Extinction debt of plants, insects and biotic interactions: interactive effects of habitat fragmentation and climate change

Aussterbeschuld von Pflanzen, Insekten und biotischen Interaktionen: interaktiv Auswirkungen der Fragmentierung von Lebensräumen und des Klimawandels

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I hereby confirm that my thesis entitled ”Extinction debt of plants, insects and biotic interactions: interactive effects of habitat fragmentation and climate change” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation ”Aussterben von Pflanzen, Insekten und biotischen Interaktionen: interaktiv Auswirkungen der Fragmentierung von Lebensräumen und des Klimawandels” eigenständig, d.h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

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At some point, I was apparently very adamant about the conservation measures I supported: the use of ”energetic fences” to ”protect nature” seemed like a proposition reasonable enough to be plastered on the walls of my elementary school. Since then, naivety gave some place to understanding, which (for now) culminated in this thesis. Hopefully, I have developed more grounded and reasonable propositions and I hereby thank the ones who helped me during this last part.

Ludmilla Figueiredo, *untitled*, ca. 1998, marker on paper, Marta da Silva Braga, personal collection.

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Contents

Abstract

The importance of understanding species extinctions and its consequences for ecosystems and human life has been getting increasing public attention. Nonetheless, regardless of how pressing the current biodiversity loss is, with rare exceptions, extinctions are actually not immediate. Rather, they happen many generations after the disturbance that caused them. This means that, at any point in time after a given disturbance, there is a number of extinctions that are expected to happen. This number is the extinction debt. As long as all the extinctions triggered by the disturbance have not happened, there is a debt to be paid. This delay in extinctions can be interpreted as a window of opportunity, when conservation measures can be implemented. In this thesis, I investigated the relative importance of ecological and evolutionary processes unfolding after different disturbances scenarios, to understand how this knowledge can be used to improve conservation practices aiming at controlling extinctions.

In the Introduction (chapter 1), I present the concept of extinction debts and the complicating factors behind its understanding. Namely, I start by presenting i) the theoretical basis behind the definition of extinction debts, and how each theory informed different methodologies of study, ii) the complexity of understanding and predicting eco-evolutionary dynamics, and iii) the challenges to studying extinctions under a regime of widespread and varied disturbance of natural habitats.

I start the main body of the thesis (chapter 2) by summarizing the current state of empirical, theoretical, and methodological research on extinction debts. In the last 10 years, extinction debts were detected all over the globe, for a variety of ecosystems and taxonomic groups. When estimated - a rare occurrence, since quantifying debts requires often unavailable data - the sizes of these debts range from 9 to 90% of current species richness and they have been sustained for periods ranging from 5 to 570 yr. I identified two processes whose contributions to extinction debts have been studied more often, namely 1) life-history traits that prolong individual survival, and 2) population and metapopulation dynamics that maintain populations under deteriorated conditions. Less studied are the microevolutionary dynamics happening during the payment of a debt, the delayed conjoint extinctions of interaction partners, and the extinction dynamics under different regimes of disturbances (e.g. habitat loss vs. climate change). Based on these observations, I proposed a roadmap for future research to focus on these less studies aspects. In chapters 3 and 4, I started to follow this roadmap.

In chapter 3, I used a genomically-explicit, individual-based model of a plant community to study the microevolutionary processes happening after habitat loss and climate change, and potentially contributing to the settlement of a debt. I showed that population demographic recovery through trait adaptation, i.e. evolutionary rescue, is possible. In these cases, rather than directional selection, trait change involved increase in trait variation, which I interpreted as a sign of disruptive selection. Moreover, I disentangled evolutionary rescue from demographic rescue and show that the two types of rescue were equally important for community resistance, indicating that community re-assembly plays an important role in maintaining diversity following disturbance. The results demonstrated the importance of accounting for eco-evolutionary processes at the community level to understand and predict biodiversity change. Furthermore, they indicate that evolutionary rescue has a limited potential to avoid extinctions under scenarios of habitat loss and climate change.

In chapter 4, I analysed the effects of habitat loss and disruption of pollination function on the extinction dynamics of plant communities. To do it, I used an individual, trait-based eco-evolutionary model (Extinction Dynamics Model, EDM) parameterized according to real-world species of calcareous grasslands. Specifically, I compared the effects of these disturbances on the magnitude of extinction debts and species extinction times, as well as how species functional traits affect species survival. I showed that the loss of habitat area generates higher number of immediate extinctions, but the loss of pollination generates higher extinction debt, as species take longer to go extinct. Moreover, reproductive traits (clonal ability, absence of selfing and insect pollination) were the traits that most influenced the occurrence of species extinction as payment of the debt. Thus, the disruption of pollination functions arose as a major factor in the creation of extinction debts. Thus, restoration policies should aim at monitoring the status of this and other ecological processes and functions in undisturbed systems, to inform its re-establishment in disturbed areas.

Finally, I discuss the implications of these findings to i) the theoretical understanding of extinction debts, notably via the niche, coexistence, and metabolic theories, ii) the planning conservation measures, including communicating the very notion of extinction debts to improve understanding of the dimension of the current biodiversity crisis, and iii) future research, which must improve the understanding of the interplay between extinction cascades and extinction debts.

Zusammenfassung

Die Tatsache, dass es wichtig ist das Aussterben von Arten und dessen Folgen für Ökosysteme und das menschliche Leben zu verstehen, findet zunehmend öffentliche Beachtung. Unabhängig davon, wie dringlich und besorgniserregend der derzeitige Verlust an biologischer Vielfalt ist, finden Aussterbeereigniss, mit seltenen Ausnahmen, nicht unmittelbar nach einer Störung (z.B. Habitatverlust und Klimawandel) statt. Sie geschehen vielmehr viele Generationen nach der eigentlichen Störung. Dies bedeutet, dass nach einer Störung zu jeder Zeit eine bestimmte Anzahl von noch auszusterbenden Arten zu erwarten ist . Diese Anzahl wird Aussterbeschuld (ëxtinction debt”) genannt. Solange nicht alle durch die Störung ausgelösten Aussterbeereignisse eingetreten sind, ist diese Schuld zu begleichen. Durch diese Verzögerung des Aussterbens von Arten entsteht ein Zeitfenster, in dem Erhaltungsmaßnahmen umgesetzt werden können. In dieser Forschungsarbeit untersuche ich die Bedeutung von ökologischen und evolutionären Prozessen als Folge verschiedener Störungsszenarien, um zu verstehen, wie dieses Wissen zur Verbesserung von Naturschutzmaßnahmen verwendet werden kann, um Aussterbeereignisse zu minimieren.

In der Einleitung (Kapitel 1) stelle ich das Konzept der Aussterbeschuld vor und verschiedene Faktoren, die unser Verständnis dieses Sachverhaltes erschweren. Kapitel 1 fokussiert sich auf i) die theoretischen Grundlagen hinter der Definition der Aussterbeschuld und wie diese unterschiedliche Untersuchungsmethoden beeinflussten , ii) die Komplexität, ökologische Evolutionsdynamik zu verstehen und vorherzusagen, und iii) die Herausforderungen, die es mit sich bringt Aussterbeereignisse zu einer Zeit zu untersuchen, in der Störungen in natürlichen Lebensräumen weit verbreitet und vielfältig sind.

Ich beginne den Hauptteil meiner Arbeit (Kapitel 2) mit einer Zusammenfassung des aktuellen Standes der empirischen, theoretischen und methodischen Forschung zur Aussterbeschuld. In den letzten 10 Jahren wurden Aussterbeschulden weltweit in einer Vielzahl von Ökosystemen und taxonomischen Gruppen festgestellt. Wenn der Größenwert der Aussterbeschuld geschätzt wird - was selten ist, da für eine Quantifizierung häufig nicht verfügbare Daten erforderlich sind -, liegt er zwischen 9 und 90% des aktuellen Artenreichtums und variiert zwischen einer Dauer von 5 und 570 Jahren. Ich identifiziere zwei Hauptprozesse hinter der Aussterbeschuld, nämlich 1) Merkmale, die verschiedene Lebensstadien betreffen und dadurch das Überleben des Einzelnen verlängern, und 2) Populations- und Metapopulationsdynamiken, die es Populationen erlauben auch unter verschlechterten Bedingungen zu überleben. Weniger untersucht sind die mikroevolutionären Dynamiken, die während der Dauer der Aussterbeschuld auftreten, wie das verzögerte gleichzeitige Aussterben von Interaktionspartnern und die Aussterbedynamik unter verschiedenen Störungsregimen (z. B. Habitatverlust vs. Klimawandel). In den Kapiteln 3 und 4 widme ich mich diesen Fragen.

Im dritten Kapitel verwende ich ein genomisch explizites, Individuen-basiertes Modell einer Pflanzengemeinschaft, um die mikroevolutionären Prozesse zu untersuchen, die nach Habitatverlust und Klimawandel ablaufen und möglicherweise zur Minderung der Aussterbeschuld beitragen. Ich zeige, dass eine demografische Erholung der Population durch Anpassung der Arteigenschaften, d.h. Rettung durch Evolution, möglich ist. In diesen Fällen äußert sich eine Änderung der Merkmale, anstatt in einer direktionalen Selektion, in einer Zunahme der Variation der Merkmale, was ich als Zei-

chen einer disruptiven Selektion interpretiere. Darüber hinaus kann ich die „evolutionäre Rettung“ von der „demografischen Rettung“ trennen und zeigen, dass diese beiden Arten der Rettung für die Widerstandsfähigkeit einer Gemeinschaft gleich wichtig sind. Dies weist darauf hin, dass die Wiederherstellung von Artengemeinschaften eine wichtige Rolle bei der Aufrechterhaltung der biologischen Vielfalt nach Störungen spielt. Meine Ergebnisse zeigen, wie wichtig es ist, ökologische Evolutionsprozesse auf Artgemeinschaftsebene zu berücksichtigen, um den Wandel der biologischen Vielfalt zu verstehen und vorherzusagen. Darüber hinaus zeigt sich, dass die „evolutionäre Rettung“ ein begrenztes Potenzial hat, um Aussterbeereignisse unter Szenarien von Habitatverlust und Klimawandel zu vermeiden.

Im vierten Kapitel vergleiche ich die Auswirkungen von Lebensraum- und Bestäubungsverlust auf die Aussterbedynamik einer Pflanzengemeinschaft. Dazu verwende ich ein Individuen- und Merkmal-basiertes Öko-Evolutionsmodell (Extinction Dynamics Model, EDM), welches für reale Magerrasen-Arten parametrisiert worden ist. Insbesondere vergleiche ich die Auswirkungen dieser Störungen auf das Ausmaß der „extinction debt“ und die Zeitspanne bis zum Aussterben einer Art sowie darauf, wie sich die Funktionsmerkmale der einzelnen Arten auf die Aussterbedynamik der Artgemeinschaften auswirken. Ich zeige, dass Habitatverlust zu einer höheren Anzahl von unmittelbar aussterbenden Arten führt, aber der Verlust von Bestäubung eine höhere „extinction debt“ mit sich bringt, da Arten hierbei länger brauchen, um auszusterben. Darüber hinaus beeinflussten insbesondereFortpflanzungsmerkmale (klonale Fähigkeit, Abwesenheit von Selbstbestäubung und Insektenbestäubung) das Artensterben zur Tilgung der Aussterbeschuld. Bestäubung ist daher ein wesentlicher Faktor bei der Entstehung von Aussterbeschuld. Renaturierungsvorgaben müssen daher darauf abzielen, den Status ökologischer Prozesse und Funktionen in ungestörten Systemen zu überwachen, um diese in gestörten Gebieten zu verbessern. Abschließend diskutiere ich die Auswirkungen dieser Ergebnisse i) auf das theoretische Verständnis der Aussterbeschuld, insbesondere mit Hilfe der Nischen-, Koexistenz- und Metabolischen Theorie, ii) auf die Planung von Erhaltungsmaßnahmen, einschließlich der Vermittlung des Begriffs der Aussterbeschuld, um das Verständnis der Dimension der aktuellen Biodiversitätskrise zu erweitern, und iii) darauf, wie die zukünftige Forschung die Herausforderung angehen kann, das Zusammenspiel zwischen Auslöschungskaskaden und Aussterbenschuld zu verstehen.

Part I

General introduction

Chapter 1

Extinction debts

Recent studies report one million species currently threatened with extinction (IPBES, 2019a), decreasing vertebrate populations (WWF, 2020), and expected increase in number of extreme weather and climate events that threaten remaining populations (Maxwell et al., 2019), the importance of understanding species extinctions and its consequences for ecosystems and human life is ever more pressing. With the exception of catastrophic, large scale events that immediately extirpate entire populations (e.g. volcanic explosions obliterating entire islands, Quammen, 1996), extinctions are processes that can last up to decades and even thousands of years (e.g. Cousins & Vanhoenacker, 2011; Cristofoli, Piqueray, Dufrene, Bizoux, & Mahy, 2010; Otto et al., 2017). This happens because species have different resistance to a given disturbance (Hylander & Ehrlen, 2013; Kuussaari et al., 2009), depending on species traits, and (meta)population and genetic dynamics (explicitly discussed in chapter 2). From species differential responses emerges a period of relaxation (the ”relaxation time”, coined by J. M. Diamond, 1972), during which the community rearranges itself, as some populations perish and go extinct while others adapt and thrive, until a new equilibrium is attained. During that time, extinctions happen, and since they are not necessarily immediate nether simultaneous, at any point in time, there is a number of extinctions that can be expected to happen until relaxation is complete. This number is the extinction debt (Tilman, May, Lehman, & Nowak, 1994; Kuussaari et al., 2009). Until all these extinctions have not happened, there is a debt to be paid.

In this thesis, I investigate the relative importance of ecological and evolutionary processes unfolding after different disturbances scenarios, to understand how this knowledge can be used to improve conservation practices aiming at controlling extinctions. My objective is to provide insights into how debts can be waived, rather than paid with extinctions. In this Introduction, I present the historical development of the concept of extinction debt, the importance of accounting for ecological and evolutionary processes to understand ecosystems responses, and the difficulties of studying extinction processes in a world where ecosystems dynamics are often disturbed by a variety of factors.

1.1 Theoretical origins of extinction debts

The concept of extinction debt has its origins in the island biogeography, metapopulation, and niche theories (Malanson, 2008).

From the theory of island biogeography comes the idea that when the equilibrium between immigration and extinction rates is unbalanced, species richness varies until equilibrium is reached again (MacArthur & Wilson, 1963). Based on this idea, J. M. Diamond (1972) estimated the ‘relaxation time’ for bird species in New Guinea satellite islands as the time required for species diversity to return to an area-based expected equilibrium number of species after being displaced by volcanic eruptions and deglaciation events that had destroyed the fauna and flora in different degrees. In some of those islands, he observed that the equilibrium number of species had not yet been attained, so further extinctions were expected. He also observed that, for smaller areas, extinction rates were higher, and thus, the relaxation time was shorter, and the number of species yet to be extinct, smaller.

From the metapopulation and niche theories came the first actual definition of extinction debt: the number of superior competitors driven extinct by habitat destruction (in a metapopulation model Tilman et al., 1994). Even if not immediately extinct, those species would be deterministically set for extinction under the new habitat conditions, due to limited dispersion capability. While they were not extinct, there was a debt of extinction to be paid (Tilman et al., 1994; Hanski & Ovaskainen, 2002). As Malanson (2008) details, Tilman et al. (1994) was the first to expand the idea of delayed extinctions and consider which species were the most susceptible to extinction. Much of the following development of the concept continued his explorations of the competition-colonization dynamics (Tilman et al., 1994; Malanson, 2008) and the use of metapopulation models (further discussed in chapter 2, Hanski & Ovaskainen, 2002; Ovaskainen & Hanski, 2002).

1.2 Ecological and evolutionary dynamics of communities

Communities are composed of species that interact with each other and the environment. As a consequence, species abundances vary over time and space, originating ”ecological dynamics”. These include population changes in response to variation of a resource or abiotic condition (Fortini, Bruna, Zarin, Vasconcelos, & Miranda, 2010; Molofsky, Danforth, & Crone, 2014; Thibault, Ernest, White, Brown, & Goheen, 2010), and in relation to each other, since they are involved in mutualistic, parasitic, competitive, and trophic interactions (e.g. Miele, Ramos-Jiliberto, & Vázquez, 2020; Rodríguez-Rodríguez & Valido, 2011; Agulova et al., 2016; Springer, Kappeler, & Nunn, 2017; Liu et al., 2014).

Inside these populations, genotype and phenotype frequencies also vary over time and space (e.g. Willemsen, Cui, Reichard, & Valenzano, 2020; Salojärvi et al., 2017), due to ”evolutionary dynamics”. These changes result from selection and genetic drift acting on genetic (and phenotypic) variability arising from mutations and gene flow. The relative importance of each of these processes has long been studied in population genetics, with abundant empirical data on model organisms (e.g. Zhong et al., 2016; Yashima & Innan, 2017), and application in conservation biology (e.g. Ellstrand & Elam, 1993; Koizumi, 2011).

Initially addressed separately, the empirical and theoretical recognition that ecological and evolutionary processes can influence each other, particularly in ecological time-scales due to ”rapid evolution” (e.g. Yoshida, Jones, Ellner, Fussmann, & Hairston, 2003), gave rise to the study of ”eco-evolutionary dynamics” (Fussmann, Loreau, & Abrams, 2007; Pelletier, Garant, & Hendry, 2009). Eco-evolutionary dynamics arise when variation in populations genotype frequencies, i.e. evolutionary dynamics, cascades into phenotypical changes that affect a species population growth and the strength of its interaction with other species, i.e. ecological dynamics — or vice-versa (Fussmann et al., 2007; Pelletier et al., 2009). For example, in plants, increased flower attractiveness is selected for by pollinators, but increased self-compatibility and selfing are favored if herbivores are present (Ramos & Schiestl, 2019). Since ecological processes can influence evolutionary ones and vice-versa, ”eco-evolutionary feedbacks” can also be expected (Post & Palkovacs, 2009; Pelletier et al., 2009). For example, herbivory induces change of plants chemical, morphological, and phenological traits, which in turn indirectly affect other herbivores of the community (Utsumi, 2011). Moreover, eco-evolutionary processes might also result in altered ecosystem functions, whereby phenotypic evolution of performance traits affects species population dynamics, which cascade into affected ecosystem functions if the biomass flux inside the ecosystem is altered (Matthews et al., 2011). Such cascades can happen from a variety of mechanisms. For example, increased primary production in aquatic systems can emerge from photosynthetic traits of algae affecting population dynamics, and thus primary production as a consequence, or from predator (invertebrates) and prey (zooplankton) mismatching body sizes, leading to algae proliferation (Matthews et al., 2011). Importantly, extinction is a process involved in both ecological (e.g., due to competitive exclusion Kramer & Drake, 2014) and evolutionary (e.g. during natural selection Davis, Shaw, & Etterson, 2005) dynamics.

Eco-evolutionary processes have been shown to affect community stability and composition (e.g. Jones et al., 2009; de Andreazzi, Guimarães, & Melián, 2018; Cortez, Patel, & Schreiber, 2020). Therefore, their role in ecosystems responses to current environmental threats has been the focus of an increasing amount of research (e.g. Legrand et al., 2017; Norberg, Urban, Vellend, Klausmeier, & Loeuille, 2012; Lavergne, Mouquet, Thuiller, & Ronce, 2010; Thuiller et al., 2013; Shefferson & Salguero-Gómez, 2015). Under fragmentation, the effects of decreased population sizes and connectivity are the most often studied factors, for their effects on populations susceptibility to demographic stochasticity, inbreeding depression, and maladaptation, and on the selection of species dispersal abilities (see a review of such effects by Legrand et al., 2017). Under climate change, niche evolution and dispersal abilities (also possibly evolving) determine whether species adapt to changed conditions (temperature and precipitation, for example), if they track conditions inside their tolerances (range shift Davis et al., 2005; Lavergne et al., 2010). Moreover, population size has been shown to be a better predictor of extinction risk than climate change (Vincenzi, 2014), adding evidence that evolutionary changes are rarely as fast as ecological changes (DeLong et al., 2016; Hanski, 2012). Therefore, their potential to counteract negative ecological effects (e.g. decreased intrapopulation variability due to decreased population size) is limited, and the conditions in which this potentials are realized are worth of dedicated studies.

1.3 The Anthropocene

The conception of extinction debts and relaxation times depends on the assumption of a state of equilibrium of species numbers. The idea of ecosystem equilibrium, however, is far from implying any kind of static state, and non-equilibrium is the norm for many ecosystems, which are considered to be recovering from prior disturbances (Wu & Loucks, 1995). Natural disturbances vary in their frequency and intensity (Romme, Everham, Frelich, Moritz, & Sparks, 1998). For example, fires in savannas and forests are usually seasonal (Archibald, Lehmann, Gómez-Dans, & Bradstock, 2013; Ursino, 2014), while windthrows in forests (Ulanova, 2000) or hurricanes are rarer - climate change, however, is expected to increase its frequencies (Maxwell et al., 2019). Nonetheless, these dynamics are integrated into ecosystem's functioning, contributing to the maintenance of community composition and nutrient cycling, for examples, and even end up resetting habitat conditions previously altered by human activity (Lindenmayer, Thorn, & Banks, 2017; Franklin et al., 2000). Moreover, organisms, present morphological (e.g. plants resist and reestablish via bark, root or seed resistance in plants, van Mantgem & Schwartz, 2003; Paula, Naulin, Arce, Galaz, & Pausas, 2016) and behavioral adaptations (e.g. refuge recognition in mammals Banks et al., 2011) to survive it and reestablish after disturbance.

Human activity has generated a myriad of disturbances (Bowler et al., 2020), such as habitat destruction, fishing and hunting, invasions, and climate change (Bowler et al., 2020; Pereira, Navarro, & Martins, 2012). The impact of such disturbances on Earth's climate, biogeochemical and water cycles, and species extinctions (Steffen, Grinevald, Crutzen, & McNeill, 2011) is high enough for human activity to be equated to a global geological force, and thus, capable of defining the end of the Holocene epoch and the beginning of the "Anthropocene" (Steffen et al., 2011; Crutzen, 2002) Even though the starting date of such high human influence has not been agreed upon (which impedes the Anthropocene being officially declared an epoch), its global impact is undisputed (Lewis & Maslin, 2015). Moreover, anthropogenic disturbances seldom happen isolated, composing particular combinations over terrestrial and marine realms (Bowler et al., 2020), and increasingly reinforcing each other's negative effects on biodiversity (Brook, Sodhi, & Bradshaw, 2008). Such disturbances have low level "biological legacies", which refers to the organisms and organic material that persist through disturbance and allow the following ecosystem recovery (Lindenmayer et al., 2017; Franklin et al., 2000). Organisms, however, are not as adapted to such changes, and the mechanisms of succession involved in reestablishment following human-induced disturbances have not been "evolutionarily shaped" for long enough to be in place.

Currently, 58% of the Earth's terrestrial surface is currently under intense human pressure and 75% has been altered by humans in some degree (WWF, 2020), which means that extinction debts are likely being created and will be paid in the short- and long-term future. Throughout this thesis I reinforce the importance of the concept of extinction dynamics, which encompasses the interacting eco-evolutionary and stochastic processes at play when species are going extinct in a community (Brook et al., 2008). In the current scenario of multiple, widespread disturbances, understanding such interactions is particularly challenging, but all the more necessary. For example, habitat destruction not only reduces populations, increases inbreeding depression, facilitates species invasions, decreases habitat resistance to climate change, but it also launches cascading extinctions (Brook et al., 2008). Any attempts to understand man-made extinctions must account for the synergy between extinction drivers and the consequent eco-evolutionary processes (Brook et al., 2008). In that sense, the study of extinction debts allows us to learn from the past to understand the future consequences of such pressures.

1.4 Overview of study questions

In this thesis, I present the work done to combine ecological principles and theories (section 1.1), to understand how eco-evolutionary dynamics (section 1.2) respond to the currently varied regime of current disturbances of natural habitats (section 1.3). Specifically, I concentrate on investigating eco-evolutionary processes that could be harnessed to inform conservation measures necessary to manage and potentially avoid current extinction processes. To achieve it, I use simulation models, which provide the computational power necessary to recreate eco-evolutionary dynamics based on ecological principles.

The main part of the thesis (part II) is organized as a pseudo-cumulative thesis, in which each chapter constitutes a manuscript addressing the study questions presented in the following paragraphs. Chapter 2 has been published in the peer-reviewed journal *Ecography*, chapter 3 is currently under review at the journal *Basic and Applied Ecology*, and chapter 4 is being prepared for submission to the journal *Global Change Biology*. The references of all chapters are grouped at the end of part III, to avoid redundancy among the chapters.

In chapter 2, I provide an in depth review conducted to summarize the progress in the understanding of the eco-evolutionary processes behind extinction debts since the publication of the last major review focused on the topic, Kuussaari et al. (2009). Since then, the difficulties involved in quantifying such extinctions has been increasingly discussed, because i) perturbations have shown to co-occur across various spatial and temporal scales, and ii) the relative importance of eco-evolutionary processes varies across scales, due to hierarchical responses from individuals, (meta) populations and (meta)communities. In particular, I reviewed recent empirical, theoretical and methodological studies addressing either the spatio–temporal scales of extinction debts or the eco-evolutionary mechanisms delaying extinctions. Besides summarizing the knowledge gathered regarding the importance of species traits and metapopulation and genetic dynamics to the build up of extinction debts, I identified possibly relevant processes which had been less studied up to that moment and deserved more attention. These were used to draw a roadmap for future research on extinction debts consisting of three main avenues, namely 1) the microevolutionary dynamics of extinction processes, 2) the disjunctive loss of interacting species and 3) the impact of multiple regimes of perturbations on the payment of extinction debts. In the following chapters, I follow this roadmap by addressing, in varying degrees, each of these avenues.

In chapter 3, I present a modeling study where I investigated a question pertaining to the first major avenue of research mentioned above: how much can evolutionary rescue (population recovery due to evolutionary change) contribute to save species from extinction? Up to now, studies of extinction debt have focused on understanding how functional traits affect whether a species is more likely to go extinct as payment of a debt or to survive it. However, little attention has been given to the microevolutionary dynamics affecting the distribution of such traits in the community under debt. It is possible that species adapt to disturbance regimes and escape extinction, what is known as evolutionary rescue. Therefore, in this study, I used a genomically explicit, individual-based model of a plant community (Leidinger & Cabral, 2020) to simulate the effects of habitat loss and climate change, two disturbances with high impact on eco-evolutionary processes. This model is particularly suited for this study because several species ecological traits are explicitly coded by the species genomes, and thus evolutionary change is possible via recombination, sexual reproduction, genetic drift, and selection. The results show that evolutionary rescue and demographic rescue are independent events, which are equally important for community resistance. This reinforces the importance of accounting for eco-evolutionary processes at the community level to understand and predict biodiversity change.

In chapter 4, I present a model developed to investigate questions pertaining to the second and third avenues of research detailed in chapter 2: how does the disruption of pollination function impacts the size of extinction debts and the length of species extinctions? And how do these effects differ from the ones imposed by habitat loss? An important feature of this model is that it was developed based on trait values from a real-world plant community of calcareous grasslands and thus, the results observed were compared to empirical data on the species and functional composition of a calcareous grassland community. The current results show that, as expected, habitat area is a key factor to the maintenance of biodiversity. Nonetheless, the results also indicated that the disruption of pollination function was a major factor in the creation of extinction debts. Moreover, the whole process of model parameterization and calibration is thoroughly documented. Therefore, upon similar parameterization, the model could be applied to other communities of herbal plants and their pollinators.

I conclude (part III) by discussing the implications of my findings to i) theoretical ecology, namely to the niche, coexistence, and metabolic theories, and ii) conservation biology, where the very notion of delayed extinctions and the dynamics of ecological change have yet to be more explicitly communicated. Finally, I discuss how remaining gaps can be addressed by future research.

Part II

Study questions of the thesis

Chapter 2

Understanding extinction debts: spatio – temporal scales, mechanisms and a roadmap for future research

This chapter has been published as Figueiredo, L., Krauss, J., Steffan-Dewenter, I., & Cabral, J. S. (2019). Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography*. 42(12), 1973–1990, doi:10.1111/ecog.04740.

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Extinction debt refers to delayed species extinctions expected as a consequence of ecosystem perturbation. Quantifying such extinctions and investigating long-term consequences of perturbations has proven challenging, because perturbations are not isolated and occur across various spatial and temporal scales, from local habitat losses to global warming. Additionally, the relative importance of eco-evolutionary processes varies across scales, because levels of ecological organization, i.e. individuals, (meta) populations and (meta)communities, respond hierarchically to perturbations. To summarize our current knowledge of the scales and mechanisms influencing extinction debts, we reviewed recent empirical, theoretical and methodological studies addressing either the spatio–temporal scales of extinction debts or the eco-evolutionary mechanisms delaying extinctions. Extinction debts were detected across a range of ecosystems and taxonomic groups, with estimates ranging from 9 to 90% of current species richness. The duration over which debts have been sustained varies from 5 to 570 yr, and projections of the total period required to settle a debt can extend to 1000 yr. Reported causes of delayed extinctions are 1) life-history traits that prolong individual survival, and 2) population and metapopulation dynamics that maintain populations under deteriorated conditions. Other potential factors that may extend survival time such as microevolutionary dynamics, or delayed extinctions of interaction partners, have rarely been analyzed. Therefore, we propose a roadmap for future research with three key avenues: 1) the microevolutionary dynamics of extinction processes, 2) the disjunctive loss of interacting species and 3) the impact of multiple regimes of perturbation on the payment of debts. For their ability to integrate processes occurring at different levels of ecological organization, we highlight mechanistic simulation models as tools to address these knowledge gaps and to deepen our understanding of extinction dynamics.

2.1 Introduction

Species extinctions after any ecosystem perturbation or disturbance are not all immediate (Box 1). Some populations and metapopulations can persist for extended periods below a minimum viable population size or an extinction threshold (Box 1). These delayed extinctions constitute an extinction debt (Tilman et al. 1994, see Malanson 2008 for a historical overview of the concept). This concept also suggests that extinctions are avoidable if effective conservation measures are implemented (Hanski & Ovaskainen, 2002; Kuussaari et al., 2009). Fulfilling this conservation potential, however, depends on our ability to understand the ecological processes upon which conservation measures could act (Cronk, 2016). Previous studies have reviewed the evidence of extinction debt in a variety of environments and organisms (Hanski & Ovaskainen, 2002; Essl et al., 2015b). Abiotic and biotic factors, such as perturbation intensity and species life-history traits, respectively, as well as stochasticity have been shown to influence how many extinctions happen and how long they will take (Kuussaari et al., 2009). Extinctions involve responses of individuals that scale up to patterns and processes at the population, metapopulation and species levels (Hylander & Ehrlen, 2013). At the community (and metacommunity) levels, biotic interactions add further feedbacks between these processes (Jackson & Blois, 2015; Essl et al., 2015b). The variety of processes, the ecological level at which they act, and interactions among them complicate the ability to predict which, when and why species go extinct. Understanding this extinction dynamics and the underlying processes is paramount, considering that current extinction debts represent a sizable portion of the predicted 1 million species threatened with extinction (hundreds of thousands of terrestrial species alone – Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2019a, based on Hoskins et al., 2019).

Extinction debts have been studied mainly via statistical or theoretical models due to a lack of appropriate long-term biodiversity data for estimating or directly quantifying extinctions (Kuussaari et al., 2009; Sodhi et al., 2010; Dornelas et al., 2013, 2018; Vellend, Brown, Kharouba, McCune, & Myers-Smith, 2013). Statistical models can detect extinction debts by verifying whether current species richness exceeds or corresponds to expected values under current habitat conditions (Kuussaari et al., 2009). These statistical models may suggest, but cannot mechanistically detail why, for which species or for how long extinctions are being delayed. Theoretical models, however, provide insights into relevant processes but the development of such models is slow and data-dependent for parameterization and verification (Getz et al., 2018). Mechanistic models have been, therefore, infrequently used to investigate extinction dynamics in real systems (Kuussaari et al., 2009). Nonetheless, upon detection of an extinction debt, conservation efforts must account for dynamic biodiversity change to avoid underestimating its strength, which would render conservation efforts ineffective (Kuussaari et al., 2009; Jackson & Blois, 2015; Essl et al., 2015b; Hylander & Ehrlen, 2013; Essl et al., 2015a). Because the different eco-evolutionary processes associated with biodiversity dynamics are simultaneous (Jackson & Blois, 2015; Essl et al., 2015b) and synergistic (Brook et al., 2008), our understanding of the relative roles of these processes remains challenging.

As a consequence of the mechanistic complexity related to extinction debt, recent reviews called for more mechanistic and dynamic frameworks to investigate extinction debts (Kuussaari et al., 2009; Jackson & Blois, 2015; Essl et al., 2015b; Hylander & Ehrlen, 2013; Essl et al., 2015a). With this review we acknowledge this call and aim to synthesize the contributions of individual studies to better understand eco-evolutionary processes that delay extinction, i.e. those processes that generate extinction debts. We build up on the work of Kuussaari et al. (2009), the most recent review summarizing the challenges in understanding extinction debts; of Hylander and Ehrlen (2013), who emphasize the importance of processes happening at the individual, population and metapopulation levels in generating extinction debts; of (Jackson & Blois, 2015), who highlight the importance of transient dynamics of biodiversity response to environmental change such as the co-occurrence of extinction debts and immigration credits; and of (Essl et al., 2015b), who highlight the contributions of hierarchical processes at different ecological levels and at different rates. First, we present our systematic literature search, with retrieved studies organized into three main categories: ‘empirical’, ‘theoretical’ and ‘methodological’ work. Second, with the aid of empirical and theoretical work, we characterize the range of spatial and temporal scales that extinction debts can reach. Third, we summarize the mechanisms explicitly investigated by empirical and theoretical work that delayed extinctions. Finally, we propose a roadmap for future research, to address the aspects of extinction debts that remain poorly investigated by empirical and theoretical work, particularly with respect to scales and mechanisms. As a navigational tool for this roadmap, we propose eco-evolutionary mechanistic models for their potential to integrate the multiple processes necessary to simulate the dynamics of extinctions from the individual to the metacommunity level.

2.2 Overview of literature

Our systematic search returned 397 articles, published between 2009 (year of publication of Kuussaari et al., 2009) and 2017, from which 114 fulfilled our inclusion criteria (details in Supplementary material Appendix 1 Material and methods). In this section, we summarize the findings from 83 studies in three categories, according to their main focus: A) observational or experimental empirical studies focused on detecting extinction debts in natural systems (hereafter referred to as ‘empirical work’); B) theoretical explorations of extinction debt in mathematical or computational models, which may or may not have been validated by empirical data (‘theoretical work’); and C) analyses of issues concerning the methodologies used for detecting extinction debts (‘methodological work’). We further characterized each paper within these categories in Supplementary material Appendix 1 Tables A1–A3. An additional 31 papers found in our search that did not fit into the above categories are discussed throughout this review whenever relevant (and listed in Supplementary material Appendix 1 List A1).

Box 1. Metrics and components of extinction debt

The extinctions that comprise an extinction debt can be expected based on the assumption of a new equilibrium to be achieved. This new equilibrium is also a community state that depends on how much the perturbation changes environmental conditions and community properties. The changes in species richness will then emerge from the interactions of eco-evolutionary processes over time at multiple levels of ecological organization (Cabral, Valente, & Hartig, 2017; Cabral, Wiegand, & Kreft, 2019). This reasoning emphasizes extinction debt as a community (or metacommunity) state. Therefore, we further refer to mechanisms of extinction debt as eco-evolutionary processes creating or prolonging this state, i.e. delaying extinctions and thus putting and maintaining the community into debt. Being a state, an extinction debt has to be first and foremost, detected. Once detected, it can be characterized (Fig. 2.1). The extinction debt itself is the number of extinctions expected to happen as consequence of a perturbation, therefore, the main metric is the size or magnitude of the debt. Depending on the strength of the perturbation, immediate extinctions might happen, but most extinctions are usually delayed (a and b in Fig. 2.1, respectively). Immediate extinctions are mostly relevant for strong pulse perturbations, in which entire species are wiped out by the perturbation itself. Therefore, at the time of perturbation (t_P), the extinction debt coincides with the total number of expected extinctions ($a + b$ if there are no immediate extinctions or b, if there are). As these extinctions happen, during the relaxation time (c in Fig. 2.1), the second most important metric, the extinction debt decreases. When the relaxation is over (at t_R, with $t_R - t_P$ being the relaxation time, c), the extinction debt is zero, i.e. it is paid. Other relevant metrics of an extinction debt are the half-life of extinction debt (the time necessary for 50% of the expected extinctions to happen — d in Fig. 2.1) and the time to first extinction (e, the time necessary for species to fall from S to $S - 1$, Halley, Monokrousos, Mazaris, Newmark, & Vokou, 2016). An important component of extinction debts is the extinction threshold. Derived from a patch-occupancy model (Hanski & Ovaskainen, 2002), extinction threshold refer to the metapopulation conditions where the proportion of suitable habitat patches (h) has to be higher than the ratio between a species' colonization and extinction rates (p_c and p_e , respectively — this is a demographically implicit model, therefore the rates are measured in terms of patches being occupied or unoccupied by the species). Therefore, the extinction threshold is defined as $h > p_e/p_c$. Similar to the minimum viable population size, the extinction threshold defines the minimal conditions for metapopulation persistence (number of occupied patches at equilibrium is bigger than zero; Hanski & Ovaskainen, 2002).

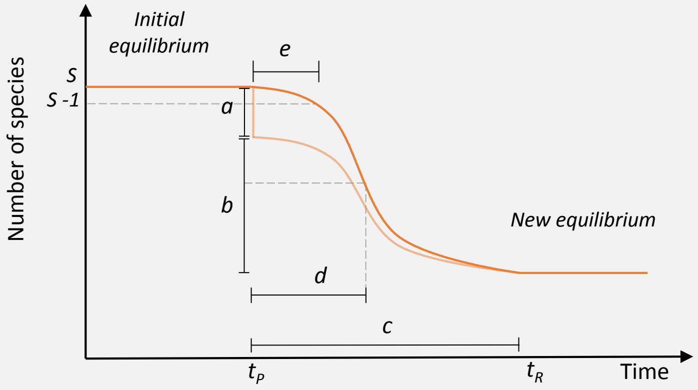

Figure 2.1: Components of the relaxation process: (a) immediate extinctions, (b) delayed extinctions, (c) relaxation time, (d) half-life of extinction debt, (e) time to first extinction. t_P is the time of perturbation, and t_R , the end of the relaxation time.

2.2.1 Empirical work

There is a consensus that current biodiversity loss lags behind anthropogenic environmental pressures (Jackson & Blois, 2015; Essl et al., 2015b) for several groups of organisms, across the globe (Fig. 2.2a). Estimates of the size of current extinction debts for natural systems range from 9% to 90% of current local species richness ($n = 8$). Not included in this range are studies that provided scenario- and/or model-dependent estimates (Wearn, Reuman, & Ewers, 2012; Fordham et al., 2016). Considering a variety of scenarios of forest loss in the Amazon,

Although we found studies conducted on all continents except Antarctica, the highest concentration of studies were in northern temperate regions, in comparison to tropical areas (Fig. 2.2a). This reflects the lead of Europe-based researchers in quantifying extinction debts, including cross-country, continent-wide studies (Krauss et al., 2010). One study, however, mapping global estimates of extinction debts and extinction risks for forest-dwelling reptile, mammal and amphibian species found areas of high extinction debt in South America, Africa and south Asia (Y. Chen & Peng, 2017). Studies in tropical communities have focused equally on plant and vertebrate species, while those in temperate regions have focused on plants and invertebrates (Fig. 2.2a; but see Dullinger et al. 2013 for a description of extinction risks to vascular plants, bryophytes, mammals, reptiles, dragonflies and grasshoppers across 22 European countries). Habitat destruction (fragmentation and/or area loss) was the predominant perturbation studied in all regions (Fig. 2.2b, Supplementary Appendix 1 Table A1). Few studies have investigated extinction debts in aquatic ecosystems (Duplisea, Frisk, and Trenkel (2016); Pandit, Maitland, Pandit, Poesch, and Enders (2017), Supplementary material Appendix 1 Table A1), reinforcing calls to address extinction debts when planning conservation of fresh-water (Olden et al., 2010; Hoagstrom, Brooks, & Davenport, 2011; Braulik, Arshad, Noureen, & Northridge, 2014) and marine environments (Briggs, 2011).

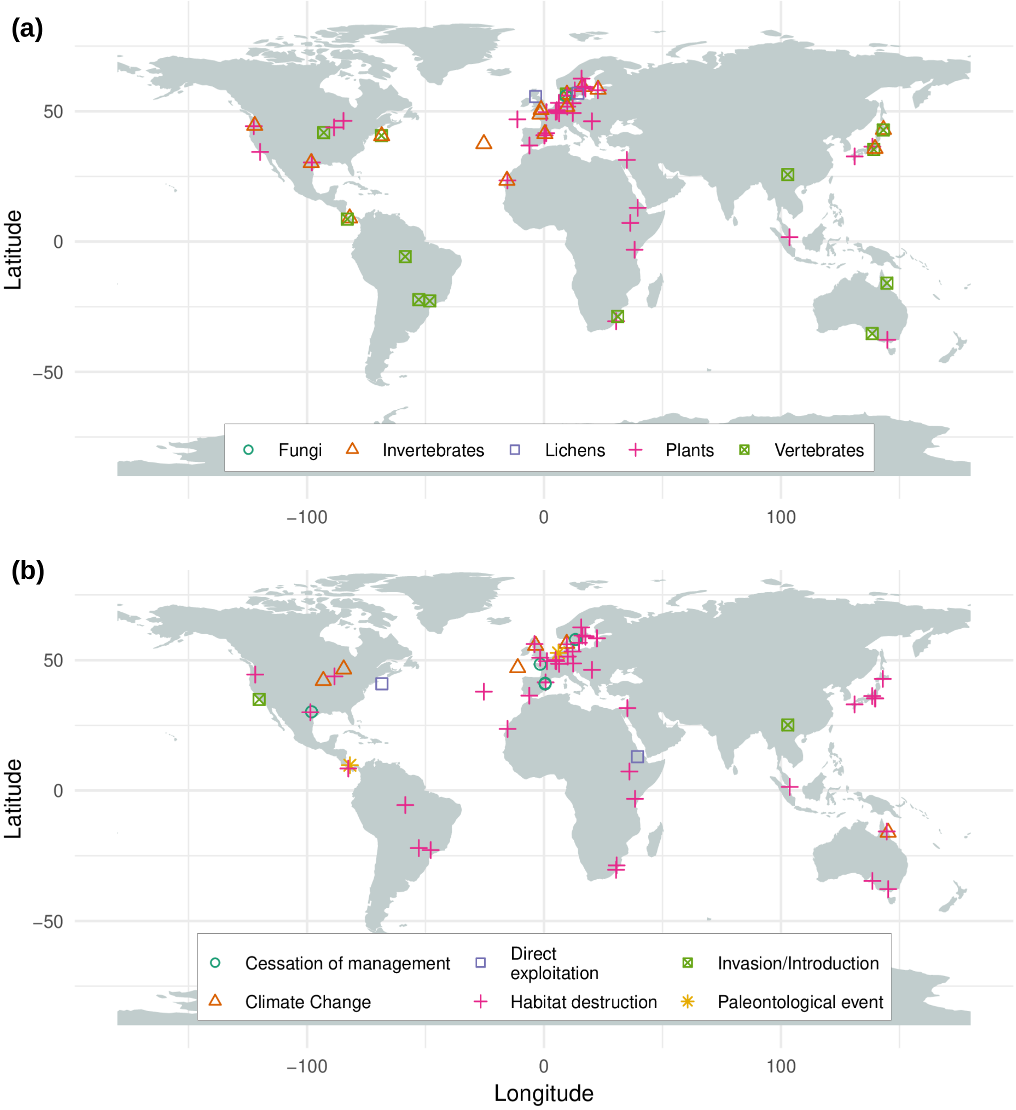

Figure 2.2: Distribution of (a) taxonomic groups for which extinction debt was investigated and of (b) the causative perturbations behind the possible extinction debts. Both panels include 58 empirical studies investigating extinction debts in real-world systems, published between 2009 and 2017. All studies are listed in Supplementary material Appendix 1 Table A1 in (studies at the continental (n = 2), global (n = 4) or microcosmic (n = 1) scales were not included). Supplementary material Appendix 1 Fig. A2a–b shows the distribution of studies in Europe.

While the availability of data on past landscape configuration (e.g. aerial photographs, Krauss et al., 2010) made it possible to standardize past and present landscape metrics, availability of past biodiversity estimates is scarce (Supplementary material Appendix 1 Table A4). Therefore, most studies use regression techniques or comparison of equilibrium numbers of species between disturbed and non-disturbed habitats to explain current biodiversity state (Fig. 2.3; see Kuussaari et al. (2009) for a summary of the possible methods of estimating extinction debts). Compared to studies from the northern hemisphere, studies conducted in tropical areas have applied a wider variety of alternative methods, such as bioclimatic models coupled with demographically explicit niche models (Fig. 2.3a, Fordham et al., 2016). Even though a relatively small number of cases have verified the debt of possibly interacting species ($n = 7$ out of 65 empirical studies, Fig. 2.3c), even fewer studies explicitly address changes in species interactions ($n = 2$). This imbalance could be related to the methodological difficulties of quantifying species interactions. To investigate extinction debts, these obstacles were overcome by the use of microcosm experiments (Gibbs & Jiang, 2017) and of regression techniques applied to network metrics (Guardiola, Stefanescu, Rodà, & Pino, 2018).

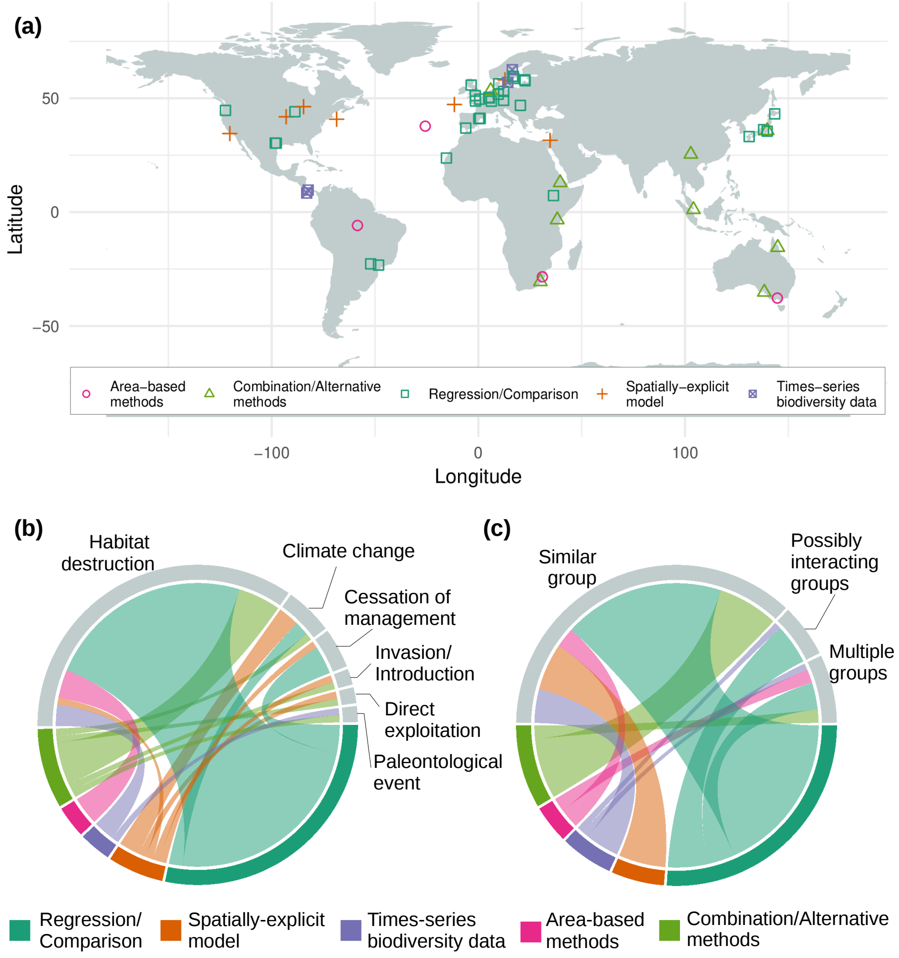

Figure 2.3: Distribution of (a) methods applied in each study detecting extinction debt, choice of methodology according to (b) perturbations generating the extinction debt, and (c) functional groups of the species for which the debt was analyzed. In panel (c): 'Similar group' refers to functionally similar species (e.g. 'plants' in Dullinger et al., 2012); 'Possibly interacting groups' refers to species that can possibly interact, meaning that extinctions in one group, would likely affect the other (e.g. 'plants' and 'butterflies' in Guardiola et al., 2018); 'Multiple groups' refers to species of different functional groups, for which the consequences of extinctions to interactions between the species are not necessarily considered (e.g. 'plants', 'bryophytes', 'mammals', 'reptiles', 'dragonflies', 'grasshoppers' in Dullinger et al. 2013). Panel (a) includes 58 empirical studies investigating extinction debts in real-world systems, published between 2009 and 2017. All studies are listed in Supplementary material Appendix 1 Table A1 (studies at the continental (n = 2), global (n = 4) or microcosmic (n = 1) scales were not included). Supplementary material Appendix 1 Fig. A2c shows the distribution of studies in Europe. Panels (b) and (c) include all 65 empirical studies.

2.2.2 Theoretical work

Theoretical studies have used different ecological theories to conceptualize extinction debt. Besides metapopulation and island biogeography theories, on which the extinction debt concept was based, neutral and niche theories have also been used in a variety of dynamic models, and have ranged from individual-based (Claudino, Gomes, & Campos, 2015) to purely mathematical models (Y. Chen & Shen, 2017). Since each theory clarifies a different aspect of extinction debts, more than one was often combined in the same study (Supplementary material Appendix 1 Table A2).

Island biogeography and metapopulation theories have been used to investigate the impact of habitat fragmentation and/or the role of dispersal capacity on different aspects of the extinction process. Larger fragments are more likely to sustain extinction debts than smaller ones (Kuussaari et al., 2009). However, as species approach the extinction threshold (Box 1), extinction dynamics are similar, independent of fragment size (Huth, Haegeman, Pitard, & Munoz, 2015). The competition–colonization trade-off, historically important for extinction debt studies (Malanson, 2008), connects principles of both niche and metapopulation theories. Trade-off models of coexistence show how coexistence mechanisms, interacting with post-perturbation metapopulation dynamics, can give rise to the heterogeneous extinction dynamics that compose an extinction debt (Holt 1993). For example, while direct extinctions happen rapidly, mostly as a result from habitat destruction affecting source–sink dynamics, indirect extinctions take longer and result from habitat destruction that destabilizes coexistence and enables competitive exclusion (Mouquet, Matthiessen, Miller, & Gonzalez, 2011). Allee effects, an expected feature of decreasing populations (Amarasekare, 1998), can invert outcomes of classical experiments on the competition–colonization trade-off (Tilman et al., 1994), with superior colonizers going extinct first if their colonization rate decreases when population size is low (L.-l. Chen, Hui, & Lin, 2009). Moreover, strong Allee effects may render habitat restoration ineffective to prevent extinctions (Labrum, 2011).

Despite the importance of niche-based differences demonstrated in the above-mentioned studies, neutral dynamics and stochasticity have been shown to be just as relevant in determining populations' fate after perturbation. For example, ecological drift can neutralize competitive superiority in meta-communities composed of small local communities, because demographic stochasticity becomes a stronger factor in determining species persistence (Orrock & Watling, 2010). At the same time, neutral theory makes it possible to identify the relative importance of different processes to extinction dynamics. Neutral theory-based estimates of extinction rates agree well with data for large areas ($1 - -10^3$ km^2, in Halley & Iwasa, 2011). However, immigration, isolation, behavioral shifts and environmental stochasticity are likely more relevant in small fragments, in which cases the neutral model is likely to underestimate relaxation times (Halley & Iwasa, 2011). In very large fragments, immigration and endemicity may explain overestimates provided by the neutral model (Halley & Iwasa, 2011). In summary, understanding extinction debts depends on integrating the principles of a variety of theories and the mechanisms evoked by these theories. The relative importance of any of them is, most likely, case-dependent.

An important asset of theoretical models, particularly computational models, is that they make it possible to explore aspects of extinction debts that are difficult to quantify in real systems. For example, the evolutionary history of a trait can generate an extinction debt if the population ceases to adapt once evolutionary pressure decreases (Osmond & Klausmeier, 2017). At the ecosystem-level, the loss of species interactions and ecosystem functions can happen more rapidly than species extinctions (Valiente-Banuet, Aizen, Alcántara, & Arroyo, 2015). Scaling up to ecosystem services, habitat destruction is estimated to have generated a debt of carbon storage loss ranging from 2 to 21 pentagrams of carbon (Isbell et al. 2015) this means that the global value of conserving vegetation for carbon storage ranges from US$0.3 to 3.1 trillion (and possibly higher values due to the uncertainties involved in these estimates; Isbell, Tilman, Polasky, & Loreau, 2015). Adding to this picture, extinction debts have been shown to decrease the sustainability of socio–ecological systems (Lafuite & Loreau, 2017; Lafuite, de Mazancourt C., & Loreau M., 2017), reinforcing the consensus about the importance of biodiversity in providing ecosystem functions and services that benefit humanity (Cardinale et al., 2012; Hooper et al., 2012).

2.2.3 Methodological work

Species–area relationships (SARs) and endemics–area relationships (EARs) are two of the main methods for estimating extinctions following habitat loss (Kuussaari et al. (2009); hereafter referred to as 'area-based methods'). The SAR describes the number of species occurring in an area A. The EAR gives the number of species restricted to area a, which is part of A. 'Backward estimates' are done by comparing the SAR for current area and species richness and the SAR for past area and species richness (Kuussaari et al., 2009). The difference between current species richness and the value expected from the SAR for past conditions provides an estimate of the debt to be paid (Kuussaari et al., 2009). The EAR can also be used to predict the number of species likely to go extinct immediately after perturbation. The adequacy of such area-based methods, however, has been debated. Concerns include the possibility of overestimating extinction rates (He and Hubbell (2011), but see response by Axelsen, Roll, Stone, & Solow, 2013), the possibility of underestimating extinctions (Halley, Sgardeli, & Monokrousos, 2013; Chase et al., 2018) and the absence of uncertainty estimates and information on individual species extinction risks (Kitzes & Harte, 2014).

Some studies explicitly investigated the mechanisms that could potentially generate under- and overestimates of extinctions (Supplementary material Appendix 1 Table A3). At least two area-based methods seem necessary to describe the dynamics of extinctions (Rybicki & Hanski, 2013; Halley, Sgardeli, & Triantis, 2014). One SAR is necessary to describe the relationships in a habitat before area loss and to predict immediate extinctions, caused by the loss of connectivity between patches (Halley et al., 2014). The other SAR is necessary to describe the relationship observed after habitat loss and to predict the total number of extinctions (Halley et al., 2014). Rybicki and Hanski (2013) attribute these two roles to a continental SAR (sampled from subareas of a continuous landscape) and to an island SAR (sampled from discrete habitat fragments). Although designed to estimate immediate extinction, EARs fail to account for short-term extinctions, which though not immediate, still happen soon after perturbation Rybicki and Hanski (2013). All studies also highlight how the incorporation of ecological features, such as minimal population size (Tanentzap, Walker, Stephens, & Lee, 2012; Kitzes & Harte, 2014), dispersal (Rybicki & Hanski, 2013), immigration (Halley et al., 2014), or coexistence (Matias et al., 2014) can improve estimates. Considering the temporal and spatial extent to which habitat destruction can progress (e.g. Triantis et al. (2010) report ¿ 95% habitat loss over 600 yr in the Azores islands), the scales at which the different processes emerge must be addressed as essential aspects for the study of extinction debts.

2.3 Spatio-temporal scales of extinction debts

Extinction debts generated by anthropogenic perturbations (habitat destruction, climate change, species invasion, change in management and fishery – Fig. 2.2b) have been investigated in remnant habitat areas measuring from 0.013 to 5.510^6 km^2 (Fig. 2.4, Supplementary material Appendix 1 Table A4). The duration over which debts have been sustained varies from 5 to 570 yr, and projections of the total period required to settle a debt can extend to 1000 yr (Fig. 2.4, Supplementary material Appendix 1 Table A4). As the most investigated group, plants are well represented at all scales (Fig. 2.4a). Global values of the half-life of extinction debt time to first extinction (Box 1) increase with remnant area for vertebrates, plants and less strongly for invertebrates (Halley et al., 2016).

The spatial scale at which to investigate extinction debt can determine whether or not they are detected. Reasons for this scale effect include 'purely' spatial factors, such as sample availability and correlations between explanatory variables (Krauss et al., 2010) and landscape context (Ernoult & Alard, 2011; Guardiola, Pino, & Roda, 2013; Alignier & Aviron, 2017; Koyanagi, Akasaka, Oguma, & Ise, 2017). Additionally, this scaling issue may be a result from 'spatial scale-varying' mechanisms, such as faster extinction at smaller scales (Cousins & Vanhoenacker, 2011; Guardiola et al., 2013) and species' sensitivity to perturbation (Cusser, Neff, & Jha, 2015).

The relative abundance distribution and spatial aggregation of individuals influence the magnitude of extinction debts and the duration of relaxation times, as highlighted by neutral models (Halley & Iwasa, 2011; Kitzes & Harte, 2015; Y. Chen & Shen, 2017; Sgardeli, Iwasa, Varvoglis, & Halley, 2017). Communities following the log-normal and broken-stick abundance distributions tend to

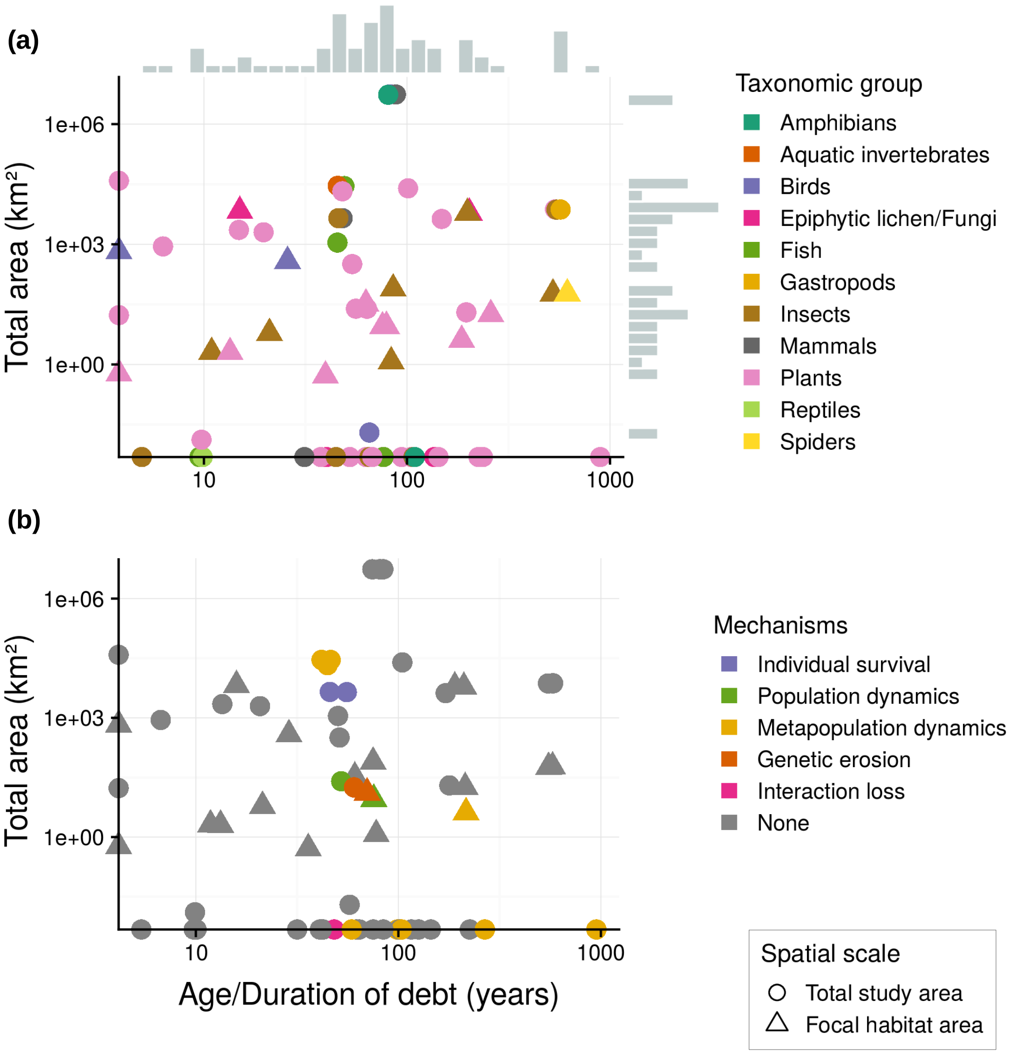

Figure 2.4: Spatio-temporal scales of extinction debts for (a) the organisms for which a debt was detected, and for (b) the mechanisms investigated. The spatial extent of the study was quantified as either the total area covered by the study, the total area of the focal habitat, or the total sampled area. Circles represent studies for which we could only approximate the total area of study. The relative sizes of focal habitat area and matrix inside the total area can vary wildly in these cases and are either hard to estimate from the provided maps or not available. Studies for which the total or the sampled area of focal habitat was identified are represented by triangles. These measures are closer proxies to the area actually 'paying' the debt. The age of debt refers to the time passed since the causative perturbation, while the duration refers to the time predicted or measured for a debt to be completely settled. Studies for which the spatial or temporal scales were not available or could not be derived are plotted in the x and y axes, respectively. The complete list of papers for which we were able to identify the spatial and/or temporal scales and their values is available in Supplementary material Appendix 1 Table A4.

exhibit extinction debt following habitat decrease, especially under conditions of low aggregation of individuals. Following destruction of contiguous fractions of habitat, a higher aggregation of individuals can result in more immediate extinctions, smaller extinction debts and shorter times (Claudino et al., 2015; Kitzes & Harte, 2015; Sgardeli et al., 2017).

While most studies of natural systems detect the 'age' of an extinction debt, i.e. the length of time since its causative perturbation, those that estimate or predict its duration are rarer (Supplementary material Appendix 1 Table A4). Moreover, some extinction debts are evaluated based on measures describing environmental conditions in periods that do not necessarily match the beginning (the measure is taken many years after it) or the frequency of perturbations (Supplementary material Appendix 1 Table A4). These studies often note that the data on past conditions used to infer extinction debt approximate those occurring before the most important perturbation. In studies aiming at detecting extinction debts through regression techniques, such an approach is sufficient (Cristofoli et al. 2010; see Supplementary material Appendix 1 Table A4 for the complete list). However, the frequency of perturbations, rather than their magnitude, has a stronger impact on the size of extinction debts generated (Claudino et al., 2015). Therefore, it is worth further investigating the impacts of perturbation frequency on extinctions.

2.4 Mechanisms generating and delaying extinctions debts

Two mechanisms generating extinction debts have been explicitly investigated in real-world systems: 1) life-history traits that prolong individual survival, and 2) population and metapopulation dynamics that maintain sink populations under deteriorated conditions (Supplementary material Appendix 1 Table A1, A2 list all empirical and theoretical studies, and the mechanisms they address). We also discuss genetic erosion, as its occurrence during relaxation time has also been addressed. However, we do not frame genetic erosion itself as a mechanism of extinction debt (i.e. it does not delay extinctions), but rather as a component of it, resulting from the two mechanisms presented above and increasing extinction risk. Hence, genetic erosion accelerates the payment of the debt. For all three of these processes, we identify the spatio–temporal scales at which they have been studied (Fig. 2.4b). Below, we detail the evidence for each of these processes.

2.4.1 Individual survival: the role of life-history traits

Life-history traits, such as dispersal ability, reproductive strategy and longevity are often considered potential causes both of detected (Dullinger et al., 2013) and undetected extinction debts (Lundell, Cousins, & Eriksson, 2015; Hu et al., 2017; Roberts, Forrest, Denham, & Ayre, 2017). The prevalence of clonality among remnant species indicates that asexual reproduction likely delays extinctions (Dullinger et al., 2012; Otsus, Kukk, Kattai, & Sammul, 2014). Trait trade-offs might also help to identify species most likely to be the first to pay extinction debts (Lindborg et al., 2012; Marini et al., 2012; Purschke, Sykes, Reitalu, Poschlod, & Prentice, 2012; McCune & Vellend, 2015; Saar, de Bello, Pärtel, & Helm, 2017). By the end of relaxation time, plant species with long-distance dispersal ability (e.g. wind-dispersal), but lower competitive and stress–tolerance abilities, were likely to have become locally extinct (Saar, Takkis, Pärtel, & Helm, 2012). Persistent species tend to be long lived and to reproduce clonally (Purschke et al., 2012; Saar et al., 2012). Assessments of such trait associations in the context of extinction debts among other guilds, however, are lacking, especially at higher trophic levels (Fig. 2.4a–b). Efforts to describe change in community trait composition (not necessarily restricted to life-history traits) should elucidate whether or not such changes can serve as early signs of population decline (Baruah, Clements, Guillaume, & Ozgul, 2019), especially if those traits respond at similar temporal scales (Takkis, Pärtel, Saar, & Helm, 2013). Detection of trait changes may also identify the role of microevolutionary processes in the payment of debts (Fagan and Holmes (2006), further discussed below).

2.4.2 Population and metapopulation dynamics maintain populations under deteriorating conditions

Extinction debts arise from population dynamics due to reduced seedling recruitment (Botzat, Fischer, & Farwig, 2015; Plue, Vandepitte, Honnay, & Cousins, 2017), rate of succession (Lehtilä et al., 2016), local dynamics of competition and colonization (Duplisea et al., 2016). Population dynamics have also been investigated together with genetic erosion (Fig. 2.4b, 2.5). These studies illustrate how both processes may occur at similar temporal scales (Fig. 2.4b, but see Takkis et al., 2013), even if different life stages contribute differently to the build up of an extinction debt (Plue et al., 2017).

Metapopulation dynamics, i.e. local extinctions and re-colonization of populations connected by long-distance dispersal, are especially important in scenarios where habitat configuration (patch area and connectivity) is perturbed (Ovaskainen & Hanski, 2002; Vellend et al., 2006). Special should be given to species remaining in habitat relics, since lack of connectivity between local populations may condemn a metapopulation in the long term (Wynne et al., 2014).

Metapopulation models have also been used to address extinction debts generated by types of perturbations beyond fragmentation, such as species invasions (Gilbert and Levine 2013) and by climate change (Dullinger et al., 2012; Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017). In the latter, metapopulation and species distribution models were combined (hybrid species distribution models) to predict range shifts; these can be interpreted as generating extinction debts at the trailing edge, and colonization credits at the leading edge (Pandit et al., 2017; Talluto et al., 2017). Because metapopulation and hybrid species distribution models are commonly used, they provide appropriate tools for generating explicit information about extinction dynamics. Moreover, colonization and extinction also depend on the species' life-history traits. Therefore, data-driven metapopulation models (Talluto et al., 2017) are particularly useful in accounting for the role of species' dispersal ability (Dullinger et al., 2013; May, Giladi, Ristow, Ziv, & Jeltsch, 2013), colonization/extinction rates (Talluto et al., 2017), and eco-evolutionary dynamics (Cotto et al., 2017) in delaying both local and metapopulation-wide extinction.

2.4.3 Genetic erosion becomes increasingly important for smaller, often clonal populations

While is it possible that fragmented populations can maintain high genetic diversity (Habel et al., 2015), life history traits and life stages that delay extinctions usually decrease genetic diversity over the long term. Long lifespans and clonal reproduction make prolonged survival possible under deteriorated conditions (Cotto et al., 2017; Hu et al., 2017). However, clonal reproduction decreases genetic diversity (Jimenez-Alfaro, Garcia-Calvo, Garcia, & Luis Acebes, 2016; Hu et al., 2017) and long lifespans limits adaptive capacity (Cotto et al., 2017). It is also possible that even if pre-perturbation levels of recruitment are maintained, the genetic diversity of seed banks becomes lower than that of adult plants (Vranckx, Jacquemyn, Muys, & Honnay, 2012; Plue et al., 2017) contributing to a genetic extinction debt (delayed loss of genetic diversity). At the same time, the seed bank can also marginally contribute to prolongation of this debt by reintroducing alleles lost by the adult population (Plue et al., 2017). In perennial species, offspring maladaptation and consequent population decrease, can occur more rapidly than range losses (Cotto et al., 2017; Dullinger et al., 2012). The late loss of populations due to stochasticity and low genetic variability has been dubbed a genetic Allee effect by Vercken et al. (2013). However, the role of genetic erosion requires further investigation because loss of genetic diversity might happen more quickly than and be decoupled from decrease in population size (as in Takkis et al., 2013). Therefore, conservation measures aimed at mitigating extinction debts should include potential loss of genetic diversity, since it adds yet another source of stochasticity, in addition to demographic and environmental sources (Ovaskainen & Meerson, 2010).

In summary, individual survival combined with population and meta-population dynamics under new landscape configuration enable transient population persistence for long periods of time despite genetic erosion. Notably, species life-history traits play a role in each of these processes, with three consequences. First, the very traits that contribute to individual survival under pre-perturbation conditions can contribute to increased extinction risk. This reinforces propositions made by Hylander and Ehrlen (2013) that individual, population and meta-population processes result in extinction debts. Second, this hierarchy of ecological processes inhibits a clear separation of factors delaying extinctions, as the different mechanisms interact with one another. Moreover, genetic erosion resulting from population and metapopulation processes does not generate debts but can accelerate debt payment. Third, an adequate appraisal of the relative importance of extinction-delaying mechanisms requires explicit consideration of how these mechanisms interact with one another. In the next section, we propose how this can be achieved.

2.5 A roadmap for future research

Previous work by Kuussaari et al. (2009) and Hylander and Ehrlen (2013) has called for more research focusing on methodological development, careful long-term monitoring of species at different organizational levels and spatial scales, and comparative studies of the impact of different types intensities of perturbations. Another shared perspective is the need to better understand the temporal dynamics of extinctions.

The importance of a cross-level view of biodiversity has been stressed by the IPBES report (2019), which summarizes trends of essential biodiversity variables (EBVs – ecosystem, ecosystem function, community composition, species populations, organismal traits and genetic composition; Pereira et al., 2013). Albeit varying differently according to the driver of change, taxonomical group, geographic region and habitat types, there is an overall decline in EBVs (IPBES, 2019a). Nonetheless, despite growing recognition of the importance of the impact of habitat perturbation on evolutionary dynamics (Legrand et al., 2017; Pelletier & Coltman, 2018; IPBES, 2019a) and the extent to which extinction cascades can reach (Roopnarine 2006, Vieira and Almeida-Neto 2015), neither mechanisms has been explicitly investigated under scenarios of extinction debt. This scarcity of studies is perhaps due to methodological and data-related difficulties in assessing microevolution and biotic interactions. Combined with system idiosyncrasies (e.g. species composition and relative abundance, habitat configuration, perturbation regime), the feedback between ecological processes at different organizational levels may generate non-linear responses (e.g. abundance decrease, loss of genetic diversity, interaction loss) that cannot be captured by static methods. It is worth investigating the extent to which mechanism-based predictions match the ones provided by statistic methods (e.g. the values reported in IPBES, 2019a). Therefore, though the detection of extinction debts remains essential, a bigger challenge in understanding extinction debts is how these processes interact with one another under different perturbed conditions. To address this challenge, we propose a roadmap for future research (Fig. 2.5) consisting of three main avenues: 1) the microevolutionary dynamics of extinction processes, 2) the disjunctive loss of interacting species and 3) the impact of multiple regimes of perturbations on the payment of extinction debts. The first two avenues address understudied processes happening during relaxation time, while the last avenue addresses an understudied aspect of extinction debt that would benefit from mechanistic understanding. We also briefly explore the potential contributions of these avenues to conservation measures (Box 2). Finally, we propose integrative mechanistic models as tools to navigate this roadmap.

2.5.1 The microevolutionary dynamics of extinction processes

Microevolutionary dynamics are especially relevant in reduced (and often clonal) populations, for the potential that genetic drift and inbreeding have to decrease populations' effective size and increase their extinction risk (Keller & Waller, 2002; Spielman, Brook, & Frankham, 2004; Dixo, Metzger, Morgante, & Zamudio, 2009; Hendricks et al., 2017). In such a scenario, extinction vortex is a theoretical construct used to illustrate the synergy between environmental, demographic and genetic factors that accelerates the descent of an already declining population towards extinction (Fagan & Holmes, 2006; Blomqvist, Pauliny, Larsson, & Flodin, 2010). Decreased genetic diversity detected during the payment of extinction debts can be interpreted as a sign of an extinction vortex (Vercken et al., 2013). We propose that extinction vortex and extinction debt could be addressed as two complementary phenomena. First, the synergy between environmental, demographic and genetic factors, i.e. the onset of the extinction vortex, takes time to happen and delays extinctions. The more deeply populations are drawn into the vortex (as they pass the extinction threshold, and/or lose genetic diversity), the more rapidly extinction rates become. Second, the extinction vortex was conceived for application to a population, while an extinction debt exists at the metapopulation or community level. This implies that population-level extinction vortexes could reinforce each other and affect the payment of extinction debts. Therefore, the reinforcement of extinction vortexes themselves is another synergistic factor that complicates our understanding of extinction dynamics. Characterizing populations decline (Fagan & Holmes, 2006) when debts are being paid could verify these predictions and potentially indicate when this synergy is triggered at the community level (Fig. 2.5a).

It is also possible that, during relaxation time, adaptive dynamics save populations from extinction via selection of traits adapted to the new conditions, i.e. 'evolutionary rescue' (Gomulkiewicz & Holt, 1995). In these instances, at least part of the debt could be waived. Although not yet empirically verified, theoretical results illustrate the complexity of the phenomenon. On the one hand, it is possible that trait evolution before perturbation pushes trait values in directions contrary to rescue, hampering rescue as a result (Osmond and Klausmeier 2017). On the other hand, genetic drift in small populations may actually facilitate evolutionary rescue from evolutionary suicide (i.e. an evolutionary attractor that becomes a disadvantage under environmental change – Ferriere & Legendre, 2013). For microbial populations, the conditions necessary for evolutionary rescue vary (G. Bell & Gonzalez, 2011, 2009), but genetic variation and population size are critical. For larger organisms, the question remains whether partial waiving of extinction debts via evolutionary rescue is possible. Longer generation times, combined with genetic erosion, low population sizes, and demographic and environmental stochasticity, have been shown to hamper evolutionary rescue in vertebrate species (Vander Wal, Garant, Festa-Bianchet, & Pelletier, 2013). Unfortunately, studies of evolutionary rescue in wild populations are rare due to demanding data requirements (Vander Wal et al., 2013). Although evolutionary rescue in wild populations is possible (Vilà Carles et al., 2003), its likelihood of occurring (Vander Wal et al., 2013) and its actual role in conservation biology (Hao et al. 2015) are still under discussion, requiring further research.

The competition–colonization trade-off may be a good candidate for exploring such dynamics. This trade-off is often studied in contexts where change in landscape configuration affects the outcome of competitive interactions (L.-l. Chen et al. (2009); Orrock and Watling (2010); Mouquet et al. (2011) – detailed in Supplementary material Appendix 1 Table A2), but it may also play a role in determining the outcome of eco-evolutionary dynamics (Legrand et al., 2017). For example, evolutionary decrease in dispersal propensity at the local scale (in response to habitat amelioration) can increase metapopulation extinction risk (Poethke, Dytham, & Hovestadt, 2011).

2.5.2 The disjunctive loss of interacting species

Considered under the network paradigm, extinctions can lead to extinction cascades (Emer et al., 2018), decreases in community stability (Spiesman & Inouye, 2013) and even network collapse (Jiang et al., 2018). Although the importance of accounting for secondary extinctions is firmly recognized (Brodie, Helmy, Brockelman, & Maron, 2009; Colwell, Dunn, & Harris, 2012), the contribution of cascading effects to the payment of extinction debts remains the least explored component of extinction debts. In our search, we found only microcosm experiments by Gibbs and Jiang (2017), a theoretical model of extinction debt of ecological interactions by Valiente-Banuet et al. (2015) and an empirical study of interaction network change in a scenario of extinction debt by Guardiola et al. (2018) (Fig. 2.4b, 2.5a).

Network sciences in ecology are still in development (Borrett, Moody, & Edelmann, 2014; Pilosof, Porter, Pascual, & Kéfi, 2017; Delmas et al., 2019). Analyses of temporal networks (Masuda & Lam-

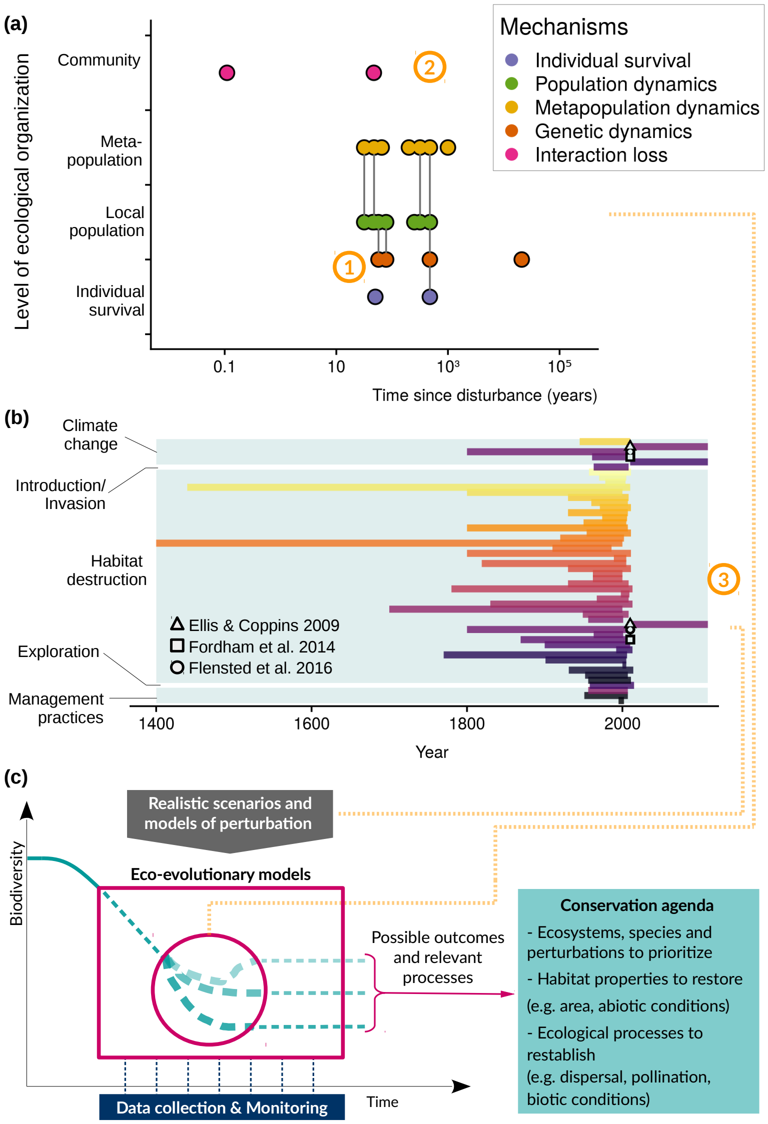

Figure 2.5: Roadmap for future research on extinction debt. (a) Ecological mechanisms investigated in scenarios of extinction debt plotted according to the ecological organizational level at which they were measured and the time scale of the debt. Studies included are the empirical studies which explicitly investigated ecological processes (n = 15; Supplementary material Appendix 1 Table A1) and Cotto et al. (2017), the only mechanistic model that was verified by empirical data (Supplementary material Appendix 1 Table A2). Lines connecting points indicate a single study that addressed more than one mechanism. Unconnected points represent studies that addressed only one mechanism. The paucity of studies addressing the microevolutionary dynamics of evolutionary processes (orange circle 1) and processes above the meta- population level, namely the disjunctive loss of interacting species (orange circle 2), justify our choice of these factors to integrate our roadmap. (b) Causative perturbations resulting in extinction debts identified in the empirical work and the age (time since perturbation) or duration of the extinction debt they generate. This panel summarizes empirical work for which we were able to assign one (or multiple) causative perturbations and an estimate of the age or duration of the debt (n = 49, listed in Supplementary material Appendix 1 Table A4). Studies reporting debt lasting more than 1000 yr were excluded to facilitate visualization. Studies are identified by color. Even though there is temporal overlap of different perturbations, few studies (n = 3, identified by different symbols) have included multiple sources of perturbations in their evaluation of extinction debts. For that reason, we included the impact of multiple regimes of perturbation on the payment of extinction debts (3) as the third avenue of our roadmap. (c) Eco-evolutionary models can provide better assessments of which ecosystems and species are critical to protect, perturbations that require priority action, as well as which abiotic and/or biotic conditions must be restored or reestablished to avoid future extinctions and waive the debt. Data collection and monitoring of model predictions are crucial to validate the models and to verify the efficiency of conservation measures.

biotte, 2016) and network robustness are particularly important (Grass, Jauker, Steffan-Dewenter, Tscharntke, & Jauker, 2018; Guardiola et al., 2018), since species go extinct at different rates during relaxation time. In this context, plant–herbivore and plant–pollinator communities represent good model systems, since plant populations promote community stability by connecting pollination and herbivory networks (Sauve, Thébault, Pocock, & Fontaine, 2016) and differential responses of pollinators and herbivores to perturbation have contrasting effects on community maintenance (Georgelin, Kylafis, & Loeuille, 2015).

Because extinctions take time to happen, we propose going beyond robustness analyses, which assume sudden extinction, and breaking down the progressive feedbacks between ongoing extinction processes in populations of interacting species during relaxation time. Species interactions are the result of spatial and temporal matching of species occurrence, population abundances and interaction traits (J. N. Thompson, 2010; Poisot, Stouffer, & Gravel, 2015). These factors can all be affected as a debt is paid. During relaxation time, interacting species go extinct at different rates (Bommarco, Lindborg, Marini, & Öckinger, 2014; Cusser et al., 2015; Guardiola et al., 2018) affecting presence and abundance matching. The loss of species interactions could be a particularly important factor behind extinctions caused by climate change (Cahill et al., 2012). Even before extinctions happen, continuous and directional perturbations such as climate change can induce phenological shifts between interacting species that alter population dynamics and community stability (Fabina, Abbott, & Gilman, 2010). As we proposed in the previous subsection, it is also worth investigating whether microevolutionary processes in small populations may generate a mismatch in interaction traits. Additionally, it is possible that there is not enough time for microevolution to allow species to adapt to new conditions before it gets excluded by an invading pre-adapted one (Holt, 1990). Therefore, evolutionary rescue and interaction networks should be studied in the context of changes in both abiotic and biotic conditions.

Beyond the change in species interactions and in biotic conditions, ecosystem functions and services can also be lost more rapidly than the extinctions occur (Valiente-Banuet et al., 2015) and feedback into ongoing extinction processes, generating nonlinear biodiversity responses (Essl et al., 2015b). Tackling these confounding effects in empirical settings is challenging , especially due to the experimental complexity required. Nonetheless, these intertwined processes (i.e. evolution, environmental change and metacommunity dynamics) should be more easily disentangled in theoretical studies utilizing mechanistic models that can integrate all these mechanisms simultaneously (Schiffers, Bourne, Lavergne, Thuiller, and Travis (2013); Cabral et al. (2019), see also Cabral et al. (2017) for a review of such integrative biodiversity models).

2.5.3 The impact of multiple regimes of perturbation on the payment of extinction debts

The concept of extinction debt relies on the perturbation of a community at an equilibrium state, leading to relaxation at another equilibrium state. However, the Anthropocene brings a series of simultaneous threats to biodiversity (e.g. climate change, invasions, fragmentation – Bowler et a. 2018, IPBES (2019a), Fig. 2.2b shows the causative perturbations included in this review and Fig. 2.5b illustrates their co-occurrence) that are likely to reinforce each other (Brook et al., 2008). This means that relaxation processes themselves are perturbed and the new equilibrium is delayed or constantly shifted. Regardless of the idiosyncrasies of relaxation processes, which are likely case-dependent, current biodiversity loss is happening rapidly. Current extinction rates have been calculated to be between 10 and 1000 times the background rate for vertebrates (Pimm et al., 2014) and up to 500 times for plant species (Humphreys, Govaerts, Ficinski, Lughadha, & Vorontsova, 2019). Current anthropogenic drivers of biodiversity change include land/sea use change, pollution, direct exploitation, species invasions and climate change (IPBES, 2019a). The effects of varied regimes (types and frequency) of perturbation on the extinction dynamics of the same system have been addressed in mechanistic modeling studies and microcosm experiments (Claudino et al., 2015; Gibbs & Jiang, 2017; Zarada &

Drake, 2017), but not verified in real-world systems. Because the relative incidence of various perturbations also varies in space and time, any cross-system comparisons (including meta-analyses) require adequate replicate sites undergoing similar combinations of perturbations and must control for confounding effects (Bowler et al. 2018 characterize and provide such threat complexes at the global scale).

Box 2. Mechanistically informed conservation

The potential to identify future extinctions is one of the main assets of the extinction debt concept. We illustrate how policy management could integrate mechanistic knowledge to realize this potential. For this, we work on a fictive case of an extinction debt for habitat–specialist plant species caused by habitat fragmentation. Knowledge of the current trait composition of the remnant species is crucial to identify which are at most risk of going extinct to settle the debt. In our example, let's assume non-clonal, wind-dispersed plants are still present, but can be expected to go extinct as the debt is settled (Saar et al. 2012). This information allows identifying which ecological processes are affected by the causative perturbation. It is important to account how ecological processes are affected by the perturbation and how they respond to conservation measures. If non-clonal, wind-dispersed species are likely to become extinct, it is possible to identify ecological mechanisms contributing to the extinction process:

A) At the metapopulation scale, the possible fates – adapt or perish – of a species, particularly if habitat specialist, can be particularly dependent to dispersal. For example, loss of connectivity in a highly fragmented landscape might indicate the highest extinction risk (Saar et al., 2012), whereas preservation of minimal connectivity may actually make population rescue possible (Huth et al., 2015). In the first case, artificial sowing or increase in connectivity may decrease extinction risk. In the second, simply maintaining the current connectivity might be enough.

B) At the local scale, competition with generalist or invasive species can increase extinction risk. Management practices would involve electrical mowing or pasture grazing to minimize fitness differences from stronger competitors. This might be crucial in conserving our example species, as by the colonization–competition trade-off, wind-dispersed species can be expected to have lower competition ability. Combined with the lower colonization success under a highly fragmented landscape, propagule pressure of dispersing seeds might not be enough to withstand the competition anyways. Therefore, increasing of dispersal rates would be ever so important.

C) Other possibilities of improving survival would tackle the reproductive success of remnant species. Reintroducing pollination services for non-clonal species could increase their recruitment rates. This, however, requires careful choice and timing of the pollinators to be used and the possible impacts on wild pollinators. The three mechanisms A, B and C are not isolated, but their relative importance will depend, among other factors, on the trait composition of the remaining populations, on the relative abundances, habitat configuration and pollination availability. Moreover, the relative importance of these mechanisms will likely also vary during the time since perturbation. In this case, a metapopulation model with explicit dispersal functions can help identify which strategy illustrated in A or B (if it is a trade-off model) would be more efficient. If it is possible to increase complexity, metacommunity models including species interactions would provide possible alternatives of management (strategy C). Moreover, if including evolutionary dynamics, such models could even illuminate unforeseen consequences of the relaxation process (Cotto et al., 2017).

2.5.4 Mechanistic simulation modeling as a navigational tool

When addressing extinction debts, simulation-based models have been used to predict relaxation times (May et al., 2013), to verify the impact of different perturbations on the size of debts (Claudino et al., 2015), to test theoretical assumptions (Halley & Iwasa, 2011; Huth et al., 2015), and to verify the effectiveness of conservation measures (Wearn et al., 2012; Fordham et al., 2016). They have also proved to be useful, yet underused, tools for investigation of the impacts of climate change and species invasions (Cahill et al., 2012; Gilbert & Levine, 2013). Our knowledge of how eco-evolutionary processes lead to delayed extinctions and the full extent of their feedbacks (Legrand et al. 2017) and ecosystem-level consequences (Valiente-Banuet et al., 2015) is still incipient. Simulation models can integrate all those processes (Thuiller et al., 2013; Urban et al., 2016; Cabral et al., 2017) and fill the gaps. An example is Cotto et al. (2017), an eco-evolutionary model used to investigate extinction debt and able to connect processes at the individual, population and metapopulation levels (Fig. 2.5a). Such an approach is especially useful for informing conservation efforts (Wood, Stillman, & Hilton, 2018), which may currently overlook delayed extinctions (Urban (2015); Y. Chen and Peng (2017) – see Box 2 for considerations of conservation policies). Specifically, accounting for extinction debt when planning conservation and management has been shown to be especially useful when funding is limited; knowledge of the dynamics of extinctions allows more effective resource allocation (Leroux, Martin, & Goeschl, 2009; Leroux & Whitten, 2014; Iacona, Possingham, & Bode, 2017). Considering the spatio-temporal scales that extinction debts can reach (Fig. 2.4, Halley et al. 2016, 2017), further investigation into their consequences, and the extension of those consequences to ecosystem service debts

2.6 Conclusion

Our review demonstrates an increasing effort to understand the mechanisms involved in extinction debts across systems and scales. To date, the contributions of niche-based, neutral and metapopulation dynamics have been fairly well characterized. Evolutionary and biotic interaction processes, however, remain less adequately addressed and thus deserve further inquiry. To this end mechanistic models make it possible to scale individual responses to the population and metapopulation levels and to better characterize feedback processes. The roadmap to improve our understanding of extinction debts includes entraining genetic dynamics into the prediction of (meta)population dynamics, scaling cascading effects to the community level, and studying the combined effects of different types of perturbations. While long-term empirical studies of community dynamics and underlying drivers of extinctions remain important to monitor biodiversity change, and to calibrate and validate model-based forecasts of extinction debts, it may be too late to counteract severe losses of biodiversity. Hence, immediate policy and conservation efforts must consider mechanisms of extinction debt explicitly in order to preserve remaining biodiversity in a rapidly changing world.

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Chapter 3

Evolutionary rescue and community re-assembly contribute to the waiving of extinction debts

The following chapter contains a manuscript currently under revision to be featured in the Special Issue "DNA sequenced-based biodiversity and interaction ecology" of the *Basic and Applied Ecology* journal.

—After disturbance, species which cannot sustain their populations under the new biotic and abiotic conditions go locally extinct. These compose an extinction debt, which is paid over the relaxation time. Extinction debt studies have hitherto focused their efforts on understanding how functional traits and ecological processes influence which species are more likely to pay the extinction debt and which go through demographic rescue, i.e. recovery in abundance. Microevolutionary dynamics, however, have received less attention despite interacting with the processes above. It is possible that species adapt to disturbance regimes and escape extinction, what is known as evolutionary rescue. To evaluate evolutionary rescue in plant communities under extinction debt, I applied a genomically- and spatially-explicit, niche- and individual-based model to scenarios involving different types of disturbance (habitat loss and temperature increase) in separate and in combination. In this model, functional traits are coded in genomic sequences, which can recombine and undergo sexual reproduction. Hence, selective pressure caused by disturbances can act upon standing variation. I was able to disentangle evolutionary rescue from demographic rescue and verified that these two types of rescue are equally important for community resistance. Moreover, I verified that community re-assembly plays an important role in maintaining diversity following disturbance. Habitat loss had an stronger effect on species response than climate change. For the species showing evolutionary rescue, rather than expected directional trait selection, I observed changes in trait variation, which I interpret as a sign of disruptive selection allowing survival in communities under extinction debt. The results demonstrate the importance of accounting for eco-evolutionary processes at the community level to understand and predict biodiversity change.

3.1 Introduction

Depending on its intensity, frequency, and type, an ecosystem disturbance can cause the extinction of a varying set of species (Figueiredo, Krauss, Steffan-Dewenter, & Cabral, 2019). Many of these extinctions are not immediate, but are delayed, creating an extinction debt (Jackson & Sax, 2010; Essl et al., 2015a). This is in particular the case for perennial plant communities which cannot directly escape habitat loss and disturbance through individual movement as in most animal taxa. Moreover, certain traits enable prolonged individual survival, such as clonality and long lifespans (Saar et al., 2017, 2012), whereas other traits prevent rapid population responses to disturbance events, such as low dispersal ability of seeds/fruits (Figueiredo et al., 2019; Hylander & Ehrlen, 2013; Purschke et al., 2012). Nevertheless, few studies reported cases of populations under debt for which clonal reproduction hampered genetic variability (Jimenez-Alfaro et al., 2016; Hu et al., 2017), or where the survival of long-living individuals reduced the population's adaptive capacity (Cotto et al., 2017). The period of time to pay the extinction debt is called the relaxation time (J. M. Diamond, 1972). During this period, species have the chance to bounce back from the disturbance and rescue themselves from extinction. This can be facilitated by intrapopulation variability and microevolutionary processes that unfold during the relaxation time. Thus, accounting for and understanding these processes may shed light on how species respond to disturbances and which mitigation policies are most promising (Figueiredo et al., 2019). However, the study of such processes is difficult due to the lack of adequate information, namely empirical demographic, genomic and/or trait data before and after a disturbance. Computational and mesocosmic experiments have shown that it is possible that rapid adaptations revert population decline under stressful conditions by increasing population fitness and growth rate, in a phenomenon dubbed evolutionary rescue (Gomulkiewicz & Shaw, 2013; G. Bell, 2013; G. Bell & Gonzalez, 2011, 2009). In these studies, rescue is characterized by a demographic recovery in the form of a U-shaped abundance curve over time, i.e. initial decrease in response to the disturbance followed by increase once the population starts to adapt to the new conditions (Fig. 3.1-A, Gomulkiewicz & Holt, 1995; G. Bell & Gonzalez, 2009). Such population responses indicate evolutionary rescue, and they can arise from the selection of favorable phenotypes from standing genetic variation, mutations, or introduction of new alleles by gene flow (D. A. Bell et al., 2019). Biological and environmental factors increase the potential of evolutionary rescue by promoting selection of adaptive phenotypes: i) a minimal population size (G. Bell & Gonzalez, 2009); ii) previous exposure to non-lethal levels of disturbance (G. Bell & Gonzalez, 2009); iii) temporally consistent disturbance (Hao, Brockhurst, Petchey, & Zhang, 2015); and iv) a match between the spatial and temporal regime of disturbance, the species dispersal ability, and genetic structure of mutating genes (G. Bell & Gonzalez, 2011; Schiffers et al., 2014). Nonetheless, evidence suggests that adaptation due to selection from genetic variation is actually faster than selection from beneficial mutations, which require long periods of time to happen (Barrett & Schluter, 2008). This is particularly relevant for the current fast pace of human disturbances, for which species may need to adapt via standing variation rather than via mutation.

Evolutionary rescue is originally a species-level concept. At the community level, it is assumed that community viability is restored, but not all species abundances, meaning that community structure likely changes in the process (with community viability being measured as the proximity of organisms density close enough to the original community, for example Low-Décarie et al., 2015). Computational, micro-, and mesocosmic experiments have also shown that the recovery of the various species in a community is not uniform and that community evolutionary rescue involves changes in species relative abundances and community composition, as species respond differently to change in environmental conditions (Osmond & Mazancourt, 2013; Fussmann & Gonzalez, 2013; Low-Décarie et al., 2015). Therefore, recovery of community viability does not depend only on can happen due to demographic rescue of some species, resulting from species sorting following disturbance and consequent community reassembly (D. A. Bell et al., 2019). Demographic rescue can also happen through species adaptive phenotypic plasticity (Snell-Rood, Kobiela, Sikkink, & Shephard, 2018), making it necessary to consider changes in heritable trait values to distinguish between evolutionary rescue from pure demographic rescue. Therefore, disentangling demographic rescue, i.e. abundance recovery, from evolutionary rescue remains challenging, and how evolutionary rescue influences or is influenced by species traits remains largely unexplored. Studies have addressed evolutionary rescue by focusing on a single species trait change (e.g. Tseng & O'Connor, 2015); by experimenting with conditions that would be lethal for all species, and would thus require adaptation if recovery is to happen (e.g. Low-Décarie et al., 2015); by focusing on the evolution of a trait directly related to the disturbance (Fussmann & Gonzalez, 2013); or by monitoring the change in phylotype frequencies (e.g. Thibodeau, Walsh, & Beisner, 2015). Therefore, when investigating community evolutionary rescue under extinction debts, one must account for the confounding effects of species sorting, because stabilizing mechanisms of coexistence are disrupted during the relaxation time, opening niche spaces which might allow dwindling populations to recover.

Climate change and habitat loss, currently two of the major threats to biodiversity (IPBES 2019), have been addressed differently in the context of evolutionary rescue. Evolutionary rescue from climate change has been shown to be enabled by a slow rate of temperature increase (Killeen, Gougat-Barbera, Krenek, & Kaltz, 2017), and to depend on the interaction with dispersal ability (Boeye, Travis, Stoks, & Bonte, 2013). At the population level, local adaptation can result in maladaptation for highly dispersing species (Bourne et al., 2014), while at the community level, fast adapting species might prevent slow adapting ones from dispersing, and thus, surviving through range shift (P. L. Thompson & Fronhofer, 2019). Besides higher temperature tolerance and dispersal, smaller body sizes can be selected for under climatic change, due to higher metabolic and reproductive rates, and thus faster life cycles (Leidinger & Cabral, 2020). While research including scenarios of habitat fragmentation reinforces the possibility of both positive and negative effects arising from the interaction between dispersal evolution and climate change (e.g. Boeye et al., 2013; Cheptou, Hargreaves, Bonte, & Jacquemyn, 2017), I could not find any experiments testing the occurrence of population or community evolutionary rescue following the loss of habitat area. In contrast, a larger body of work addressed extinction debts under habitat destruction (fragmentation and loss of contiguous area) than under climate change (Figueiredo et al., 2019). This exemplifies how little I know about the contribution of evolutionary rescue to waive extinction debt across disturbance types or even across combinations of disturbance types, which is a likely scenario worldwide (Bowler et al., 2020).

In this study, I aim at exploring evolutionary rescue after two types of disturbances (habitat loss and climate change) and their combination. I ask the following questions: 1) Can one differentiate evolutionary from demographic rescue in species under a metacommunity context? 2) Which traits allow species to undergo evolutionary rescue compared to species going extinct? 3) How do life-history traits change during evolutionary rescue? To tackle these questions, I applied a genomically explicit individual-based model to scenarios a) without disturbance (control), b) with habitat loss, c) with climate change, d) with both habitat loss plus climate change. In this model, the ecological traits of plant individuals belonging to different coexisting species are coded in their genomes (Leidinger & Cabral, 2020). In the experiments, species could only exploit genetic and intraspecific variation already present at initialization (i.e. mutations were switched off). Thus, evolutionary change could happen only via recombination, sexual reproduction and the emergent processes of drift and selection. The hypothesis for question 1 is that demographic rescue and evolutionary change are independent process. When the happen simultaneously in a population, this population is said to have gone through evolutionary rescue. Therefore, populations that went through evolutionary rescue show significant trait change in relation to pre-disturbance values, while species that were rescued solely due to demographic rescue do not (they go through demographic rescue only). The hypothesis for question 2 is that enhanced dispersal abilities, higher temperature tolerance, smaller body sizes, and low levels of gene linkage favor evolutionary rescue. The hypothesis for question 3 is that rescued species are selected for smaller body sizes, and that higher temperature tolerance and dispersal distance are jointly selected for.

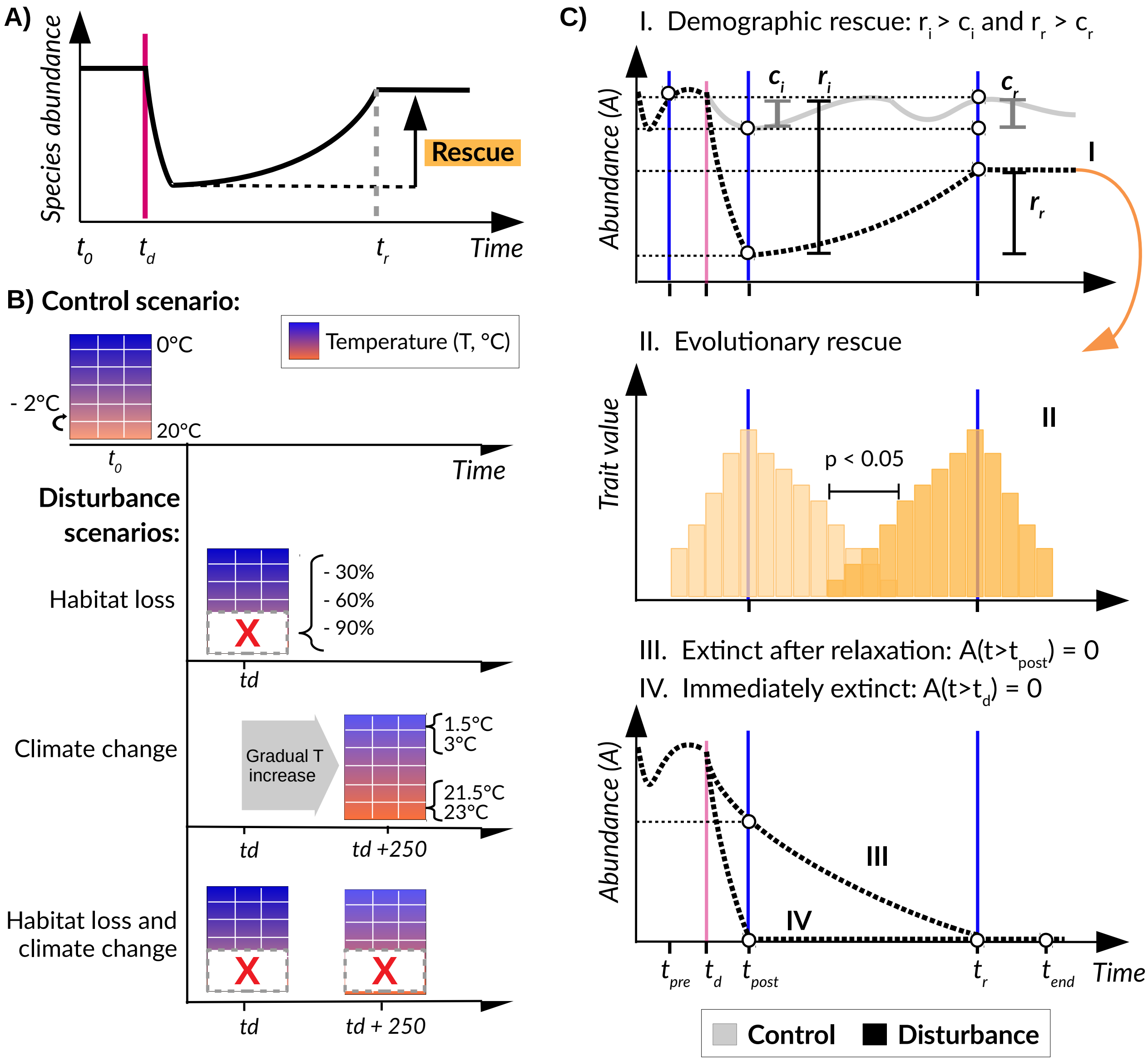

Figure 3.1: Schematic representation of A) a classic example of population demographic rescue due to evolutionary rescue, B) the experimental design of the study, and C) how species responses to disturbance were identified. t_0 refers to the start of the simulation, t_d to the time where disturbance is implemented (pink line), and t_r to the end of the relaxation time. In B, the depiction of how disturbances are implemented: habitat loss, as decrease (in %) in grid area at t_d; climate change, as global and gradual temperature (T) increase (of 1.5°C or 3°C) during 250 time steps; and habitat loss plus climate change, a combination of both. In panel C, I identified the time steps (blue lines) where abundances (A) were measured (points) to calculate species abundance change before and after disturbance ($r_i = A(t_{post})/A(t_{pre})$) and at the end of the relaxation time ($r_r = A(t_r)/A(t_{post})$). I compared these values to their equivalents in the control scenarios (c_i and c_r) to identify demographic rescue (I). Significant trait change between beginning and the end of relaxation differentiated evolutionary (II) from demographic rescue. I also identified species extinct during the relaxation time (III) or immediately after disturbance (IV).

3.2 Materials & Methods

3.2.1 Model description

I use the GeMM (version 1.2.0, Leidinger & Cabral, 2020) - a genome and spatially-explicit, niche- and individual-based model for plant metacommunities written in Julia (Bezanson, Edelman, Karpinski, & Shah, 2017). The following text summarizes the complete model description from Leidinger and Cabral (2020). The model considers explicit population and community assembly dynamics emerging from genomic and individual level processes. In the model, individuals belong to species, which are characterized by individuals with identical genetic architecture (genome size and number of linkage units), whose genome codes for ecological traits (dispersal ability, environmental niche and size). Trait values follow species-specific Gaussian trait distributions. Hence, conspecific individuals display genetic and phenotypic variation.

Eco-evolutionary processes. Yearly vegetative growth in biomass, fertility and mortality rates in the model are calculated according to the metabolic theory of ecology (MTE Brown, Gillooly, Allen, Savage, & West, 2004; Price, Gilooly, Allen, Weitz, & Niklas, 2010), whereby an individual's biological rate depends positively on environmental temperature, and negatively, on its body mass. It follows that smaller individuals have higher mortality rates than bigger ones, while individuals in cooler conditions have lower mortality rates than those in warmer conditions. Over the course of a simulation (the model considers discrete yearly time steps), individuals grow in size, passing three life stages: (1) seed, (2) juvenile, and (3) adult. Individuals disperse as seeds, establish, grow and become reproductive adults. Seed biomass and adult biomass, i.e., the threshold biomass where individuals become reproductive, are genetically-coded traits. Adults reproduce sexually with a random adult of the same species within the same grid cell to produce new seeds. Failing to find a reproductive partner, individuals may also reproduce by selfing. The probability of selfing in the absence of reproductive partners is another genetically-coded trait. Seed dispersal connects local populations, and dispersal distances are modeled after a logistic dispersal kernel with genetically-coded mean dispersal distance and shape parameters (see Bullock et al., 2017). Furthermore, all individuals have encoded temperature niche. Local temperature has a direct effect on biological rates, as described by the MTE (Brown et al., 2004) and affects density-independent mortality. Each species temperature niche is characterized by a temperature optimum and a temperature tolerance parameter (Table 3.1), which represent the mean and standard deviation of a Gauss curve, respectively. The degree of mismatch between an individual's preference optimum with the local environment, i.e. within the grid cell, determines its adaptation value, i.e. environmental fitness. During establishment, fitness is calculated for each new seed based on the local conditions and phenotypic traits. Furthermore, each time environmental conditions change, all individuals in the affected grid cell pass establishment again to re-calculate their fitness values. These fitness values are functional for density-independent mortality (Bullock et al., 2017). Mortality further scales with individual temperature adaptation, where mortality is higher for individuals which are poorly adapted to the surrounding temperature (Cook, 1979). All of the aforementioned traits are coded by one or more genes as explicit genetic sequences packed in an individual's diploid genome (i.e. polygenes). A detailed description of the genetic architecture can be found the in Supplementary material Appendix 2. A detailed model description, with justification for assumptions, equations, and default parameter values can be found in (Leidinger & Cabral, 2020). Model parameters are summarized in Table 3.1.

3.2.2 Experimental design

To generate an extinction debt and potentially observe community rescue and characterize the evolutionary rescue behind it, I simulated the eco-evolutionary dynamics of randomly assembled meta-

Table 3.1: Simulation parameters, values and references, and scope. Parameters of 'default' scope keep values used by Leidinger & Cabral (2020), upon creation of the GeMM model. Parameters of 'experiment' scope were adapted to implement the current experimental design. SD abbreviates standard deviation.

Parameter	Value or Range	References	Scope
Number of loci (n_l)	1 to 10	Leidinger & Cabral (2020)	default
Number of linkage units	1 to n_l	Leidinger & Cabral (2020)	default
Temperature optimum	10°C to 40°C	Leidinger & Cabral (2020)	default
Temperature tolerance	0°C to 1°C	Leidinger & Cabral (2020)	default
Adult biomass	e^3 to $e^{14}g$	Leidinger & Cabral (2020)	default
Biomass at seed stage	e^{-2} to $e^{10}g$	Leidinger & Cabral (2020)	default
SD among trait loci	0 to $0.1 \times \mu_{trait}$	Leidinger & Cabral (2020)	default
Base fecundity	1.4×10^{12}	Leidinger & Cabral (2020)	default
Base growth rate	8.8×10^{10}	Leidinger & Cabral (2020)	default
Base mortality rate	1.3×10^{9}	Leidinger & Cabral (2020)	default
Carrying capacity (K)	$5 \times 10^4 kg$	Bernhardt-Römermann et al. (2011)	experiment
Dispersal kernel mean	0 to 2 grid cells	-	experiment
Dispersal kernel shape	0 to 2 grid cells	-	experiment
Habitat loss	30%, 60%, 90%	-	experiment
Climate change	1.5°C, 3.0°C	IPCC (2013)	experiment

communities, in a landscape submitted to different scenarios of habitat loss and climate change. The landscape, represented by a rectangular grid of square cells, was composed of 5×10 grid cells, and contained a gradient of temperature along the latitudinal axis, with temperatures between 0°C (northernmost edge) and 20°C (southernmost edge). The gradient considered a 2°C difference between rows of grid-cells (Fig. 3.1-B). Considering a tropospheric lapse-rate of 5°C/km^{-1} (La Sorte, Butchart, Jetz, & Böhning-Gaese, 2014), the resulting grid approximates a 4 km mountain slope. Each grid cell had a carrying capacity of 1000 kg, and total landscape carrying capacity reached 510^4 kg. This carrying capacity is equivalent to 12.5 ha of a mildly mowed, unfertilized temperate grassland area, whose productivity ranges around 0.4 kg m^{-2} according to (Bernhardt-Römermann, Römermann, Sperlich, & Schmidt, 2011). Experiments and analysis were repeated in a shallower gradient of 1°C step sizes, with results that were qualitatively similar to the ones obtained for the steeper gradient. Hence, results from shallower gradients are reported only in the Supplementary material. The initial species community was generated from a random combination of ecological and and genomic traits, known to generate stable communities in the GeMM (as listed in Table 3.1, the default values from Leidinger & Cabral, 2020). To focus on selection on standing variation at ecological timescales and avoid confounding effects, mutation was disabled, and the only mechanism of increasing genetic diversity at the regional scale (whole grid, hereafter "landscape") was recombination. Gene flow within the landscape is possible, and therefore, might also contribute to changes in genetic diversity at the local scale (grid cell). Simulation experiments consisted of scenarios where different intensities of habitat loss and/or climate change were imposed to the simulation arena (3.1-B). Intensity of disturbance are listed in 3.1, and disturbance types were simulated in full-factorial design (fully described in "Experimental design" and depicted in Figs. S1-S4, in the Supplementary material).

In total, I simulated 12 scenarios, including a control scenario without disturbance. Each experiment was replicated 30 times, yielding a total of 720 simulations. Each of the 30 replicates consisted of a random initial set of species, which were subjected to all experiments, to ensure comparison. I ran each simulation for 2700 time-steps, with a burn-in period of 750 time-steps. The length of the burn-in period was chosen as the time necessary to reach quasi-equilibrium of species richness metrics in the control scenarios (Figs. S5-7 in the Supplementary material).

3.2.3 Analyses

To identify the roles of evolutionary and demographic processes in community rescue (question 1), I first identified all possible responses to disturbance: demographic rescue, evolutionary change, evolutionary rescue, survival without rescue, extinction upon disturbance, and extinction during relaxation. To identify species that exhibited demographic rescue, I calculated species abundance change (ratio between relevant time steps) at the regional scale (total abundance grid) and compared values of abundance change at key time steps t: pre-disturbance ($t = 700$), post-disturbance ($t = 800$ or $t = 1000$, for habitat loss and climate change, respectively), and at the end of the community relaxation time ($t = 1800$). Specifically, species for which abundance decreased after disturbance and then increased by the end of the relaxation time were identified as having gone through demographic rescue (Fig. 3.1-C). To avoid including (in further analysis) species for which such a rescue-like population change was part of their natural population dynamics, I only included species for which the response (demographic rescue or not) was different from the control scenario. To identify species that went through evolutionary change, I verified whether I could detect significant trait change of at least one species' trait during the relaxation time. To that end, I used a non-paired Wilcox test to detect significant change (p-value < 0.05) between populations' trait values immediately after disturbance ($t = 800$) and by the end of relaxation ($t = 1800$). Here, to assure statistical robustness and decrease the chance of detecting change due to genetic drift instead of selection, I only included populations with minimum regional abundance of 30 individuals. Moreover, the minimal abundance of 30 individuals was representative of most species included in the simulation (Fig. S8 and Table S1 in the Supplementary material). Species for which the wilcox-test was inconclusive, i.e. no *p-value* could be estimated due to ties arising from exact trait values, were considered to not have gone through evolutionary change. Species that went through demographic rescue and evolutionary change were considered to have gone through evolutionary rescue. Finally, I counted the number of species that went extinct immediately after disturbance and the number of species that went extinct by the end of the relaxation time (Fig. 3.1-c). I also verified the occurrence of community collapse, i.e., whether there were communities for which all species went extinct after the relaxation time. Such community-wide response indicates threshold conditions under which no rescue is possible. To visualize the distribution of responses per disturbance scenario (characterized by disturbance type and intensity), I calculated the proportion of species falling into each category of response (in relation to the number of species present before disturbance). I tested the effect of disturbance intensity on the number of species exhibiting each response, in each disturbance type, through Herberich's tests (Herberich, Sikorski, & Hothorn, 2010). This test constitutes a multiple comparison procedure for assessing multiple means that makes no assumptions regarding the distribution, sample sizes or homogeneity of variance. Finally, I verified whether it is possible to decouple community rescue through community reassembly from rescue through evolutionary rescue by identifying species that went through a) demographic rescue only, b) evolutionary change only, and c) demographic rescue and evolutionary change, i.e., species that went through evolutionary rescue. The occurrence of these three groups indicates the independence of the demographic and evolutionary processes.

To detect which traits contribute to the occurrence of evolutionary rescue (question 2), I compared trait values between populations that went through evolutionary rescue and populations that went extinct during the relaxation time, i.e. payed the extinction debt. For the comparison, I applied a linear mixed-effects model with species mean trait value (measured in the beginning of the relaxation time) as the response variable, response to disturbance ("evolutionary rescue" or "extinction during relaxation") as the fixed effect, and replicate as the random effect. To visualize the variation, intensity and direction of trait differences for the traits which showed significant effect of response, I used notched boxplots. Notches indicate the 95% confidence interval around the median, thus facilitating the visualization of differences in values distributions.

To assess how trait values changed during evolutionary rescue (question 3), I compared trait values that significantly changed between the beginning ($t = 800$) and the end of relaxation time ($t = 1800$) for the species showing evolutionary rescue. To visualize the trends of selective pressure on single traits, I plotted the distribution of populations' mean trait values and the distribution of coefficients of variation of populations' trait values (i.e. intraspecific variation). A species is classified as having gone through evolutionary rescue if at least one of its traits showed significant during the relaxation period. Therefore, for each trait, I only compare the distributions of the species for which it significantly changed during the relaxation time.

Linear models of question 2, and the visualizations of questions 2 and 3 were built with traits values (v) transformed as $log(v + 1)$, because the distribution of values is left-skewed. All analyses were conducted on R (R Core Team, 2018).

3.3 Results

Regarding question 1, I detected species that went through i) demographic rescue, ii) evolutionary change without demographic rescue, iii) evolutionary rescue, iv) species that went extinct during the relaxation time, v) species that went extinct shortly after disturbance, and vi) species that survived without any signs of demographic rescue (only responses i-iv are depicted in Fig. 3.2 for simplicity, but all types of responses, for both temperature gradients, are depicted in Fig.5 of the Supplementary material). I did not detect any case of community collapse. Absolute and relative quantities of species falling into each category of response to disturbance (for both temperature gradients) are listed in Tables 1 and 2, and results of the Herberich tests, in Tables 3-4 in the Supplementary material. Results for both temperature gradients were similar. I focus on the results for the steep temperature gradient, since the results for the shallow temperature gradient are similar (included in the Supplementary material).

Most species went extinct shortly after intermediate (60%) or high (90%) intensities of habitat loss, independently of the occurrence or intensity of climate change (Fig. 5 in Supplementary material). In scenarios of isolated disturbance (low (30%) or intermediate habitat loss or climate change), evolutionary change without demographic rescue was the second most frequent response, ranging between $\mu = 14.7\%$ of responses ($\sim$ 10 species) under high habitat loss and $\mu = 38.8\%$ ($\sim$ 18 species) under low (+1.5°C) climate change (Fig. 3.2-A,B and Table 1 in Supplementary material). In scenarios with both disturbances, however, evolutionary rescue was the second most frequent response under low and intermediate intensities of habitat loss, ranging between $\mu = 12.8\%$ ($\sim$ 8 species) under intermediate habitat loss (60% habitat loss, +3°C climate change) and 24.6% ($\sim$ 13 species) under low intensity (30% habitat loss, +1.5°C climate change, Fig. 3.2-C). The occurrence of demographic rescue was lower than that of evolutionary change and evolutionary rescue under lower and intermediate habitat loss ($\mu = 8.8 - 13.8\%$, $\sim 5 - 7$ species) and climate change ($\mu = 12.8 - 12.1\%$, $\sim$ 6 species) in isolation, and under low intensities of habitat loss plus climate change ($\mu = 17.6 - 18.5\%$, $\sim$ 9 species, Fig. 3.2-C and Table 1 in Supplementary material). Nonetheless, under scenarios of high habitat loss ($\mu = 3.5\%$, $\sim$ 3 species) and intermediate and high habitat loss plus climate change ($\mu = 4.42 - 15.3\%$, $\sim 3 - 10$ species), demographic rescue was the second most common response (Fig. 3.2-C and Table 1 in Supplementary material).

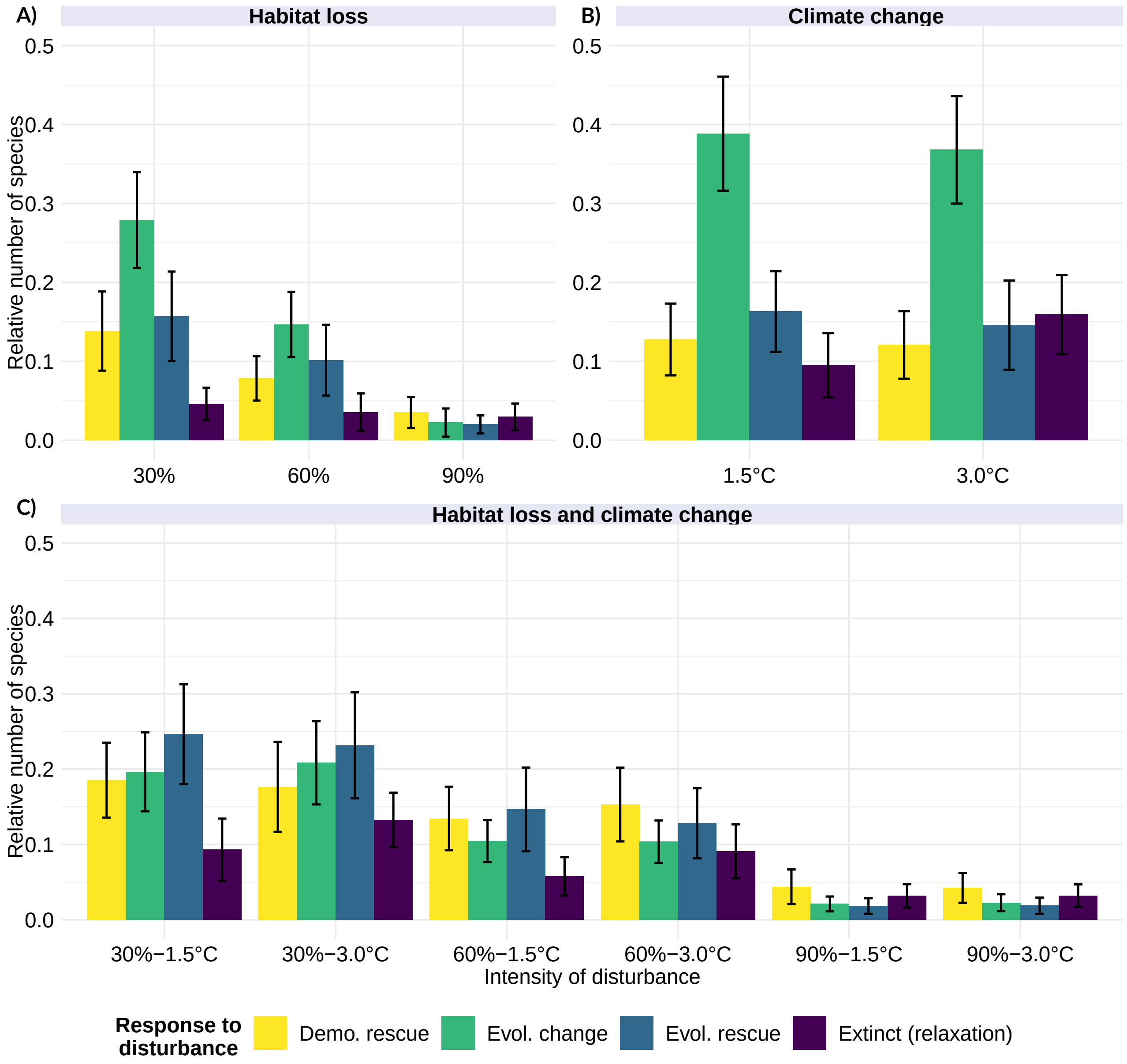

Figure 3.2: Mean relative number ($n_{response}/n_{total}$ ± sd) of species' responses to disturbance in simulations with the steep temperature gradient: demographic rescue only (U-shaped abundance curve, *Demo. rescue*), evolutionary change without demographic rescue (*Evol. change*), demographic rescue and evolutionary rescue, i.e. evolutionary rescue (*Evol. rescue*), and extinction by the end of the relaxation time *Extinct (relaxation)*. All responses, as well as results for the shallow gradient are available in Fig. 5 of the Supplementary material.

When comparing the occurrence of responses across different intensities of the same disturbance, contrary to the other responses, only the proportion of species extinct during the relaxation time significantly increased under higher climate change (Fig. 3.2-B) and did not significantly change under habitat loss in isolation (Fig. 3.2-A, Table 3 in Supplementary material). Under habitat loss plus climate change, it significantly decreased under higher levels of habitat loss (independent of the intensity of climate change) and significantly increased under higher climate change (under low and intermediate levels of habitat loss, Table S3). The other groups of response, however, significantly differed under different intensities of habitat loss, but not under climate change in isolation (Fig. 3.2-A,B, Table 3 in Supplementary material). Under habitat loss plus climate change, except for the proportion of species going through demographic rescue, the proportion of species exhibiting each of the responses considered was significantly different under different intensities of habitat loss (independent of the intensity of climate change, Fig. 3.2-C, Table 3 in Supplementary material).

Regarding question 2, the difference between trait values of species that went through evolutionary rescue and those of species that went through extinction during relaxation varied according to disturbance and intensity, as well as to the trait itself. In Fig. 3.3, I focus on traits for which differences were significant for most intensities, but Fig. 6-9 and Tables 5-6 of the Supplementary material Appendix 2 contain the results for all traits, in all scenarios simulated. Adult and seed biomass, probability of selfing, and temperature niche values were significantly different in all scenarios of disturbance (Fig. 3.3). Under habitat loss, species that eventually managed to survive through evolutionary rescue had smaller body size (significantly smaller under intermediate intensity, Fig. 3.3-A), higher probability of selfing (significantly higher for all intensities, Fig. 3.3-B), lower temperature optimum (significantly different under low and intermediate intensity, Fig. 3.3-C), and higher temperature tolerance (significantly different under low intensity, Fig. 3.3-D). Under climate change, rescued species had higher seed mass (significantly higher under high intensity, Fig. 3.3-E), and (under all intensities) higher probability of selfing (Fig. 3.3-F), temperature optimum (Fig. 3.3-G), and temperature tolerance (Fig. 3.3-H). Under habitat loss plus climate change, rescued species had significantly higher seed biomass (Fig. (3.3-I), probability of selfing (Fig. (3.3-J), temperature optimum (Fig. (3.3-K) and tolerance (Fig. (3.3-L) values under all combinations of low and intermediate habitat loss with climate change. These species also had significantly higher probability of selfing under high habitat loss and low climate change (Fig. 3.3-J).

Regarding question 3, during evolutionary rescue, I observed the increase and decrease of variation in the populations trait values, respectively (Fig. 3.4 and Fig. 10-14 in Supplementary material), rather than through change in populations mean values (Fig. 15-18 in Supplementary material). In Fig. 3.4, I focus on traits that i) albeit significantly changing during evolutionary rescue, were not significantly different to extinct species in the beginning of relaxation (i.e. not relevant for question 2 above, e.g. mean and long dispersal distances), or ii) presented both increase and decrease of variation under different intensities of the same disturbance (e.g. adult and seed biomass). Under habitat loss (Fig. 3.4-A-D), the variation of mean of mean dispersal distances increased under low intensity, but decreased under intermediate and high intensity (Fig. 3.4-A), while the variation in long dispersal distance only increased, independent of the intensity of loss (Fig. 3.4-B). On the contrary, the variation of adult biomass decreased under all intensities (Fig. 3.4-C), while the seed biomass has a response similar to the mean dispersal distance ((Fig. 3.4-D, increased under low intensity, and decreased under high). Under climate change (Fig. 3.4-E-H), the variation of mean of mean dispersal distances decreased under low intensity, but increased high intensity (Fig. 3.4-E), while the variation in long dispersal distance only increased, independent of the intensity of climate change (similar to the response under habitat loss, (Fig. 3.4-F). The variation of adult biomass decreased under low intensity but increases under high ((Fig. 3.4-G), while the seed biomass has an opposite repines, i.e. it increased under low intensity, and decreased under high ((Fig. 3.4-H, similar to the response under habitat loss, (Fig. 3.4-D). Under habitat loss plus climate change (Fig. 3.4-I-L), responses are mixed. Under low and high habitat loss, the variation in mean dispersal distance decreases, independent of the intensity of climate change (Fig. 3.4-I). Under intermediate habitat loss, it increases. The variation of long dispersal distances increased under low intensity habitat loss plus climate change, and under intermediate habitat loss (Fig. 3.4-J). Under low habitat loss and high climate change, and under high habitat loss, the variation decreased. The variation of adult biomass increased under low intensities of habitat loss plus climate change, and it decreased under intermediate intensities (Fig. 3.4-L). It also decreased under the highest intensity, but the variation at the beginning of relaxation was the lowest, if compared to the other intensities. The variation of seed biomass increased only under low intensities of habitat loss plus climate change, and it decreased for all other scenarios (Fig. 3.4-L).

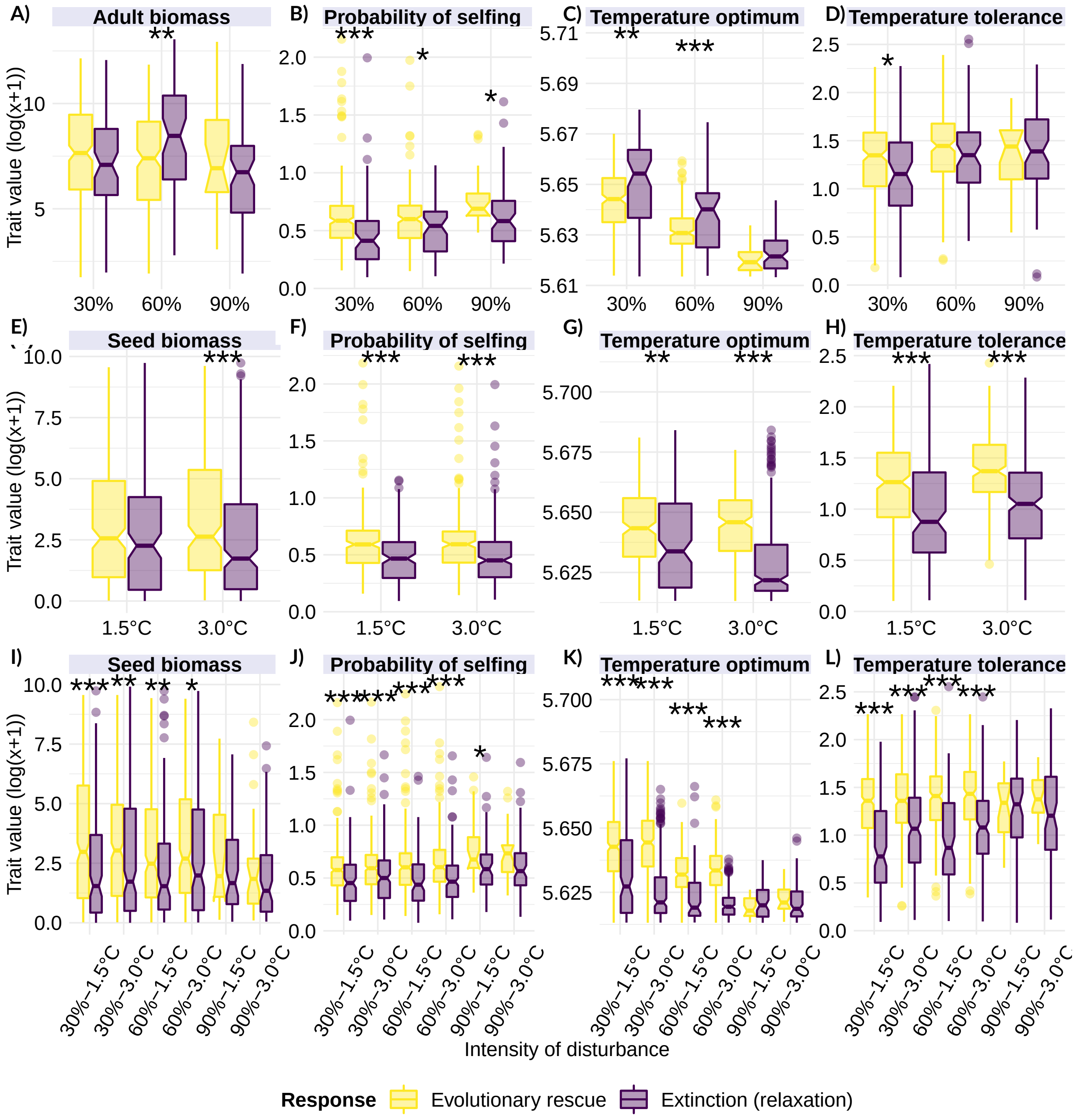

Figure 3.3: Distributions of mean trait values of species that went through evolutionary rescue and extinction during the relaxation time in simulations of (a) habitat loss, (b) climate change, and (c) habitat loss plus climate change, in the steep temperature gradient. Trait values (x) were measured immediately after disturbance started being implemented ($t = 800$ for all disturbances, for simplicity), and transformed as $log(x + 1)$. Significance levels: "***" = p-value $\leqslant 0.001$, "**" = $0.01 \geqslant$ p-value $\geqslant 0.001$, "*" = $0.05 \geqslant$ p-value $\geqslant 0.01$. Non-significant differences are not shown.

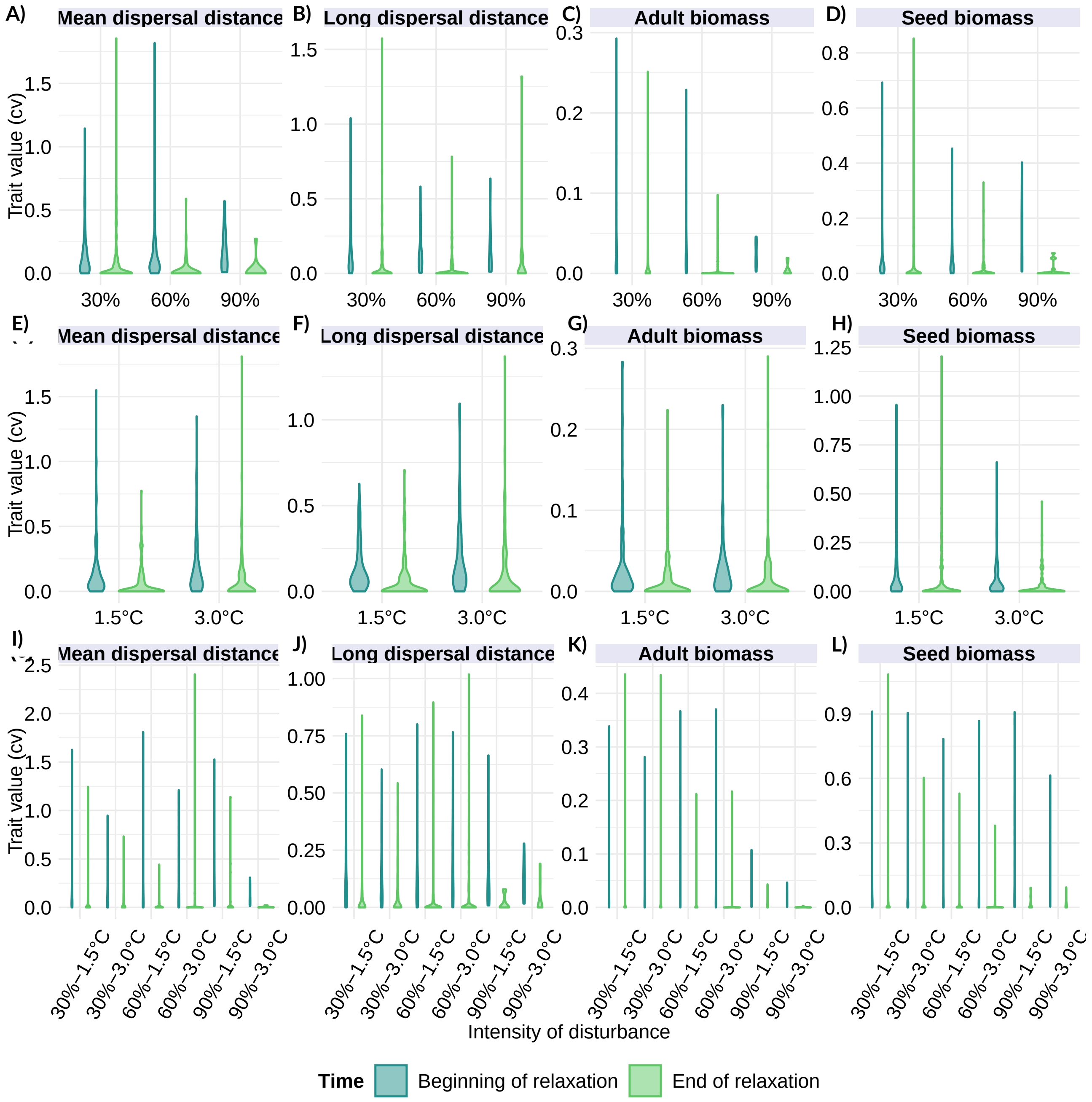

Figure 3.4: Distribution of intraspecifc variation (measured as coefficient of variation) of trait change of species that went through evolutionary rescue following a) habitat loss, b) climate change, and c) both disturbances. Change calculated as the ratio between trait values at the end and at the beginning of relaxation. Trait values measured immediately after disturbance started being implemented ($t = 800$ for all disturbances, for simplicity), and at the end of the relaxation time ($time = 1800$). Trait change was only calculated for traits for which the time steps (beginning or end of relaxation) had a significant effect on trait value.

3.4 Discussion

In this study, I verify that both evolutionary and demographic rescue contribute to community resistance to disturbance. In the following subsections I discuss whether these results verify the hypotheses I had for each of the questions and finish by listing the limitations of this study and the perspectives for future research.

3.4.1 Can one differentiate evolutionary from demographic rescue in species under a metacommunity context?

I confirm the hypothesis for question 1, by showing that demographic and evolutionary change can happen independently from one another, as well as simultaneously, i.e. evolutionary rescue. I show that the relative importance of these processes depends on the type and intensity of disturbance.

Previous work on evolutionary rescue usually used disturbances that are known to be lethal to the focus organism/community (e.g. Low-Décarie et al., 2015; G. Bell & Gonzalez, 2009). In this study, I instead simulated disturbances that take place in different regimes and affect entire communities in the real-world. Hence, the simulated meta-communities should be more representative of real-world scenarios than previous single-species, single-disturbance experiments. In that regard, the results presented here illustrate the complexity of predicting community responses to current, multivariate threats, where a variety of dynamics are possible (further discussed in Blonder et al., 2017). Both demographic and evolutionary processes contribute to populations' survival, as well as innate species characteristics that make them resistant (species that survive without any demographic nor evolutionary response).

Habitat loss was the disturbance that affected populations the most, by imposing immediate decrease in population sizes, which likely limited populations evolutionary potential, particularly under high habitat loss, where evolutionary responses were the rarest. Such population bottlenecks are are a major threat to successful conservation measures as they reduce species evolutionary potential (Frankham et al., 1999; Hoffmann, Sgrò, & Kristensen, 2017) and increase extinction risk due to demographic and environmental stochasticity. Under climate change, however, population sizes did not decrease as much, allowing high population sizes to foster evolutionary change. Under habitat loss plus climate change, particularly under low or intermediate habitat loss, climate change seems to have prompted evolutionary rescue. While habitat loss decreased population sizes by destroying habitats in the warmer margin of the landscape, climate change increased the temperature of the remaining area, allowing for evolutionary rescue to happen as the remaining habitat became more suitable to remnant populations. In the GeMM, given enough available habitat area (range change is close to 0 under high intensity of habitat loss), species surviving through evolutionary rescue also presented both range expansion and retraction (positive and negative range sizes for all disturbances), and shift (northward change of both north and southern edges under climate change). Such range dynamics are possible due to species dispersal ability (further discussed under ”Trait evolution during rescue”), but beneficial mutations (not included in the simulations done for this study) may also contribute to evolutionary rescue, if the rate of dispersal is slow enough to allow mutations to establish (Kirkpatrick & Peischl, 2013). Besides range dynamics, species that went through evolutionary rescue also increased local adaptation, which indicates that whichever was the direction of range change, competition competition was likely not too harsh in the final occupied area (Razgour et al., 2019). Regardless, the potential of evolutionary rescue to save populations under climate change is limited by high habitat loss, which not only creates population bottlenecks that reduces evolutionary potential (Frankham et al., 1999; Hoffmann et al., 2017), but also limits the range available for potential adaptation (Schiffers et al., 2013).

3.4.2 Which traits allow species to undergo evolutionary rescue compared to species going extinct?

Regarding the hypothesis for question 2, I only confirm that higher temperature tolerance would facilitate evolutionary rescue, since no significant difference was detected for values of dispersal distance or linkage degree between rescued and extinct species. I verified that species that later went through evolutionary rescue generally had larger seeds at the beginning of the relaxation period, than the species that went extinct during the same period. According to the metabolic theory of ecology (MTE, Brown et al., 2004; Sibly, 2012), seeds with higher biomass have lower metabolic mortality rates, which might have contributed to short-term survival following disturbance, increasing the chances of rescue. Larger seeds also have lower metabolic germination rates, which might have contributed to the formation of seed banks, which in turn allow population reestablishment and potentially, evolutionary rescue (if dispersal abilities maintain the seed inside the species' niche tolerance (as demonstrated by Schiffers et al., 2014). Albeit I did not detect a significantly positive effect between adult biomass and evolutionary rescue, short-lived and fast reproducing plant species (lower biomass, according to the MTE) have been shown to be more vulnerable to climate change (Compagnoni et al., 2020) and local extinction (Saar et al., 2012). The physiological effects of climate change on species ability to cope with new environmental conditions can be seen as direct, individual-level effect (Huey et al., 2012). When analyzed coupled with species dispersal abilities, an ever increasing body of research on range dynamics connects physiological and regional demographic and evolutionary processes to predict species to climate change (Diniz-Filho et al., 2019; S. E. Diamond, 2018; MacLean & Beissinger, 2017; Chuang & Peterson, 2016). These results show how the metabolic theory of ecology allows adding yet another layer of effects, by connecting species traits, physiology, and local demography.

Selfing ability was a highly important factor for species ability to go through evolutionary rescue, being significantly different from extinct species for most disturbances and intensities. This finding fuels the discussion regarding the evolution of selfing as a reproductive strategy of short term advantage (reproductive assurance, Busch & Delph, 2012; Cheptou, 2018), despite its long term disadvantages (limiting the species adaptive potential and the increased mutation load Escobar et al., 2010; Busch & Delph, 2017; Noël et al., 2017; Cheptou, 2018; Wright, Kalisz, & Slotte, 2013). Even on the short-term, it can lead to evolutionary suicide, whereby the reproductive assurance starts as an evolutionary attractor, but the inbreeding depression of selfing might increase to the point of having negative effects of the population growth rate, leading to extinction (Cheptou, 2018). I argue that the simulations constitute a representative case of the processes involved in the evolution of selfing. On the short-term, selfing provides reproductive assurance, which allows population recovery and evolutionary rescue. Agreeing with studies investigating the establishment of intermediate levels selfing (Johnston, 1998), in the results reported here, selfing does not remain the sole reproductive mode of rescued species, with maximal probability of selfing being 30% (Fig. S18 and S19 in the Supplementary material). By not being the major mode of reproduction, the negative effects of selfing did not manifest in these species, and the advantage of the strategy allowed them to be rescued. For communities under debt, therefore, it is particularly important to monitor the levels of selfing remnant populations, since i might decrease extinction risk in the short term, but not in the long term, if it increases in frequency.

Regarding species temperature niche, under climate change, rescued species had significantly higher values of temperature optimum and tolerance. These species were likely concentrated in affected areas (warmer, southern edge of the landscape), but had enough temperature tolerance and remaining abundances and habitat to reestablish in the remaining areas. Some species are known to have lower thermal tolerances (e.g. birds Khaliq, Hof, Prinzinger, Böhning-Gaese, & Pfenninger, 2014), and thus be vulnerable to more frequent heat waves and to climate change. Tropical plants, however, do not have lower tolerances, but are localized at the edge of their thermal range, which makes them more vulnerable (Sentinella, Warton, Sherwin, Offord, & Moles, 2020). These results reinforce the importance of considering populations' range dynamics when evaluating extinction risks (e.g. Leão, Fonseca, Peres, & Tabarelli, 2014; Dagnino et al., 2020). An important asset of such approach is the inclusion of species biotic context, i.e. interactions and associations, in the estimation of species distributions (e.g. Godsoe & Harmon, 2012; Tikhonov, Abrego, Dunson, & Ovaskainen, 2017). As shown in chapter 2, the study of the impact of interaction loss on extinction dynamics during the payment of debts is still meager. Requiring less detailed data than the network analysis proposed to be used in that chapter, joint-species distribution models could be an informative first approach to explore the extinction dynamics of interacting species.

3.4.3 How do life-history traits change during evolutionary rescue?

None of the hypotheses for question 3, regarding the selection of smaller body sizes, and the joint selection of higher temperature tolerance and dispersal distance during evolutionary rescue, were confirmed. Albeit significant, mean trait change trends were mild, which is expected by the limited temporal extent simulated (Hendry, 2017). Instead, I observed increases and decreases in the variation of species trait values (Fig. 3.4), which I interpret as stabilizing and disruptive selection, respectively.

Disruptive selection has been show to drive species differentiation of cichlids (van Rijssel, Moser, Frei, & Seehausen, 2018), and both selection and phenotypic plasticity (not included in the model, but a possible source of intraspecific variation) contribute to niche differentiation among grassland plant species (Meilhac, Deschamps, Maire, Flajoulot, & Litrico, 2020). Such differentiation improves coexistence by decreasing competition. Increased variation of dispersal traits can also potentially improve coexistence by allowing survival by avoidance, whereby species flee unsuitable conditions - which I observed in the simulations of climate change. Habitat loss, however, should pose strong selection on dispersal, since species quickly go extinct if they keep dispersing into unsuitable areas (Travis, 2003). It seems therefore counter intuitive that variation in long dispersal distances increased under increasing habitat loss. I interpret it as an instance of bet-hedging (Slatkin, 1974), whereby episodes of long dispersal remain rare, and thus, selection might not be as strong. Similar to the proposed interpretation regarding the increase of selfing among surviving species, a ”risky” strategy (i.e. increase in selfing at the risk of decrease genetic variability, and increase in long distance dispersal at the risk of mortality) allowed some species to survive disturbance. Nonetheless, evolutionary rescue was still the least frequent response under high intensities of habitat loss, meaning that such risky strategies work as ”risky business” do: some species that invested in them were successful, but it is not a reliable mechanism of survival. Therefore, conservation measures, specially of small populations, which are subject to demographic and environmental stochasticity, should rather focus on restorative measure, instead of counting on species ability to revert extinctions.

The decrease in variation of seed size during evolutionary rescue, under high intensities of all disturbances, reinforces the importance of higher seed sizes in allowing species survival (in the previous sections, I discussed the implications of species that went through evolutionary rescue having higher seed biomass than extinct ones). Interpreted according to the metabolic theory of ecology, this observation agrees with the demographic buffering hypothesis, which predicts reduction in variance of vital rates of with highest influence in population growth and individual fitness (Hilde et al., 2020). In this study, lower germination did not seem to have generated maladaptation, as it has been reported by other studies. Instead, the maintenance of a seedbank, sustaining population recruitment, was more important, and has been empirically verified to be a passive restoration strategy (Kiss, Deák, Török, Tóthmérész, & Valkó, 2018). Therefore, restoration plans involving seed addition have the potential of being highly effective in maintaining remaining species, as long as they follow community composition and population effective sizes over time (Kiss et al., 2018).

3.4.4 Limitations and perspectives

One limitation of this study is not including other interactions besides competition. The model is able to account for diffuse intra- and interspecific competition arising from the species relative fitness competition for area as resource, or from Allee effect following population decrease after habitat loss, for example. Competition (Osmond & Mazancourt, 2013; Fussmann & Gonzalez, 2013) and pollination (Ramos & Schiestl, 2019; Roels & Kelly, 2011) have been shown to be important selective forces, while trophic relations can mediate demographic recovery of prey and predators (D. A. Bell et al., 2019). Further model developments should include the integration of more explicit interactions, particularly pollination, and herbivory (in the form of leaf and seed herbivory, with the later entailing seed dispersal as well) Moreover, trophic interactions might be particularly important for the occurrence of evolutionary rescue under extinction debts, considering how important, albeit poorly explored, extinction cascades are for extinction debts (chapter 2). Understanding whether community evolutionary rescue might mitigate extinction debts remains a challenging due to the diversity of interactions. Still, the modeling approach used in this study can open up new research avenues for genomically-explicit, trait-based studies on the importance of microevolutionary process in the context of ongoing biodiversity loss and global change.

Individual phenotypic plasticity is expected to be an important factor in species response to disturbance, with both positive (Larson, Anacker, Wanous, & Funk, 2020) and negative effects (Gutterman, 2000). On the one hand, phenotypic plasticity might provide resistance against disturbance, and thus, buffer the selective pressure. On the other hand, phenotypic plasticity itself could be selected for during evolutionary rescue (Chevin, Gallet, Gomulkiewicz, Holt, & Fellous, 2013). In the model I used, phenotypic plasticity is possible for biological rates, which depend on local conditions. For example, individuals sizes depend on the intra-genomic variation of the traits coding for body mass and on the local temperature, as higher temperatures cause higher growth rates via metabolic constraints. This phenotypic plasticity is thus enabled by variable environmental tolerances, which constitute the main measure of plasticity in the model. Following, the genome-explicit model I used could be used to investigate the importance of genetic architecture in enabling phenotypic plasticity of traits under selection. Future efforts could hence be targeted at extending the representation of phenotypic plasticity by randomizing the genotype-phenotype association or allowing the environmental conditions to affect the expression of other functional traits considered in the model.

The results reported here illustrate the importance of considering processes at multiple ecological levels: genomic (explicit genome-trait coding), individual (species trait values), populational (metabolic dependent vital rates), and at the community level The integration of so many processes was possible thanks to the use of a genome and spatially-explicit, niche- and individual-based model (Leidinger & Cabral, 2020). In the analysis of results, I focused on phenotypic and functional responses, which can be easily verified by past empirical studies. The increasing use of genome wide association studies in natural populations (facilitated by tools such as Rönnegård et al., 2016) should facilitate future comparisons, by providing the genetic structure behind the traits included in the model (so far, the genetic structure of traits in the model is randomly set). More importantly, such modeling approaches would help close the gap that still make studies of empirical genome association rare for natural populations (Gienapp, 2020).

3.5 Conclusion

This study reinforces the importance of the interaction between eco-evolutionary dynamics (i.e., community re-assembly arising from demographic and evolutionary rescue), to communities response to disturbance. Nonetheless, evolutionary and demographic rescue, remain rare. Most of the original hypotheses regarding the occurrence of evolutionary rescue were rooted in a population-oriented conception of evolutionary rescue, through single-trait adaptation, and likely because of it, most of them were not verified. Such outcome reinforces the need for a mechanistic, community-level study of evolutionary rescue, where by species coexistence mechanisms are included as a selective pressure. Moving forward, the integration of eco-evolutionary mechanisms and genomic analysis constitutes a promising avenue to improve understanding and management of upcoming biodiversity change.

Chapter 4

Habitat loss and pollination loss trigger different extinction dynamics in a simulated multispecies community

The following chapter is being prepared for submission to the journal *Global Change Biology*.

—An extinction debt corresponds to the number of species expected to go extinct due to past ecosystem disturbance. It arises from species-specific differential responses to disturbances in biotic and/or abiotic. The various types of disturbances are seldom isolated but rather exhibit varying regimes of frequency, occurrence, and synergy. I built an individual, trait-based eco-evolutionary model (Extinction Dynamics Model, EDM) to simulate the effects of biotic and abiotic disturbances (the disruption of pollination function and loss of habitat area, respectively, simulated in isolation and combined) on plant communities parameterized according to real-world species. Besides verifying the model's ability to reproduce real-world functional patterns, I use it to investigate the effects of these disturbances on the magnitude of extinction debt and species extinction times, as well as how species functional traits affects the communities' extinction dynamics. I show that the loss of habitat area generates higher number of immediate extinctions, but the disruption of pollination function generates higher extinction debt, as species take longer to go extinct. Therefore, such delayed extinctions which compose these debts, might be avoided if pollination is reestablished. Moreover, reproductive traits (clonal ability, absence of selfing and insect pollination) where the traits that influenced species extinction as payment of the payment. Habitat area is a key factor to the maintenance of biodiversity. Nonetheless, the results demonstrate that loss of ecosystem function, pollination is this case, is a major factor in the creation of extinction debts. Considering that the role of the disruption of pollination function in the creation and payment of extinction debt is seldom explicitly explored, research must fill this gap and restoration policies need to aim at monitoring ecological processes and functions in undisturbed systems to inform its re-establishment in disturbed areas.

4.1 Introduction

Following disturbance of a community, species traits and population dynamics affect if and how species respond to the change in its biotic and abiotic conditions (Figueiredo et al., 2019). As individual species responses unfold and interact, the community enters a process of relaxation to new equilibrium, where extinctions (and colonization) take place at different speeds (i.e. species have different extinction times), until community dynamics re-stabilizes (Essl et al., 2015a; Figueiredo et al., 2019; Hylander & Ehrlen, 2013; Jackson & Sax, 2010). While new equilibrium has not been reached, the expected number of extinctions yet to happen is called the extinction debt (Figueiredo et al., 2019; Kuussaari et al., 2009). The time it takes for the community to reach equilibrium is called the ″relaxation time″ (J. M. Diamond, 1972). The detection of a debt is often interpreted as a ″window of opportunity″ to implement conservation actions to prevent upcoming extinctions (Kuussaari et al., 2009; Wearn et al., 2012; Löffler, Poniatowski, & Fartmann, 2020). However, the ecological processes behind an extinction debt are intrinsically hierarchical and non-linear, with individual responses (e.g. trait-dependent survival) scaling up to population level (e.g genetic and metapopulation dynamics Essl et al., 2015a; Figueiredo et al., 2019). Moreover, the influence of the interaction between different species responses (e.g. loss of interaction partners and ecosystem services) has been seldom explored (Essl et al., 2015a; Figueiredo et al., 2019), but see an example in Valiente-Banuet et al. (2015). As a result, it is challenging to predict the magnitude of debts and the length of extinction times, as well as to evaluate the possibility of decreasing a debt through conservation measures.

The species-area relationship (SAR) and a variety of correlative methods hereafter referred to ″static methods″, see (Kuussaari et al., 2009) for a detailed description provide a straightforward reasoning to detect extinction debts: if biodiversity at any given time is somehow higher than what would be expected for the observed habitat condition (e.g. area or connectivity), the existence of a debt is assumed (Kuussaari et al., 2009). However, static methods have limited capacity to estimate the magnitude of the debt - possible through SAR, but not through correlations - or the duration or order of extinctions (Kuussaari et al., 2009). This results from these methods often not being able to account for the effect of i) species life history traits, ii) (meta)population demographic and genetic dynamics, and iii) the status of biological interactions on species extinction processes (Figueiredo et al., 2019). While the role of life history traits for species survival can be assessed independently of the methodology (e.g. Purschke et al., 2012; Saar et al., 2017), increasingly complex, dynamic models, such as metapopulation and metacommunity models combined with different data sources, are required for predictive or descriptive studies of current extinction debts (e.g. Cotto et al., 2017; Talluto et al., 2017); see a comprehensive list in Figueiredo et al. (2019). Despite such advances, the effects of the disruption of biological interactions on community relaxation remains the least investigated ecological factor (Figueiredo et al., 2019; Valiente-Banuet et al., 2015).

Besides the inherent complexity of extinction processes, current ecosystem threats (e.g. habitat destruction, climate change, species invasions) add yet another source of dynamism, as they seldom occur isolated (neither in space nor time), but rather form “anthropogenic threat complexes”, which vary among different regions of the terrestrial and marine realms (*sensu* Bowler et al., 2020). The IPBES (2019a) estimates that one million species of animals and plants are currently threatened with extinction, with a third of the extinction risk having possibly emerged in the last 25 years, meaning they could be related to such anthropogenic threat complexes. Moreover, such threats often feed back into one another, potentiating their single (negative) effects on biodiversity (Brook et al., 2008). Therefore, considering the current state of biodiversity loss, conservation actions intended at slowing down extinctions need to account for the intrinsic complexity of extinction dynamics, but also that of its drivers.

To improve the understanding of the payment of extinction debts under complex perturbation scenarios, I present an individual and trait-based eco-evolutionary model developed to take into account the main mechanisms affecting local extinction dynamics inside a plant community. I use species trait values, composition and relative density cover data from a calcareous grassland community to parameterize the model and verify the results. I apply the model to investigate the long-term consequences of the loss of habitat area and pollination function, in isolation and in combination, for grassland plant communities. I ask three questions: 1) How disturbance regime affects the size of the extinction debt? 2) How disturbance regime affects the length of species extinction times? 3) How species functional traits affect whether they compose a debt or survive long-term? For question 1, I expect to observe extinction debts for all disturbance scenarios. When disturbances are simulated in isolation, the size of extinctions debts, the total number of extinctions, and species extinction times should be lower than when both disturbances are simulated together. For question 2, I also expect that species go extinct faster when disturbances are combined. For question 3, I further expect that, under area loss, short-distance dispersing species survive longer, due to the mass effect resulting from keeping offspring nearby, while long-distance dispersing species loose offspring in the increased unsuitable habitat. Alternatively, under disruption of pollination function, species capable of selfing or clonal reproduction should dominate the surviving community as animal-pollinated species experience reduced offspring production. In all scenarios, surviving species should have longer life spans and seed longevity, which act as temporal buffers for population and growth rate reductions, while populations of short-lived plants response faster, and are thus extinct faster.

4.2 Materials & Methods

4.2.1 Model description

I developed an individual-based model that simulates the life cycle of multiple co-occurring plant species in a landscape which may be subjected habitat destruction and disruption of pollination function. The model was written in Julia (Bezanson et al., 2017) and the code is available on GitHub[1]. Here, I present a summarized version of the model description. The complete documentation, written following the ODD (Overview, Design concepts and Detail) protocol and the TRACE (TRAnsparent and Comprehensive Ecological modeling documentation) framework (Grimm et al., 2010, 2014), is available in Appendix 4, and is referred to simply as "TRACE".

The model simulates the life cycle of plant communities in a landscape (Fig. 4.1-A). Plant individuals are characterized by state variables and species parameters listed in Table 4.1. State variables include individuals temporary statuses (e.g. developmental stage), and species-specific parameters include species traits (e.g. seed number), some of which are allowed to evolve during the simulation (Table 4.1, further described in 'Trait inheritance' subsection of 'Submodel description', below). State variables and species-specific parameters control the course of the simulation of an individual's life cycle (depicted in Fig. 4.1-B). Individuals are initialized at a random developmental stage (seed, juvenile, or adult), with species-specific trait values of their species (life span, range of first flower, maximal seed number, and duration of seed bank are initiated from a Uniform distribution due to high variability in trait measures). Seed and juveniles are initialized with seed weight, and juveniles are initialized at 75% of species's maximal weight.

All biological rates in the model (biomass growth, germination, and density-independent mortality) are calculated according to the metabolic theory of ecology (Brown et al., 2004; Sibly, 2012; Ernest et al., 2003):

$$B = b_0.m^{\alpha}.e^{\frac{-E}{k.T}} \tag{4.1}$$

where B is the metabolic rate, b_0 is a taxon and stage-specific proportionality constant, m is the individual's body mass, α is an allometric exponent, E is the activation energy, k is the Boltzmann constant, and T is the local temperature. Values of α, E, and k are constants from the MTE (Table

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[1] `https://github.com/ludmillafigueiredo/edm`

4.2). Individuals probabilities of germination (p_{germ}) and mortality (p_{death}) are calculated from the respective rates, B_{germ} and B_{death}, as

$$p = 1 - e^{-B} \tag{4.2}$$

The realization of either process is randomly drawn from a Bernoulli distribution, with probability p.

The landscape is represented as a square grid of square cells, each of area of 1 m^2 and characterized as either suitable or unsuitable habitat, according to the experimental design (Fig. 4.1, Table 4.2). The total extent of the landscape is also defined by the experimental design. Upon initialization, plant individuals of the species to be simulated are randomly placed in suitable grid cells (Fig. 4.1). Temperature is a global variable in the model (all patches have the same temperature), and affects organisms metabolic rate, according to the MTE. The model runs on weekly discrete time steps (I present results in annual scales to facilitate understanding). The list of species (and respective trait values), the landscape configuration, the regime of disturbance (type of disturbance, time of occurrence and magnitude), and the temperature time series are obligatory inputs of the model, as they define the experimental configuration of the simulations run. Hence, they are described in the "Experimental design" section below.

At each time step, each individual goes through its life cycle processes, according to its state variables, i.e., not all processes happen for all individuals at all time steps (Fig. 4.1-B, and detailed in Fig. 1 of TRACE). The processes are simulated by the following submodels:

Resource allocation: Biomass growth rate, i.e., whole organism biomass production, is calculated according to the MTE (Eq. 4.1). The total production is allocated to vegetative or reproductive biomass according to an individual's developmental stage and reproductive phenology. Juveniles and non-reproducing adults can only accumulate vegetative biomass, which is equally divided among "root", "stem", and "leaves" organs (Fig. 4.1-B). During their species-specific reproductive season, determined by the phenological traits of start and end of flowering season (Table 4.1), adults allocate biomass production to reproductive structures if they have reached a species-specific minimal vegetative biomass.

Maturation of juveniles: Juvenile individuals become adults once they reach their age of first flowering, a species-specific phenological trait (Table 4.1).

Mortality: Density-independent individual mortality is calculated according to the MTE (Eq. 4.1 and 4.2). Density-dependent mortality is calculated once total vegetative standing biomass production surpasses the carrying capacity. Individuals die according to the species local (at the grid cell level) relative adaptation to temperature (fitness).

Pollination: A global constant defined by the experimental design determines the proportion of reproductive biomass that is available for seed production (Table 4.2). Plants can be pollinated if they have enough reproductive biomass to produce at least one seed. For each species, the number of individuals pollinated is drawn from a Binomial distribution $n_{poll} \sim B(n = n_{repr} \times p_{visit}, p = p_{eff})$, where n_{repr} is the number of flowering individuals able to produce seed(s), p_{visit} is the proportion of visited flowers, and p_{eff} is the pollination vector efficiency. The proportion of visited flowers and the efficiency of pollination vectors (wind and/or insect) are global constants in the model (Table 4.2), and the pollination vector, is a species-specific trait (Table 4.1).

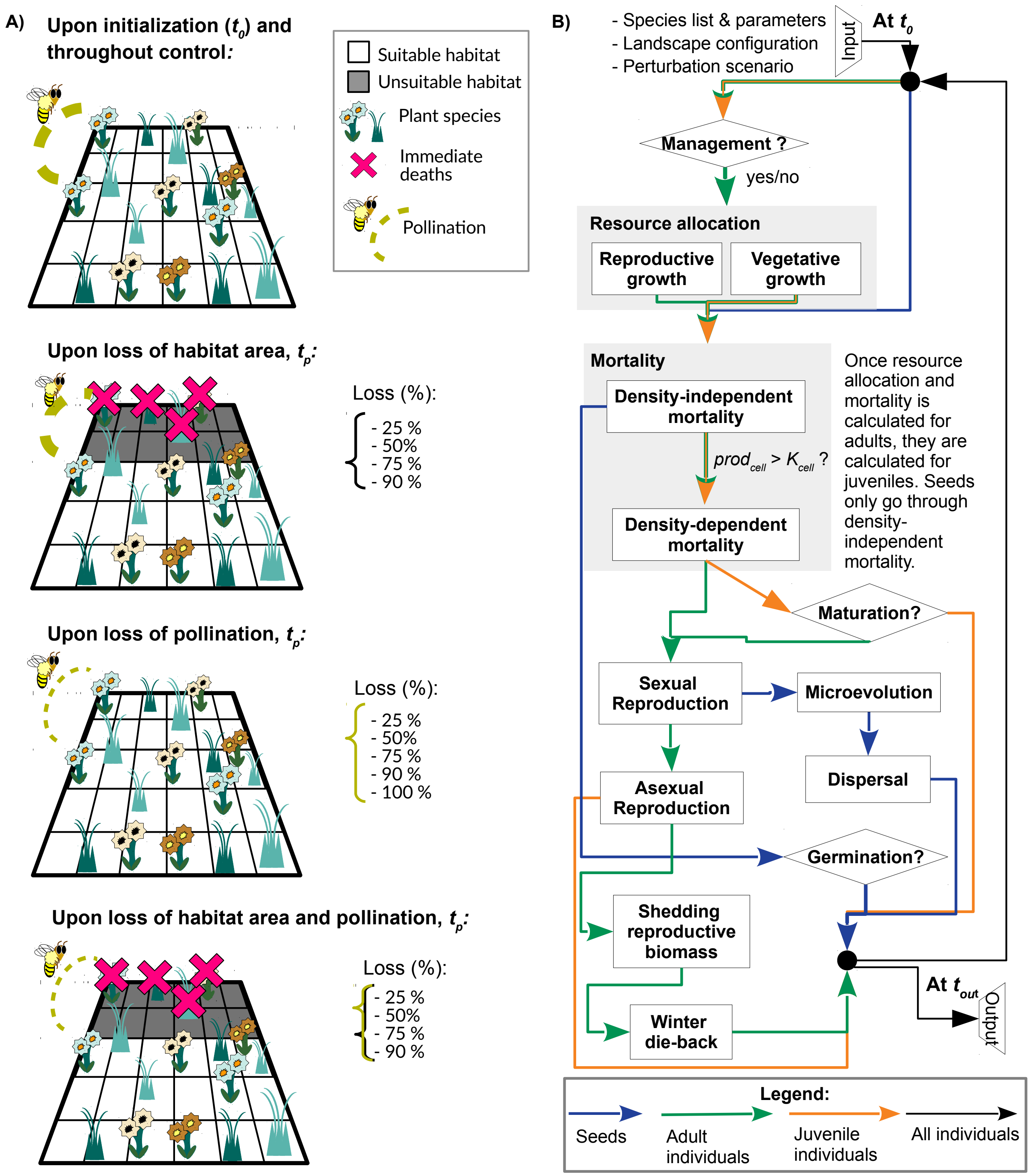

Figure 4.1: Experimental design and simplified model flowchart. A) Schematic representation of how simulations were set up and implemented in the model. All simulations are initialized ($t_0 = 0$ years) under the same conditions, and disturbances area applied at the same time step, $t_p = 50$ years (= 2600 weeks). B) Scheduling of ecological processes simulated by the model, including required inputs read upon initialization and outputs produced at frequency $t_{out}(t_{out} =$ 2 years = 104 weeks in this study). Detailed version available in the TRACE document (Supplementary material).

Sexual reproduction: Sexual reproduction happens for individuals that have been pollinated. Trait inheritance is calculated for seeds thus produced (described below). Species also have a species-specific probability of selfing (Table 4.1), in which case, no trait inheritance is calculated. The number

Table 4.1: State variables and species parameter characterizing plant individuals, range of values they might take inside their scope, and the scope over which they vary. Variables that change across time are recalculated every time step. Variables that change across the community vary among species, but not among individuals. Variables marked with an asterisk (*) also present intrapopulation variation inside a species-specific range determined by the species minimal and maximal trait values, given as input. Justification to all values is given in section 'Data Evaluation' of the the TRACE document (Supplementary material).

Variable/Parameter	Range of values	Scope of variation
State variable		
Developmental stage	seed, juvenile or adult	Time
Age	1–life span (in weeks)	Time
Vegetative biomass of leaves	$0 - 50$ g	Time
Vegetative biomass of stem	$0 - 50$ g	Time
Vegetative biomass of roots	seed mass $- 50$ g	Time
Reproductive biomass	$0 - 50$ g	Time
Pollination status	true or false	Time
Parameter		
Dispersal kernel	short, medium, long, and combinations	Community
Clonal ability	true or false	Community
Pollination vector	wind, insects, or combinations	Community
Capacity of selfing at fail of outcrossing	true or false	Community
Probability of selfing upon pollination	$0 - 95$ %	Community
Seed mass	$0.0001 - 0.003$ g	Community
Maximal plant organ mass	$30 - 150$ g	Community
Life span	1-50 years	Community *
Age of first flowering	1.5 months – 6 years	Community *
Beginning of flowering season	9^{th} – 32^{nd} week of year	Community *
End of flowering season	1^{st} - 52^{nd} week of year	Community *
Beginning of sowing season	16^{th} - 52^{nd} week of year	Community *
End of sowing season	16^{th} - 52^{nd} week of year	Community *
Maximal number of seeds	1-2000 week^{-1}	Community *
Seed bank duration	1 month – 3 years	Community *
Biomass growth proportionality constant	4.53×10^{8} - 5.97×10^{9} g/week	Community
Germination proportionality constant	$1.41 \times 10^{8}\ week^{-1}$	Community
Mortality proportionality constant	$1.11 \times 10^{9}\ week^{-1}$	Community
Temperature optimum	277.8-290 K	Community
Temperature tolerance	5.73-11.16 K	Community

of seeds produced, m_{repr}/m_{seed}, where m_{repr} is the amount of reproductive biomass of the mother plant and m_{seed} is the species-specific seed weight, is limited to species-specific values of maximal weekly seed production (Table 4.1).

Table 4.2: Global parameters of the model, their respective values, and references used to define them. Detailed justification to all values is given in section 'Data Evaluation' of the the TRACE document (Supplementary material).

Parameter	Range/Value	Justification of range/value
Probability of selfing at fail of outcrossing	50%	Arbitrary value
Allocation of reproductive biomass to seed production	5%	Weiss et al. (2014)
Proportion of plants visited by pollinators	1	Approximation from (Fishman & Hadany, 2010)
Efficiency of insect pollination	60%	King, Ballantyne, and Willmer (2013)
Efficiency of wind pollination	60%	Arbitrary value
Short-dispersal kernel	$\mu = 1, \lambda = 0.2$	Vittoz and Engler (2007); Bullock et al. (2017)
Medium-dispersal kernel	$\mu = 0.2, \lambda = 3$	Vittoz and Engler (2007); Bullock et al. (2017)
Long-dispersal kernel	$\mu = 1000, \lambda = 100$	Vittoz and Engler (2007); Bullock et al. (2017)

Asexual reproduction: If an individual is not pollinated, but is capable of clonal reproduction (a species-specific trait), it has 50% chance of producing a single clone (Table 4.2). Clones are initialized as juveniles, in the same location as the plant generating it, with 10% of adult vegetative biomass.

Trait inheritance: Trait inheritance is simulated upon sexual reproduction through a simplified model of phenotypical change of a population under panmixia. Offspring trait value (v_o) is recalculated as

$$v_o = \frac{v_{parent1} + v_{parent2}}{2} + v_{ch}, v_{ch} \sim N(\mu = 0, \sigma^2 = |\frac{(v_{parent1} - v_{parent2})}{6}|) \tag{4.3}$$

where $v_{parent1}$ refers to the individual producing seeds,$v_{parent2}$, to a randomly chosen individual of the same species, and v_{ch} to the phenotypical change. Clones and seeds produced through selfing have the exact species-specific trait values of the plant that produced them.

Seed dispersal: Seeds can be dispersed at short (0.1-100 m), medium- (100-500 m), and long-distances (1-10km), according to the species-specific dispersal parameters. The phenology of seed release is also a species-specific trait (Table 4.1).

Seed germination: Seed germination is only possible in grid-cells labeled "suitable". Seeds that disperse outside the landscape or in unsuitable grid-cells die. Individual germination is calculated according to the MTE (Eq. 4.1 and 4.2).

Shedding: At the end of the flowering season, adult plants lose all their reproductive biomass.

Winter dieback: At the last week of the year, adults lose all of the biomass allocated to leaves, and 50% of the biomass allocated to stem, due to winter dieback.

Management: Annually, the effects of management (mowing or grazing) are simulated as the reduction of above-ground biomass of juvenile and adult plants. The probability of management happening and the period of the year when might occur are defined by the experimental design. Only individuals that have accumulated at least 50% of the species maximal vegetative biomass (biomass allocated to stems and leaves) have it reduced to 50% of its maximal values and lose all reproductive biomass.

Disturbances: Loss of habitat area is simulated by calculating the amount of grid cells equivalent to the lost area, marking them as ”unsuitable”, and killing all plants located in these cells (Fig. 4.1-A). Disruption of pollination is simulated by decreasing the amount of effectively (animal) pollinated plants, n_{poll}, by a proportion defined in the experimental design (Fig. 4.1-A).

4.2.2 Experimental design

I simulated the ecological assembly of initially random plant communities in a landscape, and then applied different intensities of loss of habitat area and/or disruption of pollination.

I simulated landscapes of two sizes, 484 m^2 and 961 m^2, represented by grids of 22×22 and 31×31 square cells, respectively. These sizes were automatically calculated by the model, which created square grids for the representative sizes of 500 m^2 and 1000 m^2. The model offers the possibility of inputting a raster file, Considering the base productivity of 5 T/ha/year, equivalent to a mildly mowed, unfertilized temperate grassland (Bernhardt-Römermann et al., 2011), total landscape carrying capacity reached 242 kg and 480.5 kg, respectively. Temperature is a global variable, and the weekly temperature time-series used in the simulations was created by expanding monthly temperature measures provided by the German Weather Service for the period between 1857 to 2017 (Fig. 2 in the TRACE). Management happens once a year, in the first week of August.

The plant species pool from which communities were pooled included species listed in a density survey conducted by Krauss, Klein, Steffan-Dewenter, and Tscharntke (2004) on fragments of calcareous grasslands around the city of Göttingen, Germany. Traits values for these species were retrieved from literature (references for each value, and complete list of species available for the model and their trait values are available in Tables 12-14 of the TRACE). The range of trait values included in the present study is listed in Table 4.1.

Simulation experiments consisted of a control scenario (without disturbance) and a series of disturbance scenarios (Fig. 4.1-A). Disturbance scenarios were designed as fractional factorial combining intensities of a) area loss (25%, 50%, 75%, 90%), b) disruption of pollination function (25%, 50%, 75%, 90%, 100%), and c) both area loss and disruption of pollination function (25%, 50%, 75%, 90%) (Fig. 4.1-A).

Normalization constants of growth rate are species-specific. The values were parameterized to generate logistic growth curves with lower and upper asymptotes equivalent to seed and maximal biomass, respectively, and maximal growth rate happening at the age of first flowering (details in the model TRACE). The normalization constant of metabolic rate of germination and mortality are global parameters of the model, and were parameterized by germination and mortality rates reported in Marba, Duarte, and Agusti (2007) (Table 4.2, details in the TRACE).

I ran the same 22 initial species pools as replicates for each scenario. Each initial species pool consisted of species (59 species at 484 m^2 and 63 species at 961 m^2) taken randomly from the greater species pool described above (containing 194 species in total). This value of the initial species richness was calculated for the initial area, according to the species-area relationship derived from richness observations reported in Krauss et al. (2010) and depicted in Fig. S1 of the Supplementary material Appendix 3.

4.2.3 Analyses

Before answering the main questions, I verified the model's capability of reproducing the communities upon which simulations were based. I verified the stability of species richness in simulated communities, calculated community dissimilarity as the Euclidean distance and Bray-Curtis dissimilarity between simulated and empirical communities of similar sizes, and compared species rank curves between simulated and empirical communities through metrics of absolute difference in evenness, relative difference in species richness, relative difference in ranked biomass, and relative species gains and losses. Relative values are calculated as the proportion between the difference of the metric in both communities and the number of species unique to both simulated and empirical communities (complete description of metrics in the ”Model output verification” section of the TRACE document). Instead of abundances, the metrics of evenness and ranked biomass were calculated from species relative biomass for simulated data and species relative cover for empirical communities. Besides, I performed a Principal Component Analysis (PCA) to compare the trait spaces of simulated communities with the trait space estimated for species reported by Krauss et al. (2004) for 31 calcareous grasslands in the vicinity of the city of Göttingen (Germany), for which an extinction debt has been detected (Krauss et al. 2010). I first compared the trait space of simulated communities in the control scenarios to the trait space estimated for the communities reported in patches of areas similar ($\leqslant$) to the simulated ones (484 m^2 and 961 m^2). Second, I verify the model's ability to reproduce the effect of habitat area on trait space by comparing the trait spaces of simulated communities under different intensities of loss of habitat area (25%, 50%, 75%, 90%), and the trait space estimated for communities reported for patches of area sizes falling into the 10th, 25th, 50th, and 75th percentiles (matching, in reverse order, the intensities of habitat loss) of the areas reported by Krauss et al. (2004), which range from 314 m^2 to 51395 m^2 (percentiles range from 489 m^2 to 11528 m^2). To define trait spaces of simulated communities, quantitative traits were summarized (per replicate) as the mean of species mean trait values weighted by species respective proportion of the total biomass production at the end of the simulation. For empirical communities, quantitative traits were summarized (per replicate) as the mean of species mean trait values weighted by averaged density values sampled in the patches included in each of the two comparisons. In both cases, to summarize qualitative traits, I calculated the proportion of species falling into each category of value. The results of these analyses are reported in the model TRACE, as part of the model output verification procedure that integrates that document.

To verify the effect of disturbance regime on the size of extinction debts (question 1), I calculated, for each replicate, in each disturbance regime, the size of extinction debts as the percentage of species that went extinct after disturbance, until the end of the simulation. The percentage was derived from the proportion n_{ext}/n_{dist}, where n_{ext} is the number of extinctions that happened between the second year after the implementation of disturbance ($t = 52$ years) and the end of simulation ($t = 160$ years), and n_{dist} is the number of species that initially survived disturbance (i.e. the number of species at $t = 52$ years). Measuring the extinction debt in relation to $t = 52$ years ensured that I excluded immediate extinctions, which do not compose the extinction debt (Fig. 4.1-B).

To verify the effect of disturbance regime on the length of extinction times (question 2), I estimated the time to extinction for species that survived disturbance (i.e. species alive at $t = 52$ years), but which went extinct after. Extinction times are thus measured from the same point in time ($t = 52$ years), even if population decrease did not start then.

To compare the effect of species trait spaces on their responses to disturbance (delayed extinction or survival, question 3), I compared the trait spaces of species composing the debt and surviving species in each scenario of disturbance through a Principal Component Analysis. The trait spaces used for this comparison were built as described above, from trait values measured immediately after disturbance ($t = 52$ years), thus excluding species that went extinct with disturbance. Moreover, I only included species which, under any disturbance, had a response (delayed extinction or survival), different from the one it had under control.

All analyses were conducted in R (version 3.6.3 R Core Team, 2018): PCAs and its visualization were done with the ’FactoMineR’ (Lê, Josse, & Husson, 2008) and ’factoextra’ packages (Kassambara & Mundt, 2020), analysis of dissimilarity with the ’vegan’ package (Oksanen et al., 2019), and analysis of rank abundance with the ’codyn’ package (Hallett et al., 2020).

4.3 Results

The simulations produced stable communities (Fig. S1 in the Supplementary material Appendix 3). The Euclidean distance and Bray-Curtis dissimilarity between simulated (in the control scenarios, in the last time step of the simulation) and empirical communities is, respectively, 0.41 and 0.91 for small communities, and 0.43 and 0.91 for large ones (Table 10 of the TRACE). Both Eucledian and Bray-Curtis metrics are constrained between 0 and 1, with 0 indicating the communities compared are equal, and 1 indicating the highest difference. Small simulated communities usually had higher richness than empirical ones, but in many instances, richness also lower (Fig. 4.2 and Fig. 12 of the TRACE for comparisons between larger real-world and simulated communities). Evenness was similar between simulated and empirical communities, even though variation was higher for smaller simulations (Fig. 4.2). Larger communities usually had lower richness. Rank changes was 0.25 for both sizes of simulations (Fig. 12 of the TRACE).

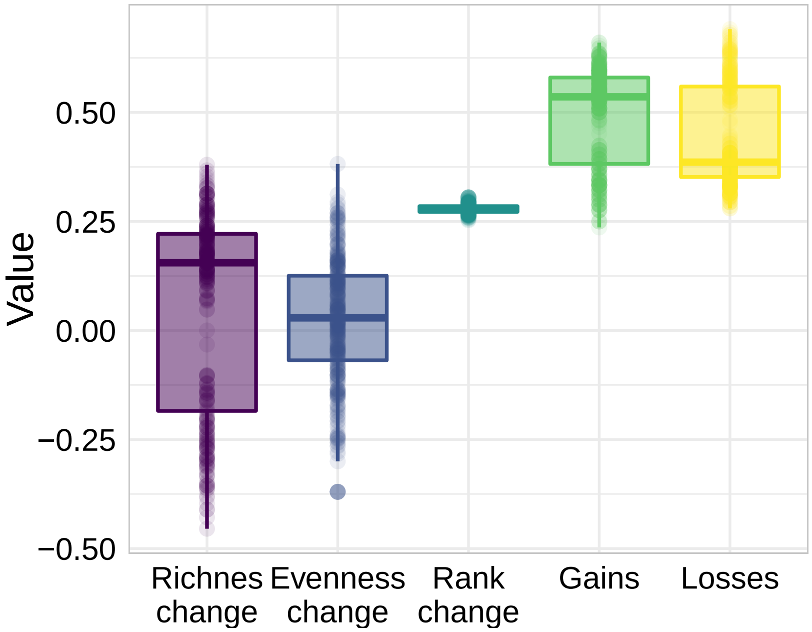

Figure 4.2: Comparison between species ranked curves of small simulated (484m^2) and empirical ($\leqslant 500\text{m}^2$) communities, measured as relative difference in species richness, absolute difference in evenness, relative difference in ranked biomass, relative gains and relative losses. Instead of abundances, the metrics of evenness and ranked biomass were calculated from species relative biomass for simulated data and species relative cover for empirical communities. Relative values are calculated as the proportion to the number of species unique to each community.

The trait spaces of simulated communities encompass most of the trait space estimated for empirical communities (Fig. 4.3-A, see a larger version in Fig. 13 in the TRACE). Independently of patch size, trait space of simulated communities was shifted towards higher proportion of insect-pollinated, non-selfing, and short-dispersing species, which mature later (Fig. 4.3-A). Figure 14 in the TRACE contains the 2^{nd} and 3^{rd} components, because the gain in variance explanation between the 2^{nd} and 3^{rd} components is higher than the gain between the 1^{st} and 3^{rd} components (Fig. 15-B in TRACE). Figures 16-17 in the TRACE shows the comparison between the trait spaces of small simulated and real-world communities ($\leqslant 484$ m^2), and Fig. 18-19, between large simulated and real-world ones ($\geqslant 484$ m^2, $\leqslant 961$ m^2). In simulated communities, area loss shifted the trait space towards non-selfing, insect-pollinated, short-distance dispersing species, that start flowering later (Fig. 4.3-B, details in Fig. 20-22 in the TRACE). In communities where area loss was simulated in combination with pollination, the response of trait space was similar (Fig. 23-25 in the TRACE). In empirical communities, the trait space of communities of smaller areas was mostly defined by reproductive traits, whereby clonal abilities and pollination vectors (wind or insects) were equally important to characterized trait spaces, as well as the ability to reproduce through selfing (Fig. 4.3-C, details in Fig. 26-28 in the TRACE). For communities from larger areas, medium-dispersal, longer lifespans and flowering and seed release seasons shaped the trait space more than reproductive strategies (Fig. 4.3-C, details in Fig. 26-28 in the TRACE).

Regarding question 1, increasing loss of habitat area increased the total number of extinctions (Fig. S2 in Supplementary material). In many replicates, no extinction debt was created (Fig. 4.4-A-D) and the absolute size of extinction debts is low (maximal three species, Table S1 in Supplementary material). However, these can correspond to up to $\sim 14\%$ of the species that survived disturbance (Fig. 4.4-A-D, Table S1 in Supplementary material). In control simulations, there is no extinction debts, rather "background extinction", which refers to the percentage of extinction happening after the time step were disturbance happened in the other scenarios, and the mean value across replicates is $\bar{b} = 1.4\%$. Under loss of habitat area, mean debts sizes ranged between 0.4% and 1.1% (Fig. 4.4-B). Under disruption of pollination, the sizes of extinction debts were slightly higher and decreased with increasing intensity of disturbance, with the mean ranging between 0.2% under high decrease of pollination and 2.2% under lowest (Fig. 4.4-C). Under both scenarios of disturbances, the mean sizes of extinction debts ranged between 0.5% and 1.6%, independent of the intensity of habitat loss (Fig. 4.4-D). Extinction debts are smaller in simulations of a landscape of 961m, and are depicted in Fig. S2 and listed in Table S1 in the Supplementary material.

Regarding question 2, in control scenarios, mean time to extinction $\bar{t} = 22.9$ (Fig. 4.4-E). Under loss of habitat area, with mean values (per replicates, $\bar{t}$) ranging between 26 and 100 years (Fig. 4.4-F). Under disruption of pollination, mean species extinction times varied between 6 and ~ 48 years (Fig. 4.4-G). Moreover, the number of replicates where extinctions happened (m) is higher in relation to the scenarios of habitat loss (compare m in Fig. 4.4-F and 4.4-G). Under loss of habitat area and disruption of pollination function, mean time to extinction varied between 23 and 61 years (Fig. 4.4-H) Mean extinction times in simulations of a landscape of 961m are depicted in Fig. S3 in Supplementary material. The number of replicates where extinctions happened and extinction times, m is similar across different disturbances and intensities (e.g. compare Fig. 4.4-F and G to Fig. S3-B and C).

Regarding question 3, in general, clonal, insect pollinated, non-selfing species went extinct in all scenarios simulated, including control (Fig. 4.5-A-D). The difference between the two groups is specially marked in the control scenario (Fig. 4.5-A) Under scenarios of loss of habitat area (in isolation or combined), the trait space of species that went extinct and species that survived are closer to each other than in the control scenario (compare Fig. 4.5-A to 4.5-B and 4.5-D). In both scenarios, the trait space of extinct species is spread over the 2^{nd} principal component (Dim.2), which is mostly defined by species phenology (begin and end) of flowering and seed release, as well as plant biomass (seed size and maximal organ size). Under disruption of pollination, the trait space of species that went extinct and species that survived are all closer to each other, but less spread over the 2^{nd} principal component (Fig. 4.5-C).

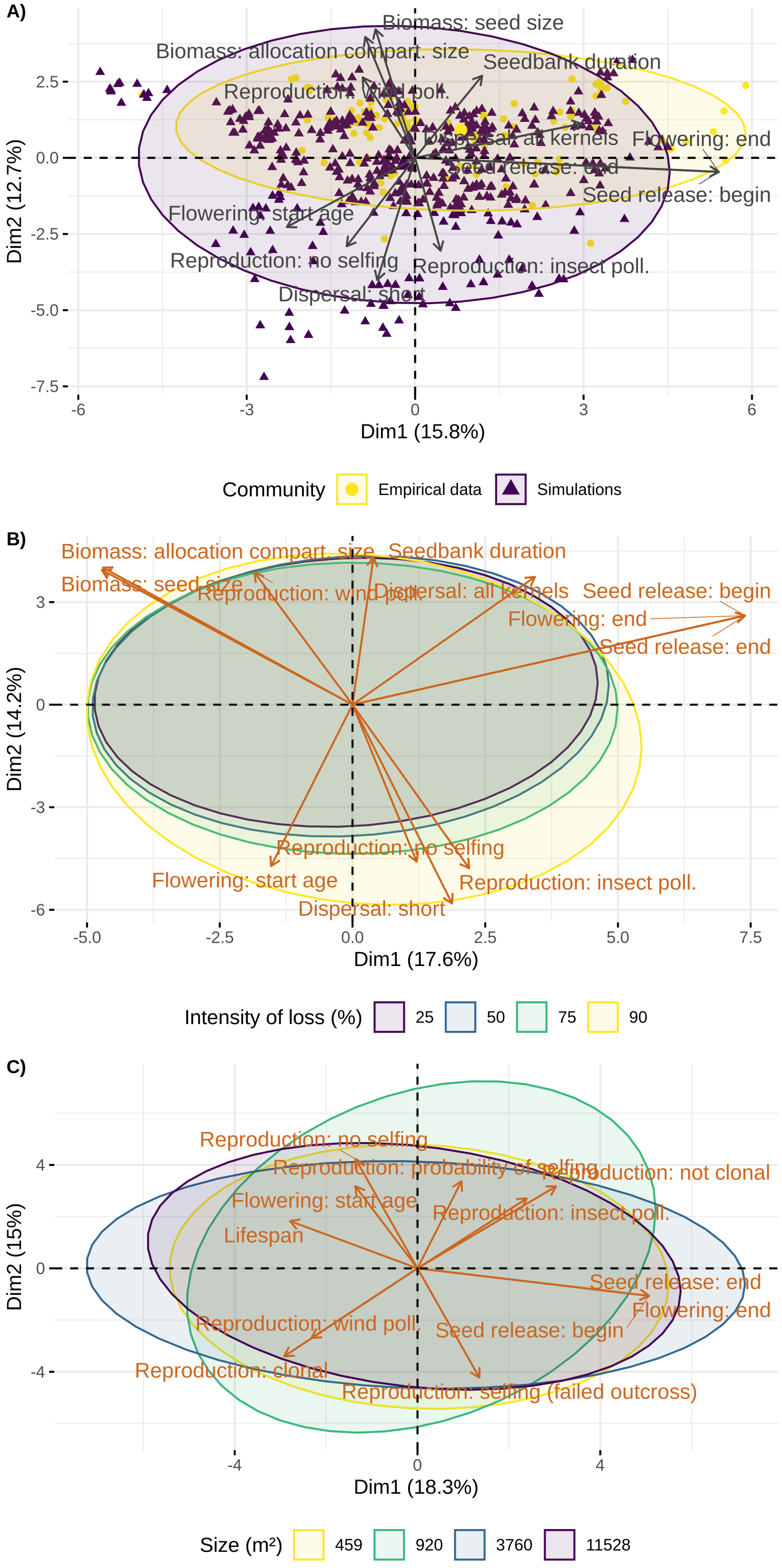

Figure 4.3: Analysis of 1^{st} (Dim.1) and 2^{nd} (Dim.2) principal components of A) final trait space of surviving communities in the control scenario (yellow) and the trait space estimated for empirical communities (purple) reported in Krauss et al. (2004), B) the trait space of surviving communities in simulations of different intensities of loss of habitat area, and C) the trait space estimated for empirical communities sampled in calcareous grasslands of sizes falling into the 10^{th}, 25^{th}, 50^{th}, and 75^{th} percentiles of the patch area distribution. Percentages indicate the amount of variance explained by each axis. For simulated communities, quantitative traits were summarized (per replicate) as the mean of species mean trait value weighted by species biomass production at the end of the simulation. For empirical communities, as the mean of species mean trait values weighted by relative density values sampled in the patches. Qualitative traits were summarized as the proportion of species presenting each category of value of the trait.

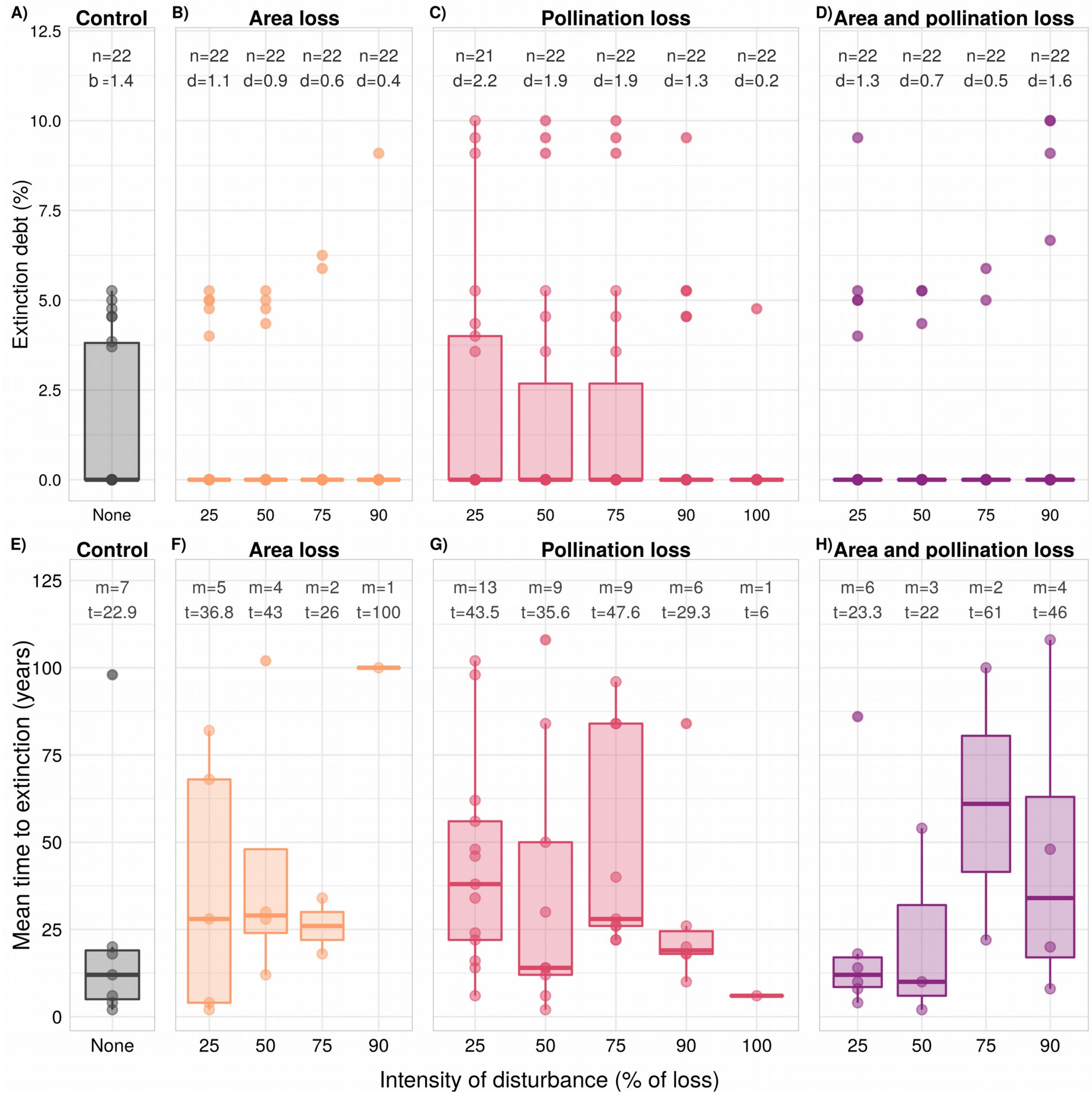

Figure 4.4: Extinction debts (A-D) and species extinction times (E-H). Extinction debts are measured as percentages (one point per replicate) of species lost in the absence of A) any disturbance (”control”), and after B) area loss, C) disruption of pollination function, and D) area loss and disruption of pollination. Extinctions were counted after the first year following disturbance*, thus excluding species that went immediately extinct. In A-D, n is the number of replicates analyzed, $\bar{d}$ is the mean (across replicates) number of ”background extinctions”, i.e. extinctions happening after the time step where disturbance happened in non-control simulations, and $\bar{d}$ is the mean size of extinction debts across replicates. Mean species extinction time (one point per replicate), in the absence of any disturbance (E), and after area loss (F), disruption of pollination (G), and area loss and disruption of pollination (H). Extinction time calculated for all species that survived through the first year after disturbance*, thus excluding species immediately extinct. In E-H, m is the number of replicates where extinction happened, and $\bar{t}$ is the mean value of the mean of species extinction times across replicates. ”*” = Output frequency was equivalent to two years, for computational efficiency.

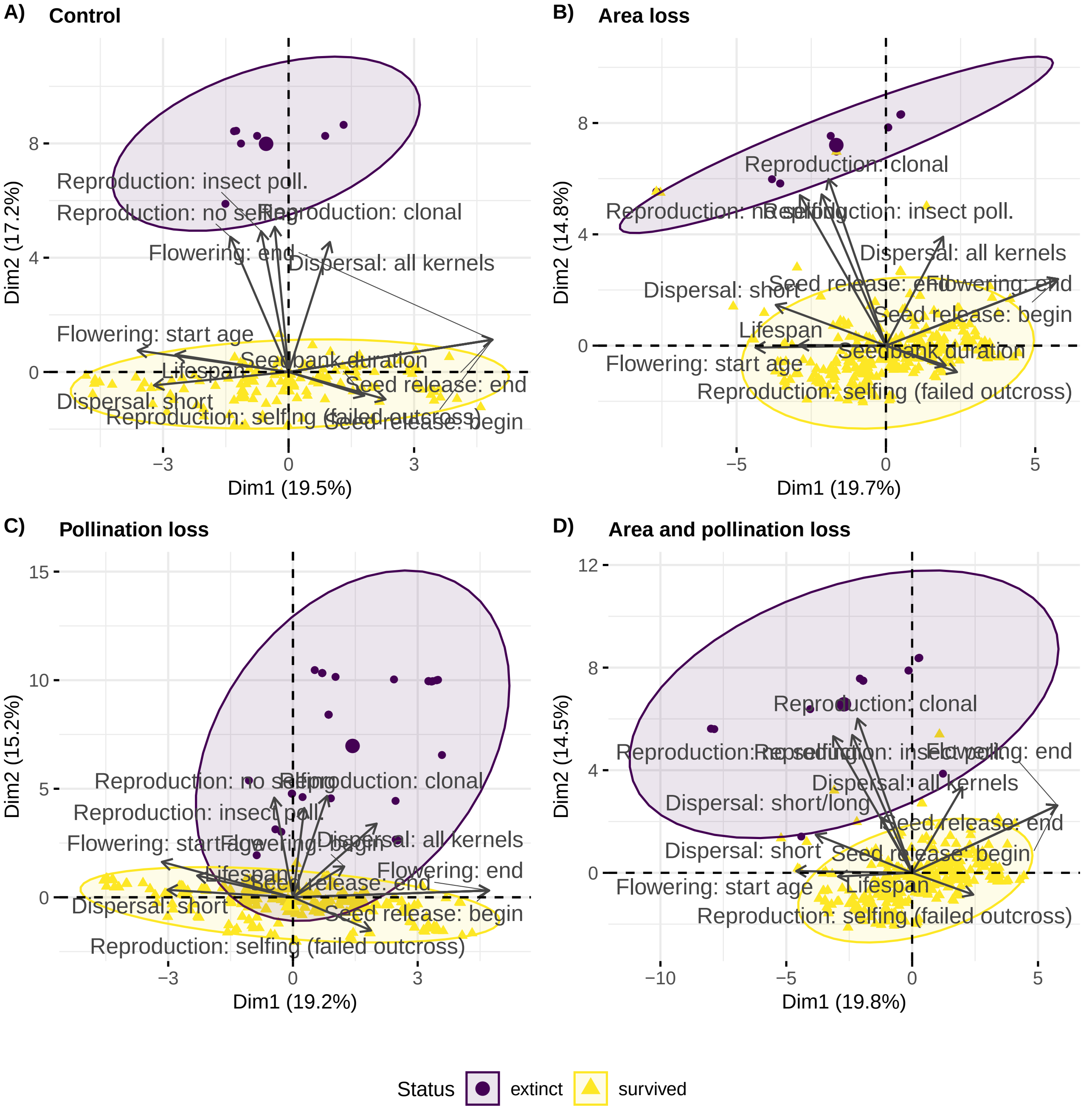

Figure 4.5: Analysis of 1^{st} (Dim.1) and 2^{nd} (Dim.2) principal components of the trait space of species following disturbance (traits measured at t=52), in a patch of 484 m^2. Percentages indicate the amount of variance explained by each axis. Species are identified according to their status at the end of the simulation: extinct during the relaxation time (i.e., as payment of the debt, dark purple) or survived (yellow). Out of the 24 variables used to define the trait space, only the 10 most contributing ones were included, to facilitate visualization.

4.4 Discussion

This work constitutes one of first comparisons of the effects of different types of biotic and abiotic disturbances on the magnitudes of extinction debts and extinction times. Moreover, it constitutes the first application, to the study of extinction debts, of an individual-based, multi-species model fully parameterized by real species traits and community composition. I show that habitat loss generates a higher number of immediate extinctions than disruption of pollination function, but smaller extinction debts. Habitat loss had a dominant effect in relation to disruption of pollination, because in simulations with both disturbances, responses were similar to those observed when habitat loss was simulated in isolation. Moreover, the functional traits of extinct species differ across disturbances. Following, I discuss the implications of these findings to the understanding of the impact of different disturbance types on extinction dynamics.

4.4.1 Model validation

In terms of species composition, the model was not able to appropriately reproduce empirical observations. While values of Eucledian distance were smaller, this metric is calculated based on composition alone. Since the simulations where run with communities pulled from the same species pools as the empirical communities, differences in species is expected to be low. The Bray-Curtis dissimilarity index, however, accounts for species relative biomass, indicating that simulations failed to reproduce the real-world species compositions, since values reached 0.91 (maximal dissimilarity happens at 1). This is confirmed by the analysis of change of species rank curves, which hshow that species relative composition of simulated communities (being different from 0) differs from the empirical ones. Nonetheless, in terms of community functional space, representation of real-world communities is better, since the space of simulated communities encompasses that of empirical ones. The main difference between the community trait spaces arises from the dispersal capability and reproductive strategies. As shown in Fig. 4.3-A, short-distance dispersing species had a larger importance to defining the community trait space of simulated communities, in relation to empirical ones, indicating that they survival was facilitated in simulations, in relation to the real-world. Two factors might contribute to this difference. The first is that simulations reported here were run in small areas (relative to the real-world patches, Fig. 3-C), where short dispersal is less risky than long dispersal, whereby seeds have a higher chance of falling outside the patch and being lost. The second is that seed dispersal into the patches, likely achieved by long-dispersing species, was not included in the model. Considering its positive effect on grassland restoration (von Blanckenhagen & Poschlod, 2005), richness (Ladouceur et al., 2020), and diversity (Stein, Auge, Fischer, Weisser, & Prati, 2008), the absence of such process in the model is likely to be major cause for the mismatch between simulation results and observations.

4.4.2 Effects of disturbance types on extinction debts

I observed that pollination loss generates higher extinction debts of plant species at low to intermediate intensities. In the simulations analyzed here, disruption of pollination affects all species equally, by decreasing the number of reproductively active individuals being effectively pollinated. Comparing this regime to the shortage of pollinating species in semi-natural ecosystems during crops mass-flowering events (Magrach et al., 2018; Kleijn et al., 2015), the results of this work verify results of analyses of the plant-pollinator networks of these ecosystems. When characterizing network robustness to the loss of pollinators, Magrach et al. (2018) indicate the existence of a threshold of random pollinator abundance loss over which network structure changes. In particular, they observe that complementary specialization, a measure of how exclusive interactions are, tends to increase under disruption of pollination. As the authors observe, higher interaction exclusiveness increases the vulnerability to secondary extinctions (Weiner, Werner, Linsenmair, & Blüthgen, 2014; Simmons et al., 2020). Nonetheless, it is important to highlight that the shortage of pollinators necessary to generate network changes in (Magrach et al., 2018) is higher than what is observed in the field and that the effects of crop flowering on pollinator availability are scale dependent - positive at local scale (Hegland, 2014) and negative at the landscape (Holzschuh et al., 2016) - as facilitation turns into competition (Braun & Lortie, 2019). Moreover, the relationship between network structure and stability is still uncertainty. Thus, although the extinctions debts generated by disruption of pollination can be expected to alter the structure of network of semi-natural ecosystems and impact its stability, long-term monitoring and scale-specific management plans are required to maintain ecosystem functioning.

Most often, reports of extinction debts address the long-term consequences of habitat destruction on the local or regional diversity correlations between past abiotic conditions (such as habitat area and connectivity) and species richness (see Kuussaari et al. (2009) for a detailed explanation, e.g. Jamin, Peintinger, Gimmi, Holderegger, & Bergamini, 2020; Semper-Pascual et al., 2018). The availability of data containing past habitat information facilitates this approach (e.g. Munteanu et al. (2020) used imagery from a Cold War spy satellite to detect an extinction debt for bobak marmots in Kazakhstan). Such approach, however, does not allow the estimation of the size of the debt Kuussaari et al. (2009) and thus, most studies detect but do not measure extinction debts (in the last 10 years, 8 out of 61 reports of extinction debt estimated it Figueiredo et al., 2019). Albeit secondary effects of habitat destruction are not explicitly included in such reports, habitat destruction, due to land-use change or intensification for example, has been shown to affect pollinators (Potts et al., 2010, 2016), specially bees, due to the consequent decrease of floral resources and nesting sites (Steckel et al., 2014; Forrest, Thorp, Kremen, & Williams, 2015; Abrahamczyk, Wohlgemuth, Nobis, Nyffeler, & Kessler, 2020). Even if the results reported here did not fully verify it, since debts in simulations of both disturbance types were qualitatively similar to simulations of habitat loss only, they verify the importance of the availability of pollination function for species maintenance, and can be thus interpreted as a successful verification of model behavior.

4.4.3 Effects of disturbance types on extinction times

Since disruption of pollination gave rise to extinction debts, so it did to delayed extinctions. I measure species extinction times, the longer of which can be interpreted as the relaxation time, since they are all measured from the same point in time ($t = 52$ years, the second year after disturbance). The extinction times generated match real-world estimations of ages of extinction debts (where relaxation time is not complete) and relaxation times (rarely reported), which range from a couple of years to, more commonly, decades or centuries, specially for vascular plants (see Kuussaari et al. (2009) and Figueiredo et al. (2019) for listings of such studies, and Halley et al. (2016) in particular, for a detailed description of the most relevant time measures during relaxation). However, these results usually arise for extinction debts following habitat loss, which is not the case for the results reported in this study. Nonetheless, despite the existence of a debate about whether extinction debts are paid faster in smaller habitats or whether relaxation times are independent of habitat area (see the complete debate in Wearn et al., 2012; Wearn, Reuman, & Ewers, 2013; Halley, Iwasa, & Vokou, 2013), both sides agree that extinction debts are paid faster in extremely small habitats, which is the case in the simulations analyzed here. Once again, such results increase confidence in the model's behavior.

The detection of debts resulting from disruption of pollination indicates that such disturbance opens a temporal window of opportunity for conservation measures to be implemented to restore this ecosystem function (Kuussaari et al., 2009). In the particular case of grassland pollination, the base scenario, restoration has been shown to effectively reestablish networks (Sexton & Emery, 2020).

4.4.4 Effects of disturbance types on community functional response

The functional difference between surviving and extinct species in communities that underwent loss of habitat area is higher than that observed under disruption of pollination function. Shorter dispersal distances, lifespans, and lower age of first flowering seed release also affected species survival. This is in accordance with previous results indicating that species sorting following disturbance plays an important role in the community dynamics (chapter 3). Nonetheless, it is important to consider that, because area loss generates higher total number of extinctions, the trait space of disturbed communities is most likely to differ from non-disturbed scenarios, since more species were extinct.

In simulations analyzed here, reproducing strategies (clonality, selfing ability, and insect pollination) were the most important traits affecting species survival. Previous studies have shown that animal pollinated plant species are more prone to local extinction following habitat degradation (Laanisto, Sammul, Kull, Macek, & Hutchings, 2015), which is verified by the results presented here. Clonality and selfing, however, have been linked to short-term reproductive assurance, but long-term increase in extinction risk (as discussed in chapter 3). This reinforces the need for restoration policies to focus on the maintenance and re-establishment of pollination function, if they are to be successful on the long-term (Menz et al., 2011). Nonetheless, further analysis of the significance of the difference between the trait spaces of species that went extinct during the payment of the extinction debt and those that survived are necessary to evaluate the potential contribution of each trait.

4.4.5 Limitations and perspectives

Any extinction-causing disturbance is expected to increase the risk of indirect extinctions, even before direct extinctions are completed, because the abundance decrease resulting from the ongoing direct extinction process causes the reduction of the species ecological function(s) (Valiente-Banuet et al., 2015). In plant-insect communities, the abundance and richness of insect species respond faster than those of plants (e.g. Krauss et al., 2010; Guardiola et al., 2018). In the simulations included here, insects are not explicitly simulated. Instead, I simulated the disruption of pollination function that would result from insects extinctions. Therefore, the plant extinctions that I analyze in these scenarios are indirect extinctions (with insects extinctions being direct), while the extinction in scenarios of habitat loss are considered direct ones. However, the size of extinction debts, species mean time to extinction, and changes in trait space could not be distinguished from simulations in which only habitat area was lost. This is likely to have happened because of the small landscape areas simulated, where the effects of loss of habitat areas were stronger than those of the disruption of pollination function. Simulations of larger areas function will likely yield more realistic results. Moreover, the number of available simulation results for analysis is also limited. Since replicates differ in the community they simulated, once I collect a higher number of simulation results, I will be able to distinguish more clear patterns of extinction.

In the simulations included here, I addressed rather simple disturbance regimes: both habitat loss and disruption of pollination (in isolation or combined) are simulated as press events, of constant intensity, and of the same duration. Real-world disturbance scenarios are, however, more complex and affect a variety of biotic and abiotic conditions simultaneously (e.g Bowler et al., 2020; Mace et al., 2014; Steffen et al., 2015). Moreover, management regimes in the model could be made more realistic: instead of biomass-based, an allometric relationship between biomass and height should determine how much individuals are affected by the use of lawnmowers or grazing activity. These where not implemented due to time constraints arising from the necessary parameterization of such growth curves and its computation during simulations. More importantly, however, is that disruption of pollination is likely to be a gradual process, resulting from spatial and temporal matching of species occurrence, population abundances and interaction traits (J. N. Thompson, 2010; Poisot et al., 2015). All of this terms can be expected to change at different rates under real scenarios of disturbance. For example, species occurrence can drastically change due to habitat loss, whereas trait values are subjected to microevolutonary dynamics that usually last longer. Moreover, pollination and herbivory have been shown to interact and select for higher self-compatibility and autonomous selfing (Ramos & Schiestl, 2019), which increase reproductive assurance. However, as discussed in chapter 3, these same traits might decrease species adaptive potential and increase mutation load in the long-term(Escobar et al., 2010; Busch & Delph, 2017; Noël et al., 2017; Cheptou, 2018; Wright et al., 2013) Therefore, the results showing that the loss of interaction might be responsible for bigger extinction debts encourages the investigation of extinction dynamics under more realistic scenarios of interaction loss, since such debts are a sign of a time period when conservation measures can be implemented to revert ongoing extinctions (Kuussaari et al., 2009). While the maintenance of habitat area remains imperative, maintaining or restoring interactions will likely contribute to the waiving of extinction debts in remnant and restored areas. Further simulations are required to identify the most suitable courses of action, specially on the long-term, when debts can be waived.

The results reported in this chapter originate from simulations ran on arbitrary values of three global parameters (Table 4.2). Even if justified by the unavailability of estimations for most the species simulated, in the absence of a sensitivity analysis, this choice limits the generalization of the current results. In this paragraph, I discuss how limited each parameter is. The Biolflor database reports whether plants have the ability to reproduce through selfing upon failure of outcrossing (Table 4.2), but not the frequency at which this happens, which could be assumed to be 1. Nonetheless, outcrossing is directly affected by one of the experiments (disruption of pollination function), and having this probability be 1 would guarantee reproduction, and thus, possibly selection, of the species with this trait, without empirical basis for it. Therefore, I introduced stochasticity to the process by giving it equal probabilities of sucess or failure. As shown by King et al. (2013), flower visitation is not a good proxy for efficient pollination, with 0%-78% (mean of 40%) of visited flowers not being effectively pollinated. Thus, I separated the two parameters. Moreover, I set the proportion of flowering plants that are visited per week (the time step of the model) at 1 (Table 4.2), which is an approximation based on foraging reportedly lasting hours (Fishman & Hadany, 2010). The efficiency of wind pollination was set to the same value as that of insect pollination (Table 4.2). However, for grasses, reported values of efficiency (*Alopecurus pratensis, Anthoxanthum odoratum*) can be as low as 5%-20% (Cresswell, Krick, Patrick, & Lahoubi, 2010). Therefore, this means that it could be expected that wind-pollinated species would be favored in scenarios of disrupted pollination function. This does not seem to be the case, because, although insect pollination is one of the most important traits defining the trait space of extinct species, the same is not observed for wind pollination, for surviving species. Nonetheless, it is still possible that the species who ”benefited” from higher than expected wind pollination have survived. As with the other parameters, a sensivity analysis is necessary to define the effect of these parameters on the simulation results.

Pollination services are vital for human well-being (Potts et al., 2010, 2016) for their importance for crop production (Klein et al., 2007; Woodcock et al., 2019) and the reproduction of wild plants (Ollerton, Winfree, & Tarrant, 2011). This dependence results from the spillover effect, i.e. the transfer of functionality between natural and managed areas (Blitzer et al., 2012), wherey crops and wild plants benefit from the populations of wild and domesticated bees maintained by both environments. In the simulations included here, I only simulated the effects of static disruption of pollination function on natural communities. As described in the TRACE document, the model has the ability to simulate temporally varying availability of pollinators and it keeps track of the proportion of flowering plants being pollinated. Thus, future, and longer, simulations could investigate the long-term effects of crop flowering (e.g. Magrach et al., 2018) on pollination of wild plant communities, and its feedback on the maintenance of the spillover effect.

Another unexplored feature of the model is the use of temperature data-series as inputs, which allows the simulations of different scenarios of climate change. In the context of extinction debts, such scenarios are specially interesting for two reasons in particular. The first relates to the metabolic consequences of temperature increase. Species life history rates and times also depend on environmental temperature (and body size), as proposed by the metabolic theory of ecology (Brown et al., 2004; Sibly, 2012), and implemented in the model. More specifically, species with higher germination and mortality rates (under increased temperature) respond faster to disturbance, while lower rates might allow species to build seed banks or survive long enough to survive temporarily bad conditions that are eventually restored. Second, in the model, species temperature tolerances affect species fitness and, thus species competitive strength. Moreover, along with dispersal and reproductive rates, species tolerances give rise to range shift dynamics under climate change. Therefore, future simulations must compare the short- and long-term consequences of temperature variation, as well as the feasibility of species range shifts under temperature change and habitat destruction.

4.5 Conclusion

With this work, I present a model designed to explore the long-term consequences of biotic and abiotic disturbances in real-world inspired plant communities. Emergent patterns of community diversity and trait composition approach those calculated for real-world calcareous grassland communities, indicating good model performance, and potential to be applied to different communities (after similar parameterization). Most importantly, the results indicate that the disruption of pollination function is a major factor behind the generation of extinction debts. Notably, extinction debts are higher and extinction times are longer under disruption of pollination. Considering that the role of disruption of pollination function in the creation and payment of extinction debt is seldom explicitly explored, our results demonstrate the importance of accounting for the loss of ecological functions, specially when those might be critical to restore communities under debt.

Part III

General discussion

Chapter 5

Insights into extinction debts from mechanistic models

In previous chapters, I have explored the eco-evolutionary processes taking place following disturbances of different types.

Specifically, I started by reviewing and summarizing the status of empirical, theoretical, and methodological research on extinction debts. I showed how extinction debts are currently being paid by fungi, lichens, plants, vertebrates and invertebrates, in a variety of ecosystems all over the globe, due to a variety of disturbances (habitat destruction being the most frequent). I also showed how the island biogeography, metapopulation, niche, and neutral theories contribute (via modeling) to assessing different aspects of extinction debts, specially those hard to assess empirically, such as the total duration of debts. Most importantly, I summarized that most of the knowledge regarding the mechanisms maintaining extinction debts addresses the roles of i) species traits, ii) metapopulation dynamics, and iii) genetic erosion, while other microevolutionary processes and extinction cascades remain largely understudied.

Following, I explored the possibility of evolutionary rescue contributing to the waiving of extinction debts. I verified that demographic rescue is just as important to species recovery as evolutionary rescue, but that both events are relatively rare, specially under higher intensity of habitat loss. Moreover, I found that, in some instances, evolutionary rescue happened through risky strategies, such as the increase in selfing and bet-hedging. These observations indicate limited capacity of evolutionary rescue to revert species extinctions, and that conservation measures would be required to facilitate it. In that sense, complex, mechanistic models constitute important tools in allowing to explore such responses.

Finally, I used a trait-based model, parameterized by species trait values from a real-world community to investigate the differences in extinction processes triggered by disturbances of different types, namely, habitat loss and pollination loss. In this study, I showed how pollination loss, by affecting a population process, generates extinction debts, while habitat loss, by affecting population size, generates more immediate extinctions.

In the next sections, I discuss the implications of my findings to ecological theory and conservation practices. I also present the shortcomings of the research presented in this thesis, and how they can be addressed moving forward.

5.1 Implications for ecological theory

I started this thesis by presenting the relevant ecological theories used to shape the study of extinction debts. As introduced in part I, the concept of extinction debt was born from the island biogeography, metapopulation, and niche theories, and in chapter 2, I reviewed the importance of principles of neutral theory to allow the identification of the relative importance of processes such as demographic and environmental stochasticity, immigration and endemicity. These four theories have dominated the interpretation of extinction debts up to now, but in chapters 3 and 4, respectively, I evoke principles of the coexistence (Chesson, 2000) and metabolic (Brown et al., 2004) theories to explore different aspects of extinction debts. In the following subsections, I discuss the contributions of the results presented in these two chapters to the theoretical grounding of the concept of extinction debts.

5.1.1 Extinctions arise from slow niche disarrange

A delayed extinction can be conceptualized as the irreversible disruption of conditions necessary for species occurrence in a certain area. In previous chapters, I have shown that extinction debts can be created by disruption of biotic (chapters 2 and 4), abiotic (chapters 2, 4, and 3), and mobility conditions (chapters 2, 4, and 3). These are the same factors affecting species fundamental and realized niches, as proposed by Soberon and Peterson (2005) in their formalization of the Biotic-Abiotic-Mobility framework (from now on BAM, Fig. 5.1-a), according to which a species occurrence depends on the existence of biotic and abiotic conditions within a given area reachable by the species. Since evolutionary adaptive capacity is essential for species survival, one could extend the BAM framework to make it explicit, originating thus, the Biotic-Abiotic-Mobility-Evolution framework; from now on BAME - Fig. 5.1-b,c). In Fig. 5.2-a-e, I summarize how each of these factors has been shown to contribute to species response to disturbance. At the community level, the understanding of extinction processes becomes even more complicated because they can interact and affect each other (Fig. 5.2-f). Besides the cascading effects of extinction processes, there might be cascading effects between the biotic, abiotic, mobility, and evolutionary factors themselves. For example, the actual effect of change in abiotic conditions in species fitness response is mediated by the interaction between its evolutionary capacity to adapt, and the availability of areas where mutants would not be maladapted (Schiffers et al., 2014). Despite the myriad of ways in which these factors can interact, addressing extinction process through the BAME framework allows compartmentalizing each factor, without loosing sight of their interactions.

5.1.2 The importance of high-order interactions for coexistence theory

In the model used in chapter 3 (Leidinger & Cabral, 2020), species in the simulations were in competition with each other, for space with other species with similar temperature niches, since density-dependent mortality is controlled by the landscape carrying capacity and species temperature-dependent fitness. Albeit not explicitly modeled (i.e. I did not assign coefficients of competition to each species), such competition could have given rise to high-order interactions - *sensu* Levine, Bascompte, Adler, and Allesina (2017), where high-order interactions are defined as arising when a competitor's per capita effect on another one depends on the population density of other species besides the two focal ones.

In the results analyzed in that chapter, I interpret the increase in intraspecific trait variation as sign of disruptive trait selection, which was observed for multiple traits. Moreover, I interpret the absence of directional single trait or trait syndrome selection as a sign that species responses depend on the biotic (other species in the simulated community) and abiotic (disturbance scenarios) contexts. Such contingency is a long discussed component of community ecology (Lawton, 1999; Simberloff, 2004). In regards to extinction debts, neutral processes (e.g. immigration rates and demographic stochasticity) may govern the extinction dynamics following disturbances, and are also likely to vary in relative importance (chapter 2). When considering coexistence mechanisms, if one conceives them as also arising from high-order interactions between multiple species (Levine et al., 2017), rather than the classical, pairwise only (Chesson, 2000), the contingency in species responses to disturbance can

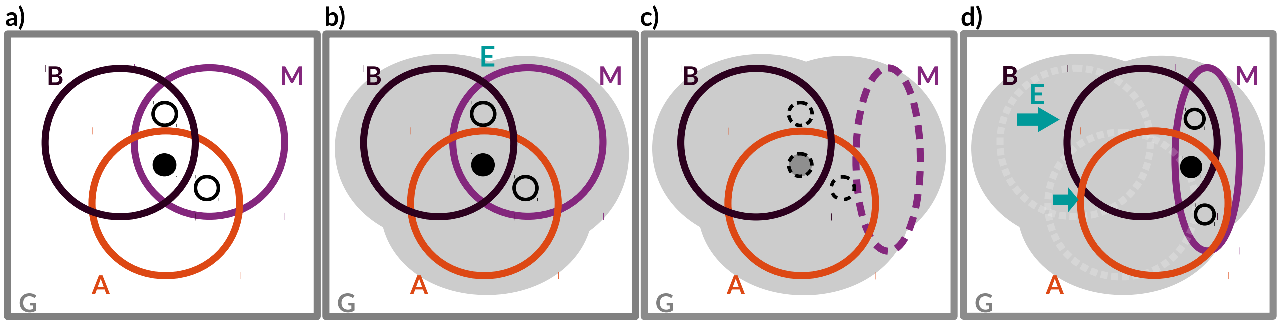

Figure 5.1: Factors affecting a species realized niche. The original Biotic-Abiotic-Mobility (BAM) framework (panel a) from Soberón & Peterson (2005) depicts the factors that influence a species realized geographic distribution (Soberon and Peterson 2005, Soberón 2007): a species occurrence in a certain area of study (square 'G') and, thus, the realized range, depends on the intersection of three factors: i) a set of abiotic conditions, i.e. the physiological limits of the species (the area were those conditions are met is represented by circle 'A'); ii) a set of biotic conditions, i.e. required mutualisms or resources and non-excluding antagonists (circle 'B'); iii) available colonizable area, i.e. area that the species can reach via dispersal ('M'). Where conditions B, A and M are present, the species can establish source populations (filled circles in circle intersections). If one of the conditions is missing, the species might establish only sink populations (white circles). The species also has some adaptive capacity to adapt to change in the previously cited conditions (area 'E' in panel b), not present in the original BAM diagram. For example, a disturbance affecting the available colonizable area enough to also affect existing populations (dashed lines in panel c), can be overcome if the species can adapt (green arrows in panel d) to the new conditions.

be understood as resulting disturbance of multiple high-order interactions being affected at the same time. High-order interactions, especially competition interactions, are notorious for their stabilizing potential (Grilli, Barabás, Michalska-Smith, & Allesina, 2017; Mayfield, Stouffer, Chesson, Venable, & Westoby, 2017; Singh & Baruah, 2019), and for emerging from mechanistic models (Levine et al., 2017; Letten & Stouffer, 2019). Therefore, it is possible that the variation in demographic and evolutionary rescue, as well as extinction events observed in chapter 3 arise from the rearrangement of these interactions. Reinforcing a proposition of Levine et al. (2017), the integration of high-order interactions would improve the prediction of species interactions (direct and high-order) influence the occurrence of extinction cascades.

5.1.3 The relevance of the metabolic theory of ecology in a warming planet

In the models used in experiments reported in chapters 3 and 4, the metabolic theory of ecology controls the biological rates of vegetative biomass growth, germination, fecundity, and mortality. According to the theory, an individual's biological rate is inversely proportional to its body mass, and directly proportional to environmental temperature. In chapter 3 in particular, where I simulated temperature increases of two intensities, adult and seed body masses are relevant traits for species survival. Specifically, species that survived disturbances through evolutionary rescue had either higher adult or seed biomass and thus, lower mortality rates, which I interpreted as allowing populations to survive for long enough (after disturbance) for the species to adapt.

On the one hand, these results contradict others reporting the selection for smaller body sizes under temperature variation reported for exothermic animals (e.g. Verberk et al., 2020) and the higher extinction risk derived for larger vertebrate species (Brook & Bowman, 2005). On the other hand, species with long lifespans are usually present in plant communities under debt (Saar et al., 2012, 2017). A possible interpretation is that these contrasts arise from differences in animals and plants eco-evolutionary dynamics, which would explain how the results of this model agree with empirical observations of plant communities, but not those of animals. Another possibility is that the equi-

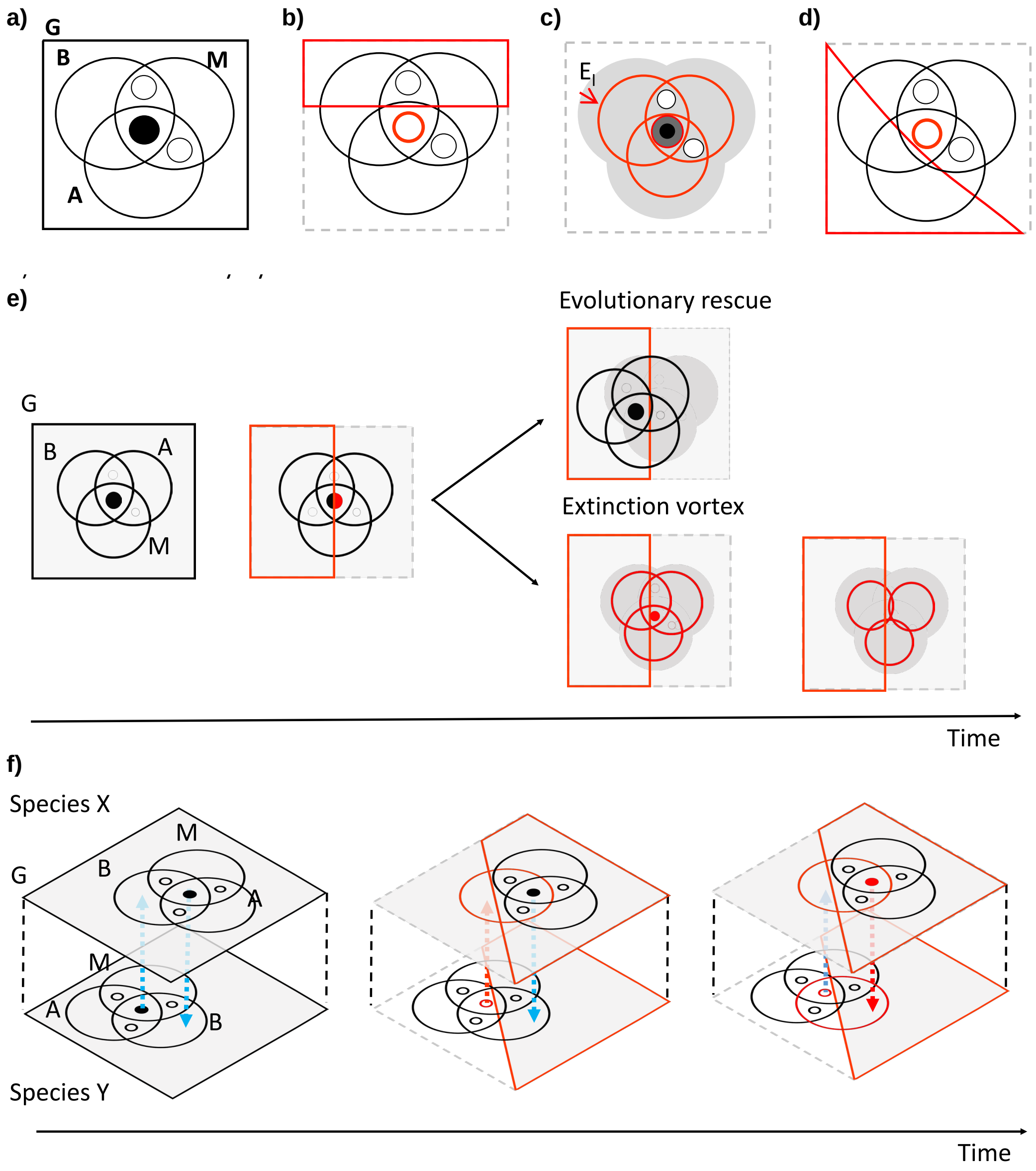

Figure 5.2: Eco-evolutionary processes happening at the individual, population, metapopulation, and community level in response to disturbance. (a) Species persistence depends on the availability of biotic ‘B‘ and abiotic ‘A‘ conditions and reachable area ‘M‘ within a geographical area of interest ‘G‘ (Soberón & Peterson 2005). Three process of delayed extinction following disturbance (red contours), most often addressed in the literature: a) sink populations (b, empty circles) persist while individuals still alive, but the later cannot assure population persistence on the long term if isolated from source populations (filled circles); adaptive capacity of smaller populations decreases over time, thus increasing extinction risk (c, smaller population effective size represented as filled black circle inside the dark grey area, E_l - red arrow - refers to the lost ability to occupy certain areas); following disturbance, landscape conditions remain close to the extinction threshold (d), it is a matter of time before colonization and extinction rates cannot sustain source populations anymore and populations die out. A species evolutionary capacity may allow it to adapt to new habitat conditions (red rectangle decreasing ‘G‘ and affecting the ‘B‘, ‘A‘ and ‘M‘ conditions) and save it from extinction due to evolutionary rescue (e), the species finds a new niche in the changed conditions – red rectangle). Otherwise, increasing loss of genetic diversity hinders adaptation pushes the species to an extinction vortex, which accelerates its extinction. When considering interacting species, X and Y, which strongly depend on each other (blue arrows), both extinction processes interact and the resultant dynamics non-linear become harder to predict (f). Upon the occurrence of a disturbance in the area occupied by both species, species Y is directly affected and falls into one of the extinction processes depicted in a-e. As species Y goes extinct, however, the population decrease affects the realization of the interaction (one red and one blue arrows) even before complete extinction. Feedbacks between both extinction processes (red arrows) affect realization of the interaction, and thus, the biotic conditions required by both species (B circles), even if they were not originally affected.

librium between ecological and evolutionary responses that allows species survival depends on the community and disturbance considered. In that case, even though smaller species show faster responses due to higher biological rates, the longevity of larger species, specially plants species, provides a constant source of offspring to be select by the new environment, until the species eventually adapts. Either way, such contrasting results justify the increasing body of research focused on the implications of climate change on the temperature-dependency of biological (e.g. physiological rates Oddou-Muratorio, Davi, & Lefèvre, 2020) and ecological rates (e.g. Gilbert et al., 2014).

5.2 Implications for conservation practices

Assessing the state of biodiversity response is no simple task. Despite the abundance of reports on the negative effects of human-action on biodiversity (e.g. IPBES, 2019a; Ceballos et al., 2015; Pimm et al., 2014), an increasing number of temporal and meta-analyses have shown that biodiversity loss is not an uniform response (van Klink et al., 2020; Dornelas et al., 2014; Pereira et al., 2012). These analyses report several instances of biodiversity change, i.e. species turnover and relative abundance variation, with both gains and losses. Nonetheless, the potential consequences of extinctions or even abundance decreases to ecosystem functioning and services (Isbell et al., 2015; Hooper et al., 2012; Valiente-Banuet et al., 2015) has not been challenged. Therefore, rather than invalidating or negating the widespread occurrence of extinctions, these results illustrate how challenging understanding biodiversity response can be and how important nuanced analysis, such as the ones I conducted of extinction processes, are (Dornelas & Daskalova, 2020). In the following sections I summarize the contributions of the results discussed in chapters 3 and 4 to planning, evaluation, and communication of conservation measures.

5.2.1 Main courses of action

In chapter 3, I showed that, without dedicated interference, evolutionary rescue has a limited potential to waive extinction debts. Specially under scenarios of habitat loss (a widespread disturbance, Bowler et al., 2020), evolutionary rescue should be limited and conservation should focus on improving demographic processes, for example, by increasing reproductive success and establishment through seed addition, or dispersal, through the establishment of ecological corridors. Otherwise, actions to facilitate evolutionary rescue involve, for example, translocating individuals from remnant species to improve populations' standing variation. Measures to maintain or restore ecological functions, namely pollination, in the disturbed communities will likely contribute in both scenarios cited above, since improved pollination increases reproductive success and genetic variability of plants. In chapter 4, I showed how pollination loss generated more delayed extinctions, meaning that these extinctions can potentially be reverted. Measures to improve it include reestablishment of nesting sites and material, as well as specific hosts and plant resources (Menz et al., 2011). It is important to take into account, however, that pollinators are less likely to exhibit extinction debts (shorter generation times). Therefore, reestablishment of the community must be guided by composition of similar area, and consider and monitor the possibility of spillover effects of adjacent managed areas (Blitzer et al., 2012). This is specially important when habitat area has been reduced, since the limited area will ultimately restrict the amount of biodiversity that can be maintained, if no supplementary actions are taken.

Long-term monitoring of disturbed areas (e.g. species richness, relative abundances, population structure, and interactions) constitutes an essential support for the continuous evaluation of extinction risks and the efficiency of conservation measures in maintaining coexistence (e.g. García-Callejas, Godoy, & Bartomeus, 2020). Before any measures are implemented, assessing the age of an extinction debt is necessary, to decide whether mitigation measures should prioritize short-term interventions on demographic processes to increase population sizes, or long-term ones, on evolutionary processes, to maintain populations of high effective sizes and adaptive genetic diversity. Considering the appropriate detection of extinction debts depends on the availability of past and present species richness data (Ridding et al., n.d.), meaning that detection might be flawed, disturbed areas should nonetheless undergo a mixture of the measures cited in the paragraph above. Nonetheless, Ridding et al. (n.d.) also show how the most efficient method of estimation of extinction debts, based on the comparison between present species richness and the number estimated by the species-area relationship calculated from past species richness. Therefore, even if not possible for debts currently being paid (because of the lack of data on past species richness), this data will facilitate the estimation and monitoring of future debts, which are being set up by current disturbances.

Equally important as restoration measures, is the conservation of currently available, undisturbed habitats. The perspective of an extinction debt must not be interpreted as a buffer against negative effects on biodiversity. Current biodiversity change in response to anthropogenic threats has been so far characterized by high species turnover (Dornelas & Madin, 2020; Dornelas et al., 2014; Dornelas & Daskalova, 2020), and further change can be expected. While the impact of such changes on ecosystem stability has not yet been understood, further change risks pushing ecosystems and the services they provide into irreversible loss (Montoya, Donohue, & Pimm, 2018).

5.2.2 Waiving debts can be as slow as paying them

One of the greatest potentials of studying extinction debts is detecting time windows for conservation measures to be implemented (Kuussaari et al., 2009). As summarized above, in each chapter of this thesis I have discussed how the same ecological processes that maintain extinction debts are the ones that should be restored to waive them, i.e. to avoid the expected extinctions. Therefore, much like final extinctions can take generations to be complete, so do restoration measures, to reach their objectives (Watts et al., 2020). For example, older grasslands restoration projects (> 10 years) have been shown to most successfully restore pollination (Sexton & Emery, 2020). This understanding of the delayed responses of ecosystems is specially important when setting and evaluating conservation targets, such as the United Nation's Convention on Biological Diversity's strategic goal "to improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity" (CBD, 2020; Mace et al., 2018). If changes are expected to be effective sooner than they can actually happen, measures risk being wrongly discarded as ineffective.

5.2.3 Information as conservation

Since the release of the Global Assessment Report on Biodiversity and Ecosystem Services by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services report (IPBES, n.d., 2019b), the threat of human-caused species extinctions has been ever more present in the media and in public consciousness. This increased attention has also fueled the movement of extinction denialists, who seek to downplay and deny the warnings regarding the expected increase in extinction numbers (Lees, Attwood, Barlow, & Phalan, 2020). One of strategies to combat such misinformation movements is to present reasonable estimates of the phenomenon one is aiming to communicate (Lees et al., 2020). Most importantly, considering the degree of uncertainty and contingency involved in estimations of biodiversity loss (e.g. van Klink et al., 2020; Dornelas et al., 2014), it is necessary to explain the origins of such estimates (Fischhoff, 1995). Indeed, discussions regarding the uncertain nature of scientific investigations should be brought to the public more often to familiarize them with the uncertain nature of scientific process, and possibly revert how, so far, uncertain declarations have actually decreased the public's trust in message being communicated (Gustafson & Rice, 2020). One of the other strategies to combat misinformation comes hand in hand at this point (Fischhoff, 1995), as it advises to show the public how this "uncertainty" has been a part of events that are familiarized with and seem to be "certain".

In chapter 3, species ultimate extinction or survival from a disturbance is shown to depend on the community and on the disturbance in question. Acknowledging and exploring such particularities of extinction processes can fuel informed discussions regarding ongoing extinctions and the understanding of biodiversity change in general (Dornelas & Daskalova, 2020), and at least caution against further interference with natural ecosystems (Lindenmayer et al., 2017).

5.3 Perspectives

In the previous chapters I have addressed most of the under-explored questions raised in chapter 2. Following, I investigated the importance of microevolutionary dynamics to the payment of debts (chapter 3) and the difference between extinction debts generated by different disturbances (chapter 4). The contribution of extinction cascades to the occurrence of extinction debts, however, was the questions least addressed. Even though I did explore the consequences of pollination loss in chapter 4, I did not investigate more complex scenarios where interacting species are both undergoing extinction processes, as proposed in Figueiredo et al. (2019). In chapter 3, I propose "breaking down the progressive feedbacks between ongoing extinction processes in populations of interacting species". To this end, I believe the population-level framework proposed by Poisot et al. (2015) to be the most appropriate, since it takes into account four factors that are affected during the payment of debts: species co-occurrence, population abundances, interaction traits, and high-order effects. These factors can all be affected as a debt is paid. Species co-occurrence and their populations abundances can be expected to mismatch because of i) extinctions happening at different rates (e.g. insects usually going extinct faster than the plants they pollinate or consume Bommarco et al., 2014; Guardiola et al., 2018; Cusser et al., 2015), and ii) phenological shifts between interacting species, expected to increase due to climate change, can also contribute to mismatching populations (Schenk, Krauss, & Holzschuh, 2018; Fabina et al., 2010; Schenk, Mitesser, Hovestadt, & Holzschuh, 2018). Interaction traits are subjected to genetic drift in smaller populations, and, as discussed above, high-order interactions can potentially influence several species responses to disturbance. Therefore, integrating all these factors should provide a more holistic understanding of communities responses to disturbance.

Species invasions constitute one of the major current biodiversity threats (Pereira et al., 2013; WWF, 2020). Considering the changes in community composition happening during the payment of extinctions, for example the abundance changes reported in chapter 3 or simply accentuation's in chapter 4, it is likely that colonization and establishment are facilitated. Future studies should characterize extinction debts caused by species invasions, which itself constitutes a slower, multi-stage process (Theoharides & Dukes, 2007), as well as the probability of communities under debt being more vulnerable to species invasions.

5.4 Conclusion

Understanding extinction processes is a necessary and daring challenge. With this thesis I have defined and partially followed a roadmap defining the main avenues of research to improve the mechanistic understanding of extinction debts, upon which conservation measures can be more precisely defined. In the first, to my knowledge, study addressing the occurrence of evolutionary rescue in a scenario of extinction debt, I have shown that evolutionary rescue has a limited potential to rescue populations. I also presented a model parameterized for real-world communities, that allows contrasting the extinction dynamics triggered by different disturbance types, namely habitat destruction, temperature increase, and pollination loss. In both cases, I showed how habitat loss ultimately restricts the possibility of reverting extinction processes, which reinforces calls to strongly reduce any further disturbance of natural systems. Each of these studies highlighted the usefulness of a mechanistic approach to bring insights into the understanding of extinctions happening during the payment of debts. In this sense, monitoring the status of biodiversity in disturbed areas constitutes an essential strategy for the control and understanding of current and future debts. Moving forward, I expect future research and conservation planning to keep focusing on the mechanistic understanding of extinction dynamics.

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Appendices

Appendix 1

Supplementary material

Materials & Methods

We searched the literature for the term *extinction debt* isolated and in combinations with the following terms: *relaxation time*, *extinction dynamics, model*, *metapopulation*, *mechanistic model*, *individual-based model*, *agent-based model*, *biotic interactions*, *temporal*, *network stability, delayed extinction* and *prediction* in the Clarivate Analytics Web of Science collection, for works published between 2009 and 2017 (Fig. A1). Although it would strictly fall outside of this time window, Guardiola et al. (2018) has been included in this review because of its date of first publication (November 10th, 2017). Furthermore, because "relaxation time" is a concept closely linked to extinction debt, we extended the period of search to for this term to 1972, when it was first used in Ecology by Diamond (1972). We restricted our searches to the Environmental Sciences & Ecology research area of the Web of Science collection. In total, we found 397 studies. The 83 studies retained by filtering the through the 'empirical', 'theoretical' and 'methodological work' categories are listed in tables A1, A2, and A3, respectively. Additionally, List A1 lists the 31 papers arising from our search and appropriately cited in the main text, but not fitting the above categories.

To assess if and how much each study addressed the spatial-temporal dynamics and mechanisms behind extinction debt, we analyzed results from each category differently. For studies in the empirical category, we read the methodology section of each paper and identified a) the type of habitat and taxonomic group(s) for which the debt was being evaluated, b) the source of data on those organisms, b) the method used to detect the extinction debt, d) whether the study estimated its duration (relaxation time) and magnitude (number of species yet to be extinct), and e) the spatial and temporal scales. We classified the methodology of each paper according to the summary presented in Kuussaari et al. (2009). Namely, these are i) regressive methods, ii) comparative methods, iii) estimations based on species-area relationships, iv) estimations from time series biodiversity data and v) (meta)population modeling (for a more thorough description of each method, please refer to Kuussaari et al. 2009). Methods that do not fall into those categories were specifically identified in Table A1 and classified as "Alternative methods" in Figs. 1, and Tables A1 and A2. Moreover, only estimations of the relaxation time made under a clearly stated assumption of new equilibrium of the system were considered estimations of relaxation time. We did not consider the time passed since the perturbation to be the relaxation time because it does not necessarily correspond to the time taken to pay the extinction debt. To identify whether any ecological mechanism was explicitly investigated in the study, we carefully read each paper, especially the section describing the methodology used, and searched for attempts to quantify factors related to the mechanism. For example, Guardiola et al. (2018) estimated associations between network metrics and current and past landscape metrics in a system paying an extinction debt. For that reason, we interpreted that the mechanism investigated was the loss of biological interactions during the relaxation time. Mechanistic explanations alluded to or presented in the discussion section were not considered as explicitly investigated and therefore are not listed.

Models in the theoretical category (listed in Table A2) were classified according to model (*e.g.,* mathematical, metapopulation, agent-based models) and theoretical background (*e.g.,* metapopulation, island biogeography, coexistence theories).

Table A1: List of reports of extinction debt published between 2009 and 2017. Papers are characterized according to (a) the ecological processes explicitly investigates, (b) the type of habitat where the debt was being evaluated, (c) the source of data on those organisms, (d) the causative perturbation of the extinction debt, (e) the taxonomic group(s) for which the debt was being evaluated, (f) the method used to detect the extinction debt, (g) whether the study estimated the magnitude of the extinction debt (i.e. number of species yet to be extinct), and (h) the spatial scale of the study. Studies published in 2009 where only included in this table if not present in Kuussaari et al. (2009).

Reference	Processes investigated	Habitat	Data collection	Perturbation	Organisms	Method	Magnitude	Spatial Scale	Notes
Alignier and Aviron (2017)	no	Field margins	Field sampling	Cessation of management	Carabid beetles	Regression	no	Regional	-
Alofs et al. (2014)	no	Savanna	Field sampling	Cessation of management	Plants	Regression	no	Regional	-
Aynekulu et al. 2016)	no	Dry afromontane forest	Field sampling	Direct exploitation	Woody plants	Inferred from species absence in seed bank	50% of current diversity	Local	-
Bagaria et al. (2015)	no	Mediterranean grasslands-forest interface	Field sampling	Forest encroachment	Plants	Regression	no	Regional	-
Bommarco et al. (2014)	no	Semi-natural grassland	Field sampling	Habitat destruction	Butterflies, bees, hoverflies, vascular plants	Regression	no	Regional	-
Botzat et al. (2015)	Local population structure and metapopulation dynamics	Scarp forest	Field sampling	Habitat destruction	Tree, seedling, sapling	Inferred from reduced recruitment	no	Regional	-

Bunnell and Houde (2010)	no	Managed forest	Literature	Cessation of management	Vertebrates, invertebrates	Inferred from review	no	Continental	-
Burst et al. (2017)	no	Forest-grasslands interface	Field sampling	Habitat destruction	Plants	Regression	no	Regional	-
Chen and Peng (2017)	no	Forest	Databases	Habitat destruction	Reptiles, amphibians, mammals	Neutral model	Up to 100 species, depending on the group	Global	-
Cousins and Vanhoenacker (2011)	no	Semi-natural grasslands	Field sampling	Habitat destruction	Plants	Regression	no	Local; Regional	-
Cristofoli et al. (2010)	no	Wet heathlands	Field sampling	Habitat destruction	Vascular plants	Regression	no	Regional	-
Cusser et al. (2015)	no	Agroecological system	Field sampling	Habitat destruction	Bees, butterflies	Regression	no	Local; Regional	-
Ding et al. (2017)	no	Lakes	Field sampling	Species Introduction	Fish	Regression and Time-series data for diversity	no	Local; Regional	-
Dullinger et al. (2012)	Local population and metapopulation dynamics	Alpine forest	Databases, literature	Climate Change	Plants	Niche model	44-50% range reduction	Regional	-

Dullinger et al. (2013)	no	NA	Databases	Habitat destruction	Vascular plants, bryophytes, mammals, reptiles, dragonflies, grasshoppers	Regression	no	Continental	-
Duplisea et al. (2016)	Local population dynamics	Sea bank	Databases	Direct exploitation	Fish, invertebrates	Occupancy model	no	Regional	-
Ellis and Coppins (2009)	no	Juniper scrub	Field sampling	Climate change, fragmentation, pollution	Lichen epyphites	Regression*	no	Regional	*Ordination analysis
Ernoult and Alard (2011)	no	Hedgerow networks	Field sampling	Habitat destruction	Vascular plants	Regression	no	Local; Regional	-
Flensted et al. (2016)	no	Temperate forest	Databases, literature	Climate change, habitat destruction	Mammals, saproxylic beetles, butterflies, vascular plants, fungi	Regression	no	Regional	-
Fordham et al. (2016)	Metapopulation dynamics	Tropical forest	Literature	Climate change, area loss	Frogs	Bioclimatic and nihe population models, compared to different species-area relationship estimates	0-25 (scenario and model dependent)	Regional	-

Gibbs and Jiang (2017)	Interaction loss	Microcosm	Experiment	Environmental warming	Bactivore protists	Time-series data	yes	Microcosm	-
Gilbert and Levine (2013)	Metapopulation dynamics	Serpetine grasslands	Field sampling	Invasion	Grass	Metapopulation model	no*	Regional	Persistence estimation for a number of species
González-Varo et al. (2015)	no	Mediterranean woodland	Field sampling	Habitat destruction	*Myrtus Communis*	Regression*	no	Regional	* Quantified presence-absence, not richness
Guardiola et al. (2013)	no	Mediterranean mountain grasslands	Field sampling	Cessation of management	Vascular plants	Regression; Comparison	10 species	Regional; Local	-
Guardiola et al. (2018)	Interaction loss	Mediterranean mountain grasslands	Field sampling	Cessation of management	Vascular plants, butterflies	Regression*	no	Regional; Local	*Regressions between network metrics and habitat conditions
Haddad et al. (2015)	no	Long Term Ecological Research Network (LTER)	Experiment	Habitat destruction	Plants, arthropods, birds, butterflies	Lagged increase in extinctions	no	Regional; Global Comparison	-
Hahs and McDonnell (2014)	no	Urban area	Literature	Habitat destruction	Plants	Backward SAR	55 % of diversity	Local	-

Hahs et al. (2009)	no	Urban area	Literature	Habitat destruction	Plants	Backward SAR	Up to 55%* of diversity	Local; Global Comparison	* Hahs and McDonnel (2009) is included in this global comparison
Highland and Jones (2014)	no	Meadow	Field sampling	Habitat destruction	Plants, nocturnal moths	Regression	no	Regional	-
Huber et al. (2017)	no	Calcareous grasslands	Field sampling	Habitat destruction	Plants	Bayesian multiple regression	no debt	Regional	-
Hylander and Nemomissa (2017)	no	Forest-agriculture mosaic	Field sampling	Habitat destruction	Epiphytes, mosses, liverworts	Regression*	no	Local	*Path model
Hylander and Weibull (2012)	no	Coniferous forest	Field sampling	Habitat destruction	Briophytes	Time-series data	no	Regional	-
Jimenez-Alfaro et al. (2016)	Genetic erosion	Mountain forests	Field sampling	Paleontological event	*Salix hastata, Juncus balticus*	Species distribution modeling; population genetics analysis	no	Regional	-
Jones et al. (2016)	no	Wet tropical, Subtropical, Mediterranean and Boreal forests; Tropical grassland	Literature	Habitat destruction	Mammals, birds, invertebrates, herptiles, plants, fungi	Inferred from depaupered richness	no	Global	-

Klaus et al. (2012)	no	Coral reefs	Field sampling	Paleontological event	Coral	Inferred from extinction rates*	no	Regional	* Calculated from stratigraphic units
Kolk and Naaf (2015)	no	Temperate forest	Field sampling	Habitat destruction	Vascular herbs	Regression	no	Regional	
Koyanagi et al. (2017)	no	Semi-naturalgrass lands	Observational	Habitat destruction	*Echinops setifer*	Regression	no	Local	-
Krauss et al. (2010)	no	Calcareous grasslands	Field sampling	Habitat destruction	Plants, butterflies	Regression	no	Regional	-
Latta et al. (2017)	no	Premontaine forest	Field sampling	Habitat destruction	Birds	Population trends model	credit	Regional	-
Lehtilä et al. (2016)	Local population dynamics	Grasslands	Field sampling	Cessation of management	*Primula Veris*	Metapopulation model	no	Regional	-
Lira et al. (2012)	no	Atlantic forest	Field sampling	Habitat destruction	Birds; Mammals	Regression	no	Regional	-
May et al. (2013)	Metapopulation dynamics	Mediterranean schrub, grassland	Field sampling	Habitat destruction	Vascular Plants	Multi species incidence model	33-60%	Regional	-
Neumann et al. (2017)	no	Woodland	Field sampling	Habitat destruction	Carabid beetles	Regression*	no	Regional	* Multivariate analysis, but still based on regressions

Niissalo et al. (2017)	no	Tropical forest	Observational	Habitat destruction	Zingiberales	Inferred from species distribution and extinction risk	no	Regional	-
Ockinger and Nilsson (2010)	no	Hemi boreal forest	Field sampling	Habitat destruction	Epiphytic lichens	Inferred from negative population growth	no	Local; Regional	-
Olivier et al. (2013)	no	Coastal forest	Field sampling	Habitat destruction	Birds	Backward SAR*	14 spp.	Local; Regional	*Combined with species distribution model
Otsu et al. (2017)	no	Semi-natural grasslands	Field sampling	Habitat destruction	Plants	Hierarchical bayesian regression model	no	Regional	
Otto et al. (2017)	no	Coastal vegetation, Euphorbia scrub, thermo-philous woodland, laurel forest, pine forest, oceanic islands	Field sampling	Habitat destruction	Vascular plants, ground beetles, darkling beetles, flies, land snails	Regression	no	Regional	-
Pandit et al. (2017)	no	Freshwater system	Literature data, secondary	Climate change	Fish	Species distribution model	no*	Regional	*Estimation of range shift, extinctoin debt

			sources						being inferred for potentially isolated populations
Piqueray et al. (2011a)	no	Calcareous grasslands	Field sampling	Habitat destruction	Plants	Regression and Comparison	28.00%	Regional	-
Piqueray et al. (2011b)	no	Calcareous grasslands	Field sampling	Habitat destruction	Plants	Comparison	20.3 – 34.1 %	Regional	-
Plue et al. (2017)	Genetic erosion and local population structure	Semi-natural grasslands	Field sampling	Habitat destruction	*Campanula rotundifolia*	Regression*	no	Regional	* Genetic extinction debt inferred from Regression
Rédei et al. (2014)		Sand grassland	Field sampling	Habitat destruction	Plants	Regression, Comparison	no	Regional	-
Rogers et al. (2009)	no	Forest understory	Field sampling	Habitat destruction	Plants	Regression	no	Regional	-
Saito et al. (2016)	no	Urban-rural gradient	Field sampling	Habitat destruction	Hare	Inferred from presen in regressive site	no	Local	-
Sang et al. (2010)	no	Calcareous grasslands	Field sampling	Habitat destruction	Butterflies	Regression	no	Regional	-
Soga and Koike (2012)	no	Decidous forest	Field sampling	Habitat destruction	Butterflies	Regression, Comparison	0.3-3.8 spp.	Regional	-
Szabo et al. (2011)	no	Woodlands	Field sampling	Habitat destruction	Birds	List length	no	Regional	-
Takkis et al. (2013)	Genetic erosion and Local population dynamics	Calcareous grasslands	Field sampling	Habitat destruction	*Briza Media*	Regression	no	Regional	-

Talluto et al. (2017)	Metapopulation dynamics	Temperate-boreal forest	Databases	Climate change	Trees	Metapopulation model*	yes (mapped)	Regional	*Combined with distribution modelling
Thijs et al. (2014)	Metapopulation dynamics	Afromontane forest	Field sampling	Habitat destruction	Trees	Species equation	9.00%	Regional	-
Triantis et al. (2010)	no	Laurisilva forest	Literature	Habitat destruction	Coleoptera, hemiptera, araneae	Backward SAR*	67-91%**	Regional	*Species-area-age relationship; ** Varying for taxonomical group and at the local scale
Uezu and Metzger (2016)	no	Atlantic forest	Field sampling	Habitat destruction	Birds	Regression	no	Regional	-
Wearn et al. (2012)	no	Amazonian forest	Databases	Habitat destruction	Vertebrates	Dynamic SAR	16 spp.	Regional	-
Yamanaka et al. (2015)	Individual survival	Oak forests	Field sampling	Habitat destruction	Carabid beetles, bats	Regression	no	Regional	-

Table A2: List of studies considered to be ‘theoretical work. These studies are modelling explorations of different aspects of extinction debt (specified in the *Motivation* column).

Reference	Modelling strategy	Theoretical framework(s)	Explicitly simulated processes	Simulated impact	Motivation	Empirical verification	Mechanistic findings	Considerations on spatio-temporal
Chen et al. (2009).	Multi-species hierarchical competition model	Metapopulation theory	Mortality, colonization, competition	Habitat loss	To verify the importance of Allee-like effect on extinction debt size and order.	no	Allee efect affects the extincitons order and the extinction debt; the stronger the Allee effects, the more sensitive species are to habitat destruction.	Strong Allee effect decreases time lag of extinction but also depends on the initial abundance of the best competitor.
Orrock and Watling (2010)	Hierarchical competition model	Metapopulation, neutral and niche theories	Mortality, colonization, competition	Habitat (patch) loss and degradation (reduction in community size)	To verify relative roles of niche and neutral dynamics in metacommunities.	no	In small comminuties, demographic stochasticity has stronger effect on species survival than competitive ability.	-
Halley and Iwasa (2011)	Hyperbolic model of relaxation time	Neutral theory	Phenomeno-logical model: Relaxation curve derived from species	Habitat loss	To predict extinction rates.	yes	-	Estimations from the neutral model agree well with data for large areas (1-10 km) ; immigration, isolation, behavioural shifts and environmental stochasticity are likely more relevant in small

			abundance distribution					fragments, where the neutral model underestimated relaxation times; in very large fragments, speciation, immigration and endemicity might explain overestimations yielded by the neutral model; estimation of extintion times based on the broken-stick produce better fit than the ones based on the log-series model.
Mouquet et al. (2011)	Source-sink metacommu nity models	Niche and Metapopulation theory	Competition, reproduction, mortality, dispersal	Habitat destruction (via removal of local communities)	To verify effects of landscape perturbation on species coexistence (under competition-colonization trade-off) under source-sink dynamics.	no	Dispersal and relative competitive abilities generate different patterns of extinction, depending on the importance of source-sink dynamics.	Extinctions resulting "directly" from habitat loss (*i.e.* loss of source populations) happen faster than "indirect" extinctions, resulting from decreased regional similarity between species competitive abilities; the relaxation time for direct extinctions increases with dispersal but not for very low regional similarity, where source-sink dynamics are less relevant.
Claudino et al. (2015)	Individual-based model	Neutral theory	Mortality, speciation, dispersal	Habitat fragmentation	To verify the impact of dynamic fragmentation on extinction debts.	no	Dispersal leads to lower biodiversity than SAR estimations in a scenario of dynamical	The time between disturbance events affects the extinction debt but not their magnitude. Destruction of contigous fractions of habitat lead to smaller extinctoin debts.

							disturbance.	
Huth et al. (2015)	Metapopulation model	Metapopulation theory	Colonization, extinction	Habitat fragmentation	To differentiate the role of short and long-distance dispersal in the maintenance of regional persistence in fragments	no	-	Large islands dominate the slow dynamics of extinction away from the critical threshold; slow extinction dynamics due to heterogenous island size distribution is different from extinction debt.
Kitzes and Harte (2015)	Mathematical model	Neutral theory	Phenomenological model	Habitat loss (including climete-driven range contraction)	To verify how abundance distribution and spatial aggregation affect the magnitude of extinciton debt.	yes	-	Communities following lognormal and broken-stick abundance distributions will present extinction debt under low spatial aggregation, or immgiration credit under high aggregation; increasing species spatial aggregation decreases the extinction debt.
Halley et al. (2016)	Population-based model	Neutral and island biogeography theories	Extinction	Habitat loss	To describe dynamics of extinction debts.	yes	-	Half-life of extinction and time to first extinction increase with remnant area; biodiversity loss might not be detected if surveys are conducted too early (before first extinction) or too late (after the debt has been paid).
Chen and Shen (2017)	Expansion of the model by Kitzes and Harte (2015)	Neutral theory	Phenomenological model	Habitat loss	To include time delayed responses in the model of Kitzes and Harte (2005).	no	-	Depending on the species distributions and the pattern of habitat destruction, species contribute to either extinction debt or immigration credit.

Hugueny (2017)	Species loss equation	Neutral and island biogeography theories	Phenomenological model wih diversity dependent extinction rate	Habitat fragmentation (increased isolation)	To account for area and age of fragments/islands and diversity-dependence when estimating extinction rates over large time intervals.	yes	Isolate age, rather than diverisity-dependence, has a stronger impact on species loss rates	-
Sgardeli et al. (2017)	Neutral model community model	Neutral theory	Extinction, speciation	Any disturbance	To derive the relaxation curve for neutral communities where speciation introduces new species	no	-	Relaxation time is quicker for higher speciation rates, which depends on community size.
Zarada and Drake (2017)	Population logistic model	Population theory	Birth, death	Any disturbance (via effects on birth and death rates)	To verify extinciton times in continuously deteorating environments	no	Population dynamics alone (ignoring metapopulation dynamics) can have important effects on extinction delays.	When birth rates are affected by declining carrying capacity, extinction delay is the largest, but extinction debt is the smallest. The contrary is true when mortality rates are affected.

Table A3: List of studies addressing issues arising from estimations of extinction debts using species-area relationships (SARs) or endemics-area relationships (EARs) using an alternative modelling strategy (other studies addressing the same issue are listed in the main text).

Reference	**Modelling strategy**	**Theoretical framework(s)**	**Explicitly simulated processes**	**Empirical verification**	**Motivation**	**Mechanistic findings**	**Considerations on area-based estimations (SARs or EARs)**
Halley et al. (2014)	Neutral model of relaxation time	Neutral and Metapopulation theories	Reproduction, mortality, dispersal (immigration)	yes	To understand SAR estimations in the context of extinction debt.	Inclusion of immigration helps differentiate between imminent and delayed extinctions.	Two SAR curves emerge, one predicting immediate extinctions, and one predicting the total number of extinctions. The difference between the two is the number of delayed extinctions (*i.e.* the total extinction debt).
Matias et al. (2014)	Individual-based spatially-explicit model	Niche, Neutral and ommunity assembly theories	Mortality, reproduction, dispersal, competition, coexistence mechanisms	no	To verify SAR estimations of extinctions	Coexistence mechanisms and environmental heterogeneity affect species abundance distributions, which affect how species respond to different patterns of habitat loss.	SARs and EARs underestimate extinctions; SAR estimations are higher than EARs and closer to equilibrium values, indicating that EARs are better suited for estimations of immediate loss; both effects were higher with higher habitat-loss.

Rybicki and Hanski (2013)	Spatially explicit stochastic patch occupancy model	Metapopulation and Niche theories	Colonization, extinction, dispersal	no	To compare SAR and EAR estimations of extinctions in a dynamic context of habitat fragmentation.	SAR are unlikely to have the same slopes in areas where species distribution is more affected by spatial dynamics (low dispersal between isolated fragments).	Remaining species-area relationship underestimates future extinctions; SARs produce large underestimations in highly fragmented landscapes with small areas of remnant habitat.
Tanentzap et al. (2012)	Probabilistic endemic species-area relationship	Island biogeography and Metapopulation theories	Phenomenological model	yes	To adapt EAR to account for future extinctions.	Population size and remnant habitat area influence delayed extinctions.	EARs underestimate future extinctions. However, it is possible to adapt EARs to include the effects of population size and remnant habitat area that generate delayed extinctions.

Table A4: List of studies reporting extinction debts for which information regarding the spatial and/or temporal scales was retrieved. Details on how the scales were identified – or not – are specified in the *Observation* column. Studies from Table A1 which reported that the debt had already been paid where not plotted. Notation used to describe the frequency of data compilation: ";" indicates repeated measures, and "-" indicates a range of dates where measures were taken (regularly or not). Values marked with * entail further details in the *Observation* column.

Reference	Biodiversity sampling	Begin of disturbance	Habitat condition data/ Simulation duration	Age/ Duration of debt (years)	Focal habitat area (km)	Observation
Alignier and Aviron (2017)	2001/2002	NA	1995-2002*	5	NA	* Annually measured
Alofs et al. (2014)	2007	NA	1951; 1980; 1995; 2004; 2008	56	33.43*	* Sum of 3 study sites
Aynekulu et al. (2016)	NA	NA	NA	NA	16.87	-
Bagaria et al. (2015)	2011	1940	1956; 2009	55	320*	* Total study area
Bommarco et al. (2014)	2007	NA	1952-2005*	12	2.0205*	* Measures taken at variable intervals ** Approximated from mean patch area (45 patches)
Botzat et al. (2015)	2010	1860*	NA	~150*	NA**	* Approximated from range informed in the text ** Unable to approximate total area from map
Bunnell and Houde (2010)	NA	NA	NA	NA	NA*	* Unable to approximate total area from compiled literature
Burst et al. (2017)	2014	1826	1931-2014*	21	2000*	*Measures taken approximately every decade. ** Total study area
Chen and Peng (2017)	NA	NA	1500; 2000; 2005	Not applicable	Not applicable	* Global study
Cousins and Vanhoen (2011)	2005	NA	1901	14	2250	* Total study area
Cristofoli et al. (2010)	2006	NA	1770; 1880; 1950; 1970; 2006	236	17.65*	* Current total area of focal habitat in the study area

Cusser et al. (2015)	2013	NA	1992; 2006	21	6	* Current total area of focal habitat in the study area
Ding et al. (2017)	1940-2015 (literature data)	1958-1965; 1970-1980	same as biodiversity	50	1102.5*	*Sum of lakes areas
Dullinger et al. (2012)	Not applicable *	NA	2010-2100 (simulation)	> 100*	Not applicable *	* Predictions of range decline
Dullinger et al. (2013)	1995-2010 (national redlist data)	NA	1900; 1950; 2000	110 (plants, insects, mammals); 10 (fishes, reptiles)	NA*	* Unable to determine total area, because focus is on organisms
Duplisea et al. (2016)	1963-2008 (annual)	1800*	Not applicable	45	~28800**	* Approximated value ** Approximated from map https://soundwaves.usgs.gov/2005/01/fieldwork4.html
Ellis & Coppins (2009)	2005/2006	NA	1961-2000 (climate); 1869 – 2004 (fragmentation);	44 (climate); 136 (fragmentation)	NA*	* Unable to approximate total area from map
Ernoult & Alard (2011)	2001	1950	1963; 1985; 2000	38	NA*	* Unable to approximate total area from map
Flensted et al. (2016)	1994-2013*	NA	1760-1850; 2013	200	6081**	* Database collection ** Current total area of focal habitat in the study area
Fordham et al. 2014	Williams SE et al. 2010	NA	2080; 2150; 2200 (predictive)	100*	NA	* Predictive model
Gibbs & Jiang (2017)	Microcosm experiments				Not applicable	-
Gonzales-Varo et al. (2015)	1999;2001	1500	1956; 2002	45	21 000**	* Approximated value ** Total study area
Guardiola et al. (2017)	2007	NA	1956; 2003	47	NA	-
Haddad et al.	Mesocosm experiments					-

(2015)						
Hahs et al. (2009)	1800-1900;1980-2000(literature and unpublished datasets)	1600-1800	Not applicable	250	NA	* Approximated value
Highland & Jones (2014)	2008-2010 (annual)	NA	1949;2005	61	NA	-
Huber et al. (2017)	2013*	NA	1830;2013	no debt	no debt	* Assumed to be present date
Hylander & Nemomissa (2017)	2008-2009	NA	1967-2008	7	900	* Total study area
Hylander & Weibull (2012)	1998; 2001, 2009	1998	NA	10	0.013 *	* Sum of area of compared plots
Jimenez- Alfaro et al. (2016)	NA(present)	NA	LGM (niche models)	21000; 1000*	NA	* Exact values depends on location
Jones et al. (2016)	1982-2015 (1-92 years since disturbance)	1916-2000	Not applicable	NA	NA*	* Literature data
Klaus et al. (2012)	1993-2009*	NA	~ 3.5 Ma	~1500000**	NA	* Collection of stratigraphic units ** Time between Oceanic closure of the Central American Seaway and the peak in extinctions
Kolk and Naaf (2015)	2013	NA	1780; 2008	160*	4217 **	* Duration of payment ** Total study area
Koyanagi & Akasaka (2017)	2008/2009	1930	1930; 1970; 2000	78	NA	-

Krauss et al. (2010)	2001(plants); 2007 (butterflies)	Estonia: 1930*	Estonia: 1968;2005	no debt at local scale	10.117 **	* Approximated value ** Estimated from current mean patch area (sampled patches)
Krauss et al. (2010)	2000	Finland: 1880*	Finland: 1963/65;1999-2005	no debt at local scale	0.468**	* Approximated value ** Estimated from current mean patch area (sampled patches)
Krauss et al. (2010)	2000	Germany: 1900*	Germany: 1962*; 2004-2005	38	0.5177 **	* Approximated value ** Estimated from current mean patch area (sampled patches)
Krauss et al. (2010)	2007	Spain: 1940*	1956, 2004	no debt at local scale	1.515**	* Approximated value ** Estimated from current mean patch area (sampled patches)
Krauss et al. (2010)	2007	Sweden: 1900*	1956-59*; 2003	no debt at local scale	1.38**	* Approximated value ** Estimated from current mean patch area (sampled patches)
Lehtila et al. (2016)	1995-1998,2006	NA	NA	40-250	NA	-
Lira et al. (2012)	2001-2002/2004-2005/2005-2007	1500*	1962; 1979-1981;2000-2005	40, 20	100**	* Approximated value ** Total study area
May et al. (2013)	2009; 2010/2011	NA	1000 years	<1000*	NA	* Simulation duration
Neumann et al. (2017)	2011	1940*	1930; 2011	81	1.178**	* Approximated value ** Estimated from current mean woodland patch area (sampled patches)
Niisalo et al. (2017)	1989-2005*	1819	NA	200	20	* Varying intervals for each population
Öckinger & Nilsson (2010)	1989-1998;2001-2005	Not applicable	Not applicable	16	6720*	* 70% of study region (total = 9600 km) is covered in forest

Olivier et al. (2013)	2011/2012	<1800	Backward SAR	NA	663*	* Total coastal forest area
Otsu et al. (2017)	1984; 1985, 1986; 2008-2010	1800*	1910; 1980/2000	100	25200 **	* Approximated value ** Total study area
Otto et al. (2017)	literature data	1400*	NA (approximated conditions)	600	7447**	* Approximated value ** Total study area
Pandit et al. (2017)	literature/ databases	NA	70 years*	70*	NA	* Simulated (1908-2050)
Piqueray et al. (2011)	2002; 2003	1920*	1920; 1965; 2002	82, 37 (model-dependent)	0.59 **	* Approximated value ** Current total area of focal habitat in the study area
Plue et al. (2017)	2011	1854	1954; 2011	57	25*	* Total study area
Redei et al. (2014)	2007	1800*	1783;1860;1950;1987/1989; 2005	147	NA	* Approximated value
Rogers et al. (2009)	1950;2005	NA (European settlement)	1950 (approximated); 2005	no debt	39215*	* Approximation of total study area occupied by sampled sites from map provided in paper
Saito et al. (2016)	2006-2007	1940	1950;1974;1984;1994	30	NA	-
Sang et al. (2010)	2007-2008	1930*	1930; 2004	77	78**	* Approximated value ** Current total area of focal habitat in the study area
Soga & Koike (2012)	2011	1970*	1971;2011	40	NA	* Approximated value
Szabo et al. (2017)	1997-2007 (annual)	1800*	Not applicable	60	0.02**	* Approximated value ** Total study area
Takkis et al. (2013)	2008;2011	1930	1930;2000	78	8.95*	* Sum of current areas of sampled patches
Talluto et al. (2017)	NA	NA	1945-2010	65	NA	-

Thijs et al. (2013)	NA	*1800	Not applicable	200	4.13**	* Approximated value ** Total area of flores relicts
Triantis et al. (2010)	1859-2010	1400*	1440; 1700; 1850; 2000	~570 **	58 km ***	* Approximated value ** SAR from 1700 also used for estimate the extinction debt, *** Remaining native forest area
Uezu & Metger (2016)	2003; 2004; 2005	1950	1956; 1965; 1978; 1993; 2003	26	380*	* Current forest cover corresponds to 19% of original 200000 ha
Wearn et al. (2012)	NA (IUCN)	1970	1978; 1988; 1992; 1998; 2000-2008 (annual); 2050 (simulation)	80*	5500000**	* Simulation duration; ** Total area of Amazonian region covered in the simulations (Fig. 1 of Wearn et al. 2012).
Yamanaka et al. (2015)	2011	1896	1920, 1957, 2000	50	4500 km *	* Total study area estimated from Fig. 1

List A1: List of papers arising from the literature search and which discuss relevant points related to extinction debts. These papers, however, do not fit the 'empirical', 'theoretical' nor 'methodological work' categories. These papers are cited throughout the text when relevant.

Braulik, G. T. et al. 2014. Habitat Fragmentation and Species Extirpation in Freshwater Ecosystems; Causes of Range Decline of the Indus River Dolphin (Platanista gangetica minor). - PLoS ONE 9: e101657.

Briggs, J. C. 2011. Marine extinctions and conservation. - Mar Biol 158: 485–488

Brodie, J. F. et al. 2014. Secondary extinctions of biodiversity. - Trend. Ecol. Evol. 29: 664–672.

Habel, J. C. et al. 2015. Fragmentation genetics of the grassland butterfly Polyommatus coridon: Stable genetic diversity or extinction debt? - Conservation Genetics 16: 549–558.

Halley, J. M. et al. 2013. Species-area relationships and extinction forecasts. - Annals of the New York Academy of Sciences 1286: 50–61.

Halley, J. M. et al. 2017. Extinction debt in plant communities: where are we now? - J Veg Sci 28: 459–461.

Hoagstrom, C. W. et al. 2011. A large-scale conservation perspective considering endemic fishes of the North American plains. - Biological Conservation 144: 21–34.

Hu, A.-Q. et al. 2017. Preponderance of clonality triggers loss of sex in Bulbophyllum bicolor, an obligately outcrossing epiphytic orchid. - Molecular Ecology 26: 3358–3372.

Iacona, G. D. et al. 2017a. Waiting can be an optimal conservation strategy, even in a crisis discipline. - Proc. Natl. Acad. Sci. U. S. A.114: 10497–10502.

Iacona, G. D. et al. 2017b. Waiting can be an optimal conservation strategy, even in a crisis discipline. - PNAS 114: 10497–10502.

Isbell, F. et al. 2017. Linking the influence and dependence of people on biodiversity across scales. - Nature 546: 65–72.

Lafuite, A.-S. and Loreau, M. 2017. Time-delayed biodiversity feedbacks and the sustainability of social-ecological systems. - Ecol. Model. 351: 96–108.

Lafuite, A. S. et al. 2017. Delayed behavioural shifts undermine the sustainability of social–ecological systems. - Proc. R. Soc. B Biol. Sci. 284: 20171192.

Legrand, D. et al. 2017. Eco-evolutionary dynamics in fragmented landscapes. - Ecography 40: 9–25.

Leroux, A. D. and Whitten, S. M. 2014. Optimal investment in ecological rehabilitation under climate change. - Ecol. Econ. 107: 133–144.

Leroux, A. D. et al. 2009. Optimal conservation, extinction debt, and the augmented quasi-option value. - J. Environ. Econ. Manag. 58: 43–57.

Lindborg, R. et al. 2012. Effect of habitat area and isolation on plant trait distribution in European forests and grasslands. - Ecography 35: 356–363.

Marini, L. et al. 2012. Traits related to species persistence and dispersal explain changes in plant communities subjected to habitat loss. - Divers. Distrib. 18: 898–908.

McCune, J. L. and Vellend, M. 2015. Using plant traits to predict the sensitivity of colonizations and extirpations to landscape context. - Oecologia 178: 511–524.

Ojanen, S. P. et al. Long-term metapopulation study of the Glanville fritillary butterfly (*Melitaea cinxia*): survey methods, data management, and long-term population trends. - Ecology and Evolution 3: 3713–3737.

Olden, J. D. et al. 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. - Divers. Distrib. 16: 496–513.

Osmond, M. M. and Klausmeier, C. A. 2017. An evolutionary tipping point in a changing environment. - Evolution 71: 2930–2941.

Purschke, O. et al. 2012. Linking landscape history and dispersal traits in grassland plant communities. - Oecologia 168: 773–783.

Rangel, T. F. 2012. Amazonian Extinction Debts. - Science 337: 162–163.

Saar, L. et al. 2012. Which plant traits predict species loss in calcareous grasslands with extinction debt? - Diversity and Distributions 18: 808–817.

Saar, L. et al. 2017. Trait assembly in grasslands depends on habitat history and spatial scale. - Oecologia 184: 1–12.

Semlitsch, R. D. et al. 2017. Extinction Debt as a Driver of Amphibian Declines: An Example with Imperiled Flatwoods Salamanders. - Journal of Herpetology 51: 12–18.

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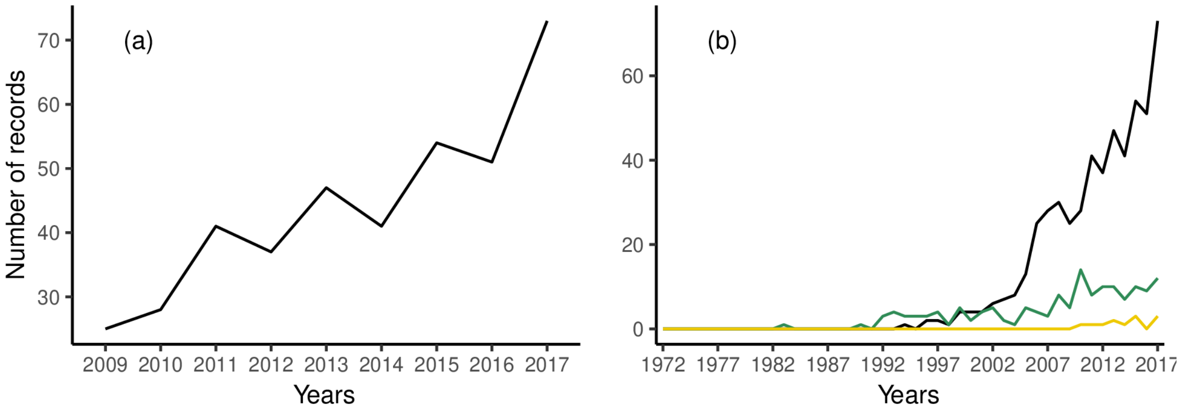

Figure A1: Number of records returned by different searches in the Web of Science collection. (a) Number of hits of "extinction debt", between 2009 and 2017 (total = 397). (b) Number of manuscripts returned for the strings "extinction debt" (black), "relaxation time" (restricted to the Environmental Sciences & Ecology research area – green, *n* = 147) and “relaxation time AND extinction debt” (yellow, *n* = 12 - first one published in 2010), between 1972 and 2017.

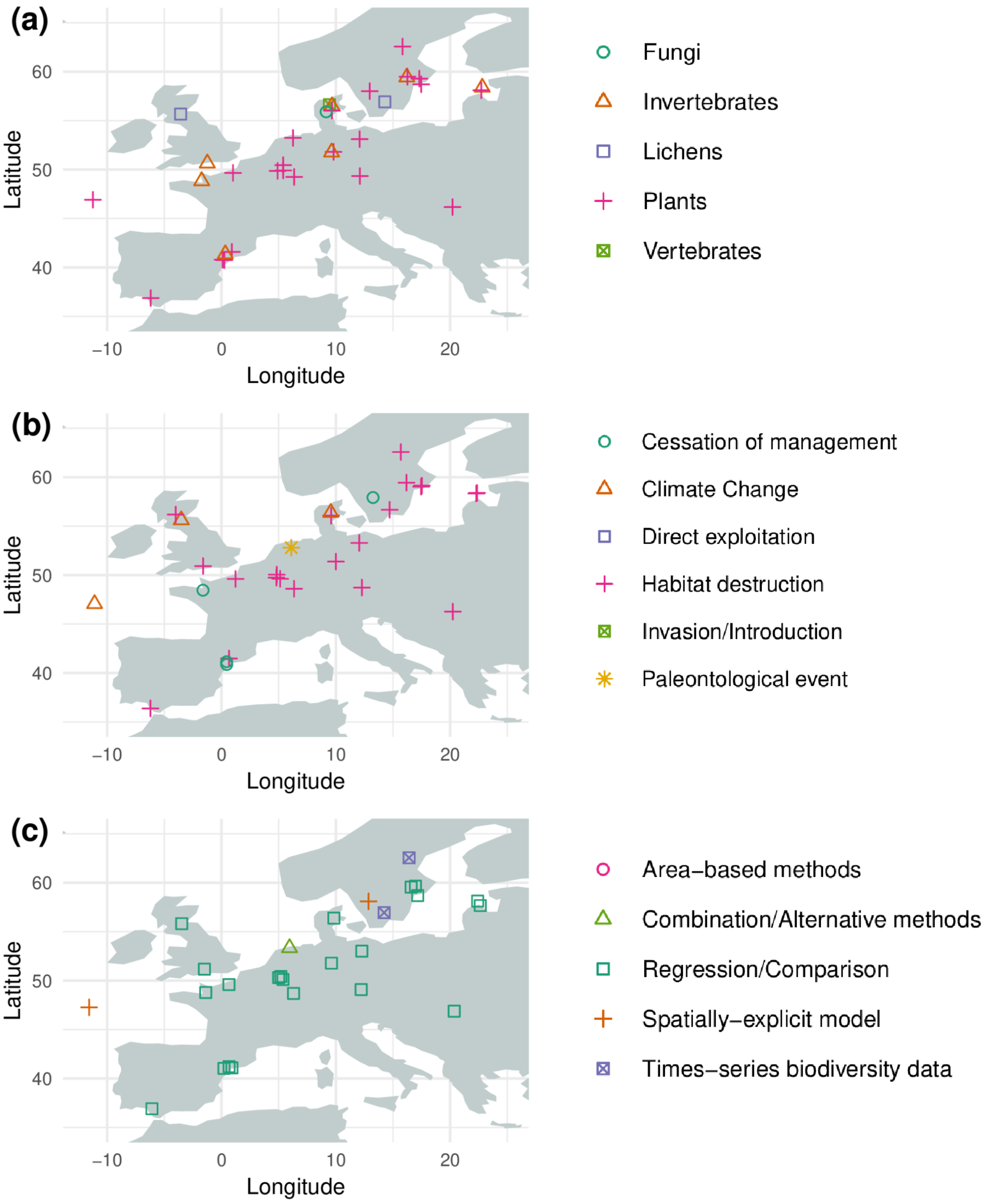

Figure A2: Distribution of (a) taxonomic groups for which extinction debt was investigated, of (b) the causative perturbations behind the possible extinction debts, and of (c) the methods applied in the studies. All panels include empirical studies investigating extinction debts in European real-world systems, published between 2009 and 2017. All studies are listed in Table A1 (studies at the continental (n = 2), global (n = 4) or microcosmic (n = 1) scales were not included).

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Appendix 2

Supplementary material

Model description: Genetic architecture

All ecological traits are coded by one or more genes as explicit genetic sequences packed in an individual's diploid genome (i.e. polygenes). Single genes can also be associated to several traits at the same time (Solovieff et al 2013). Thus, each trait can be represented more than once in the genome, i.e. through different genes at different loci. Trait representations are subject to species-specific variation both within the haploid genome at different loci and between the maternal and paternal haploid genomes or between individuals via different alleles (Nevo 1978). Realized ecological traits, i.e., an individual's phenotype, are then determined quantitatively by considering all respective loci within an individsual's genome and taking their average values. This results in a random degree of species-specific phenotypic and genetic, i.e., intra-individual or intra-genomic, trait variation (Mackay 2001). Lastly, genes may be combined to form a linkage unit, which represents a set of spatially close genes within the same chromosome arm. Linkage units thus comprise the smallest hereditary entities (Hermann 2013, Lande 1984). Haploid gametes receive a complete random set of those linkage units following a recombination process, where each linkage unit can originate from either the paternal or maternal chromosomal complement of the individual producing the gamete. During reproduction, the gametes of two mating individuals thus form an offspring's (i.e. seed) genome. The phenotypic characteristics of each offspring are then calculated on the basis of its recombined genome and local environmental conditions.

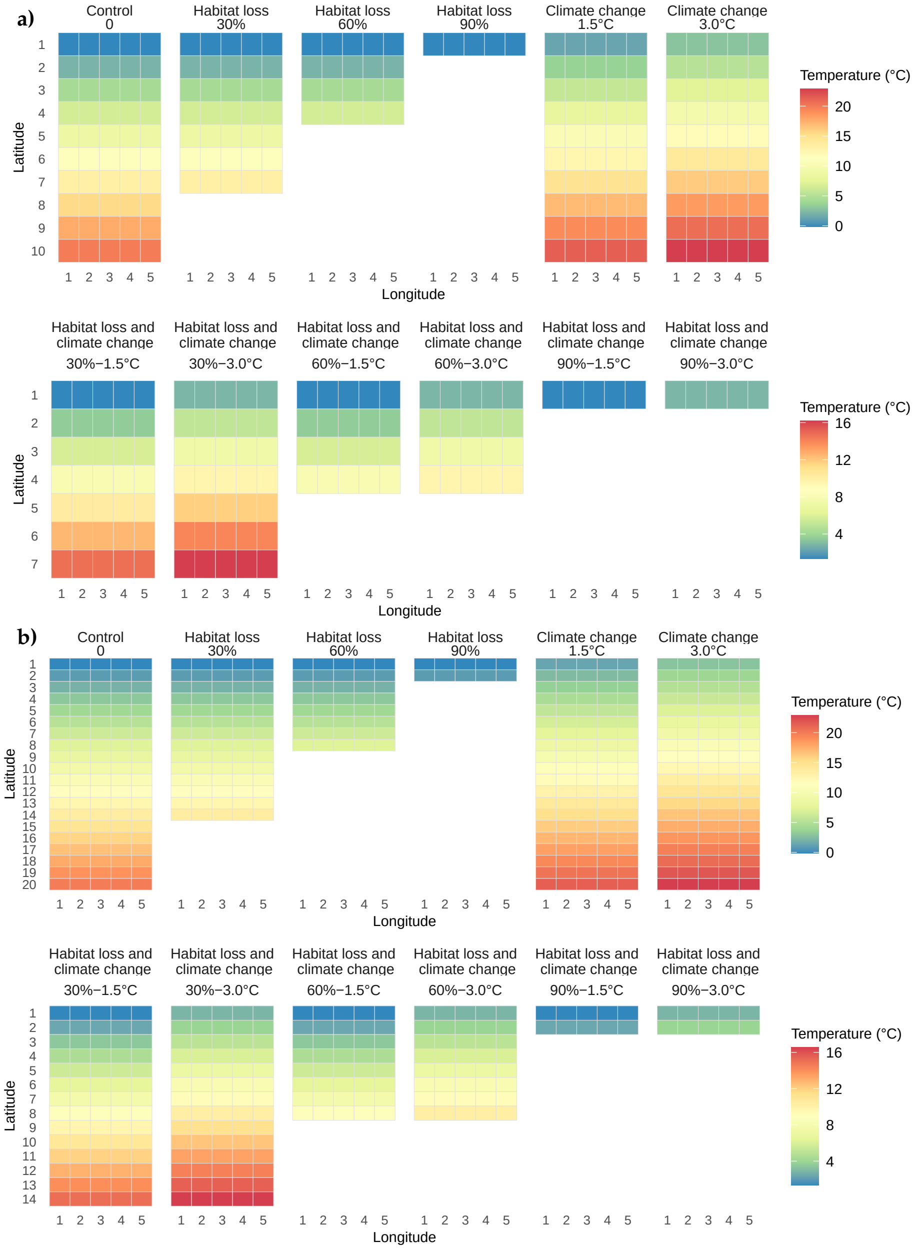

Figure 1: Schematic representation of grid cells with a steep (a) and shallow (c) temperature gradient along the latitudinal axis (2°C temperature decrease from southernmost to northernmost edge) used in the "Control", "Habitat loss", and "Climate change" simulations. Simulations under the "Control" scenario happen under the represented grid for 3000 time steps. For simulations of "Habitat loss", the "Control" grid is replaced for the grid equivalent to the amount of habitat loss being simulated (30%, 60%, or 90%), at time step 750. For simulations of "Climate change", the "Control" grid is successively replaced by grids with higher temperatures, until the temperatures have been raised 1.5°C or 3°C, according to the scenario. Temperatures were raised globally, and constantly, therefore, grids are replaced every time step over 250 time steps, starting at time step 750. This was achieved by and increase of 0.006°C/time step/cell for scenarios of final 1.5°C increase, and 0.012°C/time step(cell for scenarios of 3°C final increase (here, only the final temperature, after increase, is depicted).

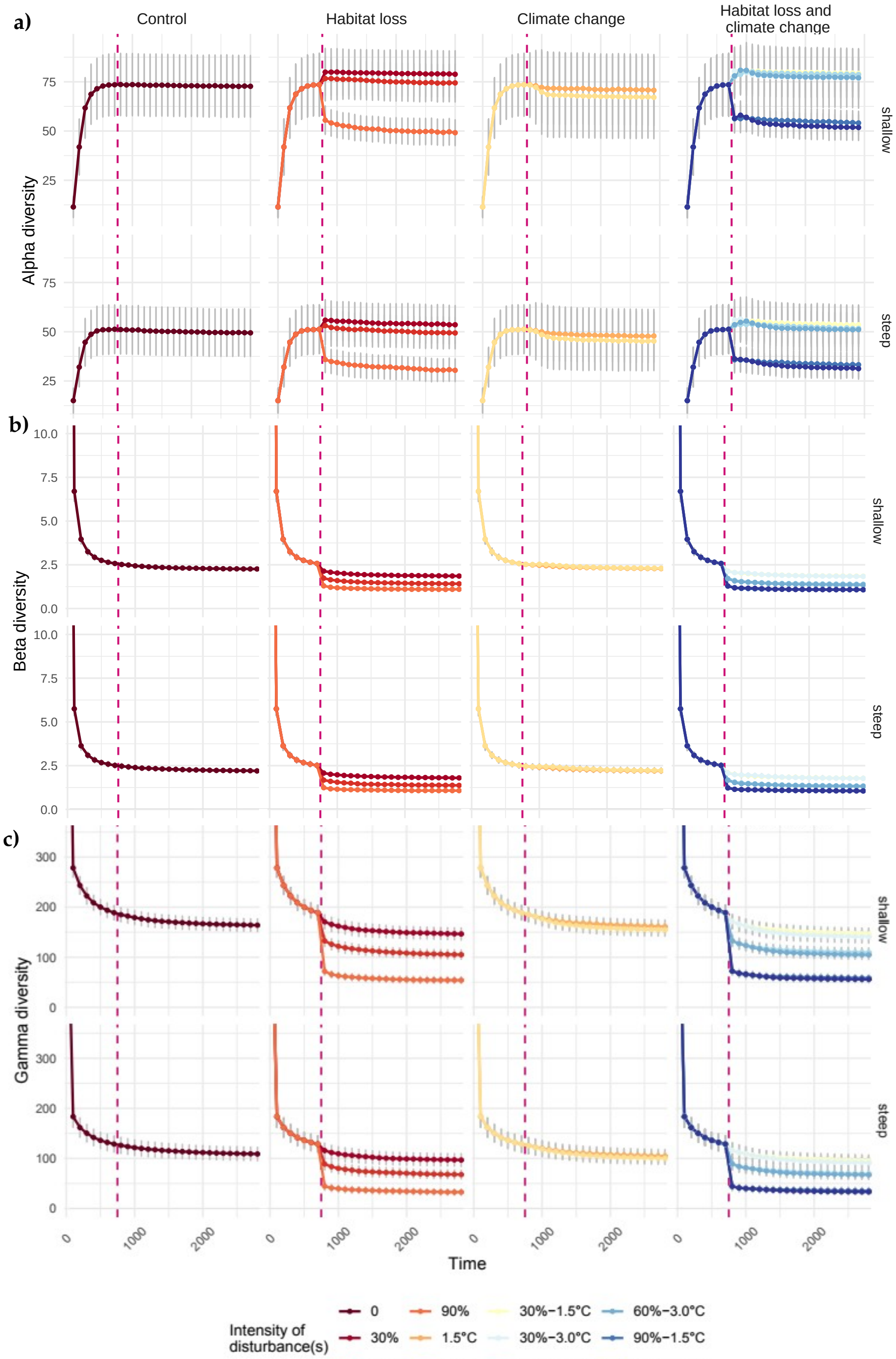

Figure 2: Diversity change over time, calculated for all scenarios of disturbance, and temperature gradients: a) local richness (alpha diversity, measured at grid-cell level), b) species turn-over (beta diversity, measured at landscape level), and c) regional richness (gamma diversity, measured at landscape level). Lines represent mean values of diversity across replicates, and grey bars, standard deviations. Colors identify different intensities of disturbance: "%" refers to the percentage of habitat loss, and "°C", to the final increase in temperature generated by climate change; "%-°C" refers to experiments where habitat loss and climate change were simulated in combination.

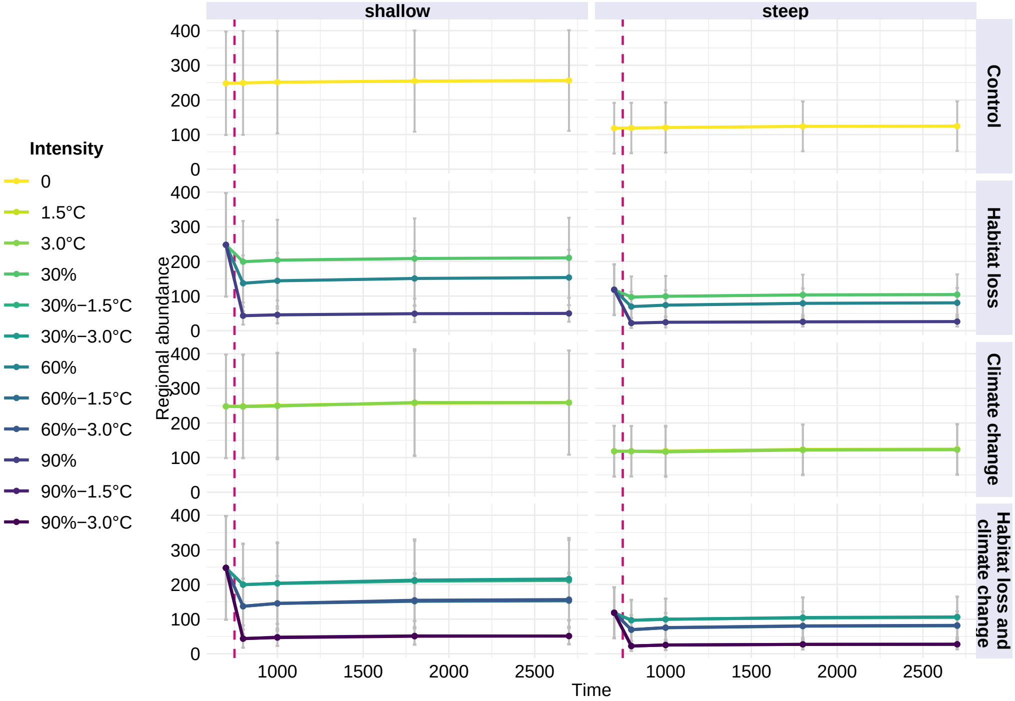

Figure 3: Regional abundance (number of individuals in the grid) change over time, calculated for all scenarios of disturbance, and temperature gradients. Lines represent mean values of diversity across replicates, and grey bars, standard deviations. Colors identify different intensities of disturbance: "%" refers to the percentage of habitat loss, and "°C", to the final increase in temperature generated by climate change; "%-°C" refers to experiments where habitat loss and climate change were simulated in combination.

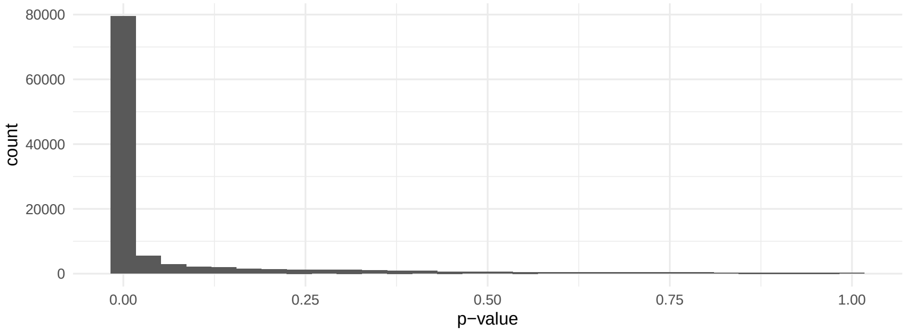

Figure 4: Distribution of p-values among tested lineages (n = 259,084), showing demographic rescuei simulations of disturbance. Tests were performed for 6802 lineages from the 31 replicates, tested for all seven traits, and 109,852 were inconclusive (could not estimate a p-value, marked as "NA").

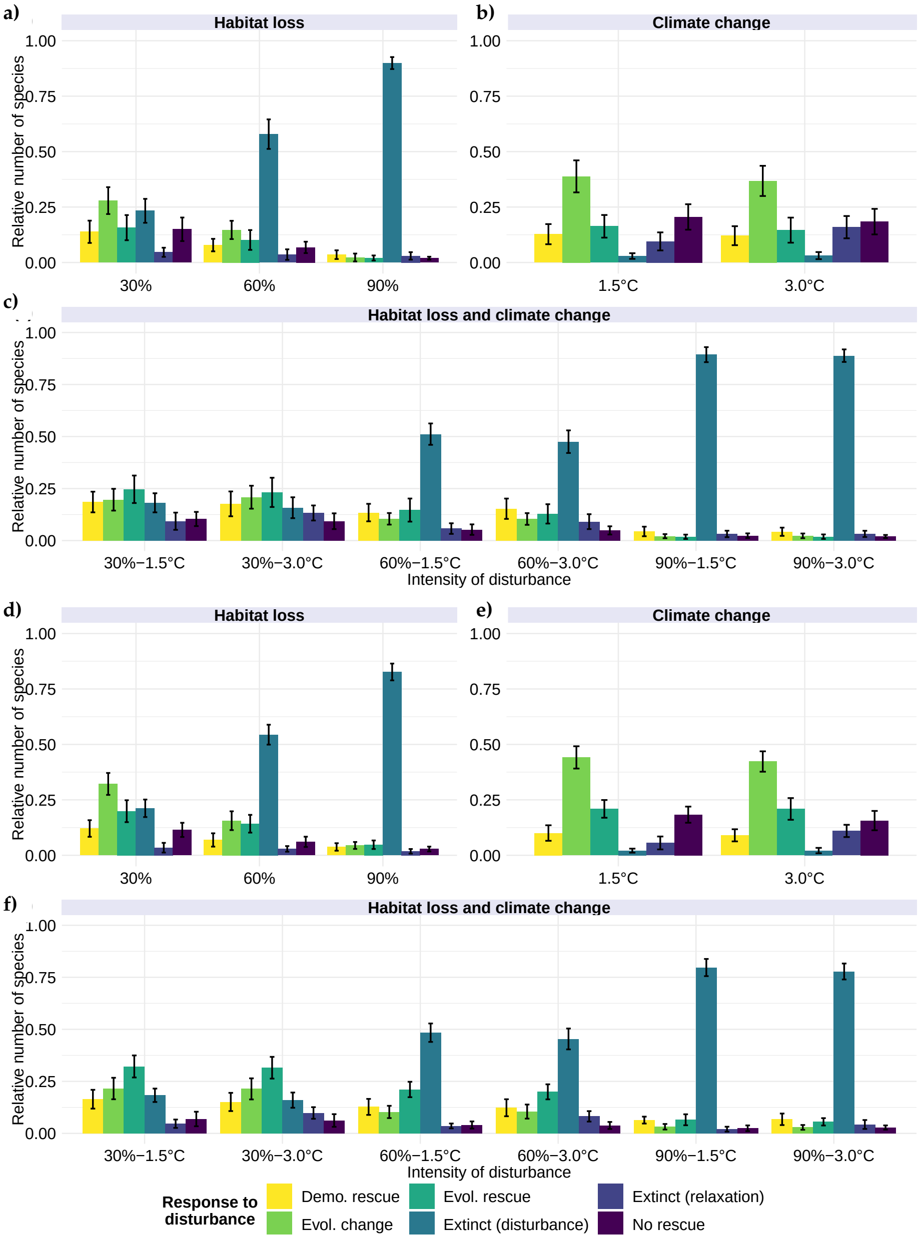

Figure 5: Mean relative number ($n_{response}/n_{total} \pm$ sd) of all species' responses to disturbance in simulations with the steep (a,b,c) and shallow (d,e,f) temperature gradient: demographic rescue only (U-shaped abundace curve, *Demo. rescue*), evolutionary change without demographic rescue (*Evol. change*), demographic rescue and evolutionary rescue, i.e. evolutionary rescue (*Evol. rescue*), immediate extinction after disturbance (*Extinct (disturbance)*), extinction by the end of the relaxation time (*Extinct (relaxation)*, or survival without no characteristic demographic response (*No rescue*).

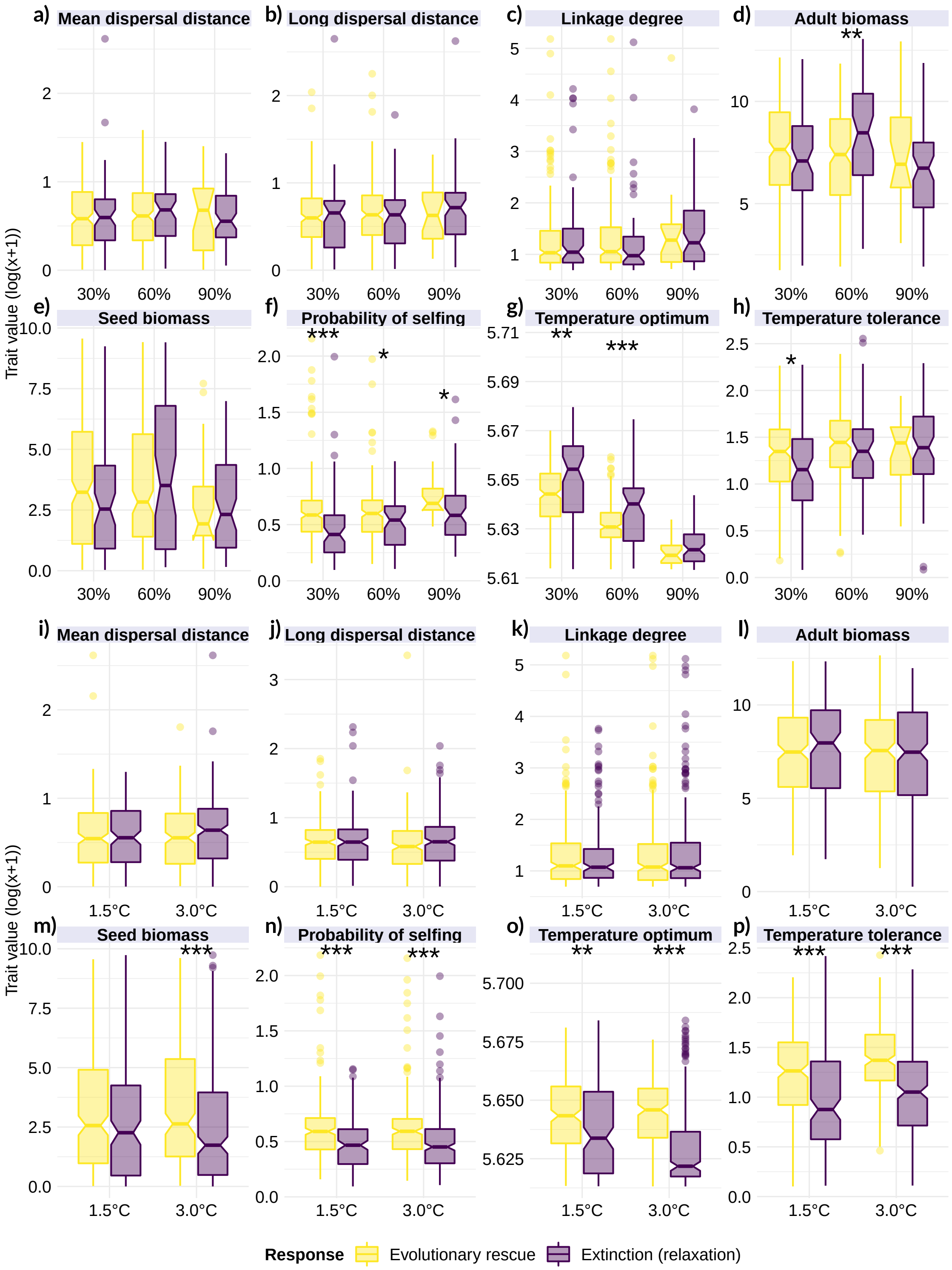

Figure 6: Distributions of mean trait values (transformed as (log x +1)) of species that went through evolutionary rescue and extinction during the relaxation time in simulations of habitat loss (a-h) and habitat loss (i-p), in the steep temperature gradient. Significance levels: “***” = p-value < 0.001, “**” = 0.01 > p-value >= 0.001, “*” = 0.05 >= p-value >= 0.01. Non-significant differences are not shown.

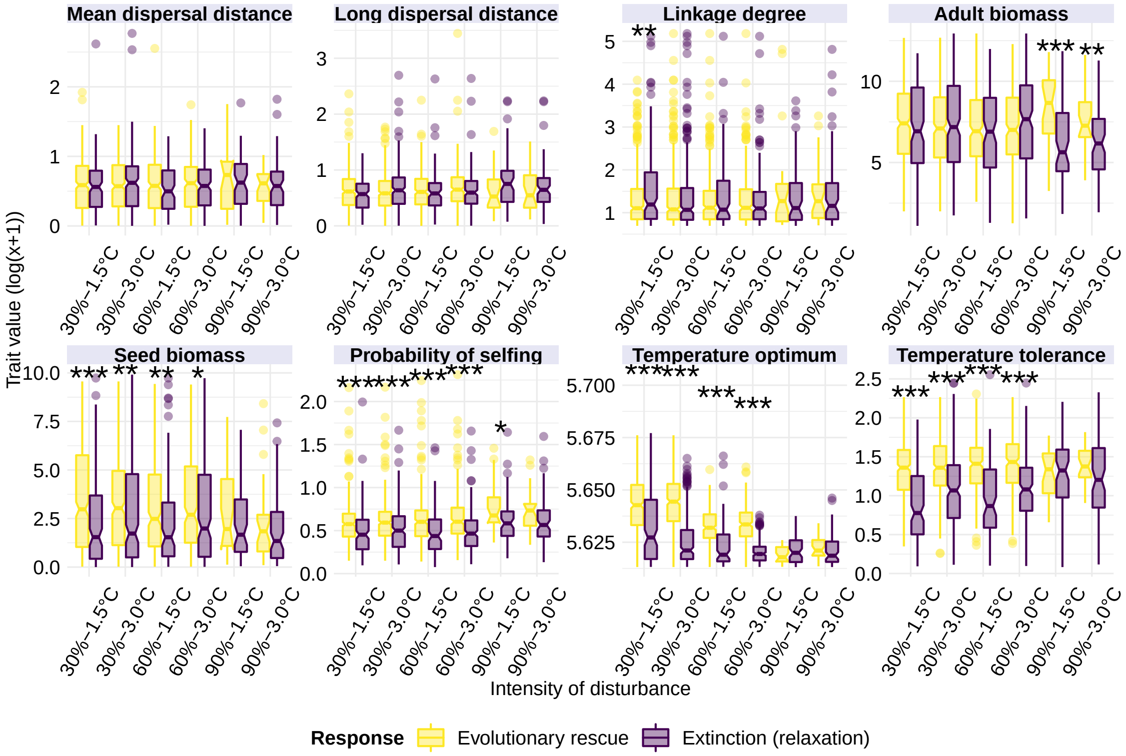

Figure 7: Distributions of mean trait values (transformed as (log x +1)) of species that went through evolutionary rescue and extinction during the relaxation time in simulations of habitat loss and climate change, in the steep temperature gradient. Significance levels: “***” = p-value < 0.001, “**” = 0.01 > p-value >= 0.001, “*” = 0.05 >= p-value >= 0.01. Non-significant differences are not shown.

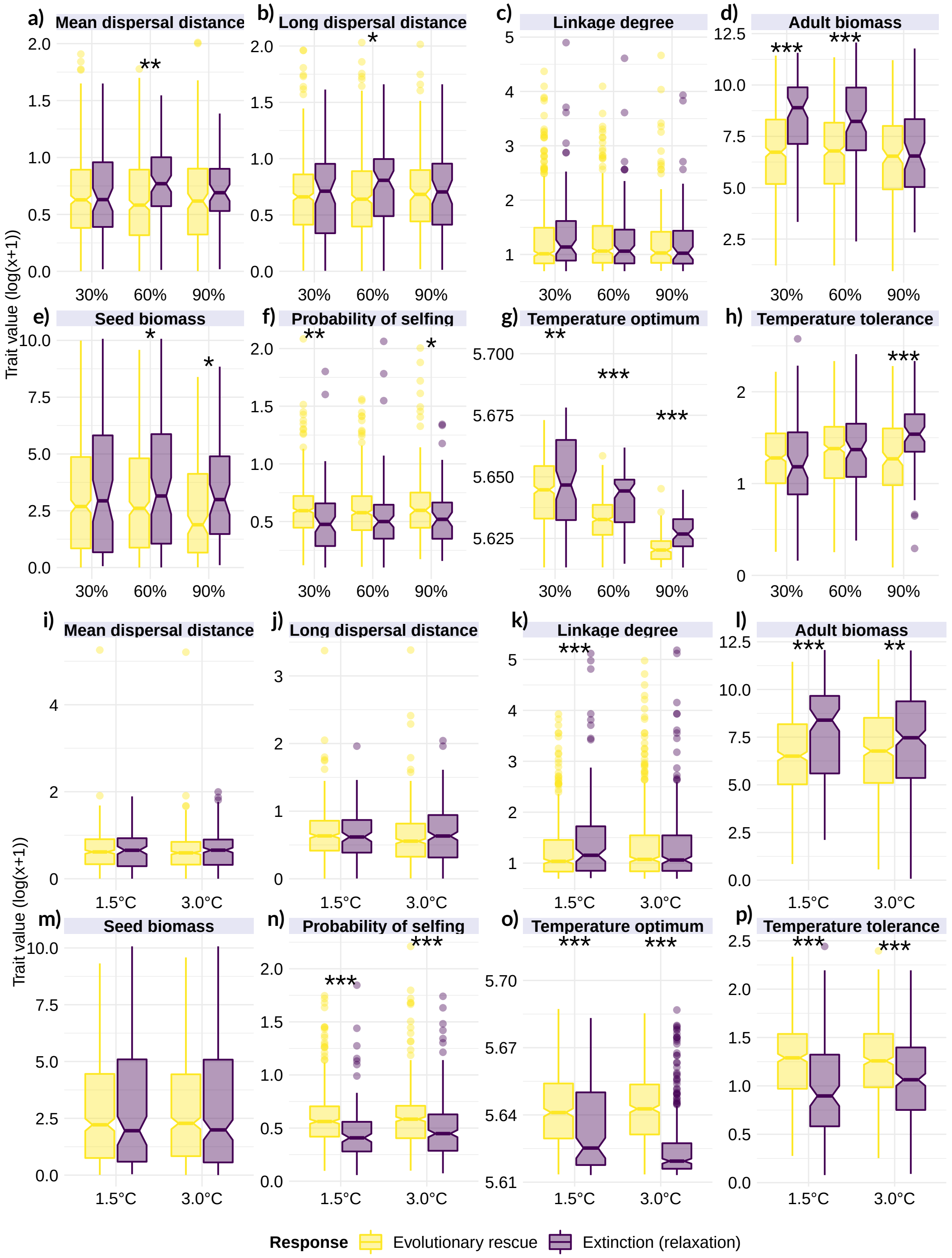

Figure 8: Distributions of mean trait values (transformed as (log x +1)) of species that went through evolutionary rescue and extinction during the relaxation time in simulations of habitat loss (a-h) and climate change (i-p), in the shallow temperature gradient. Significance levels: “***” = p-value < 0.001, “**” = 0.01 > p-value >= 0.001, “*” = 0.05 >= p-value >= 0.01. Non-significant differences are not shown.

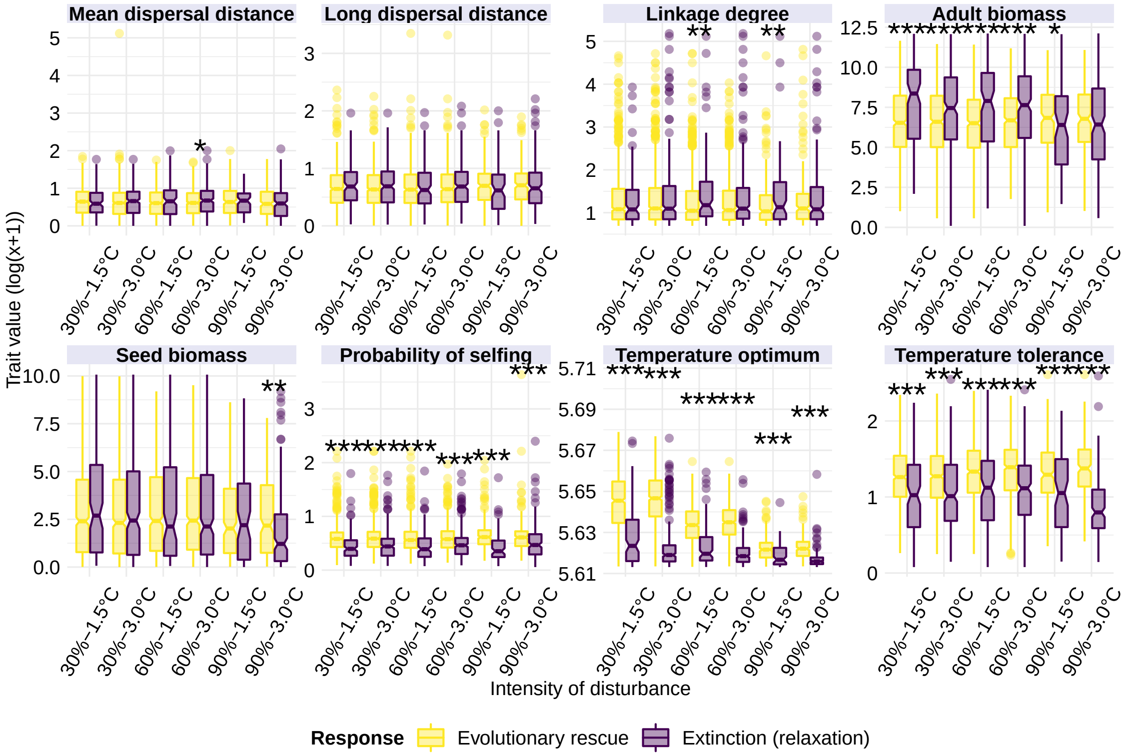

Figure 9: Distributions of mean trait values (transformed as (log x +1)) of species that went through evolutionary rescue and extinction during the relaxation time in simulations of habitat loss and climate change, in the shallow temperature gradient. Significance levels: "***" = p-value < 0.001, "**" = 0.01 > p-value >= 0.001, "*" = 0.05 >= p-value >= 0.01. Non-significant differences are not shown.

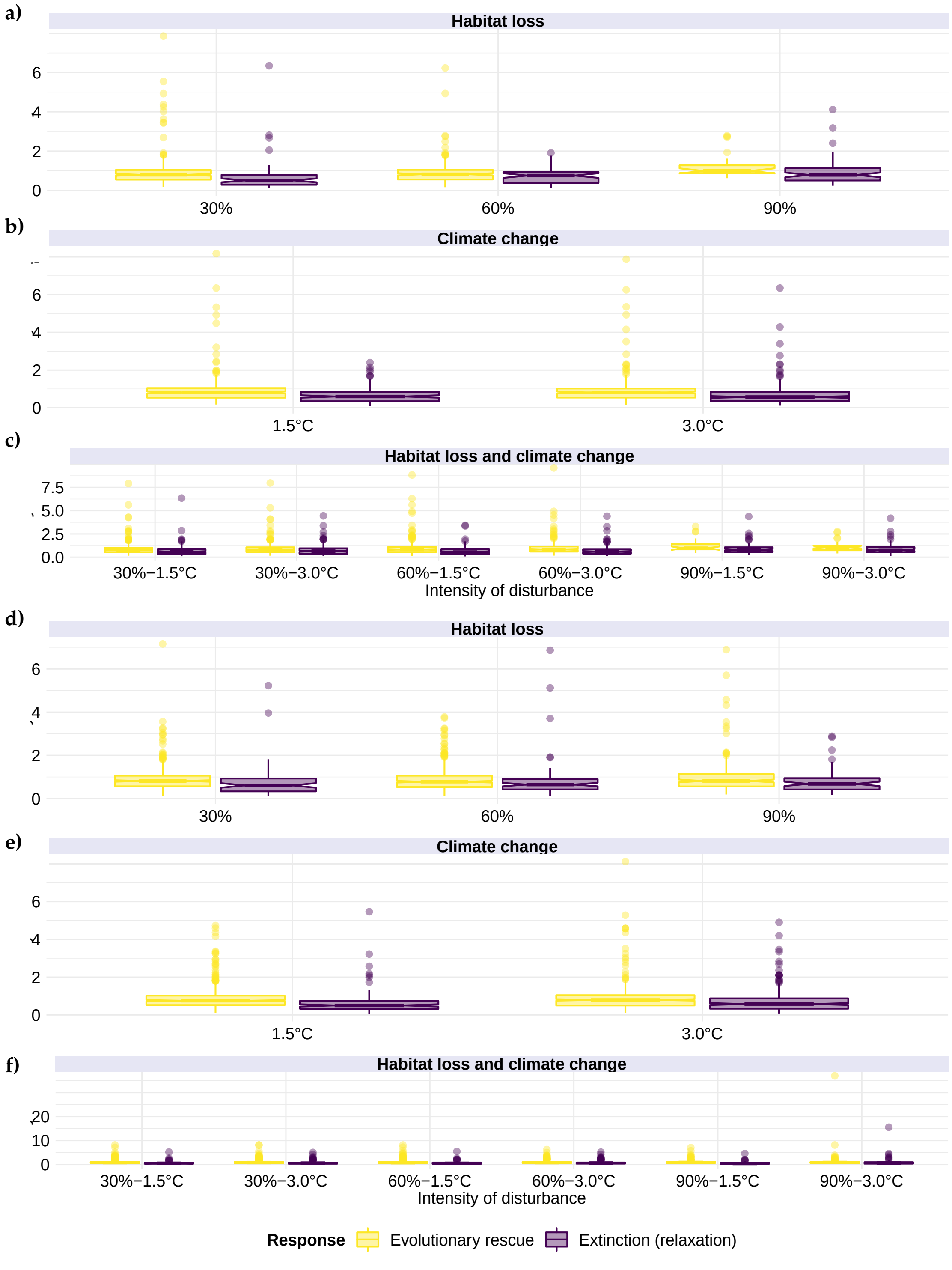

Figure 10: Species mean values of probability of selfing (y axis) in all simulations of disturbance under the steep (a,b,c) and shallow (d,e,f) temperature gradients.

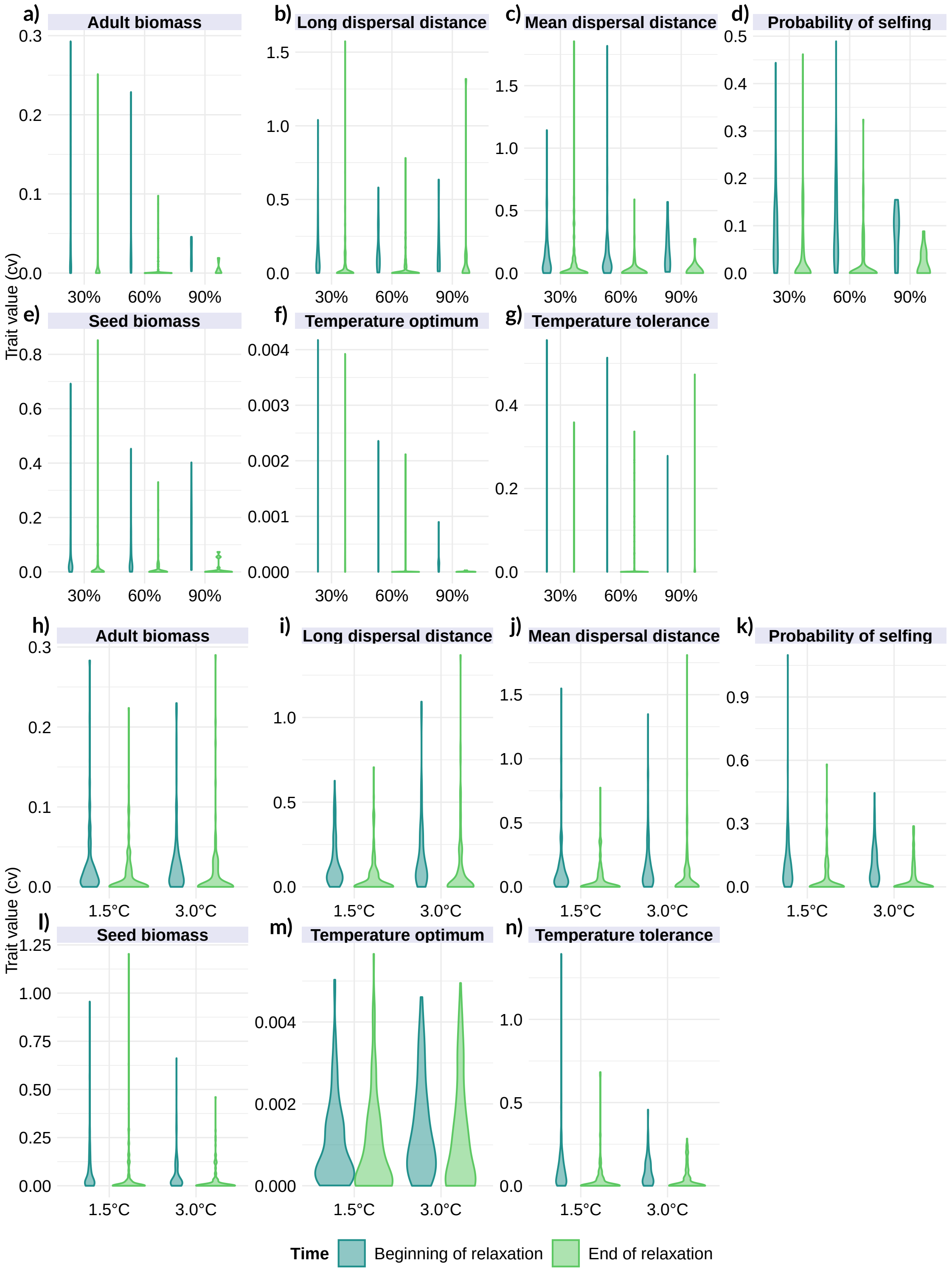

Figure 11: Distributions of the coefficent of variation of trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss (a-h) and climate change (i-p), in the steep temperature gradient.

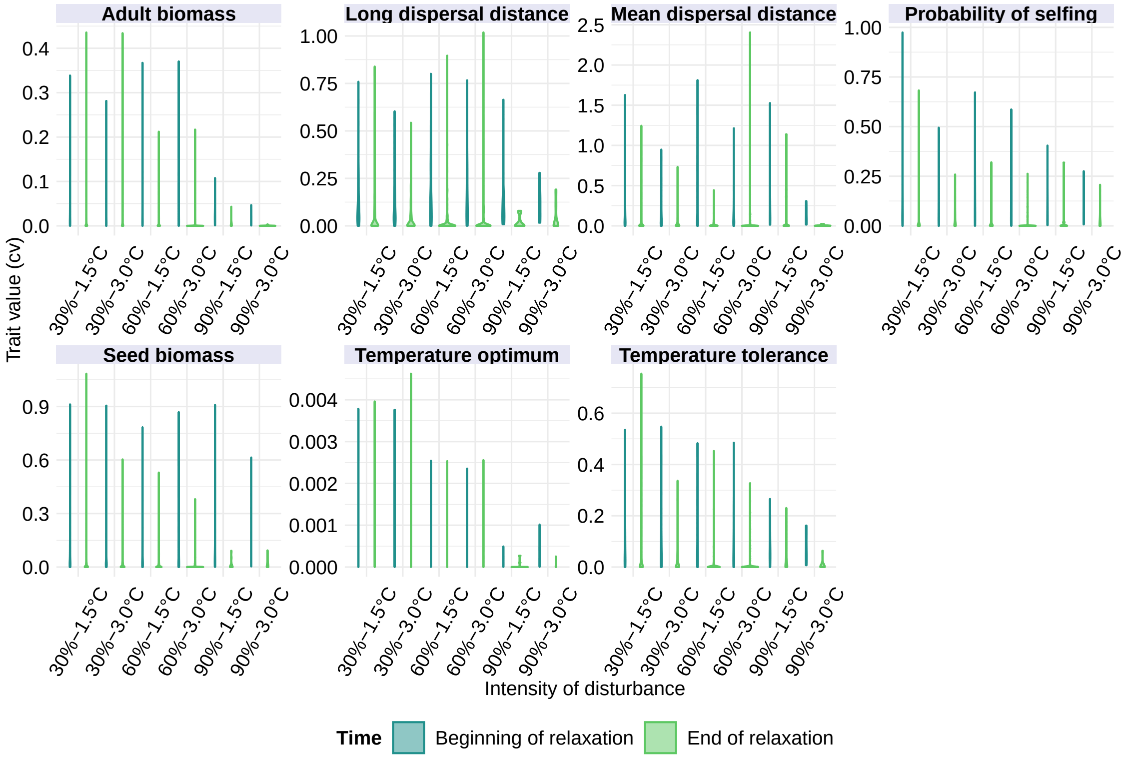

Figure 12: Distributions of the coefficent of variation of trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss and climate change, in the steep temperature gradient.

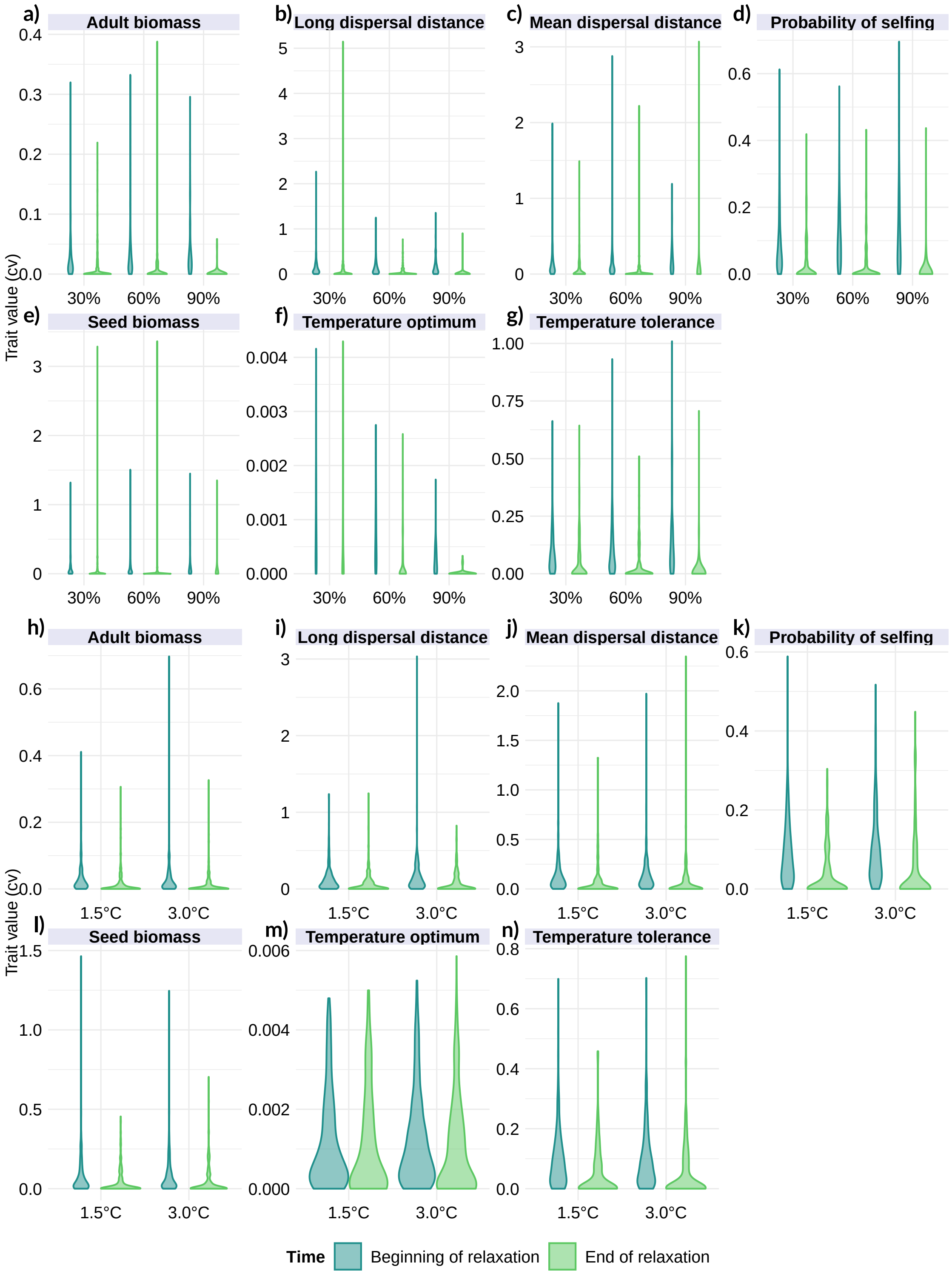

Figure 13: Distributions of the coefficent of variation of trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss, in the shallow temperature gradient.

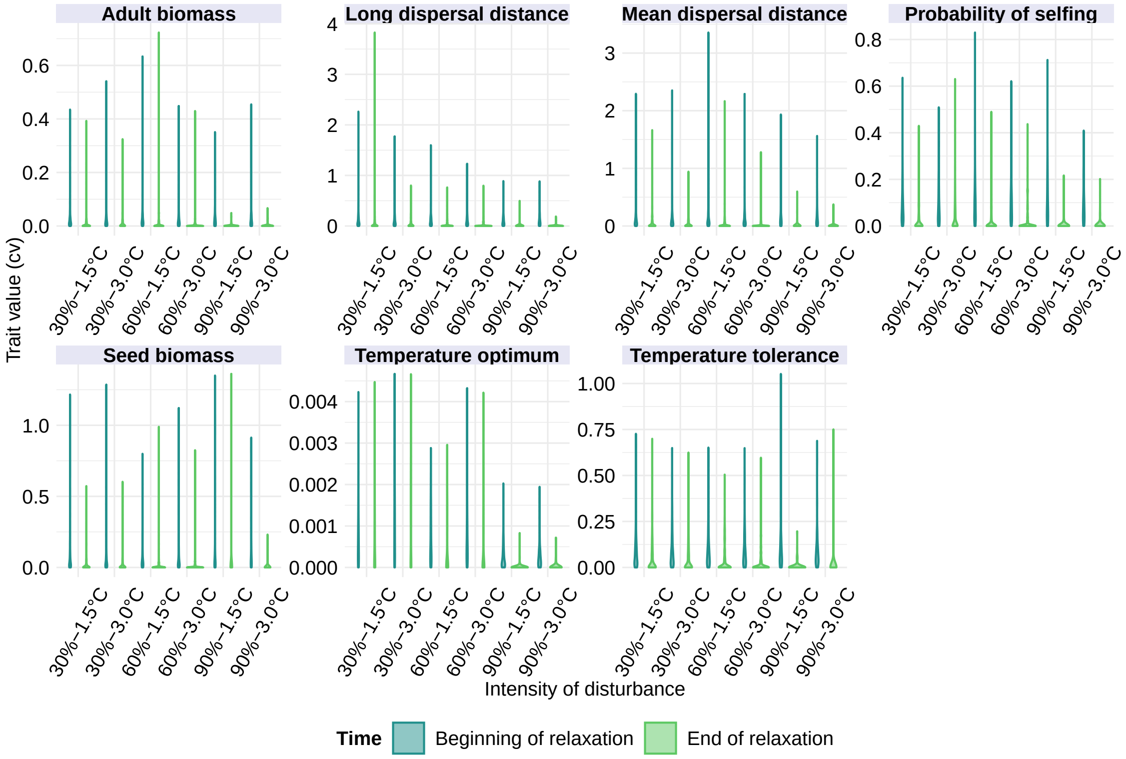

Figure 14: Distributions of the coefficent of variation of trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss and climate change, in the shallow temperature gradient.

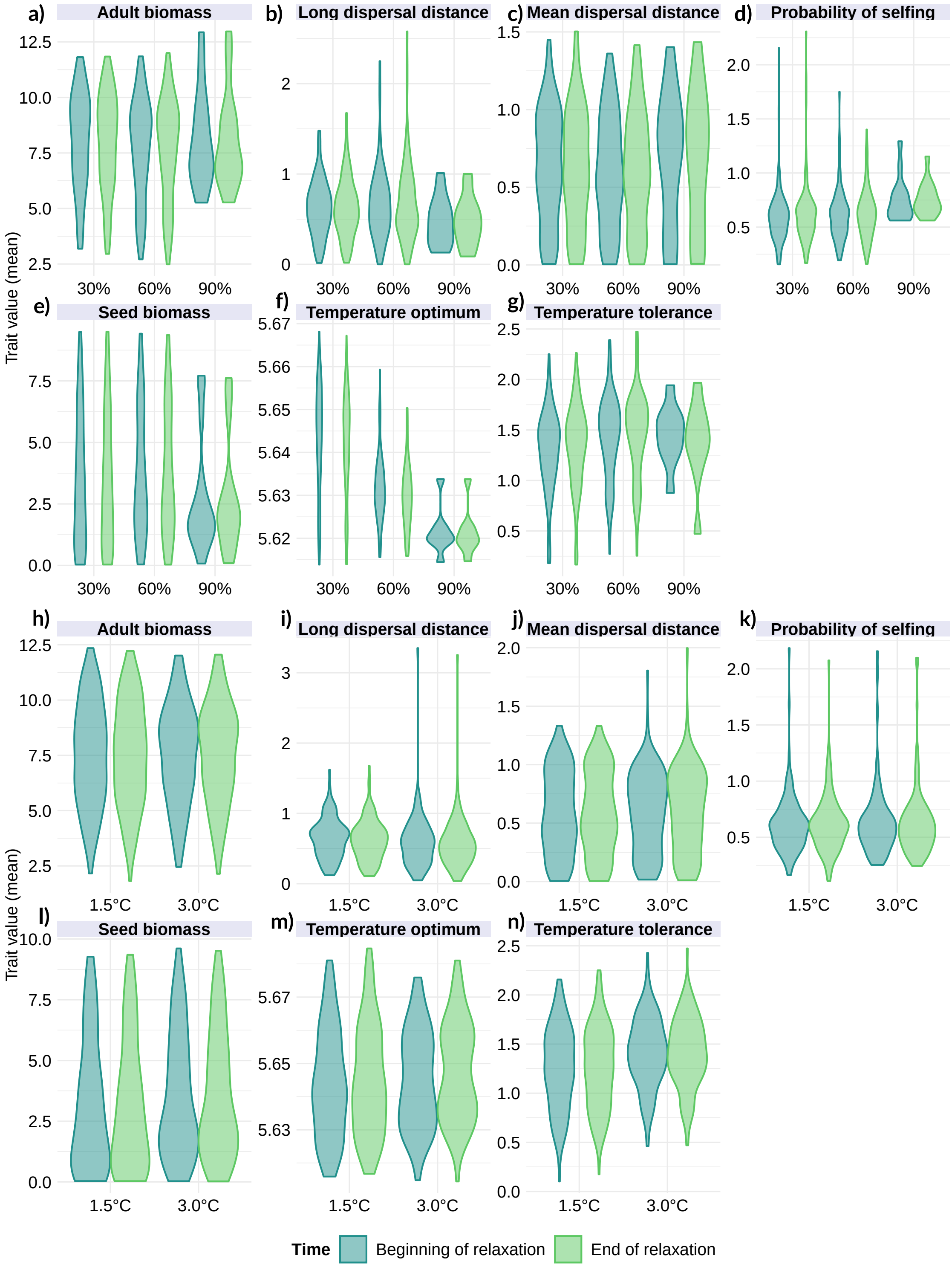

Figure 15: Distributions of mean trait values of species that went through evolutionary rescue, measured at the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss (a-h) and climate change (i-p), in the steep temperature gradient.

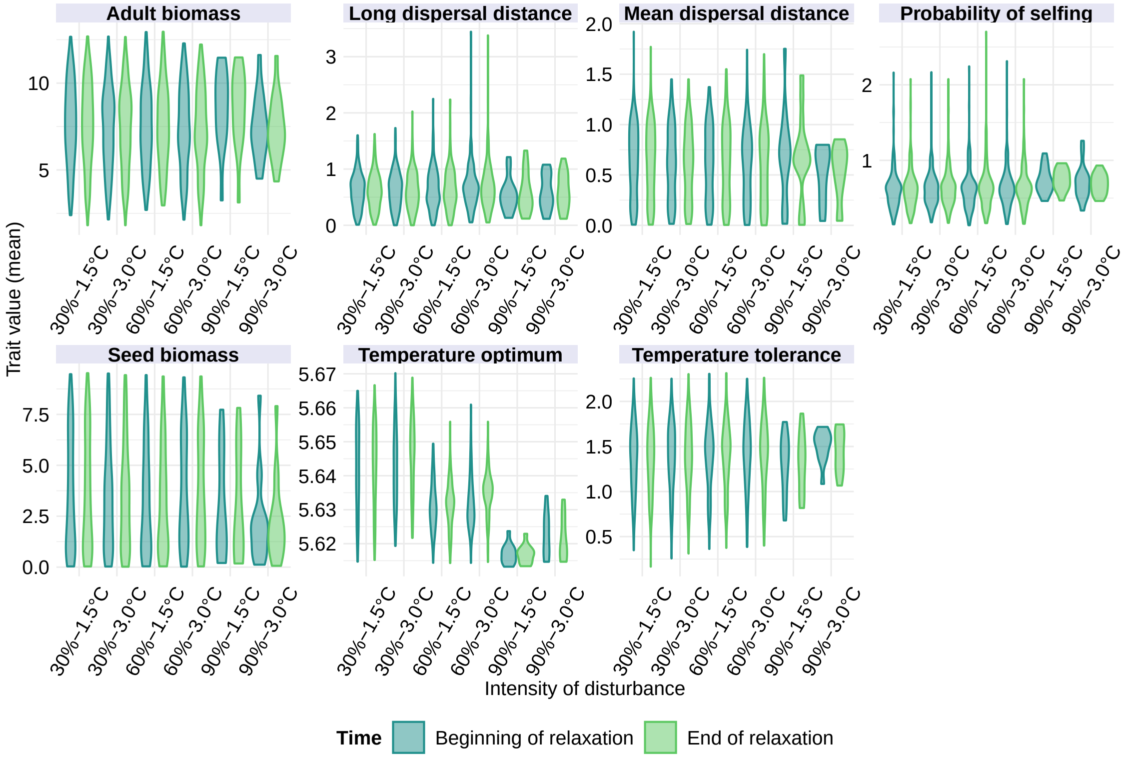

Figure 16: Distributions of mean trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss and climate change, in the steep temperature gradient.

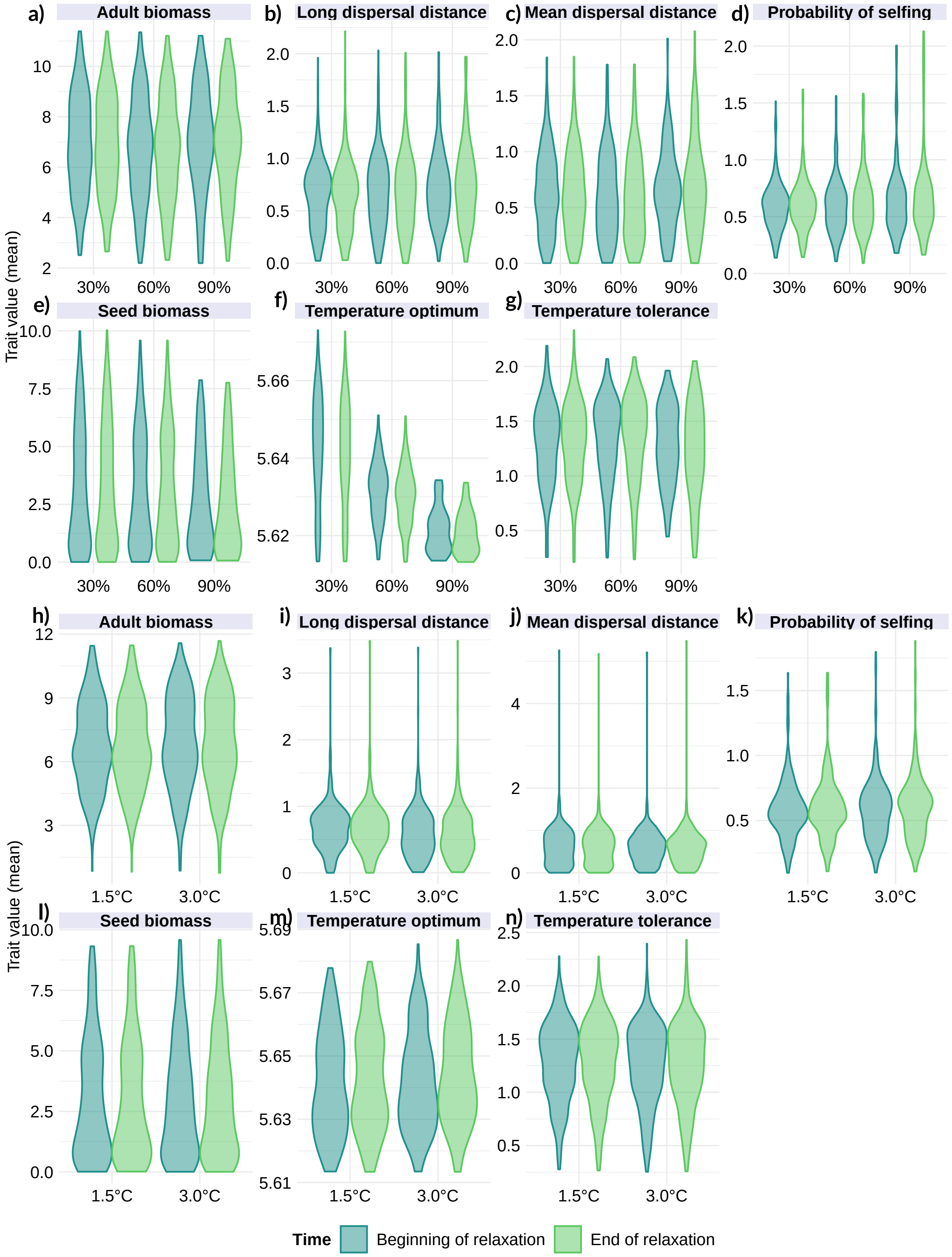

Figure 17: Distributions of mean trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss (a-h) and climate change (i-p), in the shallow temperature gradient.

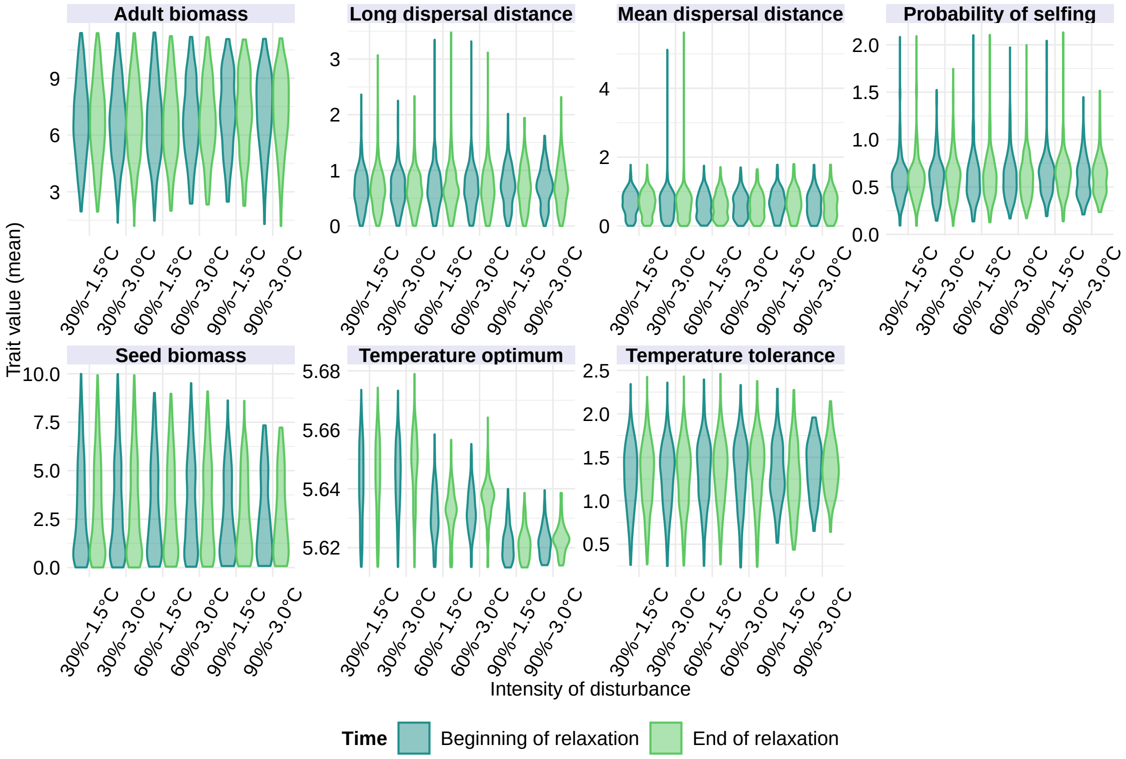

Figure 18: Distributions of mean trait values of species that went through evolutionary rescue, measured the beginning (t = 800) and at the end (t = 1800) of the relaxation time, in simulations of habitat loss and climate change, in the shallow temperature gradient.

Table 1: Mean absolute numbers and mean relative proportions (mean, sd) of species that went through demographic rescue, evolutionary change, evolutionary rescue, extinct immediately after disturbance ("Extinct (disturbance)"), extinct by the end of the relaxation time ("Extinct (relaxation)"), and species that did not exhibited a U-shaped abundance curve after disturbance, but survived nonetheless ("No rescue"), in the steep gradient.

Disturbance, Intensity	Response	Absolute (mean, sd)	Relative (mean, sd)
Climate change, 1.5°C	Demographic rescue	5.968, 2.401	0.128, 0.045
	Evolutionary change	18.032, 4.175	0.388, 0.072
	Evolutionary rescue	7.613, 2.604	0.163, 0.051
	Extinct (disturbance)	1.364, 0.581	0.029, 0.013
	Extinct (relaxation)	4.581, 2.335	0.095, 0.041
	No rescue	9.484, 2.908	0.205, 0.057
Climate change, 3.0°C	Demographic rescue	5.935, 2.38	0.121, 0.043
	Evolutionary change	17.71, 3.779	0.368, 0.068
	Evolutionary rescue	7.032, 2.811	0.146, 0.057
	Extinct (disturbance)	1.455, 0.671	0.031, 0.016
	Extinct (relaxation)	7.71, 2.661	0.159, 0.05
	No rescue	8.903, 3.208	0.184, 0.058
Habitat loss, 30%	Demographic rescue	6.903, 2.548	0.138, 0.05
	Evolutionary change	14.129, 4.153	0.279, 0.061
	Evolutionary rescue	7.968, 3.167	0.157, 0.057
	Extinct (disturbance)	11.581, 2.73	0.233, 0.054
	Extinct (relaxation)	2.345, 1.078	0.046, 0.021
	No rescue	7.516, 2.791	0.15, 0.053
Habitat loss, 60%	Demographic rescue	5.226, 2.202	0.078, 0.028
	Evolutionary change	9.774, 3.432	0.147, 0.041
	Evolutionary rescue	6.613, 2.974	0.102, 0.045
	Extinct (disturbance)	37.742, 5.586	0.579, 0.067
	Extinct (relaxation)	2.28, 1.487	0.036, 0.024
	No rescue	4.433, 1.775	0.068, 0.026
Habitat loss, 90%	Demographic rescue	2.867, 1.592	0.035, 0.02
	Evolutionary change	1.826, 1.497	0.022, 0.018
	Evolutionary rescue	1.643, 0.929	0.02, 0.011
	Extinct (disturbance)	73.194, 8.92	0.899, 0.027
	Extinct (relaxation)	2.414, 1.402	0.03, 0.017
	No rescue	1.571, 0.598	0.019, 0.007
Habitat loss and climate change, 30%-1.5°C	Demographic rescue	9.323, 2.6	0.185, 0.05
	Evolutionary change	10.065, 3.224	0.196, 0.052
	Evolutionary rescue	12.581, 3.888	0.246, 0.066
	Extinct (disturbance)	9.258, 2.683	0.181, 0.046
	Extinct (relaxation)	4.733, 2.164	0.093, 0.041
	No rescue	5.3, 2.037	0.104, 0.034
Habitat loss and climate change, 30%-3.0°C	Demographic rescue	9.452, 3.472	0.176, 0.06
	Evolutionary change	11.065, 3.183	0.208, 0.055
	Evolutionary rescue	12.355, 4.371	0.232, 0.07
	Extinct (disturbance)	8.355, 2.627	0.158, 0.05
	Extinct (relaxation)	7, 1.88	0.133, 0.036
	No rescue	5, 2.206	0.093, 0.038
Habitat loss and climate change, 60%-1.5°C	Demographic rescue	8.645, 2.893	0.134, 0.042
	Evolutionary change	6.742, 2.129	0.105, 0.028
	Evolutionary rescue	9.355, 3.592	0.147, 0.055
	Extinct (disturbance)	32.742, 5.978	0.511, 0.051
	Extinct (relaxation)	3.704, 1.75	0.058, 0.025
	No rescue	3.355, 1.644	0.053, 0.025
Habitat loss and climate change, 60%-3.0°C	Demographic rescue	9.71, 3.258	0.153, 0.049
	Evolutionary change	6.645, 2.074	0.104, 0.028
	Evolutionary rescue	8.161, 3.257	0.128, 0.046
	Extinct (disturbance)	30.29, 5.866	0.475, 0.054
	Extinct (relaxation)	5.774, 2.376	0.091, 0.036
	No rescue	3.097, 1.274	0.049, 0.02
Habitat loss and climate change, 90%-1.5°C	Demographic rescue	3.517, 1.975	0.044, 0.023
	Evolutionary change	1.733, 0.799	0.021, 0.01
	Evolutionary rescue	1.421, 0.769	0.018, 0.01
	Extinct (disturbance)	71.032, 9.3	0.893, 0.036
	Extinct (relaxation)	2.5, 1.175	0.032, 0.016

	No rescue	1.913, 0.9	0.024, 0.011
Habitat loss and climate change, 90%-3.0°C	Demographic rescue	3.414, 1.593	0.042, 0.02
	Evolutionary change	1.818, 0.958	0.023, 0.011
	Evolutionary rescue	1.45, 0.826	0.019, 0.011
	Extinct (disturbance)	70.484, 9.273	0.889, 0.03
	Extinct (relaxation)	2.548, 1.261	0.032, 0.015
	No rescue	1.667, 0.686	0.02, 0.007

Table 2: Mean absolute numbers and mean relative proportions (mean, sd) of species that went through demographic rescue, evolutionary change, evolutionary rescue, extinct immediately after disturbance ("Extinct (disturbance)"), extinct by the end of the relaxation time ("Extinct (relaxation)"), and species that did not exhibited a U-shaped abundance curve after disturbance, but survived nonetheless ("No rescue"), in the shallow gradient.

Disturbance, Intensity	Response	Absolute (mean, sd)	Relative (mean, sd)
Climate change, 1.5°C	Demographic rescue	7.355, 2.882	0.1, 0.035
	Evolutionary change	32.065, 4.604	0.441, 0.05
	Evolutionary rescue	15.226, 3.374	0.209, 0.04
	Extinct (disturbance)	1.467, 0.64	0.021, 0.009
	Extinct (relaxation)	4.097, 2.3	0.056, 0.029
	No rescue	13.355, 3.017	0.183, 0.036
Climate change, 3.0°C	Demographic rescue	6.968, 2.429	0.09, 0.027
	Evolutionary change	32.581, 5.488	0.423, 0.046
	Evolutionary rescue	16, 3.804	0.209, 0.049
	Extinct (disturbance)	1.647, 0.931	0.021, 0.012
	Extinct (relaxation)	8.419, 2.277	0.11, 0.028
	No rescue	12.065, 3.714	0.156, 0.044
Habitat loss, 30%	Demographic rescue	9.935, 3.473	0.121, 0.037
	Evolutionary change	26.355, 5.232	0.322, 0.049
	Evolutionary rescue	16.452, 4.972	0.199, 0.049
	Extinct (disturbance)	17.194, 2.88	0.212, 0.04
	Extinct (relaxation)	2.724, 1.73	0.034, 0.022
	No rescue	9.355, 2.665	0.115, 0.032
Habitat loss, 60%	Demographic rescue	7.161, 3.089	0.069, 0.03
	Evolutionary change	16.194, 4.564	0.156, 0.042
	Evolutionary rescue	14.774, 4.44	0.142, 0.04
	Extinct (disturbance)	56.548, 7.65	0.544, 0.045
	Extinct (relaxation)	3, 1.339	0.029, 0.013
	No rescue	6.29, 2.493	0.061, 0.023
Habitat loss, 90%	Demographic rescue	4.871, 2.078	0.038, 0.017
	Evolutionary change	5.774, 2.109	0.044, 0.016
	Evolutionary rescue	6.161, 2.368	0.048, 0.019
	Extinct (disturbance)	107.742, 11.593	0.827, 0.038
	Extinct (relaxation)	2.357, 1.339	0.018, 0.01
	No rescue	3.667, 1.398	0.028, 0.011
Habitat loss and climate change, 30%-1.5°C	Demographic rescue	13.516, 3.923	0.164, 0.045
	Evolutionary change	17.645, 4.355	0.216, 0.052
	Evolutionary rescue	26.484, 5.36	0.322, 0.053
	Extinct (disturbance)	14.968, 2.846	0.183, 0.032
	Extinct (relaxation)	3.806, 1.721	0.046, 0.02
	No rescue	5.581, 2.693	0.069, 0.035
	Demographic rescue	13.129, 4.153	0.151, 0.044
Habitat loss and climate change, 30%-3.0°C	Evolutionary change	18.613, 5.168	0.214, 0.051
	Evolutionary rescue	27.387, 5.766	0.315, 0.052
	Extinct (disturbance)	13.71, 2.866	0.16, 0.037
	Extinct (relaxation)	8.419, 2.363	0.098, 0.028
	No rescue	5.387, 2.679	0.062, 0.03
Habitat loss and climate change, 60%-1.5°C	Demographic rescue	13.129, 4.264	0.127, 0.038
	Evolutionary change	10.581, 2.986	0.103, 0.03
	Evolutionary rescue	21.806, 4.556	0.211, 0.037
	Extinct (disturbance)	49.935, 6.618	0.484, 0.044
	Extinct (relaxation)	3.7, 1.291	0.036, 0.012
	No rescue	4.097, 1.62	0.04, 0.017
Habitat loss and climate change, 60%-3.0°C	Demographic rescue	13.129, 4.801	0.123, 0.041
	Evolutionary change	11.065, 3.605	0.105, 0.034

	Evolutionary rescue	21.161, 4.212	0.2, 0.036
	Extinct (disturbance)	48.129, 7.228	0.454, 0.05
	Extinct (relaxation)	8.613, 2.667	0.082, 0.025
	No rescue	3.967, 1.712	0.038, 0.017
Habitat loss and climate change, 90%-1.5°C	Demographic rescue	8.161, 2.051	0.064, 0.017
	Evolutionary change	4.065, 1.692	0.032, 0.013
	Evolutionary rescue	8.387, 3.432	0.065, 0.026
	Extinct (disturbance)	102.419, 11.48	0.797, 0.041
	Extinct (relaxation)	2.586, 1.476	0.02, 0.012
	No rescue	3.172, 1.814	0.025, 0.014
Habitat loss and climate change, 90%-3.0°C	Demographic rescue	8.613, 3.413	0.068, 0.028
	Evolutionary change	3.677, 1.423	0.029, 0.011
	Evolutionary rescue	7.161, 2.325	0.056, 0.018
	Extinct (disturbance)	100.065, 11.39	0.778, 0.038
	Extinct (relaxation)	5.484, 2.731	0.043, 0.021
	No rescue	3.567, 1.223	0.028, 0.01

Table 3: Results of Herberich's tests applied to each disturbance scenario, to detect effects of disturbance intensity in species responses resulting from simulations in the steep gradient. Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1, ' ' 1.

Disturbance	Intensity	Estimate	Std.Error	t value	P(|t|)
Demographic rescue					
Climate change	3.0°C - 1.5°C	-0.0323	0.6172	-0.05	0.96
Habitat loss	60% - 30%	-1.677	0.615	-2.73	0.02 *
	90% - 30%	-4.037	0.551	-7.32	<1e-04 ***
	90% - 60%	-2.359	0.499	-4.73	<1e-04 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	0.129	0.792	0.16	1.00
	60%-1.5°C - 30%-1.5°C	-0.677	0.710	-0.95	0.93
	60%-3.0°C - 30%-1.5°C	0.387	0.761	0.51	1.00
	90%-1.5°C - 30%-1.5°C	-5.805	0.604	-9.61	<1e-04 ***
	90%-3.0°C - 30%-1.5°C	-5.909	0.562	-10.51	<1e-04 ***
	60%-1.5°C - 30%-3.0°C	-0.806	0.825	-0.98	0.92
	60%-3.0°C - 30%-3.0°C	0.258	0.869	0.30	1.00
	90%-1.5°C - 30%-3.0°C	-5.934	0.736	-8.07	<1e-04 ***
	90%-3.0°C - 30%-3.0°C	-6.038	0.702	-8.60	<1e-04 ***
	60%-3.0°C - 60%-1.5°C	1.065	0.795	1.34	0.75
	90%-1.5°C - 60%-1.5°C	-5.128	0.647	-7.93	<1e-04 ***
	90%-3.0°C - 60%-1.5°C	-5.231	0.608	-8.60	<1e-04 ***
	90%-1.5°C - 60%-3.0°C	-6.192	0.702	-8.82	<1e-04 ***
	90%-3.0°C - 60%-3.0°C	-6.296	0.667	-9.44	<1e-04 ***
	90%-3.0°C - 90%-1.5°C	-0.103	0.480	-0.22	1.00
Evolutionary change					
Climate change	3.0°C - 1.5°C	-0.323	1.028	-0.31	0.75
Habitat loss	60% - 30%	-4.355	0.984	-4.43	7.8e-05 ***
	90% - 30%	-12.303	0.823	-14.95	< 1e-05 ***
	90% - 60%	-7.948	0.703	-11.30	< 1e-05 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	1.0000	0.8271	1.21	0.82
	60%-1.5°C - 30%-1.5°C	-3.3226	0.7054	-4.71	<1e-04 ***
	60%-3.0°C - 30%-1.5°C	-3.4194	0.7000	-4.88	<1e-04 ***
	90%-1.5°C - 30%-1.5°C	-8.3312	0.6262	-13.30	<1e-04 ***
	90%-3.0°C - 30%-1.5°C	-8.2463	0.6247	-13.20	<1e-04 ***
	60%-1.5°C - 30%-3.0°C	-4.3226	0.6991	-6.18	<1e-04 ***
	60%-3.0°C - 30%-3.0°C	-4.4194	0.6936	-6.37	<1e-04 ***
	90%-1.5°C - 30%-3.0°C	-9.3312	0.6190	-15.07	<1e-04 ***
	90%-3.0°C - 30%-3.0°C	-9.2463	0.6175	-14.97	<1e-04 ***
	60%-3.0°C - 60%-1.5°C	-0.0968	0.5427	-0.18	1.00
	90%-1.5°C - 60%-1.5°C	-5.0086	0.4434	-11.30	<1e-04 ***
	90%-3.0°C - 60%-1.5°C	-4.9238	0.4413	-11.16	<1e-04 ***
	90%-1.5°C - 60%-3.0°C	-4.9118	0.4348	-11.30	<1e-04 ***
	90%-3.0°C - 60%-3.0°C	-4.8270	0.4326	-11.16	<1e-04 ***
	90%-3.0°C - 90%-1.5°C	0.0848	0.2988	0.28	1.00
Evolutionary rescue					
Climate change	3.0°C - 1.5°C	-0.581	0.699	-0.83	0.41
Habitat loss	60% - 30%	-1.355	0.793	-1.71	0.2
	90% - 30%	-6.325	0.633	-9.99	<1e-04 ***

	90% - 60%	-4.970	0.601	-8.27	<1e-04 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	-0.2258	1.0680	-0.21	1.000
	60%-1.5°C - 30%-1.5°C	-3.2258	0.9665	-3.34	0.011 *
	60%-3.0°C - 30%-1.5°C	-4.4194	0.9260	-4.77	<0.001 ***
	90%-1.5°C - 30%-1.5°C	-11.1596	0.7326	-15.23	<0.001 ***
	90%-3.0°C - 30%-1.5°C	-11.1306	0.7347	-15.15	<0.001 ***
	60%-1.5°C - 30%-3.0°C	-3.0000	1.0329	-2.90	0.040 *
	60%-3.0°C - 30%-3.0°C	-4.1935	0.9951	-4.21	<0.001 ***
	90%-1.5°C - 30%-3.0°C	-10.9338	0.8183	-13.36	<0.001 ***
	90%-3.0°C - 30%-3.0°C	-10.9048	0.8202	-13.30	<0.001 ***
	60%-3.0°C - 60%-1.5°C	-1.1935	0.8852	-1.35	0.726
	90%-1.5°C - 60%-1.5°C	-7.9338	0.6804	-11.66	<0.001 ***
	90%-3.0°C - 60%-1.5°C	-7.9048	0.6826	-11.58	<0.001 ***
	90%-1.5°C - 60%-3.0°C	-6.7402	0.6216	-10.84	<0.001 ***
	90%-3.0°C - 60%-3.0°C	-6.7113	0.6240	-10.75	<0.001 ***
	90%-3.0°C - 90%-1.5°C	0.0289	0.2621	0.11	1.000
Extinction (disturbance)					
Climate change	3.0°C - 1.5°C	0.0909	0.1937	0.47	0.64
Habitat loss	60% - 30%	26.16	1.14	23.1	<2e-16 ***
	90% - 30%	61.61	1.70	36.2	<2e-16 ***
	90% - 60%	35.45	1.92	18.4	<2e-16 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	-0.903	0.686	-1.32	0.75
	60%-1.5°C - 30%-1.5°C	23.484	1.196	19.63	<0.001 ***
	60%-3.0°C - 30%-1.5°C	21.032	1.178	17.86	<0.001 ***
	90%-1.5°C - 30%-1.5°C	61.774	1.767	34.95	<0.001 ***
	90%-3.0°C - 30%-1.5°C	61.226	1.762	34.74	<0.001 ***
	60%-1.5°C - 30%-3.0°C	24.387	1.192	20.46	<0.001 ***
	60%-3.0°C - 30%-3.0°C	21.935	1.174	18.69	<0.001 ***
	90%-1.5°C - 30%-3.0°C	62.677	1.764	35.52	<0.001 ***
	90%-3.0°C - 30%-3.0°C	62.129	1.760	35.31	<0.001 ***
	60%-3.0°C - 60%-1.5°C	-2.452	1.529	-1.60	0.57
	90%-1.5°C - 60%-1.5°C	38.290	2.018	18.97	<0.001 ***
	90%-3.0°C - 60%-1.5°C	37.742	2.014	18.74	<0.001 ***
	90%-1.5°C - 60%-3.0°C	40.742	2.008	20.29	<0.001 ***
	90%-3.0°C - 60%-3.0°C	40.194	2.003	20.06	<0.001 ***
	90%-3.0°C - 90%-1.5°C	-0.548	2.398	-0.23	1.00
Extinction (relaxation)					
Climate change	3.0°C - 1.5°C	3.129	0.646	4.84	9.4e-06 ***
Habitat loss	60% - 30%	-0.0648	0.3655	-0.18	0.98
	90% - 30%	0.0690	0.3342	0.21	0.98
	90% - 60%	0.1338	0.4028	0.33	0.94
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	2.2667	0.5285	4.29	<0.001 ***
	60%-1.5°C - 30%-1.5°C	-1.0296	0.5285	-1.95	0.3675
	60%-3.0°C - 30%-1.5°C	1.0409	0.5914	1.76	0.4846
	90%-1.5°C - 30%-1.5°C	-2.2333	0.4656	-4.80	<0.001 ***
	90%-3.0°C - 30%-1.5°C	-2.1849	0.4632	-4.72	<0.001 ***
	60%-1.5°C - 30%-3.0°C	-3.2963	0.4854	-6.79	<0.001 ***
	60%-3.0°C - 30%-3.0°C	-1.2258	0.5532	-2.22	0.2284
	90%-1.5°C - 30%-3.0°C	-4.5000	0.4159	-10.82	<0.001 ***
	90%-3.0°C - 30%-3.0°C	-4.4516	0.4132	-10.77	<0.001 ***
	60%-3.0°C - 60%-1.5°C	2.0705	0.5532	3.74	0.0032 **
	90%-1.5°C - 60%-1.5°C	-1.2037	0.4159	-2.89	0.0465 *
	90%-3.0°C - 60%-1.5°C	-1.1553	0.4132	-2.80	0.0603 .
	90%-1.5°C - 60%-3.0°C	-3.2742	0.4934	-6.64	<0.001 ***
	90%-3.0°C - 60%-3.0°C	-3.2258	0.4911	-6.57	<0.001 ***
	90%-3.0°C - 90%-1.5°C	0.0484	0.3289	0.15	1.0000
Survival (no rescue)					
Climate change	3.0°C - 1.5°C	-0.581	0.791	-0.73	0.47
Habitat loss	60% - 30%	-3.083	0.607	-5.08	<1e-05 ***
	90% - 30%	-5.945	0.527	-11.28	<1e-05 ***
	90% - 60%	-2.862	0.356	-8.05	<1e-05 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	-0.300	0.553	-0.54	0.99378
	60%-1.5°C - 30%-1.5°C	-1.945	0.483	-4.03	0.00113 **
	60%-3.0°C - 30%-1.5°C	-2.203	0.444	-4.96	< 1e-04 ***
	90%-1.5°C - 30%-1.5°C	-3.387	0.424	-7.99	< 1e-04 ***
	90%-3.0°C - 30%-1.5°C	-3.633	0.413	-8.79	< 1e-04 ***
	60%-1.5°C - 30%-3.0°C	-1.645	0.502	-3.28	0.01489 *

	60%-3.0°C - 30%-3.0°C	-1.903	0.465	-4.09	0.00086 ***
	90%-1.5°C - 30%-3.0°C	-3.087	0.446	-6.92	< 1e-04 ***
	90%-3.0°C - 30%-3.0°C	-3.333	0.436	-7.65	< 1e-04 ***
	60%-3.0°C - 60%-1.5°C	-0.258	0.380	-0.68	0.98268
	90%-1.5°C - 60%-1.5°C	-1.442	0.356	-4.05	0.00104 **
	90%-3.0°C - 60%-1.5°C	-1.688	0.343	-4.92	< 1e-04 ***
	90%-1.5°C - 60%-3.0°C	-1.184	0.302	-3.93	0.00162 **
	90%-3.0°C - 60%-3.0°C	-1.430	0.286	-5.00	< 1e-04 ***
	90%-3.0°C - 90%-1.5°C	-0.246	0.254	-0.97	0.92165

Table 4: Results of Herberich's tests applied to each disturbance scenario, to detect effects of disturbance intensity in species responses resulting from simulations in the shallow gradient. Significance codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1, ' ' 1.

Disturbance	Intensity	Estimate	Std.Error	t value	P(|t|)
		Demographic rescue			
Climate change	3.0°C - 1.5°C	-0.387	0.688	-0.56	0.58
Habitat loss	60% - 30%	-2.774	0.849	-3.27	0.0044 **
	90% - 30%	-5.065	0.739	-6.85	<1e-04 ***
	90% - 60%	-2.290	0.680	-3.37	0.0031 **
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	-3.87e-01	1.04e+00	-0.37	0.99901
	60%-1.5°C - 30%-1.5°C	-3.87e-01	1.06e+00	-0.37	0.99907
	60%-3.0°C - 30%-1.5°C	-3.87e-01	1.13e+00	-0.34	0.99933
	90%-1.5°C - 30%-1.5°C	-5.35e+00	8.08e-01	-6.63	< 1e-04 ***
	90%-3.0°C - 30%-1.5°C	-4.90e+00	9.49e-01	-5.16	< 1e-04 ***
	60%-1.5°C - 30%-3.0°C	-7.22e-16	1.09e+00	0.00	1.00000
	60%-3.0°C - 30%-3.0°C	-1.05e-15	1.16e+00	0.00	1.00000
	90%-1.5°C - 30%-3.0°C	-4.97e+00	8.46e-01	-5.87	< 1e-04 ***
	90%-3.0°C - 30%-3.0°C	-4.52e+00	9.81e-01	-4.60	0.00011 ***
	60%-3.0°C - 60%-1.5°C	-3.33e-16	1.17e+00	0.00	1.00000
	90%-1.5°C - 60%-1.5°C	-4.97e+00	8.64e-01	-5.75	< 1e-04 ***
	90%-3.0°C - 60%-1.5°C	-4.52e+00	9.97e-01	-4.53	0.00015 ***
	90%-1.5°C - 60%-3.0°C	-4.97e+00	9.53e-01	-5.21	< 1e-04 ***
	90%-3.0°C - 60%-3.0°C	-4.52e+00	1.08e+00	-4.20	0.00060 ***
	90%-3.0°C - 90%-1.5°C	4.52e-01	7.27e-01	0.62	0.98869
		Evolutionary change			
Climate change	3.0°C - 1.5°C	0.516	1.308	0.39	0.69
Habitat loss	60% - 30%	-10.161	1.268	-8.02	<1e-10 ***
	90% - 30%	-20.581	1.030	-19.98	<1e-10 ***
	90% - 60%	-10.419	0.918	-11.35	<1e-10 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	0.968	1.234	0.78	0.97
	60%-1.5°C - 30%-1.5°C	-7.065	0.964	-7.33	<1e-04 ***
	60%-3.0°C - 30%-1.5°C	-6.581	1.032	-6.38	<1e-04 ***
	90%-1.5°C - 30%-1.5°C	-13.581	0.853	-15.92	<1e-04 ***
	90%-3.0°C - 30%-1.5°C	-13.968	0.837	-16.70	<1e-04 ***
	60%-1.5°C - 30%-3.0°C	-8.032	1.090	-7.37	<1e-04 ***
	60%-3.0°C - 30%-3.0°C	-7.548	1.150	-6.56	<1e-04 ***
	90%-1.5°C - 30%-3.0°C	-14.548	0.993	-14.65	<1e-04 ***
	90%-3.0°C - 30%-3.0°C	-14.935	0.979	-15.26	<1e-04 ***
	60%-3.0°C - 60%-1.5°C	0.484	0.855	0.57	0.99
	90%-1.5°C - 60%-1.5°C	-6.516	0.627	-10.40	<1e-04 ***
	90%-3.0°C - 60%-1.5°C	-6.903	0.604	-11.43	<1e-04 ***
	90%-1.5°C - 60%-3.0°C	-7.000	0.727	-9.63	<1e-04 ***
	90%-3.0°C - 60%-3.0°C	-7.387	0.708	-10.44	<1e-04 ***
	90%-3.0°C - 90%-1.5°C	-0.387	0.404	-0.96	0.92
		Evolutionary rescue			
Climate change	3.0°C - 1.5°C	0.774	0.928	0.83	0.41
Habitat loss	60% - 30%	-1.677	1.217	-1.38	0.35
	90% - 30%	-10.290	1.005	-10.23	<1e-04 ***
	90% - 60%	-8.613	0.919	-9.38	<1e-04 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	0.903	1.437	0.63	0.98796
	60%-1.5°C - 30%-1.5°C	-4.677	1.284	-3.64	0.00449 **
	60%-3.0°C - 30%-1.5°C	-5.323	1.245	-4.28	0.00039 ***
	90%-1.5°C - 30%-1.5°C	-18.097	1.162	-15.57	< 1e-04 ***
	90%-3.0°C - 30%-1.5°C	-19.323	1.067	-18.12	< 1e-04 ***
	60%-1.5°C - 30%-3.0°C	-5.581	1.342	-4.16	0.00067 ***

	60%-3.0°C - 30%-3.0°C	-6.226	1.304	-4.78	< 1e-04 ***
	90%-1.5°C - 30%-3.0°C	-19.000	1.225	-15.51	< 1e-04 ***
	90%-3.0°C - 30%-3.0°C	-20.226	1.135	-17.82	< 1e-04 ***
	60%-3.0°C - 60%-1.5°C	-0.645	1.133	-0.57	0.99234
	90%-1.5°C - 60%-1.5°C	-13.419	1.041	-12.89	< 1e-04 ***
	90%-3.0°C - 60%-1.5°C	-14.645	0.934	-15.68	< 1e-04 ***
	90%-1.5°C - 60%-3.0°C	-12.774	0.992	-12.88	< 1e-04 ***
	90%-3.0°C - 60%-3.0°C	-14.000	0.878	-15.94	< 1e-04 ***
	90%-3.0°C - 90%-1.5°C	-1.226	0.757	-1.62	0.57295
Extinction (disturbance)					
Climate change	3.0°C - 1.5°C	0.180	0.289	0.62	0.54
Habitat loss	60% - 30%	39.35	1.49	26.4	<2e-16 ***
	90% - 30%	90.55	2.18	41.5	<2e-16 ***
	90% - 60%	51.19	2.54	20.2	<2e-16 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	-1.258	0.737	-1.71	0.49
	60%-1.5°C - 30%-1.5°C	34.968	1.315	26.59	<0.001 ***
	60%-3.0°C - 30%-1.5°C	33.161	1.418	23.38	<0.001 ***
	90%-1.5°C - 30%-1.5°C	87.452	2.159	40.50	<0.001 ***
	90%-3.0°C - 30%-1.5°C	85.097	2.143	39.70	<0.001 ***
	60%-1.5°C - 30%-3.0°C	36.226	1.317	27.51	<0.001 ***
	60%-3.0°C - 30%-3.0°C	34.419	1.420	24.24	<0.001 ***
	90%-1.5°C - 30%-3.0°C	88.710	2.160	41.06	<0.001 ***
	90%-3.0°C - 30%-3.0°C	86.355	2.144	40.27	<0.001 ***
	60%-3.0°C - 60%-1.5°C	-1.806	1.789	-1.01	0.90
	90%-1.5°C - 60%-1.5°C	52.484	2.419	21.69	<0.01 ***
	90%-3.0°C - 60%-1.5°C	50.129	2.405	20.84	<0.001 ***
	90%-1.5°C - 60%-3.0°C	54.290	2.477	21.92	<0.001 ***
	90%-3.0°C - 60%-3.0°C	51.935	2.463	21.09	<0.001 ***
	90%-3.0°C - 90%-1.5°C	-2.355	2.952	-0.80	0.96
Extinction (relaxation)					
Climate change	3.0°C - 1.5°C	4.323	0.591	7.32	7.2e-10
Habitat loss	60% - 30%	0.276	0.411	0.67	0.78
	90% - 30%	-0.367	0.416	-0.88	0.65
	90% - 60%	-0.643	0.358	-1.79	0.18
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	4.613	0.534	8.64	<0.001 ***
	60%-1.5°C - 30%-1.5°C	-0.106	0.395	-0.27	1.000
	60%-3.0°C - 30%-1.5°C	4.806	0.579	8.29	<0.001 ***
	90%-1.5°C - 30%-1.5°C	-1.220	0.420	-2.90	0.044 *
	90%-3.0°C - 30%-1.5°C	1.677	0.589	2.85	0.052 .
	60%-1.5°C - 30%-3.0°C	-4.719	0.494	-9.56	<0.001 ***
	60%-3.0°C - 30%-3.0°C	0.194	0.651	0.30	1.000
	90%-1.5°C - 30%-3.0°C	-5.833	0.514	-11.35	<0.001 ***
	90%-3.0°C - 30%-3.0°C	-2.935	0.659	-4.45	<0.001 ***
	60%-3.0°C - 60%-1.5°C	4.913	0.543	9.05	<0.001 ***
	90%-1.5°C - 60%-1.5°C	-1.114	0.368	-3.03	0.031 *
	90%-3.0°C - 60%-1.5°C	1.784	0.553	3.22	0.017 *
	90%-1.5°C - 60%-3.0°C	-6.027	0.561	-10.74	<0.001 ***
	90%-3.0°C - 60%-3.0°C	-3.129	0.697	-4.49	<0.001 ***
	90%-3.0°C - 90%-1.5°C	2.898	0.571	5.07	<0.001 ***
Survival (no rescue)					
Climate change	3.0°C - 1.5°C	-1.290	0.874	-1.48	0.14
Habitat loss	60% - 30%	-3.065	0.666	-4.60	3.9e-05 ***
	90% - 30%	-5.688	0.552	-10.31	< 1e-05 ***
	90% - 60%	-2.624	0.524	-5.01	< 1e-05 ***
Habitat loss and climate change	30%-3.0°C - 30%-1.5°C	-0.194	0.694	-0.28	0.9998
	60%-1.5°C - 30%-1.5°C	-1.484	0.574	-2.59	0.1011
	60%-3.0°C - 30%-1.5°C	-1.614	0.585	-2.76	0.0659 .
	90%-1.5°C - 30%-1.5°C	-2.408	0.599	-4.02	0.0011 **
	90%-3.0°C - 30%-1.5°C	-2.014	0.542	-3.72	0.0034 **
	60%-1.5°C - 30%-3.0°C	-1.290	0.572	-2.26	0.2089
	60%-3.0°C - 30%-3.0°C	-1.420	0.583	-2.43	0.1433
	90%-1.5°C - 30%-3.0°C	-2.215	0.597	-3.71	0.0036 **
	90%-3.0°C - 30%-3.0°C	-1.820	0.539	-3.38	0.0109 *
	60%-3.0°C - 60%-1.5°C	-0.130	0.434	-0.30	0.9997
	90%-1.5°C - 60%-1.5°C	-0.924	0.453	-2.04	0.3123
	90%-3.0°C - 60%-1.5°C	-0.530	0.373	-1.42	0.7037
	90%-1.5°C - 60%-3.0°C	-0.794	0.467	-1.70	0.5222

	90%-3.0°C - 60%-3.0°C	-0.400	0.391	-1.02	0.9050
	90%-3.0°C - 90%-1.5°C	0.394	0.411	0.96	0.9266

Table 5: Results of mixed effects model fits for trait values before disturbance, with response to disturbance (evolutionary rescue or extinction after relaxation time) as fixed effect and replicate as a random effect, for each scenario of disturbance (disturbance type and intensity) in the steep gradient. "Evolutionary rescue" was the reference value in the models.

Disturbance, Intensity	Trait	Estimate	Std.Error	DF	t value	p value
Climate change, 1.5°C	Mean dispersal distance	0.000	0.038	346	0.000	1.000
	Long dispersal distance	0.024	0.038	346	0.631	0.528
	Linkage degree	0.000	0.071	346	-0.006	0.995
	Adult biomass	0.159	0.263	346	0.605	0.546
	Seed biomass	-0.293	0.277	346	-1.057	0.291
	Probability of selfing	-0.130	0.029	346	-4.552	0.000
	Temperature optimum	-0.006	0.002	346	-2.912	0.004
	Temperature tolerance	-0.304	0.049	346	-6.231	0.000
Climate change, 3.0°C	Mean dispersal distance	0.065	0.033	425	1.929	0.054
	Long dispersal distance	0.059	0.034	425	1.732	0.084
	Linkage degree	0.047	0.073	425	0.645	0.519
	Adult biomass	-0.041	0.233	425	-0.176	0.860
	Seed biomass	-0.824	0.236	425	-3.490	0.001
	Probability of selfing	-0.122	0.026	425	-4.718	0.000
	Temperature optimum	-0.015	0.002	425	-10.069	0.000
	Temperature tolerance	-0.336	0.038	425	-8.764	0.000
Habitat loss, 30%	Mean dispersal distance	0.029	0.050	283	0.583	0.561
	Long dispersal distance	-0.013	0.048	283	-0.276	0.783
	Linkage degree	0.085	0.097	283	0.871	0.385
	Adult biomass	-0.363	0.320	283	-1.136	0.257
	Seed biomass	-0.653	0.353	283	-1.851	0.065
	Probability of selfing	-0.156	0.039	283	-3.990	0.000
	Temperature optimum	0.006	0.002	283	3.273	0.001
	Temperature tolerance	-0.146	0.057	283	-2.553	0.011
Habitat loss, 60%	Mean dispersal distance	0.023	0.051	230	0.453	0.651
	Long dispersal distance	-0.035	0.053	230	-0.659	0.510
	Linkage degree	-0.031	0.107	230	-0.292	0.771
	Adult biomass	0.996	0.346	230	2.879	0.004
	Seed biomass	0.475	0.396	230	1.199	0.232
	Probability of selfing	-0.073	0.037	230	-1.992	0.048
	Temperature optimum	0.006	0.001	230	4.065	0.000
	Temperature tolerance	-0.035	0.061	230	-0.578	0.564
Habitat loss, 90%	Mean dispersal distance	0.018	0.081	63	0.216	0.830
	Long dispersal distance	0.091	0.100	63	0.917	0.363
	Linkage degree	0.079	0.186	63	0.427	0.671
	Adult biomass	-1.029	0.561	63	-1.833	0.072
	Seed biomass	0.055	0.485	63	0.113	0.911
	Probability of selfing	-0.164	0.065	63	-2.519	0.014
	Temperature optimum	0.002	0.002	63	1.515	0.135
	Temperature tolerance	0.007	0.106	63	0.064	0.949
Habitat loss and climate change, 30%-1.5°C	Mean dispersal distance	-0.027	0.035	500	-0.771	0.441
	Long dispersal distance	-0.062	0.033	500	-1.902	0.058
	Linkage degree	0.206	0.073	500	2.825	0.005
	Adult biomass	-0.315	0.241	500	-1.305	0.192
	Seed biomass	-1.069	0.258	500	-4.147	0.000
	Probability of selfing	-0.100	0.025	500	-4.005	0.000
	Temperature optimum	-0.011	0.001	500	-8.090	0.000
	Temperature tolerance	-0.468	0.039	500	-11.942	0.000
Habitat loss and climate change, 30%-3.0°C	Mean dispersal distance	0.019	0.031	568	0.605	0.545
	Long dispersal distance	0.053	0.029	568	1.799	0.073
	Linkage degree	0.081	0.065	568	1.244	0.214
	Adult biomass	0.046	0.208	568	0.220	0.826
	Seed biomass	-0.570	0.216	568	-2.643	0.008
	Probability of selfing	-0.087	0.021	568	-4.104	0.000
	Temperature optimum	-0.018	0.001	568	-17.309	0.000
	Temperature tolerance	-0.282	0.035	568	-8.045	0.000

Habitat loss and climate change, 60%-1.5°C	Mean dispersal distance	-0.063	0.042	358	-1.487	0.138
	Long dispersal distance	-0.004	0.040	358	-0.103	0.918
	Linkage degree	0.064	0.081	358	0.797	0.426
	Adult biomass	-0.285	0.277	358	-1.030	0.304
	Seed biomass	-0.806	0.280	358	-2.877	0.004
	Probability of selfing	-0.145	0.033	358	-4.380	0.000
	Temperature optimum	-0.010	0.001	358	-10.057	0.000
	Temperature tolerance	-0.420	0.046	358	-9.240	0.000
Habitat loss and climate change, 60%-3.0°C	Mean dispersal distance	-0.002	0.033	400	-0.074	0.941
	Long dispersal distance	-0.038	0.036	400	-1.068	0.286
	Linkage degree	-0.022	0.065	400	-0.346	0.730
	Adult biomass	0.394	0.244	400	1.612	0.108
	Seed biomass	-0.510	0.250	400	-2.036	0.042
	Probability of selfing	-0.157	0.026	400	-6.047	0.000
	Temperature optimum	-0.014	0.001	400	-19.152	0.000
	Temperature tolerance	-0.325	0.037	400	-8.819	0.000
Habitat loss and climate change, 90%-1.5°C	Mean dispersal distance	-0.064	0.089	64	-0.720	0.474
	Long dispersal distance	0.180	0.103	64	1.756	0.084
	Linkage degree	-0.107	0.192	64	-0.560	0.578
	Adult biomass	-2.032	0.552	64	-3.683	0.000
	Seed biomass	-0.558	0.489	64	-1.143	0.257
	Probability of selfing	-0.151	0.061	64	-2.474	0.016
	Temperature optimum	0.002	0.001	64	1.608	0.113
	Temperature tolerance	-0.039	0.104	64	-0.375	0.709
Habitat loss and climate change, 90%-3.0°C	Mean dispersal distance	0.030	0.072	76	0.410	0.683
	Long dispersal distance	0.073	0.081	76	0.897	0.373
	Linkage degree	0.038	0.172	76	0.224	0.824
	Adult biomass	-1.329	0.433	76	-3.067	0.003
	Seed biomass	-0.240	0.411	76	-0.583	0.561
	Probability of selfing	-0.111	0.056	76	-1.963	0.053
	Temperature optimum	-0.001	0.001	76	-0.752	0.455
	Temperature tolerance	-0.176	0.097	76	-1.820	0.073

Table 6: Results of mixed effects model fits for trait values (transformed as (log x +1)) before disturbance, with response to disturbance (evolutionary rescue or extinction after relaxation time) as fixed effect and replicate as a random effect, for each scenario of disturbance (disturbance type and intensity) in the shallow gradient."Evolutionary rescue" was the reference value in the models.

Disturbance, Intensity	Trait	Estimate	Std.Error	DF	t value	p value
Climate change, 1.5°C	Mean dispersal distance	0.015	0.043	567	0.348	0.728
	Long dispersal distance	-0.009	0.035	567	-0.253	0.800
	Linkage degree	0.224	0.066	567	3.405	0.001
	Adult biomass	1.179	0.217	567	5.442	0.000
	Seed biomass	0.174	0.241	567	0.722	0.471
	Probability of selfing	-0.127	0.026	567	-4.853	0.000
	Temperature optimum	-0.008	0.002	567	-4.824	0.000
	Temperature tolerance	-0.293	0.042	567	-7.013	0.000
Climate change, 3.0°C	Mean dispersal distance	0.050	0.031	725	1.633	0.103
	Long dispersal distance	0.050	0.029	725	1.712	0.087
	Linkage degree	0.012	0.053	725	0.227	0.820
	Adult biomass	0.503	0.178	725	2.824	0.005
	Seed biomass	0.122	0.189	725	0.647	0.518
	Probability of selfing	-0.093	0.021	725	-4.533	0.000
	Temperature optimum	-0.017	0.001	725	-14.056	0.000
	Temperature tolerance	-0.174	0.032	725	-5.537	0.000
Habitat loss, 30%	Mean dispersal distance	0.006	0.044	557	0.137	0.891
	Long dispersal distance	0.008	0.041	557	0.203	0.839
	Linkage degree	0.135	0.078	557	1.731	0.084
	Adult biomass	1.755	0.247	557	7.108	0.000
	Seed biomass	0.536	0.303	557	1.766	0.078
	Probability of selfing	-0.092	0.029	557	-3.117	0.002
	Temperature optimum	0.005	0.002	557	2.649	0.008
	Temperature tolerance	-0.032	0.048	557	-0.658	0.511
Habitat loss, 60%	Mean dispersal distance	0.136	0.043	516	3.164	0.002
	Long dispersal distance	0.092	0.040	516	2.291	0.022

	Linkage degree	0.029	0.066	516	0.434	0.665
	Adult biomass	1.426	0.237	516	6.009	0.000
	Seed biomass	0.586	0.277	516	2.115	0.035
	Probability of selfing	-0.056	0.030	516	-1.894	0.059
	Temperature optimum	0.008	0.001	516	7.759	0.000
	Temperature tolerance	0.018	0.045	516	0.387	0.699
Habitat loss, 90%	Mean dispersal distance	0.043	0.055	225	0.782	0.435
	Long dispersal distance	-0.015	0.051	225	-0.287	0.774
	Linkage degree	0.013	0.090	225	0.149	0.882
	Adult biomass	0.178	0.311	225	0.572	0.568
	Seed biomass	0.753	0.312	225	2.409	0.017
	Probability of selfing	-0.099	0.041	225	-2.434	0.016
	Temperature optimum	0.006	0.001	225	6.653	0.000
	Temperature tolerance	0.216	0.055	225	3.910	0.000
Habitat loss and climate change, 30%-1.5°C	Mean dispersal distance	-0.031	0.036	907	-0.857	0.392
	Long dispersal distance	0.048	0.035	907	1.388	0.166
	Linkage degree	-0.034	0.065	907	-0.517	0.605
	Adult biomass	1.080	0.215	907	5.019	0.000
	Seed biomass	0.441	0.237	907	1.858	0.064
	Probability of selfing	-0.143	0.024	907	-5.859	0.000
	Temperature optimum	-0.016	0.001	907	-11.317	0.000
	Temperature tolerance	-0.250	0.039	907	-6.414	0.000
Habitat loss and climate change, 30%-3.0°C	Mean dispersal distance	0.028	0.028	1078	1.016	0.310
	Long dispersal distance	0.042	0.025	1078	1.702	0.089
	Linkage degree	0.067	0.050	1078	1.360	0.174
	Adult biomass	0.736	0.156	1078	4.728	0.000
	Seed biomass	0.119	0.173	1078	0.688	0.492
	Probability of selfing	-0.135	0.018	1078	-7.367	0.000
	Temperature optimum	-0.024	0.001	1078	-27.127	0.000
	Temperature tolerance	-0.202	0.028	1078	-7.123	0.000
Habitat loss and climate change, 60%-1.5°C	Mean dispersal distance	0.041	0.039	755	1.061	0.289
	Long dispersal distance	-0.001	0.038	755	-0.015	0.988
	Linkage degree	0.184	0.066	755	2.782	0.006
	Adult biomass	1.088	0.221	755	4.918	0.000
	Seed biomass	-0.032	0.238	755	-0.135	0.893
	Probability of selfing	-0.141	0.028	755	-5.110	0.000
	Temperature optimum	-0.011	0.001	755	-10.871	0.000
	Temperature tolerance	-0.234	0.041	755	-5.685	0.000
Habitat loss and climate change, 60%-3.0°C	Mean dispersal distance	0.063	0.027	891	2.379	0.018
	Long dispersal distance	0.024	0.027	891	0.923	0.356
	Linkage degree	0.081	0.047	891	1.732	0.084
	Adult biomass	0.876	0.156	891	5.609	0.000
	Seed biomass	-0.065	0.172	891	-0.376	0.707
	Probability of selfing	-0.103	0.018	891	-5.605	0.000
	Temperature optimum	-0.015	0.001	891	-25.672	0.000
	Temperature tolerance	-0.233	0.029	891	-8.050	0.000
Habitat loss and climate change, 90%-1.5°C	Mean dispersal distance	-0.019	0.049	303	-0.389	0.697
	Long dispersal distance	-0.061	0.049	303	-1.242	0.215
	Linkage degree	0.214	0.082	303	2.615	0.009
	Adult biomass	-0.580	0.294	303	-1.975	0.049
	Seed biomass	0.143	0.274	303	0.520	0.604
	Probability of selfing	-0.208	0.035	303	-5.910	0.000
	Temperature optimum	-0.003	0.001	303	-4.356	0.000
	Temperature tolerance	-0.248	0.054	303	-4.591	0.000
Habitat loss and climate change, 90%-3.0°C	Mean dispersal distance	-0.026	0.040	360	-0.666	0.506
	Long dispersal distance	-0.036	0.039	360	-0.920	0.358
	Linkage degree	0.085	0.074	360	1.143	0.254
	Adult biomass	-0.398	0.232	360	-1.714	0.087
	Seed biomass	-0.704	0.215	360	-3.268	0.001
	Probability of selfing	-0.113	0.033	360	-3.458	0.001
	Temperature optimum	-0.006	0.001	360	-10.529	0.000
	Temperature tolerance	-0.492	0.038	360	-13.061	0.000

Appendix 3

Supplementary material

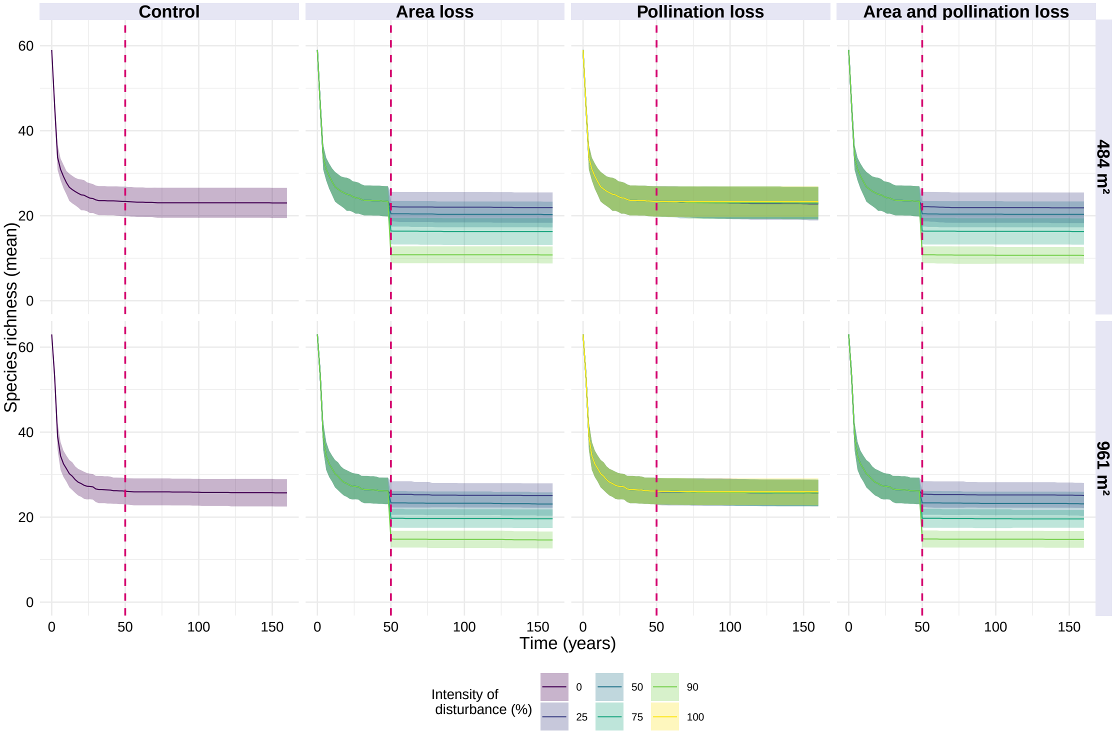

Figure 1: Mean species richness curves (+- sd, ribbon area) over time, for all simulated scenarios. Pink vertical line identifies the time disturbance was implemented (also indicated for control scenario for comparison only

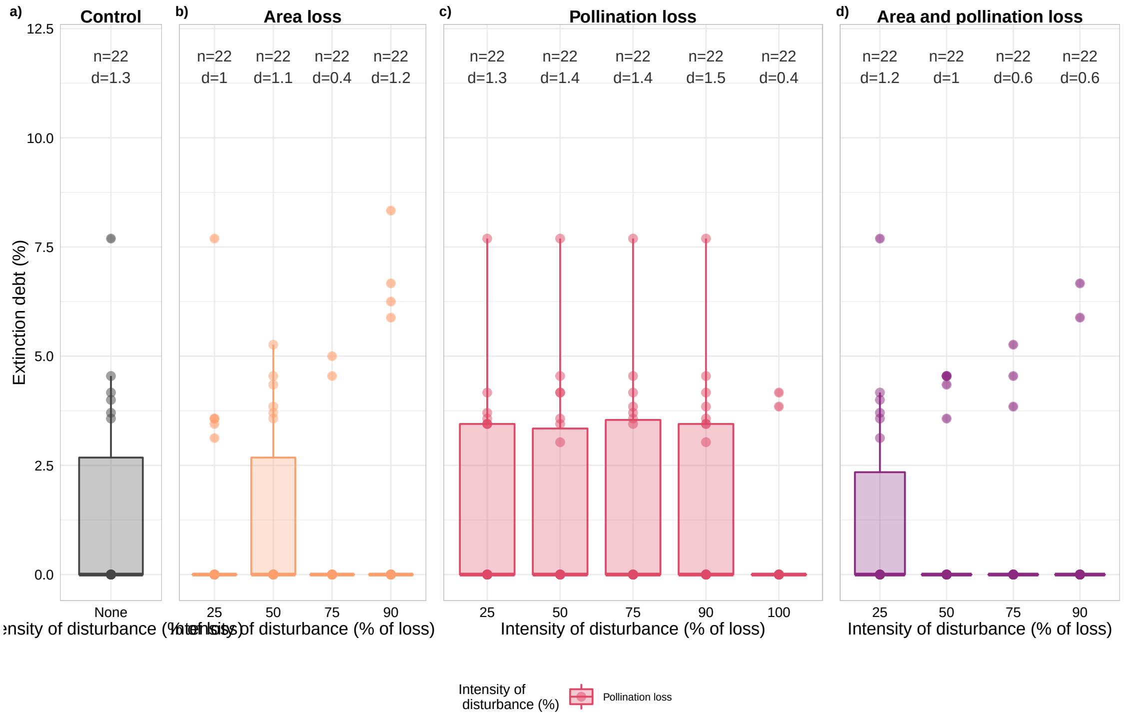

Figure 2: Extinction debts in a landscape of 961m². Proportion (per replicate) of species lost in the absence of any disturbance (A), and after area loss (B), pollination loss (C), and area and pollination loss (D). Extinctions were counted after the second year after disturbance ^{a}, thus excluding species immediately extinct. ^{a} Output frequency was equivalent to two years, for computational efficiency.

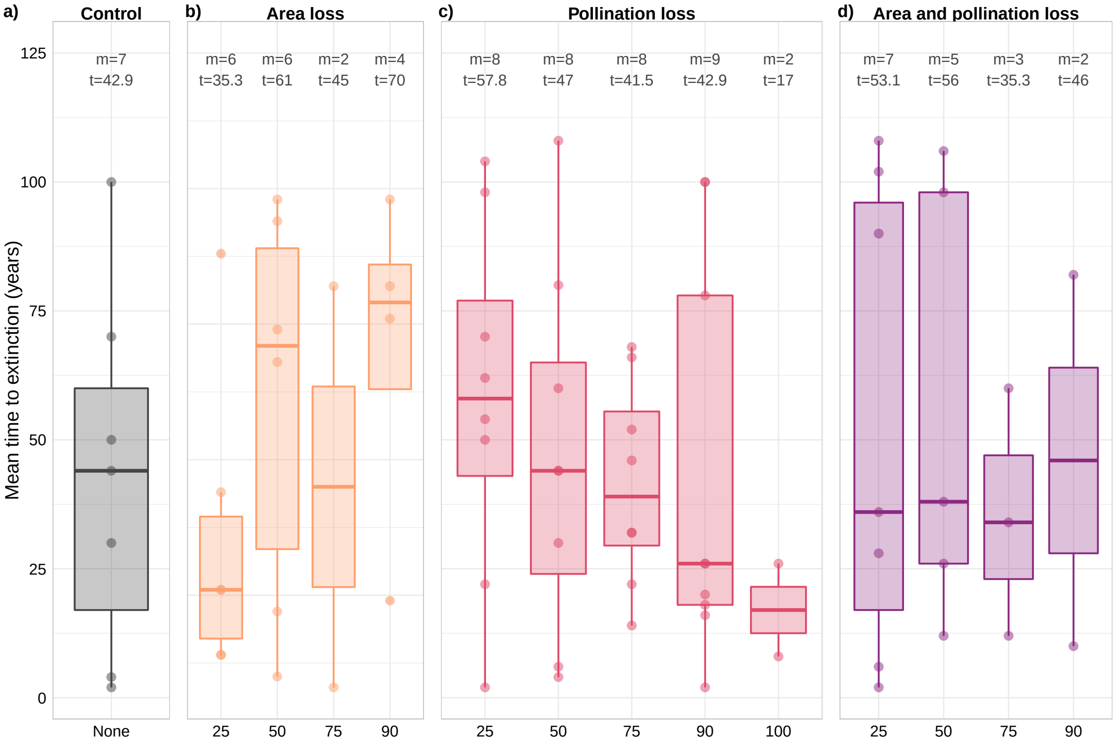

Figure 3: Species extinction times in a landscape of 961 m². Mean species extinction time (per replicate), in the absence of any disturbance (A), and after area loss (B), pollination loss (C), and area and pollination loss (E). Extinction time calculted for all species that survived the second year after disturbance ^{a}, thus excluding species immediately extinct. ^{a} Output frequency was equivalent to two years, for computational efficiency.

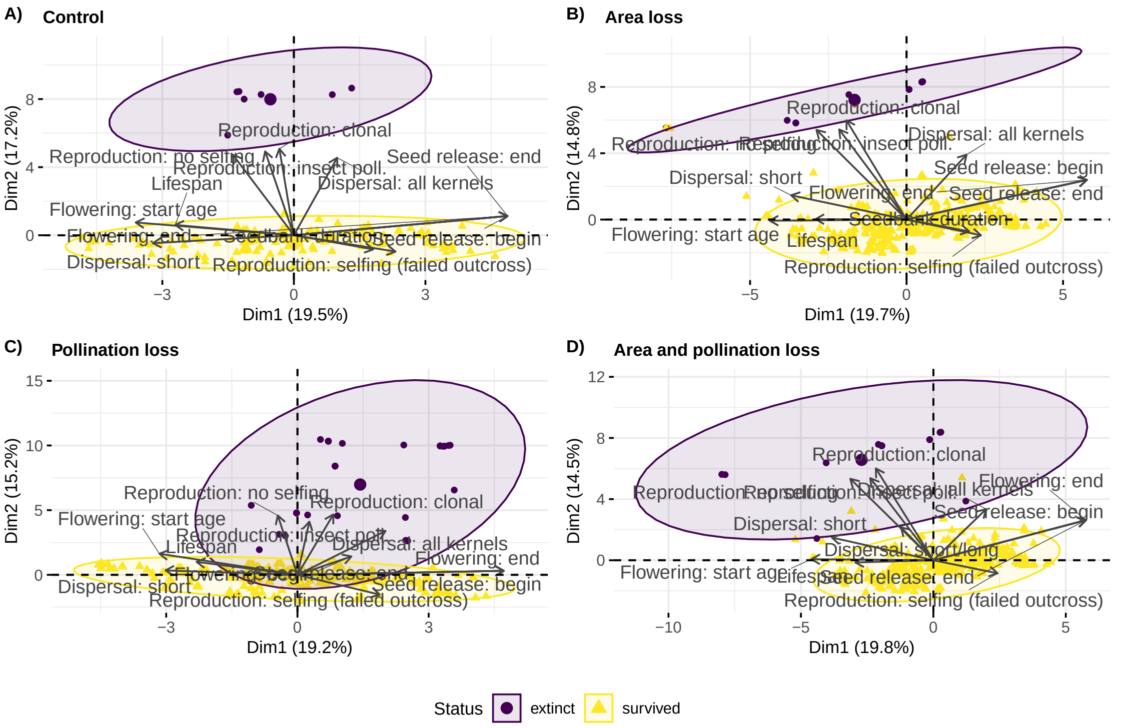

Figure 4: Analysis of 2nd and 3rd principal components of the trait space of species following disturbance (traits measured at t=52), in a landscape of 481m². Species are identified according to their status at the end of the simulation: extinct (dark purple) or survived (yellow). Out of the 24 variables used to define the trait space, only the 10 most contributing ones were included, to facilitate visualization.

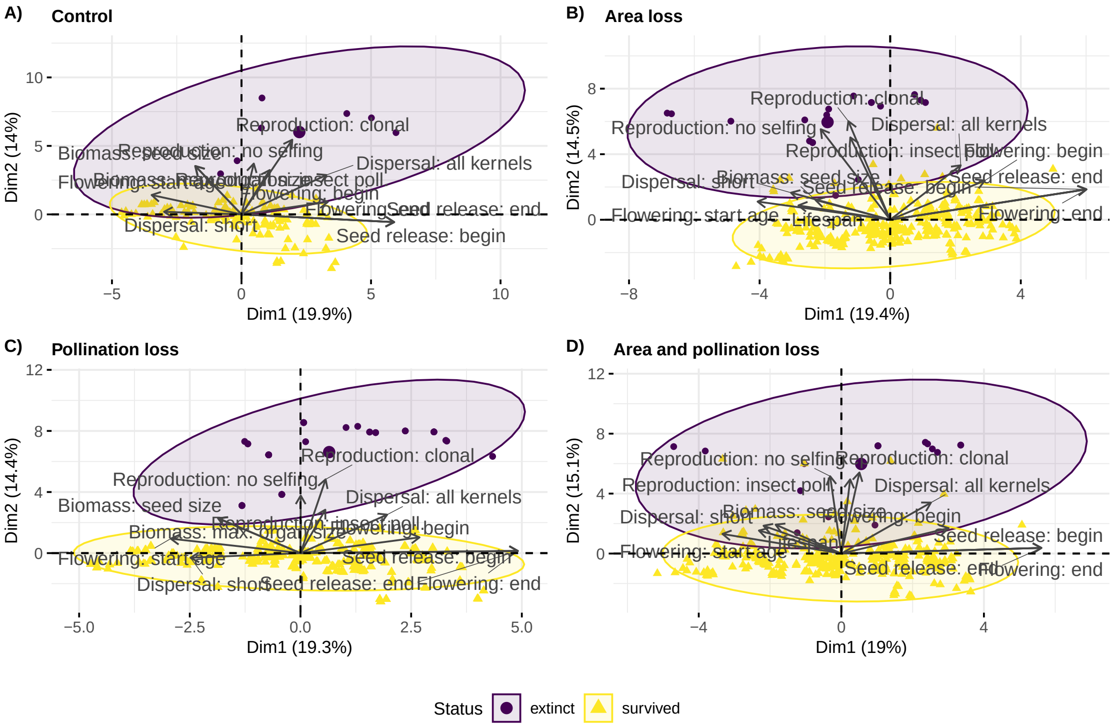

Figure 5: Analysis of principal components of the trait space of species following disturbance (traits measured at t=52), in a landscape of 961m². Species are identified according to their status at the end of the simulation: extinct (dark purple) or survived (yellow). Out of the 24 variables used to define the trait space, only the 10 most contributing ones were included, to facilitate visualization.

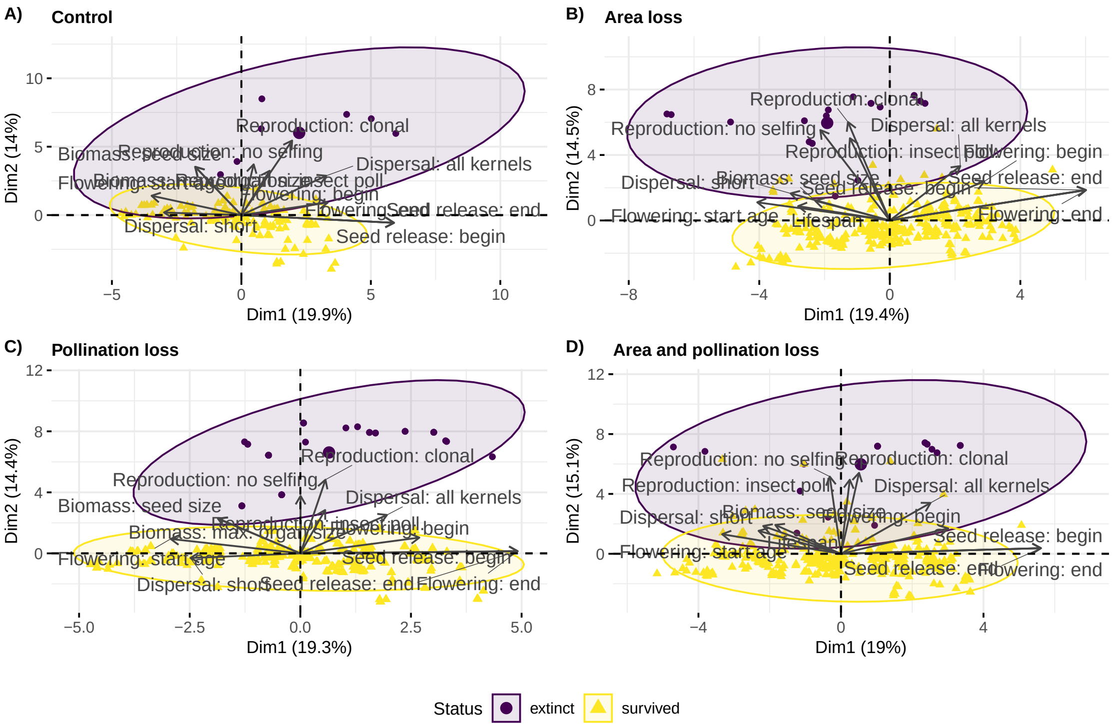

Figure 6: Analysis of 2nd and 3rd principal components of the trait space of species following disturbance (traits measured at t=52), in a landscape of 961m². Species are identified according to their status at the end of the simulation: extinct (dark purple) or survived (yellow). Out of the 24 variables used to define the trait space, only the 10 most contributing ones were included, to facilitate visualization.

Table 1: Summary of sizes of extinction debts (%) and mean of extinctions (n), summarized over all replicates, for all scenarios simulated in a landscape of 484 m^2. 'Std. dev' refers to standard deviation.

Disturbance	Intensity (%)	Mean (%)	Std. dev. (%)	Mean extinctions (n)
Control	None	1.44	2.18	0.32
Area loss	25	1.092	2.072	0.23
	50	0.88	1.92	0.18
	75	0.55	1.79	0.09
	90	0.41	1.94	0.05
Pollination loss	25	2.70	4.22	0.59
	50	1.91	3.48	0.41
	75	1.91	3.48	0.41
	90	1.32	2.67	0.27
	100	0.22	1.02	0.05
Area and pollination loss	25	1.30	2.64	0.27
	50	0.68	1.75	0.14
	75	0.49	1.61	0.09
	90	1.63	3.58	0.18

Table 2: Summary of sizes of extinction debts (%) and mean of extinctions (n), summarized over all replicates, for all scenarios simulated in a landscape of 961 m^2. 'Std. dev' refers to standard deviation.

Disturbance	Intensity (%)	Mean (%)	Std. dev. (%)	Mean extinctions (n)
Control	None	1.41	2.40	0.36
Area loss	25	1.26	2.23	0.35
	50	1.26	2.04	0.29
	75	0.56	1.59	0.12
	90	1.60	3.00	0.24
Pollination loss	25	1.31	2.29	0.35
	50	1.80	2.41	0.47
	75	1.60	2.41	0.41
	90	1.78	2.40	0.47
	100	0.47	1.33	0.12
Area and pollination loss	25	1.33	2.30	0.35
	50	1.00	1.87	0.24
	75	0.27	1.10	0.06
	90	0.74	2.09	0.12

Table 3: Summary of species time to extinction, summarized over all replicates, for all scenarios simulated in a landscape of 484 m². 'Std. dev' refers to standard deviation.

Disturbance	Intensity (%)	Mean (years)	Std. dev	Min. (years)	Max. (years)
Control	None	22.86	33.84	2	98
Area loss	25	36.80	36.68	2	82
	50	43.00	40.15	12	102
	75	26.00	11.31	18	34
	90	100.00		100	100
	25	43.54	30.16	6	102
Pollination loss	50	35.56	37.61	2	108
	75	47.56	30.98	22	96
	90	29.33	27.27	10	84
	100	6.00	-	6	6
Area and pollination loss	25	23.33	31.08	4	86
	50	22.00	28.00	2	54
	75	61.00	55.15	22	100
	90	46.00	44.60	8	108

Table 4: Summary of species time to extinction, summarized over all replicates, for all scenarios simulated in a landscape of 961 m². 'Std. dev' refers to standard deviation.

Disturbance	Intensity (%)	Mean (years)	Std. dev	Min. (years)	Max. (years)
Control	None	33.33	26.79	2	70
Area loss	25	35.33	28.05	14	88
	50	71.20	30.32	22	98
	75	45.00	52.33	8	82
	90	70.00	32.04	24	98
Pollination loss	25	50.66667	34.44803	2	98
	50	47.00	35.49	4	108
	75	37.71	18.02	14	66
	90	45.00	40.61	2	100
	100	17.00	12.73	8	26
Area and pollination loss	25	45.00000	44.12256	2	108
	50	43.50	37.85	12	98
	75	12.00		12	12
	90	46.00	50.91	10	82

Appendix 4

TRAnsparent and Comprehensive Evaludation (TRACE) document of the Extinction Dynamics Model

Problem formulation

Summary

When an ecosystem undergoes a perturbation, species extinctions are not necessarily immediate. Extreme events excluded, e.g. a volcanic island explosion, when species might be immediately extirpated (Quammen 1996), in most cases, it can take up to many decades for most extinctions to happen (Figueiredo et al. 2019), because species have different capabilities to survive in disturbed conditions. Metapopulation dynamics and resistance traits grant such capabilities (Saar et al. 2012; Saar et al. 2017). The number of such extinctions, which are bound to happen in the future is known as the "extinction debt" (Tilman et al. 1994; Kuussaari et al. 2009). The it takes for these extinction debts to happen is known as the "relaxation time" (Diamond 1972). This concept implies that, while these extinctions have not happened, i.e. the debt has not been paid by the ecosystem, extinctions can also be both accelerated and delayed by eco-evolutionary processes happening at different levels of the community (i.e., individual, populational, and community). Moreover, conservation measures could be planned to avoid them. To elucidate the relative importance of these processes, we build an individual-based model to simulate and characterize community response to different kinds of habitat perturbation at different ecological levels.

Motivation

The model is designed to elucidate how ecological processes in a plant-insect community are affected by ecosystem disturbance, and how they affect extinction dynamics. More specifically, we are interested at how species dispersal capacity and reproductive strategy, for example, delay or accelerate species extinctions.

Questions

With this model, we aim at answering the following questions:

1. How does the regime of disturbance affects extinction debt and relaxation time?

Abiotic perturbations cause biotic perturbations (e.g., pollination loss) as a secondary effect. The secondary perturbations amplify the effects of the primary disturbances alone. Thus, predictions of extinction debts and relaxation time that only consider isolated abiotic perturbations yield underestimations.

2. Which traits allow species to survive through the payment of the debt?

Following disturbance, initial species survival depends on the severity of the extinction-causing disturbance, and on the species abundance. During the relaxation process, community reassembly and microevolution affect are the main factors for species survival. Both processes either arise from (community reassembly) or affect (microevolution) species trait spaces. Our objective is, thus, to describe the change in community trait space during the relaxation process.

Use and applicability

The model is suited for theoretical explorations of eco-evolutionary dynamics.

Model description

Summary: This is a complete version of the model description presented in Figueiredo et al. (in prep.).

Overview

Purpose

The model simulates the effects of abiotic and biotic perturbations on i) plant species richness and population dynamics, and ii) community trait space.

Entities, state variables and scales

The model simulates the life cycle of plants in a landscape. Plant individuals are characterized by state variables and species traits (Table 1, which are used as parameters values in the simulation of the individual's life cycle (detailed in the next section, Process overview and scheduling).

The landscape is represented as a grid of cells. Each grid cell has an area of 1 m^2 and represents either suitable or unsuitable habitat (Table 1). There is no upper limit on the size of landscape (minimal size would be 1 m^2), but increasing the size of the landscape allows more individuals to occupy and thus, can be decrease the speed of simulations. The configuration of these cells in the grid is defined by the input, thus, by the experimental design. Temperature is a global variable in the model (all patches are subjected to the same temperature). The temperature is used to calculate the biological rates of the organisms being simulated (germination, growth, and mortality, each detailed in the Submodels section). The model runs on weekly discrete time-steps to account for the seasonality of management (mowing) and species phenology. The species to be included in the simulation, the landscape configuration, the regime of perturbation (type of perturbation, time of occurrence, and magnitude), and total duration of the simulation are determined by the user-defined experimental design (details in the Input and Disturbance submodel sections).

Process overview and scheduling

At each time-step, each individual goes through its life cycle processes, which vary according to the life history strategy determined by the individual's traits and current developmental stage (Table 1), *i.e.*, seeds, juveniles and adults go through different processes (Fig. 1).

The processes simulated in the model are the following (scheduling is depicted in Fig. 1, and further details are described in Details section):

Management: Annually, the effects of management (mowing or grazing) are simulated as the reduction of above-ground biomass of juvenile and adult plants.

Biomass growth and resource allocation: Whole organism biomass production is calculated according to metabolic theory of ecology (MTE)(Ernest et al. 2003; Brown et al. 2004). The total production is allocated to vegetative or reproductive structures, according to the individual's developmental stage and phenology. Juveniles and non-reproducing adults can only accumulate vegetative biomass, which is equally divided among "root", "stem", and "leaves" organs. During their species-specific reproductive season, determined by the phenological traits of start and end of flowering season, adults allocate biomass production to reproductive structures if they have reached a species-specific minimal vegetative biomass.

Maturation of juveniles: Juvenile individuals become adults once they reach their age of first flowering, a species-specific phenological trait.

Mortality: The probability of *density-independent* mortality is calculated for each individual, according to the metabolic theory of ecology (Brown et al. 2004). *Density-dependent* mortality is calculated once total

Table 1: Entities and their respective state variables in the model. Variables marked with (*) can evolve as described in the Microevolution submodel. Species specific parameters must be provided as input. The criteria regarding the selection and attribution of the respective values is described in the sections listed below.

Entity	State variable (unit)	Scope
Plant	Species	Species name
	Developmental stage	Temporary status
	Age(weeks)	Temporary status
	Vegetative biomass of leaves (g)	Temporary status
	Vegetative biomass of stem (g)	Temporary status
	Vegetative biomass of roots (g)	Temporary status
	Reproductive biomass (g)	Temporary status
	Pollination status	Temporary status
	Life span (weeks)*	Species specific parameter
	Age of first flowering (weeks)*	Species specific parameter
	Beginning of flowering season (week of year)	Species specific parameter
	End of flowering season (week of year)	Species specific parameter
	Pollination vector	Species specific parameter
	Beginning of sowing season (week of year)	Species specific parameter
	End of sowing season (week of year)	Species specific parameter
	Dispersal kernel	Species specific parameter
	Clonal ability	Species specific parameter
	Seed mass (g)	Species specific parameter
	Capacity of selfing at fail of outcrossing	Species specific parameter
	Probability of selfing upon pollination	Species specific parameter
	Maximal number of seeds (weeks)*	Species specific parameter
	Seed-bank duration (weeks)*	Species specific parameter
	Temperature optimum	Species specific parameter
	Temperature tolerance	Species specific parameter
	Germination proportionality constant $(week^{-1})$	Species specific parameter
	Mortality proportionality constant $week^{-1}$	Species specific parameter
	Biomass growth proportionality constant $({}^{g}/_{week^{-1}}$	Species specific parameter
Landscape grid cell	Habitat suitability	Experimental design

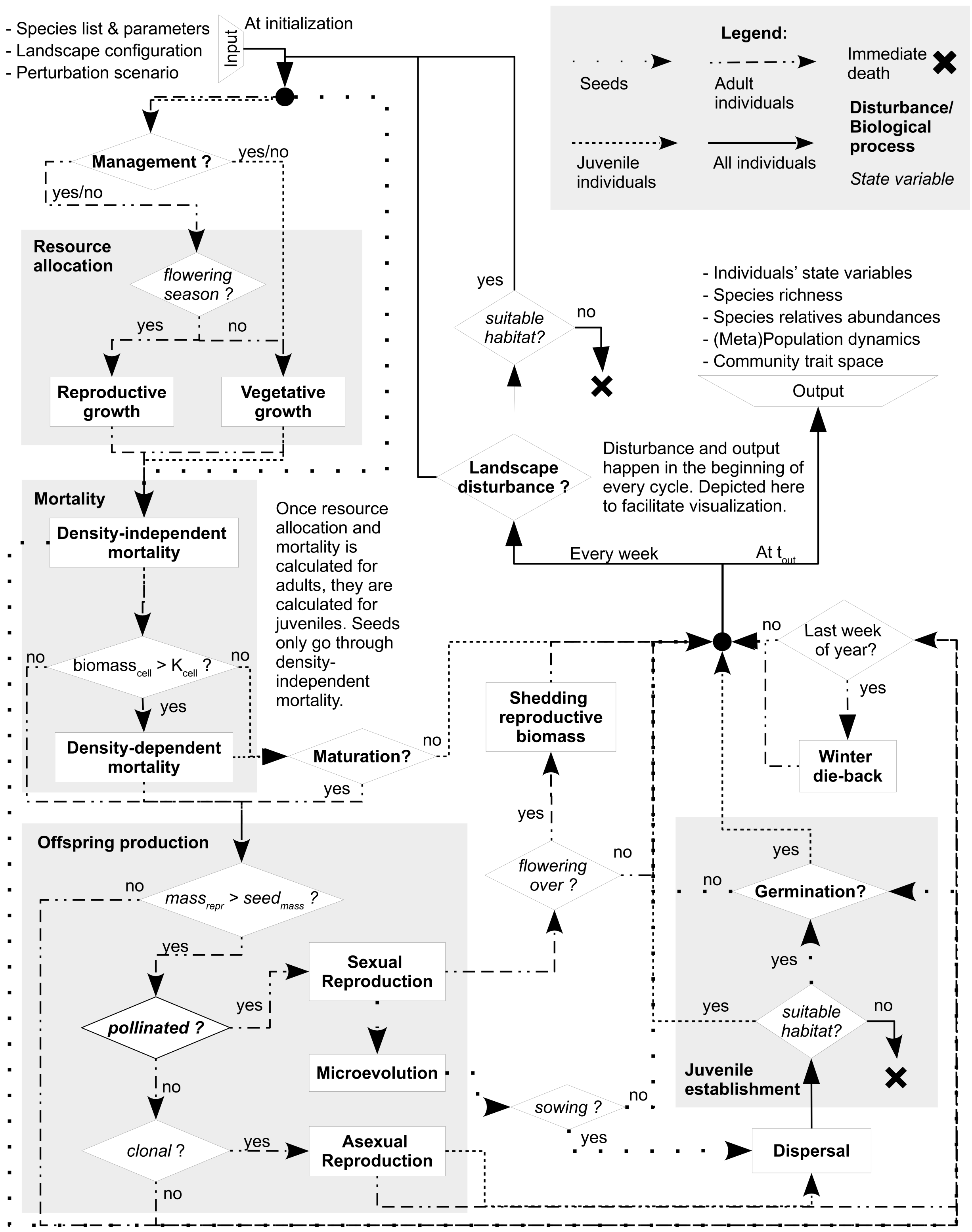

Figure 1: Flowchart of the processes simulated by the model for each individual plant. The biological processes differ between individuals according to state variables such as stage (as identified by the line type), or phenology (e.g.flowering season). The circumstances where state variables control the outcome of certain biological processes, namely pollination, maturation, germination, or excesive growth ($biomass_{cell} > K_{cell}$ refers to the biomass production being over the landscape carrying capacity) can also determine the course of an individual's life cycle.

vegetative standing biomass production surpasses the carrying capacity. Individuals die acccording to the species local (at the grid cell level) relative adaptation to temperature (fitness).

Pollination is implicitly simulated as pollination service, i.e., a plant is to sexually produce offspring only if it has been pollinated. Plants can be pollinated if they have enough reproductive biomass to produce at least one seed. The number of individuals being pollinated depends upon the number of individuals visited, pollination efficiency of the vector, and on the regime of pollination, all defined by the experimental design.

Sexual reproduction happens for individuals that have been pollinated. Trait inheritance is calculated for seeds thus produced (described below). Species also have a species-specific probability of selfing, in which case, no trait inheritance is calculated. The number of seeds produced depends on the species-specific seed weight and on the amount of reproductive biomass of the mother plant, and it is limited to species-specific values of maximal weekly seed production.

Asexual reproduction is simulated for clonal plants that do not get pollinated. Clonality is a species-specific trait. Probability of clone production is a global parameter (Table 2), and at most one clone is produced per cloning plant. Clones are initialized as juveniles, in the same location as the plant generating it.

Trait inheritance is simulated upon sexual reproduction through a simplified model of phenotypical change of a population under panmixia. Clones and seeds produced through selfing are exact copies of the plants that produced them.

Seed dispersal: Seeds can be dispersed at short (0.1-100 m), medium- (100-500 m), and long-distances (1-10km), accoding to the species-specific dispersal parameters. The phenology of seed release is also a species-specific trait (Table 1).

Seed germination is only possible in grid-cells labelled "suitable". Seeds that fall outside the landscape or in unsuitable grid-cells are considered dead and discarded from the simulation. The probability of seed germination is calculated for each individual, according to the MTE. If a seed is successful, it turns into a juvenile.

Shedding: At the end of the flowering season, adult plants lose all their reproductive biomass.

Winter dieback: At the last week of the year, adults lose all of the biomass allocated to *leaves*, and 50% of the biomass allocated to *stem*.

Disturbances can happen as **temperature change**, **loss of habitat area**, **fragmentation**, and **loss of pollination**. **Temperature change** is simulated if the obligatory the input of a temperature time series depicts the change. **Loss of habitat area** is simulated by the input of a proportion of habitat to be marked as "unsuitable" or by providing a raster file with the new habitat configuration, and the frequency of change, i.e. the time steps when the change happens. **Fragmentation** is only simulated through raster file(s) of the new habitat configuration. **Loss of pollination** is simulated by an input defining the intensity ($(0, 1]$), the frequency, and the specificity (i.e. which species are affected) of loss.

Design concepts

Basic design principles

The basic principle of the model is to capture how habitat change affects the individual, population and community levels of an ecosystem and how those processes contribute to the size of extinction debts and relaxation times. For its ability to scale individual level effects to community level patterns, the metabolic theory of ecology (Brown et al. 2004) was chosen as the guiding principle for calculating biological rates.

Emergence

Metapopulation and metacommunity dynamics arise from the local population dynamics and from species-specific dispersal abilities. Population dynamics results from individual biological demographic rates

Table 2: Global parameters of the model, their respective values, and references used to define them.

Global parameter	Value	References
Beginning of management season	$31^{st} week$ (first week of August)	Kormann et al. (2015)
End of management season	39^{st} (last week of September)	Kormann et al. (2015)
Probability of selfing at fail of outcrossing	50%	Arbitrary value
Allocation of reproductive biomass to seed production	5%	Weiss et al. (2014)
Proportion of plants visited by pollinators	1	Arbitrary value
Efficiency of insect pollination	60%	King et al. (2013)
Efficiency of wind pollination	60%	Arbitrary value
Short-dispersal kernel	$\mu = 1, \lambda = 0.2$	Vittoz & Engler (2007), Bullock et al. (2017)
Medium-dispersal kernel	$\mu = 0.2, \lambda = 3$	Vittoz & Engler (2007), Bullock et al. (2017)
Short-dispersal kernel	$\mu = 1000, \lambda = 100$	Vittoz & Engler (2007), Bullock et al. (2017)
Boltzmann constant	$8.65 - e5 - eV/K$	Brown et al. (2004)
Activation energy	$0.63 - eV$	Brown et al. (2004)
Landscape carrying capacity	$5T/ha$	Bernhardt-Romermann et al. (2011)

(biomass growth - both vegetative and reproductive biomass, germination, and mortality) that are calculated according to the MTE. Species coexistence arises from species density-dependent mortality depending on species relative adaptation to local temperature (fitness), where such limitation works as a local stabilizing mechanism. Competition arises from species relative fitness being updated locally, at every time step. Thus, extinct species leave open spaces that might be occupying by the surviving ones, according to their relative fitness.

Interactions

Organisms interact with the environment because all vital rates depend on local temperature, as determined by MTE. Plants also compete for space, since species local fitness limits its biomass growth.

Stochasticity

Reproduction, seed dispersal, germination and density-independent mortality are stochastic processes. The probability distribution used in each process is specified in their respective sub-model description. Mortality is specific for adult individuals older than their species lifespan, and for seeds falling in unsuitable habitat, or older than their seed bank duration. Density-dependent mortality is deterministic for small individuals of species going over their carrying capacity.

Observations

To keep track of extinction arising at different ecological levels (individual, population or community), the model outputs all state variables of each individual being simulated (Table 1) at user-defined intervals. From these outputs, the model readily summarizes species diversity, population dynamics (abundance and struture), biomass allocation, and life-history events (at the community level, not for each species). Other analysis can be derived by the user with the same file.

Details

Initialization

Simulations are defined by the landscape configuration, the species pool, the climatic conditions (temperature) and the type of disturbance. Landscape configuration determines which grid cells constitute suitable habitat and can, therefore, be occupied. Initial temperature (temperature is a global variable of the model) is read from an input file and updated at every time step (the file contains a time-series of weekly temperatures). Individuals are created according to the list of species list given as input. Upon initialization, each individual is randomly placed in the landscape and receives an individual identification tag. The individual's grid location is recorded because it is relevant for the calculation of density-dependent mortality (detailed in the Density-dependent mortality section). The individual's trait values (v) are read from the species list input (Table 1), except for values of seed number, seed bank duration, life span and age of first flowering. These values are highly variable (see Data evaluation section). Thus, the values for these traits are drawn from an Uniform distribution, $v \sim U(v_{min}, v_{max})$, where v_{min} and v_{max} are the minimal and maximal trait values given in the species list input file. Individuals that are initialized at random stages ("seed", "juvenile", or "adult"). Juveniles have the same biomass as seeds, since they are considered young seedlings, with four weeks old. Adults are initialized with 75% of the species maximum adult biomass and have the age of first flower of the species.

Input

Simulation scenarios are user-defined, and most parameters are specified in input files. A simulations requires:

1. Species list and trait values: The list of the species to be initialized, their respective trait values, and initial abundances (Table 1). Details on the species and trait values data used to develop the model under Data evaluation.
2. Initial landscape configuration: A raster file with binary values coding for habitat availability).
3. Time series of temperature variation: temperature values (°C) to be assigned for all grid cells, for each week of simulation. The total duration of simulation is determined by the length of the time-series. Details on the time-series data used to develop the model are provided under Environmental characteristcs in Data evaluation.
4. Type, time and magnitude of environmental disturbance: A dedicated setting identifies the type of disturbance, if any, tp be simulated. Frequency and magnitude are provided in dedicated files:
    - to simulate temperature change, the time series (item *3*) should contain the temperature values to be used.
    - to simulate area loss or fragmentation, the file must inform the time step(s) of change, and the respective proportion of area to be lost, or the raster file(s) containing the new configuration.
    - to simulate pollination loss, the file must inform the regime of pollination loss, the time steps when it happens, and how much pollination remains available.

Details on the contents of these files and how they are implemented are available in the descriptions of each disturbance submodel).

Submodels

All biological rates in the model, namely biomass growth, germination, and (density-independent) mortality, are calculated according to the metabolic theory of ecology (Brown et al. 2004):

$$B = b_0.m^{\alpha}.e^{\frac{-E}{k.T}} \tag{1}$$

where B is the metabolic rate, b_0 is a taxon and stage-specific proportionality constant, m is the individual's body mass, α is an allometric exponent, E is the activation energy, k is the Boltzmann constant, and T is the local temperature. Values of α, E, and k are constants from the metabolic theory of ecology (Brown et al. 2004, Sibly 2012a, Table 2). The proportionality constant b_0 is specifically parameterized for each process to generate (biologically) realistic rate values. We describe this parameterization in the Metabolic biological rates section of Data evaluation. Biological rates are converted into individual probabilities (of germination and mortality, only) as

$$p = 1 - e^{-B} \tag{2}$$

Management

Annually, the effects of management (mowing or grazing) are simulated as the reduction of above-ground biomass of juvenile and adult plants. The regime of mowing, i.e. the period of the year when it occurs, the probability of occurence, and the maximum annual number of occurence, is defined by the experimental design (example described in the Management section of Data evaluation). Only individuals that have accumulated at least 50% of the species maximal vegetative biomass (biomass allocated to stems and leaves) have their vegetative reduced to 50% of its maximal values and lose all reproductive biomass.

Biomass growth & Resource allocation

To simulate biomass growth, an individual's biomass (m) at time ($t + 1$) is calculated as

$$\begin{aligned} m_{t+1} &= m_t + g(t) \\ g(t) &= B_{growth} \times (m_{max} - m_t) \end{aligned} \tag{3}$$

where $g(t)$ calculates the total biomass production at a time-step t, m_{max} refers to the species total maximal biomass (vegetative and reproductive), and B_{growth} is the rate of growth (Eq. 1). This growth function approaches the S-shaped Richards growth curve (Richards 1959) parameterized according to the species minimal and maximal sizes, and age of first flowering (detailed in the Biomass growth rates section of Data evaluation).

The total production is allocated to vegetative or reproductive organs according to the allometric relationship between plant organs biomasses devised by Niklas and Enquist (2002), to the individual's developmental stage, and to the species' reproductive phenology. The allometric relationship devised by Niklas and Enquist (2002) states that standing leaf biomass scales as the $^3/_4$-power of stem biomass and that stem and root biomasses scale isometrically in relation to each other, i.e. $M_{leaf}\ M^{3/4}_{stem}\ M^{3/4}_{root}$. Moreover, the growth rates of the three biomass organs also scale isometrically, i.e. $B_{leaf}\ B_{stem}\ B_{root}$. Thus, biomass growth is equally divided among all vegetative organs ("root", "stem", and "leaves") during vegetative growth. Juveniles and non-reproducing adults can only accumulate vegetative biomass. During their species-specific flowering season (determined by the phenological traits of start and end of flowering season Table 1), adults allocate biomass production to the "reproductive" organs, if they have reached at least 50% of the species maximal size. Otherwise, they allocate to vegetative structures, as described above.

Maturation of juveniles

Juvenile individuals become adults once they reach their species-specific age of first flowering.

Mortality

Biomass growth and mortality are calculated in sequence, separately for adults and juveniles (Fig. 1). Only density-independent mortality is calculated for seeds.

Density-independent mortality is calculated for all individuals, except seeds that are still attached to the mother plant. Mortality rate, B_{mort}, and probability, p_{mort}, are calculated according to the MTE (Eq. 1 and 2). Individuals that are older than their maximal lifespan (always adults, see Maturation) are killed deterministically. Details on the parametrization of the normalization constant are described under the Mortality rates section of Data evaluation.

Density-dependent mortality is calculated once the total standing biomass in a grid-cell

$$M_{total} = \sum_{x=i}^{n_{cell}} m_i \tag{4}$$

(n_{cell} being the total number of individuals in the cell) is higher than its carrying-capacity (K_{cell}), a global, constant value defined by the experimental design (an example is given in the Data evaluation section. Mortality is then simulated only for the species whose specific share of the total standing biomass production ($M_{sp} = \sum_{x=i}^{n_{sp}} m$, n_{sp} being the number of individuals of the species) is above its relative carrying capacity ($K_{cell_{sp}}$). A species ($K_{cell_{sp}}$), i.e. its maximal standing biomass production inside a cell, depends on its temperature niche, defined by species-specific, non-evolving temperature optimum (T_{opt}) and tolerance values (T_{tol}). The temperature niche is modelled as a Gaussian function ($f(T)$, with maximum value $f_{max} = f(T_{opt}) = 1$, and $sd = T_{tol}$,

$$f(T) = f_{max} \times \exp(\frac{-(T - T_{opt})^2}{2 \times T_{tol}^2}) \tag{5}$$

where T is the mean temperature calculated over the same time period as the optimum and tolerances were defined, which is the same time period over each fitness is updated. Species temperature niches are defined by the experimental design and an example of how we defined it is described in the "Data evaluation" section.

A species relative carrying-capacity is then,

$$K_{cell_{sp}} = \frac{f_{sp}(T)}{\sum_{x=i}^{spp_{cell}} f_i(T)} \times K_{cell} \tag{6}$$

where f_{sp} is the species absolute fitness value, and spp_{cell} are the species in the cell.

Thus, once $M_{sp} > K_{cell_{sp}}$, individuals are ranked according to total biomass, and smaller (independent of stage, juvenile or adult) are killed first, until $M_{sp} \leq K_{cell_{sp}}$. Since the MTE predicts that smaller individuals have higher metabolic rates, we avoid the computational burden of drawing random processes (as it happens for density-independent mortality) by eliminating smaller individuals first.

Pollination

The occurrence of pollination is a stochastic process that depends on the availability of pollination service, which is determined by the experimental design and affects the total number of individuals that will produce offspring sexually.

The number of pollinated n_{poll} individuals is calculated (per species) from all the flowering plants with enough reproductive biomass to produce at least one seed (n_{repr}). Flowering plants are adult individuals that are in their reproductive season, a species specific trait determined (an example is decribed in Data evaluation), and the proportion of reproductive biomass available for seed production is determined by a global constant defined by the experimental design (Table 2). The number of effectively pollinated plants is drawn from a Binomial distribution

$$n_{poll} \sim B(n = n_{repr} \times p_{visit}, p = p_{eff}) \tag{7}$$

where p_{visit} is the proportion of visited flowers, and p_e. Both are global constants in the model (Table 2). In the absence of disturbance, n_{poll} individuals of the species are identified as having been pollinated and can thus, produce seeds. Pollination disturbance decreases n_{poll} according to the pollination scenario, whose implementation is detailed in the Pollination loss submodel description.

Sexual reproduction

The number of seeds produced at each reproductive event is calculated as $nseeds = m_{repr}/m_{seed}$, where m_{repr} is the amount of reproductive biomass and m_{seed} is the species-specific seed weight. The amount is limited by the species weekly maximal number of seeds, i.e., even if the plant has enough biomass to produce more than its maximum, it will not. The species weekly maximal number of seeds is a trait value given as input to the model (an example is described in the Seed number section of Data evaluation). Species have a species-specific probability of selfing upon pollination. Moreover, some species can resort to selfing in case they are not pollinated. For such species, there is a global probability of success (Table 2). The trait values of the offspring are calculated according to a simplified model of phenotypical change of a population under panmixia (described below). After offspring production, the reproducing plant loses biomass from its reproductive compartment equivalent to the weight of all the seeds produced.

Asexual reproduction

A clonal plant that has not been pollinated has a global probability of generating a ramet (Table 2). The clone is initialized as a juvenile, in the same grid cell as the mother-plant, weighing 10% of the species total maximal biomass. Thus, clonality is a global strategy to assure seedling establishment (Doust 1981).

Trait inheritance

Offspring inherits its trait values according to the type of reproduction it is generated from. For sexually, non-selfing, generated seeds, the new trait value v of evolvable traits (Table 1) is calculated as

$$v = \frac{v_{mother} + v_{mother}}{2} + N(0, |\frac{(v_{mother} - v_{father})}{6}|) \tag{8}$$

where v_{mother} is the trait value of the plant originating the seed and v_{father} is the trait value of a conspecific plant randomly chosen in the population. By using $(v_{mother} - v_{father})/6$, the introduced variability in trait hereditability is limited to the difference between the parent's values. The resulting trait value, however, is limited by the species minimal and maximal values, v_{min} and v_{max}, given as input. Individuals generated through selfing and cloning inherent the same set of traits as the plant producing them.

Seed dispersal

During the reproductive season, seeds are produced, but not necessarily dispersed. Seed dispersal during species-specific seed release season. The model simulates kernel-based dispersal. Kernel parameters characterize the distribution of distances achieved by the species mode of dispersal.

Dispersal is simulated by drawing a random radian angle $\theta = [0 - 2 \times \pi)$ from Uniform distribution, and drawing the dispersal distance $dist_{disp}$ from the species' dispersal kernel. The dispersal distance $dist_{disp}$ is drawn from an Inverse Gaussian distribution parameterized according to the species-specific dispersal vector (an example is described in the Dispersal kernels. The new location is calculated as

$$(x_{new}, y_{new}) = (x + cos(\theta) \times dist_{disp}, y + sin(\theta) \times dist_{disp}) \tag{9}$$

where (x, y) is the individual's current location (cartesian coordinates of the cell in the landscape). A species might have different dispersal kernels. Upon dispersal, one of them is randomly drawn from an Uniform probability distribution before drawing $dist_{disp}$.

Seed germination

If a seeds is dispersed and falls on an unavailable grid cell, it dies immediately and is discarded from the simulation. Otherwise, its germination rate, B_{germ}, and probability, p_{germ} are calculated according to the metabolic theory of ecology Details of the parameterization of normalization constant parameterized as described in the [Germination rate section]#germination-rate) of Data evaluation. The realization of germination is randomly drawn from a Bernoulli distribution, with probability p_{germ}. If germination happens, the new seedling is identified as a juvenile individual. Seeds that do not germinate remain in the seed bank. Seeds that reach an age older than the species-specific seed bank duration are killed deterministically.

Disturbances

The model can simulate scenarios of temperature change, loss of habitat area (with or without fragmentation) and loss of pollination. These scenarios are defined independently from each other, which allows the combination of different perturbations into a single scenario. Each type of disturbance is simulated as follows:

Temperature change

The model is dependent on a temperature time series being input (to calculate the rates of biological processes), therefore, temperature change can be simulated by providing a time series that characterizes the temperature change for the duration of the simulation.

Area loss (without fragmentation)

The simulation scenario must define a proportion of habitat to be lost at a given time-step. Then, the number of contiguous grid cells equivalent to the area lost are marked as 'unsuitable' and all individuals occupying this cells are immediately killed. It is also possible to simulate area loss if a raster file describing a new configuration of habitat suitability of the original area is provided (associated with a time-step when it should be loaded).

Fragmentation

Habitat fragmentation can only be simulated via raster files. Similarly to area loss, cells are marked as unsuitable according to the description contained in the raster file and individuals in the area are killed. Several episodes of area loss or fragmentation can be simulated if several proportions or raster files describing loss are provided, associated with different time-steps. Individuals occupying cells that become "unsuitable" upon fragmentation are killed and discarded from the simulation.

We provide the `createnlm.R` script to generate raster files of a given area, using the NLMR package (Sciaini et al. 2018).

Pollination loss

The regime of pollination loss is be defined according to its i) *intensity*, *i.e.*, the proportion of flowers still being pollinated (p_{remain} = [0,1]), ii) *frequency*, i.e, the time-step(s) when loss happens (t_d), and iii) *specificity*, i.e., which species are affected. The intensity of loss affects pollinations by decreasing the number of individuals being identified as "pollinated", $n_{poll} = n_{poll} \times p_{remain}$. The specificity of pollination loss can defined as "equal", "random", or "specific". In the scenario of "equal" pollination loss, all species are affected by p_{remain}. Under the "random" scenario, p_{remain} is applied to the total individuals potentially reproducing, among all species. Thus, the number of pollinated individuals per species is randomly set. Under the "specific scenario", a given list of species loses pollination is affected by p_{remain}. (see details in the Input section)

Data evaluation

Summary: The model uses species trait values to control entities behaviour in the simulation of a plant's life cycle under given biotic (pollination services) and abiotic (temperature and habitat availability) conditions. Because this model was developed to study the community dynamics of temperate grasslands, inspired by Krauss et al. (2010), we report how we retrieved, evaluated and adapted species trait values and temperature time series data to parameterize the model to mimick this ecosystem. The parameter values thus defined are used as model input. Therefore, users of the model can refer to this section when defining their own experiments. Data was retrieved from different literature sources and databases. Data that could not be obtained as such was imputed, as described in "Missing trait values" subsections. The final trait values chosen for each species are listed in Appendix.

Management

Management is implemented following the regime reported for Göttingen by Kormann et al. (2015). Thus, at most once a year, between August and September, the effects of management (mowing or grazing) are simulated as described in the Model description.

Temperature time series

Parametrization of metabolic rates has taken into account the monthly mean temperatures registered for the city of Göttingen, between 1857 and 2017 (station 1691, DWD 2018). Monthly temperatures values where expanded to a weekly bases by assigning the same value to all weeks of the month (code available in the chunck below). The final temperature time series is depicted in Fig. 2.

Species functional traits

Trait values used in the model Table 1 were retrieved from the LEDA Traitbase (Kleyer et al. 2008), the BiolFlor database (Klotz, Kühn, and Durka 2002), the FloraWeb database (http://www.floraweb.de), the WorldClim database ("WorldClim 1.4" 2019; Hijmans et al. 2005), and the GBIF database (GBIF 2019). The process of filtering and transformation of this data, as well as the parameterization based on it is described below.

Dispersal kernels

Species dispersal types were retrieved from the LEDA database (Kleyer et al. 2008). We used a classification of dispersal modes with similar distances (Vittoz and Engler 2007) to assign kernel parameters to the species.

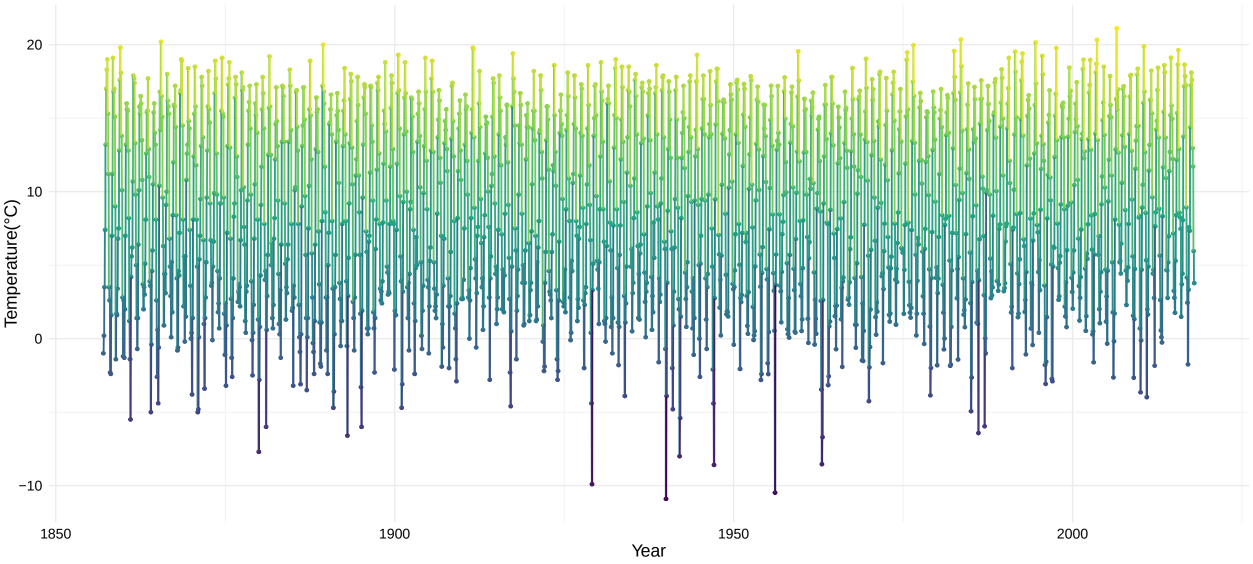

Figure 2: Temperature time-series used in the first implementation of the model. Monthly mean temperatures registered for the city of Göttingen, between 1857 and 2017(station 1691, DWD (2018) were expanded to a weekly bases by assigning the same value to all weeks of a given month.

We reorganized the seven dispersal types originally devised by Vittoz and Engler (2007) into three super-types: short-, medium-, and long-distance dispersal (Table 3). Kernels are assigned to a species according to the super-types its mode of dispersal belongs to.

When more than one dispersal kernel suits the same species, all of them are listed. If no dispersal mode was reported on neither of the references, the species can spread via any of the kernels. Because of the difficult in estimating the dispersal distances reached by nautochoric and bythisochoric species, those dispersal modes were ignored for species that had other dispersal modes. Species that only dispersed via these two modes were assigned as being able to disperse via any of the dispersal kernels. Each super-type is modeled by a set of kernel parameters (Table 4).

Seed mass

Seed mass values were retrieved from the LEDA database (Kleyer et al. 2008) and from a classification of plant sizes by Weiss et al. (2014).

In the LEDA database, mean values are reported from multiple observations diaspore ("mean"), and from a single observation ("single value"). For some species, however, both values do not match or one of them is missing. In that case, "mean" values are preferred, as they arise from multiple observations. This is also the case when both values are available and are similar ("Small difference", in Table 5). If "mean" is missing, "single value" is used. For two species for which seed mass was missing in the LEDA database, we used the values attributed in the Weiss et al. (2014) classification of species sizes: *Equisetum arvense* is $0.0001g$ *Veronica teucrium* is $0.0003g$. For species for which we could not retrieve the seed mass from the literature, values were inputed, as reported in the section "Imputation of missing trait values".

It is important to note that reported values (both "mean" and "single" values) vary according to the diaspore, i.e. dispersule or geminule, used to measure it to measure. The definitions of dispersule and germinule used by the LEDA database are:

> "Dispersule: Every morphological part of a plant that serves as a unit of dispersal and becomes detached from the mother-plant to disperse. Here we only provide data for the generative dispersules, i.e. units of dispersal that contain a seeds (see also germinule)."

Table 3: Reference values of dispersal distances (m) reported in Vittoz and Engler (2007) are used to verify the values generated by the kernels in the Dispersal kernels subsection of the Implementation section

Dispersal mode	Quantiles (50-99% m)	Details
Autochory	0.1-1	-
Blastochory	0.1-1	-
Herpochory		not included in Vittoz & Engler (2007) but assigned the same as other autochory syndromes
Ballochory	1-5	-
Boleochory	0.1-1	-
Ombrochory	0.1-1	-
Cystometeorochory	1-5	-
Trichometeorochory	2-15	-
Meteorochory		-
Pterometeorochory	2-15	-
Chamaeochory	1-5	-
Myrmechory	2-15	-
Dyszoochory	40-150	-
Agochory	500-5000	-
Anthropochory	500-5000	-
Endozoochory	400-1500	-
Epizoochory	400-1500	-
Ethelochory	500-5000	assigned the same as anthropochory
Hemerochory		-
Speirochory	500-5000	assigned the same as anthropochory
Zoochory	400-1500	-
Anemochory		-
Nautochory		-
Bythisochory		-
other		-

Table 4: Dispersal kernels simulated in the model and the range of dispersal distances generated by each.

Dispersal kernel	Function (parameters)	Range of values
Short-distance	Inverse Gaussian $(\mu = 1, \lambda = 0.2) \times 4$	$0.1 - 100m$
Medium-distance	Inverse Gaussian $(\mu = 0.2, \lambda = 3) \times 1000$	$100 - 500m$
Long-distance	Inverse Gaussian $(\mu = 1000, \lambda = 100)$	$1 - 10km$

Table 5: Species for which the "mean" and "single" seed mass values in LEDA database did not match but were close enough ("Small difference") or were missing ("Missing").

Species	Availability
Aegopodium podagraria	Small difference
Chaerophyllum temulum	
Cichorium intybus	
Daucus carota	
Geranium molle	
Geranium robertianum	
Holcus lanatus	
Rhinanthus angustifolius	
Rumex acetosa	
Tanacetum vulgare	
Trifolium dubium	
Carex leporina	Missing
Carlina vulgaris	
Cephalanthera rubra	
Cerastium holosteoides	
Cerinthe minor	
Elytrigia repens	
Equisetum arvense	
Hieracium lachenalii	
Inula conyzae	
Listera ovata	
Medicago falcata	
Mentha verticillata	
Ophrys apifera	
Ophrys insectifera	
Orchis mascula	
Orchis purpurea	
Orchis tridentata	
Potentilla neumanniana	
Senecio ovatus	
Taraxacum laevigatum	
Veronica teucrium	
Vicia villosa	

> "Germinule: Unit of germination. In many cases the dispersule is not the unit that will enter the soil after dispersal and germinate and therefore differs from the dispersule. This difference is due to morphological structures, such as pappus, wings, awns or fleshy nutrient containing tissues, that get lost between the time of dispersal and the time of germination."
>
> — Definitions used in the LEDA traitbase (Kleyer et al. 2008).

Mismatching measures could be clearly identified for the one instance of "multi-seeded generative" diaspore, which was thus discarded. Values reported for "unknown" diaspore were not used either, as it is not possible to evaluate for which reproductive unit they were measured. For species for which seed mass from other diaspores where reported, we verified the their coefficients of variation (Table 6). Values of germinule weight have precedence, as these are the reproductive structures that enter the soil and germinate (Table 6). Species for which germinule value was missing were assigned the value reported for one-seeded dispersule (Table 6). If that was also missing, the value reported for generative dispersule was used (Table 6).

Table 6: Variation (mean, standard deviation, and coefficient of variation per species) of seed mass values reported for germinule, one-seed generative dispersules, and generative dispersule in the LEDA database. Species for which standard deviation and coefficient of variation had only one value reported, which was taken as the mean.

Type of diaspore	Species	Mean value (mg)	Std. Deviation (mg)	Coeff. variation (%)
Germinule	*Achillea millefolium*	0.0001305	0.0000423	32.40
	Acinos arvensis	0.0006155	0.0006515	105.84
	Actaea spicata	0.0062603	0.0006095	9.73
	Aegopodium podagraria	0.0015825	0.0004878	30.82
	Agrimonia eupatoria	0.0130967	0.0104114	79.49
	Ajuga genevensis	0.0017540	0	0
	Ajuga reptans	0.0014652	0.0000206	1.40
	Allium schoenoprasum	0.0009167	0.0001735	18.92
	Alopecurus pratensis	0.0007005	0.0000742	10.59
	Anchusa arvensis	0.0045297	0.0015999	35.32
	Antennaria dioica	0.0000535	0.0000092	17.18
	Anthoxanthum odoratum	0.0005640	0.0002985	52.93
	Anthriscus sylvestris	0.0042036	0.0008762	20.84
	Anthyllis vulneraria	0.0032066	0.0005561	17.34
	Arabis hirsuta	0.0000926	0.0000336	36.25
	Arrhenatherum elatius	0.0025858	0.0005373	20.78
	Artemisia vulgaris	0.0001396	0.0000387	27.74
	Astragalus glycyphyllos	0.0051500	0.0004784	9.29
	Avenula pubescens	0.0019075	0.0000233	1.2
	Bellis perennis	0.0001415	0.0000809	57.2
	Brachypodium pinnatum	0.0020458	0.0012759	62.37
	Briza media	0.0003855	0.0001598	41.451
	Bromus erectus	0.0046908	0.0003932	8.39
	Bromus hordeaceus	0.0017159	0.0018782	109.46
	Calystegia sepium	0.0302720	0.0042330	13.99
	Campanula glomerata	0.0001430	0.0000268	18.72
	Campanula persicifolia	0.0000706	0.0000079	11.22
	Campanula rapunculoides	0.0001920	0.0001645	85.7
	Campanula rotundifolia	0.0000631	0.0000117	18.56
	Cardaminopsis arenosa	0.0001090	0	0

Carduus crispus	0.0016901	0.0005185	30.68
Carex caryophyllea	0.0012118	0.0003657	30.18
Carex flacca	0.0009653	0.0001954	20.25
Carex ornithopoda	0.0007596	0.0001126	14.82
Centaurea jacea	0.0020156	0.0009595	47.60
Centaurea scabiosa	0.0061623	0.0011812	19.17
Centaurium erythraea	0.0000126	0.0000043	33.94
Cerastium arvense	0.0002260	0	0
Cerastium tomentosum	0.0004492	0.0001000	22.27
Chaerophyllum hirsutum	0.0033330	0	0
Chaerophyllum temulum	0.0028661	0.0004814	16.8
Cichorium intybus	0.0019305	0.0003673	19.03
Cirsium acaule	0.0033513	0.0007729	23.07
Cirsium arvense	0.0011891	0.0001025	8.62
Cirsium oleraceum	0.0025923	0.0000881	3.4
Cirsium vulgare	0.0024458	0.0004116	16.83
Clinopodium vulgare	0.0004245	0.0000575	13.54
Convolvulus arvensis	0.0114391	0.0125680	109.87
Crepis biennis	0.0011153	0.0001645	14.75
Cruciata laevipes	0.0035856	0	0
Cynosurus cristatus	0.0005514	0.0001141	20.7
Dactylis glomerata	0.0009057	0.0002729	30.13
Daucus carota	0.0011330	0.0003149	27.8
Echium vulgare	0.0028145	0.0002831	10.06
Epilobium angustifolium	0.0000564	0	0
Epilobium montanum	0.0001204	0	0
Euphorbia cyparissias	0.0019580	0.0007750	39.59
Euphrasia officinalis	0.0001310	0.0000014	1.08
Falcaria vulgaris	0.0009300	0	0
Festuca ovina	0.0003565	0.0002150	60.3
Festuca pratensis	0.0018080	0.0003932	21.75
Festuca rubra	0.0008650	0.0003040	35.14
Filipendula vulgaris	0.0007030	0.0001601	22.78
Fragaria vesca	0.0003208	0.0000266	8.3
Fragaria viridis	0.0003751	0.0001398	37.28
Galeopsis ladanum	0.0012000	0	0
Galium aparine	0.0092078	0.0025501	27.7
Galium mollugo	0.0007562	0.0001813	23.98
Galium verum	0.0005547	0.0001168	21.05
Genista tinctoria	0.0037611	0.0005859	15.58
Gentianella ciliata	0.0001270	0	0
Gentianella germanica	0.0001544	0.0000288	18.69
Geranium dissectum	0.0025653	0.0000888	3.46
Geranium molle	0.0010464	0.0000799	7.64
Geranium pratense	0.0083606	0.0018614	22.26
Geranium pusillum	0.0007572	0.0001216	16.07
Geranium robertianum	0.0014076	0.0002583	18.35
Geum urbanum	0.0015905	0.0012141	76.33
Gymnadenia conopsea	0.0000060	0	0
Helianthemum nummularium	0.0010792	0.0003380	31.32

Heracleum sphondylium	0.0059122	0.0006622	11.20
Hieracium murorum	0.0004000	0	0
Hieracium pilosella	0.0001724	0.0000573	33.23
Hippocrepis comosa	0.0036646	0.0005812	15.86
Holcus lanatus	0.0003542	0.0001032	29.15
Hypericum perforatum	0.0000995	0.0000354	35.53
Knautia arvensis	0.0044278	0.0017531	39.59
Koeleria pyramidata	0.0023000	0	0
Lathyrus pratensis	0.0126003	0.0022036	17.49
Leontodon hispidus	0.0011093	0.0002842	25.63
Leucanthemum vulgare	0.0004056	0.0000496	12.23
Linum catharticum	0.0001529	0.0000158	10.3
Lolium perenne	0.0019982	0.0002313	11.57
Lotus corniculatus	0.0013993	0.0002433	17.39
Medicago lupulina	0.0017413	0.0002380	13.67
Melilotus alba	0.0028295	0.0012594	44.51
Melilotus officinalis	0.0025756	0.0014815	57.52
Mentha arvensis	0.0001837	0.0000666	36.24
Myosotis arvensis	0.0003060	0.0000224	7.32
Myosotis sylvatica	0.0004670	0.0001315	28.16
Onobrychis viciifolia	0.0201171	0.0023906	11.88
Ononis repens	0.0051355	0.0004122	8.03
Ononis spinosa	0.0047589	0.0015598	32.78
Orchis militaris	0.0000010	0	0
Origanum vulgare	0.0000944	0.0000147	15.57
Phalaris arundinacea	0.0007175	0.0000629	8.77
Pimpinella saxifraga	0.0012331	0.0002822	22.89
Plantago lanceolata	0.0017259	0.0004097	23.74
Plantago major	0.0002950	0.0000636	21.57
Plantago media	0.0003732	0.0000919	24.61
Platanthera chlorantha	0.0000030	0	0
Poa annua	0.0002127	0.0000610	28.7
Poa pratensis	0.0002687	0.0000318	11.8
Polygala vulgaris	0.0017736	0.0001246	7.03
Potentilla anserina	0.0010118	0.0001875	18.53
Potentilla reptans	0.0002679	0.0000220	8.23
Primula veris	0.0008156	0.0001858	22.78
Prunella grandiflora	0.0007780	0	0
Prunella vulgaris	0.0006776	0.0000659	9.72
Ranunculus bulbosus	0.0026607	0.0011067	41.6
Ranunculus repens	0.0022736	0.0007780	34.21
Rhinanthus angustifolius	0.0023213	0.0002768	11.93
Rhinanthus minor	0.0027015	0.0004292	15.89
Rumex acetosa	0.0008381	0.0002866	34.2
Rumex crispus	0.0018993	0.0008908	46.9
Salvia pratensis	0.0026018	0.0005634	21.66
Sanguisorba minor	0.0043664	0.0015513	35.5
Scabiosa columbaria	0.0017925	0.0005773	32.21
Sedum sexangulare	0.0000100	0	0
Senecio erucifolius	0.0003100	0	0

	Senecio jacobaea	0.0003171	0.0001260	39.75
	Senecio vulgaris	0.0002690	0.0000198	7.36
	Silene dioica	0.0007876	0.0001729	21.96
	Silene nutan	0.0003454	0.0001316	38.11
	Sonchus asper	0.0002943	0.0000257	8.73
	Stachys germanica	0.0015188	0.0002237	14.73
	Stellaria holostea	0.0027284	0.0004172	15.3
	Stellaria media	0.0003936	0.0000686	17.43
	Symphytum officinale	0.0111288	0	0
	Tanacetum vulgare	0.0003431	0.0001686	49.13
	Thymus pulegioides	0.0001519	0.0000300	19.72
	Tragopogon pratensis	0.0084214	0.0013562	16.10
	Trifolium campestre	0.0003186	0.0000699	21.95
	Trifolium dubium	0.0004029	0.0000441	10.94
	Trifolium medium	0.0021266	0.0004149	19.51
	Trifolium ochroleucon	0.0023984	0.0010093	42.08
	Trifolium pratense	0.0013825	0.0002395	17.33
	Trifolium repens	0.0005134	0.0001535	29.90
	Trisetum flavescens	0.0002230	0.0000753	33.79
	Triticum aestivum	0.0431250	0.0008839	2.05
	Valeriana dioica	0.0008636	0.0006056	70.13
	Valeriana officinalis	0.0008710	0.0002221	25.5
	Verbascum lychnitis	0.0001188	0.0000181	15.24
	Veronica chamaedrys	0.0001960	0.0000177	9.03
	Vicia cracca	0.0158318	0.0044573	28.15
	Vicia hirsuta	0.0059904	0.0023536	39.3
	Vicia sepium	0.0227702	0.0023650	10.39
	Vicia tenuifolia	0.0242800	0.0053457	22.02
	Vicia tetrasperma	0.0031977	0.0004474	13.99
	Vincetoxicum hirundinaria	0.0069850	0.0003323	4.76
	Viola hirta	0.0028570	0.0007985	27.95
	Viola odorata	0.0033096	0	0
One-seed generative dispersule	*Hieracium caespitosum*	0.0001065	0	0
	Melampyrum sylvaticum	0.0075550	0	0
	Phleum pratense	0.0004460	0	0
	Poa trivialis	0.0001440	0.0000581	40.35
	Galium pumilum	0.0003580	0	0
	Melampyrum nemorosum	0.0066378	0	0
	Polygala comosa	0.0014200	0	0
Generative dispersule	*Galium pumilum*	0.0003580	0	0
	Melampyrum nemorosum	0.0066378	0	0
	Polygala comosa	0.0014200	0	0

The variation of values reported in (Table 6, Fig. 3) is passed down to the model by inputing minimal and maximal values, from which individual values are drawn, following an Uniform distribution.

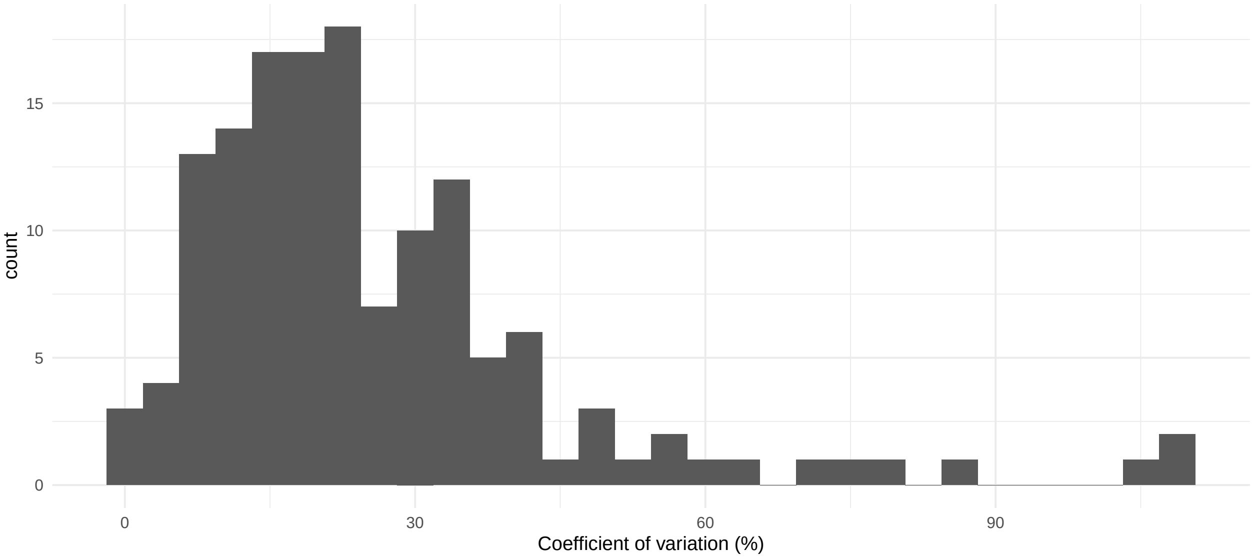

Figure 3: Distribution of coefficient of variation of measures of germinule mass reported in the LEDA database.

Table 7: Minimal and maximal sizes defined for plant functional types in Weiss et al. (2013)

Group	Seed mass (mg)	Max. size (g)
Small	0.0001	1
Medium	0.0003	2
Large	0.0010	5

Adult maximal mass

We combined the allometric relationship devised by Niklas and Enquist (2002) with the classification divised by Weiss et al. (2014) to assign species maximal (adult) weights.

Considering the biomass allometric relationship, $M_{leaf} \propto M_{stem}^{3/4} \propto M_{root}^{3/4}$ (where M_{leaf}, M_{stem}, and M_{root}, area the maximal biomasses of leaves, stems, and roots), the total maximal biomass of adult individuals is $(M_{total} = M_{organ} + 2 \times M_{organ}^{3/4}$. We used Weiss et al. (2014) size group classification Table 7 to assign organ maximal biomass (also referred to as biomass compartments) according to the species seed size. Forty-seven of the 194 species used to parameterize the model were used to devise this classification.

Seed number

Seed numbers were retrieved from the LEDA database (Kleyer et al. 2008). Similar to values of seed mass, measures from multiple ("mean value") and a single ("single value") observations, and for different types of inflorescence were reported. Because both measures are rather close 4, and there are less species for which "single value" is missing (64 out of the 936 species in the database, in opposition to 353 for which the mean value is missing), this value was used for all species.

The valuge reported varies according to the reproductive unit it was measured on. The possible reproductive units are "multiple flower stem", "ramet/tussock or individual plant", "single flower inflorescence", "multiple flower inflorescence", "per square meter", or "unknown" (Table 10 in Appendix).

The number of seeds was not measured for the same reproductive unit in all species. To make measures across species as standardized as possible, when available, we gave preferrence to values reported for "ramet/tussock or individual plant" first, "multiple flower inflorescence" or "multiple flower stem" second,

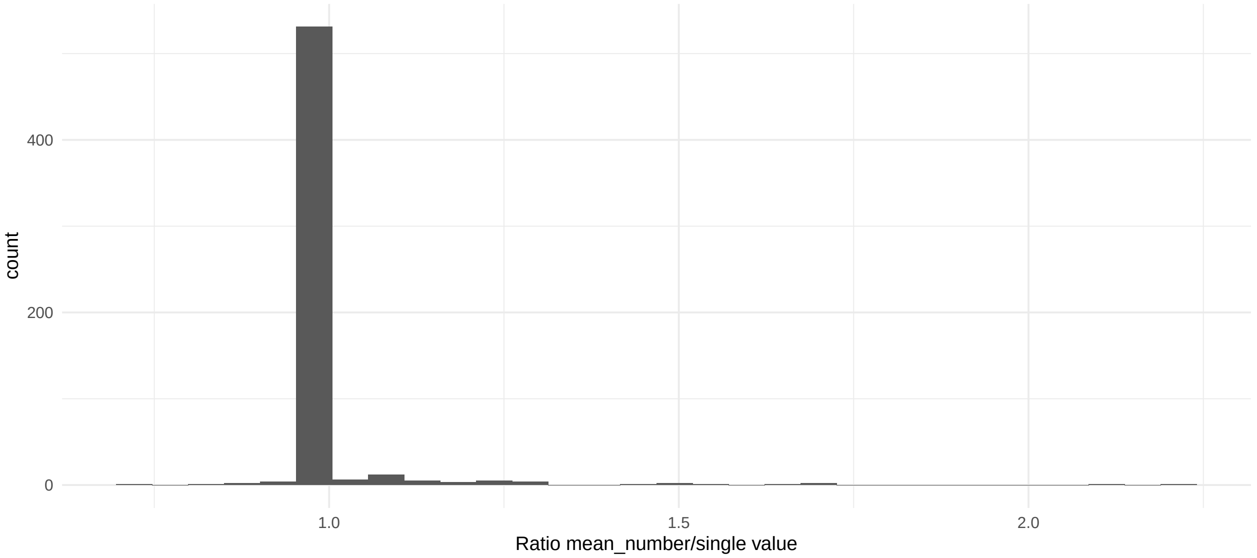

Figure 4: Ratio between values of seed number reported as "mean value" (from ultiple observations') and "single value" in the LEDA database. Ratios calculated only for species for which both values were reported.

"single flower inflorescence" third, and "unknown" at last. Measures of seed numbers taken "per square meter" where excluded because thes could not be approach to individual quantities. Similar to seed mass, the variation in trait values is passed down to the model by inputing minimal and maximal values, from which individual values are drawn, following an Uniform distribution.

Life span

Species life spans were retrieved from the LEDA database (Kleyer et al. 2008), and from the BiolFlor database (Klotz, Kühn, and Durka 2002), if not available in LEDA (detailed below). The LEDA database classification (van Groenendael, J.M.) is based upon measurements, observations, or published data: annuals, perennials, summer annuals, winter annuals, strict monocarpic bi-annuals and poly-annuals, short-lived perennials (poly-annuals < 5 years), long-lived perennials (poly-annuals > 50 years), medium-lived perennials (poly-annuals 5-50 years). In some cases, the same species is classified as both annual and perennial. Mean of span values was taken as the final value. For non-clonal or closely-knitted clones, the lifespan is the number of years of appearance of the adult.

Quantitative weekly values are necessary to control density-independent mortality during the simulation individuals older than the lifespan are killed deterministically). To achieve it, we converted LEDA's categorical classification of lifespans into weekly values by assigning values falling inside the interval defined by the categories. The variation in trait values is passed down to the model by inputing minimal and maximal values, from which individual values are drawn, following an Uniform distribution.

Missing values

Estimates of life span duration are missing for 57 species: *Achillea millefolium*, *Acinos arvensis*, *Aegopodium podagraria*, *Allium schoenoprasum*, *Anthriscus sylvestris*, *Arabis hirsuta*, *Artemisia vulgaris*, *Astragalus glycyphyllos*, *Brachypodium pinnatum*, *Briza media*, *Campanula rapunculoides*, *Campanula rotundifolia*, *Carex leporina*, *Carex ornithopoda*, *Centaurea jacea*, *Centaurea scabiosa*, *Cerastium holosteoides*, *Cichorium intybus*, *Cirsium acaule*, *Cirsium oleraceum*, *Clinopodium vulgare*, *Dactylis glomerata*, *Daucus carota*, *Elytrigia repens*, *Epilobium angustifolium*, *Equisetum arvense*, *Festuca pratensis*, *Filipendula vulgaris*, *Fragaria vesca*, *Galium mollugo*, *Galium verum*, *Geum urbanum*, *Helianthemum nummularium*, *Heracleum sphondylium*, *Hieracium lachenalii*, *Hypericum perforatum*, *Inula conyzae*, *Lotus corniculatus*, *Medicago falcata*, *Melampyrum nemorosum*, *Melampyrum sylvaticum*, *Mentha* *verticillata*, *Myosotis sylvatica*, *Onobrychis viciifolia*, *Ononis spinosa*, *Origanum vulgare*, *Plantago major*, *Plantago media*, *Poa annua*, *Poa trivialis*, *Potentilla neumanniana*, *Senecio ovatus*, *Stachys germanica*, *Tanacetum vulgare*, *Taraxacum laevigatum*, *Taraxacum officinale*, *Veronica teucrium*.

The classification of life spans in the BiolFlor database is smaller than in the LEDA database, having three, instead of five classes: annuals, biannuals, and pluriennials. For annuals and biannuals, weekly values are straightforward. For pluriennals, we atributed the same value used for LEDA's "medium-lived" perennials (30 years), to avoid the extremes of that classification, i.e. "short" and "long-lived" perennials.

Clonality

Species clonal ability was retrieved from the LEDA database (Kleyer et al. 2008), which reports the type of organ structure that enables clonal reproduction. Species that are not in listed in the LEDA database were considered to be non-clonal.

Age of first flowering

Species age of first flowering were retrieved from the LEDA database (Kleyer et al. 2008) These values are reported as intervals, but quantitative weekly values are necessary to control juvenile maturation during the simulation and to parameterize the biomass production rate (detailed in Metabolic biological rates section of Implementation verification). Weekly values were taken from an Uniform probability distribution covering the interval reported. If more than one value was reported for the same species, we use the mean value of the randomly assigned precise values. In some instances, this procedure averaged over different intervals. For that reason, if the same interval had been reported multiple times, the repetition was taken into account when calculating the mean.

Mismatching values

In some instances there was a conflict between the limit values of age of first flower and duration of life span (age of first flowering > life span). Values of age of first flowering were scaled down to fit inside the reported life span.

Flower phenology

Flower phenology, i.e. month of beginning and ending of flowering season, was retrieved from the BiolFlor database (Klotz, Kühn, and Durka 2002). Monthly ordinal values were converted to weekly values to control flowering during the simulation. Any month was assumed to contain 4.5 weeks.

Seed longevity and bank duration

Species dispersal types were retrieved from the LEDA database (Kleyer et al. 2008). The LEDA database provides two files on seed (`seed_long.txt`) and seed bank longevity, (`seed*bank.txt`). For our purposes, the files are redundant, because `seed*bank.txt` contains information on more species, including all the ones in `seed_long.txt`.

Therefore, `seed*bank.txt` is going to be used to assign seed longevity. Nevertheless, only 46 species of the 194 species listed for the calcareous grasslands in Göttingen have information on the duration of the seed-bank. The missing values will be imputed, as described in the next section.

Available data

All data retrieved from the LEDA and BiolFlor databases is listed in Appendix.

Imputation of missing trait values

Missing values are handled separately, after all the data available in LEDA and BiolFlor databases has been processed. We performed a multiple imputation of these values (Josse and Husson 2016). This procedure is performed by an iterative principal component analysis algorithm (PCA), whereby, starting from a randomly imputed value, missing values are recalculated until the algorithm converges to the principal components of the complete set of variables (Josse and Husson 2016). This procedure makes it possible to account for the global similarities between species and correlations between trait values, which can be interpreted as species trait syndromes. Imputed values, however, are not used to calibrate the model 5.

Special case: Seed number

Note that the procedure generated negative values for seed number and for seed bank duration. For the values of seed number, a separate imputation including only values of seed number and seed mass (the trait value mostly correlated to seed number) is able to retain only positive values.

For the values of seed-bank duration, however, we could not find other trait values to support multiple imputation. Thus, the mean value of all species was used.

Metabolic biological rates

The metabolic normalization constants, b_0, are taxa and region-dependent values that adapt the allometric body size-rate allometric relationship to different biological rates, for a given set of species in a given set of environmental conditions (Brown et al. 2004). Therefore, the constants should be calibrated according to a pre-defined list of temperatures and species traits values. Following, we report the calibration process for species present at calcareous grasslands in the vicinity of the city of Göttingen, Germany (Krauss et al. 2010).

Biomass growth rates

The biomass growth rate is parameterised to reproduce the Richards curve (Richards 1959), also known as generalized logistic function (S-shaped), derived from the Bertalanffy growth function and adapted to plant growth (Richards 1959).

In its original formulation, size (or weight, length, height) at any time (l_t) is defined by A, the lower asymptote; L, the upper assymptote; B_{grow}, the growth rate; t_m, the time of maximal growth; and Q, a parameter that affects the point of inflection of the curve 6:

$$l_t = A + \frac{L}{(1 + Q * e^{-B_{grow}*(t-t_m)})^{1/Q}} \tag{10}$$

We adapted plant size traits available in the literature to parameterize this equation and derive growth rates B. We used a plant's seed mass value as the lower asymptote ($size_{min}$), and the maximal size as defined by Weiss et al. (2014) (and detailed below) as the upper asymptote $size_{max}$; the age of first flowering (age_f) is set as the the time of maximum growth for all species. Parameter Q affects the height at which the point of inflection happens, while B is the rate of growth:

$$size = size_{min} + \frac{size_{max}}{(1 + Q * exp(-B_{grow} * (t - age_{1^{st} flower})^{1/Q}))} \tag{11}$$

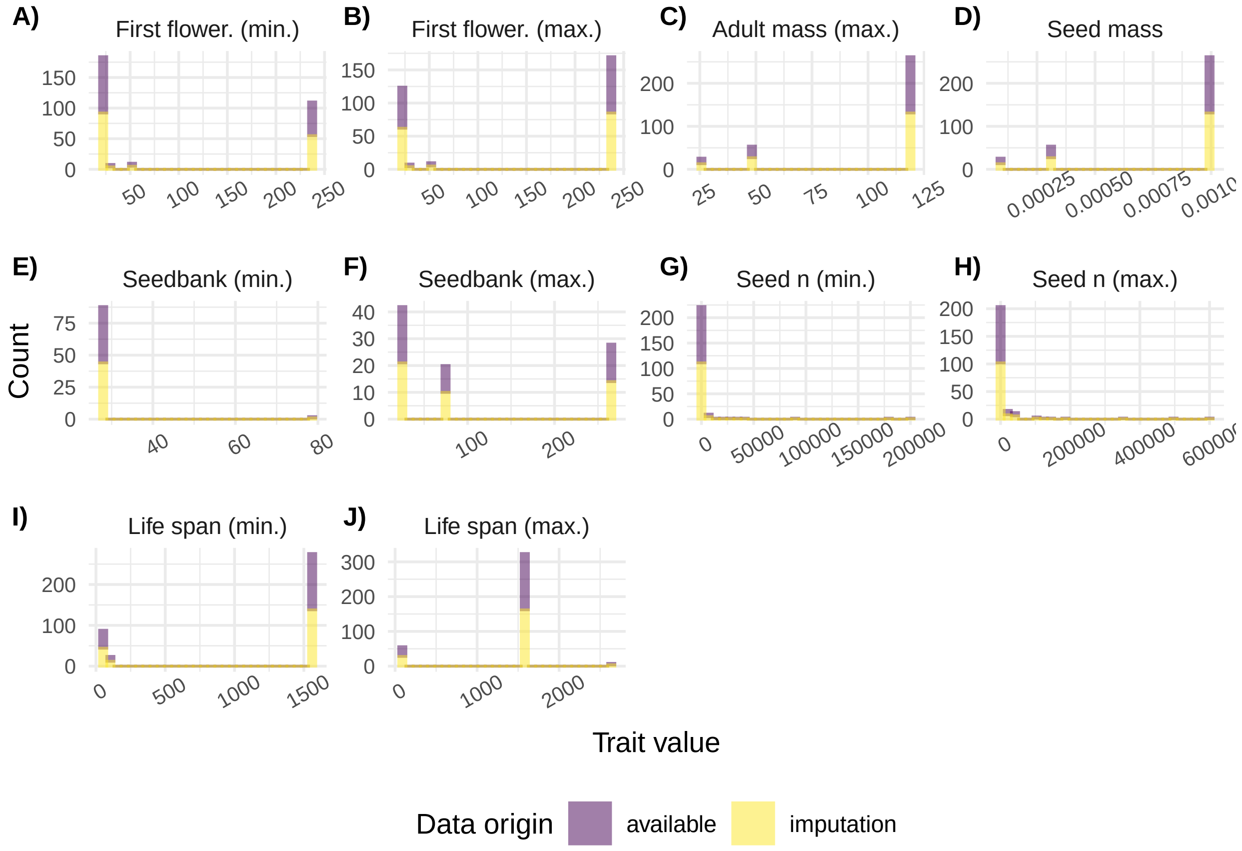

Figure 5: Comparison of the distribution of available (purple) values of each species trait and distribution of the values imputed iterative principal component analysis algorithm (yellow). Traits: A) Minimal and B) maximal age of first flowering (days), C) adult biomass, D) seed biomass, E) minimal and F) maximal duration of seedbank (weeks), G) minimal and H) maximal number of seeds, I) minimal and J) life span (weeks).

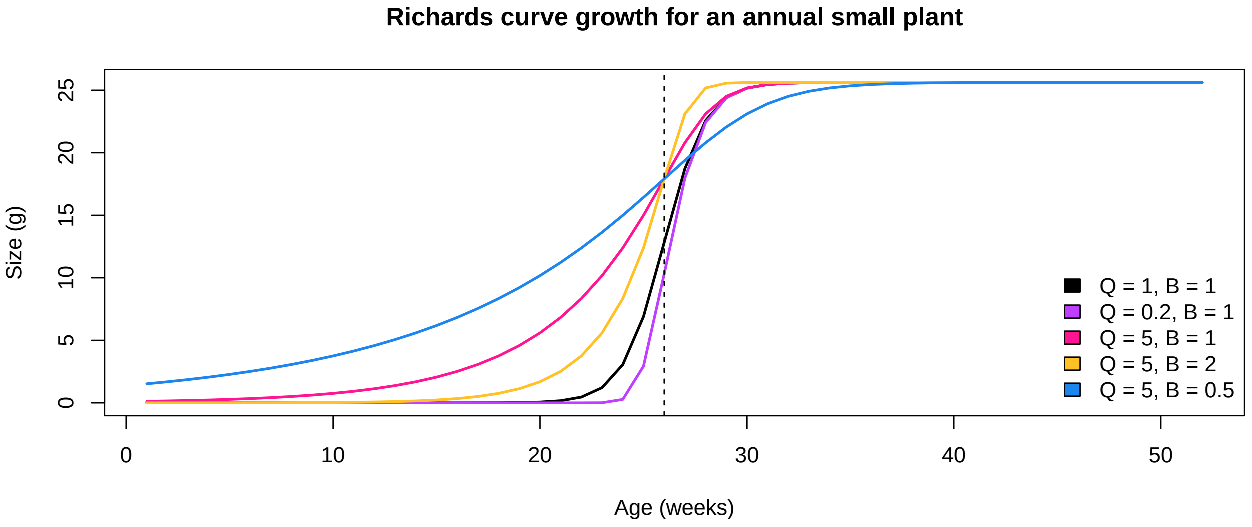

Figure 6: Sensitivity analysis of Richards growth curves calculated on weekly time steps, to different values of growth rate (B_{grow}) and the height at which the point of inflection happens (Q). The time of maximal growth (t_m) is fixed at 26, for all curves.

Growth calculated for the first time-step is particularly sensitive to the value of B_{grow} (see Fig. 6). We use $Q = 5$, as it generates higher growth during the juvenile phase of development (before the age of first flowering).

Out of the five parameters used to model the Richards curve, three can be related to plant traits available in the databases we consulted: age of first flowering, and minimal and maximal sizes. We used these three traits to identify "growth groups", i.e. groups of species that should grow between their respective minimal and maximal sizes, within the time frame of the age of first flowering. By reclassfying values of age of first flowering into one month (4 weeks) interval classes and combining it with the three size classes available (7, we obtained thirteen "growth groups" (each bin in Fig. 7 is a group).

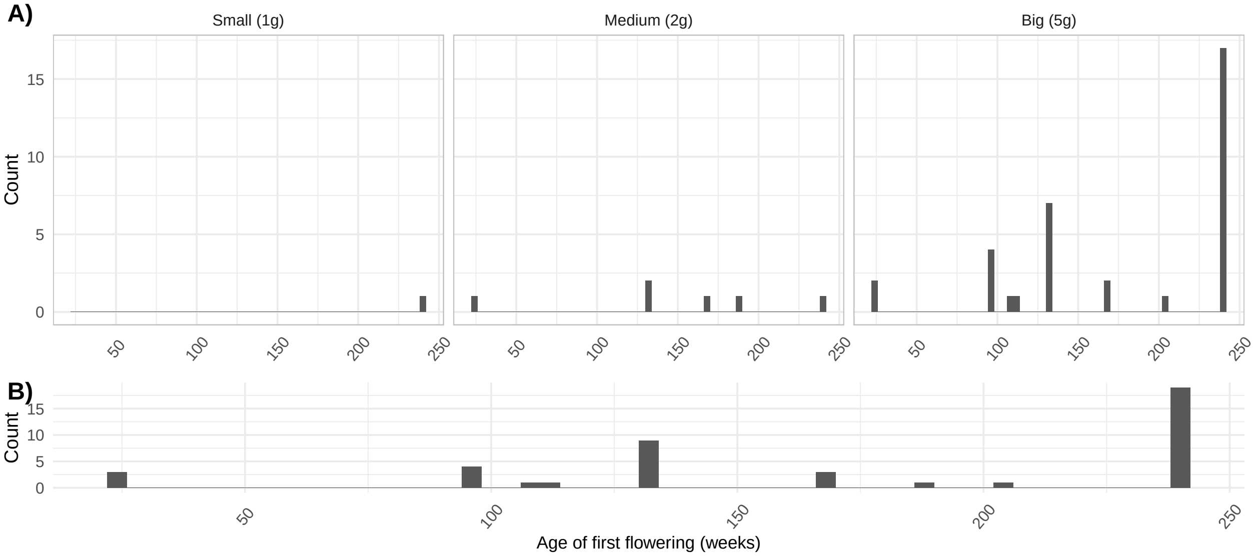

Figure 7: Growth groups characterized by age of first flowering and species sizes. A) Distribution of values of age of first flowering among species of each size group (small, medium, and large). Each bin covers an interval of 4 weeks (one month). In combination, groups of age of first flowering and groups of size give rise to 13 groups of growth. B) Overall distribution of age of first flowering, showing only eight groups of values of age of first flowering

Ideally, the growth curve would have its maximal rate of growth at the age of first flowering, and maximal size would be achieved before plants reached their maximal life span. The Richards curves has a parameter to control the first ($t_m = age_f$), but not the latter. Nonetheless, the Richards curve assures that the maximal asymptote (maximal size) is achieved shortly after the point of inflection ($t_m = age_f$, Fig. 8).

Calibration of growth normalization constants

The B value chosen above was fitted to a model (the Richards curve) that assumes continuous growth (constant rate). In the EDM model, however, growth rate depends on environmental temperature and the individual's biomass. For temperature regions, this means that growth is concentrated in warmer months and drastically decreased during colder ones (biomass actually drops due fall frost and winter dieback). When calibrating the growth normalization constant b_0, therefore, we must account for the fact that the rate must somehow balance itself during the whole year. Thus, we calibrate it using the year mean temperatures: in higher temperatures, the growth rate increases above the mean, in lower temperatures, it decreases. A caveat of this approach is the assumption of the same growth rate for all species, regardless of age of first flowering or plant size, as in (. This generates different normalization constants according to species sizes. While the proposition of metabolic theory is to use one normalization value per biological rate, variations in this values are expected at small scales (Brown et al. 2004; Sibly 2012b). Despite this shortcoming, the parameters thus chosen generate growth curves that approximate the Richard curves we indented to reproduce in the first place (Table 8, Fig. 11).

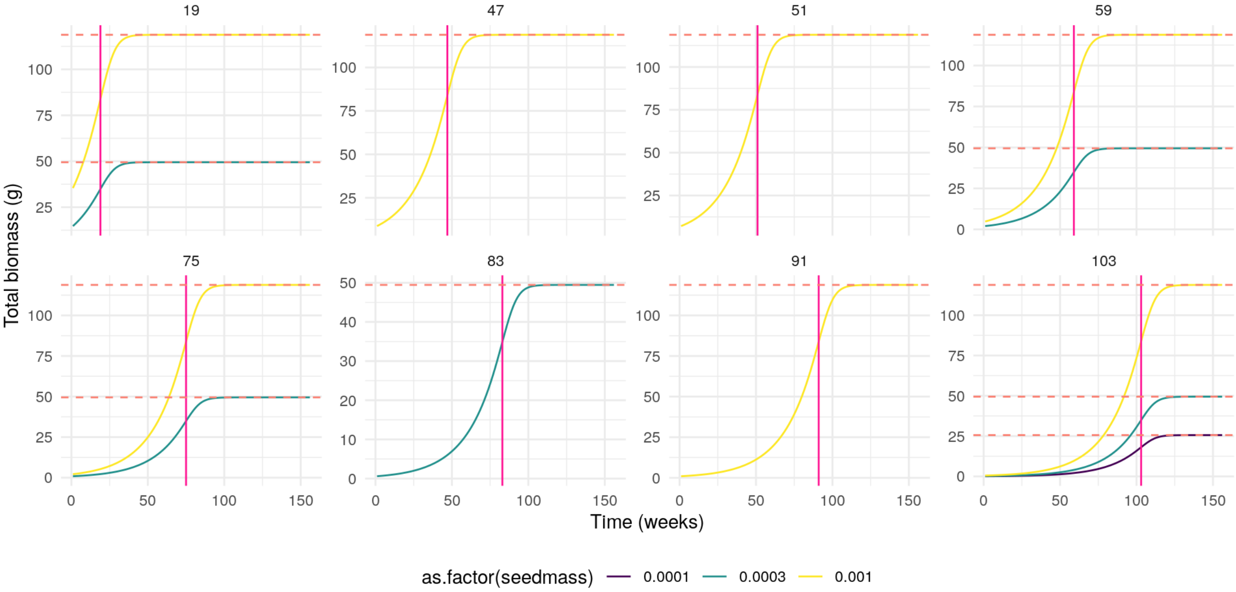

Figure 8: Comparison of tri-annual Richards growth curves calculated on weekly time steps, for the 13 growth groups (each line is a group) defined for the model based on seed (colours) and maximal adult sizes (dashed lines), and age of first flowering (pink lines, values identified above the plot). All growth curves calculated with growth rate $B_{grow} = 0.25$; the point of inflection of the curve $Q = 5$, and time of maximal growth (t_m) set to the group's age of first flowering.

Table 8: Growth parameters derived for the size-based growth groups.

Size group	Seed mass (g)	Growth rate (B)	Normalization constant (b_0)	Max. size (g)
Small (1g)	0.0001	0.25	4531446957	25.62341
Medium (2g)	0.0003	0.25	5963719581	49.45742
Big (5g)	0.0010	0.25	8058178821	118.80302

Species temperature niche

Species have a temperature niche, defined by temperature optimum and tolerance, which affects species performance as described in Mortality submodel description. To define these values, we searched the GBIF database for the species distribution, and the WordClim database for the mean annual temperatures (T_{loc_μ}), minimal temperature in the coldest month ($T_{loc_{min}}$), and maximal temperature in the warmest month ($T_{loc_{max}}$) of the retrieved locations. We used a combination of species name and the taxonomic key, to ensure all occurrence data was retrieved.

The species optimum temperature is the mean values of all mean values reported for its locations:

$$T_{opt} = \frac{\sum_{x=i}^{n_{loc}} T_{loc_\mu}}{n_{loc}} \tag{12}$$

where n_{loc} is the number of locations reported for the distribution of a species.

Following, it is necessary to choose the values that will represent the species temperature tolerance (T_{tol}), which is used as the standard deviation of the Gaussian function used to calculate the species fitness (Eq.). In a Normal distribution, the value of standard deviation approximates $^1/_6$ of the range of the distribution it generates. Thus, we use the species global temperature range $max(T_{loc_{max}}) - min(T_{loc_{min}})$ to calculate its tolerance as

$$T_{tol} = \frac{max(T_{loc_{max}}) - min(T_{loc_{min}})}{6}. \tag{13}$$

The minimal and maximal values generated by using the temperature tolerance based on the species' temperature range (Eq. 13) provide a better match to observed limits than the values generated by using the temperature tolerance based on the standard deviation around the mean temperature of the species location $sd(T_{loc_\mu})$ (Fig. 9, Table (11 in Appendix).

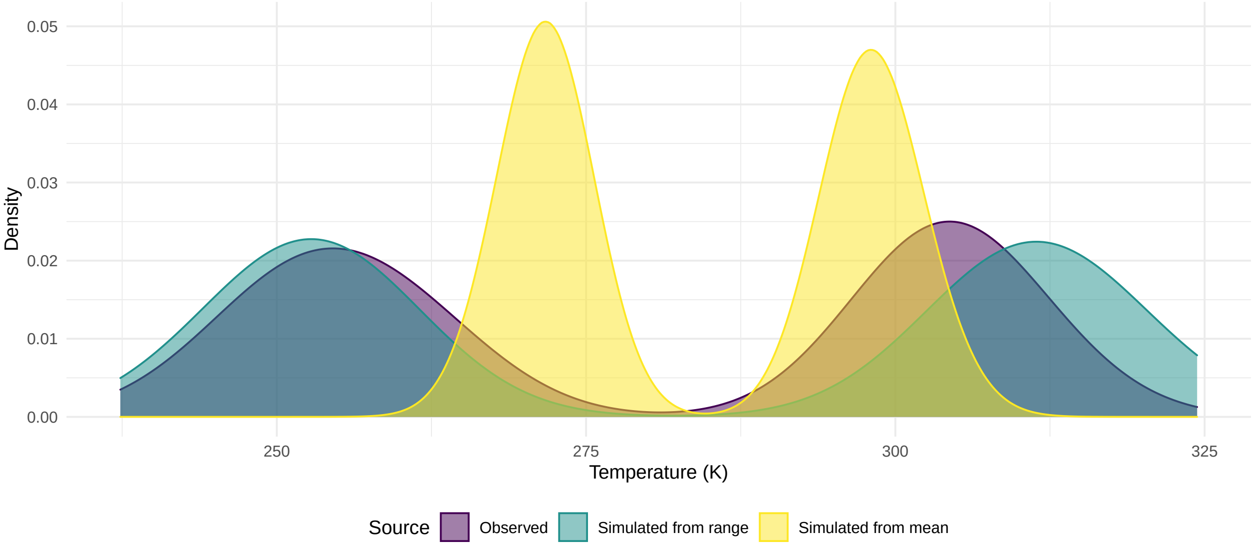

Figure 9: Comparison between the minimal and maximal temperatures of the species locations retrieved from rgbif and WordClim ("Observed", purple); the minimal and maximal values generated by a draw (n=1000) on the Normal distribution using as mean, the species temperature optimum (T_{opt}), and as standard deviation, the temperature tolerance (T_{tol}) calculated from the temperature range of the species locations ($T_{range}/_6$, "Simulated from range", green); and the minimal and maximal values generated by a draw (n=1000) on the Normal distribution using as standard deviation, the temperature tolerance calculated as the standard deviation around the mean temperatures on the species locations ($sd(T_{loc_\mu})$, "Simulated from mean", yellow).

Germination & Mortality

From the allometry study reported by Marba, Duarte, and Agusti (2007), we were able to derive a normalization constant for germination, $b_0 germ$, and for mortality, $b_0 mort$. The germination and mortality rates generated by these constant are reported in the section "Implementation verification".

Implementation verification

Summary The model relies on a series of probability functions that have been parameterized to yield values inside biologically realistic ranges for dispersal kernels, as well as growth, mortality and germination rates. These values are verified in here.

Dispersal kernels

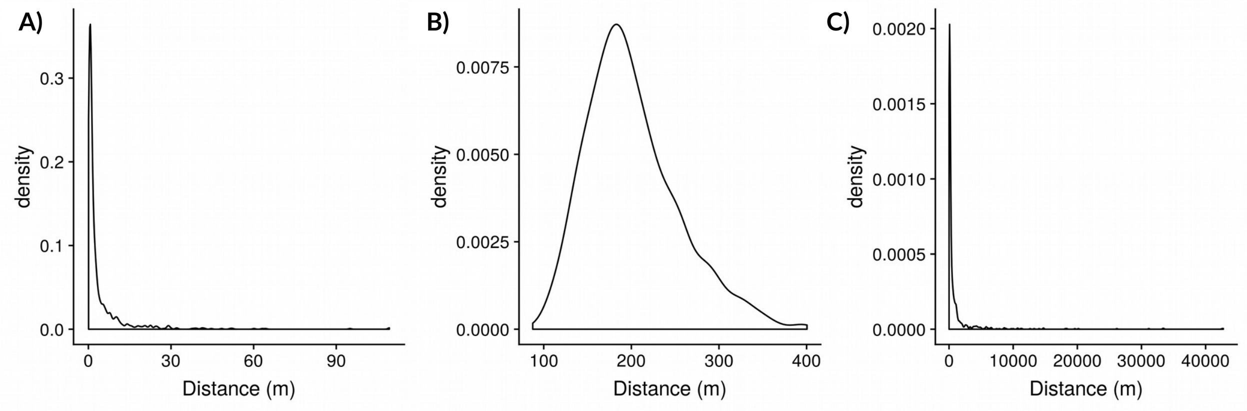

Figure 10: Density distribution of the values arising from draws ($n = 1000$) from the Inverse Gaussian distribution parameterized with the values used to simulate A) short, B) medium, and C) long distance dispersal. In the model, the Inverse Gaussian distribution is simulated with the 'Distributions' package of the Julia language.

Biomass growth

To verify the growth curve yielded by our model, we simulate the growth curve of seeds belonging to each of the size group (small, medium, and large), during a 10 year period, for the Göttingen temperature time-series used for model development (Fig. 11). This simplified simulation includes the loss of biomass during winter dieback, which is not taken into account by the calculation of the S-shaped curve alone.

Germination and mortality rates

The realized rates of germination and mortality are verified at minimal and maximal temperatures used in the simulations reported in Figueiredo et al. *in prep*, for all biomass groups and developmental stages (Fig. 12).

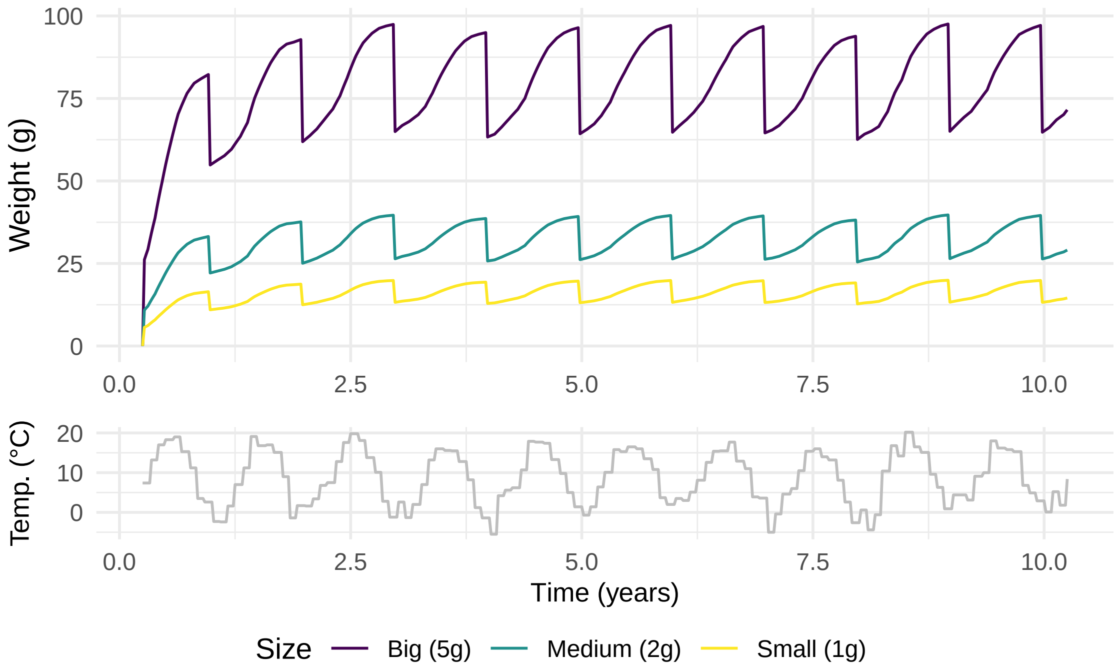

Figure 11: Verification of the simulated growth curves of seeds belonging to the three group sizes used to parameterize the Extinciton Dynamics Model ("Small", "Medium", and "Big") over 10 years, under the temperature time-series used to develop the model (DWD, 2018).

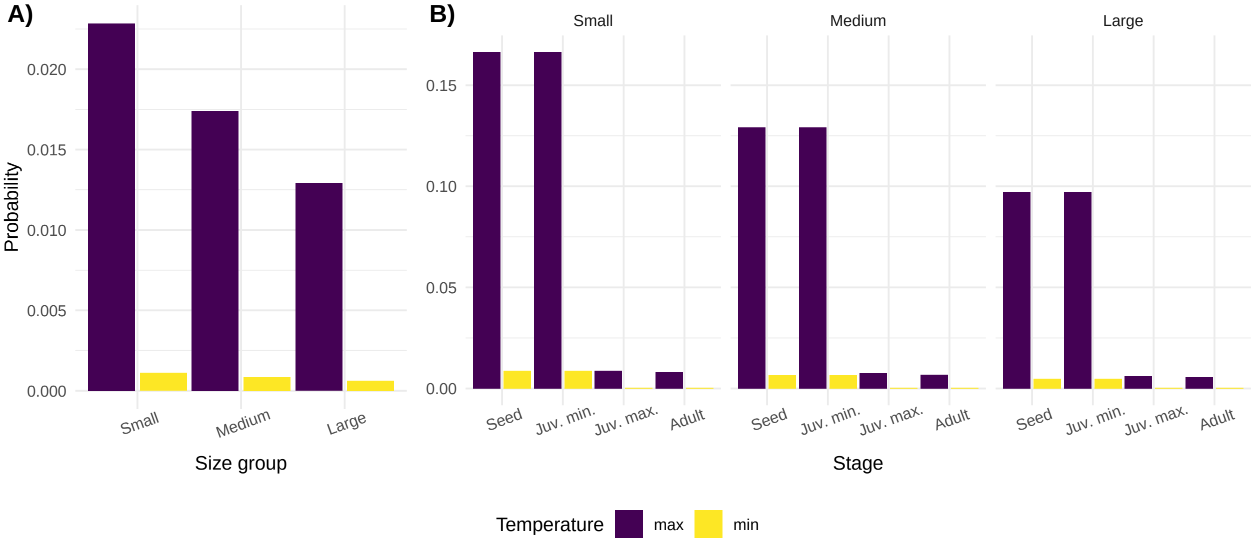

Figure 12: Germination (A) and mortality (B) rates yielded by the model, for the three biomass groups, at the minimum and maximal temperatures used for calibration. Mortality rates (B) are also distinguished among different stages, because they differ in biomass, and thus, in the resulting metabolic rate as well. In that regard, "Juv. min." refers to juveniles minimal biomass (the same as seeds), and "Juv. max.", to juveniles maximal biomass, which approaches 70% of the adult's maximal biomass, according to the Richards growth curve.

Model output verification

Summary: In this section, we report how much model outputs match observations following the parameterization and inverted callibration reported in Data evaluation.

Species composition

We verified the models capability of reproducing real-world communities by comparing the community composition of communities of similar sizes through Eucledian and Bray-Curtis distances. Values of Eucledian distance, based on species identities, are smaller than Bray-Curtis distances, which are based on species relative biomass (in the simulated communities) and relative density cover (in the real-world communities, Table 9).

Table 9: Mean ecological distances (Euclidean and Bray-Curtis) between simulated and empirical communities. Simulations of 484m² were compared to communities of patches smaller than 500m², and simulations of 961 m² were compared to communities of patches of sizes between 500m² and 1000 m².

Patch size	Distance	Mean value
$\leqslant 500\text{m}^2$	Euclidean	0.4099476
	Bray-Curtis	0.9062022
$\geqslant 500\text{m}^2, \leqslant 1000\text{m}^2$	Euclidean	0.4269850
	Bray-Curtis	0.9066383

Species rank abundances

We verified the quality of species ranked curves through five aspects calculated by the "codyn" R package (`RAC_change()` function, Hallet et al. 2020). The function was written for temporal comparisons, but we applied to simulated and empirical communities (pair-wise comparisons between each simulated community and one empirical community of similar size) and report the mean values of:

- "Richness change": the difference in richness between simulated and empirical communities, divided by the total number of unique species in both communities. A positive value indicates simulated communities had higher species richness, and a negative value, lower.
- "Evenness change": the difference in evenness between the simulated and empirical communities. Eveness itself is constrained between 0 and 1. A positive value of change indicates eveness is higher in simuated communities, and a negative value, lower.
- "Rank change": the absolute value of the average difference in species ranks between simulated and empirical communities divided by the total number of unique species in both communities.
- "Gains": the number of species present in the simulated community, but not in the empirical, divided by the total number of unique species in both.
- "Losses": it contains the number of species not present in the simulated community, but present in the empirical, divided by the total number of unique species in both.

Species trait space

Being a trait-based model, one of the most important feats of the model is reproducing the trait space of the real-world communities the simulations are set up to reproduce. To verify it, we performed a Principal Component Analysis of the trait spaces of simulated communities with the trait space of species reported by Krauss et al. (2004) for 31 calcareous grasslands in the vicinity of the city of Göttingen (Germany). We compared the trait space of simulated communities in the control scenarios and communities reported for patches of areas smaller than 484 m² and 961 m² (Fig. 14-19). We also compared the trait space of simulated communities under different intensities of habitat loss and of habitat and pollination loss (Fig. 20-23) and the trait space estimated for the communities reported by Krauss et al. (2004) in patches of different area sizes (Fig. 24-25).

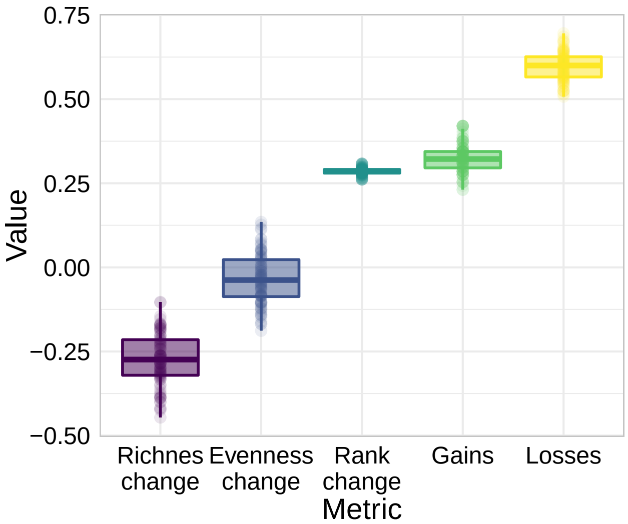

Figure 13: Comparison between species ranked curves of large simulated (484m^2) and empirical communities ($\geqslant 500\text{m}^2, \leqslant 1000\text{m}^2$), measured as relative difference in species richness, absolute difference in evenness, relative difference ranked biomass, relative gains and relative losses. Instead of abundances, the metrics of evenness and ranked biomass were calculated from species relative biomass for simulated data and species relative cover for empirical communities.

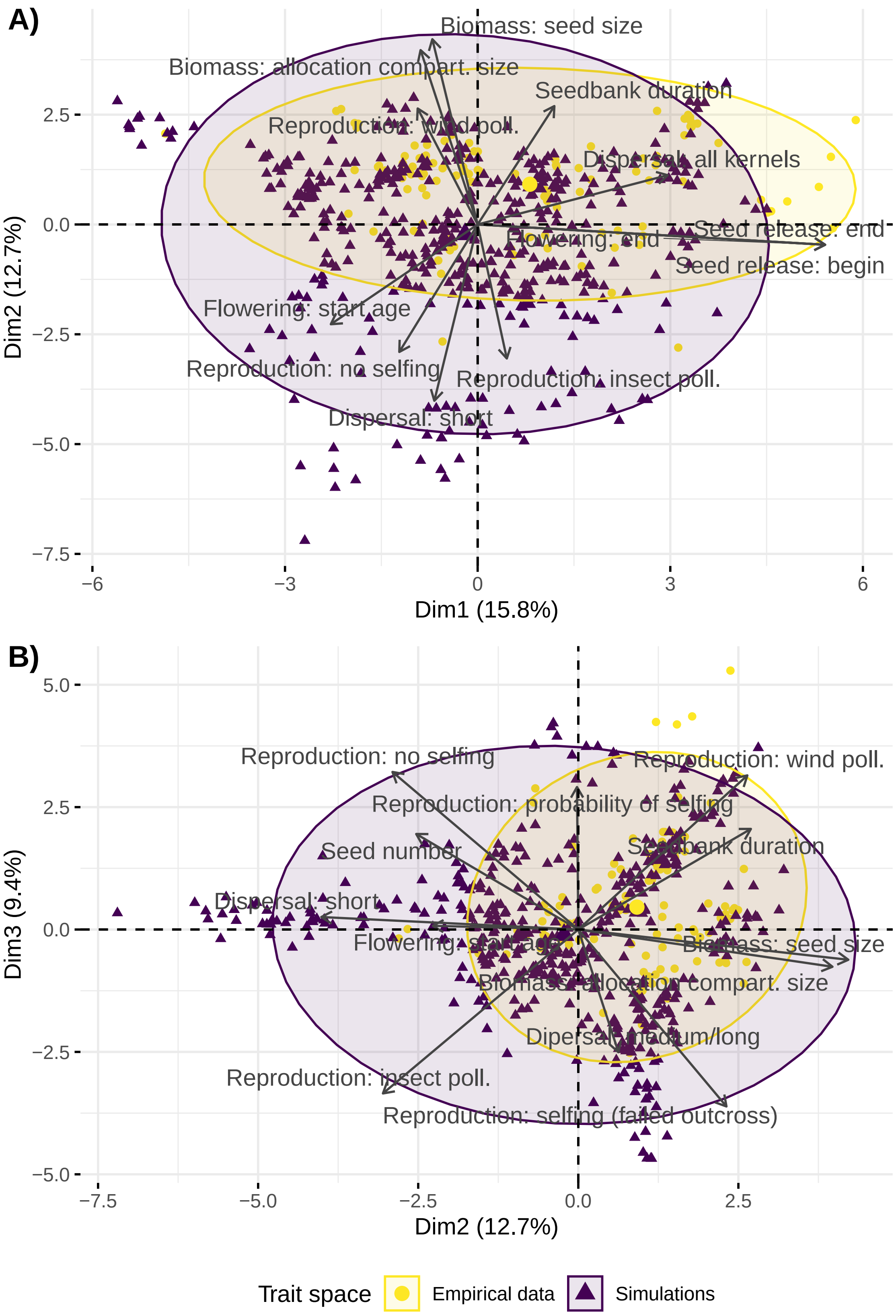

Figure 14: Analysis of A) 1^{st} (Dim. 1) and B) 2^{nd} (Dim. 2) and B) 2^{nd} (Dim. 2) and 3^{rd} (Dim. 3) principal components of the trait space of all communities simulated (dark purple) and the trait space estimated for real-world communities(yellow). Percentages indicate the amount of variance explained by each axis. Out of the 24 variables used to define the trait space, only the 12 most contributing ones were included, to facilitate visualization.

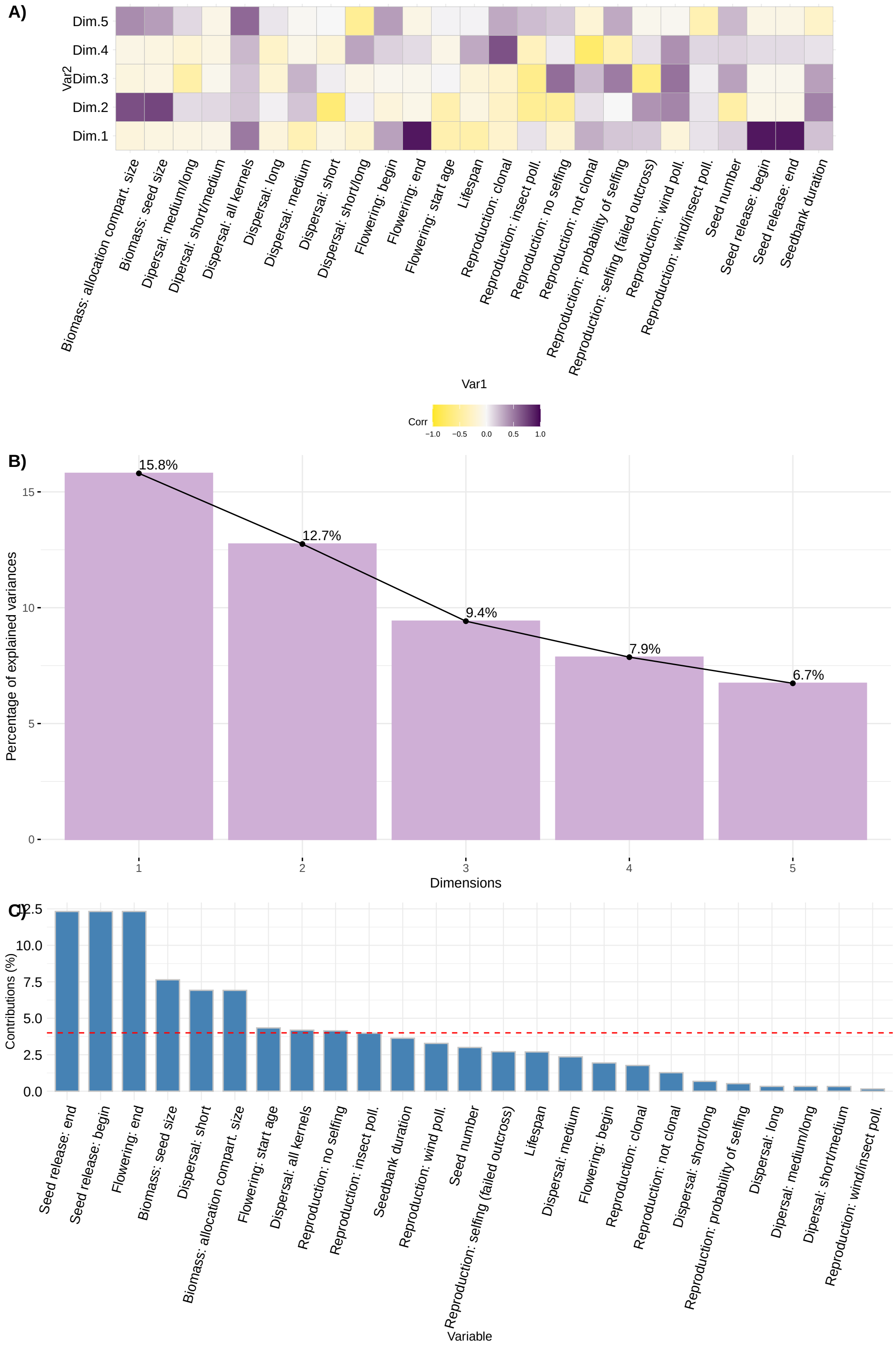

Figure 15: Representation of variables in the analysis of principal components (PCA) of the trait space of simulated communities (484 m² and 961 m²) and the trait space estimated for real-world communities (smaller than 961m²): A) Correlation between traits and the principal components defined by the PCA, B) scree plot showing percentage of variance explained by each principal component defined by the PCA, and C) percentage of contribution of each trait to the first two principal components.

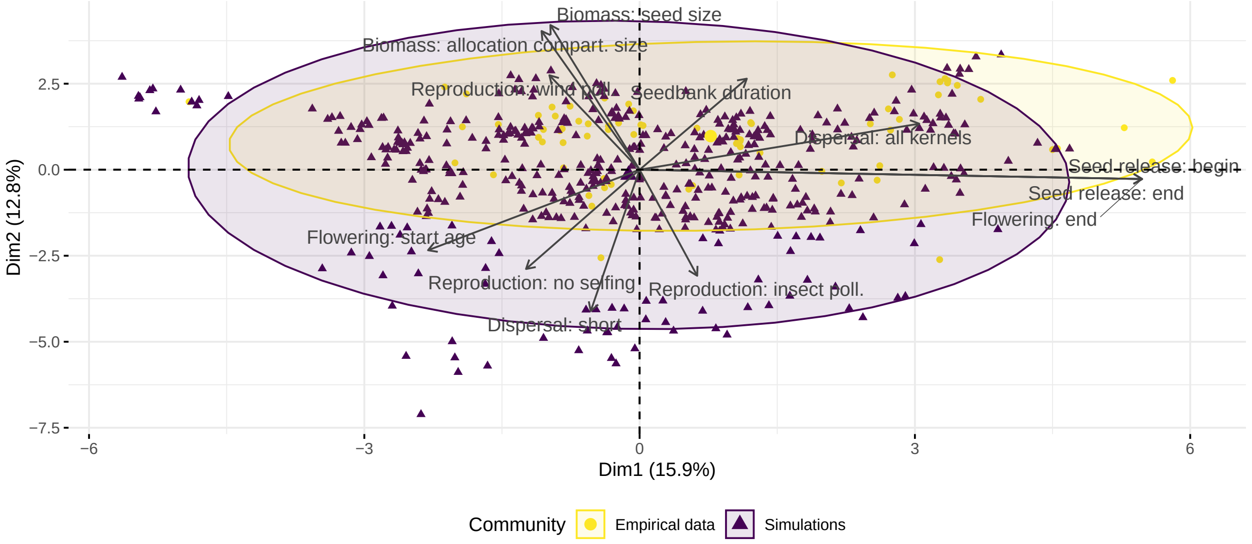

Figure 16: Analysis of the 1^{st} (Dim. 1) and 2^{nd} (Dim. 2) principal components of the trait space of a community simulated in a landscape of 484 m² (dark purple) and the trait space estimated for real-world communities (yellow). Percentages indicate the amount of variance explained by each axis. Out of the 24 variables used to define the trait space, only the 12 most contributing ones were included, to facilitate visualization.

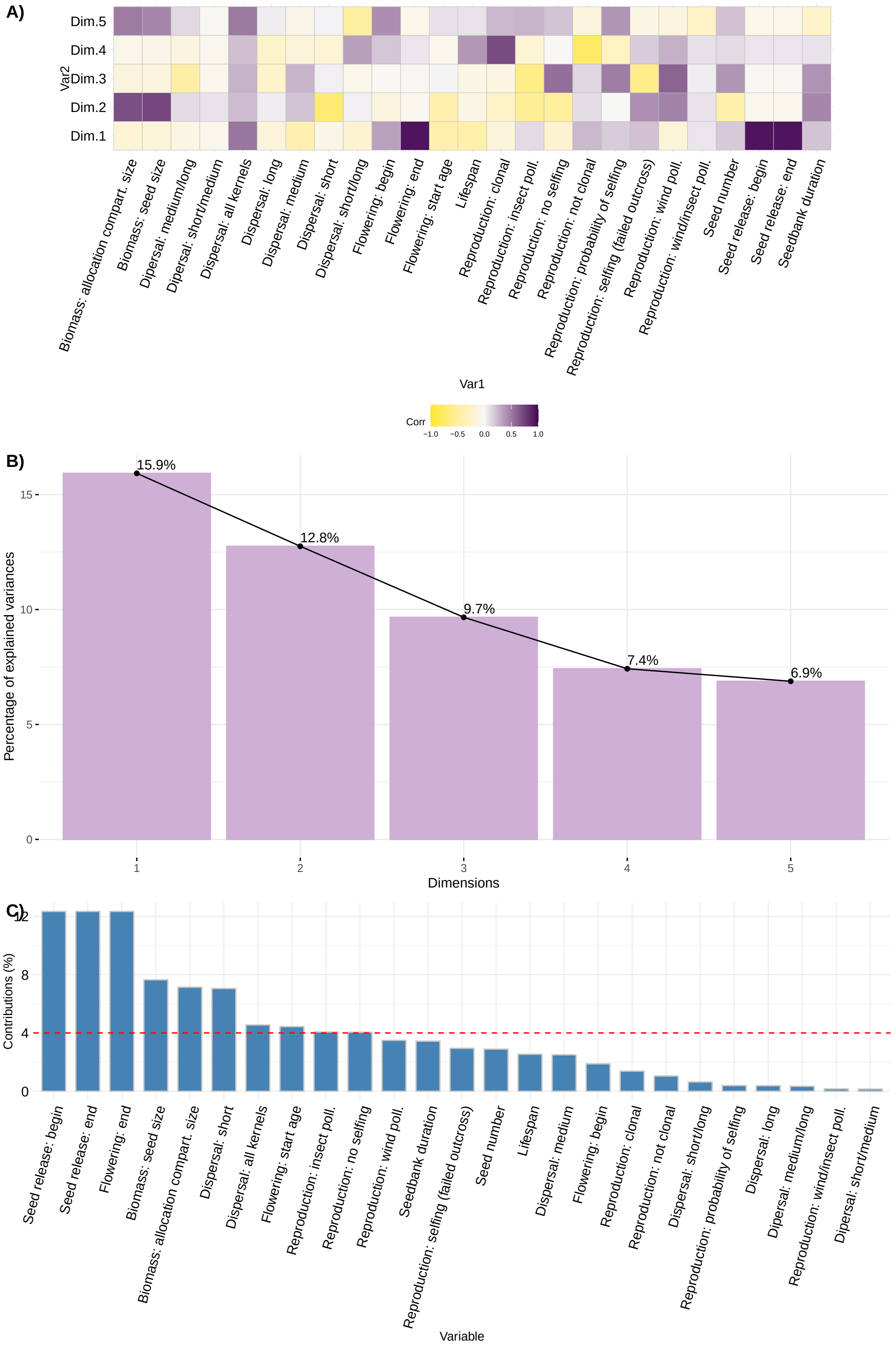

Figure 17: Representation of variables in the analysis of principal components (PCA) of the trait space of simulated small communities (484 m²) and the trait space estimated for real-world communities (smaller than 500 m²): A) Correlation between traits and the principal components defined by the PCA, B) scree plot showing percentage of variance explained by each principal component defined by the PCA, and C) percentage of contribution of each trait to the first two principal components.

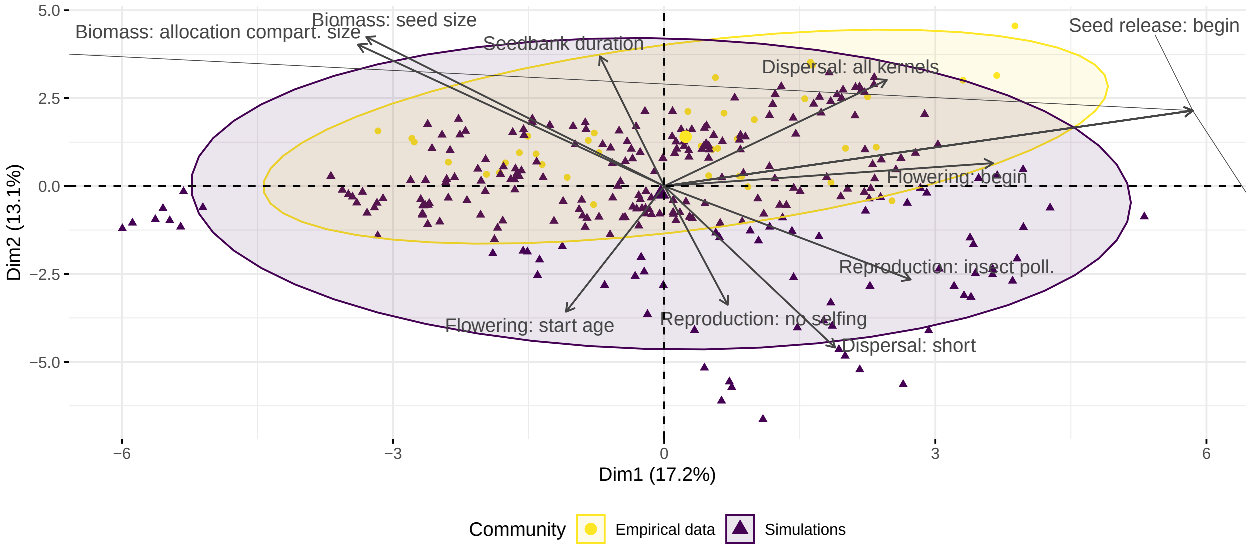

Figure 18: Analysis of the 1^{st} (Dim. 1) and 2^{nd} (Dim. 2) principal components of the trait space of a community simulated in a landscape of 961 m² (dark purple) and the trait space estimated for real-world communities(yellow). Out of the 24 variables used to define the trait space, only the 12 most contributing ones were included, to facilitate visualization.

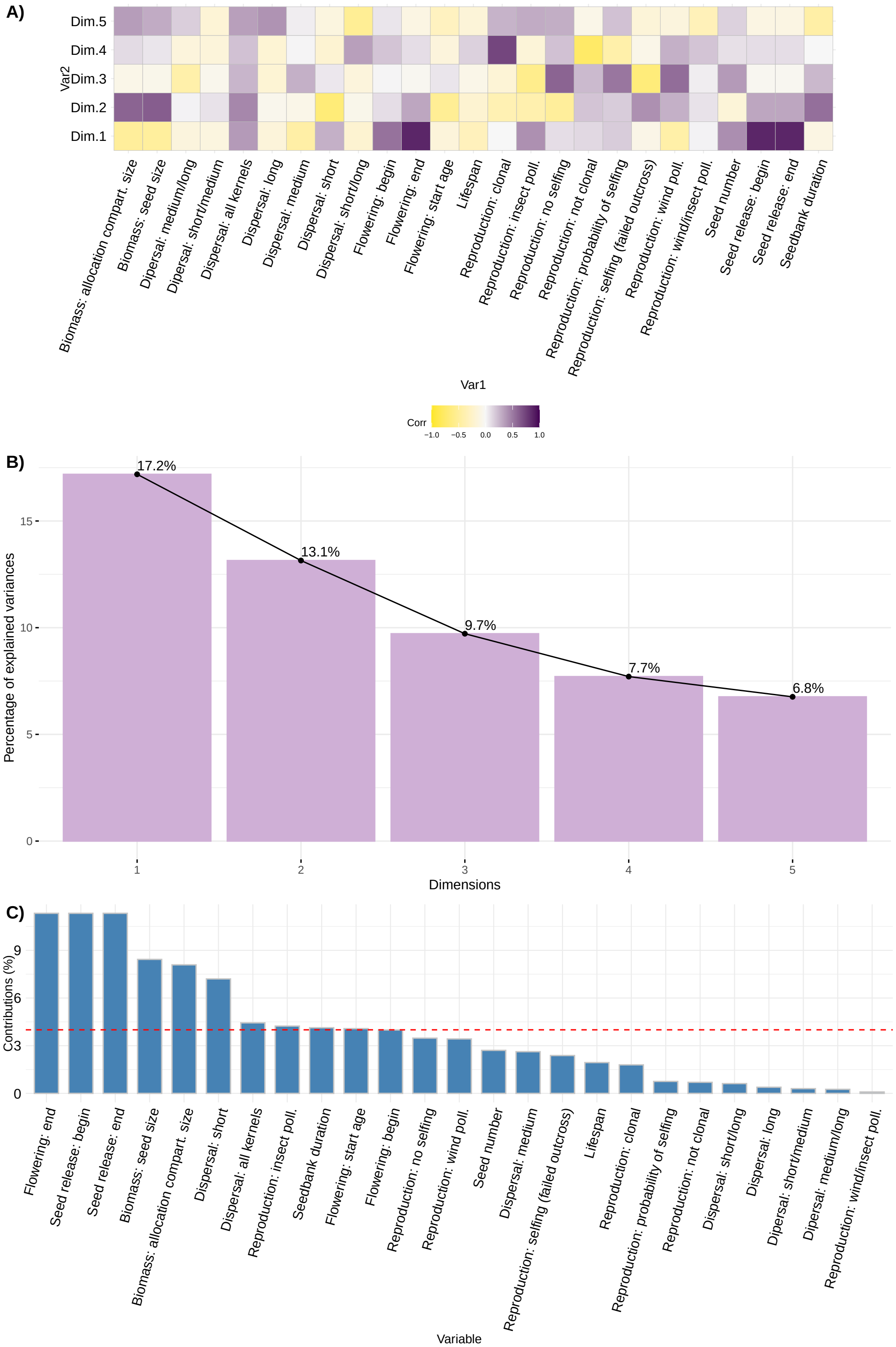

Figure 19: Representation of variables in the analysis of principal components (PCA) of the trait space of simulated communities (961 m²) and the trait space estimated for real-world communities (bigger than 500 m² and smaller than 961 m²): A) Correlation between traits and the principal components defined by the PCA, B) scree plot showing percentage of variance explained by each principal component defined by the PCA, and C) percentage of contribution of each trait to the first two principal components.

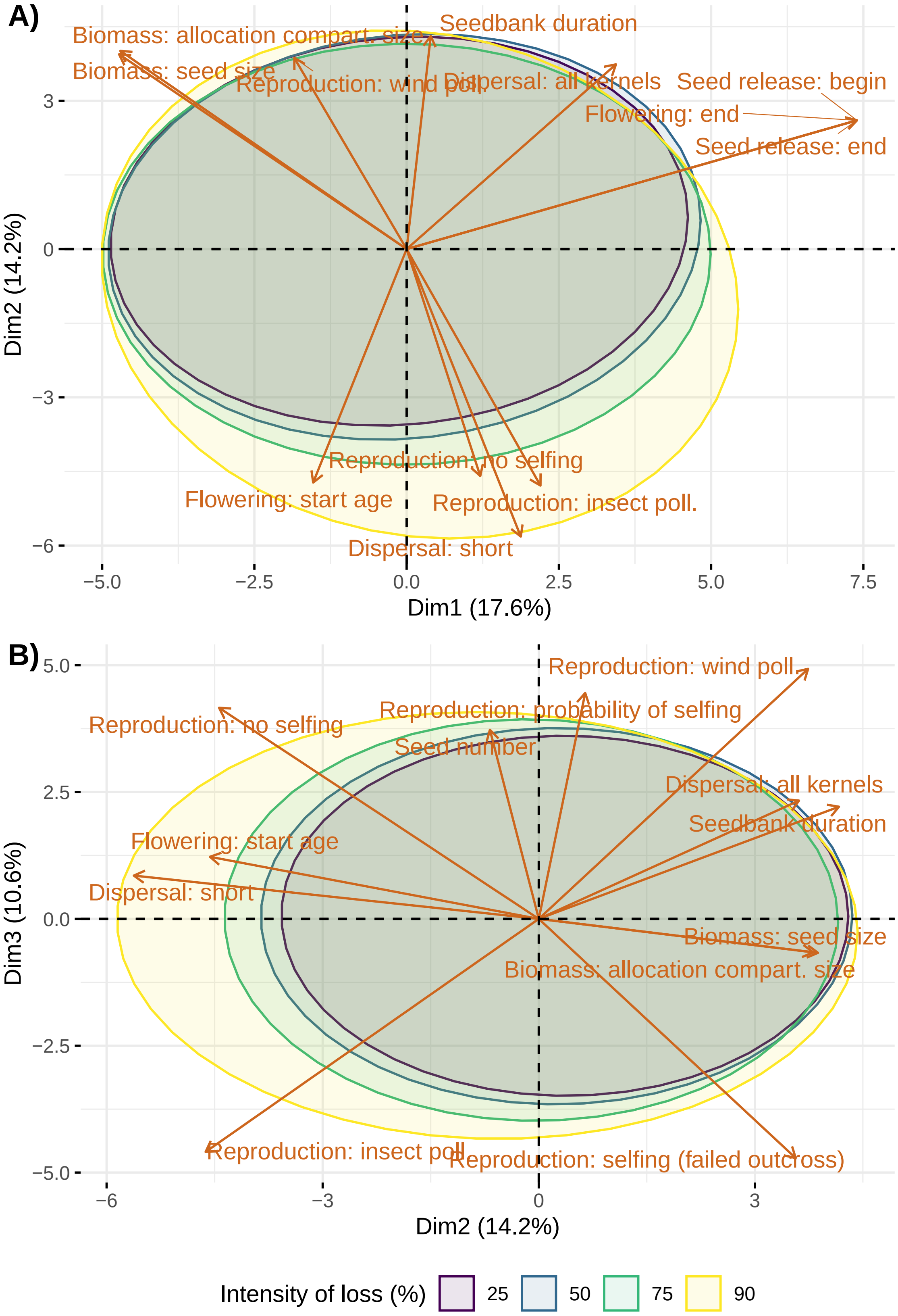

Figure 20: Analysis of A) 1^{st} (Dim. 1) and 2^{nd} (Dim. 2) and B) 2^{nd} (Dim. 2) and 3^{rd} (Dim. 3) principal components of the trait space estimated for the surviving communities in simulated communities under 25%, 50%, 75%, and 90% of loss of habitat area. Percentages indicate the amount of variance explained by each axis.

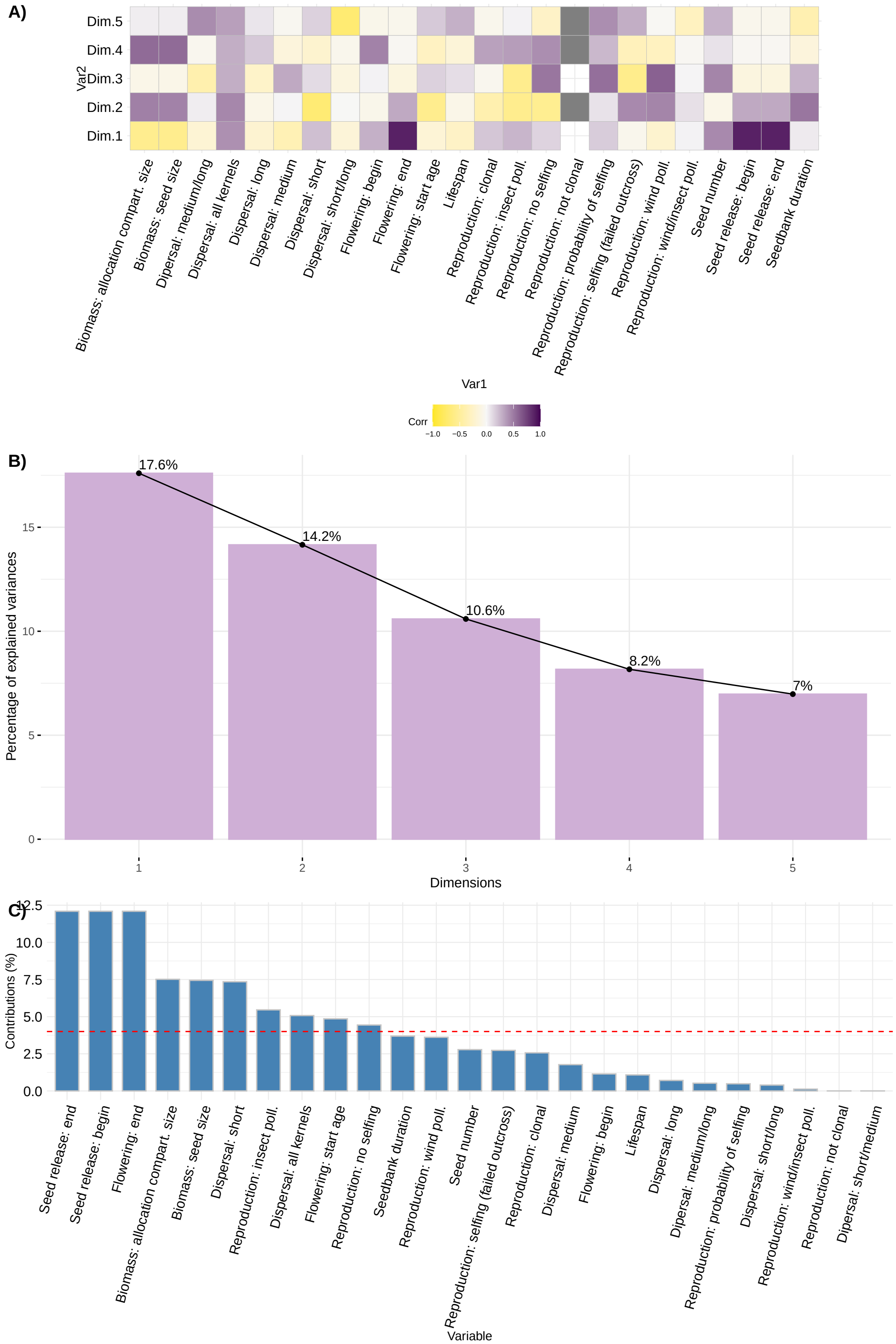

Figure 21: Representation of variables in the analysis of principal components (PCA) of the trait space estimated for surviving communities in simulated communities under 25%, 50%, 75%, and 90% of loss of habitat area: A) Correlation between traits and the principal components defined by the PCA, B) scree plot showing percentage of variance explained by each principal component defined by the PCA, and C) percentage of contribution of each trait to the first two principal components.

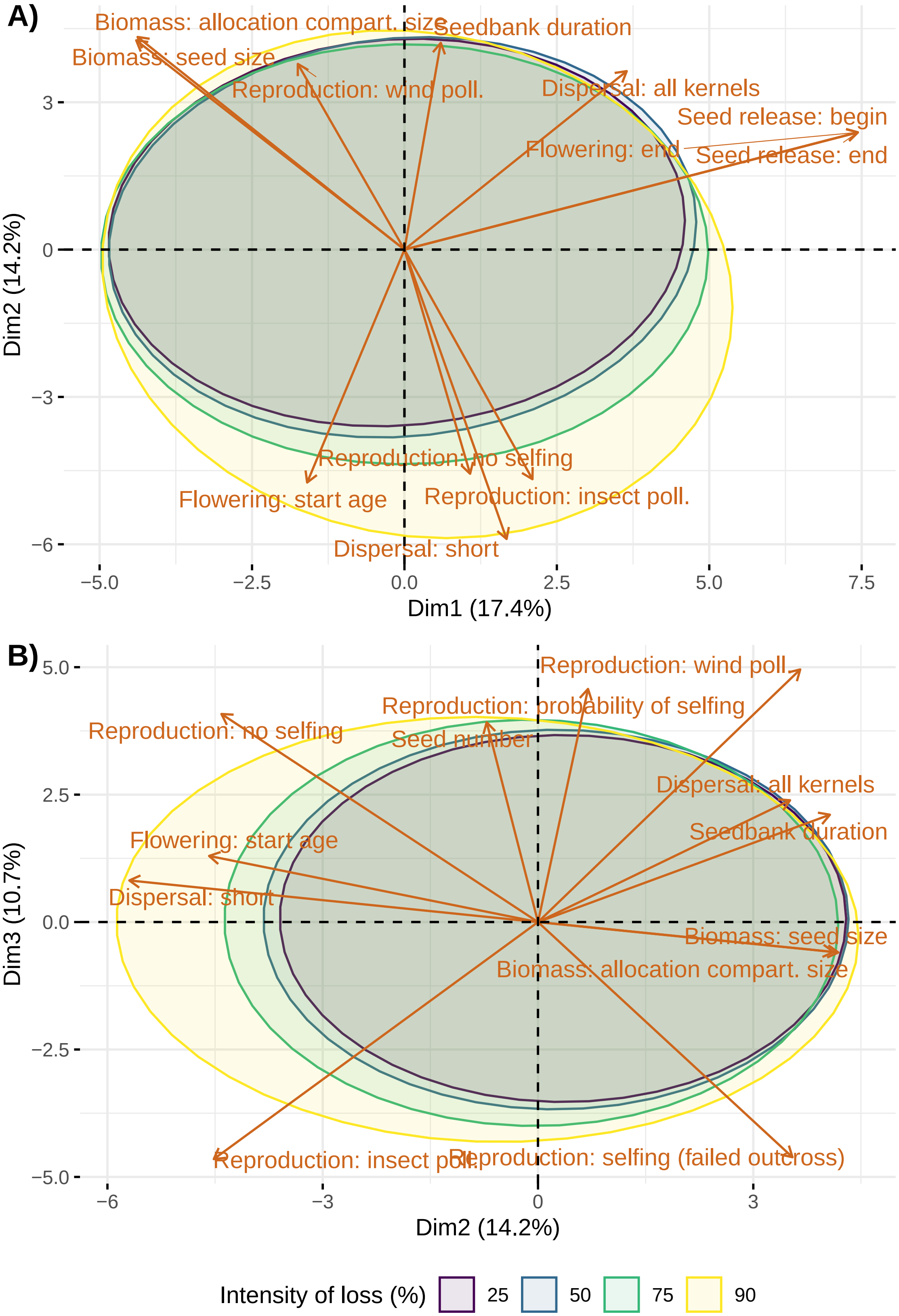

Figure 22: Analysis of A) 1st (Dim. 1) and 2nd (Dim. 2) and B) 2nd (Dim. 2) and 3rd (Dim. 3) principal components of A) the trait space estimated for the surviving communities in simulated communities under 25%, 50%, 75%, and 90% of loss of habitat area and pollination services. Percentages indicate the amount of variance explained by each axis.

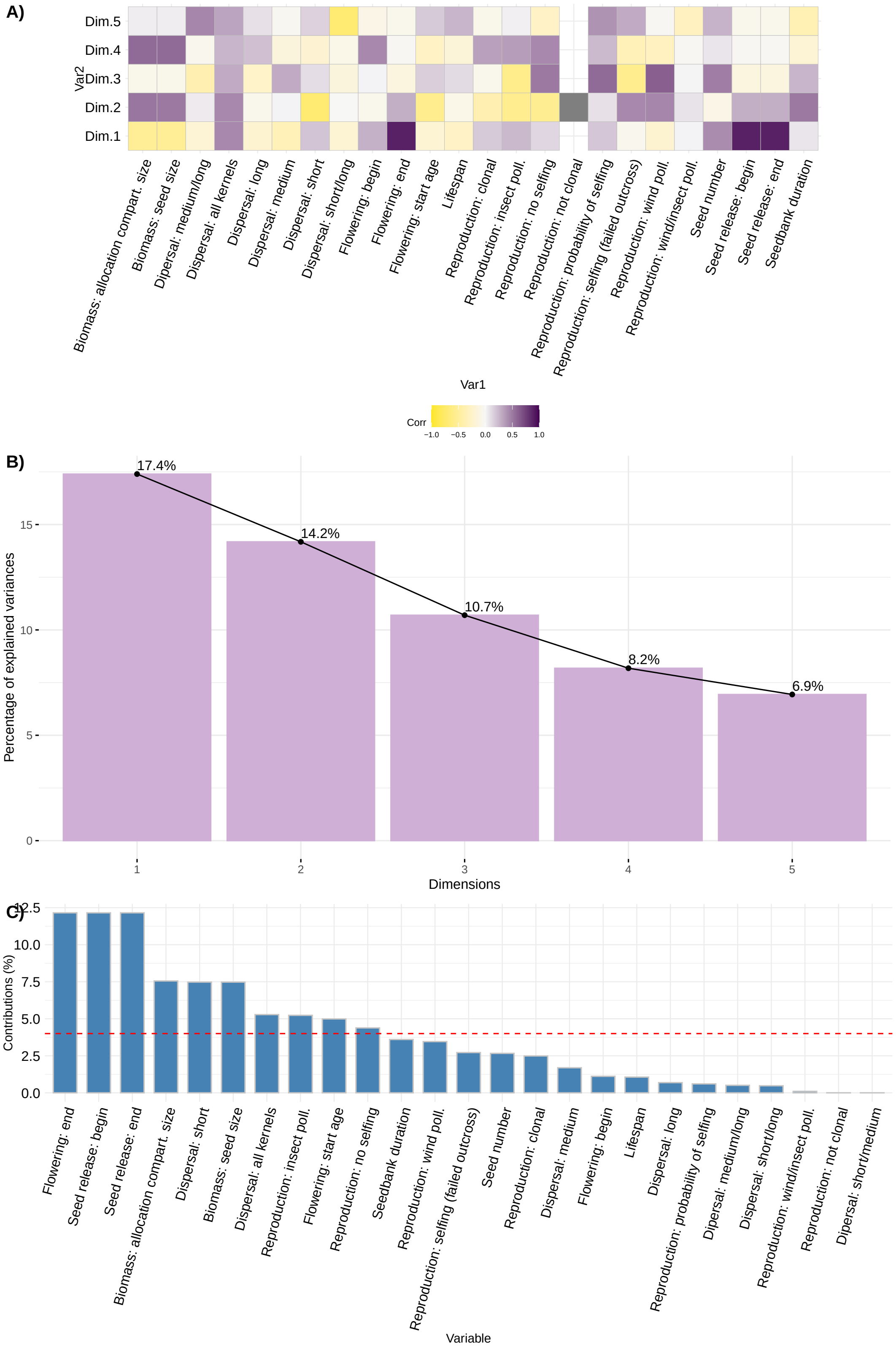

Figure 23: Representation of variables in the analysis of principal components (PCA) of the trait space estimated for surviving communities in simulated communities under 25%, 50%, 75%, and 90% of loss of habitat area and pollination services: A) Correlation between traits and the principal components defined by the PCA, B) scree plot showing percentage of variance explained by each principal component defined by the PCA, and C) percentage of contribution of each trait to the first two principal components.

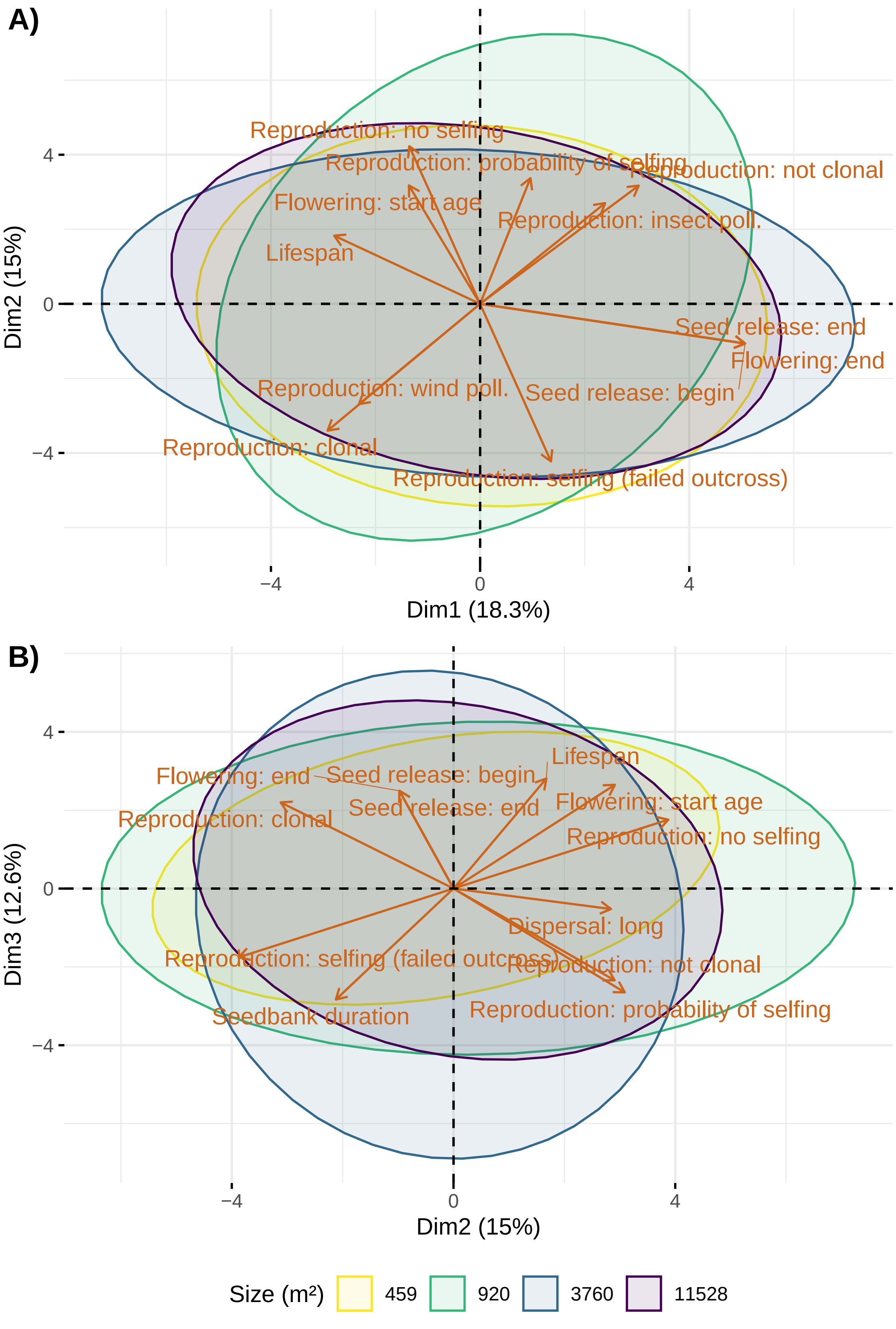

Figure 24: Analysis of A) 1^{st} (Dim. 1) and 2^{nd} (Dim. 2) and B) 2^{nd} (Dim. 2) and 3^{rd} (Dim. 3) principal components of the trait space estimated for empirical communities sampled in calcareous grasslands of sizes falling into the 10th, 25th, 50th, and 75th percentiles of the areas reported in Krauss et al. (2004).

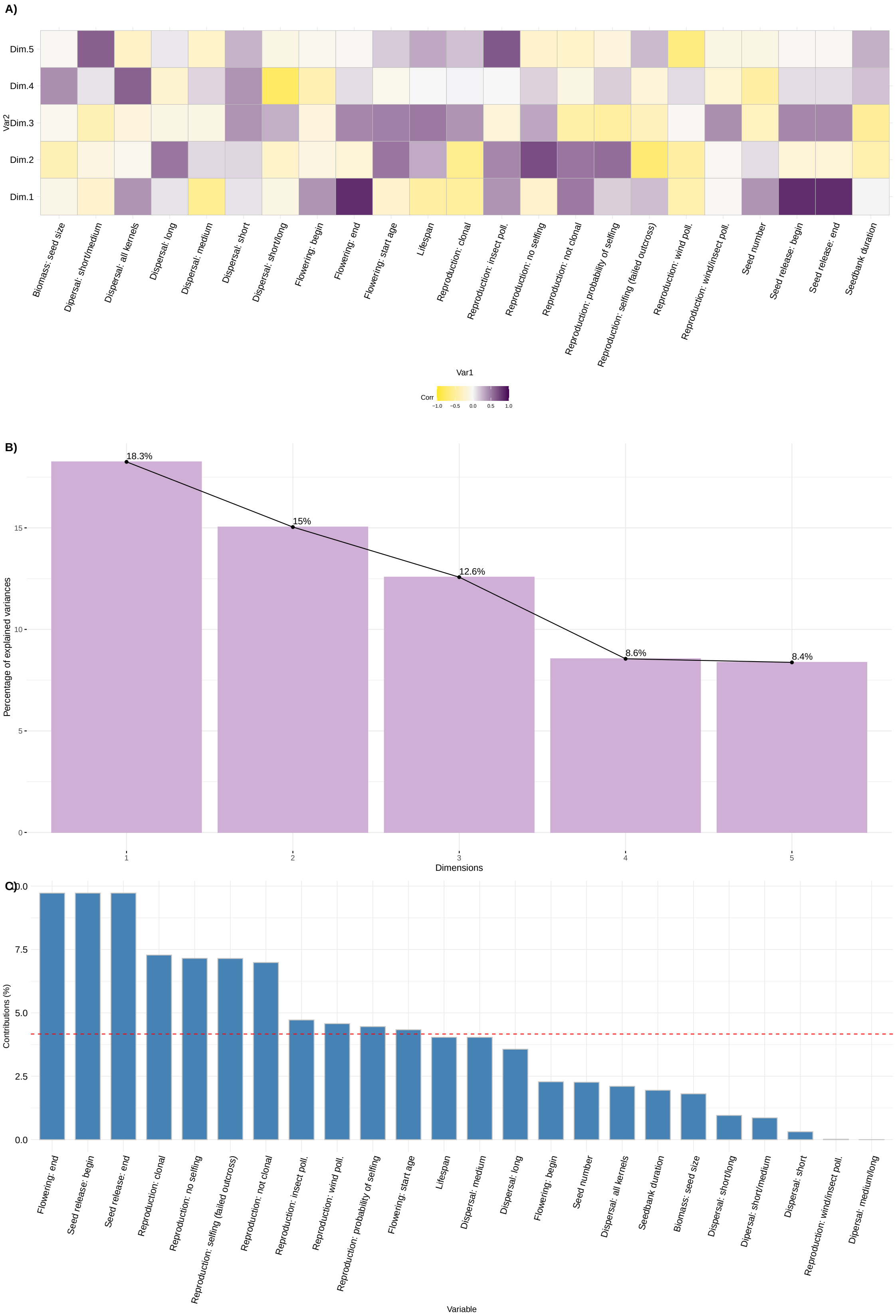

Figure 25: Representation of variables in the analysis of principal components (PCA) of the trait space estimated for empirical communities sampled in calcareous grasslands of sizes falling into the 10th, 25th, 50th, and 75th percentiles of the areas reported in Krauss et al. (2004): A) Correlation between traits and the principal components defined by the PCA, B) scree plot showing percentage of variance explained by each principal component defined by the PCA, and C) percentage of contribution of each trait to the first two principal components.

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Appendix

Table 10: Summary of variation (mean, standard deviation, minimal, and maximal) values of seed number reported in the LEDA database for the species included in the parameterization of the Extinction dynamics Model.

Species	Reproductive unit	Mean, Std. dev.	Min. - Max.)
Achillea millefolium	Multiple flower stem	822.0, 0	822.00 - 822.00
	Ramet or individual plant	2473.01, 1923.9155	190.00 - 7200.00
Acinos arvensis	Ramet or individual plant	342.00, 0	342.00 - 342.00
Actaea spicata	Ramet or individual plant	574.25, 884.159252	108.00 - 1900.00
	Single flower inflorescence	12.0, 0	12.00 - 12.00
Aegopodium podagraria	Multiple flower inflorescence	317.00, 68.69	240.00 - 402.00
	Multiple flower stem	199.9, 29.357755	164.00 - 253.00
	Ramet or individual plant	2075.16, 3589.60	46.50 - 10700.00
Agrimonia eupatoria	Multiple flower stem	50.00, 0	50.00 - 50.00
	Ramet or individual plant	66.00, 0	66.00 - 66.00
	Single flower inflorescence	2.00, 0	2.00 - 2.00
Ajuga genevensis	Multiple flower stem	221.0, 0	221.00 - 221.00
	Multiple flower inflorescence	21.00, 0	21.00 - 21.00
Ajuga reptans	Ramet or individual plant	56.75, 32.6	36.00 - 105.00
Allium schoenoprasum	Multiple flower stem	162.00, 0	162.00 - 162.00
	Ramet or individual plant	4149.0, 0	4149.00 - 4149.00
Alopecurus pratensis	Ramet or individual plant	414.00, 0	414.00 - 414.00
Anchusa arvensis	Ramet or individual plant	557.0, 286.00	128.00 - 700.00
	Single flower inflorescence	4.0, 0	4.00 - 4.00
Antennaria dioica	Ramet or individual plant	280.0, 0	280.00 - 280.00
Anthoxanthum odoratum	Multiple flower inflorescence	14.55, 2.68	9.00 - 19.60
	Ramet or individual plant	401.88, 432.510958	108.00 - 1038.50
Anthriscus sylvestris	Multiple flower inflorescence	229.5, 113.84	149.00 - 310.00
	Multiple flower stem	2457.00, 0	2457.00 - 2457.00
	Ramet or individual plant	3053.57, 3723.62	132.10 - 10000.00
	unknown	5400.0, 0	5400.00 - 5400.00
Anthyllis vulneraria	Multiple flower inflorescence	16.6, 0	16.60 - 16.60
	Ramet or individual plant	112.00, 115.965512	30.00 - 194.00
Arabis hirsuta	Ramet or individual plant	750.00, 0	750.00 - 750.00
Arrhenatherum elatius	Ramet or individual plant	10.0, 0	10.00 - 10.00
Artemisia vulgaris	Multiple flower inflorescence	200000.0, 0	200000.00 - 200000.00
	Ramet or individual plant	358333.3, 150692.84	200000.00 - 500000.00
Astragalus glycyphyllos	Ramet or individual plant	10315.00, 0	10315.00 - 10315.00
Avenula pubescens	Multiple flower inflorescence	47.90, 7.465923	43.50 - 59.00
	Ramet or individual plant	4000.00, 0	4000.00 - 4000.00
Bellis perennis	Multiple flower inflorescence	200.00, 0	200.00 - 200.00
	Multiple flower stem	125.00, 0	125.00 - 125.00
	Ramet or individual plant	1288.00, 0	1288.00 - 1288.00
Brachypodium pinnatum	Multiple flower stem	87.0, 0	87.00 - 87.00
Briza media	Ramet or individual plant	3743.50, 5040.96	179.00 - 7308.00
Falcaria vulgaris	Ramet or individual plant	2000.0, 0	2000.00 - 2000.00
Festuca ovina	Multiple flower inflorescence	38.2, 23.4	1.00 - 75.00
	Multiple flower stem	62.0, 0	62.00 - 62.00
	Ramet or individual plant	847.0, 0	847.00 - 847.00
Festuca rubra	Multiple flower inflorescence	7.2, 0	7.20 - 7.20
	Ramet or individual plant	465.0, 0	465.00 - 465.00
Filipendula vulgaris	Ramet or individual plant	324.43, 183.34	113.00 - 439.30
Fragaria vesca	Multiple flower stem	174.43, 64.89	115.40 - 243.90
	Ramet or individual plant	290.5, 53.3	225.00 - 341.00
Galeopsis ladanum	Ramet or individual plant	300.0, 0	300.00 - 300.00
Galium aparine	Ramet or individual plant	441.64, 307.13	31.00 - 1000.00
	Single flower inflorescence	2.0, 0	2.00 - 2.00
Galium mollugo	Ramet or individual plant	10867.00, 12916.012	1734.00 - 20000.00
Galium verum	Multiple flower inflorescence	550.0, 0	550.00 - 550.00
	Ramet or individual plant	58.35, 64.7	12.60 - 104.10
	Single flower inflorescence	2.0, 0	2.00 - 2.00
Gentianella ciliata	Single flower inflorescence	670.0, 0	670.00 - 670.00

Gentianella germanica	Ramet or individual plant	347.0, 187.95	160.00 - 594.00
	Single flower inflorescence	99.0, 0	99.00 - 99.00
Geranium dissectum	Ramet or individual plant	336.25, 443.2	95.00 - 1000.00
	Single flower inflorescence	5.0, 0	5.00 - 5.00
Geranium molle	Multiple flower inflorescence	16.0, 0	16.00 - 16.00
Geranium molle	Ramet or individual plant	90.5, 13.44	81.00 - 100.00
	Single flower inflorescence	4.0, 1.41	3.00 - 5.00
Geranium pratense	Single flower inflorescence	3.0, 0	3.00 - 3.00
Geranium pusillum	Ramet or individual plant	525.0, 318.2	300.00 - 750.00
Geranium robertianum	Ramet or individual plant	132.72500, 119.263165	30.00 - 300.00
	Single flower inflorescence	5.0, 0	5.00 - 5.00
Geum urbanum	Multiple flower stem	558.0, 0	558.00 - 558.00
	Ramet or individual plant	248.25, 107.84	172.00 - 324.50
Gymnadenia conopsea	Ramet or individual plant	31699.0, 0	31699.00 - 31699.00
	Single flower inflorescence	2480.0, 2093.04	1000.00 - 3960.00
Helianthemum nummularium	Ramet or individual plant	243.0, 0	243.00 - 243.00
	Single flower inflorescence	17.5, 3.54	15.00 - 20.00
Heracleum sphondylium	Ramet or individual plant	5216.0, 3508.38	850.00 - 10005.00
	Single flower inflorescence	2.0, 0	2.00 - 2.00
Hieracium caespitosum	Ramet or individual plant	612.0, 0	612.00 - 612.00
Hieracium pilosella	Multiple flower inflorescence	71.75, 22.99	55.50 - 88.00
	Ramet or individual plant	48.27, 21.83	21.00 - 75.00
Hippocrepis comosa	Ramet or individual plant	120.0, 0	120.00 - 120.00
	Single flower inflorescence	6.0, 0	6.00 - 6.00
Holcus lanatus	Multiple flower inflorescence	112.2, 0	112.20 - 112.20
	Ramet or individual plant	177000.0, 0	177000.00 - 177000.00
Hypericum perforatum	Ramet or individual plant	20933.6, 12189.77	3036.00 - 33000.00
	Single flower inflorescence	211.33, 210.57	56.00 - 451.00
Knautia arvensis	Multiple flower inflorescence	58.7, 0	58.70 - 58.70
	Ramet or individual plant	826.84, 914.92	66.00 - 2000.00
Koeleria pyramidata	Multiple flower stem	209.5, 0	209.50 - 209.50
Lathyrus pratensis	Multiple flower inflorescence	12.27, 5.52	4.80 - 18.80
	Ramet or individual plant	124.0, 120.14	38.00 - 300.00
	Single flower inflorescence	6.0, 0	6.00 - 6.00
Leontodon hispidus	Multiple flower inflorescence	67.7, 0	67.70 - 67.70
	Ramet or individual plant	68.5, 3.54	66.00 - 71.00
Leucanthemum vulgare	Multiple flower inflorescence	185.00, 148.49	80.00 - 290.00
	Ramet or individual plant	3573.79, 7961.86	66.10 - 26000.00
Linum catharticum	Ramet or individual plant	81.35, 58.9	11.40 - 183.00
	Single flower inflorescence	10.0, 0	10.00 - 10.00
Listera ovata	Ramet or individual plant	85500.0, 91216.77	21000.00 - 150000.00
Lotus corniculatus	Ramet or individual plant	6328.67 - 10108.75	345.00 - 18000.00
Medicago lupulina	Multiple flower inflorescence	15.7, 0	15.70 - 15.70
	Ramet or individual plant	2103.13, 2053.36	100.00 - 6600.00
	Single flower inflorescence	1.00, 0	1.00 - 1.00
Melampyrum arvense	Ramet or individual plant	24.67, 15.01	10.00 - 40.00
	Single flower inflorescence	4.0, 0	4.00 - 4.00
Melampyrum nemorosum	Ramet or individual plant	225.0, 301.23	12.00 - 438.00
Melampyrum sylvaticum	Ramet or individual plant	23.7, 23.51	9.40 - 76.00
Melilotus alba	Ramet or individual plant	160880.63, 177778.62	4287.50 - 350000.00
	Single flower inflorescence	2.0, 0	2.00 - 2.00
Melilotus officinalis	Ramet or individual plant	50050.0, 70639.96	100.00, 100000.00
	Single flower inflorescence	2.0, 1.41	1.00 - 3.00
Mentha arvensis	Ramet or individual plant	129.88, 87.39	19.50 - 200.00
Myosotis arvensis	Ramet or individual plant	900.0, 391.584	500.00 - 1400.00
	Single flower inflorescence	4.0, 0	4.00 - 4.00
Myosotis sylvatica	Ramet or individual plant	192.0, 0	192.00 - 192.00
Onobrychis viciifolia	Multiple flower inflorescence	16.0, 0	16.00 - 16.00
	Single flower inflorescence	1.0, 0	1.00 - 1.00
Ononis repens	Single flower inflorescence	2.5, 2.12	1.00 - 4.00
Ononis spinosa	Ramet or individual plant	300.0, 0	300.00 - 300.00
	Single flower inflorescence	4.0, 0	4.00 - 4.00
Ophrys apifera	Ramet or individual plant	40000.0, 0	40000.00 - 40000.00
	Single flower inflorescence	1000.00, 0	1000.00 - 1000.00
Orchis purpurea	Single flower inflorescence	6000.00, 0	6000.00 - 6000.00

Origanum vulgare	Single flower inflorescence	4.0, 0	4.00 - 4.00
Phalaris arundinacea	Ramet or individual plant	3000.0, 0	3000.00 - 3000.00
Phleum pratense	Multiple flower inflorescence	677.00, 0	677.00 - 677.00
Pimpinella saxifraga	Multiple flower inflorescence	122.5, 0	122.50 - 122.50
	Ramet or individual plant	2264.75, 3633.80	268.00 - 9566.00
	Single flower inflorescence	2.0, 0	2.00 - 2.00
Plantago lanceolata	Multiple flower inflorescence	28.05, 4.11	24.00 - 33.60
	Ramet or individual plant	2714.17, 3586.9823	585.00 - 10000.00
	Single flower inflorescence	2.0, 0	2.00 - 2.00
	unknown	93.50000	47.38, 60.00 - 127.00
Plantago major	Multiple flower inflorescence	2030.0, 0	2030.00 - 2030.00
	Ramet or individual plant	13835.38, 13268.55	565.00 - 40000.00
	Single flower inflorescence	19.0, 12.727922	10.00 - 28.00
Plantago media	Ramet or individual plant	2894.0, 3951.52	282.00 - 7440.00
	Single flower inflorescence	4.89, 2.98	2.78 - 7.00
Poa annua	Ramet or individual plant	3674.2, 5415.58	100.00 - 13000.00
	Single flower inflorescence	5071.25, 9952.57	50.00 - 20000.00
Poa pratensis	Ramet or individual plant	208.0, 0	208.00 - 208.00
Poa trivialis	Ramet or individual plant	299.5, 0	299.50 - 299.50
Polygala comosa	Multiple flower stem	18.0, 0	18.00 - 18.00
Polygala vulgaris	Multiple flower stem	23.0, 0	23.00 - 23.00
	Ramet or individual plant	188.0, 0	188.00 - 188.00
	Single flower inflorescence	2.0, 0	2.00 - 2.00
Potentilla anserina	Ramet or individual plant	69.9, 72.24	9.70 - 150.00
	Single flower inflorescence	36.25, 19.45	22.50 - 50.00
Primula veris	Ramet or individual plant	255.5, 21.92	240.00 - 271.00
	Single flower inflorescence	32.1, 25.3	14.20 - 50.00
Prunella grandiflora	Multiple flower inflorescence	58.0, 0	58.00 - 58.00
Prunella vulgaris	Multiple flower inflorescence	192.0, 0	192.00 - 192.00
	Ramet or individual plant	324.94, 328.63	43.30 - 854.00
	Single flower inflorescence	4.0, 0	4.00 - 4.00
Ranunculus bulbosus	Ramet or individual plant	70.62, 35.25	23.00 - 133.60
	Single flower inflorescence	22.8, 0	22.80 - 22.80
Ranunculus repens	Multiple flower stem	132.5, 10.61	125.00 - 140.00
	Ramet or individual plant	115.01, 62.72	20.00 - 215.30
	Single flower inflorescence	40.0, 14.14	30.00 - 50.00
Rhinanthus angustifolius	Ramet or individual plant	400.67, 428.29	63.50 - 1225.00
Rhinanthus minor	Ramet or individual plant	84.03, 70.43	19.40 - 187.00
	Single flower inflorescence	14.17, 3.62	10.00 - 16.50
Rumex acetosa	Multiple flower inflorescence	102.5, 34.33	64.50 - 147.50
	Ramet or individual plant	537.13, 778.82	45.40 - 2100.00
Rumex crispus	Ramet or individual plant	12122.56, 14359.60	1050.00 - 40000.00
Salvia pratensis	Multiple flower stem	95.0, 0	95.00 - 95.00
	Ramet or individual plant	3352.5, 1771.30	2100.00 - 4605.00
	Single flower inflorescence	19.85, 22.42	4.00 - 35.70
Sanguisorba minor	Single flower inflorescence	3.0, 0	3.00 - 3.00
Scabiosa columbaria	Ramet or individual plant	98.0, 142.02	24.00 - 311.00
Sedum sexangulare	Multiple flower stem	148.0, 0	148.00 - 148.00
Senecio erucifolius	Multiple flower stem	1613.25, 653.01	1151.50 - 2075.00
Senecio jacobaea	Multiple flower stem	4462.5, 0	4462.50 - 4462.50
	Ramet or individual plant	56920.0, 40538.54	2100.00 - 100000.00
Senecio vulgaris	Multiple flower inflorescence	101.0, 0	101.00 - 101.00
	Ramet or individual plant	8741.17, 14552.53	720.00 - 38000.00
Silene dioica	Ramet or individual plant	3892.92, 4102.99	220.00 - 9300.00
	Single flower inflorescence	244.00, 62.26	200.00 - 288.00
Silene nutan	Ramet or individual plant	255.80, 0	255.80 - 255.80
Sonchus asper	Ramet or individual plant	47470.53, 153108.49	330.00 - 600000.00
Stellaria holostea	Multiple flower stem	23.38, 14.24	13.00 - 44.00
	Ramet or individual plant	19.00, 0	19.00 - 19.00
Stellaria media	Ramet or individual plant	14000.00, 1732.05	11000.00 - 15000.00
	Single flower inflorescence	10.95, 4.09	8.00 - 17.00
Symphytum officinale	Multiple flower stem	72.5, 0	72.50 - 72.50
	Ramet or individual plant	808.00, 837.21	216.00 - 1400.00
Tanacetum vulgare	Multiple flower stem	232.00, 0	232.00 - 232.00
	Ramet or individual plant	6686.00, 6049.90	425.00 - 12500.00
Thymus pulegioides	Multiple flower inflorescence	33.11, 0	33.11 - 33.11

	Ramet or individual plant	528.50, 0	528.50 - 528.50
	Single flower inflorescence	4.00, 0	4.00 - 4.00
Tragopogon pratensis	Ramet or individual plant	190.00, 0	190.00 - 190.00
Trifolium campestre	Multiple flower inflorescence	29.50, 0	29.50 - 29.50
	Ramet or individual plant	142.5, 0	142.50 - 142.50
	Single flower inflorescence	1.00, 0	1.00 - 1.00
Trifolium dubium	Ramet or individual plant	92.00, 0	92.00 - 92.00
	Single flower inflorescence	1.00, 0	1.00 - 1.00
Trifolium medium	Multiple flower stem	6.30, 0	6.30 - 6.30
	Ramet or individual plant	70.00, 56.57	30.00 - 110.00
	Single flower inflorescence	1.00, 0	1.00 - 1.00
Trifolium ochroleucon	Ramet or individual plant	275.00, 0	275.00 - 275.00
Trifolium pratense	Multiple flower inflorescence	65.80, 39.17	38.10 - 93.50
	Multiple flower stem	19.80, 11.04	11.80 - 32.40
	Ramet or individual plant	530.00, 0	530.00 - 530.00
	Single flower inflorescence	1.00, 0	1.00 - 1.00
Trifolium repens	Multiple flower inflorescence	118.00, 110.31	40.00 - 196.00
	Multiple flower stem	10.10, 0	10.10 - 10.10
	Ramet or individual plant	421.33, 505.73	64.00 - 1000.00
	Single flower inflorescence	53.17, 83.87	3.50 - 150.00
Trisetum flavescens	Multiple flower stem	217.50,0	217.50 - 217.50
	Ramet or individual plant	25000.00, 0	25000.00 - 25000.00
Triticum aestivum	Ramet or individual plant	471.50, 0	471.50 - 471.50
Valeriana dioica	Ramet or individual plant	42.50, 24.75	25.00 - 60.00
Valeriana officinalis	Multiple flower stem	413.00, 0	413.00 - 413.00
	Ramet or individual plant	398.00, 366.28	139.00 - 657.00
Verbascum lychnitis	Ramet or individual plant	109830.25, 30574.24	88211.00 - 131449.50
	Single flower inflorescence	153.00, 0	153.00 - 153.00
Veronica chamaedrys	Ramet or individual plant	59.80, 115.08	3.00 - 450.00
Vicia cracca	Multiple flower stem	66.55, 31.89	44.00 - 89.10
	Ramet or individual plant	154.25, 104.72	55.00 - 300.00
	Single flower inflorescence	5.00, 1.41	4.00 - 6.00
Vicia hirsuta	Ramet or individual plant	168.48, 113.06	12.40 - 300.00
Vicia sepium	Multiple flower stem	6.10, 5.19	1.60 - 13.50
	Ramet or individual plant	76.50, 95.46	9.00 - 144.00
	Single flower inflorescence	7.00, 4.24	4.00 - 10.00
Vicia tetrasperma	Ramet or individual plant	280.42, 161.45	12.10 - 450.00
	Single flower inflorescence	4.00, 0	4.00 - 4.00
Vicia villosa	Ramet or individual plant	250.00, 50.00	200.00 - 300.00

Table 11: Comparison between the minimal and maximal temperatures of the species locations retrieved from rgbif and WordClim ("Observed", purple); the minimal and maximal values generated by a draw (n=1000) on the Normal distribution using as mean, the species temperature optimum (T_{opt}), and as standard deviation, the temperature tolerance (T_{tol}) calculated as the standard deviation around the mean temperatures on the species locations ($sd(T_{loc_\mu})$); and the minimal and maximal values generated by a draw (n=1000) on the Normal distribution using as standard deviation, the temperature tolerance calculated from the temperature range of the species locations ($T_{range}/6$).

Species	Min. observed	Max. observed	Min. $\mathcal{N}(T_{opt}, sd(T_{loc_\mu}))$	Max. $\mathcal{N}(T_{opt}, sd(T_{loc_\mu}))$	Min. $\mathcal{N}(T_{opt}, T_{range}/6)$	Max. $\mathcal{N}(T_{opt}, T_{range}/6)$
Achillea millefolium	252.35	309.75	271.9913	297.1704	246.0468	315.2280
Acinos arvensis	259.05	305.05	272.4413	298.6551	251.2799	316.0973
Actaea spicata	251.35	298.95	273.6000	299.6784	245.4221	316.8056
Aegopodium podagraria	251.45	306.15	270.8117	298.9453	257.5973	312.8530
Agrimonia eupatoria	249.55	303.25	272.3612	299.1632	249.0491	304.5230
Ajuga genevensis	255.55	303.55	270.3734	296.6527	248.2362	316.1510
Ajuga reptans	260.25	308.75	272.4653	300.3852	250.2407	307.5410
Allium schoenoprasum	250.95	306.05	271.2197	296.4063	255.1230	316.3350
Alopecurus pratensis	251.45	304.05	272.4842	298.9069	250.8666	308.5502
Anchusa arvensis	246.45	303.85	272.6076	301.6406	246.8756	310.5924
Antennaria dioica	251.35	303.55	269.7130	295.5381	247.9691	313.5711
Anthoxanthum odoratum	258.25	305.05	271.3340	305.1832	251.8056	310.7376
Anthriscus sylvestris	257.85	302.75	272.1094	299.6779	255.1937	314.9495
Anthyllis vulneraria	256.55	306.15	272.2542	298.2245	255.7452	311.7669
Arabis hirsuta	253.55	303.55	270.1528	296.8595	244.3307	311.8519
Arrhenatherum elatius	259.45	303.85	269.8638	296.6764	253.6260	309.6070
Artemisia vulgaris	248.45	305.85	270.1824	299.3564	250.2678	317.3901
Astragalus glycyphyllos	251.25	301.75	271.2779	297.2803	256.8587	310.8962
Avenula pubescens	251.25	298.75	272.8371	297.6190	253.4602	308.2638
Bellis perennis	264.25	308.75	271.5922	296.5760	249.9121	308.4771
Brachypodium pinnatum	251.35	305.35	270.1529	297.4048	252.1340	307.5409
Briza media	256.25	308.65	270.7114	299.5859	252.8763	309.8043
Bromus erectus	265.25	302.05	271.4494	295.8472	253.6521	313.6144
Bromus hordeaceus	260.55	308.65	270.5827	296.2070	254.0685	316.6008
Calystegia sepium	251.35	307.45	269.8866	297.1020	247.6411	317.8656
Campanula glomerata	237.35	304.35	271.5129	302.6452	255.5196	310.9851
Campanula persicifolia	256.45	302.05	272.6138	295.8802	253.7010	315.0017
Campanula rapunculoides	247.95	306.05	274.4884	296.5368	254.0196	313.1723
Campanula rotundifolia	249.05	303.55	272.8051	296.7435	253.9999	313.4143
Cardaminopsis arenosa	252.55	299.95	272.1995	297.6131	250.6658	311.9901
Carduus crispus	247.45	300.55	271.7866	300.3135	254.0789	309.7856
Carex caryophyllea	252.75	303.55	272.3485	298.8763	252.6954	306.9845
Carex flacca	259.65	304.85	270.1037	296.3133	254.9526	314.0697
Carex leporina	257.35	299.95	274.0692	296.2126	248.7134	310.5617

Carex ornithopoda	255.75	300.55	272.2401	303.5920	253.4595	312.4787
Carlina vulgaris	260.35	301.25	272.3249	297.4054	253.1358	308.8591
Centaurea jacea	251.35	303.15	273.1195	297.0705	256.1212	312.9503
Centaurea scabiosa	247.05	302.85	270.4698	296.1158	249.2530	314.9258
Centaurium erythraea	251.35	309.35	270.4768	295.5370	256.5062	318.4753
Cephalanthera rubra	253.25	305.45	271.4773	303.6483	244.8111	306.7876
Cerastium arvense	248.05	307.55	271.5107	295.6232	258.0235	308.6564
Cerastium holosteoides	259.45	302.55	271.7263	296.0877	251.6645	314.5873
Cerastium tomentosum	258.35	301.75	271.1094	299.4043	250.6186	317.3170
Cerinthe minor	257.25	303.35	272.4214	297.2565	247.9366	310.2951
Chaerophyllum hirsutum	260.45	298.35	273.1577	299.2368	256.4406	316.3272
Chaerophyllum temulum	260.95	302.55	272.3087	297.9936	252.8326	308.0367
Cichorium intybus	251.35	308.95	267.8817	299.2964	253.5977	306.8336
Cirsium acaule	249.45	300.15	273.4853	299.6131	251.7543	317.5739
Cirsium arvense	251.35	305.85	273.8008	296.5792	256.9199	307.3231
Cirsium oleraceum	249.45	299.65	273.0654	296.2915	252.0327	309.4643
Cirsium tuberosum	266.15	302.25	272.8264	296.7297	247.6759	318.0578
Cirsium vulgare	255.95	307.65	270.1999	299.6114	257.4823	304.7806
Clinopodium vulgare	250.55	305.65	273.8502	300.5282	255.7621	311.7134
Convolvulus arvensis	250.85	314.95	273.2551	300.7410	247.5096	312.9596
Crepis biennis	260.75	298.75	272.6145	298.1080	251.6551	308.5257
Cruciata laevipes	252.95	307.85	271.2533	300.4346	251.7106	307.1165
Cynosurus cristatus	259.65	301.75	274.0021	300.0919	253.3592	319.5059
Dactylis glomerata	256.65	305.15	272.1288	294.8130	255.4864	305.9429
Daucus carota	257.65	309.55	270.3149	300.2601	258.7113	308.0398
Echium vulgare	251.35	306.35	271.9708	296.5743	252.1409	312.8945
Elytrigia repens	254.15	295.55	269.6056	300.1611	257.5123	311.0665
Epilobium angustifolium	245.25	309.55	270.2440	297.3997	251.1903	312.3730
Epilobium montanum	251.35	298.55	269.6367	298.1539	251.4617	306.4211
Equisetum arvense	248.05	310.55	274.0457	298.6865	252.6166	308.5912
Euphorbia cyparissias	259.65	306.05	268.9412	297.7074	247.6695	312.5453
Euphrasia officinalis	249.55	298.55	272.4237	298.4730	254.8249	308.2959
Falcaria vulgaris	254.25	303.25	271.3693	299.1268	252.3341	309.7866
Festuca ovina	253.55	298.05	269.7334	297.1795	253.3290	312.1917
Festuca rubra	256.45	301.45	271.1537	293.9715	254.4016	317.6186
Filipendula vulgaris	250.95	302.05	271.3537	297.5573	248.4636	311.4833
Fragaria vesca	252.15	307.75	272.0039	298.9534	255.0400	309.1154
Fragaria viridis	246.45	302.65	272.6749	299.2681	243.8623	314.2051
Galeopsis ladanum	246.15	301.15	271.6605	294.3618	250.6469	310.8591
Galium aparine	262.45	311.45	271.1851	296.6095	247.6731	314.3189
Galium mollugo	246.45	303.65	269.3342	297.3137	255.1352	314.2945
Galium pumilum	261.35	301.95	272.9134	304.6268	251.5129	315.5710
Galium verum	246.65	304.15	273.8023	298.8334	252.8307	308.1444
Genista tinctoria	251.35	302.95	271.9765	297.7166	253.1638	310.0238
Gentianella ciliata	260.15	300.05	273.0886	296.1895	250.1031	309.2930
Gentianella germanica	259.55	298.25	271.0019	295.4218	251.2593	317.9508

Geranium dissectum	265.65	308.85	271.9655	294.5963	254.8330	314.8107
Geranium molle	263.85	309.75	270.6731	299.6686	249.1592	309.5429
Geranium pratense	246.65	299.55	271.5563	298.7168	249.8369	317.6773
Geranium pusillum	259.05	308.55	272.0182	300.0245	249.1598	313.8925
Geranium robertianum	258.35	304.15	268.3469	303.2754	252.1194	311.9078
Geum urbanum	251.35	303.75	269.6636	298.9839	256.2789	310.4844
Gymnadenia conopsea	249.35	301.45	269.4337	298.8722	253.1486	311.7797
Helianthemum nummularium	262.75	301.55	273.4579	294.3978	247.9713	314.3733
Heracleum sphondylium	250.15	306.05	272.0120	298.5743	253.2284	310.0225
Hieracium caespitosum	245.05	304.65	272.1687	302.6756	255.8339	306.4428
Hieracium lachenalii	256.35	301.65	271.3437	299.0859	253.1450	308.0908
Hieracium murorum	256.25	303.25	271.9287	299.0912	250.1351	307.4130
Hieracium pilosella	263.55	297.95	270.7488	299.3234	250.0314	307.7119
Hippocrepis comosa	262.85	302.65	271.1794	297.6768	250.2299	312.8488
Holcus lanatus	264.75	305.85	269.8060	303.8209	253.6633	308.7666
Hypericum perforatum	251.35	309.95	272.1840	298.3393	249.5758	314.3064
Inula conyzae	266.75	302.05	268.5745	299.5206	252.9695	307.4623
Knautia arvensis	255.95	308.15	271.3327	303.1635	252.9108	312.7591
Koeleria pyramidata	260.85	302.65	272.7470	301.8630	248.4618	308.7604
Lathyrus pratensis	249.55	301.05	273.8478	302.9569	250.9767	312.5682
Leontodon hispidus	256.55	304.45	272.6251	298.0446	256.7207	312.5258
Leucanthemum vulgare	257.65	308.75	272.4299	295.2001	253.4252	312.9796
Linum catharticum	259.95	298.95	270.3885	298.6054	257.2149	314.3305
Listera ovata	258.75	300.85	273.4531	295.1912	254.4431	308.0479
Lolium perenne	254.45	310.85	271.3285	296.0256	257.2935	311.6423
Lotus corniculatus	256.85	310.25	273.7545	297.3579	252.6116	314.8567
Medicago falcata	238.35	304.75	271.0792	297.8071	256.9496	315.7084
Medicago lupulina	256.95	309.65	270.2432	295.1808	252.2551	308.2210
Melampyrum arvense	253.45	303.65	268.3524	296.9476	251.3856	311.1941
Melampyrum nemorosum	248.55	300.35	267.1567	298.8969	251.7278	312.1728
Melampyrum sylvaticum	253.35	296.35	273.5182	299.6774	252.2385	314.5712
Melilotus alba	255.55	315.35	273.6517	299.4483	256.5197	312.2960
Melilotus officinalis	246.95	312.05	271.2452	301.2168	257.5404	316.6770
Mentha arvensis	242.55	304.95	272.7439	300.1750	257.2793	310.7532
Mentha verticillata	251.65	300.05	270.5340	297.8787	253.9127	311.6879
Myosotis arvensis	255.85	303.75	271.6225	299.0706	248.7663	313.7889
Myosotis sylvatica	250.45	302.85	272.9969	300.3165	250.4773	308.2800
Onobrychis viciifolia	246.65	306.35	269.5915	299.8000	253.1887	306.3587
Ononis repens	264.25	303.55	272.1914	295.8283	253.8707	310.7127
Ononis spinosa	252.45	304.75	272.7313	300.5989	259.3382	311.9998
Ophrys apifera	264.35	305.35	272.8601	297.4457	254.3779	313.7012
Ophrys insectifera	260.05	302.15	270.3375	298.3284	255.9376	306.7782
Orchis mascula	262.85	302.05	271.3473	293.7592	256.0173	308.8965
Orchis militaris	245.85	300.85	268.6722	295.9205	252.9594	309.0480
Orchis purpurea	263.15	303.25	270.4748	297.2981	255.2920	309.9377
Orchis tridentata	258.75	307.05	273.1088	298.1211	253.5223	313.1204

Origanum vulgare	249.55	308.25	272.3115	297.0389	251.8200	318.1614
Phalaris arundinacea	248.95	307.65	272.3196	297.5947	242.9220	317.6869
Phleum pratense	249.15	312.15	269.2926	300.3788	256.1122	307.9064
Pimpinella saxifraga	249.35	299.05	272.2041	300.2116	256.4888	310.4289
Plantago lanceolata	257.65	308.85	272.3717	301.4255	254.1224	307.5099
Plantago major	251.25	308.75	270.3492	296.1396	249.5138	308.7525
Plantago media	246.65	302.05	273.9663	296.6668	252.1495	313.9240
Platanthera chlorantha	259.35	301.45	273.3476	297.4140	257.2185	306.5560
Poa annua	252.15	308.85	271.6938	295.9891	250.3779	309.4506
Poa pratensis	249.55	307.65	272.7185	297.7486	256.1995	322.7312
Poa trivialis	250.95	303.35	270.0131	295.3780	253.9035	308.0971
Polygala comosa	255.85	300.65	272.8261	298.3514	256.2350	308.4919
Polygala vulgaris	258.95	302.15	270.5292	299.8805	253.5822	309.0982
Potentilla anserina	248.75	303.25	270.7556	300.8952	251.6340	306.9206
Potentilla neumanniana	264.45	301.95	271.5323	297.1231	256.0108	309.5080
Potentilla reptans	257.05	304.65	272.4032	298.6335	257.6403	317.5395
Primula veris	253.85	304.85	273.0707	295.9710	258.8037	311.3513
Prunella grandiflora	257.15	302.55	272.2142	297.8487	252.8513	312.4707
Prunella vulgaris	251.05	308.65	270.6773	300.1238	254.6302	319.6122
Ranunculus bulbosus	263.45	307.95	273.0948	299.3986	248.4533	311.7399
Ranunculus repens	257.85	308.75	272.9193	300.7073	253.2833	307.8136
Rhinanthus angustifolius	260.35	300.25	270.7263	296.9758	250.6329	314.0866
Rhinanthus minor	241.85	303.45	270.2098	298.2931	251.0218	308.0899
Rumex acetosa	256.95	304.75	272.3201	296.7122	257.8907	312.7207
Rumex crispus	250.55	313.75	270.0719	300.2709	252.0558	312.1041
Salvia pratensis	257.55	303.05	273.9683	298.6198	250.7277	312.1631
Sanguisorba minor	259.15	308.05	272.1394	301.8925	253.5455	311.3197
Scabiosa columbaria	262.35	303.15	273.3545	297.5797	249.0897	308.9493
Sedum sexangulare	255.45	304.75	272.1015	300.2827	254.2096	311.4258
Senecio erucifolius	254.45	302.05	271.2209	296.3960	251.9918	308.1157
Senecio jacobaea	265.35	300.05	272.0931	298.9244	254.1449	309.0221
Senecio ovatus	261.35	301.75	274.2304	297.8361	252.2251	308.9452
Senecio vulgaris	260.55	314.15	272.5691	301.6547	252.6029	318.8250
Silene dioica	259.65	303.95	272.7938	296.0114	251.1269	313.8320
Silene nutan	247.45	301.05	270.8226	296.6125	255.3007	306.0774
Sonchus asper	253.75	314.45	272.1424	298.4465	251.6483	307.8913
Stachys germanica	264.35	306.25	273.2375	295.8015	253.9760	308.2454
Stellaria holostea	258.85	301.35	270.3344	298.9770	258.1661	308.0253
Stellaria media	263.25	309.95	272.0308	296.9332	245.2841	314.8450
Symphytum officinale	256.25	304.55	271.5534	298.1070	254.6936	316.0077
Tanacetum vulgare	250.95	303.75	271.6448	300.1223	251.5637	308.0812
Taraxacum laevigatum	254.65	305.85	270.0531	295.9802	250.2267	315.1468
Taraxacum officinale	263.45	314.15	270.5718	295.9910	254.5225	310.6613
Thymus pulegioides	250.55	303.65	271.0233	302.0810	245.5052	315.3534
Tragopogon pratensis	254.95	308.65	272.1567	297.0067	253.5293	324.3935
Trifolium campestre	261.35	309.55	271.9624	295.9465	255.7547	315.9569

Trifolium dubium	263.45	308.25	272.4052	299.5661	255.6799	305.7898
Trifolium medium	251.75	302.25	269.6785	295.5166	252.1471	309.8364
Trifolium ochroleucon	264.35	305.75	272.2798	297.3215	253.9755	308.8568
Trifolium pratense	253.65	307.25	270.8014	298.5190	256.6391	311.8549
Trifolium repens	261.15	309.55	272.0698	295.2907	255.4797	314.8132
Trisetum flavescens	260.15	303.95	271.7579	297.1125	255.8548	313.5089
Triticum aestivum	251.45	315.45	271.6424	297.9778	251.7632	309.9724
Valeriana dioica	254.25	297.85	273.1759	294.7957	251.0340	307.4499
Valeriana officinalis	249.05	305.15	268.1814	296.2778	252.2483	307.0331
Verbascum lychnitis	246.75	302.95	268.2058	297.8396	252.2005	309.1853
Veronica chamaedrys	251.05	302.35	272.1701	299.3420	246.8682	312.8694
Veronica teucrium	249.95	302.15	267.6619	298.3473	259.6587	305.2551
Vicia cracca	246.75	307.25	272.4330	295.6431	253.9702	309.4404
Vicia hirsuta	251.65	306.65	272.3615	294.5961	251.3292	305.5972
Vicia sepium	251.05	298.55	270.6622	297.8432	254.8217	314.2523
Vicia tenuifolia	251.15	303.75	273.4414	299.8928	258.0934	310.7240
Vicia tetrasperma	256.55	308.15	272.1786	295.4854	243.0483	311.9951
Vicia villosa	269.05	309.75	273.1266	297.8104	248.9011	310.5698
Vincetoxicum hirundinaria	251.65	304.55	272.0060	296.1041	252.7377	310.6045
Viola hirta	250.65	300.75	273.5813	296.7294	249.7039	310.5084
Viola odorata	260.65	307.45	273.8921	300.4080	253.4243	315.7648

Table 12: Values of dispersal kernel (classified into distances), clonal capacity, pollen vector, selfing capacity, seed biomass (g), size of plant organ (g), probability of selfing, and minimal and maximal life span (week) for the species used in the simulations of the first implementation of the model, Figueiredo et al. (in prep.)

Species	Kernel	Clonality	Pollen vector	Selfing	Seed biomass (g)	Organ size (g)	Prob. selfing	Min. life span (week)	Max. life span (weeks)
Achillea millefolium	long-medium-short	TRUE	insects	FALSE	0.0003	20	0	1560	1560
Acinos arvensis	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Actaea spicata	long	TRUE	insects	TRUE	0.001	50	0	1560	1560
Aegopodium podagraria	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Agrimonia eupatoria	long-medium-short	TRUE	insects	FALSE	0.001	50	0.95	1560	1560
Ajuga genevensis	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Ajuga reptans	short-medium	TRUE	insects	TRUE	0.001	50	0	1560	2600
Allium schoenoprasum	short-long	TRUE	insects	TRUE	0.001	50	0	1560	1560
Alopecurus pratensis	long-short	TRUE	wind	FALSE	0.001	50	0	1560	1560
Anchusa arvensis	long-medium	FALSE	insects	TRUE	0.001	50	0	52	104
Antennaria dioica	long-short	TRUE	insects	FALSE	0.0001	10	0	1560	2600
Anthoxanthum odoratum	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Anthriscus sylvestris	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Anthyllis vulneraria	long	TRUE	insects	FALSE	0.001	50	0.5	52	1560
Arabis hirsuta	long-short	TRUE	insects	FALSE	0.0001	10	0.5	1560	1560
Arrhenatherum elatius	long-short	TRUE	wind	FALSE	0.001	50	0.05	1560	1560
Artemisia vulgaris	long-medium-short	TRUE	insects	FALSE	0.0003	20	0	1560	1560
Astragalus glycyphyllos	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Avenula pubescens	short-long	TRUE	wind	FALSE	0.001	50	0	1560	1560
Brachypodium pinnatum	short-long	TRUE	wind	FALSE	0.001	50	0	1560	1560
Bellis perennis	long-medium-short	TRUE	insects	FALSE	0.0003	20	0.5	1560	1560
Briza media	short-long	TRUE	wind	FALSE	0.001	50	0	1560	1560
Bromus erectus	long	TRUE	wind	FALSE	0.001	50	0	1560	1560
Bromus hordeaceus	long	TRUE	wind	FALSE	0.001	50	0.95	52	104
Calystegia sepium	long-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Campanula glomerata	short-long	TRUE	insects	TRUE	0.0003	20	0	52	1560
Campanula persicifolia	long-short	TRUE	insects	FALSE	0.0001	10	0	104	1560
Campanula rotundifolia	long-short	TRUE	insects	FALSE	0.0001	10	0	1560	1560
Campanula rapunculoides	long-medium-short	TRUE	insects	FALSE	0.0003	20	0	1560	1560
Cardaminopsis arenosa	long	TRUE	insects	FALSE	0.0003	20	0	52	1560
Carduus crispus	long-medium-short	FALSE	insects	FALSE	0.001	50	0	104	104
Carex caryophyllea	medium	TRUE	wind	FALSE	0.001	50	0	1560	1560
Carex flacca	long-medium-short	TRUE	wind	FALSE	0.001	50	0	1560	1560
Carex leporina	short	FALSE	wind	FALSE	0.001	50	0	1560	1560
Carex ornithopoda	long-medium-short	TRUE	wind	FALSE	0.001	50	0	1560	1560
Carlina vulgaris	long-medium-short	TRUE	insects	TRUE	0.001	50	0	52	1560
Centaurea jacea	long-medium-short	FALSE	insects	FALSE	0.001	50	0	1560	1560
Centaurea scabiosa	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560

Centaurium erythraea	short-long	FALSE	insects	FALSE	0.0001	10	0.95	52	1560
Cephalanthera rubra	short	TRUE	insects	FALSE	0.001	50	0.5	1560	1560
Cerastium arvense	long-short	TRUE	insects	TRUE	0.0003	20	0	1560	2600
Cerastium holosteoides	short	FALSE	insects	TRUE	0.001	50	0	1560	1560
Cerastium tomentosum	long-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Cerinthe minor	short-long	TRUE	insects	TRUE	0.001	50	0	104	1560
Chaerophyllum hirsutum	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Chaerophyllum temulum	short-long	FALSE	insects	FALSE	0.001	50	0	52	104
Cichorium intybus	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Cirsium acaule	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Cirsium arvense	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Cirsium oleraceum	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Cirsium tuberosum	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Cirsium vulgare	long-medium-short	FALSE	insects	FALSE	0.001	50	0	52	1560
Clinopodium vulgare	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Convolvulus arvensis	long-medium-short	TRUE	insects	FALSE	0.001	50	0.5	1560	1560
Crepis biennis	long-medium-short	FALSE	insects	TRUE	0.001	50	0	104	104
Cruciata laevipes	long	TRUE	insects	FALSE	0.001	50	0	52	1560
Cynosurus cristatus	long-medium-short	TRUE	wind	FALSE	0.001	50	0.5	1560	1560
Dactylis glomerata	long-short	TRUE	wind	TRUE	0.001	50	0.05	1560	1560
Daucus carota	long-medium-short	TRUE	insects	TRUE	0.001	50	0.05	1560	1560
Echium vulgare	long-medium-short	FALSE	insects	FALSE	0.001	50	0	104	104
Elytrigia repens	long-medium-short	FALSE	wind	FALSE	0.001	50	0	1560	1560
Epilobium angustifolium	long-medium-short	TRUE	insects	FALSE	0.0001	10	0.05	1560	1560
Epilobium montanum	long-medium-short	TRUE	insects	FALSE	0.0003	20	0.95	1560	1560
Equisetum arvense	long-medium-short	FALSE	wind	FALSE	0.0001	10	0.5	1560	1560
Euphorbia cyparissias	long-medium-short	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Euphrasia officinalis	long-medium-short	FALSE	insects	TRUE	0.0003	20	0	52	52
Falcaria vulgaris	long-medium-short	TRUE	insects	FALSE	0.001	50	0	52	1560
Festuca ovina	long-short	TRUE	wind	FALSE	0.001	50	0	104	1560
Festuca pratensis	long-short	TRUE	wind	FALSE	0.001	50	0	1560	1560
Festuca rubra	long-medium-short	TRUE	wind	FALSE	0.001	50	0	104	1560
Filipendula vulgaris	short-long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Fragaria vesca	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Fragaria viridis	short-long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Galeopsis ladanum	long-medium	FALSE	insects	TRUE	0.001	50	0	52	52
Galium aparine	long	FALSE	insects	FALSE	0.001	50	0.95	52	104
Galium mollugo	long-short	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Galium pumilum	short-long	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Galium verum	short-long	TRUE	wind-insects	FALSE	0.001	50	0.025	1560	1560
Genista tinctoria	short-long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Gentianella ciliata	short	TRUE	insects	FALSE	0.0003	20	0.05	104	1560
Gentianella germanica	short	FALSE	insects	TRUE	0.0003	20	0	52	104
Geranium dissectum	long-short	FALSE	insects	TRUE	0.001	50	0	52	104
Geranium molle	long-short	FALSE	insects	FALSE	0.001	50	0.95	52	104
Geranium pratense	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560

Geranium pusillum	long-medium-short	FALSE	insects	FALSE	0.001	50	0.95	52	1560
Geranium robertianum	long-medium-short	FALSE	insects	FALSE	0.001	50	0.95	52	104
Geum urbanum	long	TRUE	insects	FALSE	0.001	50	0.95	1560	1560
Gymnadenia conopsea	short	TRUE	insects	FALSE	0.0001	10	0	1560	1560
Helianthemum nummularium	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Heracleum sphondylium	long-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Hieracium caespitosum	long-medium-short	TRUE	insects	FALSE	0.0003	20	0.05	1560	1560
Hieracium lachenalii	short	FALSE	insects	FALSE	0.001	50	0.05	1560	1560
Hieracium murorum	long-medium-short	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Hieracium pilosella	long-medium-short	TRUE	insects	FALSE	0.0003	20	0.05	1560	1560
Hippocrepis comosa	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Holcus lanatus	long-medium-short	TRUE	wind	FALSE	0.001	50	0.5	1560	1560
Hypericum perforatum	long-medium-short	TRUE	insects	FALSE	0.0001	10	0.05	1560	1560
Inula conyzae	long-medium-short	FALSE	insects	FALSE	0.001	50	0	1560	1560
Knautia arvensis	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Koeleria pyramidata	long-short	TRUE	wind	FALSE	0.001	50	0	1560	1560
Lathyrus pratensis	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Leontodon hispidus	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Leucanthemum vulgare	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Linum catharticum	long-medium-short	TRUE	insects	FALSE	0.0003	20	0.95	52	1560
Listera ovata	short	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Lolium perenne	long-medium-short	TRUE	wind	FALSE	0.001	50	0	52	1560
Lotus corniculatus	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Medicago falcata	long-medium-short	FALSE	insects	FALSE	0.001	50	0	1560	1560
Medicago lupulina	long-medium-short	TRUE	insects	FALSE	0.001	50	0.5	52	1560
Melampyrum arvense	long-medium	FALSE	insects	FALSE	0.001	50	0	52	104
Melampyrum nemorosum	medium	FALSE	insects	TRUE	0.001	50	0	52	52
Melampyrum sylvaticum	medium-long	FALSE	insects	TRUE	0.001	50	0	52	52
Melilotus alba	long-short	FALSE	insects	TRUE	0.001	50	0	52	104
Melilotus officinalis	long-medium-short	FALSE	insects	TRUE	0.001	50	0	52	104
Mentha arvensis	long	TRUE	insects	FALSE	0.0003	20	0	1560	1560
Mentha verticillata	long-medium-short	FALSE	insects	FALSE	0.001	50	0	1560	1560
Myosotis arvensis	long-medium-short	TRUE	insects	FALSE	0.001	50	0.95	52	104
Myosotis sylvatica	long-medium-short	FALSE	insects	FALSE	0.001	50	0.95	1560	1560
Onobrychis viciifolia	short-long	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Ononis repens	short-medium	TRUE	insects	FALSE	0.001	50	0	1560	1560
Ononis spinosa	short-long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Ophrys apifera	short	TRUE	insects	FALSE	0.001	50	1	1560	1560
Ophrys insectifera	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Orchis mascula	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Orchis militaris	short	TRUE	insects	FALSE	0.0001	10	0	1560	1560
Orchis purpurea	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Orchis tridentata	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Origanum vulgare	short-long	TRUE	insects	FALSE	0.0001	10	0	1560	1560
Phalaris arundinacea	long-medium-short	TRUE	wind	TRUE	0.001	50	0	1560	1560
Phleum pratense	long-medium-short	TRUE	wind	FALSE	0.001	50	0.025	1560	1560

Pimpinella saxifraga	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Plantago lanceolata	long-medium-short	TRUE	wind	TRUE	0.001	50	0	52	1560
Plantago major	long-medium-short	TRUE	wind	TRUE	0.0003	20	0	1560	1560
Plantago media	long-short	TRUE	wind-insects	FALSE	0.001	50	0	1560	1560
Platanthera chlorantha	short	TRUE	insects	FALSE	0.0001	10	0	1560	1560
Poa annua	long-medium-short	TRUE	wind	TRUE	0.0003	20	0.05	1560	1560
Poa pratensis	long-short	TRUE	wind	TRUE	0.0003	20	0	1560	1560
Poa trivialis	long-medium-short	TRUE	wind	FALSE	0.0003	20	0	1560	1560
Polygala comosa	medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Polygala vulgaris	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Potentilla anserina	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Potentilla neumanniana	long-medium-short	FALSE	insects	FALSE	0.001	50	0.95	1560	1560
Potentilla reptans	long-medium-short	TRUE	insects	FALSE	0.0003	20	0	1560	1560
Primula veris	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Prunella grandiflora	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Prunella vulgaris	long-medium-short	TRUE	insects	TRUE	0.001	50	0	52	1560
Ranunculus bulbosus	short-long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Ranunculus repens	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Rhinanthus angustifolius	long-short	FALSE	insects	FALSE	0.001	50	0	52	52
Rhinanthus minor	long-short	FALSE	insects	FALSE	0.001	50	0.1	52	52
Rumex acetosa	long-short	TRUE	wind	FALSE	0.001	50	0	1560	1560
Rumex crispus	long-medium-short	TRUE	wind	FALSE	0.001	50	0	52	1560
Salvia pratensis	long-medium-short	TRUE	insects	TRUE	0.001	50	0.05	1560	1560
Sanguisorba minor	long-short	TRUE	wind	TRUE	0.001	50	0	1560	1560
Scabiosa columbaria	long-medium-short	TRUE	insects	FALSE	0.001	50	0	104	1560
Sedum sexangulare	long-medium-short	TRUE	insects	TRUE	0.0001	10	0	1560	1560
Senecio erucifolius	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Senecio jacobaea	long-medium-short	TRUE	insects	FALSE	0.001	50	0	52	1560
Senecio ovatus	short	FALSE	insects	FALSE	0.001	50	0	1560	1560
Senecio vulgaris	long-medium-short	FALSE	insects	FALSE	0.0003	20	0.95	52	1560
Silene dioica	short-long	TRUE	insects	FALSE	0.001	50	0	104	1560
Silene nutan	short-long	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Sonchus asper	long-medium-short	FALSE	insects	FALSE	0.0003	20	0.5	52	1560
Stachys germanica	short-long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Stellaria holostea	long-medium-short	TRUE	insects	TRUE	0.001	50	0	1560	1560
Stellaria media	long-medium-short	TRUE	insects	FALSE	0.001	50	0.5	52	1560
Symphytum officinale	medium-long	TRUE	insects	TRUE	0.001	50	0	1560	1560
Tanacetum vulgare	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Taraxacum laevigatum	long-medium-short	FALSE	insects	FALSE	0.001	50	0	1560	1560
Taraxacum officinale	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Thymus pulegioides	long-medium-short	TRUE	insects	FALSE	0.0003	20	0	1560	1560
Tragopogon pratensis	long-medium-short	TRUE	insects	TRUE	0.001	50	0	104	1560
Trifolium campestre	long-short	TRUE	insects	TRUE	0.001	50	0	52	104
Trifolium dubium	long-medium-short	FALSE	insects	FALSE	0.001	50	0.5	52	52
Trifolium medium	long-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Trifolium ochroleucon	long	TRUE	insects	FALSE	0.001	50	0	1560	1560

Trifolium pratense	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Trifolium repens	long-medium-short	TRUE	insects	FALSE	0.001	50	0	52	2600
Trisetum flavescens	long-short	TRUE	wind	FALSE	0.0003	20	0	1560	1560
Triticum aestivum	long	TRUE	wind	FALSE	0.001	50	0.05	52	52
Valeriana dioica	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Valeriana officinalis	long	TRUE	insects	FALSE	0.001	50	0	1560	1560
Verbascum lychnitis	long-short	FALSE	insects	TRUE	0.0003	20	0	104	104
Veronica chamaedrys	long-medium-short	TRUE	insects	FALSE	0.0003	20	0.05	1560	1560
Veronica teucrium	long	FALSE	insects	FALSE	0.0003	20	0.5	1560	1560
Vicia cracca	long-medium-short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Vicia hirsuta	long-medium-short	FALSE	insects	FALSE	0.001	50	0.5	52	104
Vicia sepium	short-long	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Vicia tenuifolia	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Vicia tetrasperma	long-medium-short	FALSE	insects	FALSE	0.001	50	0.95	52	104
Vicia villosa	short	FALSE	insects	FALSE	0.001	50	0	52	104
Vincetoxicum hirundinaria	short	TRUE	insects	FALSE	0.001	50	0	1560	1560
Viola hirta	long-medium-short	TRUE	insects	FALSE	0.001	50	0.05	1560	1560
Viola odorata	long-medium-short	TRUE	insects	FALSE	0.001	50	0.05	1560	1560

Table 13: Values of minimal and maximal age of first flowering (days), minimal and maximal duration of seed bank (weeks), minimal and maximal number of seeds produced, and normalization constant of growth rate for the species used in the simulations of the first implementation of the model, Figueiredo et al. (in prep.)

Species	Min. age 1^{st} flower (days)	Max. age 1^{st} flower (days)	Max. seed bank (weeks)	Min. seed bank (weeks)	Min. seeds	Max. seeds	Norm. constant growth
Achillea millefolium	18.772773	105.59588	109.590564	7.110712	47.5	1800	5963719581
Acinos arvensis	18.772773	105.59588	385.780391	3.875541	85.5	85.5	8058178821
Actaea spicata	105.59588	105.59588	3.875541	3.875541	27	475	8058178821
Aegopodium podagraria	105.59588	105.59588	385.780391	3.875541	11.625	2675	8058178821
Agrimonia eupatoria	105.59588	105.59588	149.458251	3.875541	16.5	16.5	8058178821
Ajuga genevensis	105.59588	105.59588	385.780391	3.875541	55.25	55.25	8058178821
Ajuga reptans	105.59588	105.59588	122.684719	7.110712	9	26.25	8058178821
Allium schoenoprasum	105.59588	105.59588	140.741479	7.110712	1037.25	1037.25	8058178821
Alopecurus pratensis	18.772773	105.59588	155.62625	7.110712	103.5	103.5	8058178821
Anchusa arvensis	18.772773	18.772773	149.458251	3.875541	32	175	8058178821
Antennaria dioica	105.59588	105.59588	3.875541	3.875541	70	70	4531446957
Anthoxanthum odoratum	105.59588	105.59588	141.825074	7.110712	27	259.625	8058178821
Anthriscus sylvestris	18.772773	105.59588	155.226599	7.110712	33.025	2500	8058178821
Anthyllis vulneraria	26	26	385.780391	3.875541	7.5	48.5	8058178821
Arabis hirsuta	105.59588	105.59588	81.543282	7.110712	187.5	187.5	4531446957
Arrhenatherum elatius	18.772773	18.772773	170.580602	7.110712	2.5	2.5	8058178821
Artemisia vulgaris	18.772773	105.59588	39.577009	7.110712	50000	125000	5963719581
Astragalus glycyphyllos	105.59588	105.59588	139.019233	7.110712	2578.75	2578.75	8058178821
Avenula pubescens	105.59588	105.59588	140.783097	7.110712	1000	1000	8058178821
Brachypodium pinnatum	78.283972	102.511805	146.7576	7.110712	21.75	21.75	8058178821
Bellis perennis	105.59588	105.59588	95.782183	7.110712	322	322	5963719581
Briza media	18.772773	105.59588	155.346279	7.110712	44.75	1827	8058178821
Bromus erectus	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Bromus hordeaceus	18.772773	18.772773	218.104238	7.110712	210.0389	1708.098	8058178821
Calystegia sepium	105.59588	105.59588	385.780391	3.875541	210.0389	1708.098	8058178821
Campanula glomerata	26	26	149.458251	3.875541	5113.3643	17367.398	5963719581
Campanula persicifolia	18.772773	18.772773	115.372483	7.110712	6514.3144	21841.484	4531446957
Campanula rotundifolia	18.772773	18.772773	94.852415	7.110712	6514.3144	21841.484	4531446957
Campanula rapunculoides	18.772773	105.59588	98.990475	7.110712	5113.3643	17367.398	5963719581
Cardaminopsis arenosa	18.772773	18.772773	149.458251	149.458251	5113.3643	17367.398	5963719581
Carduus crispus	52	52	385.780391	3.875541	210.0389	1708.098	8058178821
Carex caryophyllea	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821
Carex flacca	18.772773	105.59588	156.145247	7.110712	210.0389	1708.098	8058178821
Carex leporina	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Carex ornithopoda	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821
Carlina vulgaris	18.772773	18.772773	173.485193	7.110712	1472.4605	5739.778	8058178821
Centaurea jacea	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Centaurea scabiosa	18.772773	105.59588	156.145247	7.110712	210.0389	1708.098	8058178821

Centaurium erythraea	17.398469	47.747222	111.678497	7.110712	6514.3144	21841.484	4531446957
Cephalanthera rubra	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Cerastium arvense	18.772773	105.59588	79.795809	7.110712	5113.3643	17367.398	5963719581
Cerastium holosteoides	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Cerastium tomentosum	18.772773	18.772773	169.978778	7.110712	210.0389	1708.098	8058178821
Cerinthe minor	18.772773	18.772773	172.665941	7.110712	1472.4605	5739.778	8058178821
Chaerophyllum hirsutum	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Chaerophyllum temulum	6.331742	9.276826	149.458251	3.875541	210.0389	1708.098	8058178821
Cichorium intybus	105.59588	105.59588	149.458251	3.875541	210.0389	1708.098	8058178821
Cirsium acaule	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Cirsium arvense	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Cirsium oleraceum	18.772773	18.772773	169.978778	7.110712	210.0389	1708.098	8058178821
Cirsium tuberosum	18.772773	18.772773	3.875541	3.875541	1472.4605	5739.778	8058178821
Cirsium vulgare	18.772773	18.772773	191.231706	7.110712	210.0389	1708.098	8058178821
Clinopodium vulgare	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Convolvulus arvensis	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Crepis biennis	18.772773	18.772773	217.371379	7.110712	210.0389	1708.098	8058178821
Cruciata laevipes	18.772773	18.772773	3.875541	3.875541	210.0389	1708.098	8058178821
Cynosurus cristatus	18.772773	105.59588	156.145247	7.110712	210.0389	1708.098	8058178821
Dactylis glomerata	18.772773	105.59588	156.145247	7.110712	210.0389	1708.098	8058178821
Daucus carota	18.772773	105.59588	156.145247	7.110712	210.0389	1708.098	8058178821
Echium vulgare	18.772773	18.772773	385.780391	3.875541	210.0389	1708.098	8058178821
Elytrigia repens	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Epilobium angustifolium	18.772773	18.772773	94.852415	7.110712	6514.3144	21841.484	4531446957
Epilobium montanum	18.772773	18.772773	112.824005	7.110712	5113.3643	17367.398	5963719581
Equisetum arvense	63.03633	105.04578	74.979452	7.110712	6514.3144	21841.484	4531446957
Euphorbia cyparissias	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Euphrasia officinalis	18.772773	18.772773	149.458251	3.875541	5113.3643	17367.398	5963719581
Falcaria vulgaris	26	26	3.875541	3.875541	500	500	8058178821
Festuca ovina	52	52	181.360109	7.110712	211.75	211.75	8058178821
Festuca pratensis	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821
Festuca rubra	39.427771	52.331844	183.414557	7.110712	116.25	116.25	8058178821
Filipendula vulgaris	105.59588	105.59588	3.875541	3.875541	28.25	109.825	8058178821
Fragaria vesca	105.59588	105.59588	141.831881	7.110712	56.25	85.25	8058178821
Fragaria viridis	310.486899	310.486899	83.123572	7.110712	210.0389	1708.098	8058178821
Galeopsis ladanum	18.772773	18.772773	221.118505	7.110712	75	75	8058178821
Galium aparine	18.772773	18.772773	220.186553	7.110712	7.75	250	8058178821
Galium mollugo	18.772773	18.772773	169.213543	7.110712	433.5	5000	8058178821
Galium pumilum	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821
Galium verum	105.59588	105.59588	141.892395	7.110712	3.15	26.025	8058178821
Genista tinctoria	89.879767	119.343549	3.875541	3.875541	210.0389	1708.098	8058178821
Gentianella ciliata	52	52	3.875541	3.875541	167.5	167.5	5963719581
Gentianella germanica	18.772773	18.772773	174.418046	7.110712	40	148.5	5963719581
Geranium dissectum	18.772773	18.772773	220.17178	7.110712	23.75	250	8058178821
Geranium molle	18.772773	18.772773	385.780391	3.875541	20.25	25	8058178821
Geranium pratense	105.59588	105.59588	141.899512	7.110712	0.75	0.75	8058178821

Geranium pusillum	18.772773	18.772773	193.253455	7.110712	75	187.5	8058178821
Geranium robertianum	18.772773	18.772773	220.220719	7.110712	7.5	75	8058178821
Geum urbanum	18.772773	105.59588	155.68645	7.110712	43	81.125	8058178821
Gymnadenia conopsea	105.59588	105.59588	3.875541	3.875541	7924.75	7924.75	4531446957
Helianthemum nummularium	105.59588	105.59588	141.832477	7.110712	60.75	60.75	8058178821
Heracleum sphondylium	105.59588	105.59588	141.219106	7.110712	212.5	2501.25	8058178821
Hieracium caespitosum	18.772773	18.772773	3.875541	3.875541	153	153	5963719581
Hieracium lachenalii	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Hieracium murorum	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821
Hieracium pilosella	18.772773	105.59588	109.97499	7.110712	5.25	18.75	5963719581
Hippocrepis comosa	105.59588	105.59588	141.866833	7.110712	30	30	8058178821
Holcus lanatus	18.772773	105.59588	106.303418	7.110712	44250	44250	8058178821
Hypericum perforatum	105.59588	105.59588	79.452138	7.110712	759	8250	4531446957
Inula conyzae	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Knautia arvensis	105.59588	310.486899	106.764162	7.110712	16.5	500	8058178821
Koeleria pyramidata	78.242321	102.473579	146.736558	7.110712	52.375	52.375	8058178821
Lathyrus pratensis	18.772773	105.59588	155.71857	7.110712	9.5	75	8058178821
Leontodon hispidus	18.772773	105.59588	155.723208	7.110712	16.5	17.75	8058178821
Leucanthemum vulgare	18.772773	18.772773	169.307675	7.110712	16.525	6500	8058178821
Linum catharticum	18.772773	18.772773	147.58915	7.110712	2.85	45.75	5963719581
Listera ovata	105.59588	310.486899	3.875541	3.875541	5250	37500	8058178821
Lolium perenne	18.772773	18.772773	191.231706	7.110712	210.0389	1708.098	8058178821
Lotus corniculatus	18.772773	105.59588	154.78962	7.110712	86.25	4500	8058178821
Medicago falcata	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Medicago lupulina	18.772773	18.772773	193.016018	7.110712	25	1650	8058178821
Melampyrum arvense	18.772773	18.772773	149.458251	3.875541	2.5	10	8058178821
Melampyrum nemorosum	18.772773	18.772773	3.875541	3.875541	3	109.5	8058178821
Melampyrum sylvaticum	18.772773	18.772773	3.875541	3.875541	2.35	19	8058178821
Melilotus alba	26	26	199.897132	7.110712	1071.875	87500	8058178821
Melilotus officinalis	18.772773	18.772773	215.371175	7.110712	25	25000	8058178821
Mentha arvensis	105.59588	105.59588	96.127741	7.110712	4.875	50	5963719581
Mentha verticillata	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Myosotis arvensis	18.772773	18.772773	220.0589	7.110712	125	350	8058178821
Myosotis sylvatica	105.59588	105.59588	3.875541	3.875541	48	48	8058178821
Onobrychis viciifolia	18.772773	18.772773	3.875541	3.875541	4	4	8058178821
Ononis repens	18.772773	18.772773	170.58297	7.110712	0.25	1	8058178821
Ononis spinosa	18.772773	18.772773	3.875541	3.875541	75	75	8058178821
Ophrys apifera	105.59588	310.486899	61.763858	7.110712	10000	10000	8058178821
Ophrys insectifera	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Orchis mascula	310.486899	310.486899	79.624843	7.110712	1472.4605	5739.778	8058178821
Orchis militaris	105.59588	310.486899	36.356334	7.110712	6514.3144	21841.484	4531446957
Orchis purpurea	310.486899	310.486899	52.673546	7.110712	1500	1500	8058178821
Orchis tridentata	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Origanum vulgare	18.772773	105.59588	95.593185	7.110712	1	1	4531446957
Phalaris arundinacea	105.59588	105.59588	141.06241	7.110712	750	750	8058178821
Phleum pratense	78.083368	102.327697	146.656256	7.110712	169.25	169.25	8058178821

Pimpinella saxifraga	105.59588	105.59588	141.374734	7.110712	67	2391.5	8058178821
Plantago lanceolata	18.772773	18.772773	192.739234	7.110712	146.25	2500	8058178821
Plantago major	18.772773	105.59588	107.913881	7.110712	141.25	10000	5963719581
Plantago media	18.772773	105.59588	155.316104	7.110712	70.5	1860	8058178821
Platanthera chlorantha	310.486899	310.486899	3.875541	3.875541	6514.3144	21841.484	4531446957
Poa annua	18.772773	18.772773	124.171669	7.110712	25	3250	5963719581
Poa pratensis	18.772773	105.59588	109.925377	7.110712	52	52	5963719581
Poa trivialis	82.98178	120.22846	97.161759	7.110712	74.875	74.875	5963719581
Polygala comosa	54.296164	69.486893	385.780391	3.875541	4.5	4.5	8058178821
Polygala vulgaris	18.772773	105.59588	155.689375	7.110712	47	47	8058178821
Potentilla anserina	105.59588	105.59588	141.890839	7.110712	2.425	37.5	8058178821
Potentilla neumanniana	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Potentilla reptans	18.772773	18.772773	112.824005	7.110712	5113.3643	17367.398	5963719581
Primula veris	105.59588	105.59588	141.831812	7.110712	60	67.75	8058178821
Prunella grandiflora	78.293832	102.520854	146.762582	7.110712	14.5	14.5	8058178821
Prunella vulgaris	18.772773	18.772773	193.307668	7.110712	10.825	213.5	8058178821
Ranunculus bulbosus	18.772773	105.59588	155.730099	7.110712	5.75	33.4	8058178821
Ranunculus repens	18.772773	18.772773	170.568341	7.110712	5	53.825	8058178821
Rhinanthus angustifolius	18.772773	18.772773	221.128254	7.110712	15.875	306.25	8058178821
Rhinanthus minor	18.772773	18.772773	221.188756	7.110712	4.85	46.75	8058178821
Rumex acetosa	105.59588	105.59588	141.788064	7.110712	11.35	525	8058178821
Rumex crispus	18.772773	18.772773	191.177517	7.110712	262.5	10000	8058178821
Salvia pratensis	18.772773	105.59588	155.033887	7.110712	525	1151.25	8058178821
Sanguisorba minor	18.772773	105.59588	155.741048	7.110712	0.75	0.75	8058178821
Scabiosa columbaria	18.772773	18.772773	192.55308	7.110712	6	77.75	8058178821
Sedum sexangulare	62.993035	93.284943	385.780391	3.875541	37	37	4531446957
Senecio erucifolius	105.59588	105.59588	385.780391	3.875541	287.875	518.75	8058178821
Senecio jacobaea	18.772773	18.772773	188.026383	7.110712	525	25000	8058178821
Senecio ovatus	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Senecio vulgaris	18.772773	18.772773	145.592239	7.110712	180	9500	5963719581
Silene dioica	52	52	181.095047	7.110712	55	2325	8058178821
Silene nutan	18.772773	105.59588	155.670437	7.110712	63.95	63.95	8058178821
Sonchus asper	18.772773	18.772773	118.436898	7.110712	82.5	150000	5963719581
Stachys germanica	105.59588	105.59588	144.127994	7.110712	210.0389	1708.098	8058178821
Stellaria holostea	105.59588	105.59588	141.895043	7.110712	4.75	4.75	8058178821
Stellaria media	18.772773	18.772773	190.0927	7.110712	2750	3750	8058178821
Symphytum officinale	18.772773	105.59588	3.875541	3.875541	54	350	8058178821
Tanacetum vulgare	105.59588	105.59588	141.196255	7.110712	106.25	3125	8058178821
Taraxacum laevigatum	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Taraxacum officinale	76.966511	105.261698	130.743676	7.110712	1472.4605	5739.778	8058178821
Thymus pulegioides	105.59588	105.59588	95.994321	7.110712	132.125	132.125	5963719581
Tragopogon pratensis	18.772773	18.772773	149.458251	3.875541	47.5	47.5	8058178821
Trifolium campestre	18.772773	18.772773	220.202386	7.110712	35.625	35.625	8058178821
Trifolium dubium	18.772773	18.772773	221.176603	7.110712	23	23	8058178821
Trifolium medium	89.181933	118.634286	3.875541	3.875541	7.5	27.5	8058178821
Trifolium ochroleucon	78.22005	102.45314	146.725307	7.110712	68.75	68.75	8058178821

Trifolium pratense	18.772773	105.59588	155.593849	7.110712	132.5	132.5	8058178821
Trifolium repens	18.772773	18.772773	174.093581	7.110712	16	250	8058178821
Trisetum flavescens	18.772773	18.772773	117.842149	7.110712	6250	6250	5963719581
Triticum aestivum	18.772773	18.772773	221.070603	7.110712	117.875	117.875	8058178821
Valeriana dioica	78.300865	102.526838	146.767958	7.110712	6.25	15	8058178821
Valeriana officinalis	18.772773	18.772773	3.875541	3.875541	34.75	164.25	8058178821
Verbascum lychnitis	52	52	385.780391	3.875541	22052.75	32862.375	5963719581
Veronica chamaedrys	105.59588	105.59588	96.11943	7.110712	0.75	112.5	5963719581
Veronica teucrium	67.366755	105.105784	92.342268	7.110712	5113.3643	17367.398	5963719581
Vicia cracca	105.59588	105.59588	141.87311	7.110712	13.75	75	8058178821
Vicia hirsuta	18.772773	18.772773	220.224782	7.110712	3.1	75	8058178821
Vicia sepium	105.59588	105.59588	385.780391	3.875541	2.25	36	8058178821
Vicia tenuifolia	56.233035	71.316394	385.780391	3.875541	210.0389	1708.098	8058178821
Vicia tetrasperma	18.772773	18.772773	220.217579	7.110712	3.025	112.5	8058178821
Vicia villosa	18.772773	18.772773	149.458251	3.875541	50	75	8058178821
Vincetoxicum hirundinaria	105.59588	105.59588	3.875541	3.875541	210.0389	1708.098	8058178821
Viola hirta	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821
Viola odorata	81.167382	105.328987	147.551845	7.110712	210.0389	1708.098	8058178821

Table 14: Values of normalization constant of germination and mortality rates, annual day of beginning and ending of flowering, annual day of beginning and ending of seed release (sowing), temperature optimum (K), and temperature tolerance (K) for the species used in the simulations of the first implementation of the model, Figueiredo et al. (in prep.)

Species	Norm. constant germ.	Norm. constant mort	Begin flowering	End flowering	Begin sowing	End sowing	Temp. optimum (K)	Temp. tolerance (K)
Achillea millefolium	141363714	1113239249	23	44	43	47	285.6251	9.566667
Acinos arvensis	141363714	1113239249	23	40	39	43	278.8466	7.666667
Actaea spicata	141363714	1113239249	18	26	25	29	278.4126	7.933333
Aegopodium podagraria	141363714	1113239249	23	31	30	34	280.6411	9.116667
Agrimonia eupatoria	141363714	1113239249	23	40	39	43	280.4205	8.950000
Ajuga genevensis	141363714	1113239249	14	26	25	29	281.5398	8.000000
Ajuga reptans	141363714	1113239249	18	35	34	38	283.3404	8.083333
Allium schoenoprasum	141363714	1113239249	23	35	34	38	280.3545	9.183333
Alopecurus pratensis	141363714	1113239249	18	26	25	29	280.7221	8.766667
Anchusa arvensis	141363714	1113239249	18	40	39	43	281.2234	9.566667
Antennaria dioica	141363714	1113239249	18	26	25	29	278.2855	8.700000
Anthoxanthum odoratum	141363714	1113239249	18	26	25	29	281.2262	7.800000
Anthriscus sylvestris	141363714	1113239249	18	35	34	38	281.5486	7.483333
Anthyllis vulneraria	141363714	1113239249	18	35	34	38	280.7263	8.266667
Arabis hirsuta	141363714	1113239249	18	31	30	34	280.1182	8.333333
Arrhenatherum elatius	141363714	1113239249	23	44	43	47	281.2127	7.400000
Artemisia vulgaris	141363714	1113239249	27	49	48	52	283.0275	9.566667
Astragalus glycyphyllos	141363714	1113239249	23	31	30	34	279.8322	8.416667
Avenula pubescens	141363714	1113239249	18	26	25	29	279.8673	7.916667
Brachypodium pinnatum	141363714	1113239249	23	31	30	34	281.0725	9.000000
Bellis perennis	141363714	1113239249	0	49	48	52	283.4846	7.416667
Briza media	141363714	1113239249	18	26	25	29	279.9232	8.733333
Bromus erectus	141363714	1113239249	18	44	43	47	281.7318	6.133333
Bromus hordeaceus	141363714	1113239249	18	35	34	38	282.5224	8.016667
Calystegia sepium	141363714	1113239249	23	40	39	43	282.3955	9.350000
Campanula glomerata	141363714	1113239249	23	40	39	43	277.794	11.166667
Campanula persicifolia	141363714	1113239249	23	40	39	43	279.8406	7.600000
Campanula rotundifolia	141363714	1113239249	23	44	43	47	279.3996	9.083333
Campanula rapunculoides	141363714	1113239249	23	40	39	43	279.5601	9.683333
Cardaminopsis arenosa	141363714	1113239249	14	35	34	38	280.3846	7.900000
Carduus crispus	141363714	1113239249	27	40	39	43	279.9315	8.850000
Carex caryophyllea	141363714	1113239249	14	22	21	25	280.5223	8.466667
Carex flacca	141363714	1113239249	18	31	30	34	281.1753	7.533333
Carex leporina	141363714	1113239249	23	31	30	34	279.11	7.100000
Carex ornithopoda	141363714	1113239249	18	22	21	25	278.5075	7.466667
Carlina vulgaris	141363714	1113239249	27	40	39	43	280.7739	6.816667
Centaurea jacea	141363714	1113239249	23	49	48	52	280.4447	8.633333
Centaurea scabiosa	141363714	1113239249	27	35	34	38	279.9491	9.300000

Centaurium erythraea	141363714	1113239249	27	35	34	38	284.066	9.666667
Cephalanthera rubra	141363714	1113239249	23	31	30	34	281.1061	8.700000
Cerastium arvense	141363714	1113239249	14	31	30	34	281.0167	9.916667
Cerastium holosteoides	141363714	1113239249	9	26	25	29	281.2091	7.183333
Cerastium tomentosum	141363714	1113239249	18	31	30	34	281.0699	7.233333
Cerinthe minor	141363714	1113239249	18	31	30	34	280.6468	7.683333
Chaerophyllum hirsutum	141363714	1113239249	18	26	25	29	280.2983	6.316667
Chaerophyllum temulum	141363714	1113239249	18	31	30	34	282.3427	6.933333
Cichorium intybus	141363714	1113239249	27	44	43	47	283.5332	9.600000
Cirsium acaule	141363714	1113239249	27	40	39	43	280.592	8.450000
Cirsium arvense	141363714	1113239249	27	40	39	43	281.8333	9.083333
Cirsium oleraceum	141363714	1113239249	23	40	39	43	280.1936	8.366667
Cirsium tuberosum	141363714	1113239249	27	35	34	38	282.1654	6.016667
Cirsium vulgare	141363714	1113239249	23	40	39	43	283.7613	8.616667
Clinopodium vulgare	141363714	1113239249	27	40	39	43	280.3037	9.183333
Convolvulus arvensis	141363714	1113239249	23	40	39	43	284.1778	10.683333
Crepis biennis	141363714	1113239249	18	35	34	38	281.6483	6.333333
Cruciata laevipes	141363714	1113239249	14	26	25	29	282.3399	9.150000
Cynosurus cristatus	141363714	1113239249	23	31	30	34	281.0622	7.016667
Dactylis glomerata	141363714	1113239249	18	31	30	34	282.0465	8.083333
Daucus carota	141363714	1113239249	23	40	39	43	285.532	8.650000
Echium vulgare	141363714	1113239249	18	31	30	34	282.0942	9.166667
Elytrigia repens	141363714	1113239249	23	35	34	38	279.0669	6.900000
Epilobium angustifolium	141363714	1113239249	27	35	34	38	279.1531	10.716667
Epilobium montanum	141363714	1113239249	23	40	39	43	279.508	7.866667
Equisetum arvense	141363714	1113239249	9	17	16	20	281.6585	10.416667
Euphorbia cyparissias	141363714	1113239249	14	22	21	25	282.5568	7.733333
Euphrasia officinalis	141363714	1113239249	18	44	43	47	279.2117	8.166667
Falcaria vulgaris	141363714	1113239249	27	40	39	43	281.5397	8.166667
Festuca ovina	141363714	1113239249	18	35	34	38	279.3919	7.416667
Festuca pratensis	141363714	1113239249	23	31	30	34	279.8448	7.500000
Festuca rubra	141363714	1113239249	23	31	30	34	279.8448	7.500000
Filipendula vulgaris	141363714	1113239249	23	31	30	34	280.5264	8.516667
Fragaria vesca	141363714	1113239249	18	26	25	29	282.1414	9.266667
Fragaria viridis	141363714	1113239249	18	26	25	29	278.8633	9.366667
Galeopsis ladanum	141363714	1113239249	23	44	43	47	279.7941	9.166667
Galium aparine	141363714	1113239249	23	44	43	47	287.8325	8.166667
Galium mollugo	141363714	1113239249	18	31	30	34	280.4929	9.533333
Galium pumilum	141363714	1113239249	27	40	39	43	281.4022	6.766667
Galium verum	141363714	1113239249	23	40	39	43	280.0749	9.583333
Genista tinctoria	141363714	1113239249	23	35	34	38	280.7595	8.600000
Gentianella ciliata	141363714	1113239249	32	44	43	47	280.328	6.650000
Gentianella germanica	141363714	1113239249	23	44	43	47	280.6513	6.450000
Geranium dissectum	141363714	1113239249	18	35	34	38	285.291	7.200000
Geranium molle	141363714	1113239249	18	44	43	47	284.3925	7.650000
Geranium pratense	141363714	1113239249	23	35	34	38	279.96	8.816667

Geranium pusillum	141363714	1113239249	18	44	43	47	280.8284	8.250000
Geranium robertianum	141363714	1113239249	18	44	43	47	282.1439	7.633333
Geum urbanum	141363714	1113239249	18	44	43	47	281.6276	8.733333
Gymnadenia conopsea	141363714	1113239249	18	35	34	38	278.6253	8.683333
Helianthemum nummularium	141363714	1113239249	23	44	43	47	280.1858	6.466667
Heracleum sphondylium	141363714	1113239249	23	40	39	43	283.5358	9.316667
Hieracium caespitosum	141363714	1113239249	18	35	34	38	281.5453	9.933333
Hieracium lachenalii	141363714	1113239249	23	35	34	38	280.7973	7.550000
Hieracium murorum	141363714	1113239249	18	35	34	38	280.0843	7.833333
Hieracium pilosella	141363714	1113239249	18	44	43	47	282.3518	5.733333
Hippocrepis comosa	141363714	1113239249	18	31	30	34	281.8446	6.633333
Holcus lanatus	141363714	1113239249	23	35	34	38	282.6703	6.850000
Hypericum perforatum	141363714	1113239249	27	35	34	38	282.1337	9.766667
Inula conyzae	141363714	1113239249	23	44	43	47	282.6778	5.883333
Knautia arvensis	141363714	1113239249	27	35	34	38	280.4889	8.700000
Koeleria pyramidata	141363714	1113239249	23	31	30	34	281.7134	6.966667
Lathyrus pratensis	141363714	1113239249	23	35	34	38	279.4419	8.583333
Leontodon hispidus	141363714	1113239249	23	44	43	47	280.8981	7.983333
Leucanthemum vulgare	141363714	1113239249	23	44	43	47	282.6034	8.516667
Linum catharticum	141363714	1113239249	23	31	30	34	280.3002	6.500000
Listera ovata	141363714	1113239249	18	26	25	29	280.2161	7.016667
Lolium perenne	141363714	1113239249	18	44	43	47	286.1423	9.400000
Lotus corniculatus	141363714	1113239249	23	35	34	38	281.5991	8.900000
Medicago falcata	141363714	1113239249	23	40	39	43	278.8608	11.066667
Medicago lupulina	141363714	1113239249	18	44	43	47	287.8328	8.783333
Melampyrum arvense	141363714	1113239249	23	40	39	43	281.3895	8.366667
Melampyrum nemorosum	141363714	1113239249	18	40	39	43	279.1104	8.633333
Melampyrum sylvaticum	141363714	1113239249	23	40	39	43	278.0563	7.166667
Melilotus alba	141363714	1113239249	23	40	39	43	283.4032	9.966667
Melilotus officinalis	141363714	1113239249	14	40	39	43	282.2428	10.850000
Mentha arvensis	141363714	1113239249	23	44	43	47	278.4783	10.400000
Mentha verticillata	141363714	1113239249	27	35	34	38	280.1657	8.066667
Myosotis arvensis	141363714	1113239249	18	31	30	34	280.5512	7.983333
Myosotis sylvatica	141363714	1113239249	18	31	30	34	280.8248	8.733333
Onobrychis viciifolia	141363714	1113239249	18	31	30	34	281.8257	9.950000
Ononis repens	141363714	1113239249	23	31	30	34	282.5768	6.550000
Ononis spinosa	141363714	1113239249	23	31	30	34	281.1944	8.716667
Ophrys apifera	141363714	1113239249	18	26	25	29	283.7225	6.833333
Ophrys insectifera	141363714	1113239249	18	26	25	29	281.0236	7.016667
Orchis mascula	141363714	1113239249	18	26	25	29	281.6205	6.533333
Orchis militaris	141363714	1113239249	18	26	25	29	281.0057	9.166667
Orchis purpurea	141363714	1113239249	18	26	25	29	283.7867	6.683333
Orchis tridentata	141363714	1113239249	18	26	25	29	288.6735	8.050000
Origanum vulgare	141363714	1113239249	27	40	39	43	280.4336	9.783333
Phalaris arundinacea	141363714	1113239249	23	31	30	34	280.5887	9.783333
Phleum pratense	141363714	1113239249	23	35	34	38	280.0307	10.500000

Pimpinella saxifraga	141363714	1113239249	27	40	39	43	279.1678	8.283333
Plantago lanceolata	141363714	1113239249	18	44	43	47	284.8469	8.533333
Plantago major	141363714	1113239249	23	44	43	47	283.9908	9.583333
Plantago media	141363714	1113239249	18	40	39	43	279.5996	9.233333
Platanthera chlorantha	141363714	1113239249	18	31	30	34	280.114	7.016667
Poa annua	141363714	1113239249	0	53	52	56	284.4375	9.450000
Poa pratensis	141363714	1113239249	18	26	25	29	280.0435	9.683333
Poa trivialis	141363714	1113239249	23	31	30	34	280.7038	8.733333
Polygala comosa	141363714	1113239249	18	26	25	29	280.1609	7.466667
Polygala vulgaris	141363714	1113239249	18	35	34	38	279.9018	7.200000
Potentilla anserina	141363714	1113239249	18	35	34	38	281.3451	9.083333
Potentilla neumanniana	141363714	1113239249	14	26	25	29	283.0755	6.250000
Potentilla reptans	141363714	1113239249	23	35	34	38	281.6585	7.933333
Primula veris	141363714	1113239249	14	26	25	29	281.5454	8.500000
Prunella grandiflora	141363714	1113239249	23	35	34	38	280.7381	7.566667
Prunella vulgaris	141363714	1113239249	23	40	39	43	285.1315	9.600000
Ranunculus bulbosus	141363714	1113239249	18	31	30	34	281.8991	7.416667
Ranunculus repens	141363714	1113239249	18	35	34	38	282.5288	8.483333
Rhinanthus angustifolius	141363714	1113239249	23	40	39	43	281.718	6.650000
Rhinanthus minor	141363714	1113239249	18	40	39	43	279.8482	10.266667
Rumex acetosa	141363714	1113239249	18	31	30	34	280.8967	7.966667
Rumex crispus	141363714	1113239249	23	35	34	38	287.1484	10.533333
Salvia pratensis	141363714	1113239249	18	35	34	38	282.3332	7.583333
Sanguisorba minor	141363714	1113239249	18	35	34	38	282.403	8.150000
Scabiosa columbaria	141363714	1113239249	27	49	48	52	281.7792	6.800000
Sedum sexangulare	141363714	1113239249	23	35	34	38	281.2399	8.216667
Senecio erucifolius	141363714	1113239249	27	40	39	43	281.9572	7.933333
Senecio jacobaea	141363714	1113239249	27	40	39	43	282.1799	5.783333
Senecio ovatus	141363714	1113239249	27	40	39	43	280.0713	6.733333
Senecio vulgaris	141363714	1113239249	5	49	48	52	285.8002	8.933333
Silene dioica	141363714	1113239249	18	40	39	43	282.0698	7.383333
Silene nutan	141363714	1113239249	18	35	34	38	279.9228	8.933333
Sonchus asper	141363714	1113239249	23	44	43	47	289.974	10.116667
Stachys germanica	141363714	1113239249	23	35	34	38	284.642	6.983333
Stellaria holostea	141363714	1113239249	14	22	21	25	282.0927	7.083333
Stellaria media	141363714	1113239249	0	53	52	56	285.8061	7.783333
Symphytum officinale	141363714	1113239249	18	31	30	34	282.179	8.050000
Tanacetum vulgare	141363714	1113239249	27	40	39	43	280.7742	8.800000
Taraxacum laevigatum	141363714	1113239249	14	26	25	29	284.2226	8.533333
Taraxacum officinale	141363714	1113239249	9	44	43	47	287.2466	8.450000
Thymus pulegioides	141363714	1113239249	23	44	43	47	280.7396	8.850000
Tragopogon pratensis	141363714	1113239249	18	31	30	34	280.7897	8.950000
Trifolium campestre	141363714	1113239249	23	40	39	43	284.8373	8.033333
Trifolium dubium	141363714	1113239249	18	40	39	43	284.5877	7.466667
Trifolium medium	141363714	1113239249	23	35	34	38	279.1436	8.416667
Trifolium ochroleucon	141363714	1113239249	23	31	30	34	283.1174	6.900000

Trifolium pratense	141363714	1113239249	23	40	39	43	284.0001	8.933333
Trifolium repens	141363714	1113239249	18	40	39	43	289.0059	8.066667
Trisetum flavescens	141363714	1113239249	18	26	25	29	281.7958	7.300000
Triticum aestivum	141363714	1113239249	23	31	30	34	281.4158	10.666667
Valeriana dioica	141363714	1113239249	18	26	25	29	280.8733	7.266667
Valeriana officinalis	141363714	1113239249	18	35	34	38	279.324	9.350000
Verbascum lychnitis	141363714	1113239249	23	35	34	38	280.6361	9.366667
Veronica chamaedrys	141363714	1113239249	18	31	30	34	281.1476	8.550000
Veronica teucrium	141363714	1113239249	18	31	30	34	280.8409	8.700000
Vicia cracca	141363714	1113239249	23	35	34	38	280.1077	10.083333
Vicia hirsuta	141363714	1113239249	23	31	30	34	281.6091	9.166667
Vicia sepium	141363714	1113239249	18	26	25	29	280.6096	7.916667
Vicia tenuifolia	141363714	1113239249	23	35	34	38	280.9342	8.766667
Vicia tetrasperma	141363714	1113239249	23	31	30	34	280.3759	8.600000
Vicia villosa	141363714	1113239249	23	40	39	43	288.8241	6.783333
Vincetoxicum hirundinaria	141363714	1113239249	18	35	34	38	280.5451	8.816667
Viola hirta	141363714	1113239249	14	22	21	25	279.2736	8.350000
Viola odorata	141363714	1113239249	9	17	16	20	282.3458	7.800000

Publications list

Figueiredo, L., Krauss, J., Steffan-Dewenter, I., & Cabral, J. S. (2019). Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography*, 42(12), 1973–1990. doi: `10.1111/ecog.04740`

Figueiredo, L., Leidinger, L., Steffan-Dewenter, I., & Cabral, J. S. *under review*. Evolutionary rescue and community re-assembly contribute to the waiving of extinction debts.

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Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	LF	JL, JK, IS			
Data Collection	LF				
Data Analysis and Interpretation	LF	JL, JK, IS			
Manuscript Writing					
Writing of Introduction	LF	JL	JK, IS		
Writing of Materials & Methods	LF				
Writing of Discussion	LF	JL	JK, IS		
Writing of First Draft	LF				

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Figure	**Author Initials,** Responsibility decreasing from left to right				
2.1	LF	JL	JK, IS		
2.2	LF	JL			
2.3	LF	JL			
2.4	LF	JL			
2.5	LF	JL			

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