HOW GENOMIC AND ECOLOGICAL TRAITS SHAPE ISLAND BIODIVERSITY — INSIGHTS FROM INDIVIDUAL-BASED MODELS

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LUDWIG KLAUS THEODOR LEIDINGER

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Gutachter: Prof. Dr. Juliano Sarmento Cabral
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SUMMARY

Life on oceanic islands provides a playground and comparably easy-studied basis for the understanding of biodiversity in general. Island biota feature many fascinating patterns: endemic species, species radiations and species with peculiar trait syndromes. However, classic and current island biogeography theory does not yet consider all the factors necessary to explain many of these patterns. In response to this, there is currently a shift in island biogeography research to systematically consider species traits and thus gain a more functional perspective. Despite this recent development, a set of species characteristics remains largely ignored in island biogeography, namely genomic traits. Evidence suggests that genomic factors could explain many of the speciation and adaptation patterns found in nature and thus may be highly informative to explain the fascinating and iconic phenomena known for oceanic islands, including species radiations and susceptibility to biotic invasions.

Unfortunately, the current lack of comprehensive meaningful data makes studying these factors challenging. Even with paleontological data and space-for-time rationales, data is bound to be incomplete due to the very environmental processes taking place on oceanic islands, such as land slides and volcanism, and lacks causal information due to the focus on correlative approaches. As promising alternative, integrative mechanistic models can explicitly consider essential underlying eco-evolutionary mechanisms. In fact, these models have shown to be applicable to a variety of different systems and study questions.

In this thesis, I therefore examined present mechanistic island models to identify how they might be used to address some of the current open questions in island biodiversity research. Since none of the models simultaneously considered speciation and adaptation at a genomic level, I developed a new genome- and niche-explicit, individual-based model. I used this model to address three different phenomena of island biodiversity: environmental variation, insular species radiations and species invasions.

Using only a single model I could show that small-bodied species with flexible genomes are successful under environmental variation, that a complex combination of dispersal abilities, reproductive strategies and genomic traits affect the occurrence of species radiations and that invasions are primarily driven by the intensity of introductions and the trait characteristics of invasive species. This highlights how the consideration of functional traits can promote the understanding of some of the understudied phenomena in island biodiversity.

The results presented in this thesis exemplify the generality of integrative models which are built on first principles. Thus, by applying such models to various complex study questions, they are able to unveil multiple biodiversity dynamics and patterns. The combination of several models such as the one I developed to an eco-evolutionary model ensemble could further help to identify fundamental eco-evolutionary principles. I conclude the thesis with an outlook on how to use and extend my developed model to investigate geomorphological dynamics in archipelagos and to allow dynamic genomes, which would further increase the model's generality.

ZUSAMMENFASSUNG

Inseln sind nützliche Modellsysteme für das Verständnis von Biodiversität im Allgemeinen. Dies wird verstärkt durch den Umstand, dass Flora und Fauna auf Inseln eine Vielzahl einzigartiger Phänomene aufweisen: von endemischen Arten über Artenradiationen bis hin zu außergewöhnlichen Arteigenschaften. Bisherige Theorien der Inselbiogeographie berücksichtigen jedoch nicht alle Faktoren, die nötig wären, um solche Phänomene zu erklären. Derzeitige Bemühungen zielen daher darauf ab, Arteigenschaften systematisch mit bestehenden Theorien zu vereinen. Trotz dieser Entwicklung werden genomische Arteigenschaften bislang in solch einer funktionalen Inselbiogeographie weitestgehend ignoriert, obwohl es Hinweise darauf gibt, dass genomische Faktoren einige der faszinierenden Diversifizierungsmuster einschließlich Artenradiationen erklären könnten.

Die Erforschung dieser Faktoren gestaltet sich aufgrund des Mangels an umfangreichen, aussagekräftigen Daten jedoch als schwierig. Selbst unter Zuhilfenahme von paläontologischen Daten und substituierten Daten aus vergleichbaren Systemen lassen sich Unvollständigkeiten in den Daten und das Problem fehlender Kausalzusammenhänge schwer überwinden. Eine vielversprechende Alternative stellen mechanistische Modelle dar, von denen einige bereits für eine Vielzahl von Systemen und Forschungsprojekten eingesetzt wurden.

In dieser Dissertation wurden daher mechanistische Inselmodelle untersucht, um herauszufinden, inwiefern sich diese für derzeitige offene Fragen in der Inselbiogeographie eignen würden. Da keines der untersuchten Modelle gleichzeitig Artbildung and Anpassung unter Berücksichtigung von genomischen Faktoren abbildet, wurde ein neues genom- und nischenexplizites, individuenbasiertes Modell entwickelt. Dieses wurde benutzt, um drei verschiedene Phänomene im Kontext der Inselbiogeographie zu untersuchen: die Anpassung an Umweltvariation, Artenradiationen und Invasionen durch exotische Arten.

Mit diesem neuentwickeltem Modell konnte gezeigt werden, dass kleinere Arten mit flexiblen Genomen unter variablen Umwelteigenschaften erfolgreicher sind, dass eine komplexe Kombination aus Ausbreitungsfähigkeiten, Fortpflanzungsstrategien und genomischen Arteigenschaften das Entstehen von Artenradiationen beeinflussen und dass Invasionen vor allem von der Einführungsintensität und den Arteigenschaften exotischer Arten getrieben sind. Diese Ergebnisse demonstrieren, wie die Berücksichtigung funktionaler Arteigenschaften dabei helfen kann, einige bislang wenig untersuchte Phänomene der Inselbiogeographie zu verstehen.

Die Ergebnisse dieser Dissertation stehen beispielhaft für die Allgemeingültigkeit integrativer, auf Grundzusammenhängen aufbauender Modelle. Dies wird durch die Aufdeckung diverser Biodiversitätsmuster und -dynamiken im Rahmen der Bearbeitung verschiedener komplexer Fragestellungen hervorgehoben. Weitere Modelle, wie das hier beschriebene, könnten sogar in einem Modellensemble kombiniert werden, um öko-evolutionare Grundprinzipien zu identifizieren. Abschließend wird ein Ausblick auf die Möglichkeit gewährt, das Modell weiterzunutzen und zu erweitern, um beispielsweise geomorphologische Archipeldynamiken oder dynamische Genome abzubilden, und damit die Allgemeingültigkeit des Modells noch zu erweitern.

PUBLICATIONS

The following lists publications and manuscripts I co-authored as part of my PhD thesis.

Leidinger, Ludwig and Juliano Sarmento Cabral (Aug. 7, 2017). “Biodiversity Dynamics on Islands: Explicitly Accounting for Causality in Mechanistic Models.” *Diversity* 9.3, p. 30. DOI: `10.3390/d9030030`.

Leidinger, Ludwig and Juliano Sarmento Cabral (Apr. 12, 2020a). “How genomic and ecological traits affect radiations of plant species on oceanic islands: insights from a genomically-explicit model.” *in prep.*

Leidinger, Ludwig and Juliano Sarmento Cabral (Mar. 25, 2020b). “Temporal Environmental Variation Imposes Differential Selection on Genomic and Ecological Traits of Virtual Plant Communities.” *bioRxiv* (*under review at Oikos*), p. 2020.03.24.005058. DOI: `10.1101/2020.03.24.005058`.

Vedder, Daniel, Ludwig Leidinger, and Juliano Sarmento Cabral (Apr. 13, 2020). “Effects of species traits and abiotic factors during the stages of plant invasions.” *submitted to Journal of Applied Ecology*.

Change is the essential process of all existence.

— Spock

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Live long and prosper!

CONTENTS

Part I

INTRODUCTION

1

LIFE ON ISLANDS

Oceanic islands host a multitude of fascinating and unique species. This circumstance already inspired researchers like Darwin and Wallace to formulate their groundbreaking evolutionary theories on the origin of species (Darwin, 1859; Wallace, 1880; Warren et al., 2015). More than 150 years later, researchers are still working toward finding out which factors make island biota as unique as they are. The fact that islands represent comparatively small, closed systems that feature all of the relevant eco-evolutionary and environmental processes acting in other, for instance, continental, systems, makes them ideal study systems for biodiversity in general (Warren et al., 2015). Islands are recognized to feature some of the most diverse ecosystems and host a majority of the world's endemics (Kier et al., 2009). Unfortunately, this uniqueness comes at a cost: many island species are prominently at risk by neobiota, climate and land use change (Myers et al., 2000; Patiño et al., 2017). Investigating how island biodiversity is shaped and maintained therefore helps to understand biodiversity in general and thus to estimate its likely response to global change.

In this thesis, I will present my research aimed at investigating some of the factors and mechanisms that shape island biodiversity using process-based models.

1.1 PATTERNS OF ISLAND BIODIVERSITY

There are several aspects which contribute toward making island biota so intriguing. One of them is the phenomenon that island communities do not appear as random subsets of continental species pools. Instead, of all the lineages found on the continents, only a select few are represented on islands as well (Taylor et al., 2019). This so-called "island disharmony" can be explained by the fact that the only species that end up colonizing islands are those that have the ability to actually reaching them (Juan et al., 2000). Island disharmony thus exemplifies some of the many environmental and biotic filters that shape island biodiversity. A second aspect further amplifies this uniqueness. Compared to other biogeographic regions, oceanic islands exhibit a disproportionately high number of endemics, i.e. species which are found nowhere else in the world (Kier et al., 2009). Since islands are often quite isolated, *in situ* speciation rather than colonization contributes disproportionally to species richness when compared to continental systems (Whittaker and Fernández-Palacios, 2007). Furthermore, isolation of the island impedes the spread of evolved species to neighboring islands or continental land masses. The fact that many endemics within an island or archipelago are often closely related indicates the many successive speciation events within corresponding clades. These species radiations gave rise to, for example, the many species of *Aeonium* on the Canary islands (Jorgensen and Olesen, 2001) or lobeliads on Hawaii (Givnish et al., 2009). Yet, what enabled these lineages to show such outstanding diversifications (adaptive radiations), while most island species do not change markedly from the mainland lineages is unclear. So far, many of these phenomena are described primarily in a quantitative and species-agnostic manner, and species characteristics are seldom taken into account (but see Crawford et al., 2009). As a result, current research highlights these species characteristics as a promising factor to gain more insight into the origin of island biodiversity (Patiño et al., 2017; Warren et al., 2015).

Island species are in fact often associated with remarkable patterns and characteristics themselves. The phenomenon coined as the "island rule" is one of these patterns. It describes the tendency of large mainland taxa to evolve into smaller island sister taxa, and of small mainland taxa to evolve into larger island sister taxa (Foster, 1964). This is often combined with a loss of dispersal ability and responses in other traits like defensive capabilities. All of these species traits comprise the island syndrome (Burns, 2019). For most of these characteristics, there are plausible explanations. Given the vastness of ocean around islands, which represents an inhospitable matrix, reducing dispersal seems necessary to maintain viable population sizes rather than losing all offspring to the sea. Additionally, losing defensive capabilities is a way to reduce or re-allocate valuable energy in a new habitat where enemies are not around. These phenomena are exemplary for a large body of evidence of trait-related island patterns (Burns, 2019). In some of the cases, they can be attributed to particular factors: for instance, external drivers, geography or opportunism. The process of integral importance for most of these phenomena is evolution. Current theoretical frameworks hence focus on these kinds of factors to try to explain island biodiversity.

1.2 FORMAL ISLAND BIODIVERSITY THEORIES

Since Darwin and Wallace, many theories have been put forth to explain island biodiversity. One of the most influential modern frameworks on island biodiversity is MacArthur and Wilson's equilibrium theory of island biogeography (ETIB, MacArthur and Wilson, 1963). ETIB describes island species numbers as the result of two factors: island size and isolation. These factors, in turn, affect the opposing processes of immigration and extinction. This formalization makes it possible to analytically express island species numbers as a function of area — a concept known as Species-Area-Relationship (SAR). Over longer time spans, species numbers are additionally affected by speciation, i.e. the emergence of new species through evolution. But although discussed as an additional important process, speciation was not included in the original theory (MacArthur and Wilson, 1963; Warren et al., 2015).

Darwin and Wallace were also aware that present biodiversity patterns are a result of past processes, most prominently evolution. Since these processes were missing from the formal ETIB, there were several attempts to reconcile this in order to advance island biogeography theory (e.g. Chen and He, 2009; Rosindell and Phillimore, 2011). One of these attempts resulted in the formulation of the general dynamic model (GDM, Whittaker et al., 2007). Additional to immigration, extinction and speciation, the GDM considers an island's geomorphological ontogeny from island surfacing to submergence. During this interval, an island will change size, geographical features and possibly connectivity to other land masses. All of this affects ecological opportunities for species to diversify and isolation between populations. As a result, species numbers vary over time, while they are shaped by all those different processes, hence the name "dynamic" (Borregaard, Matthews, and Whittaker, 2016).

Intriguing about island biodiversity theories is that they can readily be applied to systems other than oceanic islands (Warren et al., 2015; Whittaker and Fernández-Palacios, 2007). This is because islands represent all the factors and processes that are relevant in, for instance, continental systems as well. ETIB, for instance, had a considerable impact on environmental and conservation studies. By applying SAR to a multitude of different systems, researchers were able to assess how well species numbers for a given region correspond to habitat area in comparison to SAR typical for that region. Deviations from these expectations typically indicate extinction debts or colonization credits (Cristofoli et al., 2010; Figueiredo et al., 2019; Tilman et al., 1994).

This generality of island biodiversity theory will likely still apply to future frameworks as well. A promising current development for a better understanding is the shift towards a more functional perspective in island biogeography research, i.e. to consider species' functional traits (Patiño et al., 2017; Warren et al., 2015). However, classical island biogeography frameworks do not yet represent scales at the level of detail necessary to consider traits. Hence, there are few theoretical predictions for functional island biogeography phenomena, such as island syndromes and adaptive radiations. Explaining the variety of empirical island biology patterns therefore calls for an extension of current theories to allow for the inclusion of species' functional traits and potentially of other, so far unconsidered, factors.

1.3 OPEN QUESTIONS AND CHALLENGES

Among those phenomena that current theories fail to explain are the patterns of adaptive radiations: on several oceanic islands, taxa such as *Psychotria* (Rubiaceae) or Asteraceae (Barrabé et al., 2014; Crawford et al., 2009; Nepokroeff et al., 2003) evolved a multitude of different species. The difficulty of explaining these patterns is highlighted by a subset of the 50 most pressing questions in island biology, which were compiled on the occasion of the 50th anniversary of the ETIB (Patiño et al., 2017): "What functional traits (e.g. relating to dispersal capacity, reproduction, trophic ecology) are associated with high diversification rates within and across island systems?" "What traits best predict which groups will undergo adaptive radiation on islands?" "What is the influence of gene flow among islands and/or between islands and mainland areas on speciation rates?" All of these questions refer to species characteristics. Probably the most obvious of those traits are dispersal abilities: the more dispersive a species, the more genetic exchange between populations. Consequently, many island biogeography studies use dispersal and isolation as the primary explanation for evolutionary patterns (e.g. Rosindell and Phillimore, 2011). However, genetics theory and genomic studies suggest that this might be an unwarranted oversimplification.

1.3.1 *The role of genomic traits in species performance*

Before sexual reproduction, gene variants (alleles) are selected randomly from each parent during recombination to constitute a gamete's, and thus half an offspring's, genome. Contrary to Gregor Mendel's model system in peas, this recombination is not free from certain constraints. Some genes, for example, can be located in close linear proximity on a chromosome. These genes therefore tend to be inherited together. This circumstance can be detected as the co-occurrence of particular trait alleles corresponding to seemingly unrelated genes (genetic linkage, Hawthorne and Via, 2001). An interesting phenomenon can be observed if only one of the genes is actually under selection. In this case, the frequency of the associated allele of the second gene will increase in the population, even though it is not under direct selection (divergence hitchhiking). This process can lead to quick divergence of populations, and thus speciation, since it enhances the isolation of entire genomic regions rather than only single genes (Feder and Nosil, 2010). As a result, the contained alleles have a higher chance of being fixed in the population, rather than homogenized, even in the face of gene flow between population (Via and West, 2008). This circumstance makes genomic traits therefore a good candidate to better understand why certain lineages evolve so many different species.

Genomic traits might play a role over very short time spans as well. Habitats with changing environmental conditions and possibly changing biotic composition present constant filters for species to pass in order to survive. For this, either flexibility in environmental preferences or sufficiently fast responses of species is critical. One such response comprises changing key traits in a matter of only a few generations in order to increase adaptation to the environment. This rapid evolution can be detected on the genomic side as a major shift in allele frequencies for associated traits (Thompson, 1998). For species colonizing islands, this becomes highly relevant. If lacking pre-adaptation to the novel conditions, species can only survive by rapid adaptation. Since islands often feature diverse and relatively dynamic habitats (Whittaker and Fernández-Palacios, 2007), the encountered conditions can change quickly. For the necessary rapid evolutionary response, it has been shown that selecting from already present, standing variation can be more efficient than acquiring new mutations (Barrett and Schluter, 2008, see also Crawford et al., 2009). Given the impacts of genetic linkage on recombination makes genomic traits an important factor for rapid evolutionary responses (Grant and Grant, 2014; Lamichhaney et al., 2015; Podos, 2001). Exactly how genomic traits contribute to species survival in realistic ecological settings under variable environmental conditions is still unclear, however.

1.3.2 *The threat of invasive species*

Global change presents another major challenge for island species (Myers et al., 2000). One of the largest threats to island biodiversity besides climate change and habitat destruction is presented by invasive species. The reason for the increased vulnerability of islands to invasives are the same phenomena which make islands unique in the first place: endemics and island syndromes. While the latter may increase the risk of species being replaced by invasives due to the loss of defensive or competitive abilities, the former means a replaced species might be lost forever. Understanding the process of invasions and the involved factors is therefore critical for any conservation efforts targeted to mitigate invasion impacts. Indeed, researchers have been able to identify various factors which are important for the success of invasions. One of them is the power of the many — introducing more individuals of a species in a given time period, i.e. increasing the propagule pressure, increases the chance of the introduced species to become invasive (Holle and Simberloff, 2005). Species attributes play another important role. While those alien species that end up being successful are are often those that have similar characteristics as native species (Küster et al., 2010), invasive species typically feature traits that correspond to increased recruitive and competitive capabilities, e.g. growth and size (Grotkopp and Rejmánek, 2007). These traits all contribute to a potential invasion syndrome. What is missing so far, however, is a systematic approach to put both propagule pressure and invasion syndrome in context to each other to assess their respective relative importance along the invasion process.

1.3.3 *Inferring causation*

The challenge in answering all these questions is the current lack of meaningful data. The putative causal links range from levels of genomic factors to biogeographical patterns. Hence, making any inferences requires data of appropriate scales, i.e. time series of multiple species on multiple islands together with genomic data. Fortunately, with improved and cheaper sequencing technologies, the extent of published genomic data is rapidly increasing (e.g. Alonso-Blanco et al., 2016). Additionally, there is a variety of publicly available databases which provide functional data and this still continues to grow (Kattge et al., 2011; Kattge et al., 2020). Thus, some of the necessary data is already available, albeit potentially not in sufficient extent and not harmonized.

Time series, on the other hand, are another matter. Timed data at meaningful scales, i.e. thousands to millions of years, are virtually impossible to obtain. In some cases, these gaps are therefore patched with paleontological data (e.g. Lieberman, 2012), but in the rare instances where such data is available, it is always incomplete and poorly resolved (Donoghue et al., 1989). As an alternative, many island biology studies are thus taking advantage of the fact that islands in a hotspot archipelago can be considered snapshots of different phases in an island's ontogeny and thus represent different points in an ecological and evolutionary time series (Warren et al., 2015). While this space-for-time approach produced valuable insights and inspired new hypotheses, all inferences have only a correlative foundation. Ultimately, investigating the causative effects of processes and factors on island biodiversity can only be done through systematic experiments. Again though, the spatial and temporal extents necessary to draw relevant conclusions often prohibit meaningful experiments (Warren et al., 2015). Additionally, manipulating real systems on a sufficiently large scale raises ethical considerations: Wilson and Simberloff's seminal defaunation experiments in the Florida Keyes (Simberloff and Wilson, 1969) would be unthinkable in present times, with widespread awareness of biodiversity loss, pollution and species extinctions.

Given the challenge of conducting *in situ* experiments at relevant scales, systematic manipulation has to be done elsewhere. A useful approach is employing representative models. These can also be virtual, as in the case of mechanistic simulation models. Their advantage is the ability to have complete control over all processes and parameters. The basic principle of simulation models is to define a set of rules which will dictate the behavior of the system, feed it with appropriate parameter values and analyze the emerging results. These results can then be compared to empirical data at different scales and levels in order to assess the validity of the assumptions of the model (Grimm et al., 2005). Ideally, such models consider a sufficient number of processes to be applied to several specific systems rather than some unrealistic idealization (Evans et al., 2013). This generality however, is not often the case — while most models provide some valuable biological insight, some models are not general enough to answer more complex questions which require integrating multiple processes to control for confounding effects (Cabral, Valente, and Hartig, 2017). For islands, there are already a number of mechanistic models, but they, too, often address only a limited number of systems or study questions. Whether any of these models would also qualify to answer some of the current open questions in island biogeography depends therefore on their integrated processes. Additionally, the applicability of these models to other systems or study questions depends on the level of detail their assumed processes and parameters represent. Instead of building on first principles and having higher order patterns emerge from these, some models directly simulate patterns at more abstract levels, e.g. speciation as a determined, time-delayed lineage split (Rosindell and Phillimore, 2011). As a consequence, the modeled patterns are likely context dependent on the implicit characteristics of the modeled system, which makes application to other systems difficult. And since these models do not consider the specific processes behind a pattern, their assumed mechanisms can not easily be related to any particular biological, i.e. species-specific property. Therefore, the most meaningful insights is to be expected from models that build on first principles (e.g. Cabral, Wiegand, and Kreft, 2019; Pontarp et al., 2019) and consider functional species characteristics, i.e. traits (e.g. Matthews, Leidinger, and Sarmento Cabral, 2020). As such, mechanistic models then allow integrating many different processes and established theories that, in combination, may produce unexpected patterns through complex behavior and thus new hypotheses. As per the modeling cycle, these new hypotheses can inspire empirical studies — and their observations, in turn, will motivate further modeling.

2

OVERVIEW OF STUDY QUESTIONS

This thesis aims to shed light on the role of species traits in maintenance and evolution of island biodiversity. The work thereby contributes to building an integrative, functional theory of island biology, by using mechanistic models.

After having assessed the current state of the art of island models in the literature, I closed some of the identified gaps by developing a novel simulation model. I used this model to several different phenomena related to island biology: environmental variation, diversification and invasion. The main part of the thesis (part ii) is hence structured into four separate manuscripts, each of which is devoted to one of the study questions which are briefly presented in the following. At the time of writing this thesis, one of the manuscripts has been published in a peer-reviewed journal (Leidinger and Cabral, 2017), and two others have been submitted to journals pending editor's decisions and peer reviews (Leidinger and Cabral, 2020). The remaining manuscript is currently prepared for submission to a peer-reviewed journal as well (chapter 5).

Since simulation models represent a powerful approach for investigating island biodiversity, I needed to establish an overview on mechanistic island models. This called for the investigation of which processes and factors had been considered in mechanistic models so far and the identification of potential knowledge gaps. In chapter 3, I therefore systematically searched the literature for island biogeography modeling studies and analyzed all identified models in terms of their characteristics and addressed study questions and systems.

Having identified that previous models largely neglected the process of adaptive radiation and genomic traits (chapter 3), I developed a new model to remedy both of these shortcomings by explicitly considering different species characteristics and genomic traits. To test the implementation and impact of these factors, I was interested in how genomic traits affect plant community composition under temporally variable environments — a scenario regularly encountered on oceanic islands. In chapter 4, I thus investigated how genomic traits mediated the effect environmental variation by contrasting scenarios of temporally static environmental conditions to scenarios of temporally variable environmental conditions.

The identified importance of genomic traits in ecological contexts and time scales (chapter 4) compelled me to investigate how they would impact evolutionary patterns. Since a number of studies already reported an influence of genetic linkage in speciation, I thus performed island colonization experiments in chapter 5 to find out which ecological and genomic traits affected the occurrence and extent of radiations of insular plant lineages.

Island radiations produced a major proportion of the world's endemics species. This puts island biota prominently at risk of anthropogenic influences, such as species invasions. In chapter 6, I present an application of the developed model to such a conservation- related question. The chapter describes an experiment involving in-silico species introductions on a virtual island to investigate which abiotic factors and ecological species traits cause exotic plant species to become successful invaders.

I will conclude the thesis with a general discussion of the findings of the chapters and provide an outlook to potential future research directions (part iii).

Part II

MAIN

3

BIODIVERSITY DYNAMICS ON ISLANDS: EXPLICITLY ACCOUNTING FOR CAUSALITY IN MECHANISTIC MODELS

In the quest for an integrative island biology, island simulation models will be an essential asset to mechanistically investigate factors involved in shaping island biodiversity. In the following manuscript, we systematically reviewed studies involving island models to characterize implemented factors and summarize their respective findings.

We found that island models were applied to a multitude of different study questions related to past, present, and future island biodiversity patterns, but usually restricted to only one particular system. The models themselves often considered only a few processes. In particular, adaptive radiations were touched upon by only a single model. The findings from our analyses of island model characteristics thus call for more integrative models and the reconnection of island biogeography with mainstream ecology and evolution.

The manuscript was published in *Diversity* in 2017 (Leidinger and Cabral, 2017). The article was drafted and written by myself with contributions by Juliano Sarmento Cabral. I performed all research procedures and analysis. The conceptual design was done by Juliano Sarmento Cabral. My overall contribution amounted to ca. 90 %.

diversity

Review

Biodiversity Dynamics on Islands: Explicitly Accounting for Causality in Mechanistic Models

Ludwig Leidinger * and Juliano Sarmento Cabral

Ecosystem Modeling, Center for Computational and Theoretical Biology, Faculty of Biology, University of Würzburg, 97074 Würzburg, Germany; juliano.sarmento_cabral@uni-wuerzburg.de
* Correspondence: ludwig.leidinger@uni-wuerzburg.de

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Abstract: Island biogeography remains a popular topic in ecology and has gained renewed interest due to recent theoretical development. As experimental investigation of the theory is difficult to carry out, mechanistic simulation models provide useful alternatives. Several eco-evolutionary mechanisms have been identified to affect island biodiversity, but integrating more than a few of these processes into models remains a challenge. To get an overview of what processes mechanistic island models have integrated so far and what conclusions they came to, we conducted an exhaustive literature review of studies featuring island-specific mechanistic models. This was done using an extensive systematic literature search with subsequent manual filtering. We obtained a list of 28 studies containing mechanistic island models, out of 647 total hits. Mechanistic island models differ greatly in their integrated processes and computational structure. Their individual findings range from theoretical (such as humped-shaped extinction rates for oceanic islands) to system-specific dynamics (e.g., equilibrium and non-equilibrium dynamics for Galápagos' birds). However, most models so far only integrate theories and processes pair-wise, while focusing on hypothetical systems. Trophic interactions and explicit micro-evolution are largely underrepresented in models. We expect future models to continue integrating processes, thus promoting the full appraisal of biodiversity dynamics.

Keywords: mechanistic models; island biogeography; causality

1. Introduction

Islands remain popular model systems for studying mechanisms determining species diversity [1,2]. Reasons for this include the possibility to define isolation and area [3], while still retaining a degree of connectivity via rare long-distance dispersal events. At the same time, islands showcase all major types of mechanisms thus far indicated to influence biodiversity dynamics, such as physiological, demographic, dispersal, interaction, genetic and environmental processes [4–6].

One of the most prominent and earliest theories describing island diversity as a function of ecological mechanisms and external drivers is the seminal equilibrium theory of island biogeography (ETIB; [7]). In their theory, MacArthur and Wilson suggest that species numbers on an island are determined by a dynamic equilibrium between opposing rates of colonization and extinction. These rates are, in turn, dependent on the isolation and size of an island, respectively. A decade ago, island biogeography theory received new momentum with the formulation of the general dynamic model (GDM; [8]). This conceptual model considers changes of carrying capacity and niche opportunities over the ontogeny of oceanic islands and its effect on species numbers and their rates of change, including predictions on speciation rates. The typical ontogenic trajectory of hotspot islands starts with a small island size at the time of island emergence via volcanic activity, corresponding to low carrying capacity. As the island grows older, elevation and overall area increases and, thus, also carrying capacity. Later, after the island drifts out of the volcanic hotspot, erosion leads to higher

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topographic complexity, facilitating species radiations. The last stage sees further erosion of the island and ultimately atoll formation, resulting in increased numbers of locally extinct species.

While biodiversity theories, in particular the ETIB, were developed and tested experimentally, nowadays, conservation considerations render it unfeasible to conduct experiments of a scale comparable to that of the classical experiment by Simberloff and Wilson [9]. Moreover, Borregaard et al. [10] and Whittaker and Fernández-Palacios [11] among others point out that issues such as anthropogenic disturbances and above all the long timescales relevant when considering evolution make studying phenomena affecting the dynamics and maintenance of island biodiversity difficult and complex.

As a general consequence of these limitations, many studies investigating species diversity patterns on islands can only draw conclusions of a correlative nature, often by fitting regression models [12]. This has helped in identifying many possible drivers of biodiversity distribution [13,14]. However, the underlying causal relationships remain generally debatable, considering that the representation of causality in correlative models is limited. Therefore, definitive statements on evolution and on the impact of geological processes based solely on field data are generally inconclusive. This holds true particularly for islands, due to the destructive nature of geological phenomena, such as volcanism or erosion. One way to overcome this data limitation is to employ a space-for-time substitution using islands of different ontogenic stages as snapshots in time [15]. However, archipelagic dynamics, such as geomorphological changes in island size, connectivity and heterogeneity, as well as island hopping, might have confounding effects on empirical data [16]. Another possible alternative, still involving empirical testing, is using smaller scaled model systems such as microbiota [17,18]. Yet, for studying biogeography dynamics of longer living organisms, process-explicit models remain the most viable option to date.

With the advances in technology and scientific knowledge, process-explicit simulation models have become even more feasible, both in implementation, as well as conducting. In principle, process-explicit (or mechanistic) models reflect hypotheses about how mechanisms interact to produce observed patterns. In this context, we define mechanisms (or processes) as actions that causally link elements in a model. The produced patterns are thus direct results of the interplay between integrated processes. The advantage of these models lies in their flexibility. Such flexibility can be characterized in two ways: (1) through variation of model parameter values and thus their impact [19]; and (2) switching off particular processes or varying the model structure, e.g., the order of processes [20]. The combination of both allows for a multitude of possible alternative simulation arenas or scenarios and enables us to test the robustness, but also the importance of the respective mechanistic assumptions, while maintaining complete mechanistic control of the experiments.

To get an overview of which processes and drivers have been considered thus far in mechanistic island models, what patterns they produce and what they found out about their systems, we conducted an extensive literature review. We systematically searched for aspects, like for example, the theories models are based on, whether they are stochastic or deterministic, spatially implicit or explicit and what focal level they consider. The scope of our review also entails any model explicitly assessing island biogeography theories or assumptions. In contrast to the recent review by Borregaard et al. [10], we only consider models that specifically feature causal mechanisms, detached from the scope of the GDM. Our review is similar to Cabral et al. [21], but we focus specifically on island models and perform an exhaustive, systematic literature search.

2. Results

2.1. Description

The search for “archipelago OR island OR model OR equilibrium” in the title field and “(island OR archipelago) AND (species) AND (evolution OR speciation OR theory) AND (simulation OR model)” as the topics yielded 647 hits on the Web of Science (https://apps.webofknowledge.com), spanning years from 1981 to 2017 (Figure 1), which we filtered manually on the basis of whether the papers actually contained mechanistic models and whether they were island related, i.e., whether they assessed island biogeography theories or dealt explicitly with islands and/or archipelagos. This procedure meant not including all models that could potentially be relevant to islands (e.g., metacommunity models), but which unfortunately did not explicitly state so in their text, thus making it difficult to find all of them in a systematic way. After this filtering, we attained 28 hits in total (Table 1).

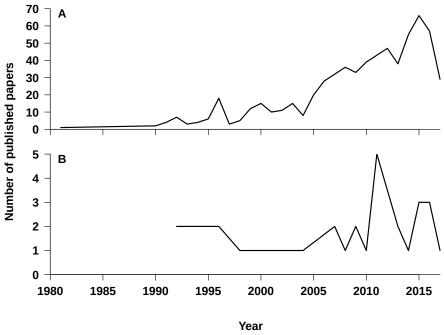

Figure 1. Number of paper hits from the literature search over publication years. (**A**) Total (raw) numbers of all paper types; (**B**) numbers of studies containing mechanistic simulation models. Note the different y-axis scales of both graphs.

2.2. *Properties*

Island biogeography models developed so far are very diverse in their properties (see the spread in Figure 2). Common to most models is the implementation of basic demographic processes (birth/death) and dispersal, but also, evolution is an often integrated process (Table 1, "processes"). A fundamental property found in the models lies in their implementation of stochasticity. Most of the studies use stochastic models (Figure 2). These are characterized by employing stochasticity in at least one of their mechanisms. This might be, e.g., the selection of the number of offspring in a reproduction event (e.g., [22]) or dispersal decisions (e.g., [23]). In contrast, deterministic models are often described purely analytically by a set of differential equations [24,25], although in some deterministic models, stochasticity can be easily switched on [26].

Some of the models explicitly consider the spatial configuration and position of state variables of their environment, i.e., they are spatially explicit. While spatially explicit and stochastic models were common in the earliest studies [22,27], more recently published models tend to be less often spatially explicit [28,29], which mirrors the popularity of the unified neutral theory of biodiversity (UNTB; [30]). Because the UNTB inspired a large portion of the later models, we considered it an additional category. Consequently, models are "neutral" if they follow neutral dynamics, i.e., ecological equivalence between individuals of different species. Additional underlying theories are also summed up in Table 1.

Models also varied in their metacommunity scenarios. The most common arena is of a mainland-island configuration (or source-sink), with a source species pool on the (continental) mainland. In some cases, more than one island is modeled, creating an archipelago-type system (Table 1). Most models furthermore explore hypothetical systems (Table 1), which represent islands in a simplified way and have no direct connection to real-world systems, although they are often inspired by real-world examples.

The integration of evolutionary processes emerges as another discriminating factor (Figure 2). This has been achieved at different levels of detail. With a genome-explicit model, Gavrilets and Vose [31] consider the accumulation of micro-evolution in genes encoding for ecological niche preferences, which leads to the isolation of populations and eventually in speciation, and recent papers opt to implement speciation in a more simplified way using submodels like "protracted speciation" [32] or point speciation as in the original UNTB [30].

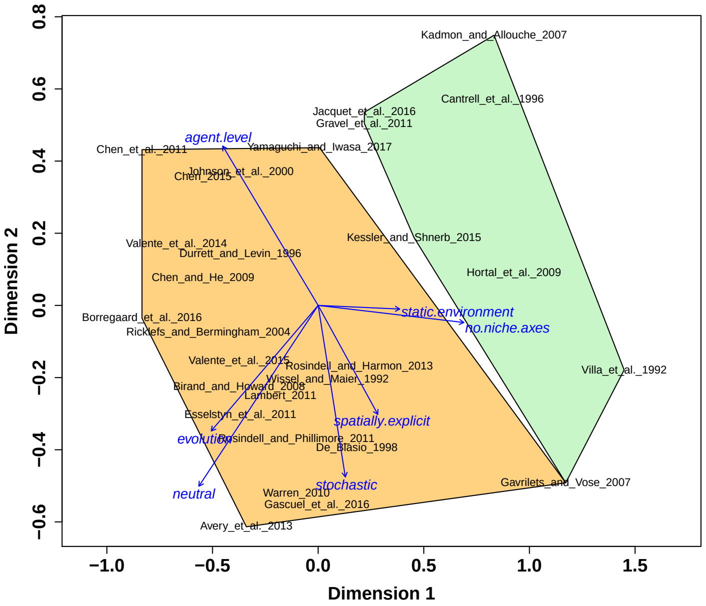

Figure 2. Multidimensional scaling of the refined list of papers according to the model characteristics ($Stress - 1 = 0.144$, better than permutation-based null solutions with $p < 0.05$). Blue arrows represent category axes with significant importance ($p < 0.05$). Arrow directions are from the absence to the presence of a property or in increasing order (number of niche axes and focal level). Clusters show groupings of papers based on whether models consider niche differences between species (green cluster) and whether they employ evolution in any form (orange cluster). Meaning of arrow labels: neutral: whether the model follows neutral theory [30]; evolution: whether the model employs evolution; stochastic: whether the model architecture is deterministic (zero) or stochastic (one); spatially.explicit: whether the model explicitly considers space; no.niche.axes: the number of parameters that relate to biological differences between species; static.environment: whether the model arena is subject to change (zero) or static (one); agent.level: the organizational level at which the model processes act (from individual, one, to population, two, to species, three). The underlying data are shown in Table 1. Note that for the creation of the plot, a jitter was applied to the data to make points better distinguishable.

An important factor contributing to the distribution of the studies' models is the implemented agent level, which determines whether processes directly act on individuals, populations or species. This also shows a positive trend with stochasticity, with deterministic analytical models usually focusing on higher organizational levels (see the diametrical axes "focal.level" and "stochastic" in Figure 2), such as population or species numbers [26,33]. In contrast, stochastic models often are individual based [22,31]. The agent level often also determines the focal level (Table 1), which is on the same or a higher organizational level as the agent level. Noteworthy here are two studies, which integrate genetic properties into their models to investigate the genetic structures of populations [34,35].

While in most of the models, there is no differences between species, some models allow species to carry their own particular parameter values. This can, for instance, be the reproductive output [22,24] or the competition strength [36] and is reflected as the number of non-neutral niche axes (Table 1). The total number of parameters ranges from one to 14 (Table 1). However, as parameters were not equally apparent in all papers, these numbers might be underestimated.

Furthermore, we discriminated models with static environments and models where the environment was subject to change. This change affects the geographic configuration of the environments, altering island size, suitability or carrying capacity. Examples for this are the models inspired by the GDM, which simulate island ontogenies [25,26,37].

Lastly, we took into consideration whether studies investigated purely hypothetical scenarios (models marked "h" in the system column of Table 1) or if they applied their models to real-world systems, e.g., by fitting or calibrating them to empirical data (models marked "**r**"). Of the 28 included studies, only five studies include a systematic comparison with real-world systems. For instance, Birand and Howard [38] and Rosindell and Phillimore [39] use parameter screening to obtain realistic rates of extinction, reproduction, speciation and migration compared with archipelago species numbers (including information on endemics) from plants and arthropods, or birds, respectively. Two other studies used representations of real geography as their model arena [23,34] for the investigation of radiation or speciation histories. Only a single study actually fitted their model to data, using a maximum likelihood approach and dated phylogenies of Galápagos land birds to obtain rates of diversification and radiation [29].

Some of the aforementioned characteristics often go together, representing commonly-used model structures (Figure 3). For example, island models following the framework of the UNTB usually employ evolution, as well. This highlights especially those studies that extend classical neutral dynamics with speciation [28,39,40]. Another example of a frequent characteristics combination are spatially-explicit models with static environments, which can be found among the earliest published models included in this study [22,24,27,41]. This co-occurrence of spatially-explicit and static environment properties is further strengthened by a number of studies displaying the exact opposite of this combination, namely spatially-implicit models with dynamic environments, as implemented by models having a GDM background [25,26,37]. One interesting property that is rather isolated in the property space is the consideration of inter-specific differences (niche-based, Figure 3). While the contrast of niche-based models to neutral models could be expected, the accompanying opposition to models including evolution is surprising. In fact, when marking the relevant studies according to whether models consider niche differences between species (green cluster, Figure 2) and whether they employ evolution in any form (orange cluster, Figure 2), only one study [31] joins both of these clusters and can thus be understood as the only one to investigate evolution in an explicitly adaptive context.

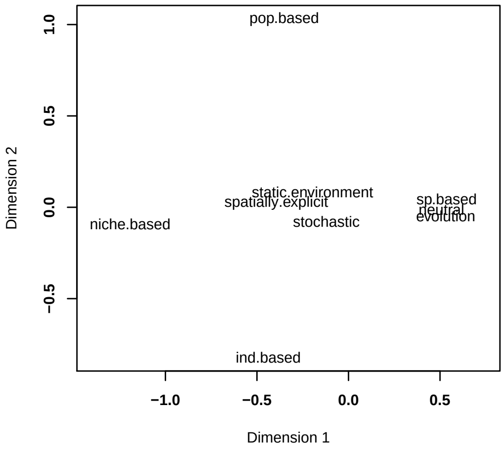

Figure 3. Multidimensional scaling of the model properties in the refined list of papers ($\mathit{Stress} - 1 = 0.126$). The closer two properties are, the more often these properties are implemented simultaneously in models. The underlying data are shown in Table 1. ind.based: individual-based; pop.based: population-based; sp.based: species-based; other properties as in Figure 2. For this analysis, we used the same data as for producing Figure 2 .

Table 1. Studies with process-based models for island biogeography. Papers are sorted chronologically. The system column also contains information on whether the model simulates a purely hypothetical (h) or real-world system (calibrated with data, **r**). Columns that were used for Figures 2 and 3 are marked with an asterisk (*). A: archipelago; AID: area-isolation-dependency; com.: community; comp.: competition; dep.: dependent; disp.: dispersal (includes immigration for species-based models and establishment for population-based models; dist.: disturbance; div.: diversity; E: endemics; eq.: equilibrium; ETIB: equilibrium theory of island biogeography; Ev.: evolutionary processes; ext.: extinction; GDM: general dynamic model of oceanic island biogeography; I: island; ind.: individual; MA: mainland-archipelago; MI: mainland-island; mut.: mutation; No. nn.: number of non-neutral niche axes, specific to species or individuals; No. par.: minimum number of easily identifiable parameters (e.g., constants, rates); Nt.: neutral; phyl.: phylogenetic; pop.: population; repr.: reproduction; SAD: species-abundance-distribution; SAR: species-area-relationship; SHR: species-heterogeneity-relationship; SIR: species-isolation-relationship; spec.: speciation; sp.: species; Spt. exp.: spatially explicit; st/dn: static or dynamic environment; Stoc.: stochastic; th.: theory.

Study	Year	System (h/r)	Theoretical Background	Processes (st/dn) *	No. par.	Stoc. *	Spt. Exp. *	Ev. *	Nt. *	No. nn. *	Agent Level *	Focal Level	Investigated Patterns
Wissel and Maier [42]	1992	MI (h)	ETIB, target effect	disp., repr., (st)	7	yes	no	no	yes	0	pop.	com.	SAR
Villa et al. [22]	1992	MA (h)	ETIB	disp., repr., dist., (st)	9	yes	yes	no	no	4	ind.	com.	SAR, eq.
Durrett and Levin [27]	1996	A (h)	ETIB	disp., comp., spec., (st)	4	yes	yes	yes	yes	0	sp.	com.	SAR
Cantrell et al. [24]	1996	MI (h)	ETIB, Allee effects	disp., repr., comp., (st)	6	no	yes	no	no	2	pop.	sp.	trait-dep. colonization
De Blasio [41]	1998	MI (h)	ETIB	disp., comp., (st)	5	yes	yes	no	yes	0	pop.	com.	SAR
Johnson et al. [43]	2000	MI (h)	ETIB, genetic divergence	disp., spec., ext., divergence, (st)	7	no	no	yes	yes	0	pop.	pop.	AID of diverging lineages over time
Ricklefs and Bermingham [44]	2004	MI (h)	[43]	mut., spec., (st)	6	yes	no	yes	yes	0	sp.	sp.	SIR, divergence-dep. no. of lineages
Gavrilets and Vose [31]	2007	MI (h)	sympatric spec.	disp., sex. repr., mut., (st)	6	yes	yes	yes	no	5	ind.	com.	time- & niche-dep. trait distribution
Kadmon and Allouche [33]	2007	MI (h)	ETIB, UNTB, niche	disp., repr., ext., (st)	5	no	no	no	no	1	ind.	com.	SAR, SHR
Birand and Howard [38]	2008	A (h)	[45]	disp., spec., ext., (st)	4	yes	no	yes	yes	0	sp.	com.	sp.-div.-dep.E
Chen and He [46]	2009	MI (h)	ETIB	disp., spec., ext., (st)	4	no	no	yes	yes	0	sp.	com.	rate-dep. E
Hortal et al. [47]	2009	MI (**r**)	[33]	disp, repr., (st)	5	yes	no	no	no	2	ind.	com.	SAR, SHR
Warren [48]	2010	MA (h)	UNTB	disp, spec., (st)	6	yes	no	yes	yes	0	ind.	com.	SIR, rate-dep. β-div.
Rosindell and Phillimore [39]	2011	MI (**r**)	UNTB	disp., repr., spec., (st)	5	yes	no	yes	yes	0	ind.	com.	SAD, SAR, SIR
Lambert [49]	2011	MI (h)	ETIB, UNTB	disp., repr., mut., (st)	6	yes	no	yes	yes	0	pop.	com.	rate-dep. SAD
Esselstyn et al. [23]	2011	A (**r**)	*not explicit*	disp., (st)	1	yes	yes	yes	yes	0	sp.	sp.	radiation history
Gravel et al. [50]	2011	MI (**r**)	ETIB, trophic th.	disp, ext., (st)	2	yes	no	no	no	1	sp.	com.	SAR

Table 1. *Cont.*

Study	Year	System (h/r)	Theoretical Background	Processes (st/dn *)	No. par.	Stoc. *	Spt. Exp. *	Ev. *	Nt. *	No. nn. *	Agent Level *	Focal Level	Investigated Patterns
Chen et al. [25]	2011	MI (h)	GDM, ETIB	disp, spec., ext., (dn)	12	no	no	yes	yes	0	sp.	com.	time-dep. E & sp. richness
Avery et al. [34]	2013	MI (r)	*not explicit*	disp., repr., mut., (dn)	6	yes	no	yes	yes	0	ind.	pop.	colonization history
Rosindell and Harmon [28]	2013	MI (h)	UNTB, ETIB	disp., death, (st)	6	yes	no	no	yes	0	ind.	com.	rate-dep. SAD
Valente et al. [37]	2014	MI (h)	GDM, ETIB	disp., spec., ext., (dn)	4	yes	no	yes	yes	0	sp.	com.	rate- & time-dep. sp. richness
Chen [51]	2015	MA (h)	[45,46]	disp., ext., spec., (st)	3	no	no	yes	yes	0	sp.	sp.	rate-dep. E & β-div.
Kessler and Shnerb [36]	2015	MI (h)	ETIB, UNTB, Lotka-Volterra	disp., repr., comp., (st)	4	yes	no	no	no	1	pop.	com.	comp.-dep. com. assembly
Valente et al. [29]	2015	MI (r)	UNTB, ETIB	disp., spec., ext., (st)	6	yes	no	yes	yes	0	sp.	com.	time-dep. phyl. rates
Borregaard et al. [26]	2016	I (h)	GDM	disp., spec., ext., (dn)	13	no	no	yes	yes	0	sp.	com.	time-dep. SAR, SHR
Gascuel et al. [40]	2016	MA (h)	UNTB, [39]	repr., disp., spec., (st)	6	yes	yes	yes	yes	0	ind.	com.	SIR, E in A
Jacquet et al. [52]	2017	MI (h)	ETIB, trophic th.	disp., ext., (st)	14	yes	no	no	no	1	sp.	com.	AID of traits
Yamaguchi and Iwasa [35]	2017	A (h)	pop. genetics	disp., mut., (st)	4	yes	no	yes	yes	0	pop.	pop.	time-dep. SIR

2.3. Findings

The reviewed studies investigate a variety of patterns in the spectrum of biodiversity. Commonly investigated patterns include the proportion of endemism and species-area relationships (SAR). For SAR, studies found that in additional to the extinction and immigration rates as proposed by MacArthur and Wilson [7]) [27,41,42], species numbers also depend on explicit competition [41], trophic interactions [50,52], environmental heterogeneity [33,47] and evolutionary processes, like mutations and speciation [25,38]. Figure 4 shows a representation of all of the processes and drivers implemented in the models, explicitly highlighting causal relationships and under-explored links.

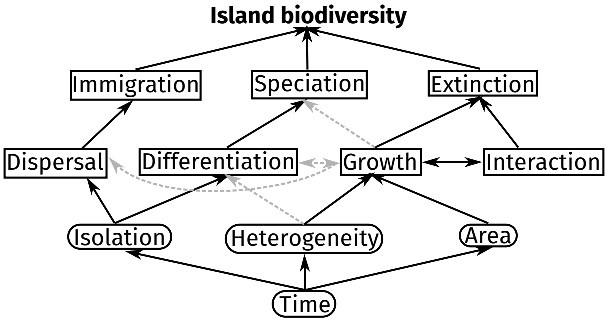

Figure 4. Summary of typical processes and drivers affecting island biodiversity implemented in the models with their assumed causal relationships (Table 1, columns "processes", "focal level", "agent level", "investigated patterns"). Round and square boxes denote drivers and processes, respectively. The bottom row of processes represents processes usually acting on individual-/population-levels, the top row of processes metacommunity-level processes. Black boxes and text mark factors and relationships regularly integrated in models, while grey arrows stand for thus far under- or un-explored relationships. Note that authors may opt to implement models that skip certain organizational levels, for example for investigating the direct effect of isolation on extinction as predicted by the ETIB. Additional relationships not explicitly stated in the chart include rescue-effects [53] between isolation and extinction and target effects [54] from area to immigration. For clarity, these kinds of relationships have been excluded from the graphic. Furthermore, "growth" combines both birth and death processes, while "interactions" include positive, neutral and negative interactions, for example competition or trophic interactions, and "differentiation" encompasses micro-evolutionary processes, such as mutation and gene flow. For a more complete overview of processes, patterns and organizational levels, the reader may refer to Figure 5.

A group of models simulating hypothetical systems concentrated on testing particular predictions from theoretical frameworks like ETIB and was thus able to confirm power law species-area-relationships [27,41,42] or the hump-shaped trajectories following island ontogenies of the GDM [26,37]. This investigation of theoretical prediction includes a trend of models integrating different existing theories or improving theory considering additional mechanisms, mostly on the basis of classical island biogeography, such as disturbance [22], trophic interactions [50], evolution and speciation [39,43], competition [24,36] and inter-specific differentiation (e.g., niche-based) [47]. In many cases, these extended models are able to explain field observations that could not be explained by any one isolated theoretical component, e.g., the ETIB (model generality [20]).

The models that simulate real-world systems [23,29,34] shed light on the mechanisms behind distribution patterns of real-world species; for instance, diversification of Philippine shrews shaped by competitive exclusion over dispersal ability [23], bluebirds on Bermuda as cryptic introductions [34] or presently increasing species richness in some bird lineages on the Galápagos, while other lineages already attained equilibrium dynamics [29]. The models of Birand and Howard [38] and Rosindell and Phillimore [39] were able to produce realistic species distribution and endemism patterns, when compared to empirical data of species numbers, while Valente et al. [29] used Bayesian information criterion weights for selection of the best model that explains current diversification patterns on the basis of phylogenetic data.

Some models reveal the impacts of spatial and temporal factors and mechanisms on island biodiversity. For instance, along island chains, species richness does not necessarily decrease, but can even increase with distance from the mainland, if speciation rates are adequately high [40]. When considering temporal scales relevant for geological dynamics, island biodiversity follows island ontogeny as predicted by the GDM [26,37]. Moreover, island biodiversity does not necessarily follow either equilibrium or non-equilibrium dynamics exclusively [29]. Furthermore, species abundances provide a better measure of immigration/extinction rates on islands than only species richness: low abundances follow immigration and may precede extinction [28]. Interestingly, the extension of island biogeography with niche theory leads to complex emergent patterns. For example, Kadmon and Allouche [33] revealed a uni-modal relationship between species richness and habitat heterogeneity, owing to the reduced suitable area on a given island at high degrees of heterogeneity. Relaxing the habitat specificity of species to allow for a niche breadth, however, restores the positive relationship between species richness and habitat heterogeneity as predicted by classical niche theory [47]. Thus, integrating multiple processes results in both complex emergent patterns and provides detailed information about the study system.

3. Discussion

3.1. General Modeling Trends

Although actual mechanistic models in island biogeography are still scarce in comparison to other fields in ecology [21], the rate of publication of models has increased (Figure 1). This reflects a renewed popularity in island biogeography theory over the past two decades (Figure 1), highlighting the importance of islands as model systems for biodiversity dynamics. Therefore, we expect a persistence of the increasing trend in the number of island models in the near future, particularly because several processes and process combinations remain un- or under-explored.

The sequence of underlying theories that studies try to test or extend shows that modelers are often inspired by the important current theories. Early papers [22,42] are mainly based on MacArthur and Wilson's ETIB. In the 2000s, the popularity of the neutral theory of island biogeography [30] inspired a series of studies following the publication of the theory [28,39,55]. More recently, the general dynamic model of oceanic island biogeography [8] is also employed in models [26,37]. This regular switching in underlying theories suggests that a universal theory of ecology is highly sought after (see Lawton [56]). The effort to develop such a universal theory is often made explicit in the usage of adjectives like "generalized" or "unified" in paper titles [25,29,36,39]. Yet, unifying studies have only integrated parts, mostly pair-wise, of the many ecological theories. More importantly, the majority of mechanistic models do indeed integrate theories by simulating processes particular to each theory. Exemplary processes include colonization and extinction, representing the ETIB [22,42], or island ontogeny, representing the GDM [26,37].

The advantage of island models simulating hypothetical systems [42,43,50] is that they facilitate understanding the effects of fundamental processes. Furthermore, hypothetical systems are more easily employed, because they do not need data to setup simulation arenas and have parameters set by assumptions and study design, which follow the model's theoretical background and study question, respectively. However, more specific questions can only be answered by simulating real-world systems [23,34]. The gained knowledge can also be used to extrapolate the development of the system into the future, taking into account different climate or disturbance scenarios. A mechanistic model is thus a powerful tool for conservation biology. These kinds of models do not have to be specific for a particular system. The model of Valente et al. [29], for instance, was later used to assess the impact of anthropogenic extinctions on equilibrium dynamics in another system, namely Caribbean bats [57].

3.2. Integrated Processes and Emergent Patterns

The observed studies often focus on specific ecological aspects, which affect the implemented processes (or characteristics of the state variables), for example spatial arrangement [40,48] or inter-specific variability [33,47]. However, some of the mechanisms, like disturbances or explicit competition, were rarely explicitly integrated (e.g., [22,24,27]). Most notably, only one model considers trophic interactions [50]. Given the importance of higher trophic levels acting as top-down regulators on biodiversity [58], it is surprising that not more direct species interactions are being considered yet.

A possible reason for this limited process integration is the required mechanistic complexity and resulting computational demand. The latter is an issue that still seems to scare ecologists and showcases that despite today's computational feasibility, ecological modeling is not as developed as other fields in biology (e.g., -omics studies) or other natural science fields. This underdevelopment of computational abilities highlights the need for teaching computer programming to undergraduate students of ecology. To also educate today's researchers, current modelers should explain their models better and make them more accessible, by, e.g., user-friendly interfaces and proper documentation. As a first step, however, it should be considered good practice to always publish computer code alongside the publication [59,60].

Another particularly understudied field in island models is evolution based on the accumulation of explicit gene mutations that result in fitness differences. Only one study of the investigated papers employed such a detailed micro-evolutionary mechanism, with a palm population adapting to different soil types and diverging in its phenology [31]. Given that selection on oceanic islands has been one of the foundations of evolution theory [61], the explicit evolution of traits and species will hopefully be more often implemented in island models. A first step towards this is the concept of protracted speciation, where a mutation event triggers a speciation process, but the new species emerges only after a certain period of implicit accumulation of mutations and genomic isolation from the sister clade [32]. Among non-island models there are further examples for such micro-evolutionary processes and consideration of genetic diversity (e.g., [62–64]). Some of their integrated evolutionary processes could ultimately result in reproductive isolation of populations and thus speciation, and there are already examples for actual adaptive speciation and radiation in landscape ecology and metacommunity models [65–67]. Applying their findings to island systems could provide the perfect framework to increase and unify efforts in studying the (micro-)evolution of species.

Biological models for nowadays complex questions should aim at producing patterns over different spatial, temporal or organizational scales (pattern-oriented modeling; [68,69]). The mechanistic complexities of many models, with up to ten model parameters or more (Table 1), would easily be able to produce more patterns, but the respective studies concentrated on only a few patterns at a time, for instance species numbers [27] or biogeographic rates [28]. One model that investigated the interaction between micro-evolutionary and ecological mechanism [6], thus producing eco-evolutionary dynamics, was unfortunately not considered by our web of knowledge search. Another example of a very complex stochastic archipelago model including evolutionary dynamics, niche theory and geomorphological processes was not captured in our search, as it represents a book chapter [70]. This reduction of investigated processes and patterns, and thus complexity, can be a consequence of the peer-review process, which often requires a focus on one or few specific and simple questions, or it can result from models developed specifically to only address a certain problem.

While simple models do have their place for, e.g., preliminary investigations of particular processes in a hypothetical system, they do not need to be developed from scratch. For example, if one is interested in assessing the role of positive density dependence (i.e., Allee effects) on islands, one would not need to implement a model de novo, but could simply apply a pre-existing model with Allee effects to islands. In the quest for more cooperation, reproducibility and re-use of code, we thus encourage modelers to rather develop existing models further. For this to work, modeling scientists should embrace open source principles. A complex model integrating multiple processes and generating multiple patterns could thus be used to investigate multiple questions, problems and systems (e.g., higher model generality [20]). For example, a model integrating trait evolution (changes in individual or species function) could be used to investigate both neutral and niche-based assumptions and is thus more general than purely neutral models.

3.3. Limitations and Modeling Agenda

Two great difficulties in constructing process-based models lie in the number of parameters and the calibration of these parameters with adequate values, as some of the investigated models did for example with phylogenetic data. The number of parameters increases with each additional process, which requires additional empirical data for parameterization. Additionally, after calibration, calibrated parameter values should be cross-checked with field observations, which further increases the need for specific data. Furthermore, additional processes and parameters increase the risk of equifinality, i.e., a model that will produce similar results, despite different parameter combinations [12]. To deal with this issue, more detailed data are needed to correctly identify processes and parameters. Due to the destructive nature of geomorphological processes acting on islands, the wish for comprehensive data for island systems over evolutionary timescales will likely never be fulfilled, but many hypotheses generated through simulations models could be selectively tested with fieldwork. For this to work, modelers and empiricists will need to collaborate more closely. This can be achieved if modelers communicate what kind of data they need and if the empiricists consider model predictions to be testable hypotheses.

Until now, island models mainly focused on single islands, preventing confounding effects emerging from archipelagic dynamics, such as archipelago biodiversity positively correlating with archipelago island number [14]. Borregaard et al. [26] considers archipelago dynamics implicitly by employing an emigration function, which represents individuals migrating between islands. Notable exceptions are the models of Warren [48] and Gascuel et al. [40], which both provide a simplified framework of archipelagos using island chain systems and dispersal between neighboring islands. This way, they are able to reveal that archipelago species richness is higher than species richness on a single island with a matched size. However, the linear, evenly-spaced arrangement of islands is one simple representation of an archipelago and cannot capture more diverse connection patterns of archipelagos that occur in nature. Additionally, theory predicts that real-world archipelagos are also subject to change over time, due to geomorphological and climatic processes, which in turn affects biodiversity [8].

Other processes known to have major impacts on biodiversity, but hitherto absent explicitly in models, include glaciation-induced sea level oscillations [71,72] or anthropogenic influences [73]. However, one initialization scenario of Rosindell and Harmon [28] reflects a sea level change that separates a landmass from the mainland, which thus harbors a subset of the mainland species pool. Furthermore, processes like range shifts under climate change and resulting evolutionary effects, which currently are a hot topic in ecological modeling in general [62,74], are not explored by island models yet. A more collaborative approach between researchers of these different ecological fields is thus a promising perspective for ecological modeling in general. With models integrating many different processes, which are able to produce several plausible patterns, researchers will have a valuable tool to make new hypotheses and thus guide field ecologists efficiently to conduct necessary experiments.

3.4. Conclusions

In this paper, we reviewed mechanistic island models, revealing a high diversity of investigated questions and integrated processes. Integrated processes were often inspired by current influential theories and highlight the search for a universal theory of ecology/island biogeography. An important step towards this will be the development of models integrating evolutionary, ecological and environmental processes, thus far recognized as relevant by biodiversity theories.

While in island models, patterns and processes at intermediate ecological levels (e.g., population, species) predominate, more realistic, and thus more widely applicable, models will need to integrate more processes at the individual level, such as interactions, genetics and behavior. These individual-level processes should not only affect individuals, but should also influence patterns at the population, community and metacommunity level (Figure 5). Additionally, processes acting on higher spatial and temporal scales, like archipelago structure and geomorphological changes, as well as human-induced environmental change will also need to be considered explicitly (far right in Figure 5). While most of these processes are already implemented in the reviewed models, hardly any model integrates more than two aspects at a time. Yet, the models were able to shed light on a variety of ecological questions in island biogeography regarding the past, present and future. Therefore, we anticipate that integrating multiple processes should untap an even larger number of potential (more complex) questions by increasing model generality.

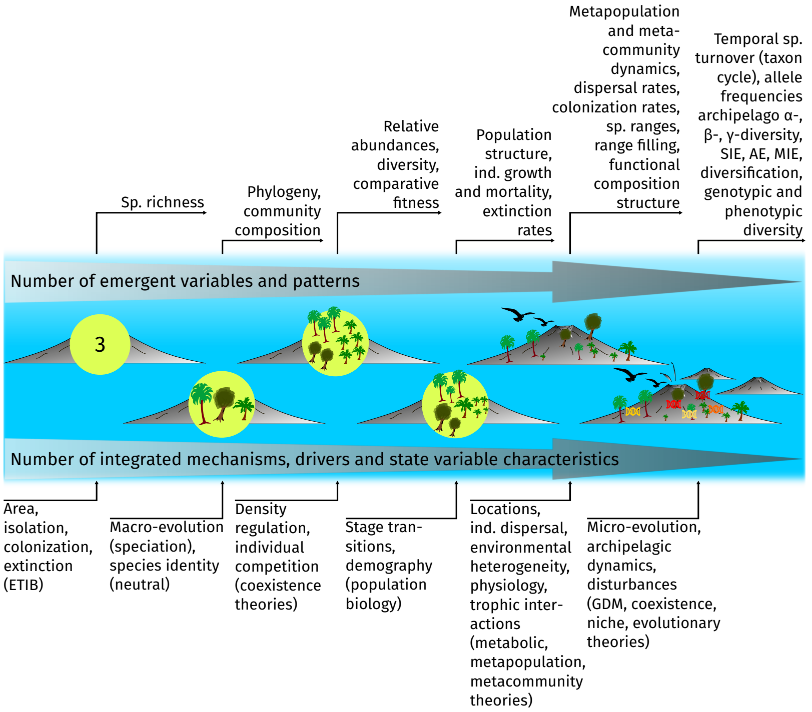

Figure 5. Representation of exemplary integrated processes and drivers in island models (bottom) and emerging variables and patterns (top). Model complexity, and thus generality [20], increases from left to right. We assume that processes and drivers add up from left to right. Thus, a given model representation includes also all processes and drivers of the less complex models to its left and is therefore also able to produce the respective patterns. Mechanisms and drivers are closely related to different theories (exemplary theories are shown in brackets at the bottom), e.g., colonization and extinction as the fundamental rates of the equilibrium theory of island biogeography (ETIB). As can be seen, some emergent patterns of more complex models are the same as the drivers for simpler models. For instance, the second model on the right produces colonization rates as an emergent pattern, which at the same time are necessary input parameters for the far left model. AE: archipelago endemics; ind.: individual. MIE: multiple island endemics; SIE: single island endemics; sp.: species; GDM: general dynamic model.

Lastly, island biogeography theory was never applied solely to islands, as several ETIB-inspired metapopulation and metacommunity studies indicate. We regret that we had to exclude many potentially relevant metacommunity studies from our review, because they did not specifically relate their models to islands, but hope that in the future, researchers will more often apply their models to other related systems, as well. Because of their many advantageous qualities, like clearly-defined isolation and structure, islands will likely remain an ideal model system for studying biodiversity dynamics in general. The next generation of island models will therefore, much like the ETIB did and still does, continue to inspire fields like landscape ecology, metapopulation and metacommunity ecology, marine biology and be applied to systems such as sky islands, coral reefs and forest fragments. This will help with promoting the usefulness of mechanistic models to an even wider range of researchers, which ultimately will result in increasingly better models and better predictions.

4. Materials and Methods

The raw compilation of studies was obtained by running an ISI Web of Science search with the string "archipelago OR island OR model OR equilibrium" in the title field and "(island OR archipelago) AND (species) AND (evolution OR speciation OR theory) AND (simulation OR model)" as the topics. We did also try a more restrictive title search string ("(archipelago OR island) AND (model OR equilibrium)"), but this string resulted in far fewer hits and missed some modeling papers we knew explicitly included islands. This conservative search captured a broad range of studies even if it resulted in many false positives. The initial search result was refined by manual review of all 647 found studies evaluating two criteria: (1) whether the study has a direct island relation; and (2) whether the study employs a mechanistic model. Only if both of these questions could be answered with yes was a study incorporated into our review. We are aware that this focus on island-specific studies is somewhat arbitrary, as many metacommunity- and metapopulation-like systems, such as lakes, caves or coral reefs, could also be applied to islands (e.g., [75,76]). However, finding all of them would be systematically challenging via a structured literature search, because although plentiful and highly relevant to islands, these models failed to explicitly relate their findings to island biogeography theory, which was one of our manual screening targets. Additionally, metapopulation and metacommunity studies are usually restricted to ecological timescales and, thus, often lack evolutionary and/or (geomorphological) environmental processes, which are relevant to island biodiversity. Nevertheless, we believe that summarizing the findings of such models and relating them to island biogeography theory, as well as to other biodiversity theories would be a very useful exercise and should be aimed for in future reviews.

We analyzed the obtained paper list with special attention on the nature of the employed models and the theoretical backgrounds. For this, we characterized the models by several categories: (a) whether they employ stochasticity, e.g., in the demographics; (b) whether or not they are spatially explicit, that is the spatial position and arrangement actually impacts the system; (c) if they consider their environments to be static (yes) or if islands for example follow an ontogenic trajectory (no); (d) if they consider evolutionary processes like mutation, speciation or selection; and (e) whether they regard their systems as following neutral theory [30]. Some categories rather represent spectra like the agent level, i.e., the organizational level of the state variables on which processes act (individuals, populations, species) or the number of niche axes (number of biological parameters, whose values may be different between species in the case of niche-based models). Furthermore, we considered the focal level: the organizational level at which most emergent patterns are investigated. Additionally, we included the year of publication, the type of system that is modeled (single island, archipelago, mainland-island, mainland-archipelago) and whether this is real-world or hypothetical, as well as the theoretical background of the model, if specified. We also looked for the integrated processes, the number of model parameters as we were able to identify them and the investigated patterns.

We then used some of this information (agent level, static environment, number of niche axes, spatially explicitness, stochasticity, neutrality and evolutionary processes) to conduct multidimensional scaling (MDS) employing the R packages `MASS`, `vegan` and `smacof` [77–79] and thus get an overview of how different studies are assembled and whether there are specific under-explored areas to be found. For the ordination of papers, we used `mds` from the `smacof` package [79] and `metaMDS` from the `MASS` package for the ordination of model properties. Contrary to ordination methods like principal component analyses, in MDS, the goodness of fit is not indicated by the sum of explained variance of the first dimensions, but the Stress-1 value, with values close to zero indicating a good fit [79]. The code for running these analyses and producing the plots can be found in the Supplementary Materials.

Supplementary Materials: The following are available online at https://github.com/lleiding/mechislandmodels, code.R: R-code for running MDS and producing plots.

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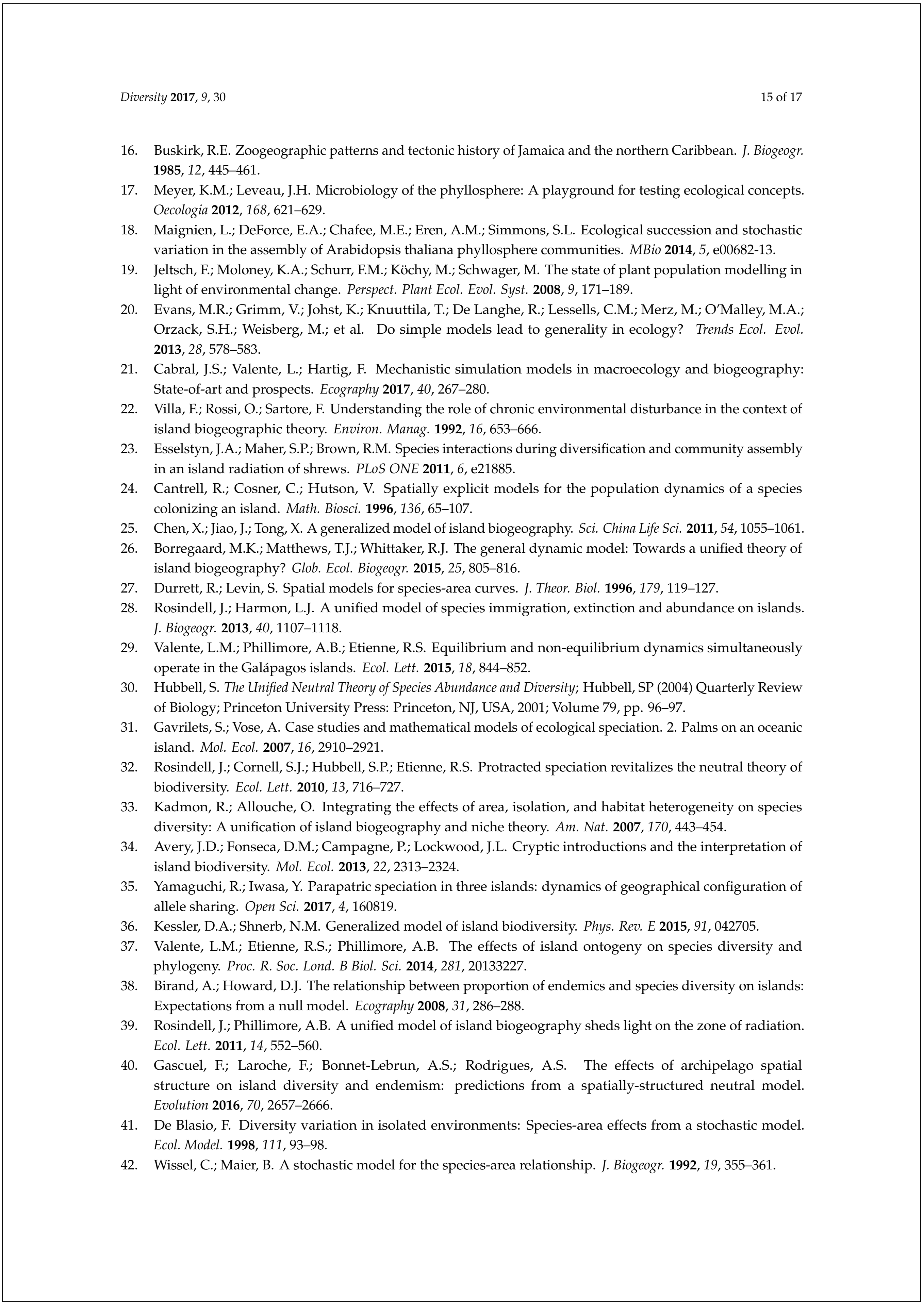

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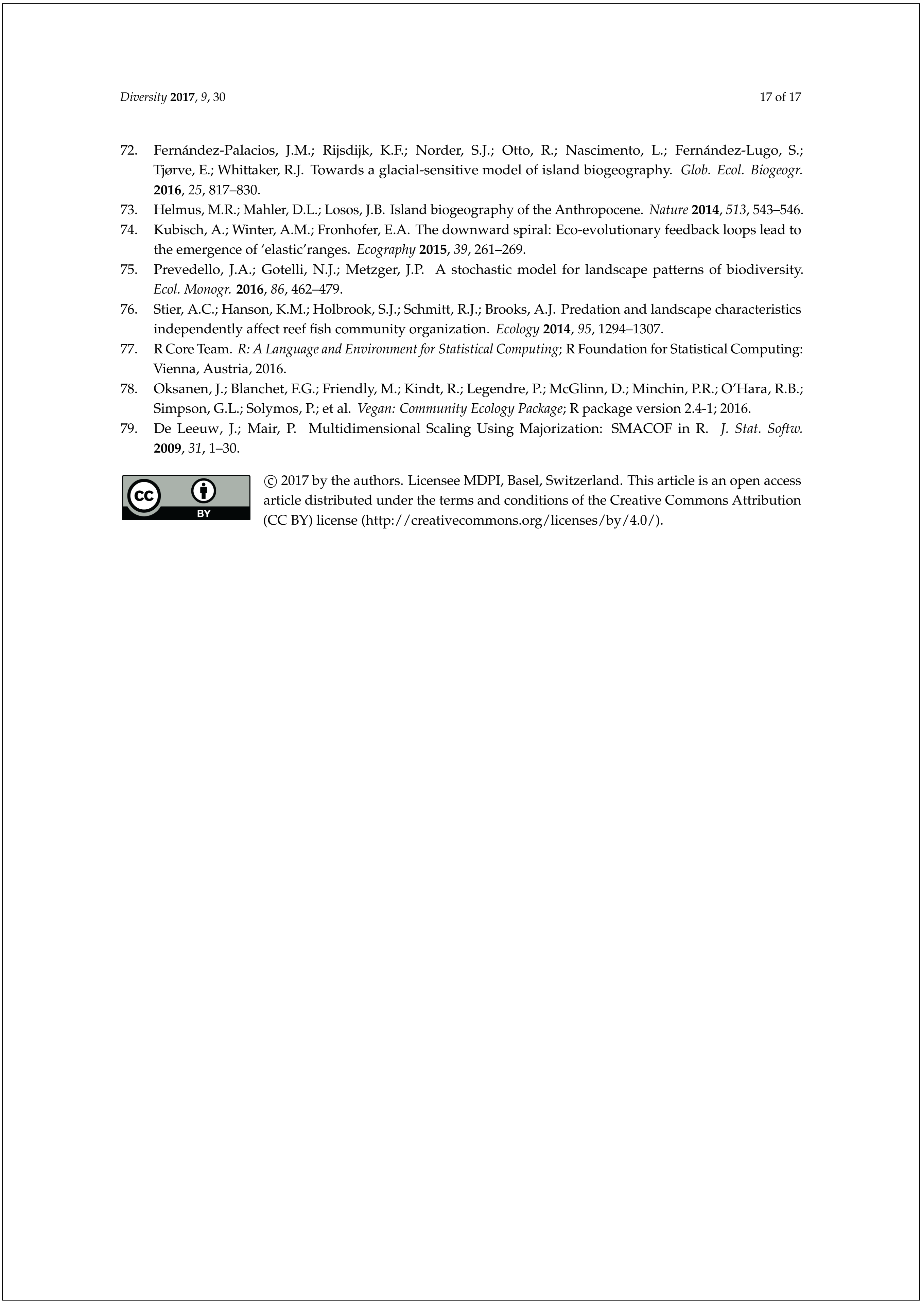

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4

TEMPORAL ENVIRONMENTAL VARIATION IMPOSES DIFFERENTIAL SELECTION ON BOTH GENOMIC AND ECOLOGICAL TRAITS

Having hypothesized that species traits, including genomic characteristics are important factors in determining how successful species are in surviving variable environmental conditions, for instance after island colonization, I wanted to test this hypothesis with a mechanistic model. Unfortunately, none of the models analyzed in the systematic literature review allowed to do that, because they either disregarded species functional differences or considered only superficial evolutionary processes and factors, including genomic traits (chapter 3). Hence, I developed a novel model aimed at closing this gap and used it to investigate the role of genomic and ecological traits of plant species in temporally variable environments. This gets described in the following manuscript.

We found that temporal environmental variability imposes a constant filter on inter- and intraspecific variation. While the loss of interspecific variation could be observed as a loss of species richness, genomic traits, in particular an intermediate genetic linkage, could slow down some of the loss of genetic variation. Ecological traits that promoted species' survival under variable environments constituted increased environmental tolerances and accelerated life cycles, enabled by decreased body sizes.

At the time of writing, the manuscript has been submitted to *Oikos*, and is currently under review. A non-peer-reviewed preprint of the article is available as Leidinger and Cabral (2020). The article was drafted and written by myself with contributions by Juliano Sarmento Cabral. I performed all research procedures and analysis. The conceptual design was done by myself and Juliano Sarmento Cabral. My overall contribution amounted to ca. 95 %.

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Temporal environmental variation imposes differential selection on genomic and ecological traits of virtual plant communities

Ludwig Leidinger[1]* (https://orcid.org/0000-0002-5008-683X), Juliano Sarmento Cabral[1] (https://orcid.org/0000-0002-0116-220X)

1 Center for Computational and Theoretical Biology, Faculty of Biology, University of Würzburg, 97074 Würzburg, Germany

* ludwig.leidinger@uni-wuerzburg.de

Abstract

The reaction of species to changing conditions determines how community composition will change functionally — not only by (temporal) species turnover, but also by trait shifts within species. For the latter, selection from standing variation has been suggested to be more efficient than acquiring new mutations. Yet, studies on community trait composition and trait selection largely focus on phenotypic variation in ecological traits, whereas the underlying genomic traits remain relatively understudied despite evidence of their role to standing variation. Using a genome-explicit, niche- and individual-based model, we address the potential interactions between genomic and ecological traits shaping communities under an environmental selective forcing, namely temporal variation. In this model, all ecological traits are explicitly coded by the genome. For our experiments, we initialized 90 replicate communities, each with ca. 350 initial species, characterized by random genomic and ecological trait combinations, on a 2D spatially-explicit landscape with two orthogonal gradients (temperature and resource use). We exposed each community to two contrasting scenarios: without (i.e. static environments) and with temporal variation. We then analyzed emerging compositions of both genomic and ecological traits at the community, population and genomic levels. Communities in variable environments were species poorer than in static environments, populations more abundant and genomes had a higher numbers of genes. The surviving genomes (i.e. those selected by variable environments) coded for enhanced environmental tolerance and smaller biomass, which resulted in faster life cycles and thus also in increased potential for evolutionary rescue. Even under the constant environmental filtering presented by temporal environmental variation, larger, more linked genomes allowed selection of increased variation in dispersal abilities. Our results provide clues to how sexually-reproducing diploid plant communities might react to increased environmental variation and highlights the importance of genomic traits and their interaction with ecological traits for eco-evolutionary responses to changing climates.

Keywords

standing variation, genomic traits, environmental variability, mechanistic model, rapid evolution, eco-evolutionary feedbacks

Introduction

Communities of plant species are the result of different abiotic and biotic conditions (Huntley 1991). Changes in those conditions will therefore also reflect on communities and their trait composition. Response strategies that enable species survival under changing conditions may vary across species. They can, for instance, select for survival (Holt 1990), for lower body mass (Parmesan 2006), for dispersal (Berg et al. 2010), or for adaptation to new conditions (Joshi et al. 2001, Jump and Peñuelas 2005, Bell and Gonzalez 2009). Given enough time, this will result in the communities passing through ecological species successions (Huston and Smith 1987) and evolutionary taxon cycles (Ricklefs and Bermingham 2002). Even in short periods, populations within communities can change their traits in response to environmental variation via rapid evolution (Maron et al. 2004). In this case, selection on standing variation can be more efficient than aquiring novel mutations (Barrett and Schluter 2008, Bolnick et al. 2011). This standing variation can be both intraspecific and intra-individual, i.e., within-genome variation. A high standing variation thus provides a resource for populations to quickly respond to changing environments (Cochrane et al. 2015). However, the genomic traits which enable and maintain standing variation remain largely understudied in ecological and eco-evolutionary studies (but see Schiffers et al. 2012, Matuszewski et al. 2015).

Many functional species traits are quantitative and subject to genetic interactions, such as epistasis, pleiotropy and genetic linkage. To infer a direct connection between phenotype and genotype is therefore complex (Korte and Farlow 2013). Still, all this genomic background determines standing genetic variation, which in turn will constrain which individual phenotypes are possible and thus a population's evolutionary potential. With the increasing availability of exhaustive genetic data, considering detailed genetic factors in eco-evolutionary models has become more feasible, especially for model species (Frachon et al. 2019, Exposito-Alonso et al. 2019). Indeed, there is an increasing amount of genetic data at the population or even at the individual level (e.g. Domingues et al. 2012, Alonso-Blanco et al. 2016). Nevertheless, manipulating real-world systems to conduct meaningful experiments to isolate factors on both functional and genetic levels is difficult (but see Booth and Grime 2003). Thus, although the importance of genetic factors for ecological processes has long been recognised (Holt 1990), investigating its effects in real-world systems remains challenging (Hughes et al. 2008).

Simulation models provide a powerful alternative to overcome the empirical challenges of investigating and manipulating genetic traits and all the trait-mediated ecological functions they control. Modeling studies can cover any organisational level in biology, from genomes over species to communities (Matuszewski et al. 2015, Kubisch et al. 2014, Münkemüller et al. 2012, Saupe et al. 2019), and thus are suitable tools to explore potential eco-evolutionary regulations of species traits. Therefore, we developed a Genome-explicit Metacommunity Model (GeMM, Fig. 1) to address the interplay of genomic and ecological traits in species communities under an environmental selective force, namely temporal environmental variation. Specifically, we address the following questions. (a) Which ecological and genomic traits enable survival in temporally variable environments? (b) How do temporally variable environments shape standing variation (phenotypic and genetic)? We designed a simulation experiment under two different environmental scenarios, namely with versus without temporal environmental variation (variable and static environments, respectively) and analyzed genomic and ecological trait characteristics of surviving communities. We expected communities in variable environments to select for higher tolerances (Holt 1990), higher dispersal abilites (Berg et al. 2010) and lower biomass (Parmesan 2006) and to exhibit increased standing variation, both genetic and phenotypic (Cochrane et al. 2015). While our expectations on trait responses were largely confirmed, we find that standing variation is decreased for most traits except dispersal. Our findings on virtual communities suggest how eco-evolutionary dynamics of real plant communities might unfold under changing environments.

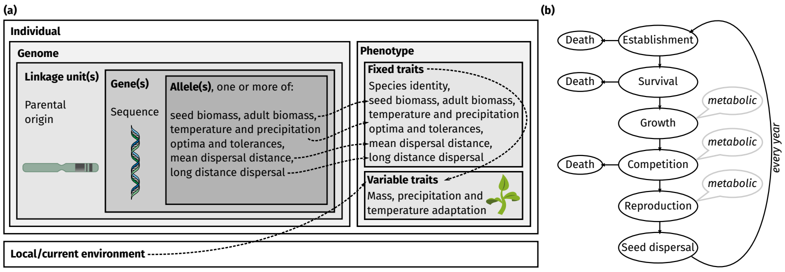

Figure 1. Schematic of the model. (a) Individuals represent the base agents in the model. They are comprised of a phenotype which interacts with other individuals and the environment, and a genome. The genome is diploid and consists of maternal and paternal sets of linkage units, which combine genes as one hereditary unit. Each gene may code for one or more alleles of functional traits. The expressed trait in the phenotype results as the average of all associated alleles in the genome. The expression of some of the traits ("variable traits") additionally depends on the local current environment and may change over time. (b) Flow of processes each individual passes every year. Some of the processes are dependent on the local temperature and individual biomass (marked "metabolic"), while all processes depend on an individual's phenotypic traits (see (a)). Dashed arrows represent influences, solid arrows represent sequence of events.

Materials and Methods

The model

General structure. We use GeMM (version 1.0.0) — a genome- and spatially-explicit, niche- and individual-based model for plant metacommunities written in julia (Bezanson et al. 2017, Fig. 1). The model generates metacommunity dynamics (Hanski 2001, Leibold et al. 2004) and it considers explicit local population and community assembly dynamics emerging from genomic and individual level processes. The model simulates discrete time steps, which can be translated to one year. In the model, individuals belong to species, which are characterized by individuals with identical genetic architecture (i.e. genome size and linkage) and ecological traits (dispersal ability, environmental niche and size) falling within a species-specific Gaussian trait distributions (Fig. 1 (a)). Thus, individuals of the same species are not functionally identical, depicting intraspecific phenotypic variation. Dispersal of individuals (i.e. seeds) interconnects grid cells, while the position of individuals is characterized by the grid cell coordinates, i.e., all individuals are concentrated in the center of the respective grid cell.

Eco-evolutionary processes. Like some previous ecosystem models (Harfoot et al. 2014, Cabral et al. 2019, see Cabral et al. 2017 for a review), yearly vegetative growth in biomass, fertility and mortality rates in the model are controlled following the metabolic theory of ecology (MTE, Brown et al. (2004), Price et al. (2010)). Accordingly, the model considers discrete yearly time steps. In MTE, a biological rate b depends on the temperature T and individual mass M, scaling a base rate b_0 as:

$$b = b_0 M^c e^{-\frac{E_A}{k_B T}} \tag{1}$$

where E_A is the activation energy and k_B the Boltzman constant. The exponent c is $\frac{3}{4}$ for biomass growth and reproduction, and $-\frac{1}{4}$ for mortality (Brown et al. 2004). This results in smaller individuals having a higher mortality than bigger ones, while individuals in cooler conditions have a lower mortality than those in warmer conditions. Using the MTE means reduced parameterization effort, since b_0 values for the different processes are global constants and thus identical for every species. Additionally, the emerging longevity-fecundity tradeoff that comes with mass-regulated rates has been shown to inherently supress the evolution of "super-species" (Cabral et al. 2019).

Over the course of a simulation, individuals thus grow in size, passing three life stages: (1) seed, (2) juvenile, and (3) adult. Individuals disperse as seeds, establish, grow and become reproductive adults (Fig. 1 (b)). Both seed biomass and adult biomass, i.e., the threshold biomass where individuals become reproductive, are two of the central, genetically-coded traits that define individuals (Fig. 1 (a), Table 1). Adults are monoaecious and reproduce sexually with a random adult of the same species whithin the same grid cell to produce new seeds. Seed dispersal follows a logistic dispersal kernel with genetically-coded mean dispersal distance and shape parameter μ and s, respectively (see Bullock et al. 2017). In our discrete landscapes, dispersal is modeled as centroid-to-area, with expected mean dispersal distances usually around equal to the length of the grid cells (cf. Chipperfield et al. 2011). Furthermore, all individuals have encoded preferences concerning two different environmental measures: the first, temperature, has a direct effect on biological rates, as described by the MTE (Brown et al. 2004) and affects density-independent mortality, while the second is a surrogate for environmental resources, e.g., water. Thus, from here on this second axis is called precipitation for simplicity. Individuals' adaptation to precipitation conditions determine their competitive abilities. Both these preferences are characterized by an optimum and a tolerance, which are represented as 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). Near their optimum, individuals with higher niche tolerance have lower adaptation values than individuals with narrower breadth (i.e. specialists, Griffith and Sultan (2012)). During establishment, the adaptation values toward temperature and precipitation are calculated for each new seed based on the local conditions and phenotypic traits (Fig. 1 (b)). Furthermore, each time environmental conditions change, all individuals in the affected grid cell pass establishment again to re-calculate their adaption values. These adaptation values are functional for two different subsequent processes. First, individuals experience a metabolic, density-independent mortality (Brown et al. 2004). This mortality further scales with individual temperature adaptation, so that mortality is higher for individuals which are poorly adapted to the surrounding temperature (Cook 1979). Second, all individuals in a cell compete for the limited available space in the grid cell, i.e., total sustainable biomass. If the combined biomass of all individuals in a cell exceeds the grid cell's carrying capacity biomass, individuals are removed from the community until biomass is within grid cell limits. The choice which individuals to remove is based on pair-wise comparisons of random pairs of individuals. From any of such two individuals, the individual less adapted to local precipitation conditions is removed.

Genetic architecture. All of the aforementioned traits (see Table 1) are coded by one or more genes in an individual's diploid genome (polygenes). Single genes can also be associated to several traits at the same time (pleiotropy, Solovieff et al. (2013)). Thus, each trait can be represented more than once in the genome (i.e. through different genes at different loci). Since trait representations are subject to species-specific variation, they can constitute different alleles — both within the haploid genome at different loci, but also between the maternal and paternal haploid genomes or between individuals (cf. Nevo 1978). Realized ecological traits y, i.e., an individual's phenotype, are then determined quantitatively by considering all respective loci y_l within an individual's genome and taking their average. This results in a random degree of species-specific phenotypic and genetic, i.e., intra-individual or intra-genomic, trait variation (cf. Mackay 2001). Lastly, genes may be combined to form a linkage unit, which represent a set of spatially close genes within the same chromosome arm. Linkage units thus comprise the smallest hereditary entities (Hermann et al. 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 (Fig. 1 (a)).

A detailed model description with justification for assumptions, equations and parameter values can be found in Supplementary material Appendix 1 (Grimm et al. 2006, 2010). Model parameters are summarized in Table 1.

Experimental design

Simulation arena. We set our simulation experiments in a rectangular landscape of a grid of 5 by 7 grid cells (Fig. 1). Each grid cell had a carrying

Table 1. Model parameters, their meaning and relevance. Phenotypic traits y (M_r, M_s, μ, s, $\overline{P}$, σ_P, $\overline{T}$, σ_T) are always the average of all corresponding trait loci y_l in the genome. Values are arbitrary, but within empirically or theoretically supported ranges (see main text and supplementary materials for details) and dimensionless unless otherwise specified. The variability column describes whether and how values might change. Constant: values are global constants across scenarios; genome: values might differ within an individual's genome, potentially giving rise to different phenotypes; scenario: values differ between scenarios, but stay constant within scenarios; species: values might differ between species, but stay fixed within species. SD: standard deviation

Parameter	Description	Value or Range	Variability
E_A	Activation energy	1×10^{-19} J (adapted from Brown et al. 2004)	constant
k_B	Boltzman constant	$1.38 \times 10^{-23}\,\mathrm{J\,K^{-1}}$	constant
K	Carrying capacity	100 kg	constant
r_0	Base fecundity	1.4×10^{12} (modified after Brown et al. 2004)	constant
g_0	Base growth rate	8.8×10^{10} (modified after Brown et al. 2004)	constant
m_0	Base mortality rate	1.3×10^{9} (modified after Brown et al. 2004)	constant
δ_P	Temporal precipitation SD	0.0 or 0.2	scenario
δ_T	Temporal temperature SD	0.0 °C or 0.2 °C	scenario
n_l	Number of loci	1 to 20 (Fournier-Level et al. 2011)	species
n_u	Number of linkage units	1 to n_l	species
σ_l	SD among trait loci	0 to 0.1 × mean of trait	genome
M_r	Biomass at reproductive stage	e^{3} g to e^{14} g (Brown et al. 2004)	genome
M_s	Biomass at seed stage	e^{-2} g to e^{10} g	genome
μ	Dispersal kernel mean	0 to 1 grid cells	genome
s	Dispersal kernel shape	0 to 1 grid cells	genome
$\overline{P}$	Precipitation optimum	0 to 10	genome
σ_P	Precipitation tolerance	0 to 1	genome
$\overline{T}$	Temperature optimum	10 °C to 40 °C	genome
σ_T	Temperature tolerance	0 °C to 1 °C	genome

capacity of 100 kg of total biomass, which approximately relates to 100 m^2 of grassland (Deshmukh 1984, Bernhardt-Römermann et al. 2011). Landscape size and carrying capacity was arbitrary but ensured computational feasibility. Two perpendicular environmental gradients (temperature and precipitation) ran along the long and short axis of the landscape, respectively. The rectangular shape of our simulation arena provided a longer gradient in the physiologically important temperature direction.

Initialization. We initialised each grid cell of the landscape with a different local community of random species. The species characteristics (i.e. genomic and ecological traits) as well as local abundances were chosen randomly from large ranges of uniform-distributed values. On the genomic level, species differed by the number of loci, n_l (maximum = 20, cf. Fournier-Level et al. 2011, Schiffers et al. 2012), intragenomic variation between trait values, i.e., genetic variation, σ_l (maximum = 0.1×trait value), and number of linkage units, n_u (between one and n_l, Table 1). To obtain the ecological characteristics of a species, first an average phenotype was defined by randomly selecting a value for each phenotypic trait. These traits, more specifically, the adult biomass trait, were then used to calculate the number of offspring a single individual of this species would have. Given an already determined genetic architecture (i.e. n_l, n_u, and σ_l), each individual of a species was then initialized as follows. For each trait representation (i.e. gene) within the genome, the associated trait value was chosen randomly following a Normal distribution with the trait value of the average phenotype as mean and standard deviation the product of σ_l and the trait value (Table 1). Afterwards, the initial phenotype for each individual was calculated based on all genes in the genome. This resulted in varying degrees of intragenomic and intraspecific standing variation. We disabled mutations in our experimental design so that this standing variation was the only resource for selection. Grid cells were then filled with populations of several species until carrying capacity was reached. Because species vary randomly in their traits, including biomass, initial grid cell communities varied in richness. This resulted in initial communities with on average 10 species per grid cell and a total of 350 species in the landscape.

Values for simulation, global and species-specific parameters that were not varied in the different experimental scenarios were chosen to ensure plausible patterns, most importantly to achieve species co-existence by adjusting the mortality-to-fecundity ratio. Species-specific parameter values were drawn at random from a range that extended beyond what would be realisable in simulations to reduce geometric artifacts within the parameter space (Table 1). This also kept the need for additional assumptions at a minimum, since viable species emerged via environmental filtering and ecological interactions. Global parameter values were either adapted from the literature (Brown et al. 2004, Fournier-Level et al. 2011) or fine-tuned via trying out a range of realistic values.

Scenarios. For investigating our general study question about the interplay of environmental variation and ecological and genomic traits, we designed two scenarios. In the first, temperature and precipitation gradients arbitrarily ranged through constant values of 16.85 °C to 22.85 °C (290 K to 296 K) and 3 to 7 (arbitrary quantity), respectively, during the entire simulation run ("static environment"). In the second, initial temperature and precipitation values were the same as in static environments, but could change at each year ("variable environment"). The change followed a gaussian random-walk trajectory to yield positive auto-correlation (Fung et al. 2018). The amount of change (δ_P and δ_T, Table 1) was drawn randomly from a Normal distribution with a standard deviation of 0.2. This value corresponds to a moderate rate of change of no more than 0.5 degrees per year in the majority (ca. 99 %) of cases, which we found by trying different values to produce noteable environmental change that did not kill all individuals in a short amount of time. Since our simulation arena represents a small spatial scale, all grid cells changed always by the same value at each timestep. The change of temperature was independent from that of precipitation and vice-versa. Confounding effects, such as landscape configuration, different temporal dynamics, complex dispersal behavior and macro-evolutionary processes (e.g. clade diversification) have been studied elsewhere and were thus not included in the present study (Münkemüller et al. 2012, Kubisch et al. 2014, Aguilée et al. 2018). Table 1 contains the parameters which were varied for the scenarios, their meaning and their values. We simulated 90 different replicates. Each replicate terminated after 1000 simulated years. This duration was adequate to allow quasi-equilibrium (see Results) and short enough to warrant our selection-on-standing-variation rationale (Hermisson and Pennings 2005). Each replicate, i.e., each unique initial community, was subjected to both scenarios. This yielded 180 simulations in total.

We recorded the complete state of the individuals in our simulation world at the start and every 50 years of a simulation run. This data encompassed individual phenotypic and genotypic values. Thus, for every year, we tracked the state of local species populations including location, abundance, demographics, median adaptation, and trait values for all ecological and genomic traits.

Analyses

To make the individual information more accessible, we calculated summary statistics at the population level. We defined a population as a group of conspecific individuals co-occurring in the same grid cell. For each population, we then calculated median values of each phenotypic trait, the variance of each phenotypic trait (phenotypic intraspecific variation), and medians of the individual genetic variation in each trait. We scaled all variance values by the respective population-specific medians to get coefficients of variation of the median (CV median). In order to compare emerging ecological patterns and identify when equilibrium is reached, we calculated a set of ecological metrics, namely species-richness, i.e., the average number of species per grid cell, α (α-diversity), the total number of species across the landscape, S (γ-diversity), β-diversity, $\beta = S/\alpha - 1$ (Whittaker 1960), population demographic structure (i.e. number of juveniles and number of adults) and range-filling from the data on surviving communities. For diversity indices, we converted our data to community matrices and analyzed them using vegan (Oksanen et al. 2018) in R (R Core Team 2019). To assess demographic structure within communities, we analyzed average numbers of juveniles and adults. Range-filling was calculated as the fraction of grid cells that was occupied by a species over all the grid cells that were potentially suitable for the given species. Suitability was asserted as an arbitrary cut-off where environmental parameters (temperature and precipitation) fell within a species' tolerance (optimum ± tolerance).

For our study questions, we analyzed the trait composition of surviving communities genomic trait composition (study question (a)), and differences in phenotypic and genetic standing variation (study question (b)) between environments. Since we were interested in general patterns of the effect of environmental variability, rather than the effects of warming or cooling trends, we excluded precipitation and temperature optimum traits from our analyses. We transformed trait and variation distributions before analysis and visualization using a $\log(x+1)$ transformation, because they were strongly left-skewed and contained values < 1. Additionally, we calculated the degree of genetic linkage as $\frac{n_l}{n_u}$, because due to our method of initializing species, n_u directly depended on n_l.

To ascertain whether and how trait composition differs between environmental conditions (study question (a)), we first compared species numbers and identities. Because each community is subjected to both environments, we analyzed what proportion of species was shared by both environments, and which were unique to one of the environments. To assess how ecological and genomic traits respond to variable environments, we compared trait characteristics between scenarios by performing principal component analyses on the population trait data. This way, we were able to describe general patterns in trait space between scenarios by relating the total trait space shift to the principal components and correlated trait axes. Additionally, we compared community trait distributions pairwise between environments to identify trends in traits specific to the environments. For this, we calculated linear mixed models using the R package lme4 (Bates et al. 2015) with trait as response, environment as fixed effect and replicate as random effect.

To find out whether there is a selective force on standing variation (both phenotypic and genetic) specific to environmental conditions (study question (b)), we compared the phenotypic and genomic trait variances of surviving communities between scenarios for all traits in separate. We again calculated linear mixed models, with trait variances as response, environment as fixed effect and replicate as random effect.

The model code, experiment definition files and analysis scripts are available at https://github.com/lleiding/gemm. Albeit reporting of significance values is generally inappropriate for simulation models (White et al. 2014), we use significance here to identify which responses are stronger than others.

Results

Differences of ecological patterns between environments

Surviving communities in our simulation experiments (Fig. 1) differed in a number of ecological characteristics. Compared to communities in static environments, communities in variable environments were only about half as species-rich on a local level (α-diversity, Fig. 2(a)) and exhibited less β-diversity (Fig. 2(b)), which resulted in decreased species richness on a regional scale (γ-diversity, Fig. 2(c)). Summing over all replicates, a total of 108 species survived in both enviroments, while 256 and 64 surviving species were unique to static and variable environments, respectively. Emerging functional differences comprised higher total abundances in all demographic stages (Fig. 2(d), (e)) and decreased range filling for communities in variable environments (Fig. 2(f)). While all aforementioned metrics were constantly changing during the entire simulation course in the variable environments, in static environments they reached a quasi-equilibrium by year 500. For the following trait-based analyses, we thus used data from that year.

Response of ecological and genomic traits

Surviving communities showed subtle differences in their trait syndromes combining all traits in a PCA. In the first two principal components, populations from variable environments occupied for the most part a subset of the trait space of populations from static environments (mostly overlapping ellipses in Fig. 3). Nevertheless, the trait space of variable environment communities was shifted towards increased environmental tolerances and dispersal abilities and decreased mean genetic variation (negative direction of second principal component - Fig. 3). With the exception of the first, all principal components and thus correlated traits, contributed similarly to the overall explained variance

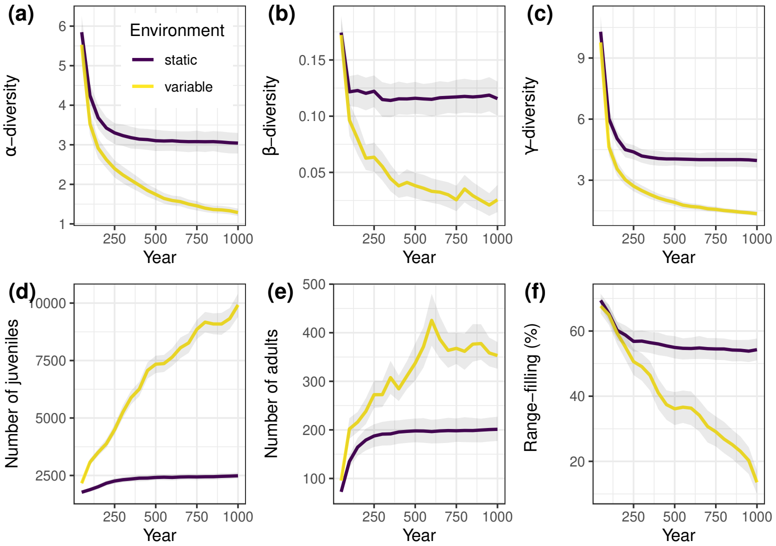

Figure 2. Averaged ecological patterns across the entire simulation arena over time after initialisation. Dark/violet: static environment, light/yellow: variable environment. Grey ribbons represent 95% confidence intervals. (a) local species richness (α-diversity) as numbers of species, (b) β-diversity (Whittaker 1960), (c) total species richness (γ-diversity) as numbers of species, (d) mean number of juveniles, (e) mean number of adults, (f) range-filling, i.e., the percentage of potentially suitable habitat that is actually occupied. Spikes are due to single replicates with extreme values.

(Supplementary material Appendix 1 Fig. A2).

Focusing on single traits, communities showed several differences between the two types of environments (Fig. 4(a), Supplementary material Appendix 1 Table A3). Compared to static environments, surviving communities in variable environments showed on average an increased number of genes (n_l), increased precipitation and temperature tolerances (σ_P and σ_T, respectively), increased long distance dispersal (s), decreased adult biomass (M_r), and decreased genetic variation (σ_l). Seed biomass, mean genetic variation and genetic linkage exhibited no significant differences (Supplementary material Appendix 1 Table A3).

Differences in standing variation (phenotypic and genetic)

Additionally to differences in the phenotypic characteristics, we found distinct patterns between environments in both phenotypic and genetic trait variation (Fig. 4(b)). While the phenotypic variation of mean dispersal distance and both phenotypic and genetic variation of long distance dispersal was increased in variable environments, all other trait variations (phenotypic and genetic) were decreased in variable environments. The trend towards a decrease in genetic

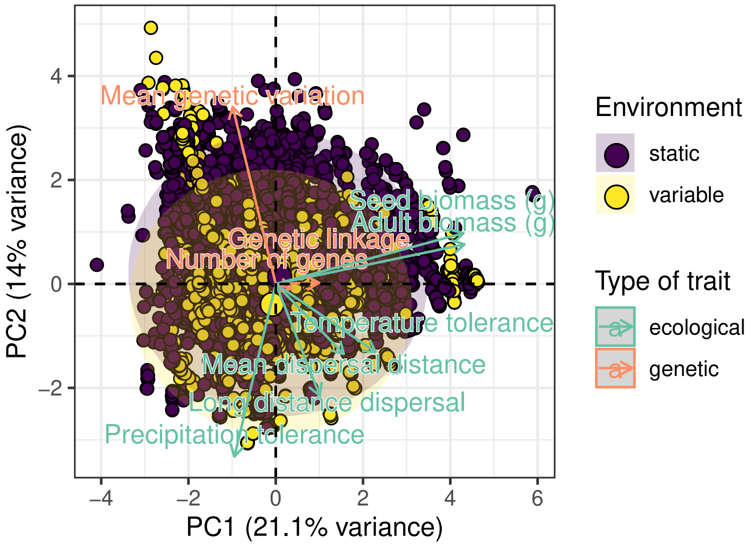

Figure 3. Principal component analysis (PCA) showing trait space characteristics (ecological and genomic) of surviving populations. Biplot of surviving populations and trait axes along the first two principal components. Populations without temporal environmental variation (dark/violet) vs. with temporal environmental variation (light/yellow). Shadowed ellipses highlight areas of 95 % confidence.

variation of temperature tolerance was not significant.

Discussion

General differences between scenarios

Our results show how community trait composition of plant metapopulations may differ between static and temporally variable environments in a genomically-explicit eco-evolutionary model. The changing abiotic conditions in variable environments act as a constant environmental filtering mechanism (Kraft et al. 2015), where only those species survive that are able to adapt to or track environmental changes. As a result, communities are species poorer (see also Menge and Sutherland 1976). The decreased β-diversity furthermore suggests that these fewer species in variable environments are rather generalistic, in comparison to static environments where species seem more specialized to local environmental conditions, as evidenced by the higher β-diversity (cf. Gilchrist 1995). The fact that, furthermore, range-filling is reduced in the variable environments is likely a mid-domain-like effect (cf. Colwell and Lees 2000), where due to the ongoing temporal variability, the margins of a potential range will often become

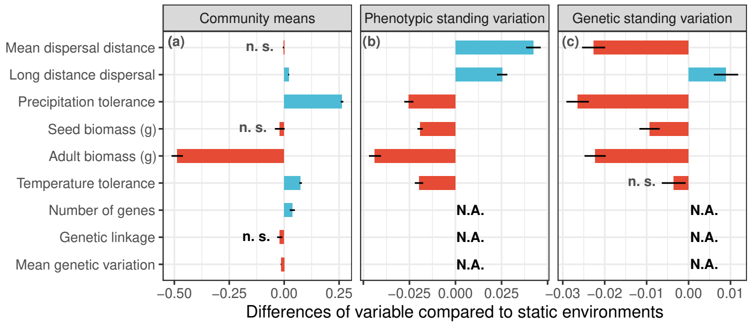

Figure 4. Community trait responses to temporal environmental variation along three organisational levels. (a) Differences in trait means in variable environments compared to static environments. (b) differences in phenotypic trait variances, and (c) differences in genetic trait variances in variable environments compared to static environments. Error bars show standard errors. Red and blue colors indicate negative and positive differences, respectively. Note the different axis scales. The abbreviation "n.s." denotes differences that are not significant ($p > 0.05$). "N.A." marks trait differences that are not available at the given level.

unsuitable quickly, impeding establishment and survival. Moreover, because the environmental change in our simulations was random rather than periodical or directional, the probability for species to find alternating suitable conditions is low. This alternating suitability, however, is the prerequisite for temporal environmental variability to favor species co-existence and increased species richness (cf. Tilman and Pacala 1993, Descamps-Julien and Gonzalez 2005). In contrast, most communities in static environments passed environmental filtering already after the first 200 years, after which species were distributed according to their environmental preferences and ecological patterns became stable.

Study question (a): Which ecological and genomic traits enable survival in temporally variable environments?

The trait characteristics of communities in the respective environments represent successful strategies in surviving random environmental variation. The decreased values of precipitation tolerance in communities in static environments indicate increased environmental specialization. This is in contrast to communities in variable environments, where the variability in precipitation conditions favors species with higher tolerance values (i.e. specialization to local conditions are detrimental in variable environments, Gilchrist 1995, Kassen 2002). Additionally, temperature tolerance directly affects individual survival due to metabolic constraints (Fig. 2(d)). Since a high temperature tolerance decreases fitness, species are forced to keep tolerances low if they occur at their respective environmental optimum. In variable environments, this environmental optimum is hardly met. As a consequence, selection acts rather on enhancing temperature tolerance to gain long-term fitness. Therefore, our experimental design captures the evolution towards bet-hedging strategies in terms of adaptation to variable environments (Slatkin 1974).

The second aspect of survival strategies lies in the biomass patterns. In general, species in variable environments were smaller than in static environments. Since growth rates and fecundity follow MTE, smaller species are more fecund than bigger species at the expense of survival. A higher and more frequent number of offspring will spread the risk over time in variable environments (McGinley et al. 1987, Philippi and Seger 1989). Additionally, the larger range of different biomasses in static environments can be interpreted as temporal partitioning (Pronk et al. 2007), because it means that co-occurring species will reproduce at different times and intervals. This allows species to alternate dominance and thus produce temporally variable biotic conditions (cf. Olff et al. 2000, Wilson and Abrams 2005). Furthermore, both biomass and tolerance patterns suggest that specialization to avoid competitive exclusion plays a larger role in shaping communities in static environments, while communities in variable environments are primarily shaped by generalism and environmental filtering (cf. Menge and Sutherland 1976, Hulshof et al. 2013).

In order to track suitable conditions, dispersal abilities are of crucial importance in changing environments (Bourne et al. 2014). While mean dispersal distances in our simulations showed little differences between environments, long distance dispersal indeed increased in variable environments. Besides primary dispersal traits, the dispersal rate also increased in variable environments via the indirect effect of metabolic rates: the high demographic turnover that comes with higher fecundity due to decreased biomass leads to more frequent dispersal. This further explains why there was little change in mean dispersal distance between environments. With the rate of change in our simulations and the small spatial extent of our landscape, dispersal distance (which is what is controlled by dispersal traits) is less important than dispersal rate (cf. Johst et al. 2002). However, this might change in fragmented landscapes, where dispersal distance is critical to maintain connection between habitable patches (Bacles et al. 2006, Boeye et al. 2013, Bonte et al. 2010).

Lastly, species may survive by adapting to changing conditions (Jump and Peñuelas 2005). This constant adaptation requires an appropriate genetic architecture: we expected genomes to contain a high variation of trait alleles (Holt 1990) which can be recombined easily for a species to quickly respond to novel conditions (Schiffers et al. 2012, Matuszewski et al. 2015) by producing new phenotypes. Indeed, we found increased gene numbers in variable environments, which allow potentially larger range of possible expressed trait values, and thus more recombination potential. Since genetic linkage did not differ between environments, the genome size increase is due to an increased number of linkage units. Species with these larger genomes can be thought of having undergone polyploidisation or ascedent dysploidy. In fact, polyploidisation correlates with latitude and, arguably, with environmental stress (Rice et al. 2019), but direct tests of this are difficult due to feasibility (Van de Peer et al. 2017). Moreover, increased fecundity also increases adaptation potential as it leads to more recombination in a given time interval. According to our results, the adaptation response to variable environments is mainly characterised by increasing environmental tolerances. However, the changes in genomic traits did not prevent the general decrease of mean genetic variation in variable conditions, which contradicts results from a previous modeling study (Matuszewski et al. 2015).

With more detailed data on the levels of variation, we will attempt to offer an explanation to this in the following section.

Study question (b): How do temporally variable environments shape phenotypic and genetic standing variation?

Having identified survival strategies on a population phenotypic level, we wanted to know whether there are selection patterns on the standing variation within the populations — both at the phenotypic intraspecific and genetic levels. Our results enable us to identify which traits are under increased selection pressure and in which traits species benefit from variation in the different environments. Most traits, such as tolerance for environmental conditions and biomass, were more specialized, i.e., had lower variation, in variable environments at both intraspecific and genetic levels. However, it appears to be beneficial for species to maintain plasticity in dispersal distances when coping with temporal environmental variation, as evidenced by the fact that dispersal traits, especially long distance dispersal, maintained similar to higher levels of variation.

Since variation in our experiments could be increased neither by mutation (Josephs et al. 2017), nor by external gene flow (Cornetti et al. 2016), selection could only act on standing variation. Under these conditions, a higher linkage of genes preserves variation in the associated trait (cf. Teotónio et al. 2009), while low linkage genes allows faster specialization. This differentiated selection pressure might explain why we don't see a net change in genetic linkage, because variation and specialization benefit from contrasting degrees of genetic linkage. Specialization in any given ecological function and thus the emergence of different phenotypes could also be facilitated by a low number of loci for associated traits (Schiffers et al. 2014). In contrast, phenotypic uniformity might arise from increased number of loci which stabilize variation (Fraser and Schadt 2010). Thus, the number of loci represents a potential trade-off between specialization and phenotypic robustness, which might warrant further investigation. These findings suggest that increasing the number of loci could act as a stabilizing coexistence mechanism by promoting intraspecific competition caused by phenotypic uniformity and thus greater intraspecific niche overlap. In light of this, further experiments should focus on whether phenotypic variation impacts species coexistence negatively (Hart et al. 2016) or if low species numbers first allow higher phenotypic variation (Hulshof et al. 2013).

Our results furthermore exemplify that intraspecific and genetic variation do not need to be correlated. In case of mean dispersal distance, phenotypic variation increased in variable environments. However, the genetic variation of mean dispersal distance decreased. Thus, the phenotypic variation in mean dispersal distance is due to very different phenotypes, which, in turn, exhibit relatively specialized genotypes. This further stresses the essential role of ecotypes to ensure species survival under changing environments.

Limitations and perspectives

The fact that our simulations produced low coexistence in terms of the total number of species across the landscape might be a result of too large a trait space in the initial species pool, most of which would be filtered by the relatively narrow environmental conditions. Since the initial species pool was on average

350 species large, the probability is also high for it to contain a few strong generalist species, which outcompete other species. On the other hand, an average initial number of 10 species per grid cell means a low probability for one or more species to be sufficiently adapted to the local conditions. Nevertheless, the coexistence level obtained is also in accordance with theoretical expectations, considering that a niche partitioning along the two gradients would explain the average of four species we count in static environments (i.e. one specialized species per environmental gradient combination, see Armstrong and McGehee 1980). The filtering is also evidenced by the reduction of trait value ranges over all traits after simulation initialisation (not shown). In fact, additional post-hoc simulations with more constrained initial communities in terms of species traits resulted in a two-fold increase of surviving species numbers (not shown). This did not, however, change the general results. Small-scale disturbance or trophic interactions, e.g., herbivory could further increase coexistence, as theoretical and empirical studies suggest (Shea et al. 2004, Roxburgh et al. 2004, Chesson and Kuang 2008). But since these processes likely produce additional confounding effects, we chose not to include them in our model at this stage, albeit we identify them as potential directions for further model development. Trophic and other interactions such as mutualism, can have important effects on species survival under climate change (Berg et al. 2010) and even lead to extinction cascades if keystone species get lost (Brook et al. 2008). Since keystone species would be affected by genetic factors in the same way as any other species, our model likely underestimates net species loss effects mediated by genetic factors.

Furthermore, our model simplifies complex genetic factors and dynamics which could potentially have confounding effects on resulting patterns. For instance, linkage between genes in reality is not a binary decision, but rather a consequence of the physical distance between those genes. The larger the distance, the higher the probability of crossing over during meiosis. Additionally, genetic architecture is dynamic, especially in plants. Genomes can grow, e.g., by polyploidisation (Van de Peer et al. 2017), and shrink in size, both of which affects genetic linkage and potentially genetic variation. Since polyploidisation is often a stress response in plants it will arguably affect survival (Rice et al. 2019). Subsequent gene loss may then even initiate speciation, therefore providing new opportunities for emerging species (Albalat and Cañestro 2016). Our model hence represent the effects of genetic linkage and genome sizes without explicitly considering their respective genetic origins. Nevertheless, our findings on the interaction betweeen genetic and ecological traits call for empirical works identifying the factors that trigger these genomic processes and assessing their evolutionary relevance (Van de Peer et al. 2017).

To make our model and the findings on genomic and ecological traits under temporal environmental variation more applicable and relevant to real-world systems, the model could be constrained by real data in further studies. For instance, the model could be initiated with simulation arenas which can be directly derived from actual landscapes, including environmental conditions (e.g. from Karger et al. 2017). Species-specific parameters could be taken from databases for phenotypic traits (Kattge et al. 2011) and occurence records (GBI) and enriched by genomic information (Dong et al. 2004, Howe et al. 2020) to constrain initial parameter space for the creation of random communities. Thus, our model represents an oppurtunity to integrate different datasets from genomes over traits and occurrences to environmental in a single mechanistic framework.

Even in the current state, our model addresses a number of eco-evo-environmental phenomena (cf. Govaert et al. 2019). The emerging patterns additionally inspire new hypotheses which can be used to guide fieldwork and experimental studies. The consideration of genomic traits, for example, implicates the explicit consideration of new perspectives on biodiversity dynamics during impending climate change (Fig. 5). For scenarios of short-term change of environmental conditions, i.e., warming, lower or increased precipitation and more frequent extreme events, adaptation can only exploit standing intraspecific or genetic variation, rather than novel mutations. Species with high phenotypic variation will likely have good adaptation potential, regardless of genetic characteristics. For species with low phenotypic variation, adaptation potential depends on genomic traits. Species that have highly specialized, i.e., uniform, phenotypes, and show little or no genetic variation will only be able to survive rapidly changing conditions by tracking their specific favourable conditions. Fragmented environments or poor dispersal abilities therefore will likely lead to the extinction of those species. Even if species have high genetic variation, genetic architecture is crucial for their performance. With a high degree of genetic linkage, species might not be able to adapt critical traits in time to react to changing conditions, since a beneficial trait allele might likely be linked to other disadvantageous trait alleles. Thus, net fitness is unlikely to increase. Low linkage, on the other hand, might lead to species who quickly adapt to new environments as they are not impeded by genetic hitchhiking. However, if linkage is too low, species will also quickly lose genetic variation, rendering them unfit to react to subsequent change. Any conservation measures targeted at particular species should thus consider population structure and genomic traits of species. Hence, while the importance of genetic diversity is already acknowledged in conservation biology (Ramanatha Rao and Hodgkin 2002) — additional to functional diversity (Díaz and Cabido 2001), it is genetic architecture that will determine adaptation success.

Conclusion

In this study we have demonstrated complex interactions between genetic and ecological realms by using a simulation model that explicitly considers genetic architecture of plant communities in changing environments. These eco-evolutionary feedbacks broaden our understanding of the role of trait-specific standing variation in species survival and adaptation (Fig. 5). This enabled identifying ecological strategies of species to survive variable environmental conditions. Variable environments select species with higher tolerances and faster life cycles while species maintain variable dispersal abilities that facilitate tracking favorable environmental conditions. These adaptations are, however, mostly enabled by large genomes, which allow maintaining a high degree of genetic variation. Furthermore, we could show that selection pressure differs between traits and that there might even be positive selection pressure to maintain higher genetic variation for dispersal traits.

Our findings suggest that genomes are subject to opposing forces — especially under changing conditions. While constant environmental filtering impoverishes genomes, there is a selective force to maintain variation in the genome to adapt for future change. This conflict can be mediated to a certain degree by genetic architecture, namely a higher number of genes which allows more

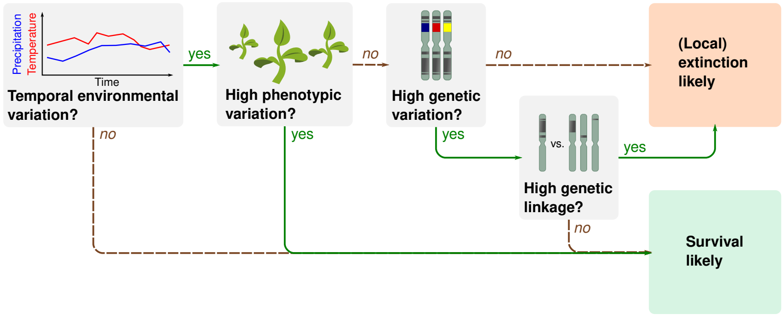

Figure 5. Ecological and genomic factors influencing species survival under variable environmental conditions.

genetic variation and a high linkage of loci which impedes the loss of variation. However, traits that need quick specialization require a low number of weakly linked loci. These complex interdependencies of genomic traits may thus further promote the high diversity in genetic architecture and ecological strategies in real-world species.

Additionally, our theoretical approach provided potential mechanisms responsible for the incongruence of phenotypic and genetic variation, which is sometimes found in nature. A mechanistic link between negative correlation in those types of variation means that special care is called for when inferring genetic variation from phenotypic variation and vice-versa.

In summary, this study highlights the importance of genomic traits for the functional assessment of local populations, species and metacommunities. We hope that conservation studies make more use of these characteristics to prioritize conservation efforts and expect future studies to investigate the genetic architecture of specific traits in natural populations.

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Contributions

JSC designed the research with input by LL. LL implemented the model, ran the simulations, performed the analysis and wrote the manuscript. JSC contributed to the writing of the manuscript.

Code availability

The model code, experiment definition files, and analysis scripts are available at https://github.com/lleiding/gemm.

Data availability

The results should be reproducible by using provided simulation codes and configuration files (see Code availability). Any data and codes associated with this study will be made accessible upon request.

Competing interests

The authors declare no competing interests.

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Supplementary material Appendix 1

1.1 Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, 2010).

1.1.1 Purpose

This model is designed to simulate a (meta-)community of plant-like individuals (Hanski 2001, Leibold et al. 2004) . For this, the model considers factors and processes across genetic, population and ecological levels. The model is able to produce several patterns across genetic, individual, population and (meta-)community levels, including adaptation and speciation through divergence of populations. Thus, the model expands from basic principles to richer representation of real-world scenarios.

1.1.2 Entities, state variables and scales

Individuals are the basic entity in the model. Given their attributes and life-history, these individuals most closely resemble plants. Individuals belong to different species, which are characterized by similar ecological traits and identical genetic architecture. The genetic architecture of each individual is comprised of a diploid set of one or more linkage units, which, in turn, combine a set of genes. Linkage units are always inherited in their entirety during the recombination phase of a reproduction event. The higher the number of genes per linkage unit, the higher the degree of genetic linkage. Some of the genes code for one ore more traits (pleiotropy, Solovieff et al. 2013), while a trait can be dependent on more than one gene (polygene). The realized trait value is the mean of all the trait alleles (quantitative trait loci). Traits thus controlled encompass the initial body mass (size) of offspring, M_s, the body mass determining onset of maturity and thus reproductive capability, M_r, mean dispersal distance, μ, the shape of the dispersal kernel, controlling long-distance-dispersal, s, and values representing the optimum and the tolerance (standard deviation) of a physical niche parameter, such as temperature and precipitation ($\overline{T}$ and σ_T or $\overline{P}$ and σ_P, resp.). Alternatively to be controlled by mutable genes, traits can also be fixed. Additionally, individuals carry attributes which describe their bodymass, M, and their adaptation to the abiotic environmental conditions (fitness), F_T and F_P. Furthermore, every individual carries a Boolean marker used to store whether a given individual has newly arrived to a grid cell or discriminate individuals from the rest of the community.

The base rates for processes governed by the metabolic theory of ecology (Brown et al. 2004) — growth, reproduction, mortality — are global constants. Mutation rate is also a global constant, if mutations are considered in a given experiment.

Every individual is placed inside an arena of grid cells, each of which has a location (coordinates) and is characterized by the physical properties temperature, precipitation and size (carrying capacity). Over the course of the simulation, these properties (location or physical parameters) might change, reflecting geomorphological dynamics. All individuals within one grid cell constitute a community. The characteristics of the grid cells combined with the state of inhabiting individuals constitute the state variables of the model. Additional patterns or summary statistics may be calculated based on these individual information.

Processes and updates are repeated every timestep, while each timestep can be considered as one year.

1.1.3 Process overview and scheduling

In each discrete, yearly timestep each individual in each grid cell will (in no particular order unless otherwise stated) undergoes the following processes: (1) establishment, (2) density independent mortality influenced by adaptation to temperature, (3) growth, (4) competition (individuals are sorted according to their adaptation to precipitation), (5) reproduction (6) mutation of offspring, (7) filtering of unviable individuals, (8) seed dispersal.

After seed dispersal, the physical environment of a grid cell might change. If that happens, all individuals within that cell are marked to undergo establishment again.

Updates to individuals and thus the local communities happen instantaneously after a specific process has been executed (asynchronous updating).

1.1.4 Design concepts

Basic principles. Metabolic theory of ecology (submodel level). Adaptive and non-adaptive radiation/evolution (submodel level). Sexual reproduction. Niche theory (system and submodel level): each individual carries unique ecological and/or functional traits, as well as preferences for their physical environments. Resource/energy limitation (carrying capacity - system level property, but invoked at submodel level).

Emergence. Species/Populations/ecotypes. Only constrained via genetic properties. Community trait composition. Interplay of physical properties (environment, geographical properties) and within community (competition strength via reproduction, growth, etc.). Species numbers, endemics, speciation rate.

Adaption and objectives. See entities. Traits follow evolution: a trait changes its value randomly within a given phylogenetic constraint. The success of the change (fitness) emerges as the result of adaption to the physical environment and the reproductive success of an individual over its competitors.

Sensing. Individuals are directly affected by the properties of their physical environment (e.g., temperature).

Interaction. Individuals directly interact when sexually reproducing. However, they are not affected by this interaction themselves. Instead, the interaction aims solely at determining the genotype of their offspring. Additionally, competition for resource/energy/space between individuals represents indirect interaction.

Stochasticity. Most of the submodels are carried out by all eligible individuals. Some submodels (Survival, Competition, Mutation and Dispersal), however, happen with particular probabilities. In these cases, execution of submodels is decided at random, taking into account individual characteristics, such as body size, fitness, genome size, or dispersal abilities. All decisions inside all of the submodels are stochastic (e.g., number of offspring) to maintain variability and relax assumptions.

Observation. At the start and end of the simulation and at definable regular time intervals, the properties of all individuals (including the properties of their locations) are recorded and written to files.

1.1.5 Initialization

The initialization step creates lineages with randomly chosen genetic and ecological trait values (see Table A1) in each grid cell that is designated to receive an initial community. This encompasses choosing the number of genes for a lineage, the number of linkage units and the intra-genomic variance of trait values. Traits with thus distributed trait values are the distributed randomly among the genes for each individual of a lineage. Population size (number of individuals) of a lineage is determined by the adult body size of individuals from a lineage. At this point all individuals of a population are identical. Values for ecological traits are then varied in each gene where a given trait is found, for all individuals of a lineage. The variation is Normal distributed with the average lineage trait value as mean and the product of σ_l (phylogenetic constraint) and the lineage trait value as standard deviation. This ensures initial genetic variation within a lineage population. Thus created populations are added to a grid cell's community until the additional mass of another population would exceed the grid cell's carrying capacity. In the experiment configuration file, it is possible to specify other methods of initializing communities, e.g., "single", where each grid cell receives only one species. Whether a grid cell receives an initial community depends on the map definition. At the end of initialization each of the thus populated grid cells holds one or more different populations, each from a separate lineage.

1.1.6 Input

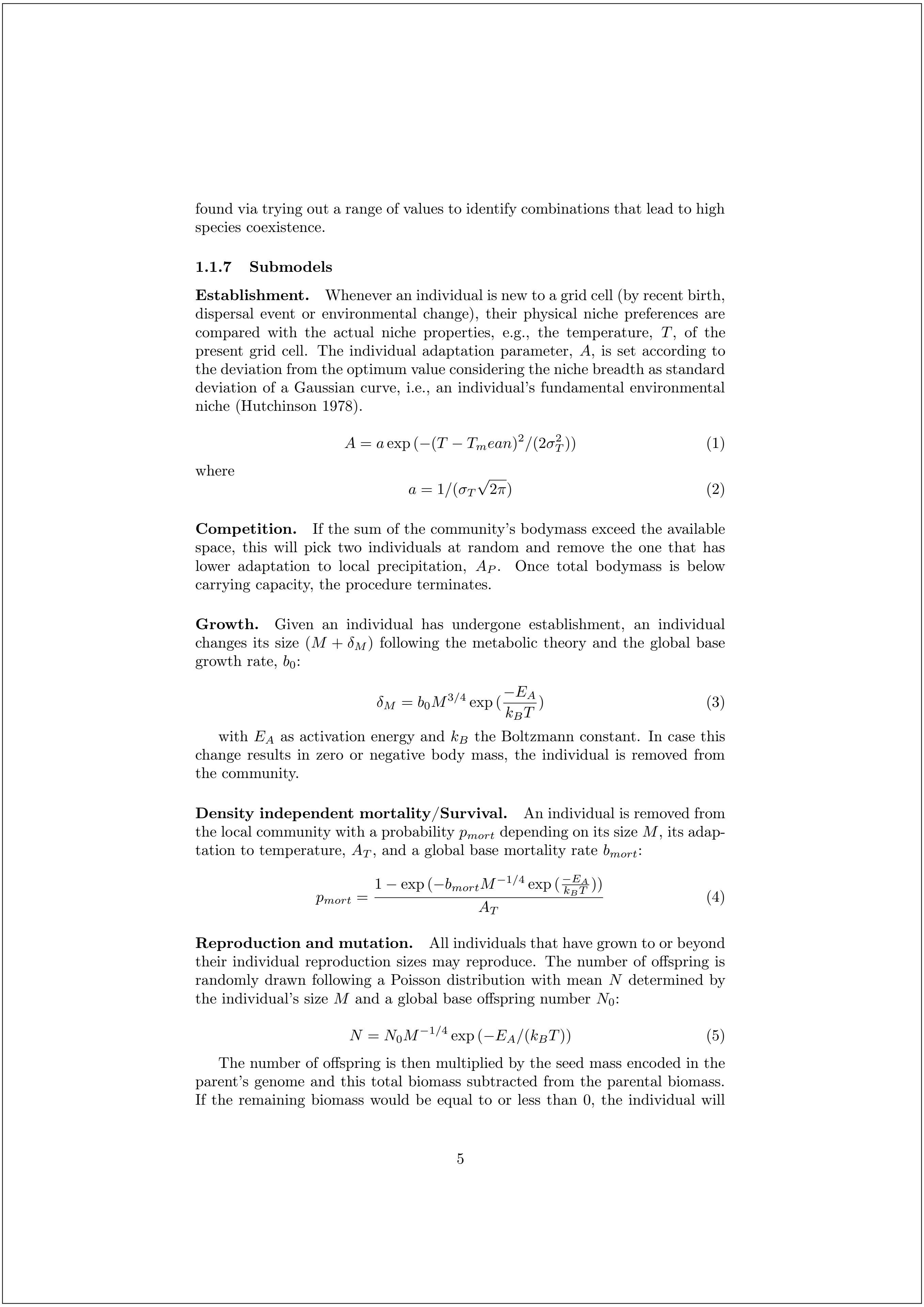
At the start of a simulation, user defined parameters are read, containing also a definition of the simulation arena (map definition). This definition is provided in a separate plain text file. Within the text file, a line at the top containing a single number defines the number of timesteps the arena definition is valid for. Every other non-empty line defines one grid cell with a unique identifier (a number), and the location of the grid cell as two coordinates. Optionally, one can define the type of the grid cell (island or continent), its temperature and precipitation values, and size.

Other optional parameters can be set in a separate configuration file and pertain to defining simulation scenarios (Table A1).

If a parameter value is not specified by the user, its default value is assumed, which is defined in the simulation code. Global parameter values were either adapted from the literature (Brown et al. 2004, Fournier-Level et al. 2011) or

Table A1: Model parameters with variable names as used in the source code.

Name/Function	**Default value**	**Description**
"avgnoloci"	1	average number of loci
"cellsize"	20e6	maximum biomass per hectare (g)
"config"	"simulation.conf"	configuration file name
"debug"	false	write out debug statements
"dest"	current date	output folder name
"fasta"	false	record fasta data?
"fertility"	exp(28.0)	global base reproduction
"growthrate"	exp(25.2)	global base growth
"indsize"	"seed"	initial individual stage
"lineages"	false	record lineage and diversity data?
"linkage"	"random"	gene linkage type ("random"/"full"/"none")
"logging"	false	write output to logfile
"maps"	""	comma-separated list of map files
"maxdispmean"	10	maximum mean dispersal distance
"maxrepsize"	14	log maximum repsize (g)
"maxseedsize"	10	log maximum seedsize (g)
"maxtemp"	313	maximum optimum temp (K)
"minrepsize"	3	log minimum repsize (g)
"minseedsize"	-2	log minimum seedsize (g)
"mintemp"	283	min optimum temp (K)
"mortality"	exp(22)	global base mortality
"mutate"	true	mutations occur
"mutationrate"	3.6e10	one mutation per individual
"nniches"	2	number of environmental niches
"outfreq"	100	output frequency
"phylconstr"	0.1	phylogenetic constraint
"phylo"	false	record phylogeny?
"popsize"	"metabolic"	population size initialization algorithm
"precrange"	10	range from 0 for precipitation optimum
"quiet"	false	don't write output to screen
"sdtemp"	0.0	temperature change per time step
"sdprec"	0.0	precipitation change per time step
"seed"	0	seed for the random number generator
"static"	false	mainland individuals stay static
"traitnames"	["compat", "dispmean", "dispshape", "precopt", "prectol", "repsize", "reptol", "seedsize", "tempopt", "temptol"]	list of traitnames



found via trying out a range of values to identify combinations that lead to high species coexistence.

1.1.7 Submodels

Establishment. Whenever an individual is new to a grid cell (by recent birth, dispersal event or environmental change), their physical niche preferences are compared with the actual niche properties, e.g., the temperature, T, of the present grid cell. The individual adaptation parameter, A, is set according to the deviation from the optimum value considering the niche breadth as standard deviation of a Gaussian curve, i.e., an individual's fundamental environmental niche (Hutchinson 1978).

$$A = a \exp\left(-(T - T_m ean)^2/(2\sigma_T^2)\right) \tag{1}$$

where

$$a = 1/(\sigma_T \sqrt{2\pi}) \tag{2}$$

Competition. If the sum of the community's bodymass exceed the available space, this will pick two individuals at random and remove the one that has lower adaptation to local precipitation, A_P. Once total bodymass is below carrying capacity, the procedure terminates.

Growth. Given an individual has undergone establishment, an individual changes its size ($M + \delta_M$) following the metabolic theory and the global base growth rate, b_0:

$$\delta_M = b_0 M^{3/4} \exp\left(\frac{-E_A}{k_B T}\right) \tag{3}$$

with E_A as activation energy and k_B the Boltzmann constant. In case this change results in zero or negative body mass, the individual is removed from the community.

Density independent mortality/Survival. An individual is removed from the local community with a probability p_{mort} depending on its size M, its adaptation to temperature, A_T, and a global base mortality rate b_{mort}:

$$p_{mort} = \frac{1 - \exp\left(-b_{mort} M^{-1/4} \exp\left(\frac{-E_A}{k_B T}\right)\right)}{A_T} \tag{4}$$

Reproduction and mutation. All individuals that have grown to or beyond their individual reproduction sizes may reproduce. The number of offspring is randomly drawn following a Poisson distribution with mean N determined by the individual's size M and a global base offspring number N_0:

$$N = N_0 M^{-1/4} \exp\left(-E_A/(k_B T)\right) \tag{5}$$

The number of offspring is then multiplied by the seed mass encoded in the parent's genome and this total biomass subtracted from the parental biomass. If the remaining biomass would be equal to or less than 0, the individual will not reproduce. Otherwise, possible mates are selected within the same grid cell based on whether they belong to the same lineage, have reached maturity (which includes having established on the grid cell) and whether their compatibility sequences are sufficiently similar. If a suitable partner is found, both partners produce gametes, i.e., complete haploid sets of all linkage units, where each linkage unit is randomly picked either from the maternal or paternal set. The two gametes, one from each mating partner, comprise the genome for the offspring. At this point, mutations in the offspring's basecode may happen with a set probability P_m. In the case of mutation all traits associated with the respective gene will randomly change value V by ϵ, which is normally distributed and has as standard deviation the product of σ_l, i.e., the phylogenetic constraint, and V.

The new individuals' trait values are then calculated as the means of all alleles and the individuals added to the community, with their size set to the initial biomass M_s (seed biomass).

Dispersal. After reproduction and mutation, each offspring individual may disperse. For each dispersal event, a new location (i.e. x and y coordinates) is drawn randomly following a logistic distribution with mean and shape parameters (which controls long-distance-dispersal) taken from the individual's traits (Bullock et al. 2017). If a suitable grid cell is found at the drawn coordinates, the dispersing individual will be placed there and removed from the original community. The removal happens even when there is no destination grid cell to be found, thus killing the individual. Special attention is paid when the destination grid cell is of island type, while the origin is on the mainland and the simulation runs in "static" mode. In this case, the dispersing individual is copied to the new destination instead of moved.

Habitat change. If enabled, both environmental habitat parameters - temperature and precipitation - change values throughout the simulation arena. The amount and direction of change is the same for all grid cells across the landscape. Changes to temperature and precipitation happen independently from one another. The change is randomly drawn from a Normal distribution with the current value as the mean and a user defined standard deviation ("sdtemp" and "sdprec").

1.1.8 Output/Calculation

The main simulation data output is stored in two separate formats. The first is a table containing data characterizing the individuals. Each line represents on individual. The columns describe an individual's current state. This is characterized by location, environmental conditions, ecological traits and summary of the genetic architecture. Additionally or alternatively to the individual level data, the data can be summarized at the population level (i.e., all individuals of a common lineage within the same grid cell). The second format is a fasta file containing the entire genome of all individuals. Association of sequences to individuals, linkage units, genes and coded traits is defined in the fasta headers. Output is stored at the beginning and end of a simulation and at user-definable intervals. The output considers the state of all non-seed individuals at those times.

1.2 Change of variance along principal components depending on the number of replicates

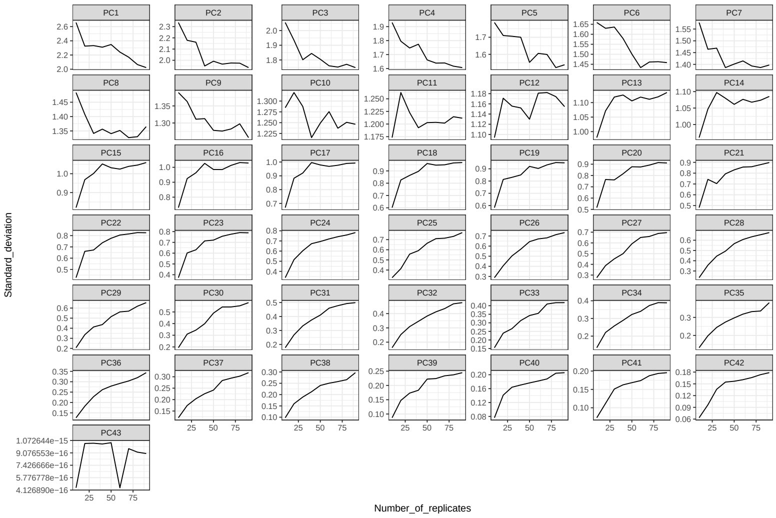


Figure A1: Standard deviations of principal components based on the simulations' output of trait data at the investigated year 500. There is no noticeable change in standard deviations prior to reaching 90 replicates.

1.3 Results from principal component analysis and mixed effects models

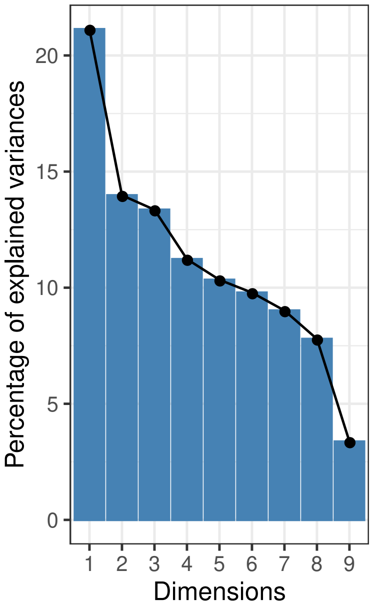


Figure A2: Scree plot of the proportion of explained variance by each of the principal components for the PCA of trait data at year 500.

Table A2: Quality of representation of traits on the principal component dimensions ("PC").

Trait	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**
Mean dispersal distance	0.223	-0.237	0.364	-0.228	-0.669	0.331	0.195	-0.335	-0.052
Number of genes	0.053	-0.016	-0.704	0.325	-0.045	0.278	0.017	-0.562	-0.012
Precipitation tolerance	-0.136	-0.584	0.097	0.201	-0.120	-0.288	-0.684	-0.156	0.030
Adult biomass (g)	0.619	0.134	0.123	0.095	0.141	0.117	-0.231	-0.021	0.699
Temperature tolerance	0.327	-0.230	-0.178	-0.011	-0.097	-0.753	0.464	-0.099	0.083
Genetic linkage	0.141	0.004	-0.549	-0.516	-0.375	0.011	-0.296	0.428	0.030
Mean genetic variation	-0.141	0.599	0.093	-0.346	-0.090	-0.357	-0.287	-0.525	0.008
Long distance dispersal	0.144	-0.378	-0.022	-0.609	0.596	0.141	0.005	-0.275	-0.119
Seed biomass (g)	0.615	0.172	0.073	0.191	0.056	-0.042	-0.237	0.055	-0.697

Table A3: Results of mixed effects model fits for the different trait as a function of the type of environment (static or variable), with replicate as a random effect.

Trait	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
Temperature tolerance (σ_T)	0.075	0.006	15232	13.082	0.000
Seed biomass (g, M_s)	-0.020	0.022	15215	-0.896	0.370
Precipitation tolerance (σ_P)	0.263	0.006	15217	44.525	0.000
Number of genes (n_G)	0.037	0.012	15205	3.228	0.001
Mean genetic variation ($\overline{\sigma_G}$)	-0.014	0.001	15212	-9.727	0.000
Mean dispersal distance (μ)	-0.003	0.003	15215	-1.178	0.239
Long distance dispersal (s)	0.021	0.002	15215	8.578	0.000
Genetic linkage (L)	-0.020	0.012	15216	-1.751	0.080
Adult biomass (g, M_r)	-0.487	0.026	15212	-18.621	0.000

Table A4: Results of mixed effects model fits for the variation of traits in phenotypic and genetic levels as a function of the type of environment (static or variable), with replicate as a random effect.

Trait	**Level**	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
Mean dispersal distance	phenotypic	0.042	0.004	15228	10.651	0.000
Mean dispersal distance	genetic	-0.023	0.003	15204	-8.244	0.000
Long distance dispersal	phenotypic	0.025	0.003	15250	9.053	0.000
Long distance dispersal	genetic	0.009	0.003	15219	3.083	0.002
Precipitation tolerance	phenotypic	-0.025	0.002	15222	-10.156	0.000
Precipitation tolerance	genetic	-0.026	0.003	15207	-9.873	0.000
Seed biomass (g)	phenotypic	-0.019	0.001	15246	-13.153	0.000
Seed biomass (g)	genetic	-0.009	0.002	15230	-3.832	0.000
Adult biomass (g)	phenotypic	-0.044	0.003	15218	-13.344	0.000
Adult biomass (g)	genetic	-0.022	0.003	15222	-8.836	0.000
Temperature tolerance	phenotypic	-0.020	0.002	15231	-8.684	0.000
Temperature tolerance	genetic	-0.004	0.003	15221	-1.242	0.214

1.4 Spatial structuring of ecological patterns in the simulations

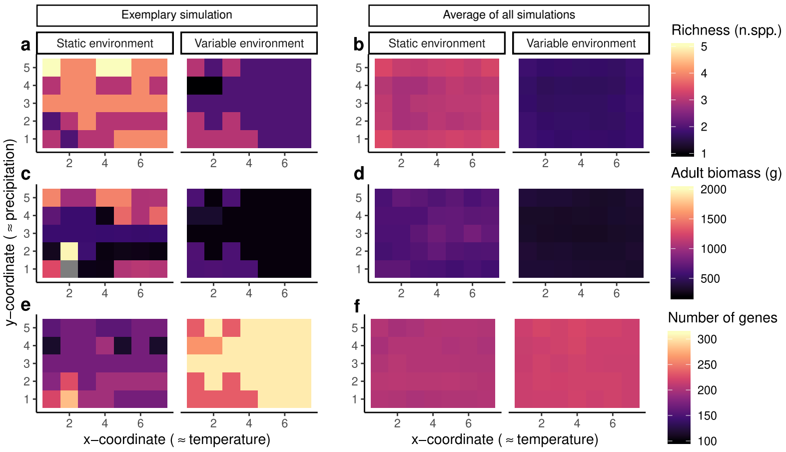
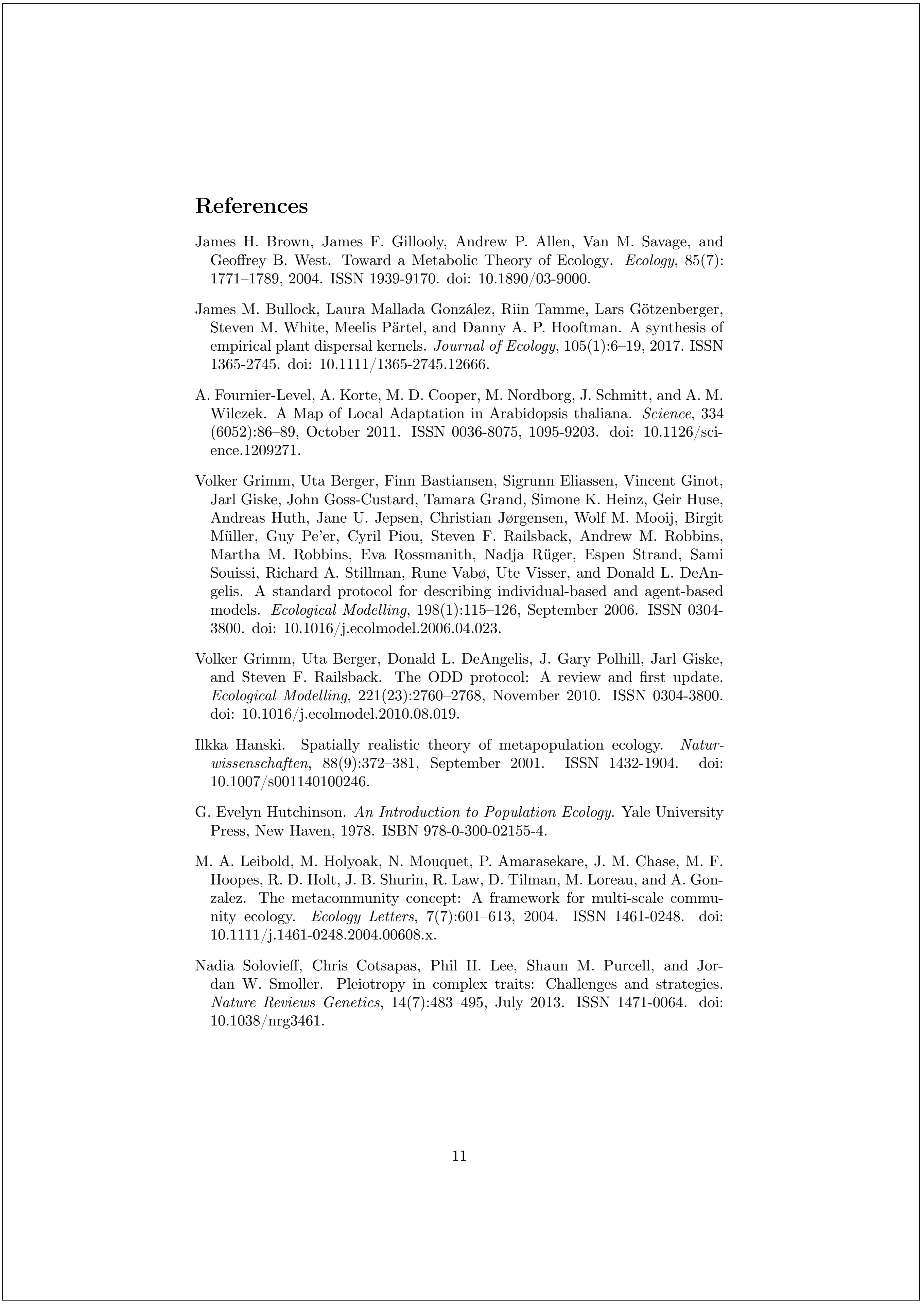


Figure A3: Spatial structuring of ecological variables and traits in static and variable environments. (a) Local richness (α-diversity) in an exemplary simulation run, (a) Local richness (α-diversity) averaged over all simulations, (c) mean adult biomass in an exemplary simulation run, (c) mean adult biomass averaged over all simulations, (e) mean number of genes in an exemplary simulation run. (f) mean number of genes averaged over all simulations. The abbreviation "n.spp." denotes number of species. Shown is data from time step 500. The initial conditions for both environments were identical.



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5

GENOMIC TRAITS AFFECT OCCURRENCE AND SPEED OF INSULAR SPECIES RADIATIONS

Since certain species properties, including genomic traits, all contribute to a trait syndrome that makes species more likely to survive in variable environments (see chapter 4), I was interested in whether the same traits could also explain why some species diversify more than others. Therefore, I conducted island colonization experiments with the same model as the one developed and presented in the previous chapter to find out which lineage attributes lead to increased numbers of evolving species.

The findings of the study show that only few lineages diverged into different species. The lineages that did diverge exhibited a complex initial trait combination of low dispersal abilities, flexible reproductive strategies, intermediate genetic linkage and pre-adaptation to environmental conditions. Later evolution of these lineages resulted in trait syndromes that largely match empirical observations: increased body sizes, loss of long-distance dispersal, and increased self-compatibility.

At the time of writing, the corresponding manuscript is in preparation to be submitted to a peer-reviewed journal. The article was drafted and written by myself with contributions by Juliano Sarmento Cabral. I performed all research procedures and analyses. The conceptual design was done by myself and Juliano Sarmento Cabral. My overall contribution amounted to ca. 95 %.

How genomic and ecological traits affect radiations of plant species on oceanic islands: insights from a genomically-explicit model

Ludwig K. T. Leidinger, Juliano Sarmento Cabral

April 12, 2020

Abstract

Species radiations on oceanic islands are fascinating evolutionary phenomena. While the effect of external factors like area, age, isolation, and environmental heterogeneity on radiations is easily investigated, the role of eco-evolutionary mechanisms and how species traits shape such radiations remains understudied. Current data indicates that at any given island or archipelago, only a small fraction of lineages radiate. Evidence for the importance of genome size and genetic linkage for speciation and adaptation suggests that genomic factors could help explain these patterns. Unfortunately, comprehensive genomic and ecological trait data for island taxa are scarce. Therefore, we employ a genomically-explicit, individual- and niche-based model to assess the influence of different genomic and ecological traits on the occurrence and extent of plant radiations on oceanic islands. In the model, genomic traits encompassed genetic linkage and genome size, whereas ecological traits coded by the genome were body sizes (seed and adult), dispersal abilities, environmental preferences and reproductive strategies (selfing and strength of pre-zygotic barriers). We performed simulation experiments by connecting hypothetical islands to source pools of species with random trait compositions via long-distance dispersal to identify the trait syndromes of successful radiators. We expected low long-distance dispersal and large, intermediately-linked genomes to promote both the occurrence and extent of radiations. Results show that only few colonizing lineages diverge into different species. The species-richest lineages are characterized by high genetic linkage, low to intermediate long-distance dispersal, and a high propensity to selfing. Over time, species evolve island syndromes comprised of similar, mostly increased, body and seed sizes, a loss of barriers to hybridization, and increased selfing. Our results based on fundamental ecological and evolutionary theory shed new light on the hypothesized island rule in plants and highlights the importance of genomic traits for evolutionary dynamics and thus species' adaptive potential.

1 Introduction

Species radiations of animal and plant lineages are fascinating phenomena that inspired researchers across the last centuries. Radiations taking place on oceanic islands have been the most emblematic. Examples include adaptive radiations of *Aeonium* on the Canary islands (Jorgensen and Olesen, 2001) or lobeliads on Hawaii (Givnish et al., 2009). A number of abiotic factors have been suggested to influence such radiations: area (Kisel and Barraclough, 2010; Losos and Schluter, 2000), time (Borregaard, Matthews, and Whittaker, 2016; Whittaker et al., 2007), isolation (Steinbauer et al., 2016), and environmental heterogeneity (Cabral et al., 2019; Cabral, Wiegand, and Kreft, 2019), all positively affect lineage divergence, and thus radiations. While correlating these abiotic factors with the extent of radiations may reveal the role of extrinsic drivers influencing radiations, several patterns remain poorly investigated. For example, most of the abiotic factors, such as intra-insular isolation, do not explain why only few lineages radiate, even though they might have similar geographic opportunities and colonization histories as species-rich lineages (Price and Wagner, 2011). Many of these few successfully radiating lineages radiate repeatedly in several different locations, i.e. wherever they colonize islands or archipelagos (Takayama et al., 2018), for instance *Psychotria* (Rubiaceae) and Asteraceae (Barrabé et al., 2014; Crawford et al., 2009; Nepokroeff et al., 2003). This suggests that a species-centered, functional perspective might be promising approach to address plant radiations on oceanic islands. (Patiño et al., 2017; Warren et al., 2015). The fact that some putative traits are already reported to have a strong importance on radiations like growth-form, breeding system and dispersal capabilities (Price and Wagner, 2004), warrants a more general, systematic investigation. However, such a study of traits related to lineage radiations in empirical systems may be confounded by the fact that many island plant species evolve similar island syndromes of traits, characterized, for instance, by a loss of dispersal abilities (Biddick, Hendriks, and Burns, 2019; Burns, 2019). This makes it difficult to infer the exact characteristics of the successful founder lineages, even when taking into account the closest mainland relatives or scarce paleontological data.

Among the species characteristics that might play important role on radiations on oceanic islands might be traits related to gene flow. This importance can be inferred from the strong focus on isolation-related abiotic factors in recent island biogeography research (Warren et al., 2015), in which increasing isolation increases both non-adaptive (Rosindell and Phillimore, 2011) and adaptive (Cabral et al., 2019) radiations. However, even though these eco-evolutionary studies represent valuable contributions to our biogeographical understanding, genetic and genomic evidence suggests that assumptions such as “protracted speciation” might be an oversimplification since they ignore genetic architecture and its effect on recombination potential (Feder, Egan, and Nosil, 2012; Malinsky et al., 2015). In fact, genomic traits can facilitate the divergence of populations and thus incipient speciation even under continuing gene flow (Nosil and Feder, 2012). One of the traits that plays an important role here is genetic linkage, which describes the tendency of genomic regions to be inherited in combination (Hawthorne and Via, 2001). This genetic linkage enables the selection and isolation of genomic regions associated with adaptive traits while other parts of the genome are still subject to gene flow with the diverging population ("divergence hitchhiking", Feder and Nosil, 2010). Another genomic trait with functional aspects that may affect speciation is genome size. A number of processes can change genome size over the course of a lineage's evolutionary history, e.g. gene duplication and loss, polyploidization and transpositions (Albalat and Cañestro, 2016; Casacuberta and González, 2013; Kraaijeveld, 2010; Van de Peer, Mizrachi, and Marchal, 2017). These processes often precede major evolutionary transitions such as speciation. Evidence from island floras indeed suggests that many genera recently underwent polyploidization prior to colonization (Crawford et al., 2009). Given that populations on islands are not necessarily isolated enough (neither from the mainland nor within the island) to support speciation-by-isolation (non-adaptive radiation), these genomic traits could hence be an important factor in understanding island radiations.

We aim therefore at identifying the genomic and ecological traits that influence island species radiations. For this purpose, we employed a theoretical approach using a mechanistic agent-based model. Mechanistic simulation models have already proven useful in a number of ecological settings (Cabral, Valente, and Hartig, 2017) and have also been applied to island biodiversity (Leidinger and Cabral, 2017). Since existing island models lack the necessary level of detail regarding genomic factors, we applied our own, recently developed, individual-based, genome-explicit model for eco-evolutionary dynamics of virtual herbaceous plant metacommunities to address these patterns (Leidinger and Cabral, 2020). Specifically, we addressed the following questions: (1) Do indeed only few colonizing lineages diverge? We expect that only few colonizers initiate radiations on islands and that the island communities will show the typically observed trend that most colonizers remain as the single, original species, i.e. monospecific, and only few lineages showing species-rich radiations, i.e. divergences (Price and Wagner, 2011). (2) Which trait characteristics and trait combinations determine lineage divergence on islands (i.e. a divergence syndrome)? We expect that there is a particular combination of traits that enables lineage divergence, for instance, large genome sizes, flexible reproductive systems, and decreased dispersal abilities (Cabral et al., 2019; Crawford et al., 2009). (3) Do the diverging lineages maintain these trait values? We expect that diverging lineages optimize their ecological traits to island life (e.g. island syndrome) by, for instance, losing their long-distance dispersal ability (Biddick, Hendriks, and Burns, 2019; Burns, 2019). We find that only a few of the colonizing lineages diverge, that the divergence syndrome is a complex combination of limited dispersal abilities, increased propensity to selfing, and low to intermediate genetic linkage, and that diverging lineages evolve an island syndrome comprised of decreased long-distance dispersal, increased seed and adult biomass, high selfing, low reproductive barriers, and environmental specialization. Our results suggest that genomic traits should be considered alongside ecological traits to assess species' evolutionary potentials and thus their potential reactions to future environmental change.

2 Material and Methods

2.1 The model

Most of the previous island models lacked the level of detail required for a genomic-focused study on drivers of species radiations (Leidinger and Cabral, 2017). Therefore, we took advantage of a previously developed model (Leidinger and Cabral, 2020, `https://github.com/lleiding/gemm`) to address our study questions. The model generates spatially-explicit dynamics of plant metacommunities (Hanski, 2001; Leibold et al., 2004) and considers explicit eco-evolutionary dynamics at the genomic and individual levels. In the model, individuals are characterized by ecological traits for mean dispersal distance, long-distance dispersal, seed biomass, reproductive biomass, optima and tolerances toward two environmental conditions (temperature and a surrogate for resources, e.g. water, from here on called precipitation for simplicity), propensity to selfing in the absence of reproductive partners and a sequence-similarity threshold determining reproductive compatibility to potential mates. This compatibility represented the individual species boundary, concordant with the biological species concept (Mayr, 1982). Each expressed ecological trait is represented at least once in the haploid genome. Genomic traits encompass the number of genes and linkage units, which combined will determine the degree of genetic linkage, i.e. the number of genes per linkage unit. A gene is characterized by a nucleotide sequence and potential associated trait alleles. Individuals' states are mainly characterized by their current mass, which, in combination with their expressed trait for adult biomass, determines their demographic stage. Demographic stage can be seed, juvenile and adult. Adults are monoaecious and able to reproduce sexually, which includes gene recombination. When new offspring, i.e. seeds, are produced, they can experience mutations in their genome. The number of mutations, N_m, is determined by a global mutation rate, m_0, scaled by the local temperature, T, following the exponential function term of the metabolic theory of ecology (MTE, Brown et al., 2004) as:

$$N_m = m_0 \times \exp\left(\frac{-E_A}{k_B \times T}\right) \tag{1}$$

where E_A is the activation energy (1×10^{-19} J) and k_B the Boltzmann constant ($1.38 \times 10^{-23} \times \mathrm{J} \times \mathrm{K}^{-1}$). Each mutation causes a nucleotide change in a randomly chosen gene, which, in turn, results in the change of the values of all associated trait alleles, concurrent with the potentially pleiotropic genetic architecture in the model. This change is drawn from a Normal distribution with the current value as mean and the product of current trait value and a phylogenetic constraint, c_p, (0.1 in the simulations) as standard deviation.

2.2 Experimental design

We set our experiments in a mainland-island system. The mainland was characterized by a single grid cell and acted as the source pool of species. We initialized the mainland with individuals from random species in terms of identity, ecological and genomic traits. Once populated with species, the state of the mainland, including individuals, was preserved throughout the duration of the simulation (i.e. no eco-evolutionary dynamics takes place in the mainland). The only active process on the mainland was seed dispersal, based on species-specific dispersal traits. Seed dispersal from the mainland did not affect mainland communities, i.e. all dispersing individuals were clones of mainland individuals. By chance, most of the dispersed seeds ended up in the ocean and perished, but some seeds could hit the second landmass, i.e. the island. To reduce confounding effects like intra-archipelagic dispersal and geological dynamics (cf. Whittaker et al., 2007), we considered only a single, environmentally stable island which was initially sterile. This contrasts our system from oceanic islands which originate from continental land masses, like Madagascar. The island was comprised of 9 x 9 grid cells with 100 kg carrying capacity each. A radial temperature gradient increased from the center to the periphery (294 K to 297 K) or 21 °C to 24 °C), reflecting an elevational gradient with a central mountain peak. A second environmental gradient of an arbitrary, dimensionless quantity (from here on called precipitation for simplicity) ran perpendicular to the mainland-island axis and represented a surrogate for environmental resources, e.g. water. The geographic characteristics represents a mountain structure with a central peak which receives more precipitation from one side than the other. These environmental properties are typical for many oceanic islands of volcanic origin, e.g. in the Canaries, and increase within-island environmental heterogeneity.

For identifying the traits that enable lineage divergence, we ran 90 different replicates, each with a mainland community between ca. 1000 and 3000 lineages. A lineage comprises individuals of identical genetic architecture and initially similar trait values. Each of the lineages was characterized by a set of random trait values in terms of their ecological and genomic traits. We recorded the complete state of the individuals in our simulation world at the start and at each 500 timesteps of a simulation run. This data encompassed individual phenotypic values, individual genotypic values and nucleotide sequences, including associated trait alleles. Thus, for every time step, we could track the state of all individuals, including location, abundance, demographics, adaptation, and trait characteristics for all ecological and genomic traits.

Some of our simulations ran for several days, and a few did not finish after weeks. Therefore, we only analyzed those runs which reached 750000 simulated years. Thus, we retained 80 replicates in total.

2.3 Analyses

Our simulations provided us with detailed information on each individual present on the island at the time of recording. To make sure we only retain those individuals that were the offspring from those individuals colonizing the island from the mainland, and thus successfully founded island populations, we excluded all mainland individuals from the data prior to analysis. We further only retained data on adult individuals (i.e. individuals whose size was equal to or greater than their adult biomass trait) to reduce overall data size. We combined timed data on the individuals from these founder populations with the nucleotide sequences of their compatibility genes to infer dated phylogenetic trees for each lineage. For this, we clustered the raw distances between sequences using Ward's method. From the individual clustering, we inferred species by cutting the tree at the maximum lineage-specific sequence dissimilarity reproduction threshold from the mainland individuals and combining all tips below that threshold to one species. This value directly exploits the actual reproductive biology of the lineages. The rationale behind using these lineage-specific values is that when individual on the island have diverged sufficiently to not be compatible to the most tolerant mainland individual, they can truly be considered separate species. We then used these individual-species associations to define first and last appearances of each species from the individual data, which we input into `paleotree` to produce dated phylogenies (Bapst, 2012).

This provided us with species numbers over time for each lineage. As a central measure for lineages' divergence potential, we calculated the maximum number of species per lineage that coexisted at a given time on the island.

For addressing our study question on the proportion of radiating lineages (question (1)), we counted all successfully colonizing lineages (i.e. those that managed to actually found populations) and related that number to the number of successful colonizers that evolved at least two species during their time on the island. Additionally, we created a lineage-rank plot showing the maximum number of evolved species for each successfully colonizing lineage. Since only one to three lineages colonized the island on average per replicate, we pooled the data on evolving species numbers per lineage from all replicates.

To identify ecological and genomic traits affecting radiations, we keep only the trait values of the founder individuals (i.e. individuals that most closely resemble the original mainland trait characteristics), since traits might change over time on the island. We then compared the distribution of trait values between lineages that diverged and lineages that remained monospecific. We additionally conducted a principal component analysis of these values to identify any recurrent trait syndromes. To find out which traits were most important in determining whether a lineage diverged (question 2), we conducted a "Herberich" test (Herberich, Sikorski, and Hothorn, 2010) with the different ecological and genomic traits as response variable and the divergence (diverged or monospecific) as explanatory variables. The test we used makes no assumptions regarding the distribution, sample sizes or homoscedasticity. Although significance levels are deemed inappropriate for simulation model results (White et al., 2014), we use the reported significance to identify the traits with the most notable differences.

To answer the third question regarding island syndromes, we identified trait syndromes of island lineages considering the evolved trait values from the most recent years in the data. For this, we again conducted a "Herberich" test with the different ecological and genomic traits as response variable and the phases (terminal vs. initial) of the two lineage groups (diverged or monospecific) as explanatory variables to identify the strongest trait responses. Additionally, the comparison of these patterns with empiric plant island syndromes (Burns, 2019) allows us to validate our model and to get an idea of the generality of our findings (Grimm and Railsback, 2012).

3 Results

Of the 964 lineages that managed to reach the island throughout our simulation replicates, 29 lineages reproduced on the island, thus temporarily establishing populations. Of these 29 colonizing lineages only nine lineages diverged (Fig. 1. The average maximum number of species per lineage was 5.1 ($\sigma = 6.8$).

These nine lineages exhibited complex trait syndromes that can be associated with their divergences (Fig. 2). In terms of differences in means, the most notable trait is a low to intermediate long-distance dispersal (reduced in diverged lineages by $\delta = -3.9$, standard error $\epsilon = 1.2$, $p = 0.0086$). Some other traits do not show a notable difference in mean, but their spread is reduced in diverging lineages. These traits encompass a intermediate to high propensity to selfing ($\delta = 0.078$, $\epsilon = 0.100$, $p = 0.85$), intermediate temperature optima ($\delta = -2.8$,

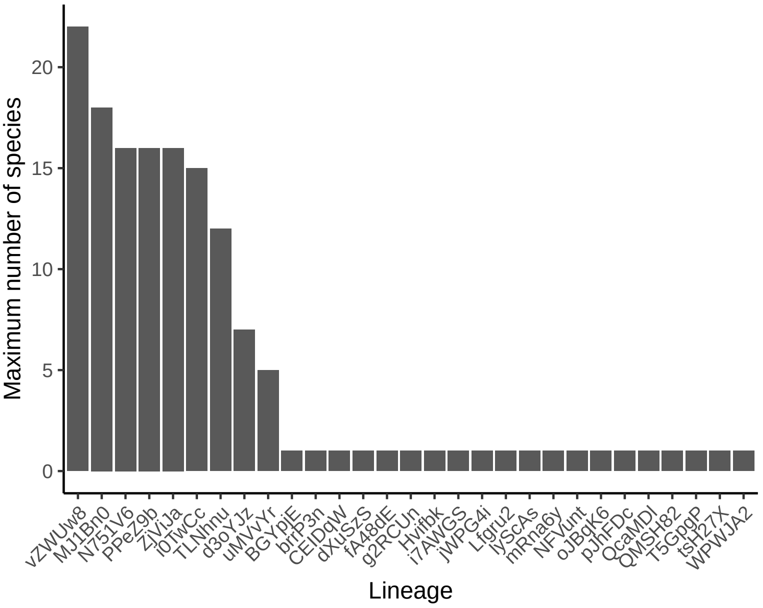

Figure 1: Lineage-rank plot showing the maximum evolved number of species for each successfully colonizing lineage.

$\epsilon = 1.3$, $p = 0.123$), and low to intermediate genetic linkage ($\delta = -30$, $\epsilon = 19$, $p = 0.38$; Fig. 3). All other traits do not differ markedly and have a similar spread in both diverged and monospecific lineages (see also Fig. 4).

The lineages that show high evolutionary activity, i.e. lineage divergence, also exhibit some common responses in their trait characteristics over time after colonization (Fig. 4). They show a tendency toward increased adult biomasses (difference of average evolved to average initial trait values, $\delta = 2.0$, standard error $\epsilon = 1.1$, $p = 0.233$; Fig. 4 a), decreased long-distance dispersal $\delta = -9.9$, $\epsilon = 0.9$, $p < 0.001$; Fig. 4 b), decreased precipitation tolerance ($\delta = -2.3$, $\epsilon = 0.4$, $p < 1\times10^{-4}$; Fig. 4 e), increased propensity to selfing ($\delta = 0.26$, $\epsilon = 0.1$, $p = 0.0012$; Fig. 4 f), a tendency toward increased seed biomass ($\delta = 2.5$, $\epsilon = 1.3$, $p = 0.23644$; Fig. 4 g), decreased reproductive barriers ($\delta = -0.40$, $\epsilon = 0.12$, $p = 0.0049$; Fig. 4 h), and a tendency toward decreased temperature tolerance ($\delta = -0.78$, $\epsilon = 0.35$, $p = 0.12$; Fig. 4 j). Mean dispersal distance, precipitation optimum, and temperature optimum (Fig. 4 c, d, i) do not differ noticeably in their means, but their spreads appear decreased. Monospecific, i.e. non-diverged species, evolved increased long-distance dispersal ($\delta = 6.9$, $\epsilon = 2.1$, $p = 0.0070$; Fig. 4 b). Other than that, they showed no noticeable change in trait characteristics between the start and end of their respective colonization histories (Fig. 4).

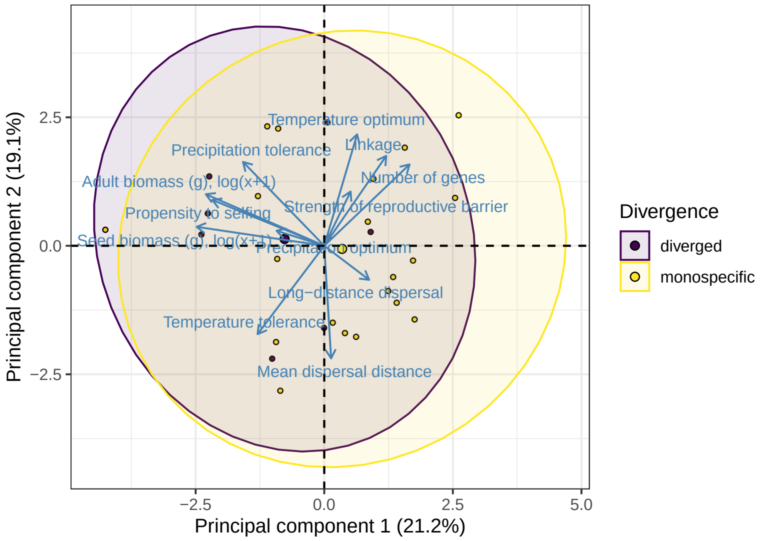

Figure 2: Principal component analysis of trait characteristics of colonizing lineages. Arrows represent traits (ecological and genomic). Lineages which subsequently undergo radiation are marked in purple, monospecific lineages in yellow. Ellipses show areas of 95 % confidence.

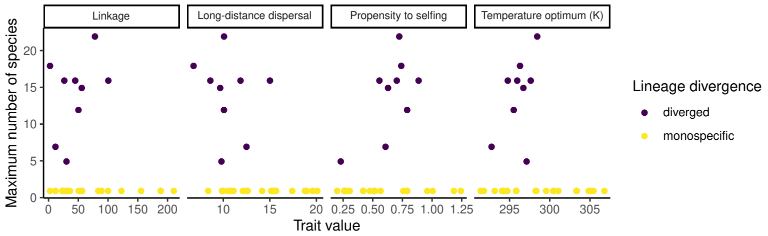

Figure 3: Traits affecting lineage divergence. The probability of a lineage to diverge is associated with low to intermediate genetic linkage, low to intermediate long-distance dispersal abilities, intermediate to high propensity to selfing, and intermediate temperature optima. Yellow: diverged lineages, purple: monospecific lineages. Trait values are dimensionless unless specified otherwise.

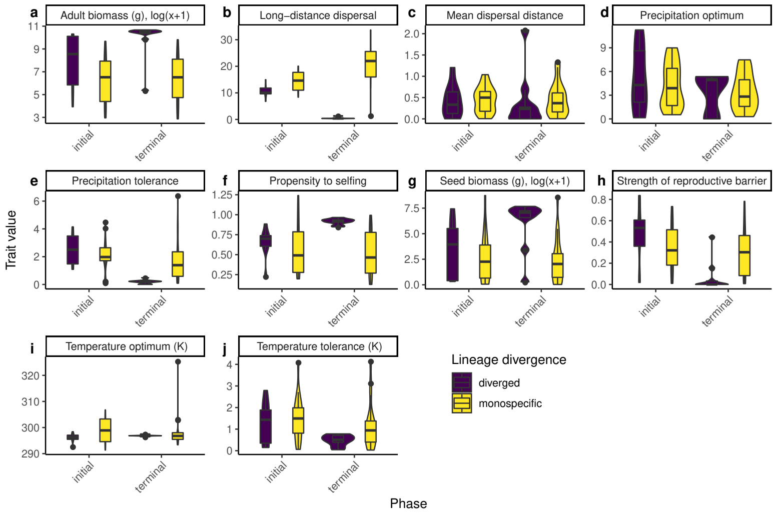

Figure 4: Traits distributions of diverged and monospecific lineages at the time of colonization (“initial”) and at the end of their evolution (“terminal”). Trait values are dimensionless unless specified otherwise.

4 Discussion

4.1 Trait syndromes of great speciators

In line with empiric evidence, only a fraction of lineages managed to diverge into distinct species (Price and Wagner, 2011; question 1). This is indicative of the many environmental and biotic filters which have to be surpassed to allow lineage divergence. Our results suggest that there is a complex set of single trait characteristics which increases the probability of lineages to pass all these filters (i.e. a "divergence syndrome"). One of the lineage characteristics we identify to increase the probability of a radiation is low long-distance dispersal. This is in line with findings describing the "zone of radiation" as a range of intermediate isolation of islands to the mainland or between islands, where the number of radiations peak (Rosindell and Phillimore, 2011). Since in our model the distance between island and mainland is constant for all lineages and replicates, effective isolation is a result of the lineages’ dispersal abilities. In fact, Cabral et al. (2019) show that isolation based on dispersal traits has similar effects on insular biodiversity as isolation based solely on distance. Accordingly, the zone of radiation in our simulations is where individuals just reach the island (as evidenced by the low long-distance dispersal abilities), but in a sufficiently low frequency as to impede gene flow. However, the fact that our results include examples of lineages with similar long-distance dispersal abilities which both radiate or remain monospecific already suggests that this “zone of radiation” is not enough to determine lineages’ radiation potential.

Indeed, the trend we identify in three additional traits could further explain divergence potential. The decreased distribution of temperature optima ensures sufficient pre-adaptation to the temperature conditions on the island and thus increase the chances of successful establishment. Additionally, an increased propensity to selfing allows reproduction of established populations even at critically low densities, a trait regularly found on real islands as well and hence termed “Baker’s law” (Baker, 1955; Baldwin, 1998). Lastly, in our simulations, divergence is associated with low to intermediate levels of genetic linkage. While low linkage levels will allow accelerated adaptation at the cost of a rapid loss of variation and would thus in fact represent an “evolutionary dead end” (Day, Hua, and Bromham, 2016), intermediate linkage ensures that genetic variation is maintained and could thus counteract disadvantages introduced by a high self-compatibility (cf. Carlquist, 1966). The divergence of this genetic variation seems to eventually result in increased species numbers of lineages with intermediate linkage.

Our modeling results hence suggest that the question whether a lineage will or will not diverge on an island depends on the probability to reach the island in the first place, the probability to establish and reproduce and the probability to adapt quickly without losing too much genetic variation. How important the associated traits are for lineage evolution on islands is indicated by the ensuing trait evolution in diverging lineages, which we will discuss in the following section.

4.2 Island syndromes in virtual plant radiations

One of the most striking evolutionary responses in the traits of diverging lineages is a loss of long-distance dispersal. This loss of dispersibility is regularly found in island plant endemics as well and reduces the loss of seeds to the ocean (Burns, 2019). The trait responses of diverging species in terms of reproductive strategies also highlights the crucial role of population-size reproductive effects, i.e. Allee effects, on island populations (Stephens, Sutherland, and Freckleton, 1999). Since species populations on islands are usually small, finding reproduction partners is unlikely. Therefore, a decrease in pre-zygotic barriers will maximize probabilities of finding mates, even if they are distantly related. This loss of "barriers to hybridization" can also be observed on real island plant taxa (Jorgensen and Olesen, 2001). Failing that, a high propensity to selfing will allow reproduction also for single mature individuals. In this case, the high reproductive tolerance will ensure gene flow to diverged populations to alleviate potential harmful effects, e.g. through inbreeding depression. However, in the evolved species, we can actually observe two contrary reproductive strategies. Either species will maintain reproductive compatibility with any individuals from their own lineage or they will only reproduce with the most similar individuals. We hardly observed an intermediate strategy. Thus, lineages evolve to be reproductively isolated specialists or frequent hybridizing species.

This later evolution of selfing propensities hints toward a differentiated selection on lineage cohesion. Lineages with low selfing and thus relatively obligate out-crossing maintain reproductive contact, whereas lineages with high selfing are more independent and can therefore more readily colonize empty habitats. This pioneering characteristic will increase the probability of population divergence following lineage splits. In fact, high self-compatibility is found in many island floras, e.g. Hawaii (Baldwin, 1998). However, breeding systems in island floras is diverse and can encompass, e.g. outcrossing, and (leaky) self-incompatibility (Crawford et al., 2009). In our model, there is apparently no selection pressure that favours evolution towards these more restrictive reproductive systems. It should be pointed out, though, that outcrossing is always the prefered reproductive mode in our model when made possible by the existence of reproductive partners, even if individuals have a high propensitiy for selfing. Thus, it could be argued that we do not model strict self-compatibility, but rather a reproductive mode closer to leaky self-incompatibility. Still, future studies could extend the model with additional processes and assumptions to identify the factors that facilitate the evolution of all these diverse reproductive systems.

4.3 Challenges and perspectives

The fact that we observed only 9 radiating lineages throughout our simulations makes assessing the relative importance of the various traits for enabling radiations difficult. Unfortunately, running more replicates, which would have also increased the number of successful colonizers, and thus, radiations, was not feasible in the time at hand due to limited computational resources. Additionally, we observed only lineage splits through divergence in our simulations, i.e. adaptive radiation, but no direct instances of anagenetic evolution, e.g. as gradual change of the original mainland species on the island that would lead to monospecific endemics. This is indicative of most species retaining their reproductive cohesion with the mainland populations throughout the simulation. A possible reason for this circumstance is our choice of number of replicates (i.e. number of colonizing lineages), which could have resulted in too few sufficiently pre-adapted, small-bodied lineages with short generation times that could have accumulated the necessary evolutionary changes to reach reproductive isolation even in the limited time span of our simulations. The choice for this temporal extent of our simulations, as well as the number of replicates, was due to computational feasibility. We therefore expect future studies to increase both the number and extent of simulations to obtain clearer patterns of the role of traits in island radiations. The number of successfully colonizing lineages could also be increased in our model by restricting the potential trait space of mainland lineages to values that are more suitable for establishment on the island. Nevertheless, even with our limited number of colonizers and simulations, we can identify distinct trends which are in accordance with available empirical evidence.

Another potential factor in lineage divergence are the details of genetic architecture: whether, how, and which traits are linked together in the genome can play an important role in incipient speciation (Hawthorne and Via, 2001). For instance, traits like host choice, habitat preference and sexual selection are often linked, which accelerates divergence of populations (Hermann et al., 2013; Via and West, 2008). A similar circumstance might be occurring in our simulations as well. In principle, the detailed genomic data would even provide us with the information which traits are linked on which linkage units in which lineages. However, due to computational constraints and feasibility of analyses, we chose not to retain this information. Therefore, we identify the investigation of which trait linkages are associated with increased population divergence in island lineages as promising avenues for future studies.

Our virtual island has both a certain geographic extent and an environmentally heterogeneous landscape that provides different ecological opportunity. Hence, dependent on species properties, lineage splits (non-adaptive radiations) could have been possible as well in our experiments besides the divergences we investigated (Lieberman, 2012). In empirical systems, testing which mode majorly contributes to a radiation is difficult. This issue of contrasting the causes for a radiation could be addressed by our model, which allows explicit definition of abiotic conditions during potential radiations. For example, with scenarios that contrast high environmental heterogeneity and low geographic isolation with low environmental heterogeneity and high geographic isolation, we could identify in resulting radiations the phylogenetic and functional signatures of the different radiation modes. These signatures could then be translated to empirical data to find clear evidence for particular radiation modes. Thus, follow-up theoretical simulation experiments with our approach can help define patterns in empirical data to advance our general understanding of biodiversity.

Lastly, theory and empirical patterns suggest that island evolutionary history is influenced by geomorphological dynamics and archipelago structure (Borregaard, Matthews, and Whittaker, 2016; Cabral et al., 2019; Whittaker et al., 2007). In fact, islands may even provide the origin of other island species and even mainland species (Nicholson et al., 2005). At the same time, the frequent disturbances during island ontogenies might increase divergence and coexistence (Shea, Roxburgh, and Rauschert, 2004; Whittaker et al., 2007). Including these processes and factors into our model would likely lead to more complex and diverse radiation patterns. To avoid confounding effects, however, we did not investigate these factors in the present study. Nonetheless, the generality of our model would easily allow investigation of appropriate scenarios. We therefore expect future studies to take into account functional-genomic factors for the investigation of real radiations across islands with dynamic geomorphological history within an archipelago.

4.4 Conclusion

Species radiations on islands are fascinating phenomena. With the findings of this study, we could shed light on some of the potential functional-genomic species characteristics which influence these radiations. These include reduced long-distance dispersal, flexible reproductive systems and intermediate genetic linkage. While the patterns of functional traits support concepts such as the “radiation zone” and increased divergence potential of specialist genera, the patterns of genomic traits have to our knowledge not yet been observed or considered in island biogeography studies in a comparable extent. Our theoretical results agree with empirical findings on island syndromes in plants, which supports the generality and validity of our model while providing a mechanistic explanation of these syndromes. Although we mainly focused on the impact of traits on the evolutionary history of species, it is likely that the same traits which enable rapid radiations will also enable taxa to cope with changing conditions. In light of current environmental trajectories, studying functional-genomic species characteristics enables us therefore not only to understand how a species came to be, but also where it is likely to go in evolutionary terms.

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6

THE INTERPLAY OF TRAITS AND ABIOTIC FACTORS ACROSS THE FOUR STAGES OF INVASION

Species traits are likely to play a role in island invasions as well. The following manuscript therefore describes the investigation of the relative roles of abiotic factors and species traits on invasion success. This study also showcases the applicability of the model to conservation-related issues.

We found that the intensity of species introductions was one of the major factors which determined invasion success. Successful invaders were characterized by a relative functional similarity to native species, but they were in comparison larger, more dispersive, and had enhanced environmental tolerances. This suggests that the invasion syndrome is comprised of increased competitive and dispersal abilities, and relative environmental generalism.

At the time of writing, the manuscript has been submitted to *Journal of Applied Ecology*. The article was drafted and written by Daniel Vedder. I described and performed the trait analysis part, wrote parts of results and discussion section and produced the figures showing the ordination of species traits and the differences in traits between species groups. Both Juliano Sarmento Cabral and myself contributed to all sections of the manuscript. Daniel Vedder performed research procedures and I provided materials in the form of the model used to address the study question. The conceptual design was done by Daniel Vedder, Juliano Sarmento Cabral and myself. Both Daniel Vedder and myself performed the analysis. The first authorship of the article is shared by Daniel Vedder and myself. My overall contribution amounted to ca. 40 %.

Effects of species traits and abiotic factors during the stages of plant invasions

Daniel Vedder, Ludwig Leidinger, and Juliano Sarmento Cabral

Ecosystem Modeling Group, Center for Computational and Theoretical Biology,
University of Würzburg

DV and LL should be considered joint first author.

Correspondence:

Ludwig Leidinger, email: ludwig.leidinger@uni-wuerzburg.de

Daniel Vedder, email: daniel.vedder@stud-mail.uni-wuerzburg.de

Abstract

1. The success of species invasions depends on multiple factors acting over the four invasion stages transport, colonisation, establishment, and landscape spread. Each of these stages is influenced simultaneously by particular species traits and abiotic factors. While the importance of many of these determinants has already been investigated in relative isolation, they are rarely studied in combination and even then mostly ignore the final phase, i.e., landscape spread.
2. Here we address this shortcoming by exploring the effect of both species traits and abiotic factors on the success of invasions using an individual-based mechanistic model, and relate those factors to the stages of invasion. This approach enables us to explicitly control abiotic factors (temperature as surrogate for productivity, disturbance

and propagule pressure) as well as to monitor whole-community trait distributions of environmental adaptation, mass and dispersal abilities. We simulated introductions of plant individuals to an oceanic island to assess which abiotic factors and species traits contribute to invasion success.

3. We found that the most influential factors were higher propagule pressure and a particular set of traits. This invasion trait syndrome was characterized by a relative similarity in functional traits of invasive species to natives, while invasives had on average higher environmental tolerances, higher body mass and increased dispersal abilities, i.e., were more generalist and dispersive.
4. Our results highlight the importance in management practice of reducing the import of alien species, especially from similar habitats.

Introduction

Species invasions are highly complex phenomena, influenced by several interacting factors, such as species traits, disturbance, or evolutionary history (Theoharides & Dukes, 2007). Gaining an understanding of these factors is necessary to understand the whole invasion process (Fleming & Dibble, 2015) and establish effective countermeasures (Mehta, Haight, Homans, Polasky, & Venette, 2007). Yet, the relative importance of various factors are difficult to derive from studies focussing only on single invasion events (Catford, Jansson, & Nilsson, 2009). Considering the impending global change scenarios and increased rate of biotic exchange, however, generalizable findings about biological invasions are still urgently needed (van Kleunen et al., 2015).

In the last decades, a number of single factors could be identified that contribute to the success of species invasions. A prominent role falls to the number of introduced individuals, i.e., propagule pressure, as it ensures minimal viable population sizes (Lockwood, Cassey, & Blackburn, 2005). Other abiotic factors such as enhanced productivity and increased disturbance have also been suggested to facilitate invasions in some circumstances (Huston, 2004). Beyond these abiotic factors, species traits may also determine invasibility. Arguably the most obvious of these traits is sufficient pre-adaptation to the abiotic environmental conditions of the invaded habitats (Carboni et al., 2016). Furthermore, invasive species need to be able to compete with native species to establish (Hui et al., 2016). Lastly, increased dispersal abilities and broad environmental niche preferences, i.e. generalism, will enable alien species to spread (Rejmánek, 2000). All these invasion factors and stages vary in their level of expression, depending on the system and taxa.

Theoharides and Dukes (2007) put forward a helpful framework integrating many of these factors and stages. They divide the entire invasion process into four stages: transport, colonisation, establishment, and landscape spread. These stages represent a set of community assembly filters that must be overcome before an alien species may be considered “invasive”. The stages do not represent a strict chronology, but rather a set of interlocking and interdependent factors and processes. Hence, for a species to become invasive, it must (a) arrive in sufficient numbers, (b) be adapted enough to the environment to survive, (c) overcome the competition of native species and reproduce, and (d) disperse to establish new neighbouring populations (Theoharides & Dukes, 2007). The main filters involved in these stages are Allee effects, environmental filtering, biotic resistance, and dispersal ability, respectively. Each of these may be influenced by species traits as well as environmental conditions, as illustrated in fig. 1. Concurrent with this framework, it has been demonstrated that the combination of both abiotic factors and species traits has considerable effects on the success of invasions (e.g. Küster, Durka, Kühn, & Klotz, 2010; Mata, Haddad, & Holyoak, 2013; Thuiller, Richardson, Rouget, Proches, & Wilson, 2006). However, many studies in the invasion literature still treat species traits and environmental conditions separately, and frequently only consider one factor at a time. To address this shortcoming, Catford et al. (2009) proposed an experimental design that varies propagule pressure, species composition, and abiotic conditions in a full-factorial setup to assess their relative importance for invasion success. An experimental approach like this will be necessary to arrive at a generalised understanding of the invasion process. However, previous experimental studies focused mainly on the earlier stages of invasion and thus, generalized insights that include landscape spread are still missing (cf. Alzate, Onstein, Etienne, & Bonte, 2020; Kempel, Chrobock, Fischer, Rohr, & van Kleunen, 2013).

For generalizing invasion processes, islands can be useful model systems. Firstly, islands are highly susceptible to invasion-related degradation. For example, invasive predators have caused multiple species extinctions on islands (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016), and there have been observed cases of complete “invasional meltdown” after native keystone species were displaced (O’Dowd, Green, & Lake, 2003). Secondly, their small size, isolation, and comparatively simple ecological dynamics mean that islands are popular study systems in ecology in general (Patiño et al., 2017). These characteristics therefore lend themselves to comprehensively study biological invasions in the context of the stages of invasion (Theoharides & Dukes, 2007). Unfortunately, even for islands, exhaustive data to investigate invasion factors are difficult to obtain and conducting systematic experiments is often unfeasible.

As an alternative, mechanistic models offer a powerful approach to supplement field studies. Such models have previously been used in invasion biology, although usually in the context of specific invaded sites (e.g. Buckley, Briese, &

Rees, 2003). However, they also hold great promise for exploring fundamental processes within a more generalised setting (Cabral, Valente, & Hartig, 2017; Grimm & Railsback, 2005; Leidinger & Cabral, 2017), and are very useful for gaining a mechanistic understanding of complex ecological patterns (Grimm & Railsback, 2011). The fact that mechanistic models allow both complete control over all environmental variables, as well as complete knowledge of every individual's traits makes them an ideal tool to help us better understand the intricacies of the invasion process.

Here, we therefore used a recently developed trait-explicit, individual-based mechanistic model of island plant communities (Leidinger & Cabral, 2020) to investigate the relative roles of propagule pressure, productivity, and disturbance, as well as the traits of invasive species relative to natives. Guided by the framework of Theoharides and Dukes (2007), we wanted to know which factors and trait syndromes increase the success of alien species during the stages of invasions on islands (cf. Pyšek et al., 2015). The specific questions we asked are found in table 1, covering all stages of invasion and including both trait-based and environmental factors. Our experimental setup enabled us to go both broad (covering a wide range of ecological factors) and deep (analysing the resulting species communities down to the trait level) in our investigation of the invasion process. We find that propagule pressure and trait syndromes relative to the native community are the most influential factors promoting invasion success, and discuss how these factors relate to the stages of invasion.

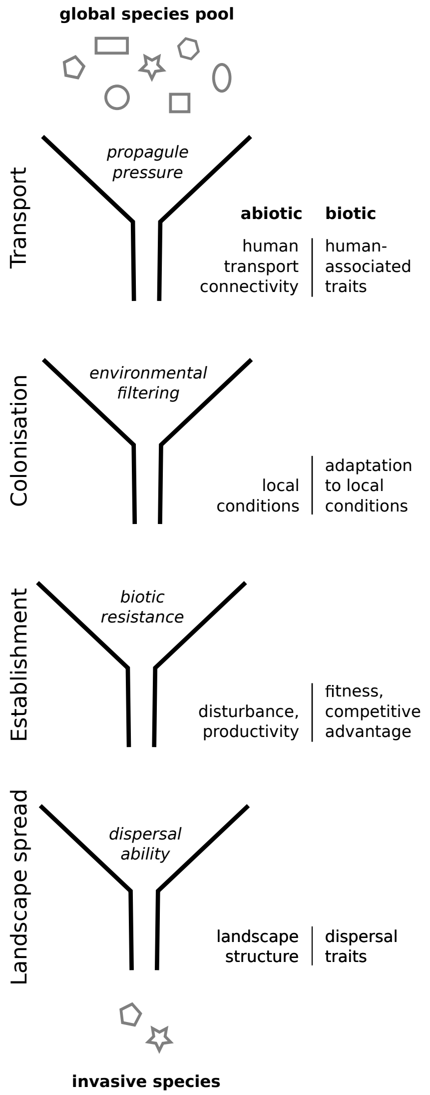

Figure 1: The four stages of invasion (from top to bottom) with their associated filters and abiotic (left label) and trait (right label) factor groups (Theoharides & Dukes, 2007). Apart from the transport factor groups, all factor groups were explicitly modelled (transport factors were combined in a single "introduction" process.)

Table 1: Questions regarding species invasions to be explored with the model.

No.	Stage	Question	Expectation
1	*Transport*	How important is propagule pressure for invasibility and why?	Very, because it helps to establish a minimum viable population (Lockwood et al., 2005)
2	*Colonisation*	Do invasives share a common trait space with native species?	Yes, as they need to be sufficiently adapted to the environment (Carboni et al., 2016)
3	*Establishment*	How do productivity and disturbance affect invasibility?	Maximum invasibility should be reached at high productivity and high disturbance levels (Huston, 2004)
4	*Establishment*	Do invasives have a higher fitness than natives?	Yes, as they have to outcompete the natives to establish successfully (Hui et al., 2016)
5	*Landscape spread*	Are invasives more generalistic and dispersive than natives?	Yes, as this enables them to spread after introduction (Rejmánek, 2000)

Methods

The model

We extended the model of Leidinger and Cabral (2020) to simulate species invasions to plant communities on a virtual oceanic island (fig. 2). The island consisted of a 5×5 grid depicting a radial elevation (and corresponding temperature) gradient. Additionally, there was a linear (lee-luv) precipitation gradient, which is typical for many oceanic islands. We chose to call this second gradient "precipitation" for simplicity, although it could also be interpreted as any other environmental characteristic like soil type. Each grid cell was assumed to be one hectare in size, with a biomass carrying capacity of two tonnes. Each cell could hold its own community, comprised of individuals belonging to one or more species. Individual body sizes could range between 150 g and 1.2 tonnnes, which puts our system along a range between grassland and shrubland (cf.

Deshmukh, 1984). Island geometry and extent were chosen arbitrarily to ensure computational feasibility and to provide different environmental combinations, to increase coexistence of native species (see Armstrong & McGehee, 1980).

In the model, each individual had a genome consisting of multiple genes that code for a set of traits, which in combination determine the individual's phenotype. These traits were functional for one or more processes (i.e. traits as parameters of biological functions, table 2). They encompassed environmental optima and tolerances to temperature and precipitation conditions, seed size, reproductive (adult) size, and mean and shape parameters of a logistic dispersal kernel (Bullock et al., 2017). Reproduction only takes place with adult members of the same species within the same grid cell and includes genetic recombination.

The probabilities for growth, density-independent mortality, and seed numbers were determined using the Metabolic Theory of Ecology (MTE, Brown, Gillooly, Allen, Savage, & West, 2004), which links yearly biological rates to body mass and to the local temperature. An individual's adaptation to the local grid cell temperature additionally scaled the metabolic density-independent mortality probability, whereas adaptation to local precipitation was used to compete individuals when determining density-dependent mortality.

At the initialisation, two species pools were formed with randomly generated species (i.e. each species was characterized by a random combination of genomic and ecological traits). One species pool was used to initialise the island community, and was allowed to stabilise during a "burn-in period" of 500 years. This period length was enough to ensure quasi-equilibrium. Depending on the scenario, native species numbers per island and replicate ranged between one and 15, with a mean of six (Supporting Information, fig. 2). As additions to the original model, the second (alien) species pool had a fixed number of 100 species and was used as a source of alien seeds. After the burn-in period, a

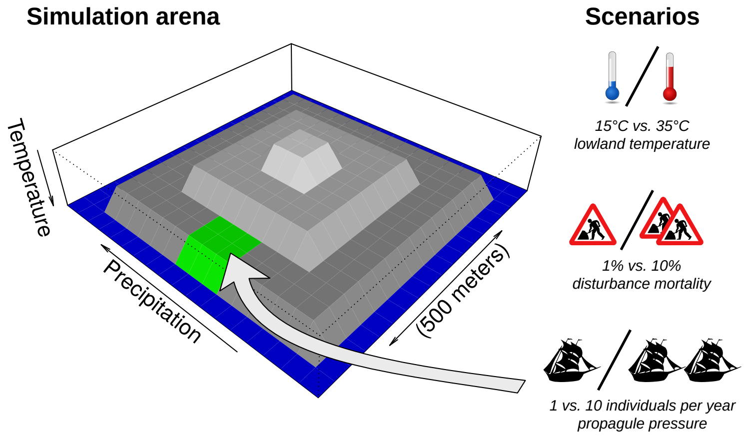

Figure 2: Schematic representation of the simulated island. Temperature decreased with altitude, giving a radial gradient with a step size of 2°C per unit of height (greyscale). A second gradient of an abstract environmental resource (termed “precipitation” for simplicity) was applied longitudinally. The green grid cell denotes the point of entry for alien species. Pictograms show the three factors that were varied in the experimental setup, namely temperature, disturbance, and propagule pressure.

fixed number of individuals, regardless of species identity, was drawn from this alien pool and introduced to a specified grid cell on the island (“point of entry”, fig. 2). To further mimic human activities, disturbances also started after the burn-in period, consisting of a given percentage of individuals being randomly removed from each grid cell every year, in addition to the previously mentioned causes of mortality. The model was allowed to run for a total of 1500 years.

For the choice of parameter values, etc., the reader is refered to the full model description in the ODD format (Grimm et al., 2010), found in the Supporting Information. The source code for the model was written in Julia (Bezanson, Edelman, Karpinski, & Shah, 2017), and is available at `https://github.com/lleiding/gemm`, along with its documentation.

Table 2: Ecological and life-history processes included in the invasion model, in the order of execution.

Process	**Details**
Survival	Density-independent mortality relative to an individual's temperature adaptation.
Growth	Individuals increase in body size until they reach reproductive size.
Competition	If the total biomass in a grid cell exceeds its carrying capacity, compete pairs of individuals and kill the one with the lower precipitation adaptation (density-dependent mortality).
Reproduction	Sexual reproduction including recombination of the parents' genomes by meiosis, produces multiple seeds.
Disturbance	Species- and density-independent mortality of a given percentage of individuals in each grid cell.
Transport	Introduction of aliens (i.e. individuals from the alien species pool) into the point of entry.
Dispersal	Dispersal of seeds produced during reproduction, the distance is calculated with a dispersal kernel.

Experimental design

We varied the three factors propagule pressure, productivity, and disturbance in a full-factorial design across two levels of each factor to give a total of eight scenarios (cf. Catford et al., 2009; fig. 2). 60 replicates of each scenario were run, resulting in 480 simulations.

We used temperature as a proxy for productivity, varying the base (lowland) temperature between 15°C and 35°C. These values were arbitrary but provided a sufficiently large contrast while maintaining realism. Due to our use of the MTE, higher surrounding temperatures lead to an increase in growth and reproduction rates and thus satisfy the general requirements for productivity (Huston, 2004). Propagule pressure (1 or 10 individuals per year) and disturbance (1% or 10% mortality per year) were explicitly implemented in the model, as described above (cf. Buckley, Bolker, & Rees, 2007; Kempel et al., 2013, for factor values).

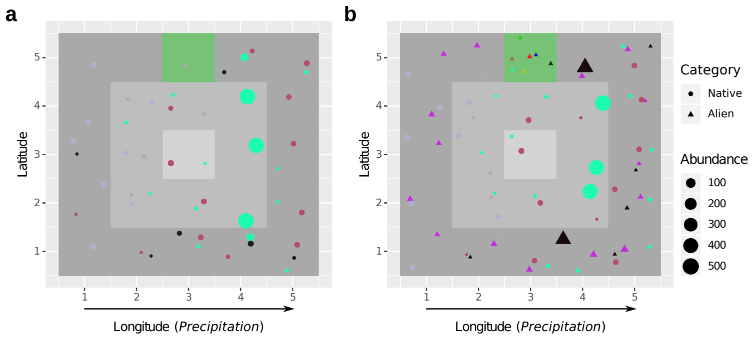

Figure 3: **a)** Island map after the burn-in period ($t = 500a$), and **b)** at the end of the simulation ($t = 1500a$) for one example run. Each marker represents one population, colours signify species. Natives are circles, aliens triangles. The green grid cell is the point of entry, grey scale denotes temperature (cf. fig. 2).

Data recording and analysis

Every year, the model recorded a log file with the mean and variance of each population's trait values. All data analyses were carried out in R 3.2.3 using `ggplot2` for visualisation (R Core Team, 2017; Wickham, 2016).

To quantify the effect of the varying factors on the success of species invasions (study questions 1 and 3, table 1), we classified species as native, alien, or invasive (species type). Natives were species from the original island species pool that were still extant at the end of the burn-in period. Aliens were all species introduced to the island from the alien species pool. Invasives were the subset of alien species that had established at least one population outside of the point of entry, i.e., had undergone landscape spread (Ricciardi & Cohen, 2007). We then identified all species that became invasive across all replicate runs and summed these up by scenario. During each run, we generated island maps at regular intervals, showing size, location, and species of all populations (e.g. fig. 3).

To compare the environmental adaptation A_{ind} of natives, aliens, and invasives, (study question 4, table 1) we combined the model's internal calculation of adaptation to temperature and precipitation as follows:

$$A_{ind} = \mathrm{G}(T_{opt}, T_{tol}, T_{env}) \times \mathrm{G}(P_{opt}, P_{tol}, P_{env}) \tag{1}$$

where $\mathrm{G}(b, c, x)$ is the Gauss function at point x with mean b and a standard deviation of c; T is the temperature and P the precipitation; N_{opt} the individual's niche optimum value, N_{tol} its niche tolerance, and N_{env} the actual environmental niche value in the individual's grid cell.

For trait comparisons between alien, invasive and native species (study questions 2 and 5, table 1), we pooled population data per species type ('alien', 'invasive' or 'native') from all scenarios. From this pooled data, we used native populations at the onset of invasion (year 500), and invasive and alien populations over the entire invasion period. The traits we were interested in comprised mean dispersal distance, long distance dispersal, precipitation tolerance, temperature tolerance, adult biomass in grams, and seed biomass in grams. Since precipitation and temperature optima traits were primarily influenced by geography and the particular temperature scenarios, we omitted them from our analysis of the pooled data. Furthermore, we log $(x + 1)$-transformed all trait and adaptation values to improve normality, because the original distributions were left-skewed and contained values < 1. We then performed a principal component analysis (PCA) on standardized trait medians of that data to investigate general patterns of trait space by comparing the size and location of 95% confidence interval ellipses corresponding to the different species types. For the PCA, we omitted alien populations, since their increased spread in trait values made comparison of natives versus alien species unfeasible. To assess how the trait characteristics in single traits of native species differed from invasives and identify the most important traits that distinguish native species from invasives, we performed linear mixed models with the particular trait as response, species type as fixed effect, and the specific replicate as random effect, using the R package `lme4` (Bates, Mächler, Bolker, & Walker, 2015). We do not report statistical significance of results, since this is mostly meaningless for mechanistic simulation models, as spurious significance emerges by simply increasing replicate number (White, Rassweiler, Samhouri, Stier, & White, 2014).

Results

A total of 28 species became invasive over all runs, one of them across two different scenarios. We found a strong link between propagule pressure and invasibility, with almost four times as many invasives occurring in high-pressure compared to low-pressure scenarios (fig. 4). Temperature also had a strong influence, with a two- to three-fold difference between levels. There was no clear relationship between invasibility and disturbance.

In terms of the total trait space, invasive populations exhibit a larger spread than natives (fig. 5). The center of the invasive populations' trait space is shifted along the second PCA dimension towards higher long distance dispersal, higher mean dispersal distance, and higher precipitation tolerance compared to native populations.

The difference in total trait space is associated with specific differences of the particular traits between species category. Specifically, mean dispersal distance (fig. 6a), long distance dispersal (fig. 6b), precipitation tolerance (fig. 6c), temperature tolerance (fig. 6d), and adult biomass (fig. 6e) were all increased in aliens and invasives compared to natives. Seed biomasses were increased in aliens, but slightly decreased for invasives (fig. 6f). For long distance dispersal,

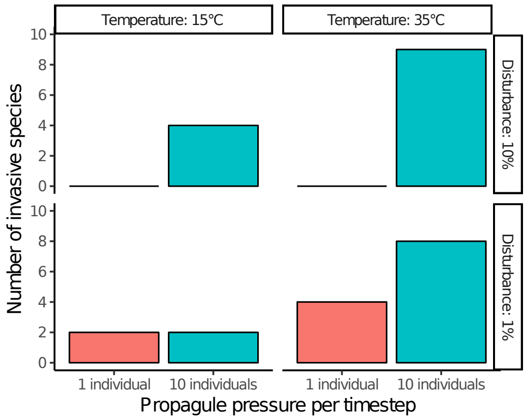

Figure 4: Cumulative number of invasive species observed in each of the eight scenarios (60 replicate runs per scenario).

precipitation tolerance, temperature tolerance, and adult biomass, the differences in means between natives and invasives were smaller than between natives and aliens. The differences in precipitation and temperature tolerance resulted in the lowest adaptation values for aliens and highest adaptation values for natives, while invasives shows intermediate adaptation value (fig. 6g).

The results from the linear mixed models revealed what traits were most important to distinguish invasive species from native (table 3). The difference in biomass explained by far the most variance, followed by precipitation tolerance, temperature tolerance, long distance dispersal and seed biomass. Mean dispersal distance explained only a small amount of variance.

Discussion

Although not explicitly imposed by the model, we observe the filtering functions of the stages transport, colonisation, establishment, and landscape spread (fig.

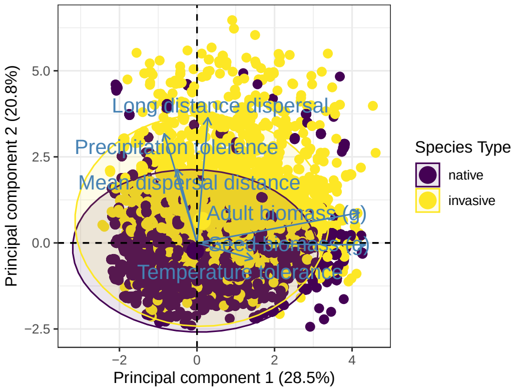

Figure 5: Principle component analysis (PCA) showing the distribution of population trait medians in the trait space. Each axis arrow represents one trait, each marker is one population. All traits were $\log(x+1)$ transformed and normalized before PCA calculation. Natives in purple, invasives in yellow. Ellipses represent 95 % confidence envelopes.

Table 3: Results of linear mixed-effects model fits comparing the means of species' traits with the type of species (native or invasive, with invasive as reference) as fixed effect and replicate as random effect. Note that invasive species were more dispersive and generalist with heavier adults, but lighter seeds than native species. Std. Error: standard error, D.f.: degrees of freedom, Mean Sq: mean squares.

Trait	Estimate	Std. Error	D.f.	*t* value	Mean Sq
Mean dispersal distance	-0.044	0.003	32467	-16.915	8.668
Long distance dispersal	-0.148	0.004	32438	-41.012	96.768
Precipitation tolerance	-0.360	0.005	32502	-68.964	572.091
Temperature tolerance	-0.214	0.005	32521	-40.307	203.051
Adult biomass (g)	-1.040	0.025	32519	-41.395	4790.100
Seed biomass (g)	0.144	0.028	32521	5.130	92.142

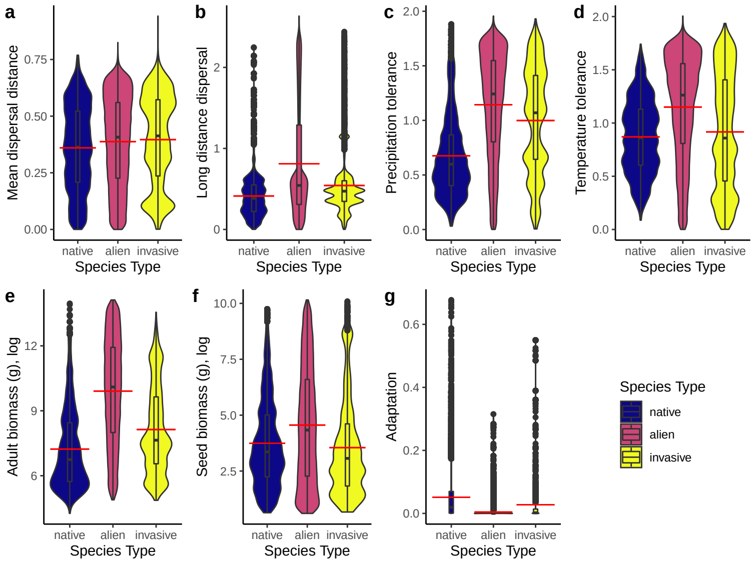

Figure 6: Distributions of single trait values. (a) Mean dispersal distance, (b) long distance dispersal, (c) precipitation tolerance, (d) temperature tolerance, (e) adult biomass in grams, (f) seed biomass grams, (g) adaptation to local temperature and precipitation conditions. All values were $\log(x+1)$ transformed before visualisation. Boxes show medians and interquartile range. Red lines highlight the means. Blue: populations of native species, red: populations of alien species, yellow: populations of invasive species.

1). Therefore, the general patterns of our model results conform to current knowledge from the empirical and theoretical literature (Theoharides & Dukes, 2007). In line with the requirements of the pattern-oriented modelling paradigm (Grimm & Railsback, 2011), these emergent patterns are found at different ecological levels (individual, population, community, and metacommunity).

Propagule pressure

Concerning the question on the importance of propagule pressure for the success of invasions (question 1, table 1), our findings mirror ample evidence from empirical studies, including macroecological analyses (e.g. Carr, Hooper, & Dukes, 2019; Seebens et al., 2018). Indeed, propagule pressure is well-known as the leading driver of invasion success in the current literature (Cassey, Delean, Lockwood, Sadowski, & Blackburn, 2018; Lockwood et al., 2005). This is mainly due to Allee effects in introduced populations (Keitt, Lewis, & Holt, 2001; Taylor & Hastings, 2005). Only sufficiently large populations will grow fast enough to overcome adverse abiotic conditions and inter-specific competition by native species. As described in Allee effects theory, this relation of population growth to density is typically hump-shaped, and will decrease again beyond a critical density (Courchamp, Clutton-Brock, & Grenfell, 1999; Stephens, Sutherland, & Freckleton, 1999). Thus, increasing propagule pressure will not increase invasion success indefinitely.

Indeed, Cassey et al. (2018) found a sigmoidal relationship between propagule pressure and establishment success. This was also reflected in additional post-hoc experiments with our model. With propagule pressure increased to 100 individuals per year, we did not observe an increase in the number of successful invasions (Supporting Information, fig. 1). Unfortunately, a direct comparison of our values with those of Cassey et al. (2018) is difficult. This is because

Cassey et al. (2018) do not relate their measure of propagule pressure to time, but assume a single initial release, which runs counter to the design of our study. Rather, the repeated introductions in our model increase our *de facto* propagule pressure beyond the one or ten individuals introduced in one year; but the stochastic nature of introductions makes it impossible to quantify exact values per species. Nevertheless, the results of our subsequent simulations indicate that we did reach propagule saturation as well. The reason for this is likely increased intra- and interspecific competition among juvenile alien individuals in already saturated communities. This saturation is an effect of our initial simulation conditions, where we initialize communities with more species populations than they will eventually hold. Given that real islands are known to have lower species richness than continents (Whittaker & Fernández-Palacios, 2007) and are thus likely un-saturated in terms of species numbers, they will therefore be much more susceptible to increased introductions than saturated continental systems. This highlights again the vulnerability of island biota to global change processes.

Temperature and disturbance

The interaction between temperature (our surrogate for productivity) and disturbance was not as straight-forward as we had expected (question 3, table 1). The dynamic equilibrium model (Huston, 2004) predicts that invasibility approximately increases with native diversity, which is high when both productivity and disturbance are high, or when both are low. This is because high productivity with low disturbance leads to population extinction through competitive exclusion, while low productivity with high disturbance means small populations that go extinct stochastically (Huston, 2004). Indeed, as described by Huston (2004), we did observe a clear peak of mean native species richness in the low-temperature, low-disturbance scenarios (Supporting Information, fig. 2). Despite this, maximum invasibility did not coincide with either low-temperature/low-disturbance or high-temperature/high-disturbance scenarios, but was driven almost entirely by temperature (fig. 4). This apparent mismatch of our model with theory may raise some questions at first, but can be explained by a closer look at disturbance and its influence on invasion processes.

The interplay between productivity and disturbance and its effect on species richness and composition has long been discussed in the theoretical literature (e.g. Catford et al., 2012; Chesson, 2000) and shown in multiple empirical studies (e.g. Huebner, Regula, & McGill, 2018; O'Connor, Falk, Lynch, Swetnam, & Wilcox, 2017). However, these interactions are subject to several preconditions. Firstly, Buckley et al. (2007) point out that disturbance may increase the invasibility of a habitat, but can also be a cause of mortality for alien species, reducing invasibility again. Thus, if disturbance affects natives and aliens equally, these two contrary effects may cancel each other out, leaving no net change. This was the case in our model, as disturbance-driven mortality was species-agnostic. Secondly, the effects of disturbance on native and alien communities are likely to change over the full gradient of disturbance intensity (Catford et al., 2012). Analysing that many disturbance levels was beyond the scope of this study, however. Therefore, our experiment only reflects two points on this gradient and may thus give an incomplete picture. And thirdly, an invaded community's response to disturbance can be strongly modulated by the trait composition of its native and alien species (Kempel et al., 2013; Mata et al., 2013). This includes traits that are represented in our model, which will be discussed in the next section.

Traits of invasive species

Although sometimes questioned in studies on species invasions (cf. Catford et al., 2009, but see Thuiller et al., 2006), our results provide some insights into an "invasion syndrome" relative to the native community and the stages of invasion (question 2, table 1; Novoa et al., 2020). In fact, invasive species are more similar to native species than alien species in terms of their trait characteristics (cf. Küster et al., 2010). This suggests that invasive species have to pass similar environmental filters to natives in order to complete the colonization and establishment stages.

However, this trait similarity is not sufficient to surpass native species in terms of environmental adaptation (question 4, table 1). Instead, invasive species have on average lower environmental adaptation. The fact that some invasive species are still successful, and even end up replacing native species, again highlights the importance of propagule pressure. This might offset some of the maladaptation and the priority effect advantage enjoyed by native species (Chase, 2003). Such interaction of traits and propagule pressure is in line with recent evidence from field and laboratory experiments (Alzate et al., 2020; Kempel et al., 2013). Still, propagule pressure alone does not explain why invasives also manage the fourth phase, landscape spread.

In order for invasives to spread, we expected increased dispersal abilities and a rather generalistic niche strategy (question 5, table 1). Indeed, invasive species in our simulations not only feature increased mean and long distance dispersal, but also have higher environmental tolerances on average (see Grotkopp & Rejmánek, 2007; Schultz & Dibble, 2012). These latter trait characteristics suggest the generalist nature of invasive species, at least in comparison to natives. A larger biomass and thus reduced mortality in invasives additionally makes them stronger competitors (cf. Kempel et al., 2013). This circumstance will also help offsetting relative maladaptation, besides propagule pressure.

Furthermore, the difference in trait characteristics between species categories might also indicate different evolutionary backgrounds. In this respect, our island communities are the result of several hundreds of years of ecological interactions between species and the environment. This is especially evidenced by their decreased dispersal ability, which is a typical island adaptation (Burns, 2019). They are, therefore, sensitive toward invasive species that (1) were not restricted by those interactions, and (2) exhibit trait syndromes different from those represented in the community. Additionally, invasive species are bigger than natives, but not as big as (unsuccessful) alien species. Thus, the invasion syndrome features adaptation to similar conditions as the invaded native community, but sufficiently different other key traits (e.g. biomass), unbounded by the local evolutionary history, to fill areas of the trait space with the least overlap with native species. If this overlap is enough to induce competitive exclusion, superior competitive abilities allow invasive species to outperform, and thus replace, native species, which we could observe in some of our simulations (cf. Flory & Clay, 2010; Pyšek et al., 2012).

Future considerations

In our simulations, we could not account for most biological interactions except for competition. Mutualisms between native species will likely lead to secondary extinctions, or even extinction cascades, if keystone species get lost (Christian, 2001; Schachtschneider & February, 2013). Trophic interactions can also allow effects like enemy-release of alien species. Therefore, the effects of invasions on our simulated communities might be very conservative and underestimated. We anticipate that the consideration of additional interactions into our modeling framework will further increase the impact of species invasions on the native communities.

In this study, we corroborated the importance of propagule pressure for the invasion success. It is important to point out, however, that previous studies frequently conflated this with the related but separate concept of colonization pressure, i.e., the number of species (rather than individuals) introduced per time (Lockwood, Cassey, & Blackburn, 2009). Although the two may interact and are difficult to differentiate in the field, they do in fact address two quite dissimilar mechanisms: propagule pressure determines how quickly a minimum viable population can be established, whereas colonization pressure increases the chances of introducing a suitable species. Our experiment does not completely disentangle these two aspects, but by using an alien species pool of constant size, we still arguably test the more specific understanding of “propagule pressure”. However, future investigations could use a model such as ours to fully separate the effects of both these factors in designated experiments.

Increasing the runtime of the model may lead to additional insights. A number of studies have pointed to the impact of longer time scales on the invasion process. For example, Pyšek et al. (2015) and Carr et al. (2019) show a link between residence time or sustained propagule pressure and establishment rates. On the other hand, Sheppard and Schurr (2019) observed an increase in biotic resistance over time, which decreases the performance of alien species. Investigating such long-term and large-scale effects of invasion factors further is possible with our model, although this will require significant computational resources.

Although beyond of the scope of this study, the current model allows us to consider genomic traits in the characterisation of species. In a previous study, Leidinger and Cabral (2020) show how environmental variation interacted with the number of genes and genomic variation of communities. Similarly, invasive species might display particular genomic profiles which enable them to quickly adapt to novel environments, for example by high standing variation or phenotypic plasticity (Zenni, Lamy, Lamarque, & Porté, 2014). To increase computational feasibility and preclude possible confounding effects, we chose not to include these effects in the present study. However, we expect future experimental designs to account for variation in genomic traits and to allow for mutations when investigating species invasions.

This study demonstrates the utility of individual-based mechanistic models for understanding biological invasions. Our results hold relevance for policy and management, as they reinforce the importance of reducing the import of alien species. This is true of alien species in general, but even more so for those showing high environmental tolerances and dispersal abilities, as well as those coming from habitats with similar conditions as native ecosystems.

Conflict of interests

The authors declare no conflict of interests.

Data Accessibility

All data should be reproducible by using the simulation codes found at `https://github.com/lleiding/gemm`.

Author contributions

DV, LL, and JSC conceived the ideas and designed methodology; DV performed simulations; DV and LL analysed the data; DV led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Effects of species traits and abiotic factors during the stages of plant invasions

Vedder, Leidinger & Cabral

1 Figures

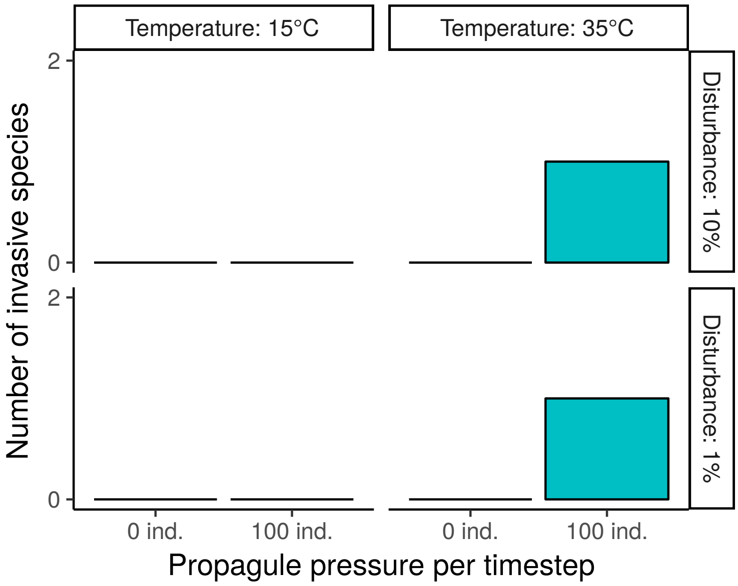


Figure 1: Number of successful invasions per scenario at higher propagule pressure levels (post-hoc simulation data, 10 runs per scenario).

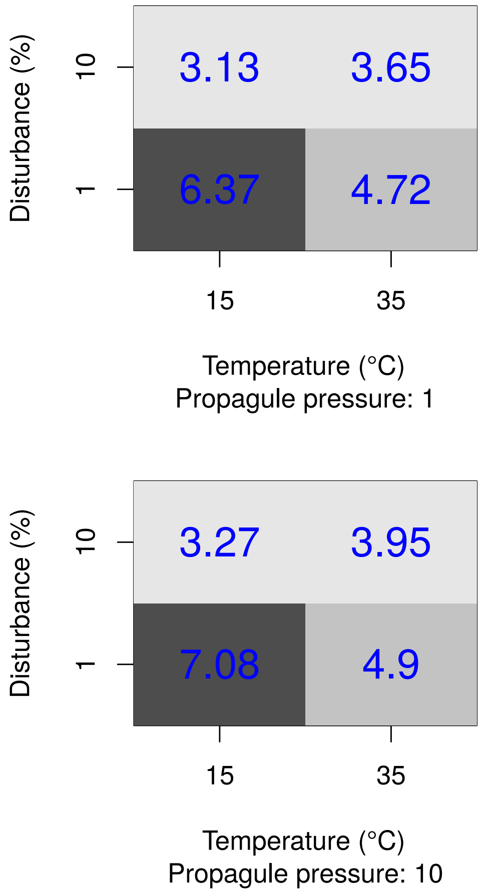


Figure 2: Average native species richness per scenario (main simulation data, 60 runs per scenario).

2 Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010).

2.1 Purpose

This model is designed to simulate a (meta-)community of plant-like individuals. For this, the model considers factors and processes across genetic, population and ecological levels. The model is able to produce several patterns across genetic, individual, population and (meta-)community levels, including adaptation and speciation through divergence of populations. Thus, the model expands from basic principles to richer representation of real-world scenarios.

2.2 Entities, state variables and scales

Individuals are the basic entity in the model. Given their attributes and life-history, these individuals most closely resemble plants. Individuals belong to different species, which are characterized by similar ecological traits and identical genetic architecture. The genetic architecture of each individual is comprised of a diploid set of one or more linkage units, which, in turn, combine a set of genes. Linkage units are always inherited in their entirety during the recombination phase of a reproduction event. The higher the number of genes per linkage unit, the higher the degree of genetic linkage. Some of the genes code for one ore more traits (pleiotropy), while a trait can be dependent on more than one gene (polygene). The realized trait value is the mean of all the trait alleles (quantitative trait loci). Traits thus controlled encompass the initial body mass (size) of offspring, M_s, the body mass determining onset of maturity and thus reproductive capability, M_r, mean dispersal distance, μ, the shape of the dispersal kernel, controlling long-distance-dispersal, s, and values representing the optimum and the tolerance (standard deviation) of a physical niche parameter, such as temperature and precipitation ($\overline{T}$ and σ_T or $\overline{P}$ and σ_P, resp.). Alternatively to be controlled by mutable genes, traits can also be fixed. Additionally, individuals carry attributes which describe their bodymass, M, and their adaptation to the abiotic environmental conditions (fitness), F_T and F_P. Furthermore, every individual carries a Boolean marker used to store whether a given individual has newly arrived to a grid cell or discriminate individuals from the rest of the community.

The base rates for processes governed by the metabolic theory of ecology (Brown et al., 2004) - growth, reproduction, mortality - are global constants. Mutation rate is also a global constant.

Every individual is placed inside an arena of grid cells, each of which has a unique location (coordinates) and is characterized by physical properties such as temperature, precipiation and size (carrying capacity). Over the course of the simulation these properties (location or physical parameters) might change, reflecting geomorphological dynamics. All individuals within one grid cell constitute a community. The characteristics of the grid cells combined with the state of inhabiting individuals constitute the state variables of the model. Additional patterns or summary statistics may be calculated based on these individual information.

Processes and updates are repeated every timestep, while each timestep can be considered as one year.

2.3 Process overview and scheduling

In each discrete, yearly timestep each individual in each grid cell will (in no particular order unless otherwise stated) undergoes the following processes: (1) establishment, (2) density independent mortality influenced by adaptation to temperature, (3) disturbance, (4) growth, (5) competition (individuals are sorted according to their adaptation to precipitation), (6) reproduction (7) mutation of offspring, (8) filtering of unviable individuals, (9) seed dispersal.

Before seed dispersal, alien individuals might be introduced to designated grid cells during an invasion process. After seed dispersal, the physical environment of a grid cell might change. If that happens, all individuals within that cell are marked to undergo establishment again.

Updates to individuals and thus the local communities happen instantaneously after a specific process has been executed (asynchronous updating).

2.4 Design concepts

Basic principles

Metabolic theory of ecology (at the submodel level). Adaptive and non-adaptive radiation/evolution (mostly submodel level, but geomorphological change at the system level). Sexual reproduction. Niche theory (both at system and submodel level). Each individual carries unique ecological and/or functional traits, as well as preferences for their physical environments. Resource/energy limitation (carrying capacity: system level property, but invoked at submodel level).

Emergence

Species/Populations/ecotypes. Only constrained via genetic properties. Community trait composition. Interplay of physical properties (environment, geographical properties) and within community (competition strength via reproduction, growth, etc.). Species numbers, endemics, speciation rate.

Adaption & Objectives

See entities. Traits follow evolution: a trait changes its value randomly within a given phylogenetic constraint. The success of the change (fitness) emerges as the result of adaption to the physical environment and the reproductive success of an individual over its competitors.

Learning

N/A

Prediction

N/A

Sensing

Individuals are directly affected by the properties of their physical environment (e.g., temperature).

Interaction

Individuals directly interact when sexually reproducing. However, they are not affected themself by this interaction. Instead, the interaction aims solely at determining the genotype of their offspring. Additionally, competition for resource/energy/space between individuals represents indirect interaction.

Stochasticity

Most of the submodels are carried out by all elegible individuals. Some submodels (Survival, Competition, Mutation and Dispersal), however, happen with particular probabilities. In these cases, execution of submodels is decided at random, taking into account individual characteristics, such as body size, fitness, genome size, or dispersal abilities. All decisions inside all of the submodels are stochastic (e.g., number of offspring) to maintain variability and relax assumptions.

Collectives

N/A

Observation

At the start and end of the simulation and at definable regular time intervals, the properties of all individuals (including the properties of their locations) are recorded and written to files.

2.5 Initialisation

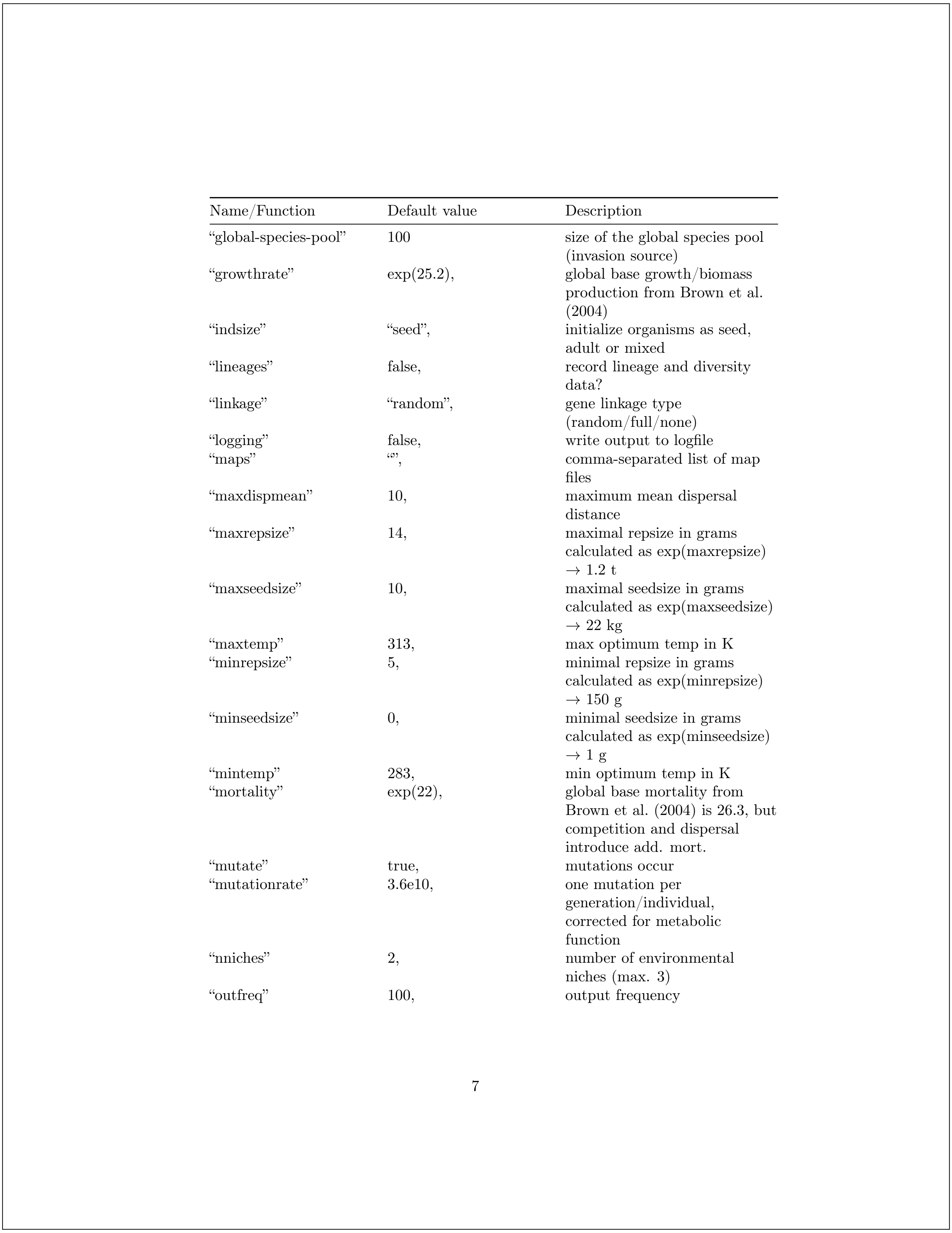
The initialisation step creates lineages with randomly chosen genetic and ecological trait values in each grid cell that is designated to receive an initial community. This encompasses choosing the number of genes for a lineage, the number of linkage units and the within genome variance of trait values. Trait with thus distributed trait values are the distributed randomly among the genes. Population (number of individuals) size of a lineage is determined by the adult body size of individuals from a lineage. At this point all individuals of a population are identical. Values for ecological traits are then varied in each gene where a given trait is found, for all individuals of a lineage. The variation is Normal distributed with the lineage trait value as mean and the product of σ_l (phylogenetic constraint) and the lineage trait value as standard deviation. This ensures initial genetic variation within a lineage population. Thus created populations are added to a grid cell's community until the additional mass of another population would exceed the grid cell's carrying capacity. In the experiment configuration file, it is possible to specify other methods of initializing communities, e.g., "single", where each grid cell receives only one species. Whether a grid cell receives an initial community depends on the map definition. At the end of initialisation each of the thus populated grid cells holds one or more different populations, each from a separate lineage.

2.6 Input

At the start of a simulation user defined parameters are read, containing also a definition of the simulation arena (map definition). This definition is provided in a separate plain text file. Within the text file a line at the top containing a single number defines the number of timesteps the arena definition is valid for. Every other non-empty line defines one grid cell with a unique identifier (a number), and the location of the grid cell as two coordinates. Optionally, one can define the type of the grid cell (island or continent), its temperature and precipitation values, and size.

Other optional parameters can be set in a separate configuration file and pertain to defining simulation scenarios:

Name/Function	Default value	Description
"avgnoloci"	1	average number of loci/copies per gene
"biggenelength"	200,	Sequence length of long genes
"burn-in"	500,	timesteps before invasion starts
"cellsize"	2e6,	maximum biomass per hectare in gramm (cf. Deshmukh, 1984; Clark et al., 2001)
"config"	"simulation.conf",	configuration file name
"debug"	false,	write out debug statements
"dest"	string(Dates.today()),	output folder name
"disturbance"	0,	percentage of individuals killed per update per cell
"fasta"	false,	record fasta data?
"fertility"	exp(28.0),	global base reproduction rate 23.8 from Brown et al. (2004), alternatively 25.0, default 30.0
"fixtol"	true,	Reproductive tolerance does not evolve



Name/Function	Default value	Description
“global-species-pool”	100	size of the global species pool (invasion source)
“growthrate”	exp(25.2),	global base growth/biomass production from Brown et al. (2004)
“indsize”	“seed”,	initialize organisms as seed, adult or mixed
“lineages”	false,	record lineage and diversity data?
“linkage”	“random”,	gene linkage type (random/full/none)
“logging”	false,	write output to logfile
“maps”	“”,	comma-separated list of map files
“maxdispmean”	10,	maximum mean dispersal distance
“maxrepsize”	14,	maximal repsize in grams calculated as exp(maxrepsize) → 1.2 t
“maxseedsize”	10,	maximal seedsize in grams calculated as exp(maxseedsize) → 22 kg
“maxtemp”	313,	max optimum temp in K
“minrepsize”	5,	minimal repsize in grams calculated as exp(minrepsize) → 150 g
“minseedsize”	0,	minimal seedsize in grams calculated as exp(minseedsize) → 1 g
“mintemp”	283,	min optimum temp in K
“mortality”	exp(22),	global base mortality from Brown et al. (2004) is 26.3, but competition and dispersal introduce add. mort.
“mutate”	true,	mutations occur
“mutationrate”	3.6e10,	one mutation per generation/individual, corrected for metabolic function
“nniches”	2,	number of environmental niches (max. 3)
“outfreq”	100,	output frequency

Name/Function	Default value	Description
“phylconstr”	0.1,	phylogenetic constraint during mutation and inter-loci variation. scales trait value as sd.
“phylo”	false,	record phylogeny?
“popsize”	“metabolic”,	initialisation algorithm: metabolic/bodysize/minimal/single
“precrange”	10,	range from 0 for precipitation optimum
“propagule-pressure”	0,	number of non-native individuals introduced per invasion event
“quiet”	false,	don’t write output to screen
“sdtemp”	0.0,	SD of temperature change per time step
“seed”	0,	for the RNG, seed $= 0 \rightarrow$ random seed
“smallgenelength”	20,	Sequence length of regular/small genes
“static”	true,	mainland sites don’t undergo eco-evolutionary
“tolerance”	0.8,	sequence similarity threshold for reproduction
“traitnames”	[“compat”, “dispmean”, “dispshape”, “precopt”, “prectol”, “repsize”, “reptol”, “seedsize”, “tempopt”, “temptol”],	minimal required traitnames
“usebiggenes”	true	Whether to use longer genes

If a parameter value is not specified by the user, the default value for that parameter set in the simulation code is assumed. Global parameter values were either adapted from the literature or found via trying out a range of values to identify combinations that lead to high species coexistence.

2.7 Submodels

Establishment

Whenever an individual is new to a grid cell (by recent birth, dispersal event or environmental change), their physical niche preferences are compared with the actual niche properties, e.g., the temperature, T, of the present grid cell. The individual adaptation parameter, A, is set according to the deviation from the optimum value considering the niche breadth as standard deviation of a

Gaussian curve, i.e., an individual's fundamental environmental niche.

$$A = a \times \exp\left(-(T - \overline{T})^2/(2\sigma_T^2)\right) \tag{1}$$

where

$$a = 1/(\sigma_T \sqrt{2\pi}) \tag{2}$$

Competition

If the sum of the community's bodymass exceed the available space, this will pick two individuals at random and remove the one that has lower adaptation to local precipitation, A_P. Once total bodymass is below carrying capacity, the procedure terminates.

Growth

Given an individual has undergone establishment, an individual changes its size $(M + \delta_M)$ following the metabolic theory and the global base growth rate, b_0:

$$\delta_M = b_0 \times M^{\frac{3}{4}} \times \exp\left(\frac{-E_A}{k_B \times T}\right) \tag{3}$$

with E_A as activation energy and k_B the Boltzmann constant. In case this change results in zero or negative body mass, the individual is removed from the community.

Density independent mortality / Survival

An individual is removed from the local community with a probability $p_m ort$ depending on its size M, its adaptation to temperature, A_T, and a global base mortality rate $b_m ort$:

$$p_m ort = \left(1 - \exp\left(-b_{mort} \times M^{-\frac{1}{4}} \times \exp\left(\frac{-E_A}{k_B \times T}\right)\right)\right) \times {A_T}^{-1} \tag{4}$$

Reproduction and mutation

All individuals that have grown to or beyond their individual reproduction sizes may reproduce. The number of offspring is randomly drawn following a Poisson distribution with mean N determined by the individual's size M and a global base offspring number N_0:

$$N = N_0 \times M^{-\frac{1}{4}} \times \exp\left(\frac{-E_A}{k_B \times T}\right) \tag{5}$$

The number of offspring is then multiplied by the seed mass encoded in the parent's genome and this total biomass subtracted from the parental biomass. If the remaining biomass would be equal to or less than 0, the individual will not reproduce. Otherwise, possible mates are selected within the same grid cell based on whether they belong to the same lineage, have reached maturity (which includes having established on the grid cell) and whether their compatibility sequences are sufficiently similar. If a suitable partner is found, both partners produce gametes, i.e., complete haploid sets of all linkage units, where each linkage unit is randomly picked either from the maternal or paternal set. The two gametes, one from each mating partner, comprise the genome for the offspring. At this point, mutations in the offspring's basecode may happen with a set probability P_m. In the case of mutation all traits associated with the respective gene will randomly change value V by ϵ, which is normally distributed and has as standard deviation the product of σ_l, i.e., the phylogenetic constraint, and V.

The new individuals' trait values are then calculated as the means of all alleles and the individuals added to the community, with their size set to the initial biomass M_s (seed biomass).

Dispersal

After reproduction and mutation, each offspring individual may disperse. For each of these, a new location (i.e. x and y coordinates) is drawn randomly following a logistic distribution with mean and shape parameters (which controls long-distance-dispersal) taken from the individual's traits. If a suitable grid cell is found at the drawn coordinates, the dispersing individual will be placed there and removed from the original community. The removal happens even when there is no destination grid cell to be found. Special attention is paid when the destination grid cell is of island type, while the origin is on the mainland and the simulation runs in static mode. In this case the dispersing individual is copied to the new destination instead of moved.

Habitat change

If enabled, both environmental habitat parameters - temperature and precipitation - change values throughout the simulation arena. The amount and direction of change is the same for all grid cells across the landscape. Changes to temperature and precipiation happen independently from one another. The change is randomly drawn from a Normal distribution with the current value as the mean and a user defined standard deviation.

Disturbance

If enabled, a set percentage (determined by the `disturbance` setting) of individuals in each cell is killed each turn, regardless of species or individual properties. Disturbance only begins after the `burn-in` period.

Invasion

If enabled, a global species pool is initialised with `global-species-pool` random species. After the `burn-in` period, `propagule-pressure` individuals from this pool are randomly selected and copied to the simulation arena's point of entry (multiple selection of the same species per turn is possible).

2.8 Output/Calculation

The main simulation data output is stored in two separate formats. The first is a table containg data characterising the individuals. Each line represents on individual. The columns describe an individual's current state. This is characterised by location, environmental conditions, ecological traits and summary of the genetic architecture. Additionally or alternatively to the individual level data, the data can be summarized at the population level (i.e. all individuals of a common lineage within the same grid cell). The second format is a fasta file containing the entire genome of all individuals. Association of sequences to individuals, linkage units, genes and coded traits is defined in the fasta headers. Output is stored at the beginning and end of a simulation and at user-definable intervals. The output considers the state of all non-seed individuals at those times.

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Part III

DISCUSSION

7

TRAITS AND MECHANISMS IN ISLAND BIODIVERSITY

In the context of global change and species mass extinctions, understanding biodiversity patterns has become one of the most pressing challenges of ecology. Islands, because of their suitability as "natural laboratories", present an ideal context in which to study such patterns (Whittaker and Fernández-Palacios, 2007). However, functional traits are still under-represented in island biodiversity theory. This thesis therefore aims at investigating the role of functional and genomic traits on the maintenance and evolution of island biodiversity using an individual-based model that combines explicit genomes with basic ecological and evolutionary principles.

In the previous chapters, I established an explicitly functional perspective on island biodiversity that includes genomic traits to investigate some of the trait-related mechanisms that shape island biodiversity, such as environmental variability and adaptive radiations. This enabled me to address a number of different, and in parts thus far unexplained, island biodiversity patterns. I will lay out further implications of this approach and its results in the following, along with directions for future work.

7.1 TOWARD A FUNCTIONAL-GENOMIC PERSPECTIVE ON ISLAND BIODIVERSITY

As stressed throughout this thesis, island evolutionary phenomena can not be explained satisfyingly without taking into account species traits, and how these traits are represented in the genome. This was made especially evident by analyzing previous island models (chapter 3). By choosing a niche- and genome-explicit approach, my model thus fills a gap that was left by previous island models that were not able to address adaptive radiations in a general manner. By explicitly considering a functional genome, I was able to find out that genome architecture can help in maintaining genetic variation under variable environmental conditions that would normally impoverish genomes (chapter 4). Species can thus retain more raw material for selection to act on when conditions change, which increases their chances of survival. In order for these reactions to happen in time, plants with smaller body sizes and thus faster life cycles are more successful, since selective adaptations can only arise in new offspring.

Some of these genomic traits were also important over an evolutionary relevant time scale that considers speciation (chapter 5). Comparable to survival in variable environments, intermediate genetic linkage maintains a higher degree of genetic variation, which, over time will increase species numbers due to genetic drift. At the same time, low genetic linkage enables species to quickly adapt to the new conditions after colonization of the island. Additional characteristics that determine high species divergence on islands encompass a complex set of ecological traits, such as decreased dispersal abilities and more flexible reproductive systems (i.e. increased self-compatibility and probability for hybridization). In fact, a certain degree of self-compatibility was found to be prevalent for most real island plant species (Crawford et al., 2009). Over time, this divergence syndrome becomes more distinct. A high propensity to selfing, combined with a considerable loss of dispersal ability will even accelerate divergence. Conflicting strategies with regard to reproductive compatibility to conspecifics provide a new perspective on the evolution of, and through, hybridization. While some species will evolve high pre-zygotic barriers to inhibit reproduction with distant relatives, most species go the opposite way and reduce such barriers to a minimum. These species will therefore hybridize frequently with potentially strongly diverged populations of the same lineage (cf. Jorgensen and Olesen, 2001). As a result, they might therefore evolve a smaller number of species as the lineages with increased reproductive barriers. The gain of such a strategy, however, is that populations maintain connection to a large pool of genetic variation which they can exploit to overcome constraints of streamlined genomes specialized to particular conditions. This could thus counteract the problem of evolutionary "dead ends" in specialized species (Day, Hua, and Bromham, 2016), which would render species unable to quickly adapt to new conditions. This suggests that hybridizations might not be random incidents that may give rise to new species, but rather the result of natural selection on the reproductive mode. While these trait syndromes have not yet been investigated in such a systematic way and can therefore not easily be validated with empirical data, concurrent body size evolution which accord with empirical evidence for an island syndrome in plants suggest my simulated patterns are plausible (Burns, 2019).

As the study on invasion factors could show (chapter 6), additionally to important abiotic factors such as propagule pressure, invasion success is affected by functional traits as well. The study suggested an "invasion syndrome" that encompassed increased environmental tolerances which enhanced population establishment, larger body sizes in comparison to native species which increased competitive ability, and higher dispersibility, which promoted spreading across the island. All these factors have not yet been studied in combination and over a larger spatial and temporal extent, which demonstrates the power of simulation approaches. Since the study on environmental variability (chapter 4) and island radiations (chapter 5) already highlighted the importance of genomic traits for ecological and evolutionary performance of species, future efforts should consider the impact of these traits for biological invasions as well (cf. Bock et al., 2018; Lee, 2002).

In general, this thesis provides a perspective on island biogeography that goes beyond immigration, extinction and (simplified) speciation. Congruent with a call for a new kind of island biogeography (Jacquet et al., 2017; Lomolino, 2000), I consider not only species differences with regard to their ecological traits but also differences in genome structure. I could show that trait differences affect survival under variable environmental conditions, speciation abilities and invasion potential. Given the disharmonic nature of real islands — not only in terms of species, but also functional composition (Taylor et al., 2019) — the results presented in this thesis highlight the consideration of traits as a high priority for future empirical and theoretical island biogeography research.

This functional island biogeography should not only consider phenotypic, but also genomic traits, which affect both short term (ecological) and long term (evolutionary) species performance, reflected in this thesis as species survival (chapter 4) and radiation potential (chapter 5), respectively. In empirical studies, sequence data should therefore be viewed not only as morphological information to infer relatedness and thus phylogenies, but also as functional data. After all, the way a genome is arranged is an important information that can tell us how genetic variation is passed on. There are already several studies from both non-island and island systems which set the methodological foundation (Alonso-Blanco et al., 2016; Blankers et al., 2018; Burri et al., 2015), but more empirical evidence will be needed to identify general patterns and to assess whether the theoretical results presented in this thesis reflect valid mechanisms. The theoretical results of this thesis could help to guide such empirical studies.

Ultimately, the eco-evolutionary effects of genomic traits offer a new perspective on the debate about "junk DNA" (Doolittle, 2013; Palazzo and Gregory, 2014) — those segments in the genome that do not seem to code for proteins or functional RNA (Biémont and Vieira, 2006; Orgel and Crick, 1980). Even if genomic segments do not provide some direct function, they will contribute to the molecular structure of a chromosome. This structure, however, will determine the crossing-over potential during meiosis and thus affect recombination. Anything that modifies the physical distance between genes will thus have an effect on the linkage between those genes, regardless of whether such a DNA segment is translated into protein or not. "Junk DNA", including transposable elements, could therefore be an important eco-evolutionary factor, since it directly modifies genetic linkage and thus adaptation potential as evidenced in my simulation experiments. Comparative genomics should therefore use the abundant sequence information to also infer and analyze genome structure (cf. Fournier-Level et al., 2011). This could shed new light on the dynamics of plants' adaptive strategies.

7.2 ISLAND MODELS AS A TOOL TOWARDS A SYNTHESIS OF BIOLOGICAL THEORIES

Since the formulation of the equilibrium theory of island biogeography (ETIB), there were several attempts to extend the theory with additional relevant factors and process and to unify it with theories from other disciplines (Chen and He, 2009; Rosindell and Phillimore, 2011; Whittaker et al., 2007). This is often hampered by the difficulty to intellectually grasp the resulting complex interactions of factors. Simulation models provide an elegant way out of this issue. As evidenced in this thesis, models can easily integrate any number of processes and factors. In most cases, the emerging patterns can, in retrospect, be explained as plausible outcomes or even match empirical patterns. Sometimes, the results are initially unexpected, but, once understood, they inspire new hypotheses which can be tested experimentally. The positive effect of genetic linkage on emerging species numbers presented in chapter 5 is one such example.

The study on island invasion (chapter 6) exemplifies how detailed models are often more general than simple models, because their integrated processes and structures can be turned on or off as needed (Evans et al., 2013). In this case, we addressed a study question, namely factors of invasion success, that did not require mutations or consideration of genomic traits. Hence, we simply turned off mutations and set genomic traits to fixed values for all species. We can proceed similarly for many different possible study questions. The added benefit of this modularity is that the effect of any factor or processes can easily be isolated by comparing the results of the model with disabled versus enabled module (cf. Cabral, Wiegand, and Kreft, 2019). Contrary to empiric experiments, we can control any confounding effects and ensure identical initial conditions. Finally, if done right, i.e. built on first principles in a modular manner, island models, albeit designed to investigate island phenomena, are not restricted to only one system. Instead they may easily be adapted to fit other systems, by simply changing the geography of the simulation arena. This is evidenced by the study on environmental variation (chapter 4): even though relevant in the island context, the geography could also reflect a continental system. Therefore, having synthesized theories, island models provide a direct interface to other biological systems, following a tradition established by ETIB.

Besides unifying theories, island models could also help in unifying concepts. In evolutionary biology, many categories revolve around the process of speciation. Albeit an arbitrary delimitation in itself, speciation is commonly classified according to its geographic extent ("sympatric" vs. "allopatric"), the rate of change and the occurrence of divergences or lineage splits ("anagenesis" and "cladogenesis"). However, as was pointed out, these concepts are arbitrary categorizations that often do not reflect the actual underlying mechanisms (Vaux, Trewick, and Morgan-Richards, 2016). The reason for this incongruency lies in spatial and temporal scales that can vary hugely for different taxa and the scarcity of informative data. If we take into account the findings of this thesis, that genomic traits, especially genetic linkage, relativize even the putative underlying mechanisms such as lineage splits and hybridization, all these concepts become even more diffuse. Hence, future efforts should work toward a genome-explicit theory of "speciation modes". Since mechanistic models provide us with an omniscient perspective, they could help in identifying the exact discriminating characteristics of all these concepts as well as commonalities. Some of these might then likely turn out to be opposing ends across a continuous spectrum rather than mutually exclusive, discrete categories.

This is but one example for identifying shared, general principles instead of focusing on discerning characteristics (cf. Lawton, 1999). Mechanistic models are useful tools in helping to find processes that produce realistic patterns for a large range of systems and scales and thus qualify for such general principles. A set of premises follow from that paradigm. For one, processes should represent rather small scales, since scaling up from them is only a computational hurdle, whereas scaling down from too coarse processes is much more challenging, if not impossible. Where possible, processes should therefore even relate to natural laws of physics and chemistry, e.g. metabolism (Brown et al., 2004). Second, so far the one identified fundamental biological process is evolution by selection of variation and mutation. It is therefore critical for any biological system at any scale that spans generations. Third, only by comparing to and calibrating with empirical data will models produce realistic patterns. As it happens, the model I presented in this thesis conforms to most of these premises. However, some of the implemented processes, e.g. dispersal following a dispersal kernel, still only reproduce patterns. Even then, there is a lot of opportunity to finding fundamental mechanisms using mechanistic models.

8

OUTLOOK

I was able to address a variety of topics concerning the impacts of genomic traits on ecological functioning and island biogeography. For the quest of a more integrative island biology and identifying fundamental principles, however, there are a number of additional related phenomena which could very well be addressed with my model. Most of these pertain to two different scale levels: the macro-ecological or biogeographic scale and the genomic scale. In the following I will present some possible research avenues for each of these, including their respective implementation. First, however, I will address the issue of bias introduced by model choice and parameter uncertainty and an approach to alleviate this.

8.1 ECO-EVOLUTIONARY MODEL ENSEMBLES TO IDENTIFY GENERAL PRINCIPLES

In all experimental approaches, results are often biased by the choice of employed methods. This holds true especially for mechanistic models, since models can and will only produce patterns based on their defined behavior. While the implementation of agents and processes giving rise to a model's behavior should always be informed by established theories and empirical findings, and built on first principles, the choice of processes and theories is often subjective. Even with the same processes modeled, models' output might still differ, because of developers' differences in coding style, language choice and general programming approach. Reliable conclusions drawn from models should therefore include not one, but many different models — similar to how meteorology has been proceeding for decades (Lewis, 2005; Urban et al., 2016).

The center of such as multi-model approach could be represented by a central repository which collects and combines different models (a "model base"). Requirements for a model to be included in the model base should encompass processing similar input data and returning comparable output, in terms of the level of detail. At least, models should produce patterns at comparable organizational levels (Radchuk et al., 2019; Zurell et al., 2016). To achieve this, all models need to be characterized systematically in terms of the type of input, the implemented factors and processes, and the produced patterns. This model base would then allow comparing the results of different models that match certain characteristics to address the same study question and assess how robust particular patterns are or how much they depend on implementation. Additionally, the model base might be used by empiricists to find models for making hypotheses or conducting exploratory simulations prior to intended experiments. And lastly, this model base would allow compiling model ensembles for predictive purposes. For such an application, a set of appropriate models would be fed with the same input parameters and run until all simulations reached the situation in question.

In order to increase predictive quality, the model base could be connected to resources which store environmental, geographical or organismal data, for example the TRY database (Kattge et al., 2011). This would enable a potential user to not only select one or multiple models from the model base, but also select the specific organisms and geographic region she is interested in. The model base would then retrieve the appropriate data from the respective databases. Ideally, it would consider all of the provided details, so that when the user specifies both species and region, and the species occurs in several regions, only the data corresponding to the populations in the specified region would be selected. However, given the incompleteness of most of today's databases in terms of intraspecific variation, this functionality might only be feasible in a couple of years.

In a further step, components of the individual models might be made modular, so that one model is able to use processes from several other models (Cabral, Valente, and Hartig, 2017). This is no small task, since it calls for standardization of interfaces between components. The potential user might then select processes she needs for a given experiment and the order these processes should occur in. This mix-and-match model toolbox, will ultimately allow to assess whether a single processes depends on implementation. Only processes independent from implementation can be considered general enough to qualify for the representation of putative fundamental principles.

A suite of different and detailed mechanistic models will generate biological patterns which can directly be traced back to the underlying processes. This makes it possible to infer processes also in empiric data, where mechanisms are obfuscated in the system's complexities or the patterns hidden in the sheer extent of the data. In such scenarios, output from models could help guide analysis, since researchers would already know what to look for. Alternatively, mechanistic models could help validate assumed causalities behind correlations in empirical data by directly testing hypotheses with designated simulation experiments. Advances in artificial intelligence methods even provide another alternative: the data from simulations could, for instance, be used to train neural networks, which are then applied to empiric data to infer the underlying conditions. This exemplifies one of the qualities of a model as detailed as the one I developed, namely that it may produce complex data, i.e. data of many different types and organizational levels, all from one single, synchronized system. This harmonized data allows direct causal inference between processes and patterns at different levels, contrary to integrating several different empirical data sources to substitute missing data between systems or points in time. Thus, the combination of mechanistic models with integrated empirical data supported by modern artificial-intelligence methods might offer unprecedented insights into the processes of real biological systems — on islands and beyond.

8.2 COMPLEX BIOGEOGRAPHY

In my modeling experiments, I used geographically static systems with a single isolated island. However, in a spatial or temporal extent larger than those considered in my experiments, this is hardly a realistic assumption. Islands do not appear out of nowhere, but rather gradually emerge from the ocean - into which they ultimately disappear more or less dramatically. Especially islands of volcanic origin usually follow a defined trajectory of emergence, erosion and submergence (Whittaker et al., 2007). The hypothesized impact of temporal biodiversity patterns could already be investigated experimentally using mechanistic models (Borregaard, Matthews, and Whittaker, 2016; Cabral et al., 2019). The detailed genomic aspects considered in my model, however, would allow assessing if the assumptions in those previous models are plausible. One common assumption in those models is the way a species cladogenetically gives rise to two species. This process is often represented by a point speciation mode, where speciation happens always after a specified time of population isolation. My model could reflect the effects of population bottlenecks and divergence hitchhiking, both of which have been found to affect speciation. Under the conditions of dynamic island geography, which imposes frequent changing of conditions and thus adaptation, genomic traits might play an even more important role than under static conditions, as indicated in chapter 4.

A number of studies investigated the effect of gene flow not only on speciation but also on population divergence within an island (Johnson, Adler, and Cherry, 2000; Rosindell and Phillimore, 2011). The predictions of these models, however, are based on very simplified modes of gene flow and genetic architecture. Thus, these hypotheses should be re-evaluated in light of the evidence of the impact of genetic linkage on the extent of population divergence. The genome-explicit nature of my model would be a useful opportunity to investigate the effects of intra-insular isolation on speciation under more realistic assumptions of population genomics. Gene flow also plays role in the biogeography of island groups, i.e. archipelagos. Colonization events between islands in an archipelago shaped many island communities of today (Emerson, Oromí, and Shaw, 2005; Juan et al., 2000). Since this might result in frequent hybridization, only by considering genomic traits will we be able to understand how species maintained their respective ranges. This evidence furthermore highlights the need to systematically investigate the effect of the past and present structure of archipelagos on evolutionary patterns on islands.

8.3 GENOME DYNAMICS

The structure of the genomes of all individuals in my model remain static throughout the simulation. Only at the genesis of a species is genome structure determined and then fixed for all species originating from that lineage. Albeit a sensible simplification, numerous examples from empiric genomic studies show that static genomes are seldom the case. Instead, genomes may grow and shrink in size, e.g. through whole genome duplication (Baduel et al., 2018), polyploidization (Van de Peer, Mizrachi, and Marchal, 2017), and subsequent gene loss (Albalat and Cañestro, 2016). Additionally, mobile elements, such as transposons, can change genome structure and lead to loss or gain of function in affected genes (Casacuberta and González, 2013). These processes often initiate evolutionary transitions and are thus good candidates for improving our understanding of speciation, but they can also be a response to changing conditions, e.g. stress (Rice et al., 2019). And while these phenomena have often been observed in nature, there is few, if any, attempts at experimentally investigating or modeling genome dynamics, especially in the eco-evolutionary contexts exemplified in this work. Thus, the direct causal effects and origins of these type of genome dynamics remain unclear. However, they too could be addressed with my model with some modification.

8.4 POSSIBLE IMPLEMENTATION

The model used in this thesis to address the respective experiments is designed to be flexible and modular. This flexibility allows (i) applying the model to diverse study questions by adapting the respective model parameters as shown above, and (ii) easy extensibility by adding processes or specific model behavior not considered in the present version. Examples for additional applications include studying the impact of geo-morphological dynamics on island biodiversity (cf. Whittaker et al., 2007) or the consideration of multiple islands, i.e. archipelagos (Gascuel et al., 2016; Triantis et al., 2015). Both of these applications could be realized by providing suitable simulation arena definitions, taking advantage of the possibility of inputting a sequence of definitions to represent geomorphological changes. To include genome dynamics, some aspects of the model would need to be extended and changed. Besides adding the necessary functions to carry out genome dynamics themselves, e.g. polyploidization, transposition or gene loss, the functions assessing compatibility of two individuals need to be adapted to allow for mismatch in genome structure. Additionally, genomes might need to be subjected to energetic constraints to impose an opposing force to accumulate genetic material. To allow backwards-compatibility with previous versions of the model, these changes should include additional parameters defaulting to values which disable the novel behavior.

9

CONCLUSION

Islands are an ideal context in which to study biodiversity patterns. For this reason, island biology remains an exciting research discipline. While island phenomena motivate a lot of primary research, island characteristics like confinement make findings relevant for other disciplines as well. In this thesis, I exemplified an approach based on process-based models to investigate island phenomena in a mechanistic matter. To achieve this, I closed a gap in the landscape of current island models by developing a model that explicitly considers genomes and micro-evolution. I used this model to investigate the effect of ecological and genomic traits on species survival under environmental variation and radiation potential. Furthermore, I presented an application of the model to a current conservation-related research topic, namely the invasiveness of species on islands. These examples highlight the generality of the model and its potential to address many other research questions. However, for a new synthesis of island biology theory, there remains a lot to be done. Only adding additional processes and levels and comparing them to alternative implementations and empiric evidence will allow identification of fundamental principles — not only in island biology but in ecology and evolution in general. This thesis represents one small step towards this goal.

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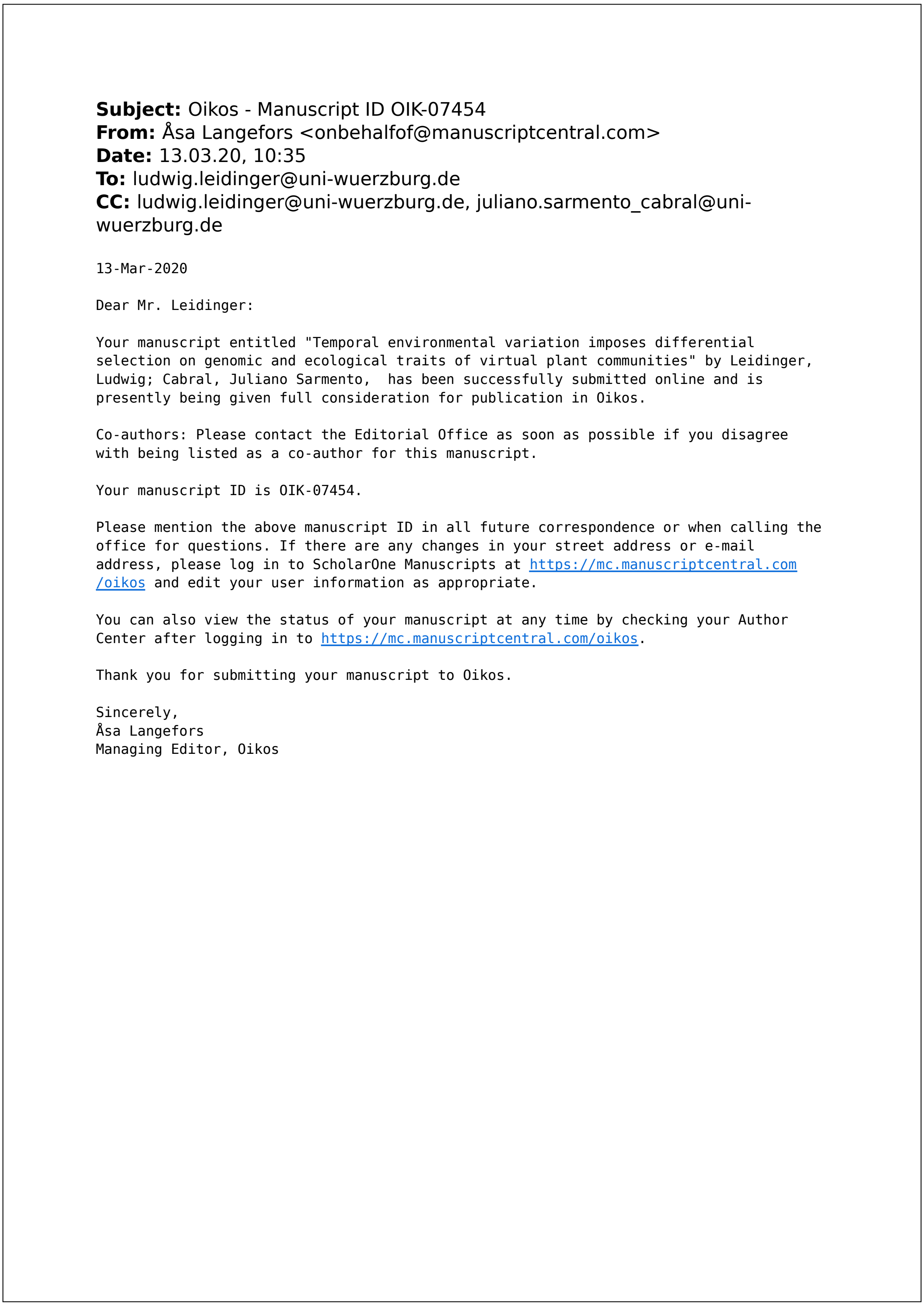
APPENDIX

A

CONFIRMATIONS OF MANUSCRIPT SUBMISSIONS



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13-Mar-2020

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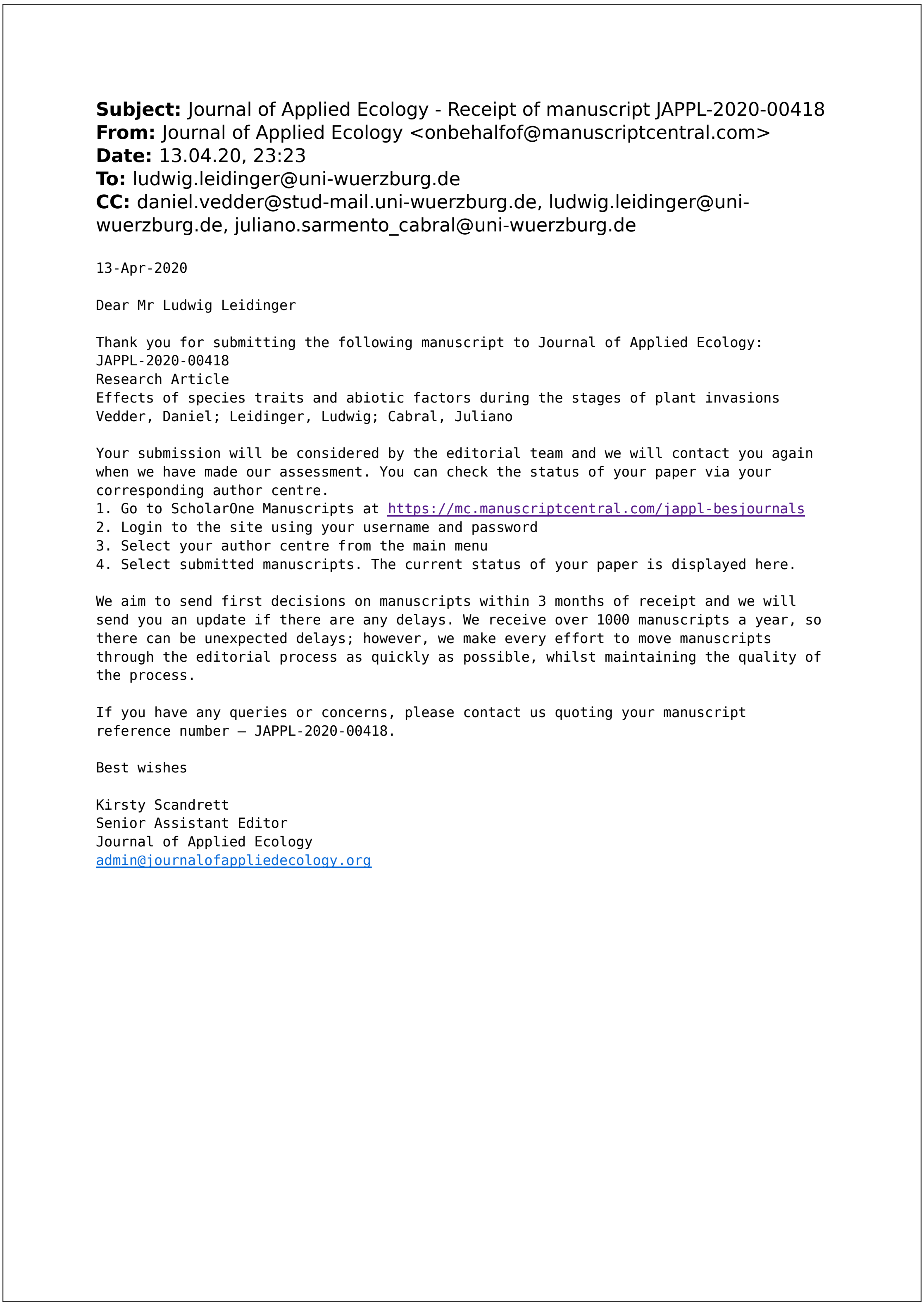

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