LINKING SPECIALISATION AND STABILITY OF PLANT-POLLINATOR NETWORKS

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Am 6. 11. 2007 verlieh mir die Universität Würzburg den akademischen Grad der "Diplom–Biologin Univ.". Weder erwarb ich weitere akademische Grade, noch versuchte ich den Erwerb dieser.

Würzburg, den 22. Januar 2013

Gita Benadi

Für meine Eltern.

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1

INTRODUCTION

> *"Es ist gewiß, dass viele Blumen von mehrern Arten von Insekten befruchtet werden . . . Es ist aber auch gewiß, dass viele Blumen bloß von einer Art von Insekten, und zwar auf eine sehr bestimmte Art, befruchtet werden . . . "*
>
> Christian Konrad Sprengel, "Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen", 1793

1.1 PREAMBLE

Plant-pollinator networks are not only a fascinating object of study in its own right, they are also important systems both from an ecologist's and an economist's point of view. This dissertation examines the relationship between specialisation and stability of plant-pollinator networks, with the aim of understanding how diversity in these systems is maintained and how robust pollination networks are against disturbances such as those caused by global climate change. In this first chapter, I briefly describe the role of plant-pollinator interactions in natural ecosystems and agriculture, introduce the concepts of ecological stability and specialisation, and provide an outline for the remaining chapters of this thesis.

1.2 PLANT-POLLINATOR INTERACTIONS

1.2.1 *Why should we care about plant-pollinator interactions?*

For an aspiring scientist, the choice of a subject for a research project of several years is of considerable importance. As an ecologist, focusing on plant-pollinator interactions is a good choice in several respects. For one thing, these systems provide an opportunity to study a wide range of general issues in ecology and evolution, such as coevolution (e.g. Kiester *et al.*, 1984; Anderson & Johnson, 2008; Rodriguez-Girones & Llandres, 2008), the evolution of cooperation (e.g. Ferriere *et al.*, 2002; Jandér & Herre, 2010), communication (Schaefer *et al.*, 2004, and references therein), community assembly (e.g. Sargent & Ackerly, 2008), species coexistence (section 1.3.2) and specialisation (section 1.4). Moreover, the pollination mutualism plays an important part both in natural ecosystems and in agricultural production. According to a recent estimate, approximately 87.5% of all angiosperm plant species are pollinated by animals (Ollerton *et al.*, 2011). Since flowering plants fulfil an essential function as primary producers in all terrestrial ecosystems, the integrity of these ecosystems depends on the pollination services provided by insects and other animals. However, the degree of dependence on animal pollination varies among plant species and ecoregions. For example, whereas wind-pollinated plants always constitute a minority in terms of species numbers, they dominate with respect to biomass in most arctic and temperate plant communities (Schemske *et al.*, 2009). Furthermore, many animal-pollinated plant species are able to reproduce in the absence of pollinators, either asexually or through self-fertilisation, thereby reducing the risk of reproductive failure (Bond, 1994; Busch & Delph, 2012). The dependence of these plants on animal pollination is more difficult to assess than for obligatory mutualists. It requires knowledge about the fitness of selfed versus outcrossed offspring and the importance of genetic diversity for the continued existence of populations.

By offering nectar and pollen in exchange for pollination services, flowering plants sustain a diverse guild of flower-visiting animal species, mostly insects, but also vertebrates such as birds, bats and primates. To my knowledge, no estimates of species numbers of pollen and nectar feeding insects in relation to species with other feeding strategies exist, but numerous flower-visiting species are found in major insect orders such as Coleoptera, Diptera, Hymenoptera and Lepidoptera (Kevan & Baker, 1983). As with flowering plants, the degree of dependence of these insects on the pollination mutualism varies from occasional flower visits to complete dependence of all life stages on floral resources.

Beside the ecological importance of plant-pollinator interactions, the pollination services of animals also constitute a considerable economic value. In a recent review article, Klein *et al.* (2007) estimated that animal pollination has a positive effect on the production of 70% of the world's most important crops. The global economic value of pollination services to all crops directly used as human food has been estimated as €153 billion or 9.5% of the value of worldwide agricultural production (Gallai *et al.*, 2009). While the production of most staple food such as cereals does not depend on animal pollination, other essential ingredients of a balanced human diet such as vegetables, fruits, nuts and spices largely depend on pollinator services (Klein *et al.*, 2007). Thus, although it is unlikely that a worldwide decline of pollinators could bring the human population to the brink of extinction, wild pollinators as well as managed honey bee populations greatly contribute to our health and well-being.

1.3 ECOLOGICAL STABILITY

1.3.1 *The concept of ecological stability*

Like many important concepts in ecological research, the term stability is widely used with a number of different connotations. The idea of ecological stability was originally borrowed from mathematics and its applications in physics and engineering (Holling, 1973). At first, it was closely linked to the notion of a dynamic system at equilibrium, in agreement with the traditional idea of the "balance of nature" (Wu & Loucks, 1995). The view of ecosystems being in a stable equilibrium state or at least close to it was subsequently contested, with several authors pointing out that biological systems are constantly changing in response to seasonal and stochastic fluctuations of environmental conditions, and that some systems also show intrinsic oscillations or other non-equilibrium behaviour (e.g. Connell & Sousa, 1983). Others suggested that the concept of an equilibrium state acting as an attractor is still helpful to understand the dynamics of fluctuating systems (Silvertown, 1987). More recently, ecological stability has become a generic term for various attributes of equilibrium and non-equilibrium systems related to their persistence over time (Grimm & Wissel, 1997). Despite its ambiguity, the concept has proven useful for at least two purposes: First, it has helped in elucidating the conditions under which species competing for resources can coexist or, in other words, the mechanisms of maintenance of species diversity (*sensu* Chesson, 2000). In addition, it can be used to understand the conditions that allow ecological systems to recover from a natural or anthropogenic disturbance. Below, each of these applications is discussed in greater detail.

1.3.2 *Mechanisms of diversity maintenance*

At least since the time of Volterra (1928), ecologists strived to understand the mechanisms that allow coexistence of species sharing one or more resources, thereby explaining the existence of species-rich communities or guilds. The plethora of possible mechanisms was reviewed by Chesson (2000), who classified them based on their properties as equalising or stabilising, and as fluctuation-dependent or -independent. Equalising mechanisms have the effect of reducing fitness differences between species, while stabilising mechanisms increase the strength of intraspecific competition relative to interspecific competition. Equalising mechanisms often involve trade-offs between traits, for example, a trade-off between the quality and quantity of offspring produced or between adaptations to the use of different resources, with the result that the mean fitness of species pursuing different strategies can be nearly identical. If only equalising mechanisms are at work, a community can at best be in a state of unstable coexistence in which species are lost through the slow process of ecological drift that may be counterbalanced by immigration, or, on a larger time scale, by speciation (Hubbell, 2001). Additional stabilising mechanisms are required for stable coexistence as defined by the ability of a rare species (an invader) to increase in the presence of the rest of the community. Whether such stable coexistence represents the dominant force in community assembly, however, is still a matter of debate between ecologists (e.g. Leibold & McPeek, 2006).

The two most intensively studied fluctuation-independent stabilising mechanisms are niche differentiation – the partitioning of resources between species (Levine & HilleRisLambers, 2009) – and frequency-dependent predation or parasitism. Both mechanisms result in higher average fitness of individuals of rarer species, in the former case because these individuals experience less resource competition, in the latter because the per-capita mortality rate of rarer species is lower. In addition, several fluctuation-dependent stabilising mechanisms exist. These mechanisms have in common that different species are favoured under different conditions, and competitive exclusion is prevented by variability of conditions in time and/or space. One of the best-known mechanisms, which allows coexistence of two consumers on one shared resource, has been termed "relative nonlinearity of competition" by Chesson (2000). It requires oscillations of resource density such as those driven by a time lag between peaks of predator and prey abundance in the classical Lotka-Volterra model of predation, and a nonlinear relationship between resource density and the growth rate of at least one of the two consumers (Armstrong & McGehee, 1980). A further mechanism, known as the "storage effect", is based on three requirements: 1) Differential responses of species to the environment, 2) covariance between environmental conditions and the strength of competition and 3) buffered population growth, for example through longevity of individuals or a dormant life stage that can survive under unfavourable conditions. All of the above-mentioned mechanisms can in principle work for more than two species, although with multiple species the requirements for coexistence may be more complex in comparison to the two-species case.

Whereas in earlier decades ecological research focused on antagonistic interactions such as predation and competition, in the last twenty years ecologists have come to appreciate the importance of positive (facilitative) interactions for community dynamics (Bruno *et al.*, 2003). Today, numerous examples of facilitation are known. In the case of species that also compete for resources, it is often unclear whether the net effect of one species on another is positive or negative. Facilitative interactions between members of the same guild seem to be especially common in harsh environments such as deserts and salt marshes, where the presence of one species may ameliorate physical stress for another (Stachowicz, 2001). Overall, the importance of facilitation as a mechanism of diversity maintenance is not fully understood.

1.3.3 *Defining and measuring stability in the face of disturbances*

The earth's ecosystems have always been subject to perturbations from a variety of sources. Some, for example many geological events, occur on the scale of millennia, while others, such as weather extremes and volcanic eruptions, operate on much shorter time scales. Today, human activities have become an additional major source of disturbances. These include land use change, pollution of air, water and soil, introduction of alien species, and climatic changes triggered by greenhouse gas emissions (Vitousek, 1994; Crowl *et al.*, 2008).

Given the increasing pressure that human activities put on ecosystems, studying their stability against disturbances has become more relevant than ever. However, since "stability" is a generic term comprising many different concepts (section 1.3.1), a clear definition is required in order to avoid confusion and inappropriate generalisation (Nilsson & Grelsson, 1995; Grimm & Wissel, 1997). First, a state variable of interest needs to be selected whose response to a disturbance is to be evaluated. Frequently chosen variables include species diversity, community composition, biomass and ecosystem services such as carbon sequestration. Further, statements about system stability can only be made in relation to a specific type of disturbance.

Disturbances may vary in their frequency and intensity, and affect the variable of interest directly or indirectly. Some types of disturbances are temporary (e.g. extreme climatic events), while others have a lasting effect on ecosystems (e.g. long-term changes in mean temperature). Moreover, a decision has to be made regarding the criterion of stability. Grimm & Wissel (1997) distinguish between three main categories of stability criteria: Staying essentially unchanged (constancy), returning to a reference state after a temporary disturbance (resilience) and persisting over time (persistence). The first two criteria require the specification of a reference state, which may be a stable equilibrium, oscillations with a certain amplitude and period, or stochastic fluctuations within predefined boundaries.

With diversity or community composition as the variable of interest, there is a close relationship between community stability against disturbances and the mechanisms of diversity maintenance mentioned above (section 1.3.2). In reality, species-rich communities can only exist if they are able to withstand at least minor disturbances.

1.4 SPECIALISATION

1.4.1 *Defining and measuring specialisation*

Like ecological stability, specialisation is one of the key concepts in ecology, and as with stability, its definition and measurement are far from clear and easy. In general, specialisation refers to a restricted niche width of organisms (Futuyma & Moreno, 1988). The concept can be applied to different levels of organisation, from individuals to communities. In the remainder of this chapter, I will focus on specialisation at the species level and briefly touch upon community-wide specialisation (see section 1.4.4).

Different concepts of specialisation can be distinguished based on the type of ecological niche to which they refer (Devictor *et al.*, 2010, and references therein). The Grinnellian niche describes species' responses to environmental variables such as food resources or physical conditions (Grinnell, 1917), while the Eltonian niche refers to species' impact on the environment or, in other words, their functional role in the ecosystem (Elton, 1927). An extension of the Grinnellian niche to all possible environmental variables is the ecological niche as defined by Hutchinson (1957): An n-dimensional hypervolume comprising all conditions that permit a species to maintain a viable population. In his seminal paper, Hutchinson distinguished between the fundamental niche of a species in the absence of biotic interactions and the realised niche – the fundamental niche modified by interspecific interactions. This distinction can be applied to the Grinnellian as well as the Eltonian niche concept. Biotic interactions may reduce (e.g. competition, predation) or expand (e.g. facilitation, mutualism) the fundamental niche of a species. In practice, the majority of studies on specialisation focus on only one niche axis, most often either habitat type or food resources. Moreover, in observational studies it is often impossible to determine to what extent the fundamental niche of a species has been modified by biotic interactions.

In addition to these limitations, the measurement of species specialisation poses several challenges (Poisot *et al.*, 2012). Often, for lack of more detailed data, species are simply divided into specialists and generalists, although most authors acknowledge that specialisation is in reality a continuous trait. The simplest continuous specialisation metrics only consider the number of resource types used by a species, for example, the number of prey species hunted by a predator. More elaborate metrics additionally account for the proportional use of each resource type. Their relationship to simpler metrics is similar to that of diversity indices such as Shannon or Simpson diversity to species richness. Indeed, these diversity indices can be used to quantify specialisation. Relatively few specialisation metrics consider not only the use of resources, but also resource availability (Blüthgen *et al.*, 2006; Devictor *et al.*, 2010). If resource availability is ignored, a species without any preferences may appear highly specialised simply because some resource types are much more common than others. A famous example is the koala (*Phascolarctos cinereus*), an Australian marsupial feeding almost exclusively on eucalypt leaves. Yet, since its habitat is a type of forest dominated by eucalypt trees, its feeding habits alone should not be taken as evidence of specialisation (Colwell & Futuyma, 1971). For conservation-related questions, on the other hand, the absolute number of resources used may be more important than the proportional use in relation to resource availability (Sahli & Conner, 2006). Finally, specialisation metrics vary in the way they handle incomplete information (Colles *et al.*, 2009; Devictor *et al.*, 2010; Poisot *et al.*, 2012). Most indices tend to overestimate the degree of specialisation of rare or rarely observed species, although it is possible to correct for this bias by using null models (Blüthgen *et al.*, 2006; Dormann, 2011).

1.4.2 *Causes of specialisation*

Why should a species confine itself to the use of a restricted range of resources? Clearly, if no costs are involved in being a generalist, generalisation should always be favoured over specialisation. Traditionally, specialisation has been regarded as an adaptation resulting from trade-offs between traits that allow efficient exploitation of different types of resources ("the jack of all trades is a master of none", MacArthur 1972). This general idea is still accepted, but the existence of trade-offs between morphological, physiological or behavioural traits related to the use of different resources cannot always be demonstrated (Poisot *et al.*, 2011, and references therein). The failure to find such trade-offs may be due to methodological difficulties, for example, the fact that in any empirical study only a subset of all possible fitness-relevant traits can be measured. An alternative explanation is that present-day specialisation is the consequence of phylogenetic constraints (i.e., the result of adaptation of ancestral species to past environmental conditions).

The conditions favouring the evolution of specialisation over generalisation are not always easy to identify. For example, spatial heterogeneity may promote adaptation of populations to local environmental conditions, but gene flow through migration between patches can prevent the formation of locally adapted genotypes (Poisot *et al.*, 2011, and references therein). In general, the effect of spatial heterogeneity seems to depend on the spatial scale of habitat patches in relation to the dispersal distances of organisms. Temporal heterogeneity, on the other hand, is usually thought to have a negative effect on the tendency to specialise. Existing specialisation can be reinforced by covariance between individual preferences and performance on different types of resources (Ravigné *et al.*, 2009). The conditions that allow coexistence of specialists and generalists are likewise not fully understood. So far, theoretical studies have demonstrated the importance of the shape of the trade-off function for generalist and specialist coexistence (Egas *et al.*, 2004).

A special situation arises when the resources themselves are biological organisms. In this case, coevolution of interacting species can promote or impede the evolution of specialisation (e.g. Abrams, 2006). In enemy-victim interactions, the development of different defence strategies by victim species is generally thought to constrain natural enemies to a restricted set of victims due to the costs involved in overcoming several defence strategies at once (Futuyma & Moreno, 1988). In mutualistic associations between plants and their symbionts, specialisation may be promoted through preferential allocation of resources by plants to the most efficient symbiont (Kiers *et al.*, 2003; Bever *et al.*, 2009).

1.4.3 *Consequences of specialisation*

Whatever the cause of specialisation may be, it has long been argued that specialised species are potentially at higher risk of extinction than generalists, because their dependence on the continued existence of a specific subset of resources is greater. Indeed, in the majority of studies examining the effects of anthropogenic environmental change on species persistence, a positive relationship between habitat specialisation and extinction risk was found (reviewed by Colles *et al.*, 2009). The evidence for dietary specialisation, on the other hand, is more ambiguous: Some studies showed a positive relationship between specialisation and extinction risk, while others found none. The difference between the effects of habitat and diet may be due to the fact that human alteration of the environment usually affects habitat availability directly, but food resources only indirectly (Colles *et al.*, 2009). A possible confounding factor in correlations of species specialisation and extinction risk is the fact that specialisation is often linked to other traits such as low population density and a limited geographic range which are themselves known to increase the risk of extinction (McKinney, 1997). If a specialised species is deprived of resources, it may adapt to the situation in one of several ways: Provided that the traits related to resource use are sufficiently plastic, the species may shift to the use of new resources. Alternatively, if the environment has only locally been changed, it may be able to migrate to undisturbed habitat, but this requires sufficient habitat connectivity and dispersal abilities. A third route of escape from extinction exists in the form of evolutionary changes of species traits. Evolution can occur within a few generations provided that the selection pressure is sufficiently strong and the population is genetically diverse. Phylogenetic studies have shown that specialisation is not an evolutionary dead end as some authors suggested (e.g. Moran, 1988), and that generalist species may evolve from specialist ancestors (reviewed by Colles *et al.*, 2009).

In systems with specialised interspecific interactions, a species may become extinct as a consequence of the loss of its host, prey or mutualist. This type of extinction has been termed "coextinction" or "secondary extinction" in the literature. Some models predict that coextinctions should be common, indeed possibly the most common type of extinction (Koh *et al.*, 2004), but observations of coextinctions are exceedingly rare (Dunn *et al.* 2009; but see Biesmeijer *et al.* 2006). There are two possible reasons for this paradoxical situation: Either many coextinctions are overlooked or misinterpreted as being caused by some other factor, or interspecific interactions are generally more flexible (phenotypically plastic or evolvable) than assumed.

While most studies of specialisation only consider species' resource requirements (their Grinnellian niche, see section 1.4.1), a growing number of studies also examine the functional role of species (the Eltonian niche) and the possible consequences of species loss for the integrity of ecosystem functions. If each species in a community represents a unique function, the community is said to show complementarity of ecological functions. By contrast, communities consisting of species with overlapping functions are called redundant. A high degree of redundancy is expected to act as a buffer against loss of ecological functions (Walker, 1995; Naeem, 1998; Rosenfeld, 2002; Blüthgen & Klein, 2011). In principle, the existence of functional complementarity can be inferred from a positive relationship between species diversity and ecosystem functions such as biomass production, but care is needed to distinguish actual complementarity from sampling effects (a larger community is more likely to contain the most effective species) and numerical effects (more diverse communities often contain a higher total number of individuals; Blüthgen & Klein 2011).

1.4.4 *Specialisation of plant-pollinator interactions: A short history*

The foundation for the scientific study of plant-pollinator interactions was laid in the 18th century by the German botanist Joseph Gottlieb Kölreuter (reviewed by Waser, 2006). Kölreuter was the first to show, through observations and experiments, that flower-visiting insects were fertilising plants by transferring pollen, and that exclusion of insects caused failure of fruit set in several plant species he studied. Moreover, Kölreuter observed that some plants were visited by multiple insect species, and some insects in turn visited multiple flowering plants. He concluded that this behaviour would allow hybridisation between plant species, which he regarded as "unnatural". This view, which was based on the belief that species are unchangeable entities created by God, was challenged by Charles Darwin (1859), who argued that extant species are only a snapshot in the ongoing process of evolution by natural selection. Darwin also directly contributed to the field of pollination ecology through his book on orchid pollination (1862). During his travels in Madagascar, he observed that flowers of the species *Angraecum sesquipedale* possess an extremely long spur, and correctly predicted that this orchid must be pollinated by a hitherto unknown hawkmoth species with an equally long proboscis. The idea that the type of pollinator can be inferred from floral characteristics was further developed by the Italian botanist Federico Delpino, who devised two classification schemes of floral phenotypes. In the 20th century, several researchers proposed simpler and more consistent classifications, which culminated in the definition of "pollination syndromes" in the 1960s (e.g. van der Pijl, 1961; Faegri & van der Pijl, 1966).

Pollination syndromes are common sets of floral characteristics of unrelated plant species which were thought to have originated from convergent evolution as an adaptation to common pollen vectors. In the case of pollination by animals, syndromes were defined for each of the major flower-visiting insect orders as well as for birds and bats (van der Pijl, 1961). The classification also included a generalised or unspecific floral type, which was thought to be the ancestral state from which the specialised syndromes originated.

Although it was based on collections of case studies rather than proper statistical analyses, the concept of pollination syndromes became popular, probably because it satisfied the human desire for finding patterns in nature and allowed to infer the pollen vector of a plant without the need for long hours of observations. However, at the end of the 20th century, the syndrome concept was increasingly questioned by field ecologists who observed an apparent paradox: Floral traits of many plant species seemed to be specialised on a certain type of visitor, but in reality flowers were often visited by a variety of animal species that did not fit the syndrome (Ollerton, 1996). A possible solution was offered by an older study by Stebbins (1970; see also Fenster *et al.* 2004), who proposed that the evolution of floral traits should be shaped by the most effective pollinator. This recognises that not all flower visitors contribute equally to the reproduction of a plant, and that some do not pollinate at all. More recently, the idea of pollination syndromes was subjected to modern multivariate statistics (Ollerton *et al.*, 2009). Ordination of floral traits from multiple communities showed that most plant species' traits did not match any of the traditional syndromes. Moreover, for about two thirds of all plant species the most frequent pollinator could not be predicted from the pollination syndrome that was closest in phenotype space. Nevertheless, while the traditional pollination syndromes turned out to be too strong a simplification, the underlying idea that floral traits are shaped by coevolution with flower visitors remains uncontested (e.g. Anderson & Johnson, 2008; Gomez *et al.*, 2009; Harder & Johnson, 2009).

The discussion about the validity of the pollination syndrome concept triggered a general interest in the mechanisms that promote the evolution of specialisation or generalisation in flowering plants and pollinators. In a frequently cited paper, Waser *et al.* (1996) proposed that plant-pollinator interactions are much more generalised than previously assumed. Using simple mathematical models, they showed that flowering plants should specialise on the single most effective pollinator in a stable environment, but generalisation should be favoured if pollinator abundances fluctuate in time and/or space. Pollinators should benefit from specialisation on the most rewarding plant only if the quality or quantity of rewards differs greatly between plant species and the costs of travels between flowers are low. The authors noted that these conditions do not seem to be met by most pollination systems. Moreover, they argued that a pollinator can only specialise on a single plant species if the flowering phase of the plant is long enough to encompass the whole life cycle of the pollinator. Therefore, they concluded that a moderate degree of generalisation of plant-pollinator interactions should be the rule rather than the exception. In response to this paper, Johnson & Steiner (2000) noted that numerous cases of remarkably specialised pollination systems are known from the tropics and the temperate zone of the southern hemisphere. They acknowledged that specialisation on a restricted number of pollinator species increases the risk of reproductive failure for a plant species, and suggested that long-lived plants and those with means of vegetative reproduction should be better able to cope with that risk. Moreover, they proposed that rare or dispersed plants should favour specialised pollinators to avoid the loss of pollen through heterospecific flower visits and clogging of stigmas by pollen of other plant species.

Whereas earlier ecological studies of plant-pollinator interactions mostly focused on one or a few species and their interaction partners, recent years have seen a surge of interest in community-wide interaction patterns (reviewed by Mitchell *et al.*, 2009a). One reason for this shift was the growing realisation that plant-pollinator interactions are often quite generalised, with most plant species being visited by multiple animals and most animal species visiting multiple plants (Waser *et al.*, 1996). Another important factor was the adoption of network analysis as a new method to describe the complex relationships between communities of plants and pollinators. Originally, network analysis was derived from the mathematical field of graph theory and its applications, but it became prominent in ecology long before pollination biologists discovered its uses for their field. At least since the early 1970s (see review by Ings *et al.*, 2009), multispecies predator-prey relationships had been described as food webs consisting of nodes (species) and links (trophic interactions). From the late 1980s onwards (e.g. Jordano, 1987), researchers began to analyse mutualistic interactions, mainly those between plants and their pollinators or seed dispersers, using the same tools.

Ecological networks are primarily a tool to describe and visualise multispecies interactions. Thus, it is not surprising that many of the earlier studies of plant-pollinator networks were purely descriptive (e.g. Memmott, 1999). From the basic structure of a network consisting of nodes and links, a large number of indices have been derived that describe different aspects of network structure (Bascompte & Jordano, 2007; Dormann *et al.*, 2009). Qualitative indices only account for presence or absence of interactions between species, while quantitative indices incorporate some measure of interaction strength. The simplest qualitative metric is the connectance of a network, the proportion of realised links, a simple measure of specialisation at the community level. Another frequently studied aspect of network structure is the degree of nestedness (Bascompte *et al.*, 2003). If the number of links of a species is taken to be a simple measure of species-level specialisation, a network is perfectly nested if each more specialised species interacts with a subset of the interaction partners of the next most generalised species. Unlike connectance, nestedness has no simple biological interpretation. In a nested structure, specialists tend to interact with generalists, while generalists also interact with other generalists. For a given distribution of links per species, nestedness maximises the overlap in the identity of interaction partners of different species of the same community.

A common issue with many network metrics is their sensitivity to incomplete sampling (Blüthgen *et al.* 2008; see also section 1.4.1). For instance, it can be shown that the observed negative relationship between connectance and size (number of species) of mutualistic networks can be explained by lower sampling intensity (average number of observations per species) in larger networks. Similarly, a nested network structure naturally emerges when communities consist of complete generalists with a skewed distribution of numbers of observations per species. Since incomplete sampling of species and interactions is inevitable in community-wide studies, new metrics have been developed that account for sampling artefacts by using null models. For example, the H_2' index is a quantitative metric of network-level specialisation whose empirical value can be compared to randomized networks to detect a significant deviation from the null expectation (Blüthgen *et al.*, 2006).

In the last few years, the community approach to studying plant-pollinator interactions has enabled researchers to address a number of new questions and to rephrase some old questions in a community context. For example, recent studies have described the variation of plant-pollinator interactions in space and time, with the aim of understanding the factors that determine this variation (Alarcon *et al.*, 2008; Olesen *et al.*, 2008; Burkle & Alarcon, 2011). Others have explored the consequences of variation in interaction patterns for the evolution of floral traits (e.g. Gomez *et al.*, 2009). Still others have tried to quantify the contribution of different mechanisms to the structure of plant-pollinator networks, for instance the influence of morphology (Stang *et al.*, 2006), olfactory and visual cues (Junker *et al.*, 2010), phenology (Encinas-Viso *et al.*, 2012) and resource competition (Mitchell *et al.*, 2009a) as structuring mechanisms. As the number of studies and the diversity of topics have greatly increased, a full account of all recent developments is beyond the scope of this overview. This thesis contributes to the branch of pollination ecology that investigates the consequences of specialisation of plant-pollinator interactions at the species and community level. It presents the results of studies on the influence of specialisation on diversity maintenance and robustness of pollination networks against environmental change.

1.5 OUTLINE OF THIS THESIS

The following chapters of this thesis can be divided into two parts based on their main focus. Chapters 2 and 3 address the effects of plant-pollinator interactions on the diversity of animal-pollinated plant communities. Chapters 4 and 5 deal with the stability of plant-pollinator systems faced with environmental changes such as those produced by climate change. Alternatively, the first three chapters (2, 3 and 4) may be grouped together since they all use mathematical models in contrast to chapter 5, an empirical study of plant-pollinator interactions along an altitudinal gradient. The final chapter (6) synthesises the findings of all four studies and provides an outlook on avenues of future research.

1.5.1 *Diversity maintenance in animal-pollinated plant communities*

Several authors of the earliest models of mutualistic systems commented on their apparent instability compared to antagonistic systems (e.g. May, 1973; Goh, 1979). Some of the instabilities of these first models were artefacts of greatly simplified model systems, such as the assumption of unlimited exponential growth of two mutualistic species, which Robert May (1982) called an "orgy of mutual benefaction". However, some other destabilising mechanisms were not so easily dismissed. In 1970, Levin & Anderson published a model of two plant species competing for pollination by a generalist pollinator. Their stability analyses showed that the two plants could not stably coexist, because each time one of them slightly decreased in abundance compared to the other, it would suffer from a reproductive disadvantage which would result in further decline and eventual extinction. This disadvantage resulted from the fact that the probability that a visiting pollinator carries conspecific pollen is lower for a rarer plant species. Although several later studies came to the same conclusion (Waser, 1978; Goulson, 1994; Kunin & Iwasa, 1996), the apparent paradox that species-rich communities of animal-pollinated plants exist despite their predicted instability was never resolved. In chapter 2, we develop a mechanistic model of the population dynamics of plant and pollinator communities that incorporates niche differentiation of plant species, a classical stabilising mechanisms (see section 1.3.1). Using this model, we conduct stability analyses of systems with two plant and two pollinator species. The aim of this study is to examine the interplay between the stabilising effect of niche differentiation and the destabilising influence of pollination to resolve the paradox of diversity in animal-pollinated plant communities.

In a more recent study, Bastolla *et al.* (2009) suggested that under certain conditions, mutualistic interactions with pollinators or seed dispersers can increase the maximum number of coexisting plant species in a community. Specifically, they showed that fully connected or nested interaction networks (see section 1.4.4) had a positive effect on plant diversity, while networks with little overlap in the identity of interaction partners tended to reduce the number of coexisting plant species. However, the authors of this study used a generic model of mutualism that did not account for the specific mechanisms of plant-pollinator interactions (see above). Moreover, the positive effect of mutualistic interactions was based on an increase in the size of the overall plant population in the presence of mutualists, disregarding the fact that the total number of individuals in the community is often limited by other factors such as abiotic resources or simply space. In chapter 3, we employ a modified version of the model developed in chapter 2 to investigate the effect of the presence of pollinators on species richness and evenness of a plant community. In accordance with Bastolla *et al.* (2009), we compare plant species richness for fully connected, nested and diagonal interaction networks. Unlike this earlier study, we examine plant communities that fill nearly all available habitat in the absence of pollinators as well as communities with a total population size far below the habitat capacity in the absence of pollinators. In addition, we study the effect of a trade-off in effectiveness of generalised pollinators on different plant species (see section 1.4.2). This analysis clarifies the conditions under which interactions with pollinators may promote plant diversity.

1.5.2 *Stability of plant-pollinator networks in the face of anthropogenic disturbances*

According to current knowledge, the anthropogenic increase of greenhouse gas emissions has two main effects on the global climate: A long-term rise in mean global temperature and an increase in the frequency and intensity of extreme climatic events (IPCC, 2007). In chapter 4, we examine the stability of multispecies plant-pollinator systems in the face of temporary disturbances such as those caused by extreme climatic events. Since stability is a generic term for system responses to different types of perturbations (see section 1.3.3), we compare results for four criteria of stability that differ in the the state variable under consideration and relate to different intensities of disturbances. The main aim of this study is to understand the relationship between specialisation and stability of plant-pollinator systems. Many studies have emphasised the destabilising effect of specialisation through an increased extinction risk (see section 1.4.3). However, as a form of resource partitioning specialisation may also have a stabilising effect by reducing the risk of competitive exclusion (see section 1.3.2). Using a variant of the model presented in chapter 2, this chapter examines the interplay between the two contrasting effects of specialisation.

Chapter 5 is concerned with the second aspect of climate change, the worldwide increase in mean temperatures. There is now sufficient evidence that rising temperatures are causing a shift in the phenology of many plant and animal species in temperate and arctic regions (Parmesan, 2006; Cleland *et al.*, 2007). While the general trend is towards earlier occurrence in the season, there is considerable variation in the magnitude and direction of phenological shifts of different species (e.g. Fitter & Fitter, 2002). If plant and pollinator species respond differently to climate change, their interactions may be disrupted. Therefore, several authors have suggested that many plant and pollinator species may be threatened by phenological desynchronisation (Stenseth & Mysterud, 2002; Memmott *et al.*, 2007), in particular specialised species whose dependence on the availability of specific mutualists is greatest (see also section 1.4.3). Others have pointed out that the structure of plant-pollinator networks seems to be quite flexible in space and time (see section 1.4.4) and that temperate pollination systems are likely to be buffered against climate change by the high degree of functional redundancy in these systems (Willmer 2012; see also section 1.4.3). In chapter 5, we study phenology and interactions of plant and pollinator communities along an altitudinal gradient in the Alps over the course of a flowering season. Using the altitudinal gradient as a model for the effects of climate change in time, we examine the relationship between specialisation and phenological synchrony of flower visitors with particular plant species. These analyses shed light on the importance of phenological synchrony for different groups of pollinators. Thus, they allow to assess the risk of species extinctions and loss of ecological functions as a result of phenological desynchronisation.

2

POPULATION DYNAMICS OF PLANT AND POLLINATOR COMMUNITIES: STABILITY RECONSIDERED[1]

2.1 ABSTRACT

Plant-pollinator networks are systems of outstanding ecological and economic importance. A particularly intriguing aspect of these systems is their high diversity. However, earlier studies concluded that the specific mechanisms of plant-pollinator interactions are destabilising and should lead to a loss of diversity. Here, we present a mechanistic model of plant and pollinator population dynamics with the ability to represent a broad spectrum of interaction structures. Using this model, we examined the influence of pollinators on the stability of a plant community and the relationship between pollinator specialisation and stability. In accordance with earlier work, our results show that plant-pollinator interactions may severely destabilise plant coexistence regardless of the degree of pollinator specialisation. However, if plant niche differentiation, a classical stabilising mechanism, is sufficiently strong to overcome the minority disadvantage with respect to pollination, interactions with pollinators may even increase the stability of a plant community. In addition to plant niche differentiation, the relationship between specialisation and stability depends on a number of parameters that affect pollinator growth rates. Our results highlight the complex effects of this particular type of mutualism on community stability and call for further investigations of the mechanisms of diversity maintenance in plant-pollinator systems.

2.2 INTRODUCTION

A central problem in ecology is understanding the impact of interspecific interactions on the dynamics of the populations and communities involved. Despite an early interest in mutually beneficial relationships between species (e.g. Pound, 1893), mutualism has only recently begun to receive the same amount of attention as for example predator-prey or competitive interactions. Considering the ubiquity of mutualistic interactions in

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[1] Article by G. Benadi, N. Blüthgen, T. Hovestadt and H.-J. Poethke
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natural ecosystems (Bronstein *et al.*, 2006), the question of their effect on community stability is one of great importance. It has far-ranging implications both for the development of ecological theory and for applied problems of biodiversity conservation.

One of the most common types of mutualistic interactions in terrestrial ecosystems is that between plants and their animal pollinators (Ollerton *et al.*, 2011). Plant-pollinator systems often comprise complex networks of interactions between highly diverse species assemblages (Bascompte & Jordano, 2007), yet it is still an open question how diversity in these systems is generated and maintained. Based on simple models of competition between two plant species for a generalist pollinator, several previous studies predicted that plant coexistence should be destabilised by interactions with pollinators (Levin & Anderson, 1970; Waser, 1978; Goulson, 1994; Kunin & Iwasa, 1996). In these model systems, the fact that the same animal must visit two conspecific flowers in close succession for pollination to occur leads to lower pollination success of an initially rarer plant species, and to the subsequent decline of that plant. This specific property of pollination was not considered in recent papers on stability of mutualistic communities that used more general models of mutualism (Bascompte *et al.*, 2006; Okuyama & Holland, 2008; Bastolla *et al.*, 2009). Thus, it remains unclear what factors maintain diversity in natural plant-pollinator systems despite the inherent reproductive disadvantage of less abundant plant species.

One factor that could possibly reduce competition between co-flowering plant species is specialisation of plant-pollinator interactions (Rathcke, 1988). Natural plant-pollinator systems exhibit a continuum from exclusive one-to-one relationships to diffuse mutualisms involving hundreds of species (Waser *et al.*, 1996; Johnson & Steiner, 2000), with the majority of networks at an intermediate level of specialisation (Blüthgen *et al.*, 2007). By specialising on a subset of all available pollinators, the loss of pollen to heterospecific flowers can be reduced (Muchhala *et al.*, 2010).

In this paper, we develop a flexible model of plant and pollinator population dynamics that allows inclusion of any number of species in the two communities, and representation of many kinds of interaction network structures. Our model is based on a mechanistic representation of plant-pollinator interactions that accounts for the specific properties of this type of mutualism. Using this model, we investigate two main questions: 1) What effect does the addition of interactions with pollinators have on the stability of a plant community and 2) How does the degree of specialisation of plant-pollinator interactions influence stability of plant-pollinator systems? In analogy to the above-mentioned studies, we began with a simple model community of two competing plant species, and compared the stability of coexistence of these two plants alone to the stability of a system with pollinators of varying degrees of specialisation. In order to establish stable coexistence of plant species in the first place, we introduced a classical stabilising mechanism, niche differentiation of the two plant species with respect to abiotic resources (Chesson, 2000), and determined the stability of plant-pollinator systems at different levels of plant niche differentiation. Furthermore, we examined the influence of other model parameters, such as the degree of pollen carryover and the amount of nectar per plant, on community stability. These analyses shed light on the complex ways in which mutualistic interactions can affect species coexistence. In future, our model may serve as a basis for investigating the stability of empirical plant-pollinator networks, and the influence of interaction structure on robustness of these systems.

2.3 THE MODEL

We first derive equations describing the dynamics of a plant community without pollinators comprising m species. All adult plants reproduce at equal per-capita rates b_{veg} through self pollination or vegetative propagules, and die at a constant rate d_P. The offspring compete for suitable sites for establishment. New plants can only establish if the total density of all plant species lies below the habitat capacity H_P. The overlap in habitat requirements of two plant species i and k is described by parameter γ_{ik}, the competition coefficient of the classical Lotka-Volterra model that varies from zero (complete niche separation) to one (complete niche overlap). The growth of a plant population of species i within one time step, ΔP_i, is thus represented by a difference equation of the form:

$$\Delta P_i = b_{veg}\left(1 - \frac{\sum\limits_{k=1}^{m} \gamma_{ik} P_k}{H_P}\right) P_i - d_P P_i \tag{2.1}$$

When pollinators are present, a second term is added to the birth rate of plant populations. This term represents the per-capita amount of pollen received by a plant, which is in turn determined by pollinator abundance and behaviour.

A key assumption of our model is that the likelihood of an interaction between a specific plant-pollinator species pair depends both on the species' relative abundances in their respective communities (a variable component) and on species-specific traits of the plant and pollinator (a fixed component). In the model, this concept is implemented in the following way (Fig. 2.1): From the pool of plant individuals a plant is randomly selected for each pollinator individual. Thus, the probability that a pollinator encounters a plant of species i is equal to species i's relative abundance, $\frac{P_i}{\sum_{k=1}^{m} P_k}$. The pollinator's decision to visit the selected plant depends on the degree of trait matching between the plant and pollinator species (Vazquez *et al.*, 2009). It comprises both traits that influence the attraction to the plant, for example preferences for certain flower colours or scents (Junker *et al.*, 2010), and traits that may act as barriers to a pollinator visit such as a complex flower morphology (Stang *et al.*, 2007). In the model, the degree of trait matching is represented by parameter α_{ij} which takes a specific value between zero and one for each plant-pollinator species pair. The total probability that an animal of species j finds and accepts a plant of species i is thus $\frac{P_i}{\sum_{k=1}^{m} P_k}\alpha_{ij}$. If a pollinator does not visit the plant it encounters, it cannot visit another plant during the same time step. By constructing different matrices of α_{ij} values, it is possible to implement any kind of interaction network structure in the model, and to explore the consequences of varying degrees of pollinator specialisation for community stability.

A distinctive attribute of pollination is that a plant can only be fertilized if the animal has visited a plant of the same species prior to the current flower visit. Moreover, pollen may be lost in intervening visits to flowers of other species (Campbell & Motten, 1985; Feinsinger *et al.*, 1988; Karron *et al.*, 2009). Therefore, in our model a flower visit only results in pollination if the visiting animal has been on a plant of the same species during at least one of its last B visits, not counting time steps without a successful flower visit. Variation of parameter B allows for an investigation of the effects of different degrees of pollen carryover on the stability of plant-pollinator systems. The probability that a pollinator of species l has visited a flower of species i in at least one of its last B visits is $1-\left(1-\frac{P_i\alpha_{il}}{\sum\limits_{k=1}^{m} P_k\alpha_{kl}}\right)^B$. The expected amount of pollen received by a plant of species i within

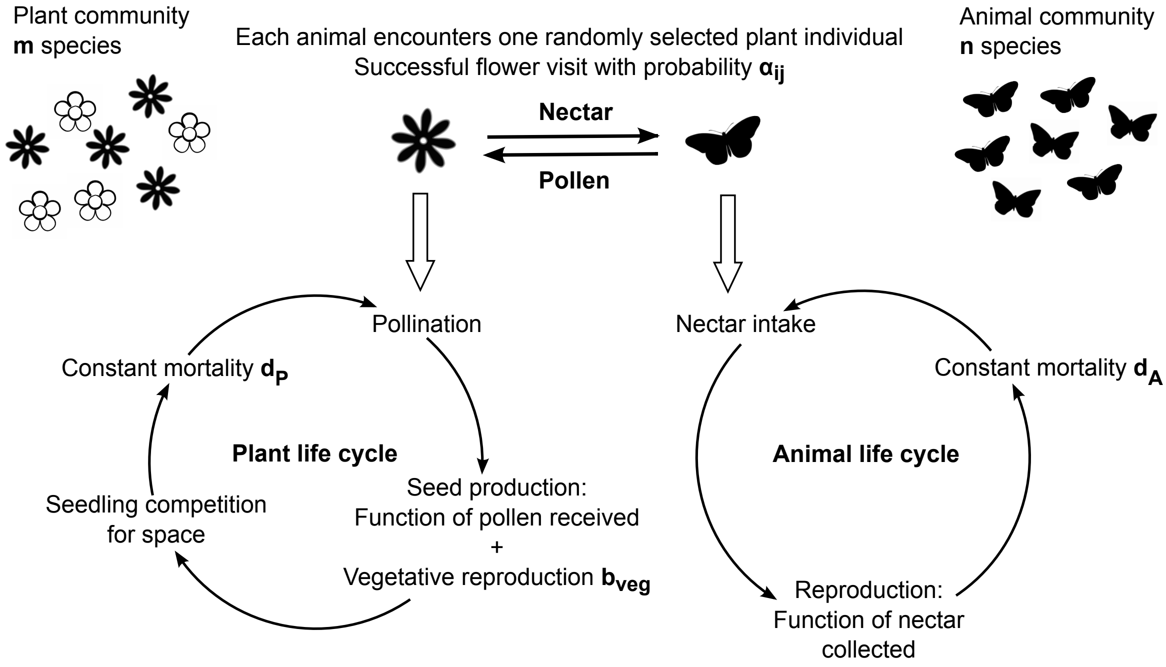

Figure 2.1: Schematic overview of the model of plant and pollinator population dynamics.

one time unit, summed over all n pollinator species with densities A_l, is thus:

$$F_i = \frac{1}{P_i}\sum_{l=1}^{n}\left(\frac{P_i}{\sum\limits_{k=1}^{m} P_k}\alpha_{il}\left(1-\left(1-\frac{P_i\alpha_{il}}{\sum\limits_{k=1}^{m} P_k\alpha_{kl}}\right)^{B}\right)A_l\right) \qquad (2.2)$$

The growth of a plant population in the presence of pollinators is then described by:

$$\Delta P_i = (F_i\beta_P + b_{veg})\left(1-\frac{\sum\limits_{k=1}^{m}\gamma_{ik}P_k}{H_P}\right)P_i - d_P P_i \qquad (2.3)$$

Here, β_P denotes the conversion of pollen to seeds. Throughout the main body of this article we assume a linear (Holling type I) functional response for both plant and animal reproduction (see below). As demonstrated in Appendix A, a saturating (Holling type II) functional response does not fundamentally change the results of our analyses.

During a flower visit, an animal receives a nutritional reward, subsequently termed "nectar", although this reward could in reality include both nectar and pollen. Here, the assumption is that collection of the reward does not have a negative effect on the plant's reproductive success, as might be the case for pollen collection. For simplicity, the amount of nectar per plant is assumed to be constant, that is, nectar is refilled instantly at the end of each time step. If several pollinators visit the same plant within a single time step, the total nectar volume N is divided equally among all visitors. Assuming that the distribution of pollinators on plants follows a Poisson distribution with mean μ_i for plants of species i, the expected amount of nectar received by a focal pollinator on a plant of species i is calculated as

$$E(\mu_i) = \sum_{k=0}^{\infty} \frac{N}{k+1} \frac{\mu_i^k e^{-\mu_i}}{k!} \tag{2.4}$$

where k denotes the number of additional pollinator individuals visiting the same flower. This expression simplifies to:

$$E(\mu_i) = \frac{N}{\mu_i}(1 - e^{-\mu_i}) \tag{2.5}$$

Setting

$$\begin{aligned} \mu_i &= \frac{\sum\limits_{k=1}^{n} A_k \alpha_{ik} \frac{P_i}{\sum_{h=1}^{m} P_h}}{P_i} && (2.6) \\ \mu_i &= \frac{\sum_{k=1}^{n} A_k \alpha_{ik}}{\sum_{h=1}^{m} P_h} && (2.7) \end{aligned}$$

and summing up over all plant species weighted by the probability of a visit to each plant gives the expected amount of nectar collected by a pollinator of species j within one time unit:

$$R_j = \sum_{i=1}^{m} \frac{P_i}{\sum\limits_{h=1}^{m} P_h} \alpha_{ij} \frac{N}{\frac{\sum_{k=1}^{n} A_k \alpha_{ik}}{\sum_{h=1}^{m} P_h}} \left(1 - e^{\frac{-\sum_{k=1}^{n} A_k \alpha_{ik}}{\sum_{h=1}^{m} P_h}} \right) \tag{2.8}$$

In analogy to the dynamics of plant populations, animal reproduction is a function of the per-capita amount of nectar, with β_A denoting the conversion of nectar to offspring. All animal populations experience a constant mortality rate d_A. Thus, the dynamics of the jth pollinator population is described by:

$$\Delta A_j = R_j \beta_A A_j - d_A A_j \tag{2.9}$$

Note that unlike plant birth rates, pollinator growth rates are assumed to be density-independent. However, density regulation of the overall pollinator population results from the limited amount of nectar provided by all plants, which in turn are limited by the habitat capacity. Thus, density regulation of plant populations is sufficient to ensure that pollinator populations also do not grow unbounded.

2.3.1 *Model Analyses*

We performed numerical analyses in order to examine how the stability of plant communities is affected by the addition of interactions with pollinators of varying degrees of specialisation. Parameter values were chosen so as to represent realistic values for a time step length of ten seconds, the time span assumed for a pollinator to find and visit a single flower. Population densities at equilibrium were found by iterating the system of difference equations until the difference between population densities in two successive iterations fell below a threshold value of 10^{-5}. Through systematic variation of initial population densities we determined the starting conditions leading to an equilibrium state that allowed all plant and animal species to persist. The analyses presented in this paper are for systems of two plant and two animal species, but the results do not change qualitatively if further species are added.

Community stability was measured by calculating the dominant eigenvalue $\hat{\lambda}$ of the Jacobian matrix at the equilibrium point with coexistence of all species (May, 1972, 1974; Otto & Day, 2007; Okuyama & Holland, 2008). The dominant eigenvalue $\hat{\lambda}$ determines the type of equilibrium (stable or unstable) as well as the rate of movement of the system back to the equilibrium (if the equilibrium is stable) or departure from the equilibrium (in case of an unstable equilibrium) following a small perturbation. For a discrete time model $|\hat{\lambda}| < 1$ indicates a stable equilibrium, $|\hat{\lambda}| > 1$ an unstable equilibrium.

Numerical analyses were performed over a wide range of parameter values and initial conditions. We used Maxima 5.20.1 (Maxima.sourceforge.net, 2010) for symbolic calculations and R 2.11.1 (R Development Core Team, 2010) for numerical analyses and preparation of figures.

To be able to vary the degree of specialisation of plant-pollinator networks continuously from a fully connected network with identical trait matching values for all interactions to a maximally specialised network with exclusive one-to-one relationships, we defined a measure of specialisation S in the following manner (Fig. 2.2): In a plant-pollinator network with n species in both communities, each pollinator species interacts preferentially with one plant species and with a lower probabil-

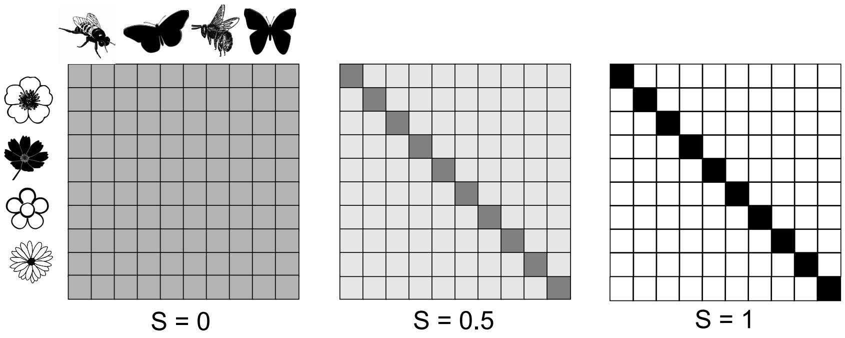

Figure 2.2: Illustration of the method used to vary the degree of specialisation ($0 \leqslant S \leqslant 1$) of plant-pollinator networks in numerical simulations. Each grid cell symbolizes an interaction between plant (rows) and pollinator species (columns). The shade of grey indicates the degree of trait matching α_{ij} of the plant and pollinator species that varies between 0 (white) and 1 (black). α_{ij} summarizes all species-specific traits that determine the likelihood of a successful flower visit, such as the proboscis length of a pollinator in comparison to the corolla length of the plant. Note that these are matrices of trait matching values, not realized interactions: The distribution of realized interactions depends on species abundances as well as on trait matching.

ity with all other plant species, such that each plant is visited preferentially by one pollinator. Trait matching of a pollinator of species j with its preferred plant species i is calculated as $\alpha_{ij} = \frac{1}{n} + \frac{S(n-1)}{n}$, and trait matching with all other plant species $k \neq i$ as $\alpha_{kj} = \frac{1}{n} - \frac{S}{n}$. Thus, $\alpha_{ij} = \alpha_{kj}$ for a completely generalised network ($S = 0$). In the most specialised network ($S = 1$), each pollinator interacts exclusively with its preferred plant, hence $\alpha_{ij} = 1$ and $\alpha_{kj} = 0$. Note that this definition of specialisation implies that a trade-off between specialist and generalist feeding behaviour exists, i.e., a generalist pollinator has a lower degree of trait matching α_{ij} with each of the plant species it utilizes compared to the respective plant species' specialist pollinators. Although it is reasonable to assume such a trade-off (Egas *et al.*, 2004; Sargent & Otto, 2006), the general patterns presented below do not qualitatively change without this assumption (see Appendix B).

2.4 RESULTS

Since all parameter values except trait matching were assumed to be equal for both species in a community, an equilibrium state with coexistence of all species was necessarily restricted to system states with exactly equal population sizes of both plant and both pollinator species. The effect of pollinator specialisation S on the stability of this equilibrium varied with the degree of niche overlap of the two plant species with respect to abiotic resources (Fig. 2.3): With a high degree of plant niche overlap (Fig. 2.3A), coexistence in plant-pollinator systems was generally unstable. The rate of movement away from the coexistence equilibrium after a small perturbation increased with increasing pollinator specialisation. Whereas community stability of completely specialised systems ($S = 1$) remained unaffected by pollen carryover, for systems with a lower degree of specialisation ($S < 1$) the speed of movement away from the equilibrium decreased with increasing pollen carryover. At an intermediate value of plant niche overlap (Fig. 2.3B), coexistence remained unstable except for highly specialised systems. Here, the rate of movement away from the coexistence equilibrium was largest for intermediate degrees of pollinator specialisation, but the difference between stability of intermediate and more extreme values of pollinator specialisation became less pronounced with increasing pollen carryover. With a further decrease in plant niche overlap, coexistence of the two plant and pollinator species became stable, at first only for specialised plant-pollinator interactions (Fig. 2.3C), then for all degrees of specialisation (Fig. 2.3D). At these low levels of plant niche overlap, a positive relationship between pollinator specialisation and the return rate to the equilibrium after a perturbation was found. Higher degrees of pollen carryover resulted in increased community stability of systems with intermediate degrees of pollinator specialisation.

The absolute values of plant niche overlap (γ_{ik}) that lead to a negative (Fig. 2.3A), negative hump-shaped (Fig. 2.3B) or positive (Fig. 2.3C and 2.3D) relationship between pollinator specialisation and community stability varied with the amount of nectar per plant (N): With sufficiently high nectar amounts, stable coexistence and a positive relationship between specialisation and stability even existed for values of plant niche overlap close to one (Fig. 2.4). Increasing the rate of conversion of nectar to pollinator offspring (β_A) or reducing the pollinators' mortality rate (d_A) had the same effect as increasing the amount of nectar per plant (results not shown). These changes resulted in higher pollinator densities at equilibrium, while plant population densities remained unchanged. For example, with increasing nectar amount (Fig. 2.4), the number of pollinator individuals per plant individual at the coexistence equilibrium changed from 0.61 (left panel) to 0.98 (middle panel) to 2.00 (right panel).

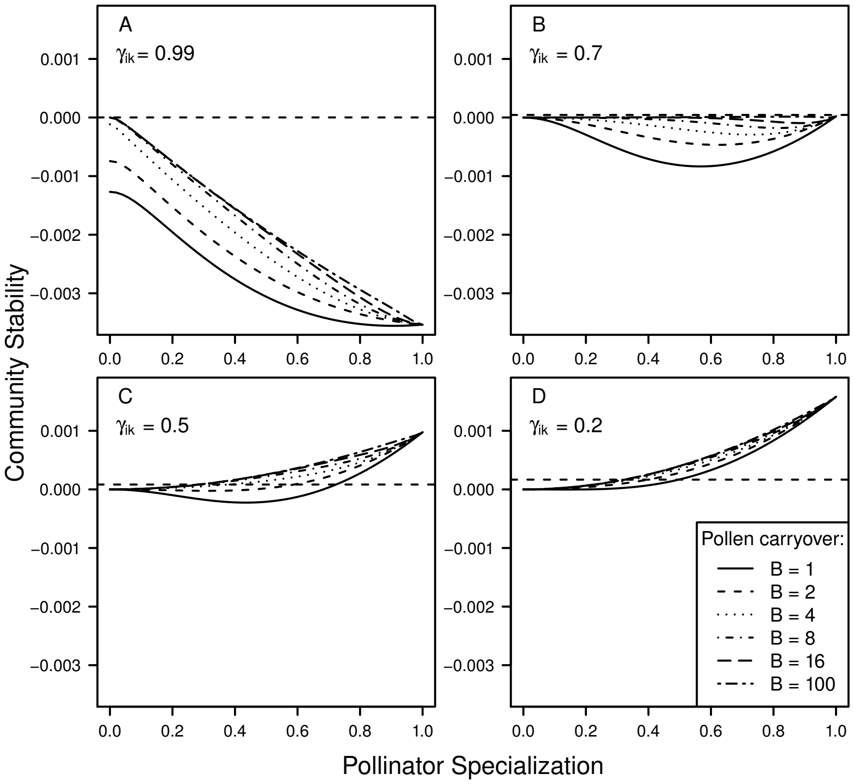

Figure 2.3: Relationship between pollinator specialisation and stability of plant-pollinator systems at four different levels of plant niche overlap. Community stability was defined as $C = 1 - |\hat{\lambda}|$, where $\hat{\lambda}$ is the leading eigenvalue of the Jacobian matrix for the equilibrium at which all four species coexist. Results are shown for six different values of pollen carryover (parameter B), the maximum number of flower visits between pollen removal and deposition, and for decreasing values of plant niche overlap with respect to abiotic resources (γ_{ik}). The dashed horizontal line indicates the stability of a plant community without pollinators. Other parameter values used for this figure: $\beta_P = 3.75 \cdot 10^{-6}$, $\beta_A = 6.33 \cdot 10^{-7}$, $d_P = 3 \cdot 10^{-8}$, $d_A = 3 \cdot 10^{-7}$, $b_{veg} = 3.5 \cdot 10^{-8}$, $N = 1.1$, $H_P = 10000$.

In comparison to the stability of a plant community without pollinators (dashed horizontal lines in Fig. 2.3 and 2.4), plant-pollinator systems exhibited higher or lower community stability depending on the combined effects of all parameters mentioned above. Since completely generalised plant-pollinator systems ($S = 0$) always had stability values of exactly zero or lower, an increase in stability compared to a plant community with only vegetative reproduction required a certain degree of pollinator specialisation. The same factors that resulted in increased community stability of plant-pollinator systems in general (see

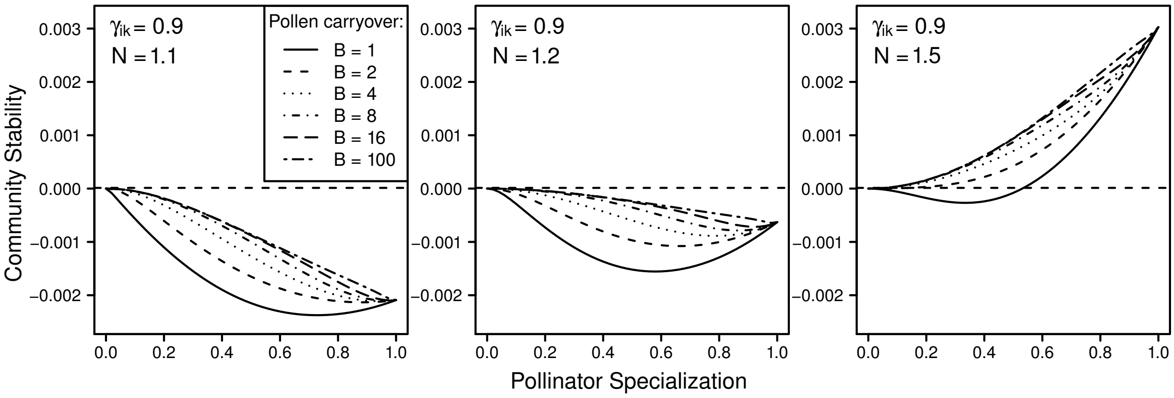

Figure 2.4: Effect of an increase in the amount of nectar per plant on stability of plant-pollinator systems. The relationship between pollinator specialisation and community stability is shown for three different values of the amount of nectar per plant (*N*), while plant niche overlap is kept constant at $\gamma_{ik} = 0.9$. All other parameter values are the same as in Fig. 2.3.

above) also facilitated greater stability of plant-pollinator systems in relation to a plant community without pollinators.

2.5 DISCUSSION

Whether certain types of interspecific interactions promote or impede species coexistence is a central question in ecological research. For mutualistic interactions between plants and pollinators, earlier studies predicted a reproductive disadvantage of less abundant plant species that would lead to rapid exclusion of any initially rarer plant if no other factors halted its decline (Levin & Anderson, 1970; Waser, 1978; Goulson, 1994; Kunin & Iwasa, 1996). Our quantitative analyses of community stability in plant-pollinator systems confirm this result. However, the destabilising effect of pollination may be compensated by stabilising mechanisms such as niche differentiation. Our results demonstrate that with sufficiently strong niche differentiation interactions with pollinators may even increase the stability of plant species coexistence.

In our stability analyses we analysed system behaviour in response to small perturbations from the equilibrium. For plant-pollinator systems with two species in each community, three different relationships between pollinator specialisation and community stability were found: A negative relationship with high degrees of plant niche overlap, a unimodal relationship at an intermediate level of plant niche overlap, and a positive relationship when plant niches were largely separated. The situation at high levels of plant niche overlap corresponds to the case described by Levin & Anderson (1970) and others for generalised pollination. Here, species coexistence is generally unstable, and a slight disturbance affecting a system at the coexistence equilibrium results in extinction of the initially rarer plant species. Interestingly, we found that species coexistence was unstable regardless of the degree of specialisation of plant-pollinator interactions. The causes of this general instability become clear through a closer examination of the extremes of pollinator specialisation.

In a system with two or more plant species sharing generalist pollinators, rare plant species receive as many visits on a per-capita basis as more common species, but the probability that a visiting pollinator carries conspecific pollen is lower for plant species with lower relative abundance. As a consequence, rare plant species produce a lower number of seeds per capita. If all plant species are almost equal in competition for space (i.e., $\gamma_{ik} \approx 1$ for $i \neq k$), the probability that a plant of species i will establish at a given site is mainly determined by the proportion of all seeds produced by that species. Thus, plants of a less abundant species have fewer successfully established offspring per capita, and the species becomes successively rarer with each time step. The extent of pollen carryover determines the speed of extinction of a rare plant species. The higher the maximum number of flower visits between pollen removal and deposition (parameter B), the smaller the reproductive disadvantage of a rare plant species.

When each pollinator species is completely specialised on one plant species, the probability that a plant receives conspecific pollen is independent of its frequency in the community. However, a specialist pollinator of a rarer plant species needs to spend more time searching for its preferred plant; hence its mean rate of nectar intake and population growth rate are lower compared to those of a pollinator specialised on a more abundant plant. As a consequence, the rare plant receives fewer pollinator visits on a per-capita basis and produces fewer seeds than its more abundant competitor. This places the rare plant at a disadvantage in seedling competition for space. Thus, the situation creates a positive feedback that results in rapid extinction of the plant-pollinator species pair. In plant-pollinator systems with an intermediate degree of specialisation, rare plant species experience a mixture of the two different mechanisms that lead to reduced growth rates in completely generalised and specialised systems.

Whereas plant species without pollinators stably coexist as long as all $\gamma_{ik} < 1$, a higher degree of plant niche separation is necessary to overcome the minority disadvantage in plant-pollinator systems. As γ_{ik} decreases, the relationship between pollinator specialisation and community stability changes from negative (highest rate of departure from the equilibrium at high degrees of pollinator specialisation) to unimodal (highest departure rates at intermediate degrees of specialisation). Here, the combined effects of both types of reproductive disadvantages experienced by rare species in specialised and generalised pollination systems lead to a faster decline of initially rarer species than either disadvantage alone. This strong effect in systems of intermediate degrees of specialisation diminishes, however, with increasing pollen carryover.

At sufficiently low levels of plant niche overlap, species coexistence in plant-pollinator systems becomes stable for all degrees of specialisation except completely generalised systems. In completely generalised plant-pollinator systems, community stability cannot rise above zero, because in this case the two pollinator species are identical in all respects. Therefore, their coexistence is neutral. In a real ecosystem subject to environmental and demographic stochasticity, such a neutral community would slowly loose pollinator species through random ecological drift until eventually only one species remains. Although the assumption of two or more pollinator species with exactly identical traits is somewhat hypothetical, our analyses show that stability of marginally specialised systems is also close to zero. With increasing pollinator specialisation, the rate of return to the coexistence equilibrium after a small perturbation rises and becomes even larger than the return rate of a plant community without pollinators. Apparently, the increase in plant birth rates produced by interactions with pollinators leads to a faster recovery after a disturbance. Interestingly, whereas in a recent paper Bastolla *et al.* (2009) found that generalised mutualistic networks allowed a maximum number of species to coexist, in our analyses community stability was maximized at high degrees of pollinator specialisation. Whether this difference is due to the specific properties of pollination in comparison to other types of mutualism, or a result of the different measures of stability applied, merits further investigation.

In our analyses, the degree of plant niche differentiation necessary to enable stable coexistence in plant-pollinator systems varied with the values of three parameters that influence pollinator growth rates: the amount of nectar per plant (N), the rate of conversion of nectar to pollinator offspring (β_A), and pollinator mortality (d_A). The effect of these factors on community stability can be most easily understood by considering a system with two plant species P_i and P_k and perfectly specialised pollinators A_j (with $\alpha_{ij} = 1$ and $\alpha_{kj} = 0$) and A_l (with $\alpha_{il} = 0$ and $\alpha_{kl} = 1$). Here, even with niche differentiation of the two plant species and no interspecific competition between pollinators for food resources, the presence of P_i has an indirect effect on the pollinator of P_k: The higher the relative abundance of plant species *i*, the more time do pollinators of species *l* need to spend searching for their preferred plant species *k*. Thus, if the relative abundance of plant *i* increases, the nectar intake rate of pollinator *l* may fall to a level where its birth rate cannot compensate its mortality. In that case, A_j will decline and may become extinct if its birth rate at low density is still not high enough to balance its death rate. Increasing the amount of nectar per plant or the conversion rate of nectar to pollinator offspring, or decreasing pollinator mortality, allows a pollinator of a rarer plant species to survive under conditions that would otherwise result in its extinction. As long as the plant niches are sufficiently separated and b_{veg} is large enough to maintain a plant population in the absence of pollinators, plant species *k* will survive even if its pollinator dies out. On the other hand, if plant competition for space is strong, plant *k* may not be able to compete with plant *i* in the absence of its pollinator, and may therefore also become extinct. However, our measure of local stability does not distinguish between these two cases.

As we have now identified the degree of plant niche overlap and the three parameters affecting pollinator growth rates as the most important factors that determine the effect of plant-pollinator interactions on plant coexistence, it is clear that empirical estimates of these parameters are needed in order to draw conclusions about the stability of real plant-pollinator systems. As for plant niche overlap, very few studies provide experimentally derived estimates of Lotka-Volterra competition coefficients (Goldberg & Barton, 1992; Silvertown, 2004), a fact that may partly be due to the lack of a mechanistic basis of the Lotka-Volterra model (Chesson, 2000; Dormann & Roxburgh, 2005). However, since resource requirements and mode of resource use of different plant species within communities such as a meadow are often strikingly similar, it seems likely that levels of plant niche overlap close to one are the norm rather than the exception in natural plant communities. Consequently, there is an ongoing debate about the question whether differential resource use alone can explain coexistence of diverse plant communities even in the absence of a minority disadvantage mediated through pollination (e.g. Bell, 2001; Silvertown, 2004; Leibold & McPeek, 2006; Levine & HilleRisLambers, 2009). This raises the question whether growth rate parameters of real pollinator populations are such that stable coexistence in plant-pollinator systems is possible even at high degrees of plant niche overlap. Rather than trying to find estimates for each parameter separately, it may be helpful to consider the fact that all three parameters affect the ratio of pollinators per plant at the coexistence equilibrium. To our knowledge, no estimates of this ratio have been published, but in a few cases the amount of flower resources required to rear a bee larva has been quantified (Müller *et al.*, 2006, and references therein). These studies seem to indicate that the number of flowers needed to raise one bee varies widely, from less than one flower head of *Helianthus annuus* (Asteraceae) to several dozen flowers of *Campanula rapunculus* (Campanulaceae). Therefore, it may well be that the effect of interactions with pollinators on plant coexistence varies from one community to the other.

In conclusion, our analysis of population dynamics in plant-pollinator systems has shown that interactions with pollinators may impede or facilitate plant coexistence, and identified a number of parameters that influence the stability of plant and pollinator communities. However, apart from the task of finding empirical estimates for these parameters, our approach has its limitations and several open questions remain. For example, the measure of community stability applied here is just one of several possible choices (Grimm & Wissel, 1997), and one that is only based on a system's behaviour in the immediate vicinity of an equilibrium state. It would not be surprising if a measure that accounts for the effects of larger perturbations produced a different relationship between pollinator specialisation and stability. Moreover, niche differentiation of plant species is by no means the only mechanism that may induce stable coexistence in plant-pollinator systems. From the literature, a number of other potentially stabilising mechanisms are known that are not specific to plant-pollinator interactions, but can contribute to species coexistence in a variety of ecological contexts (Chesson, 2000). Likewise, competition between pollinators could be modelled differently. In the current model, pollinators do not compete for resources other than nectar. Thus, the strength of interspecific competition solely depends on the probability that two pollinators of different species visit the same flower. Inclusion of pollinator competition for other resources, e.g. nesting sites for bees or larval host plants for butterflies, could affect the stability properties of the system in several ways. Niche differentiation of pollinator species with respect to these other resources could have a stabilising effect similar to that produced by plant niche differentiation. However, while populations of some pollinator species such as stem-nesting solitary bees may be strongly limited by availability of nesting sites (Steffan-Dewenter & Schiele, 2008), other important pollinator groups are unlikely to be limited by resources required for larval development. As a further group of mechanisms that contribute to species coexistence, other equalising mechanisms besides pollen carryover could reduce the reproductive disadvantages of rare species in plant-pollinator systems. Some of these, such as flower constancy (Goulson, 1994; Kunin & Iwasa, 1996) or spatial aggregation of conspecific plants (Levin & Anderson, 1970; Campbell, 1986) were already mentioned by the authors of the papers that first pointed out the distinctive features of pollination and their consequences for species coexistence. While it is beyond the scope of this paper to examine the differential effects of each of these factors, studying their relative importance for diversity maintenance may provide valuable insights to guide conservation efforts. Finally, the simple model systems with symmetric specialisation examined in this study are of course an ideal. In real pollinator communities, a mixture of different degrees of specialisation is usually found. Our model provides the means to study the stability properties of real plant-pollinator networks in order to gain a deeper understanding about the relationship between interaction structure and robustness. This knowledge may help in making informed conservation decisions in order to preserve diverse plant-pollinator systems under rapidly changing conditions.

2.6 APPENDIX

2.6.1 *Effect of a Holling type II functional response on community stability.*

With saturating functional responses, the dynamics of plant (P_i) and pollinator populations (A_j) are described by the following equations:

$$\Delta P_i = \left(\frac{F_i S}{h_P + F_i} + b_{veg}\right)\left(1 - \frac{\sum_{k=1}^{m} \gamma_{ik} P_k}{H_P}\right) P_i - d_P P_i$$

$$\Delta A_j = \frac{R_j T}{h_A + R_j} A_j - d_A A_j$$

Here, *S* and *T* denote the maximum number of seeds or pollinator offspring, respectively, that a single individual can produce within one time step. h_P and h_A are half-saturation constants. All other parameters are as defined in the main text.

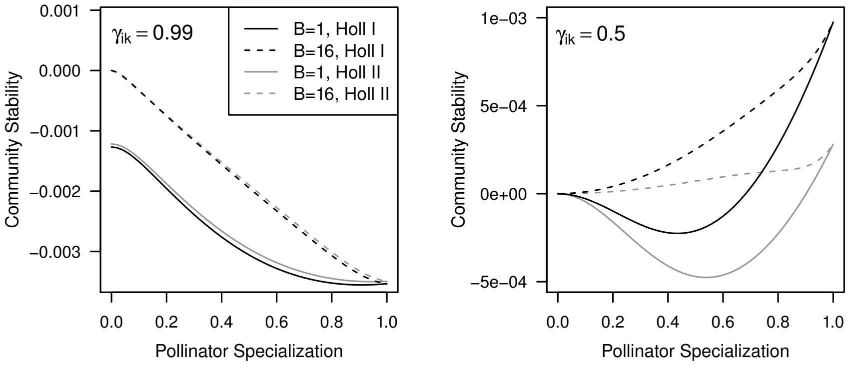

Figure 2.5: Effect of a Holling type II functional response on community stability. In both graphs, community stability of a system with two plant and two pollinator species is plotted against the degree of specialisation of plant-pollinator interactions for Holling type I (black lines) and Holling type II functional responses (grey lines) of both plant and animal birth rates. Results are shown for two degrees of plant niche overlap (γ_{ik}, left and right panel) and two different values of pollen carryover (B). Community stability was measured as $C = 1 - |\hat{\lambda}|$, where $\hat{\lambda}$ is the largest eigenvalue of the Jacobian matrix at the coexistence equilibrium. The following parameter values were used for this figure: $S = 1 \cdot 10^{-5}$ and $h_P = 2.6666$ or $\beta_P = 3.75 \cdot 10^{-6}$, respectively, $T = 1 \cdot 10^{-5}$ and $h_A = 15.5797$ or $\beta_A = 6.33 \cdot 10^{-7}$, respectively, $d_P = 3 \cdot 10^{-8}$, $d_A = 3 \cdot 10^{-7}$, $b_{veg} = 3.5 \cdot 10^{-8}$, $H_P = 10000$, $N = 1.1$.

The introduction of a saturating functional response for plant and pollinator reproduction did not induce a fundamental change in the relationship between pollinator specialisation and community stability (Fig. 2.5). However, a decrease in plant niche overlap from $\gamma_{ik} = 0.99$ to $\gamma_{ik} = 0.5$ had a stronger effect on a system with Holling type I functional responses. Otherwise, effects of pollinator specialisation and pollen carryover were identical.

2.6.2 *Relationship between specialisation and community stability without a trade-off between generalist and specialist feeding behaviour*

The measure of specialisation of plant-pollinator networks S used in the main article implies that a trade-off between specialist and generalist interactions exists. In order to investigate if the relationship between specialisation and community stability would be altered without this assumption, we constructed matrices with $\alpha_{ij} = 1$ for an existing interaction and $\alpha_{ij} = 0$ for no interaction, and varied the number of interactions of each plant and pollinator species from a fully connected network to a network with exclusive one-to-one relationships (Fig. 2.6). In accordance with the patterns found for networks with a specialist-generalist trade-off, at high levels of plant niche overlap the rate of departure from the equilibrium after a small disturbance increased with increasing network specialisation (Fig. 2.7, $\gamma_{ik} = 0.99$). Likewise, community stability of generalised networks approached zero for high degrees of pollen carryover, and a decrease in plant niche overlap resulted in a positive relationship between pollinator specialisation and community stability (Fig. 2.7, $\gamma_{ik} = 0.5$). Thus, the qualitative results of the stability analyses presented in this paper do not depend on the assumption of a trade-off between generalist and specialist feeding behaviour.

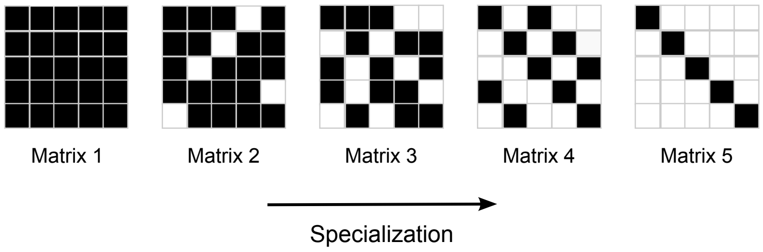

Figure 2.6: Illustration of the method used to vary the degree of specialisation of plant pollinator networks without a trade-off. For the analyses presented in Fig. 2.7, matrices of trait matching values (α_{ij}) for interactions between five plant and five pollinator species were constructed. The number of interaction partners per species was gradually reduced from five to one for successively more specialised networks. Trait matching values were set to $\alpha_{ij} = 1$ (black) for existing interactions and $\alpha_{ij} = 0$ (white) for no interaction.

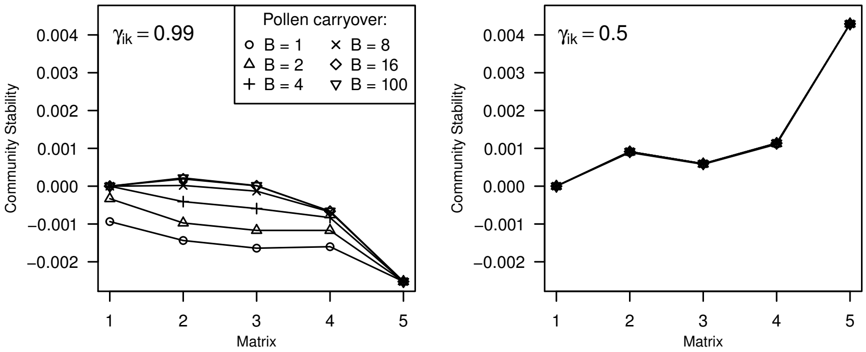

Figure 2.7: Community stability without a trade-off between generalist and specialist feeding behaviour. For the interaction matrices depicted in Fig. 2.6, community stability was calculated as $C = 1 - |\hat{\lambda}|$, where $\hat{\lambda}$ is the leading eigenvalue of the Jacobian matrix for the equilibrium at which all species coexist. Results are shown for six different values of pollen carryover (parameter B), the maximum possible number of flower visits between pollen removal and deposition, and two different degrees of plant niche overlap (γ_{ik}). Other parameter values used for this figure: $\beta_P = 3.75 \cdot 10^{-6}$, $\beta_A = 2 \cdot 10^{-6}$, $d_P = 3 \cdot 10^{-8}$, $d_A = 3 \cdot 10^{-7}$, $b_{veg} = 3.5 \cdot 10^{-8}$, $N = 1$, $H_P = 10000$.

3

CAN PLANT-POLLINATOR INTERACTIONS PROMOTE PLANT DIVERSITY?[1]

3.1 ABSTRACT

In the light of rapid losses of biodiversity worldwide, it has become more important than ever to study the factors that ensure the continued existence of diverse ecological communities. Whereas the diversity-enhancing effects of antagonistic interactions are relatively well understood, much less is known about the contribution of mutualistic interactions to the maintenance of biodiversity. The current study assesses the influence of the presence of pollinators on the diversity of plant communities with alternative means of reproduction beside animal pollination. In contrast to the conclusions of a recent more general model of plant-animal mutualisms, the results of our numerical simulations suggest that interactions with pollinators do not generally promote plant diversity. Despite a potential for increased plant species richness through the positive effect of pollinators on plant birth rates, species richness of plants was mostly negatively affected by the presence of pollinators, regardless of the structure of the interaction network. Our results imply that for plant communities with alternative means of reproduction, the loss of pollinators will usually not lead to decreased diversity. However, whereas the immediate effects of pollinator loss on plant community composition may be negligible, the long-term population genetic consequences are likely to be severe.

3.2 INTRODUCTION

Confronted with the fact that biodiversity is not evenly distributed across space and time, ecologists have long sought to understand the mechanisms underlying the observed diversity patterns. Whilst rates of speciation and global extinction determine the size and composition of the pool of regionally occurring species, the subset of species that form a local community is a product of colonization and extinction processes on a shorter time scale. Interspecific interactions play an impor-

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[1] Article by G. Benadi, N. Blüthgen, T. Hovestadt and H.-J. Poethke
Submitted to *The American Naturalist*

tant part in determining which species become established in a given locality. Clearly, interactions between members of the same guild, such as resource competition (e.g. Goldberg & Barton, 1992) and facilitation (Bruno *et al.*, 2003), have a strong impact on community diversity, but interactions with other trophic levels can be just as influential. Predators, for example, may mediate the outcome of competitive interactions among prey species if they preferentially target the most abundant species or the strongest competitor (Paine, 1969). In many cases it has been shown that natural enemies exert a major influence on the diversity of their target species and associated competitors (e.g. McCauley & Briand, 1979; Olff & Ritchie, 1998; Hastings & Godfray, 1999; Petermann *et al.*, 2008; Bagchi *et al.*, 2010).

Whereas the diversity-enhancing effects of natural enemies have been the subject of a well-developed body of theoretical studies (Chesson, 2000, and references therein), much less is known about the possible ways in which mutualistic interactions may influence biodiversity. Empirical studies and conceptual models exist for certain types of interactions (Stachowicz, 2001), most notably those between arbuscular mycorrhizal fungi and their host plants (Urcelay & Diaz, 2003). However, in many cases generalisation of these insights to other mutualisms is made difficult by the heterogeneous nature of mutually beneficial interactions.

Beside plant-mycorrhiza systems, interactions between plants and pollinating animals are one of the most common types of mutualisms in terrestrial ecosystems (Ollerton *et al.*, 2011). In the last decades, declines of pollinator populations have been recorded worldwide, raising concerns about the loss of the important ecological function of pollinators for wild plant communities and agricultural systems (Potts *et al.*, 2010). While some plant species rely completely on animal pollination to reproduce, many plants possess alternative modes of reproduction such as wind pollination, selfing and production of vegetative propagules. A key question is how the loss of pollinators will affect these plants, and whether the presence of pollinators is required to maintain the current level of plant diversity.

To our knowledge, until now, the influence of the presence of pollinators on plant diversity has only been addressed in a single study. Using an analytical approach, Bastolla *et al.* (2009) compared the maximum number of species that can stably coexist in plant-pollinator or plant-seed disperser systems in the absence and presence of mutualistic interactions between the two communities. Furthermore, they explored the effects of different configurations of the network of mutualistic interactions on the maximum number of coexisting species. The authors concluded that these interactions can increase the number of coexisting species in both communities by reducing the strength of interspecific competition between community members. With regard to network structure they found that fully connected networks allowed the highest number of species to coexist, while in networks with a lower connectance the number of coexisting species increased with the degree of nestedness of the interaction matrix.

Inspired by the work of Bastolla *et al.* (2009), the current article aims to undertake a more detailed examination of the effect of plant-pollinator interactions on plant diversity. Recent analyses showed that the stability properties of plant-pollinator systems differ from those of other types of mutualistic interactions (Benadi *et al.*, 2012a). This difference is due to the fact that pollination requires a previous visit of a pollinating animal to a flower of the same species. The generic models of mutualistic systems used in several recent articles (Bastolla *et al.*, 2009; Bascompte *et al.*, 2006; Okuyama & Holland, 2008) did not account for this specific property of pollination, although it is now known to have a considerable effect on species coexistence (Benadi *et al.*, 2012b). Furthermore, these models were based on the assumption that no competition between plants for flower visits or between flower visitors for floral resources occurs, although empirical evidence indicates that both intra- and interspecific competition for mutualistic services are common in plant-pollinator systems (pollinator competition: Heinrich 1976; Inouye 1978; Carpenter 1979; Laverty & Plowright 1985; plant competition: Mitchell *et al.* 2009b, and references therein).

How could interactions with pollinators affect plant population dynamics and ultimately, the diversity of a plant community? Most simply, the presence of pollinators may increase a plant population's birth rate provided that births are not limited by other factors such as the availability of resources required for seed production. Because a population's equilibrium density results from the balance of births and deaths, a higher birth rate translates into a larger population at equilibrium. It is a well established fact that, all else being equal, larger communities in terms of total number of individuals can contain a higher number of species, because a larger total population allows more species to maintain populations above a threshold size below which the risk of extinction due to stochastic fluctuations is high (Lawton, 1995). However, the presence of pollinators can only result in a larger total population if free space for establishment of additional individuals is available. If the total plant population already fills all available habitat in the absence of pollinators, animal pollination should have no effect on the total population size, and thus also no effect on the number of coexisting plant species.

In addition to possible effects on the size of the overall plant population, interactions with pollinators may influence the outcome of competitive interactions between plant species. Unless plant-pollinator species pairs are completely specialised, plant species compete for pollinator visits as well as for abiotic resources such as water, light and nutrients, or simply for space. Our previous analyses of plant-pollinator systems with two species in each group showed that the effect of the presence of pollinators on the stability of plant coexistence varies with the degree of overlap of the plant species' abiotic niches and the degree of specialisation of plant-pollinator interactions (Benadi *et al.*, 2012b). For more speciose mutualistic systems, several recent studies have pointed out the significant role of the structure of the interaction network for species coexistence (Bastolla *et al.*, 2009; Okuyama & Holland, 2008). An important structural parameter is the connectance of a network, the proportion of realized interactions, a measure of network-level specialisation that only accounts for qualitative information, i.e., information about the presence or absence of interactions between a pair of species. Another characteristic feature of mutualistic networks is their degree of nestedness, the propensity of specialists to interact with proper subsets of the interaction partners of more generalised species (Bascompte *et al.*, 2003). Empirical studies of mutualistic networks often report high degrees of nestedness (e.g. Bascompte *et al.*, 2003; Alarcon *et al.*, 2008; Petanidou *et al.*, 2008), but others have pointed out that nestedness may often be the result of incomplete sampling rather than a true feature of the interaction network (Blüthgen, 2010). Nevertheless, for a theoretical comparison of interaction structures nested networks represent a realistic mixture of generalised and specialised interactions in comparison to the extreme cases of uniformly generalised or specialised networks.

While Bastolla *et al.* (2009) examined the effects of these qualitative network parameters on the number of coexisting species, their study did not address the quantitative aspects of network structure. Specifically, they did not consider the possibility of a trade-off between the number of interaction partners of a species and its effectiveness in handling each interaction partner. However, the existence of such a trade-off is the most widely accepted explanation for specialisation of organisms on certain types of resources (e.g. Egas *et al.*, 2004; Rueffler *et al.*, 2007). Evidence for a generalist-specialist trade-off in the efficiency of flower handling has been found in several pollination systems (Laverty & Plowright, 1988; Thøstesen & Olesen, 1996).

In the present article, we perform numerical analyses of a mathematical model of plant and pollinator population dynamics to study the effect of the presence of pollinators on the diversity of a plant community. Following Bastolla *et al.* (2009), we compare numbers of coexisting species for three types of interaction matrices: a fully connected matrix, a matrix with lower connectance and maximally nested interactions, and a matrix with the same connectance, but with interactions clustered along the diagonal. Each matrix type is tested with and without a trade-off between generalised and specialised flower visitation of pollinator species. Furthermore, we examine the pollinators' influence on a plant community whose combined equilibrium density lies far below the habitat capacity in the absence of pollinators, and a plant community that fills nearly all available habitat even without the added benefit of animal pollination. Since species richness is just one aspect of diversity, we also consider the impact of interactions with pollinators on the evenness of plant abundances. In contrast to our previous stability analyses of simple 2x2-species systems (Benadi *et al.*, 2012a,b), here we consider the diversity of realistically large plant and pollinator communities with a mixture of different degrees of specialisation (nested network) as well as uniformly generalised (full network) and specialised (diagonal network) interaction patterns.

3.3 THE MODEL

The model employed in this study consists of a number of difference equations of Lotka-Volterra type that each describe the growth of a plant or pollinator population. Unlike classical Lotka-Volterra models, this model comprises a fairly detailed mechanistic representation of interactions between individual plants and pollinators. Here, we give only a brief overview of the underlying assumptions of the model. Further information is provided in Online Appendix A. See Benadi *et al.* (2012b) for a discussion of the stability properties of this model in the context of simple 2x2 species systems.

In the absence of pollinators, each plant population with density P_i is characterized by its intrinsic rate of reproduction through self pollination and vegetative propagules, b_{veg}, and its mortality rate d_P. Whereas the mortality rate is assumed to be density-independent, the number of successfully established plant offspring declines with the amount of available empty habitat. Here, H_P, the habitat capacity, denotes the maximum number of coexisting plant individuals the patch of habitat can support, assuming identical habitat requirements of all individuals. The overlap in habitat requirements of two plant species i and k is described by parameter γ_{ik}, the competition coefficient of the classical Lotka-Volterra model that varies from zero (complete niche separation) to one (complete niche overlap). Interactions with pollinators add a second term to the birth rates of plant populations. This term represents the per-capita amount of pollen received by a plant, which is in turn determined by pollinator abundance and behaviour.

In the model, interactions between individual plants and pollinators are implemented as follows: During a small time step, each pollinator individual encounters a randomly selected plant individual. The decision to visit the encountered plant depends on the degree of trait matching between the plant and pollinator species (α_{ij} for interactions between plant species *i* and pollinator species *j*, with $0 \leqslant \alpha_{ij} \leqslant 1$). The degree of trait matching encompasses all species-specific traits that affect the likelihood of a successful flower visit, such as a preference for the flower's colour or scent (Junker *et al.*, 2010) or a morphological barrier that prevents the pollinator from reaching the flower's nectar (Stang *et al.*, 2007). For a community with *m* species, the total probability that an animal of species j finds and accepts a plant of species i is thus $\frac{P_i}{\sum_{k=1}^{m} P_k}\alpha_{ij}$. If a pollinator does not visit the plant it encounters, it cannot visit another plant during the same time step.

Since a flower visit only results in pollination if the animal has recently visited a flower of the same species (e.g. Feldman *et al.*, 2004; Karron *et al.*, 2009), a further parameter in the model represents the maximum number of flower visits that may lie between pollen removal and pollen deposition, i.e., the degree of pollen carryover, *B*. The probability that an animal of species *j* has visited a plant of species *i* during at least one of its last *B* flower visits (not counting time steps without a successful flower visit) equals $1 - \left(1 - \frac{P_i \alpha_{ij}}{\sum\limits_{k=1}^{m} P_k \alpha_{kj}}\right)^B$. Thus, the expected amount of pollen received by a plant of species i within one time unit, summed over all n pollinator species with densities A_j, is:

$$F_i = \frac{1}{P_i} \sum_{j=1}^{n} \left(\frac{P_i}{\sum\limits_{k=1}^{m} P_k} \alpha_{ij} \left(1 - \left(1 - \frac{P_i \alpha_{ij}}{\sum\limits_{k=1}^{m} P_k \alpha_{kj}} \right)^{B} \right) A_j \right) \tag{3.1}$$

The growth of a plant population is then described by

$$\Delta P_i = (F_i \beta_P + b_{veg}) \left(1 - \frac{\sum\limits_{k=1}^{m} \gamma_{ik} P_k}{H_P} \right) P_i - d_P P_i \tag{3.2}$$

with $F_i = 0$ for a plant population in the absence of pollinators. Here, β_P denotes the conversion of pollen to seeds.

Unlike the plant species that are able to survive in the absence of pollinators, in our model pollinators obligatorily depend on floral resources. Upon arrival at a flower, a pollinator collects nectar from the flower. If several animals visit the same flower in one time step, the total amount of nectar *N* is divided equally between them. For simplicity, the amount of nectar per flower is assumed to be constant. Assuming that the distribution of pollinators on flowers follows a Poisson distribution, the expected amount of nectar collected by a pollinator of species *j* during one time unit is:

$$R_j = \sum_{i=1}^{m} \frac{P_i}{\sum\limits_{h=1}^{m} P_h} \alpha_{ij} \frac{N}{\frac{\sum_{k=1}^{n} A_k \alpha_{ik}}{\sum_{h=1}^{m} P_h}} \left(1 - e^{\frac{-\sum_{k=1}^{n} A_k \alpha_{ik}}{\sum_{h=1}^{m} P_h}} \right) \tag{3.3}$$

In analogy to the dynamics of plant populations, animal reproduction is a function of the per-capita amount of nectar, with β_A denoting the conversion of nectar to offspring. All animal populations experience a constant mortality rate d_A. Thus, the dynamics of the *j*th pollinator population is described by:

$$\Delta A_j = R_j \beta_A A_j - d_A A_j \tag{3.4}$$

3.3.1 *Model analyses*

In order to examine the influence of interactions with pollinators on plant diversity, we performed numerical simulations starting with as many plant species as the habitat could support if all available space was occupied. For a given habitat capacity H_P, a minimum population size P_T, and a degree of niche overlap of different plant species γ_{ik}, the maximum number of coexisting plant species was calculated as:

$$m_{full} = \frac{H_P - P_T}{P_T \gamma_{ik}} + 1 \tag{3.5}$$

Simulations were initialized with m_{full} plant species (rounded down to a full integer), and in the case of simulations of plant-pollinator systems, with an equal number of animal species.

With the exception of specific trait matching values for each plant-pollinator species pair, population parameters were set to identical values for all species in a community so as to focus on the effects of the different interaction structures. A further exception was made for the plants' interspecific competition coefficients. If the degrees of niche overlap of all plant species in the absence of pollinators were exactly equal, the evenness of such a community at equilibrium would be maximal, and interactions with pollinators could only lead to a decrease in evenness. In order to avoid this unrealistic symmetry and allow for the possibility of a positive effect of pollinators on evenness of the plant community, interspecific competition coefficients were drawn from a uniform distribution with a reasonable range of values. The mean of this distribution was used for the calculation of m_{full}. Reciprocal effects of plant species on one another were assumed to be identical (i.e., $\gamma_{ik} = \gamma_{ki}$). Within a species, all individuals were assumed to have identical resource requirements (i.e., all $\gamma_{ii} = 1$). In general, the choice of parameter values was guided by empirical estimates wherever possible (Table 3.1), and all relevant parameters were varied systematically to assess their effects on the diversity of the plant community. For parameters of population growth, values were chosen based on a time step length of ten seconds, the typical time span assumed for a pollinator to find and visit a single flower. In order to compare the effects of the addition of pollinators on plant communities close to the habitat capacity versus communities far below the habitat capacity in the absence of pollinators, two different rates of vegetative reproduction were chosen. Through the balance of reproduction and mortality, the lower of these values resulted in a small total population at equilibrium, while the larger rate of reproduction allowed the plant population to fill nearly all available habitat even in the absence of animal pollinators.

To simulate systems with animal pollination, the structure of the six types of interaction matrices (full, nested and diagonal, each with and without a generalist-specialist trade-off) was defined using the trait matching values (α_{ij}) for pairwise

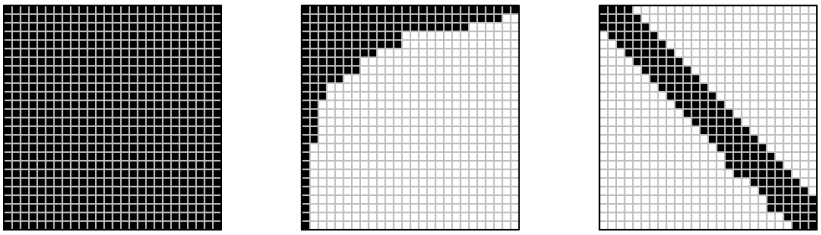

Figure 3.1: Illustration of the three types of interaction matrices examined in this study. From left to right: full, nested and diagonal matrix. Each cell of a matrix represents an interaction between a plant-pollinator species pair. Rows correspond to plant species, columns to pollinator species. Realized interactions are in black.

interactions (Fig. 3.1). For interactions without a trade-off, trait matching values were set to one for an existing interaction and to zero for no interaction. A trade-off between the number of plant species visited by a pollinator and its effectiveness in handling each of them was implemented by keeping the sum of all trait matching values of each pollinator species constant. Thus, a specialist pollinator for a certain plant species would match the plant's traits perfectly ($\alpha_{ij} = 1$), while a generalist pollinator visiting x plant species would have a trait matching value of $\alpha_{ij} = \frac{1}{x}$ with each of them. Perfectly nested trait matching matrices were generated by assigning a degree (the number of interaction partners) to each pollinator species in the following manner: In order to ensure that each plant species would be visited by at least one pollinator species, the first pollinator species received a degree of m, the number of plant species. Following Okuyama & Holland (2008), the degrees of the remaining species were drawn from a modified power distribution with probability density function $P(k) = Ck^{-\gamma}$, where $k = 1...(m-1)$ and $C = \sum_{k=1}^{m-1} k^{-\gamma}$ is a normalization factor introduced to account for the fact that the largest possible degree is constrained by the number of plant species. Based on empirical estimates, a value of 1.5 was chosen for the exponent γ of the power distribution (Okuyama & Holland, 2008, and references therein). The pollinator species were then ordered according to their degree so as to obtain a perfectly nested matrix. For the diagonal network the same connectance as for the nested matrix was used, but interactions were distributed first along a diagonal line from the upper-left to the lower right corner of the matrix, then along parallel lines on either side of the diagonal, until the desired number of interactions was reached. If the remaining number of unassigned interactions was not sufficient to completely fill a diagonal line, interactions were distributed randomly along the line.

Simulations were started with initial population densities randomly drawn from the interval $\{P_T, 2P_T\}$. The system of difference equations was subsequently iterated until an equilibrium state was reached, as indicated by the largest difference between population densities in successive time steps falling below a threshold value of 10^{-5}. 100 simulations were performed with each combination of parameter values. All parameter combinations were tested with the same sets of random numbers for initial population densities and plant competition coefficients, so as to allow for pairwise comparisons of simulation runs with and without pollinators. For the calculation of m_{full}, a population size of $P_T = 100$ individuals was assumed, resulting in simulations with 26 plant species with a habitat capacity H_P of 2000 individuals and an average degree of niche overlap of $\gamma_{ij} = 0.75$ (Eq. 3.5). To test for the effect of the choice of the extinction threshold on the results of the analyses, total population sizes, species richness and evenness of the plant community were calculated including all species with a population size of at least 100, 10 and 1 individuals at equilibrium. Evenness was calculated based on the Shannon diversity index H' as $E = \frac{H'}{\log(S)}$ (Pielou, 1969, 1975), where S is the number of species with densities above the extinction threshold.

3.4 RESULTS

As predicted, interactions with pollinators had a positive effect on the overall population size of the plant community at equilibrium when the plants' rate of vegetative reproduction was low, and virtually no effect on a plant community with a high rate of vegetative reproduction (Fig. 3.2, upper panel). In the absence of a trade-off between generalist and specialist flower visitation, all three types of interaction networks resulted in approximately equal total population sizes. With a trade-off, diagonal matrices produced the strongest increase of the plant population, followed by nested and full matrices.

Despite the positive effect of pollinators on the total population size, in nearly all cases species richness of plant communities was reduced by the presence of pollinators (Fig. 3.2, middle panel). While species richness of communities with a high rate of vegetative reproduction was only slightly affected by the presence of pollinators, pollinators had a strong negative effect on plant species richness for communities with a

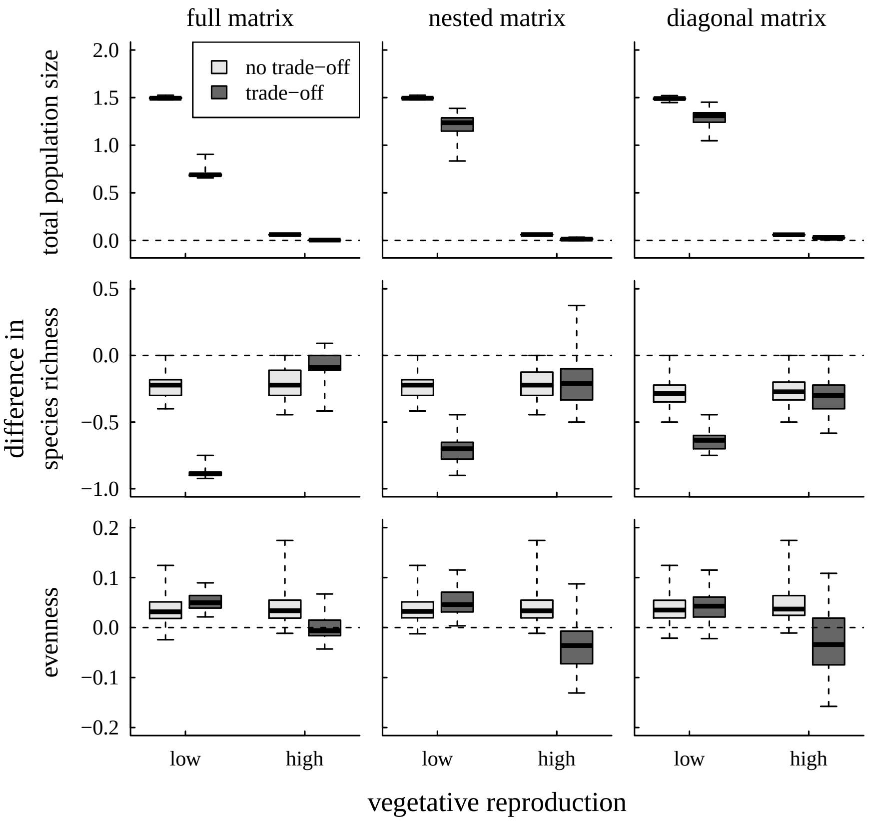

Figure 3.2: Effects of interactions with pollinators on total population size, species richness and evenness of plant communities at equilibrium. Boxplots show the proportional difference between values with and without pollinators for 100 simulation runs. Negative values indicate a decrease in the respective community property in the presence of pollinators. Results are presented for the default parameter values listed in Table 3.1, with an extinction threshold of 10 individuals. The calculation of the three community properties included all plant species with equilibrium population sizes above the extinction threshold.

low rate of vegetative reproduction, especially with a generalist-specialist trade-off. This negative effect was most pronounced for systems with a fully connected interaction matrix, followed by nested and diagonal matrices. Whereas for extinction thresholds of 1 and 10 individuals the median effect of pollinators on plant richness was always negative, with an extinction threshold of 100 individuals, a low rate of vegetative reproduction and no trade-off species richness increased by up to 100% (Fig. 3.3). The increase was most pronounced for full and nested interaction matrices. On the other hand, the same configuration of parameter values with a trade-off penalizing generalised

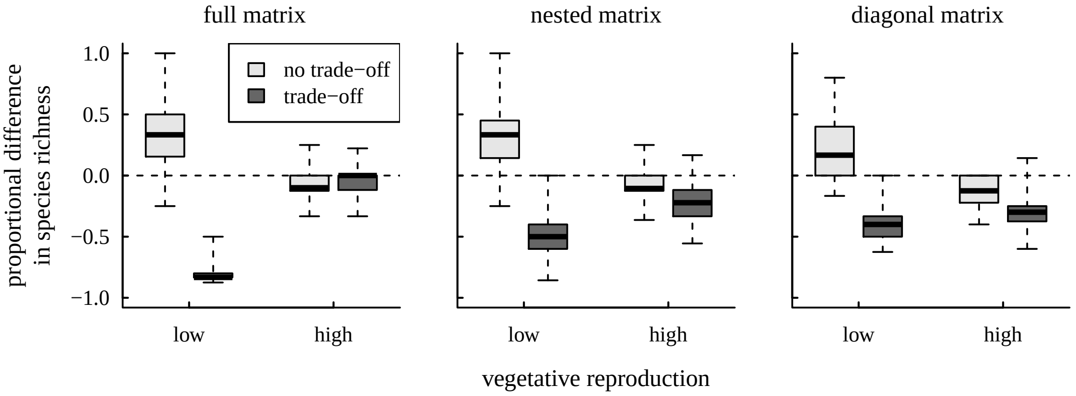

Figure 3.3: Effect of plant-pollinator interactions on plant species richness with a high extinction threshold (100 individuals). Boxplots show the proportional difference between values with and without pollinators for 100 simulation runs. All parameter values are identical to those of Fig. 3.2.

flower visitors resulted in markedly decreased species richness, particularly for full and nested networks.

Evenness of the plant community remained largely unaffected by the presence of pollinators (Fig. 3.2, lower panel). However, in most simulation runs plant evenness increased slightly under the influence of pollinators. A further increase of evenness would not have been possible, since the evenness of the community of surviving plant species was already close to its maximum in the absence of pollinators (Table 3.2).

Direct examination of the distribution of plant abundances at equilibrium showed that even in those cases with a positive effect of pollinators on plant species richness the observed increase in species richness fell short of the expected increase based on the size of the total plant population (Fig. 3.4). This discrepancy was due to the fact that not all plant species benefited from the presence of pollinators. Whereas the distribution of plant abundances ordered by rank showed a gradual decrease from most- to least-abundant in the absence of pollinators, the addition of pollinators resulted in a sharp transition between a group of highly abundant plant species and a second, larger group of species with population sizes close to zero.

Deviations from the default parameter set did not result in major changes concerning the effects of the presence of pollinators on plant community composition (Figs. 3.5-3.7). While the results for moderately higher pollen carryover ($B = 5$) were nearly identical to those of $B = 1$, at $B = 50$ the negative effect of pollinators on species richness was reduced, particularly

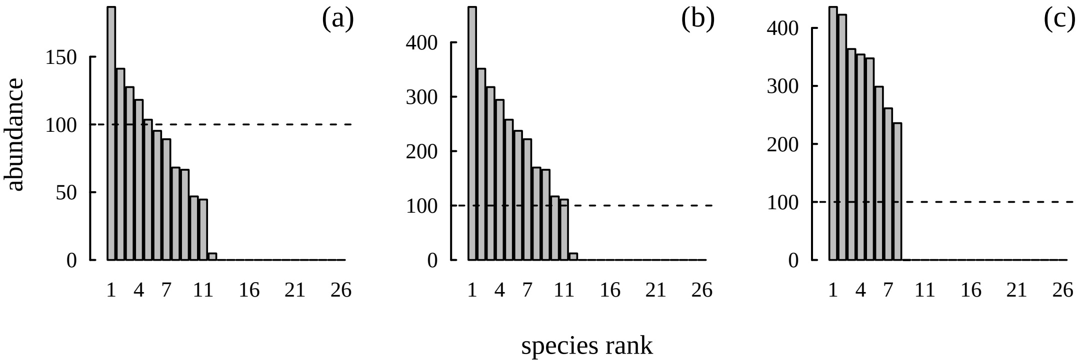

Figure 3.4: Potential and realized influence of pollinators on the abundance distribution of a plant community at equilibrium. Panel A shows the equilibrium abundance distribution of an exemplary plant community in the absence of pollinators, panel C the same community with plant-pollinator interactions, with a fully connected interaction network and no generalist-specialist trade-off. In panel B, the same abundance distribution as in A is shown, but all abundances have been increased by a constant factor so as to obtain the same total population size as in panel C. The dashed horizontal line marks the extinction threshold of 100 individuals. Species richness was determined as the number of plant species with population sizes above the extinction threshold. The same parameter values as in Fig. 3.2 were used for this figure, and a low rate of vegetative reproduction was chosen ($b_{veg} = 5 \cdot 10^{-8}$).

for fully connected matrices (Fig. 3.5). Regarding the amount of nectar per plant N, a lower limit was defined by the minimum amount needed to sustain the pollinator community with a trade-off in trait matching. Increasing the amount of nectar above this level ($N = 4$) reduced the difference between the effects of pollinator presence with and without a trade-off (Fig. 3.6). On the other hand, a wider range of degrees of plant niche overlap (values taken from a uniform distribution with boundaries {0.5, 1} instead of {0.65, 0.85}) reduced the positive effect of animal pollination on plant species richness with a high extinction threshold and no trade-off (Fig. 3.6).

3.5 DISCUSSION

Understanding the factors that explain the variation of biodiversity in space and time is one of the main challenges in ecological research. In the current study, we assess the potential influence of plant-pollinator interactions, one of the most common types of mutualism, on plant diversity. The results of our numerical simulations suggest that the addition of pollinators rarely enhances the diversity of a plant community with alternative means of reproduction. This result is in contrast to the predictions of a recent more general model of plant-animal mutualistic systems (Bastolla *et al.*, 2009).

In our simulations, the presence of pollinators most strongly affected plant community composition when the plants' intrinsic rate of reproduction in the absence of pollinators was too low to occupy all available habitat. This seems plausible, given that unlike some other types of mutualistic services (e.g. corals offering shelter for microalgae: Stachowicz, 2001), pollination does not create new habitat, nor does it allow plants to colonize habitat types where they could not grow in the absence of pollinators. In reality, underutilized habitat usually occurs in early successional stages of community dynamics, but rarely at equilibrium. However, in environments subject to frequent disturbances accompanied by high mortality, the balance between reproduction and mortality may well result in equilibrium densities far below the habitat capacity. For such situations, our model predicts that the addition of animal pollinators will increase the total population size of the plant community at equilibrium simply because the added fertility (seed production) induced by pollination increases population growth. Plant-pollinator systems without a trade-off penalizing generalist flower visitors produce the highest increase, due to the fact that both the size of the overall animal population and their rate of successful flower visitation are highest in the absence of such a trade-off (data not shown).

Although the establishment of a larger overall population would principally allow for the coexistence of more species above the extinction threshold, in most cases species richness declined in the presence of pollinators. This is due to the fact that typically only a small number of plant species benefit from the pollinators' services in terms of increased abundance at equilibrium, at the expense of other plant species. The fact that this negative effect of animal pollination diminishes as pollen carryover increases indicates that its cause lies in the reduced quantity of pollen that rare plants receive under conditions of limited pollen carryover (Benadi *et al.*, 2012b). Introducing pollination thus amplifies existing differences in plant species abundance. Interestingly, interaction matrices with a trade-off had a much stronger negative effect on species richness compared to matrices without such a trade-off. This difference can be understood by considering the dual effect of animal pollination on plant birth rates. First, pollination generally leads to an increase in the mean number of seeds per plant. Yet secondly, pollination also increases the variation in per-capita seed production between species. The effect of a certain absolute difference in seed numbers between species on the relative difference in seed numbers is largest when the mean number of seeds per plant is low. Consequently, the negative effect of variation in seed numbers on plant coexistence is most pronounced when plant birth rates are generally low, as is true in the case of a trade-off limiting pollinator effectiveness. For the same reason, pollinator presence has a stronger negative effect on plant species richness with a lower rate of vegetative reproduction.

Only for specific parameter combinations, namely a low rate of vegetative reproduction, a narrow range of plant competition coefficients, the absence of a generalist-specialist trade-off and when assuming a high extinction threshold of 100 individuals, does the addition of pollinators have a positive effect on species richness of the plant community. For real ecosystems, assuming a higher extinction threshold in relation to the habitat capacity is justified if communities underlie larger fluctuations of environmental conditions (Pimm *et al.*, 1988). However, even though according to our model under such conditions interactions with pollinators indeed promote plant diversity, the positive effect on plant diversity is still less pronounced than it could be if pollinators increased the equilibrium population sizes of all plant species in equal proportion. Instead, the presence of pollinators enhances the growth of some populations, while inhibiting that of rarer ones due to the above mentioned disadvantage in pollination rates. As a consequence, at equilibrium medium-sized populations are largely absent, and the evenness of the community of surviving plant species is close to its theoretical maximum.

The three types of interaction network structures examined in this study differ in their degrees of specialisation: While full and diagonal matrices represent extreme cases of uniformly generalised and specialised interactions, respectively, a nested matrix contains a mixture of specialist and generalist species interacting in a way that maximizes the number of shared interactions between members of the same guild (Bastolla *et al.*, 2009). In this study, we used nested and diagonal matrices of the same connectance, and thus also the same mean number of interactions per species. These two matrix types differ only with regard to the distribution of links among species. Depending on the structure of the interaction network, limited pollen carryover and a trade-off in trait matching influence population growth rates to different degrees. The effect of limited pollen carryover is most pronounced for full interaction matrices, because here the probability that a flower visitor has previously visited flowers of other species is greatest. Likewise, systems with full matrices are most strongly affected by a trade-off in trait matching, since the difference between trait matching values with and without a trade-off is largest for completely generalised interactions. Although nested and diagonal matrices have the same network-level degree of specialisation, their effects on total population size and composition of the plant community are not identical owing to the specific effects of the distribution of interactions in a nested matrix: In the absence of a trade-off, the most generalised pollinator species in a nested network outcompetes all other pollinators. Therefore, the dynamics of the system is dominated by generalised interactions, similar to a fully connected network. With a trade-off in pollinator effectiveness several pollinator species may coexist, and the degree of specialisation of the group of abundant species at equilibrium depends on the configuration of initial population densities and plant competition coefficients that are randomly assigned for each simulation.

Due to numerous differences in model assumptions and methods of analysis, it is difficult to directly compare our study to the work of Bastolla *et al.* (2009) who come to different conclusions concerning the effects of animal pollination on plant diversity. Important mechanistic details included in our model are the assumption of within-community competition for mutualistic services, the existence of a fixed habitat capacity for plants that cannot be extended by interactions with mutualists, and the characteristic attribute of pollination systems, limited pollen carryover. The model by Bastolla and colleagues omits these details in order to retain greater mathematical simplicity and applicability to multiple systems. Despite these differences, both studies predict that under certain conditions, mutualistic interactions between plants and animals can promote plant diversity. However, whereas the results of Bastolla and colleagues suggest that most plant communities benefit from the presence of animal mutualists, our results show that at least for plant-pollinator systems, the conditions for a positive effect of the presence of pollinators on plant diversity are highly restricted, and therefore unlikely to occur in the majority of natural systems. This discrepancy in model predictions highlights the importance of carefully choosing the right balance between simplicity and attention to mechanistic detail in each modelling exercise, depending on the purpose of the analysis. Needless to say, the model used in our study also makes a number of simplifying assumptions that should be kept in mind when interpreting the results (for a discussion, see Benadi *et al.*, 2012b).

Despite the existence of unique properties of pollination systems, some aspects of the current study may be relevant for the interpretation of diversity patterns in other types of mutualistic systems. By definition, all mutualistic interactions lead to increased birth and/or decreased mortality rates of both partners. Thus, the mechanism of promotion of diversity through an increase in the community's overall population size could be important for all kinds of mutualistic systems provided that population growth in these systems is not limited by other factors. Likewise, the effect of a trade-off between the number of interaction partners and the effectiveness in handling each of them may be similar for other types of mutualisms involving multiple species.

While our results suggest that the loss of animal pollinators in most cases does not decrease the diversity of plant species possessing alternative modes of reproduction, this statement obviously does not hold for species that depend completely on the services of pollinators to reproduce. Moreover, it is important to note that even those plants that are able to produce viable offspring through selfing or vegetative propagules depend on animal pollination in order to maintain a sufficient level of genetic diversity (Ollerton *et al.*, 2011). Thus, even though the short-term population-dynamic consequences of pollinator loss can be negligible for some plants, the long-term population-genetic effects of reduced outcrossing can be severe, especially at times when adaptation to rapidly changing environmental conditions is required.

3.6 APPENDIX

3.6.1 *Further explanations concerning the derivation of the model*

3.6.1.1 *Probability of pollination*

In the model, the probability that a flower is pollinated by an animal depends on the animal's visitation history. Specifically, a flower is pollinated if the animal has visited a flower of the same species during at least one of its previous B visits. We assume that animals only lose pollen during visits to flowers of other species, but not in time steps without a successful flower visit. Therefore, the probability of pollination includes the conditional probability that an animal of species j visits a flower of species *i* given that it visits any flower during the time step in question. This conditional probability is

$$\frac{\frac{P_i}{\sum_{h=1}^{m} P_h}\alpha_{ij}}{\sum\limits_{k=1}^{m} \frac{P_k}{\sum_{h=1}^{m} P_h}\alpha_{kj}} \tag{3.6}$$

Accordingly, the probability that the animal has visited a flower of species *i* at least once in the previous *B* flower visits is

$$1-(1-\frac{\frac{P_i}{\sum_{h=1}^{m} P_h}\alpha_{ij}}{\sum\limits_{k=1}^{m} \frac{P_k}{\sum_{h=1}^{m} P_h}\alpha_{kj}})^B \tag{3.7}$$

Since the two sums of all plant densities in the numerator and denominator cancel each other out, this expression can be reduced to

$$1-(1-\frac{P_i}{\sum\limits_{k=1}^{m} P_k\alpha_{kj}}\alpha_{ij})^B \tag{3.8}$$

Note that with this expression we assume that the densities of all plant species in the previous *B* flower visits were identical to the present densities. Strictly speaking, this assumption only holds for a system at equilibrium. Under non-equilibrium conditions, the probability of pollination should reflect the changes in plant densities during the last *B* flower visits. Implementing this feature in the model would introduce a time-delayed effect of past population densities which might result in greater instability, possibly leading to population cycles or chaotic dynamics. However, one may argue that the time scale of pollen transfer (minutes and hours) is sufficiently different from that of considerable changes in plant population densities (days and months) that the changes in plant densities between pollen removal and pollen deposition are negligible. Therefore, and for the sake of simplicity, we chose to treat plant densities as constant within the time span of pollen transfer.

3.6.1.2 *Per-capita amount of nectar*

The derivation of the expected amount of nectar collected by a pollinator in one time step is based on the assumption of a Poisson distribution of flower visitors on flowers. While we could have simply divided the amount of nectar per flower *N* by the mean number of visitors μ_i, this would lead to unrealistically high nectar amounts for mean numbers of visitors below one. Assuming a Poisson distribution of flower visitors ensures that the amount of nectar per flower visitor approaches N in the limit of mean visitor numbers per flower close to zero.

Although the Poisson distribution requires infinite population sizes, it is common practice to model the distribution of finite numbers of individuals using a Poisson distribution rather than a multinomial distribution. As long as the mean number of visitors per flower is considerably lower than the total animal population, the Poisson and multinomial distributions will give very similar results. Using the Poisson distribution allows us to derive a closed expression for the infinite series describing the expected amount of nectar collected by a visitor of plant species *i*, $E(\mu_i)$. Thus, the expression

$$E(\mu_i) = \sum_{k=0}^{\infty} \frac{N}{k+1} \frac{\mu_i^k e^{-\mu_i}}{k!} \tag{3.9}$$

may be replaced by

$$E(\mu_i) = \frac{N}{\mu_i}(1 - e^{-\mu_i}) \tag{3.10}$$

which greatly simplifies the model structure.

3.6.2 *Supplementary tables and figures*

Table 3.1: List of parameter definitions and default values

SYMBOL	DEFINITION	DEFAULT VALUE
m	Number of plant species	26
n	Number of animal species	26
α_{ij}	Degree of trait matching between plant species i and animal species j ($0 \leqslant \alpha_{ij} \leqslant 1$)	
B	Maximum number of flower visits from pollen uptake to pollen deposition	1
N	Amount of nectar per plant and unit of time	2.1
H_P	Habitat capacity for plants	2000
b_{veg}	Rate of vegetative reproduction and / or selfing	$5 \cdot 10^{-8}$ (low) or $5 \cdot 10^{-7}$ (high)
γ_{ik}	Niche overlap of plant species i and k ($0 \leqslant \gamma_{ik} \leqslant 1$)	between 0.65 and 0.85
β_P	Rate of conversion of pollen to seeds	$3.75 \cdot 10^{-6}$
β_A	Rate of conversion of nectar to animal offspring	$4 \cdot 10^{-6}$
d_P	Plant mortality rate	$3 \cdot 10^{-8}$
d_A	Animal mortality rate	$3 \cdot 10^{-7}$

Table 3.2: Plant diversity at equilibrium in the absence of pollinators. These values serve as a reference for the proportional effects of the presence of pollinators presented in Figs. 2 and 3. Numbers represent median and, in brackets, minimum and maximum values of 100 simulation runs with randomly chosen initial densities and degrees of niche overlap. Results are presented for simulations with high and low rates of vegetative reproduction, and extinction thresholds of 100 and 10 individuals.

RATE OF VEGETATIVE REPRODUCTION	EXTINCTION THRESHOLD	TOTAL POPULATION SIZE	SPECIES RICHNESS	PIELOU'S EVENNESS
low	100	869 (579, 1046)	6 (4, 8)	0.9914 (0.9655, 0.9986)
	10	1082 (1062, 1100)	10 (8, 13)	0.9484 (0.8873, 0.9917)
high	100	2464 (2259, 2585)	8 (6, 11)	0.9712 (0.9386, 0.9958)
	10	2548 (2504, 2585)	10 (8, 13)	0.9431 (0.8496, 0.9853)

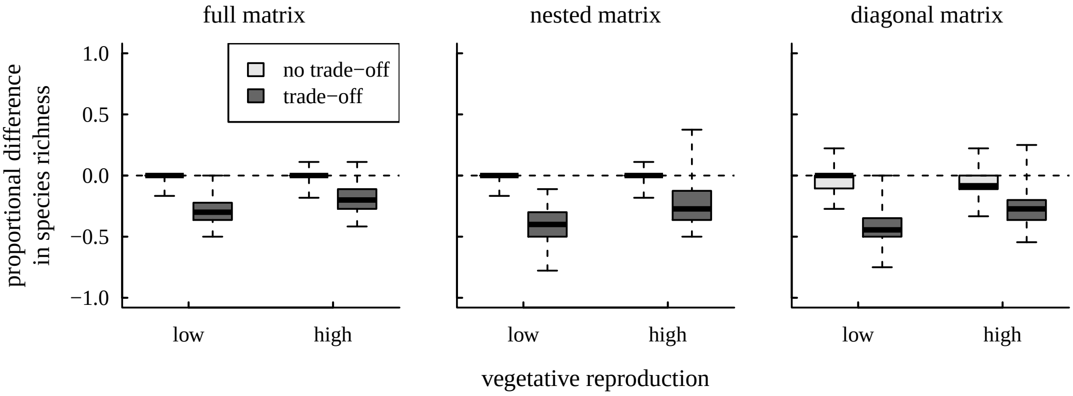

Figure 3.5: Effect of plant-pollinator interactions on plant species richness with a high degree of pollen carryover ($B = 50$). Boxplots show the proportional difference between species richness with and without pollinators for 100 simulation runs. Species richness was defined as the number of plant species with population sizes above the extinction threshold (10 individuals) at equilibrium. Except for pollen carryover, the default parameter values listed in Table 3.1 were used for this figure.

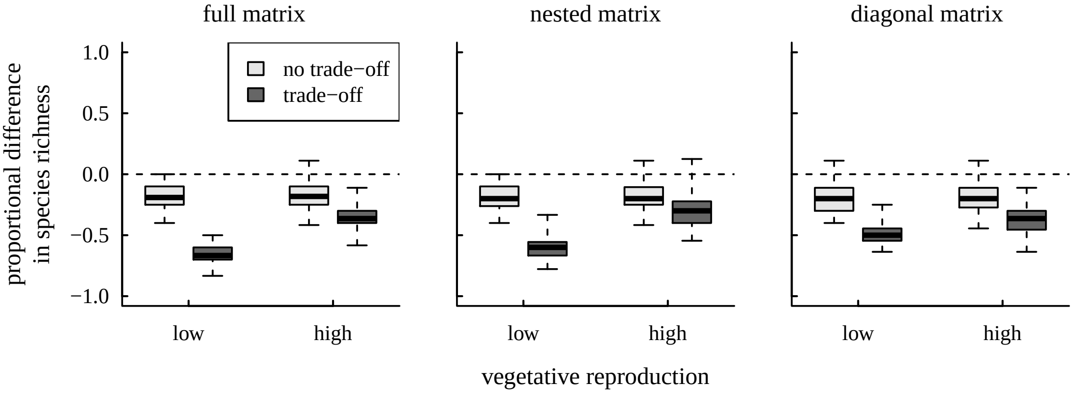

Figure 3.6: Effect of plant-pollinator interactions on plant species richness with a high amount of nectar per plant ($N = 4$). Boxplots show the proportional difference between species richness with and without pollinators for 100 simulation runs. Species richness was defined as the number of plant species with population sizes above the extinction threshold (10 individuals) at equilibrium. Except for the amount of nectar per plant, the default parameter values listed in Table 3.1 were used for this figure.

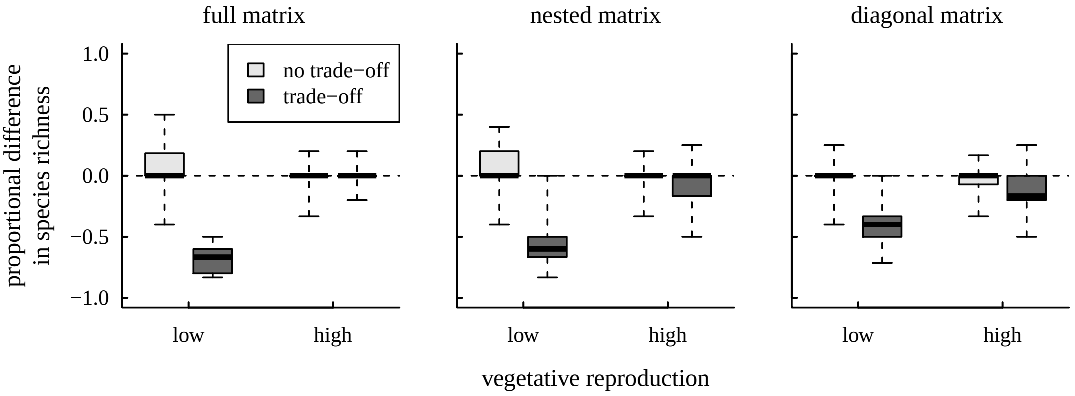

Figure 3.7: Effect of plant-pollinator interactions on plant species richness with a broad range of degrees of plant niche overlap and a high extinction threshold (100 individuals). Pairwise degrees of niche overlap of different plant species (γ_{ik} with $i \neq k$) were drawn from a uniform distribution with boundaries $\{0.5, 1\}$. Boxplots show the proportional difference between species richness with and without pollinators for 100 simulation runs. See Table 3.1 for a list of other parameter values used for this figure.

4

CONTRASTING SPECIALISATION-STABILITY RELATIONSHIPS IN PLANT-ANIMAL MUTUALISTIC SYSTEMS[1]

4.1 ABSTRACT

Specialization has often been suggested as one of the main factors influencing the stability of ecological systems at the population and community level, with highly specialised systems being the most sensitive towards disturbances. However, most previous studies did not consider the fact that specialisation contributes to community stability by reducing the risk of extinction through competitive exclusion. Moreover, since ecological stability is a highly ambiguous concept, general statements about the specialisation-stability relationship cannot be made based on a single stability criterion. In this study, we examine the relationship between specialisation and stability in plant-animal mutualistic systems using a population dynamic model with two species in each group. We compare results for four different stability criteria, both for a general type of plant-animal mutualism and specifically for a plant-pollinator system. Contrary to the commonly-held belief that specialisation increases system vulnerability to disturbances, we find that positive, negative and unimodal relationships are possible depending on the stability criterion applied and the characteristics of species interactions. Our results call for further investigations of the consequences of ecological specialisation, and emphasize the special properties of pollination mutualisms.

4.2 INTRODUCTION

Ecological stability is a central concept both in basic and applied ecological research. Research questions involving this concept include hotly debated topics such as the relationship between diversity and stability (McCann, 2000; Ives & Carpenter, 2007, and references therein), and topics of high conservation relevance such as the search for predictors of species susceptibility to anthropogenic disturbances (e.g. Colles *et al.*, 2009). Yet ecological stability is also one of the most ambigu-

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[1] Article by G. Benadi, N. Blüthgen, T. Hovestadt and H.-J. Poethke
Submitted to *Ecological Modelling*

ous concepts in ecology. More than ten years ago, Grimm & Wissel (1997) published a large inventory of stability definitions and pointed out that general statements about ecological stability are unacceptable, since application of alternative criteria for stability would often lead to different conclusions. However, until now very few studies have applied different stability criteria to the same research question (but see e.g. Chen & Cohen, 2001).

Among the numerous traits that have been proposed to be associated with the stability both of single populations and of communities, specialisation is frequently regarded as one of the most important (Devictor *et al.*, 2008; Colles *et al.*, 2009; Clavel *et al.*, 2011). In this context, the term specialisation refers to the specificity of an organism's requirements with respect to biotic or abiotic resources (its Grinellian niche, sensu Devictor *et al.* 2010). From a theoretical perspective, communities consisting of specialised species could be more or less stable than their generalised counterparts: On the one hand, specialisation is essential for diversity maintenance in many ecological communities (Chesson, 2000). Different species can only stably coexist with some kind of ecological distinction between them, be it habitat or food requirements or more subtle traits such as differential responses to environmental fluctuations. This partitioning of niches leads to stronger intraspecific competition relative to interspecific competition, and thus allow populations to recover from low density. On the other hand, each specialised species takes a risk by linking its fate to that of only one or a few resources (Den Boer, 1968; Vazquez & Simberloff, 2002). If a disturbance reduces the availability of a fraction of all resources, generalist populations should be able to persist by using the remaining resources, whereas specialists of the disturbed resources may decline. Although reality can be more complex than this simple argument, for example if generalists require a complementary diet (Blüthgen & Klein, 2011, and references therein), a positive relationship between specialisation and vulnerability of single species to disturbances has indeed been found in the majority of studies on a variety of taxa (bees and hoverflies: Biesmeijer *et al.* 2006, coral feeding fish: Graham 2007, amphibians and reptiles: Watling & Donnelly 2007, primates: Harcourt *et al.* 2002). However, other studies found no significant effect of specialisation on species extinction risk (e.g. Vazquez & Simberloff, 2002; Safi & Kerth, 2004; Fitzpatrick *et al.*, 2007).

In this paper, we use a recently developed population dynamic model (Benadi *et al.*, 2012b) to study the relationship between specialisation and stability in multispecies plant-animal mutualistic systems, particularly in plant-pollinator systems. We compare specialization-stability relationships under four different criteria of ecological stability. Compared to other types of interspecific interactions, mutualistic systems possess specific properties that may render them particularly sensitive to disturbances. In mutualistic systems, each species at the same time provides a resource for its partners and utilizes the partners' resources. Thus, in contrast to the negative feedbacks on population densities that tend to diminish the effects of disturbances in antagonistic interaction networks, positive feedbacks experienced by specialised interaction partners in mutualistic networks may amplify the impact of a disturbance (May, 1973; Boucher *et al.*, 1982; Bever, 2002). For example, a mutualistic species specialised on a declining interaction partner may suffer from a reduced growth rate due to its low encounter rate with the partner species. This reduction can then feed back onto the declining species and accelerate its downward trend.

Among mutualistic systems, pollination mutualisms are again special in that two consecutive visits of a pollinator to flowers of the same species are required for fertilization to take place. This fact results in a lower pollination probability for rare plant species with generalised pollinators as compared to more common plant species (Levin & Anderson, 1970; Waser, 1978; Campbell, 1986; Goulson, 1994; Kunin & Iwasa, 1996; Benadi *et al.*, 2012b). As a consequence, rare species are at a disadvantage both in specialised and generalised plant-pollinator systems, whereas in other types of mutualistic systems involving free-living organisms, e.g. plants and their seed dispersers, a rare species disadvantage only exists for specialised interactions.

In the present study, we analyse the stability of plant-animal mutualistic systems with two species in each group as a function of two variables: the degree of specialisation of animals on plant species and the degree of niche overlap of the two plant species with respect to abiotic resources, a measure of plant resource specialisation. In contrast to our previous work that focused solely on resilience (Benadi *et al.*, 2012b), here we employ three additional stability criteria that differ in the system property under consideration, the strength of a disturbance subject to which the respective property should remain unchanged, and the relevant time scale (Table 4.1). The first stability measure, hereafter referred to as "resilience criterion", uses the classical mathematical concept of local stability of an equilibrium state (May, 1973), and, in case of a stable equilib-

Table 4.1: Overview of the criteria for ecological stability applied in this study. Each criterion is characterized by a specific property that remains unchanged in a stable system. Furthermore, the four stability measures differ with respect to the magnitude of perturbations considered, and whether they account for the speed of recovery after a disturbance. Some are based on the assumption of an undisturbed system being at equilibrium.

CRITERION	SYSTEM PROPERTY	ACCOUNTS FOR			ASSUMES
		SMALL PERTURBATIONS	LARGE PERTURBATIONS	SPEED OF RECOVERY	EQUILIBRIUM STATE
Resilience	Species richness	Yes	No	Yes	Yes
Domain of attraction	Species richness	Yes	Yes	No	Yes
Persistence	Species richness	Yes	Yes	Yes	No
Ecosystem function	Mutualist function	Yes	Yes	Yes	No

rium, measures the rate of return to the equilibrium following an infinitely small perturbation (Otto & Day, 2007). The second measure, which is likewise related to the concept of an equilibrium state, quantifies the size of the "domain of attraction" around an equilibrium. This is the collectivity of all initial conditions from which a certain equilibrium state is reached after an arbitrarily long time period. Hence, this second stability measure does not only account for a system's behaviour in the immediate vicinity of the equilibrium state, but also considers the effects of larger perturbations. On the other hand, unlike the resilience criterion, the domain of attraction does not incorporate information on the time required for recovery following a disturbance. Both factors are accounted for by the third stability measure ("persistence criterion") that considers the starting conditions allowing all species to persist above a threshold density within a certain ecologically relevant time span. In contrast to the first two measures, this criterion does not only consider the long-term (equilibrium) behaviour of a system, but also its transient dynamics after a perturbation. For real ecological systems that are subject to frequent disturbances from a variety of sources, transients can often be more important than the stability of an equilibrium state that may never be reached (Hastings, 2004). However, many conservation projects are targeted at preserving certain ecological functions rather than individual species (e.g. Moonen & Barberi, 2008; Sutherland *et al.*, 2010). Therefore, the fourth stability measure ("ecosystem function criterion") refers to the preservation of the ecological function "pollination" (or another mutualistic service provided by animals) for the plant community and thus quantifies the fraction of starting conditions that allow persistence of both plants and at least one animal species.

4.3 THE MODEL

Here, we briefly introduce the model equations and their main underlying assumptions. See Benadi *et al.* (2012b) for a more detailed description of this model and its stability properties. Note that unlike in Benadi *et al.* (2012b), here we assume that both animals and plants are obligate mutualists, i.e., they cannot reproduce without the services offered by their mutualistic partners.

Our model describes the dynamics of a plant community comprising m species and a community of animals with n species, where P_i indicates the population density of the *i*th plant species and A_j the density of the *j*th animal species. Each species' population dynamics is represented by one difference equation. Interactions between individual plants and animals are modeled as follows: During a small time step, each animal encounters one randomly selected plant individual. However, not all encounters lead to successful visits involving an exchange of mutualistic services, because an animal may reject the plant it encounters, or it may be unable to visit the plant due to the presence of morphological or chemical barriers. In general, the probability of a successful visit is determined by the degree of trait matching between the plant and animal species (Vazquez *et al.*, 2009). It is assumed to comprise both traits that have an attractive effect on the animal, such as preferred colours or scents of fruits and flowers (e.g. Junker *et al.*, 2010), and traits that may act as a barrier, e.g. a long flower corolla in relation to the pollinator's tongue length (Stang *et al.*, 2006). In the model, the degree of trait matching is represented by parameter α_{ij} which takes a specific value between zero and one for each plant-animal species pair. Construction of different matrices of α_{ij} values allows for the variation of specialisation at the species and community level (see below). The number of visits received by an individual plant of species i within one time step, summed over all animal species, is calculated as:

$$G_i = \frac{1}{P_i} \sum_{j=1}^{n} \left(\frac{P_i}{\sum\limits_{k=1}^{m} P_k} \alpha_{ij} A_j \right) \tag{4.1}$$

Whereas for a general plant-animal mutualistic system G_i represents the benefit that a plant derives from the mutualistic interaction, in a plant-pollinator system not every flower visit results in pollination. Since fertilization of a flower requires a previous visit of the pollinator to a flower of the same plant species, the amount of pollen received by a plant depends on the probability of such a previous visit for each pollinator species. Here, the degree of pollen carryover B denotes the maximum possible number of heterospecific flower visits between pollen removal and deposition. By including parameter B in our model, we account for the fact that pollen may be lost in intervening visits to flowers of other species (Campbell & Motten, 1985; Feinsinger *et al.*, 1988; Morales & Traveset, 2008; Karron *et al.*, 2009). The amount of pollen received by a plant of species i within one time step is thus:

$$F_i = \frac{1}{P_i} \sum_{j=1}^{n} \left(\frac{P_i}{\sum\limits_{k=1}^{m} P_k} \alpha_{ij} \left(1 - \left(1 - \frac{P_i \alpha_{ij}}{\sum\limits_{k=1}^{m} P_k \alpha_{kj}} \right)^B \right) A_j \right) \tag{4.2}$$

Note that in the limit of $B = \infty$, the benefit of a plant in a pollination system (F_i) equals that of a plant in a general plant-animal mutualistic system (G_i).

In exchange for its mutualistic services, a visiting animal receives a reward from the plant. For simplicity, the total amount of reward per plant *N* is assumed to be constant, i.e., the reward is replenished instantly at the end of each time step. If several animals visit the same plant, *N* is divided equally among all visitors. Assuming that the distribution of animals on plants follows a Poisson distribution with mean G_i, the expected reward collected by an animal of species j within one time unit, summed over all plant species and weighted by the probability of a visit to each plant, is calculated as:

$$R_j = \sum_{i=1}^{m} \frac{P_i}{\sum\limits_{k=1}^{m} P_k} \alpha_{ij} \frac{N}{G_i} \left(1 - e^{-G_i} \right) \tag{4.3}$$

Birth rates of plant and animal populations are linear functions of the per capita benefit derived from the mutualistic interaction (F_i or G_i and R_j, respectively), with β_P and β_A denoting the conversion of benefit into plant and animal offspring. Plant birth rates comprise an additional term that describes seedling competition for space. We assume that the number of suitable sites for plant establishment is limited to the habitat capacity H_P, and all seedlings compete for the fraction of empty habitat. The overlap in habitat requirements of seedlings of plant species *i* and *k* is described by γ_{ik}, the competition coefficient of the classical Lotka-Volterra model that varies from zero (complete niche separation) to one (complete niche overlap). Mortality rates of both plant (d_P) and animal populations (d_A) are constant and independent of the interaction with the mutualists.

Taken together, these assumptions yield the following equations that describe the growth of plant and animal populations, respectively:

$$\Delta P_i = G_i \beta_P \left(1 - \frac{\sum\limits_{k=1}^{m} \gamma_{ik} P_k}{H_P} \right) P_i - d_P P_i \tag{4.4}$$

$$\Delta A_j = R_j \beta_A A_j - d_A A_j \tag{4.5}$$

As above, in eq. 5 G_i is replaced by F_i to represent plant growth in a plant-pollinator system.

4.3.1 *Model Analyses*

The effects of interaction specialisation and plant niche overlap on community stability were studied in numerical simulations. For specialisation of mutualistic interactions, trait matching values were varied in a symmetric fashion such that animal species 1 interacted preferentially with plant species 1 and with a lower probability with plant species 2, whereas animal species 2 preferred plant 2 over plant 1. Trait matching with the preferred plant species was calculated as $0.5 + 0.5S$ and trait matching with the other plant as $0.5 - 0.5S$, where S is a measure of interaction specialisation that varies from 0 (complete generalisation) to 1 (complete specialisation). Likewise, plant competition for resources was assumed to be symmetric (i.e., $\gamma_{12} = \gamma_{21}$). The degree of niche overlap of the two plant species varied from $\gamma_{ik} = 0$ to $\gamma_{ik} = 1$, while niches of conspecific plants were assumed to be identical (i.e., $\gamma_{11} = 1$ and $\gamma_{22} = 1$). All other parameters were set to identical values for both species in a community. Parameter values were chosen so as to represent realistic values for a time step length of ten seconds, the time span assumed for an animal to find and visit a single plant (see Table 4.2 for an overview of parameter definitions and default values). In addition, animal growth parameters were chosen so that the ratio of individual numbers of animals to plants at equilibrium with all four species was approximately 1:1 (see Benadi *et al.* 2012b and discussion). We used Maxima 5.22.1 (Maxima.sourceforge.net, 2010) for symbolic calculations and both Free Pascal 2.4 and R 2.13.1 (R Development Core Team, 2011a) for numerical analyses.

For the first two measures of community stability, the equilibrium state at which all four species coexist needed to be determined. Throughout this text, we will refer to this state as the "coexistence equilibrium". Due to the choice of parameter values, the population densities of the two plant and the two animal species at the coexistence equilibrium were always equal. Equilibrium densities were found by starting all populations at identical low densities and iterating the system of difference equations until the difference in population densities between two successive time steps fell below a threshold value of 10^{-5}.

In order to determine qualitative stability of the coexistence equilibrium and quantify the return rate of the system after a small perturbation (resilience criterion), the dominant eigenvalue $\hat{\lambda}$ of the Jacobian matrix for that equilibrium was calculated (May, 1974; Otto & Day, 2007; Okuyama & Holland, 2008). For a discrete time model, the condition for qualitative stability

Table 4.2: List of parameter definitions and default values

SYMBOL	DEFINITION	DEFAULT VALUE
P_i	Population density of plant species i	
A_j	Population density of animal species j	
m	Number of plant species	2
n	Number of animal species	2
α_{ij}	Degree of trait matching between plant species i	
	and animal species j ($0 \leqslant \alpha_{ij} \leqslant 1$)	
B	Maximum number of flower visits from pollen uptake	
	to pollen deposition	
N	Amount of reward per plant and unit of time	1.2
H_P	Habitat capacity for plants	10000
γ_{ik}	Niche overlap of plant species i and k ($0 \leqslant \gamma_{ik} \leqslant 1$)	
β_P	Conversion of mutualistic service to plant offspring	$1 \cdot 10^{-6}$
β_A	Conversion of mutualistic service to animal offspring	$2.1 \cdot 10^{-7}$
d_P	Plant mortality rate	$1 \cdot 10^{-8}$
d_A	Animal mortality rate	$1 \cdot 10^{-7}$
G_i	Number of visits received by an individual plant in one time step	
F_i	Amount of pollen received by an individual plant in one time step	
R_j	Amount of reward collected by an individual animal in one time step	

is given by $|\hat{\lambda}| < 1$. Larger values of $1 - |\hat{\lambda}|$ indicate a higher rate of return to the coexistence equilibrium.

For the purpose of estimating the size of the domain of attraction around the coexistence equilibrium, numerical simulations were performed with 2000 combinations of initial population densities of the two plant and animal species. Initial densities were drawn from an interval between one and a maximum density. As maximum initial densities we chose the equilibrium densities of a single plant species and its perfectly specialised mutualist ($\alpha_{ij} = 1$) in a world without competing species. Combinations of initial densities were drawn from a uniform distribution with these boundaries using Latin Hypercube Sampling (McKay *et al.*, 1979; Stein, 1987; Carnell, 2009). Starting with each combination of initial values in turn, the system of equations was iterated until either an equilibrium state was reached (using the same criterion as above) or the number of iteration steps exceeded a maximum number of $5 \cdot 10^{10}$ time steps (~ 15855 years). If all four populations had densities *D* close to their density at the coexistence equilibrium ($\hat{D}$) at the end of the simulation (specifically, $0.99\hat{D} \leqslant D \leqslant 1.01\hat{D}$), the simulation was counted as having reached the coexistence equilibrium. The size of the domain of attraction around the coexistence equilibrium was defined as the fraction of combinations of initial densities from which the coexistence equilibrium was reached.

A slightly modified procedure was used for the third and fourth measures of community stability. Here, a shorter maximum iteration time was chosen ($5 \cdot 10^9$ time steps or ~ 1586 years). As minimum value for the sampling of combinations of initial densities we chose a threshold population size that was assumed to be necessary for maintenance of a viable population. The results shown in this paper are for a threshold density of 100 individuals. Simulations with threshold densities of 10, 50 and 200 individuals produced similar results. The assumption of a threshold density was necessitated by the fact that in a deterministic model system such as the one used in this study the size of a population can never become exactly zero. A threshold density of 100 individuals was chosen to account for the high risk of extinction of small populations in real ecological systems due to demographic and environmental stochasticity. The population densities of the four species were monitored throughout each simulation. If all four populations (persistence criterion) or at least both plants and one animal (ecosystem function criterion) maintained population sizes above the threshold density until the end of the simulation, the community or ecological function was counted as having persisted. In analogy to the domain of attraction criterion, the fraction of simulations with persisting systems was used as a measure of ecological stability.

In the analyses involving the largest eigenvalue of the Jacobian as a measure of stability, calculations were performed for all combinations of animal specialisation ($0 <= S <= 1$) and plant niche overlap ($0 <= \gamma_{ik} <= 1$) in steps of 1/40. For the computationally more intensive analyses of attractor region

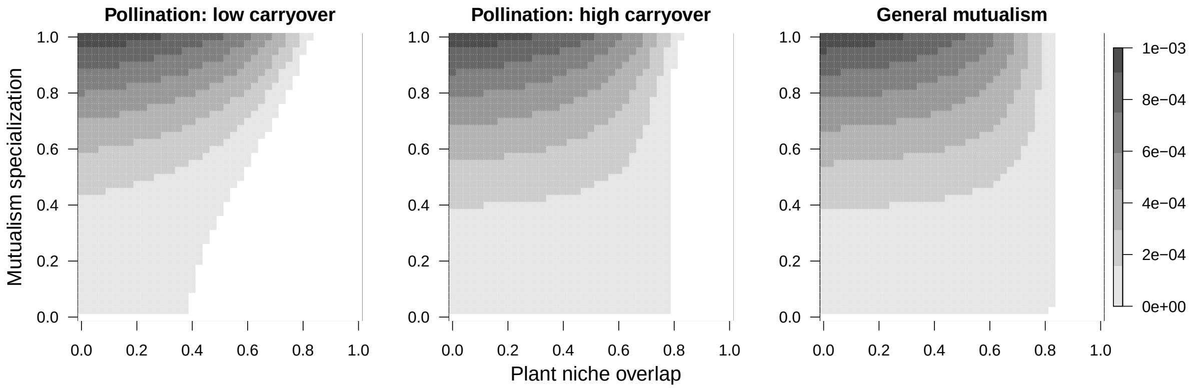

Figure 4.1: Return rate to the coexistence equilibrium after a small perturbation. The rate of return to the equilibrium with coexistence of the two plant and animal species is shown as a function of plant niche overlap with respect to habitat requirements and degree of specialisation of the mutualistic interactions between plants and animals. Darker shades of grey indicate a higher return rate. White areas denote parameter combinations where the system does not return to the coexistence equilibrium after a small perturbation. Results are presented for plant-pollinator systems with low ($B = 1$) and high ($B = 5$) degrees of pollen carryover, and for a general plant-animal mutualism. See the main text for further explanations.

sizes, persistence and ecosystem function, a coarser resolution of 1/20 was chosen.

4.4 RESULTS

As previously demonstrated (Benadi *et al.*, 2012b), the equilibrium with coexistence of all four species was only qualitatively stable at sufficiently low degrees of plant niche overlap (Fig. 4.1), and the required level of plant niche separation varied with the degree of interaction specialisation and with pollen carryover. A relatively low degree of plant niche separation was sufficient for coexistence in general plant-animal mutualistic systems, whereas plant-pollinator systems with restricted pollen carryover required a higher degree of niche differentiation. In the following, we restrict our discussion to the area of parameter space that allowed qualitative stability of the coexistence equilibrium, and focus on the effect of specialisation of mutualistic interactions on the four stability measures described above.

For the resilience criterion we found that higher levels of mutualism specialisation and lower levels of plant niche overlap resulted in an increased return rate to the coexistence equilibrium after a small disturbance (Fig. 4.1, see also Benadi *et al.* 2012b). This trend remained qualitatively unaffected by the degree of pollen carryover.

A more complex relationship between specialisation and stability was found when the domain of attraction around the coexistence equilibrium was considered (Fig. 4.2). Here, with strongly restricted pollen carryover ($B = 1$), the relationship between mutualism specialisation and attractor domain size depended on the level of plant niche overlap: for higher values of plant niche overlap, the domain of attraction increased with specialisation of mutualistic interactions, while at lower levels of plant niche overlap the smallest domains of attraction were found at intermediate values of specialisation. With increasing pollen carryover, all differences in the sizes of domains of attraction were reduced. For the general type of mutualism, in the area of parameter space that allowed stable coexistence nearly all combinations of initial population densities led to the coexistence equilibrium.

Closer examination of single domains of attraction showed that the propensity to approach the coexistence equilibrium was well explained by the initial ratios of the density of plant species 1 to the total plant population and the ratio of animal species 1 to the total animal population (Fig. 4.3). When the domain of attraction was relatively small (Fig. 4.3, $S = 0.4$), combinations of initial densities with both ratios close to 0.5, the ratio at the coexistence equilibrium, tended to approach the coexistence equilibrium, while those with both ratios strongly deviating from 0.5 did not result in coexistence. Within a narrower range of initial values, combinations with $\frac{P1}{P1+P2} > 0.5$ and $\frac{A1}{A1+A2} < 0.5$ or vice versa also approached the coexistence equilibrium, whereas combinations with both fractions either smaller or larger than 0.5 did not. As the domain of attraction increased in size ($S = 0.6$ and $S = 1$), its overall shape did not change, but more and more combinations of initial densities that deviated from a ratio of 0.5 led to the coexistence equilibrium.

For plant-pollinator systems with restricted pollen carryover ($B = 1$), further modifications of the criterion for ecological stability again changed the relationship with mutualism specialisation (Fig. 4.4). When persistence of all populations to the end of the simulation was considered (Fig. 4.4C), completely generalised plant-pollinator systems proved to be the most stable, both in terms of the range of degrees of plant niche overlap that allowed coexistence and the proportion of combinations of initial densities leading to the coexistence equilibrium. By contrast, these systems were regarded as unstable under the previous two stability criteria. Focusing on the preservation of the ecological function of animal mutualists and thus con-

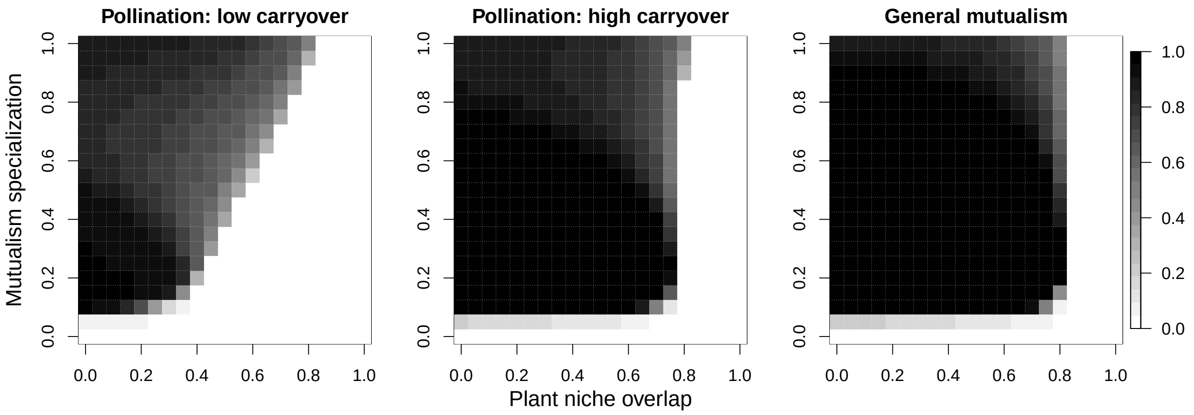

Figure 4.2: Size of the domain of attraction around the coexistence equilibrium. The size of the attractor domain was measured as the fraction of all combinations of initial population densities of the two plant and animal species that led to a point within 1% of the densities at the coexistence equilibrium. The three panels show results for plant-pollinator systems with a low ($B = 1$) and high ($B = 5$) degree of pollen carryover, and for a general plant-animal mutualism. Note that the small size of domains of attraction exhibited by generalised mutualistic systems in these simulations is a methodological artifact: With extremely low degrees of specialisation, the systems approached the coexistence equilibrium so slowly that it was often not reached within the maximum simulation time.

sidering persistence of both plant species and at least one animal brought only quantitative changes (Fig. 4.4D). The range of relatively low values of plant niche overlap and animal specialisation resulting in preservation of the animals' service in nearly all simulations increased compared to the case with persistence of all four species, but the overall effect of specialisation remained the same. As in the case of the domain of attraction, with more extensive pollen carryover the difference between generalised and specialised interaction systems diminished both for the persistence and the ecosystem function criterion (results not shown). For a general plant-animal mutualistic system, nearly all starting conditions produced a stable system according to both criteria.

4.5 DISCUSSION

It has repeatedly been suggested that specialisation is one of the main factors determining the response of organisms to disturbances (Vazquez & Simberloff, 2002; Colles *et al.*, 2009). Generally, it is assumed that a higher level of specialisation is associated with increased susceptibility to disturbances, because organisms with a wider niche can more easily adapt to changes in resource availability. However, the results of the present study show that for plant-animal mutualistic systems this is not neces-

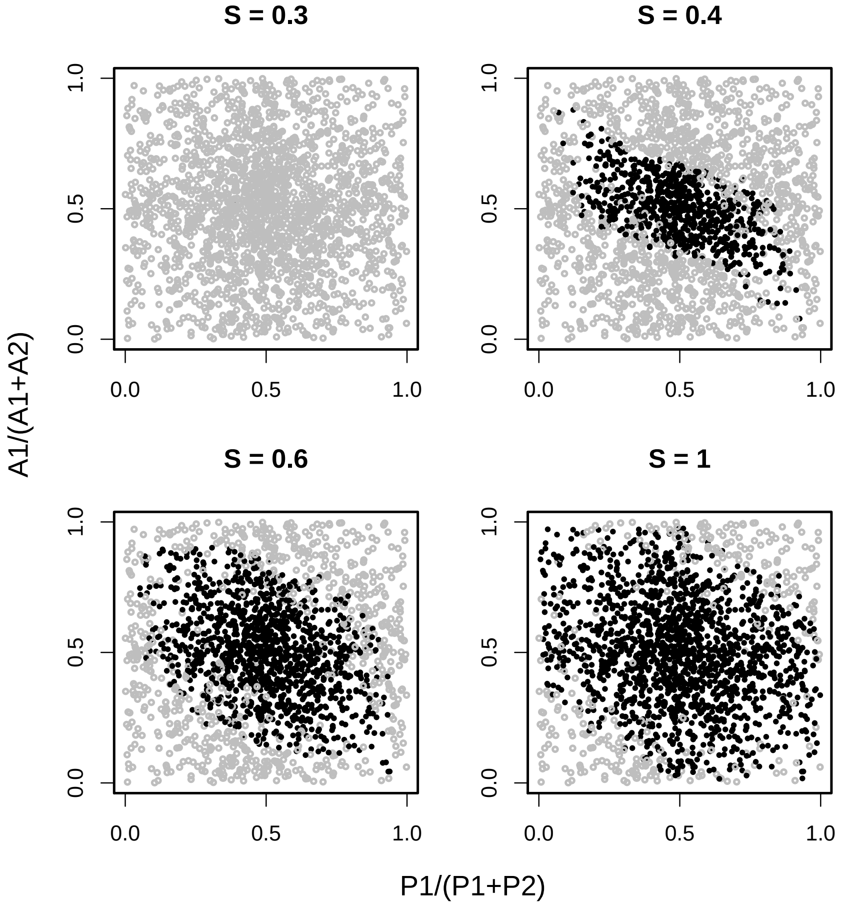

Figure 4.3: Shapes of single domains of attraction. Each graph shows 2000 combinations of initial densities plotted as the proportional densities of plant species 1 ($\frac{P1}{P1+P2}$) and animal species 1 ($\frac{A1}{A1+A2}$) relative to the total population of plants and animals, respectively. Combinations of initial densities that led to the equilibrium with coexistence of all four species are shown in black, those that did not lead to the coexistence equilibrium are in grey. At the coexistence equilibrium, the densities of both plant species and both animal species were exactly equal, thus $\frac{P1}{P1+P2} = 0.5$ and $\frac{A1}{A1+A2} = 0.5$. The graphs show results for four degrees of specialisation of mutualistic interactions (S). The degree of niche overlap of the two plant species was fixed at $\gamma_{ik} = 0.5$, the degree of pollen carryover at $B = 1$. Note that this graph gives the impression that more initial values were sampled near the coexistence equilibrium, because a combination of two high plant or animal population densities results in the same proportional density of one species relative to the total as the combination of two low absolute densities.

sarily the case: depending on the measure of stability applied, different relationships between specialisation and stability of

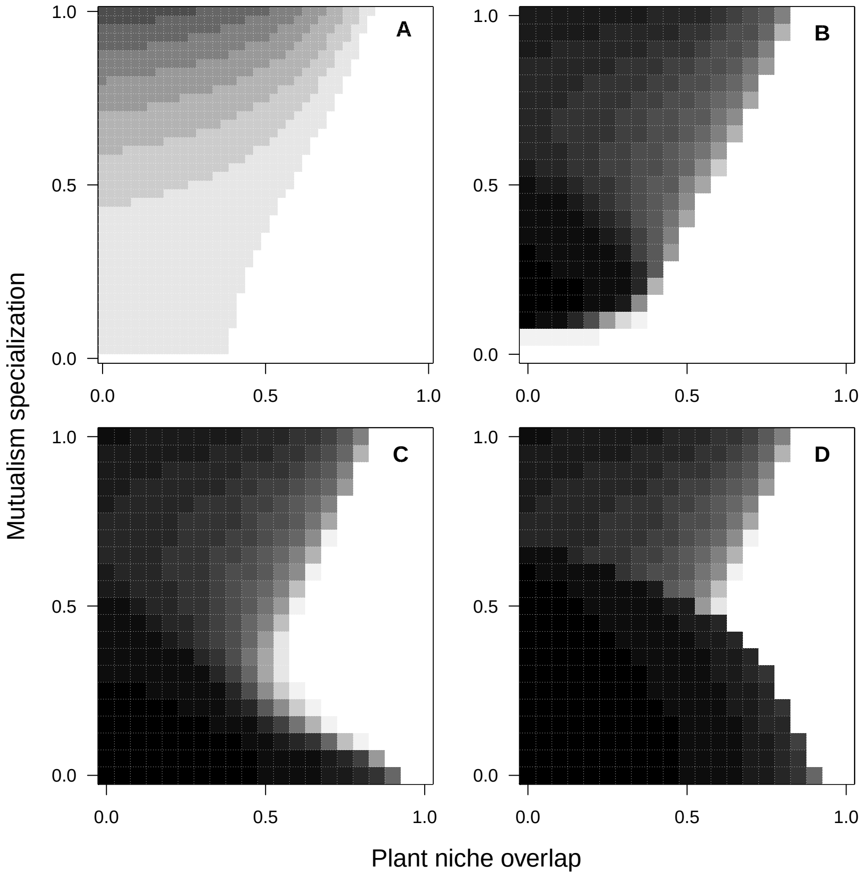

Figure 4.4: Contrasting effects of specialisation of plant-animal mutualistic interactions on four different measures of ecological stability. In all graphs, the level of stability is plotted as a function of plant niche overlap and mutualism specialisation. Darker shades of grey denote higher stability. Note that a different scale and resolution were used for Fig. A (same scale and resolution as in Fig. 1) compared to Figs. B-D (scale and resolution as in Fig. 2). The four stability measures are: A resilience criterion, B domain of attraction, C persistence criterion, D ecosystem function criterion. See Table 4.1 for a comparison of the properties of these stability criteria.

2x2-species mutualistic systems are possible. A positive effect of specialisation on system stability mainly results from the reduced risk of competitive exclusion, a fact that is rarely considered in the conservation literature. Furthermore, our results indicate that specialisation has a different effect on stability of plant-pollinator systems as compared to other plant-animal mutualistic systems, due to the reproductive disadvantage of rare plant species in generalised pollination systems.

The four criteria of ecological stability applied in this study did not produce consistent trends regarding the relationship between specialisation of mutualistic interactions, plant resource specialisation and ecological stability. The classical approach using the largest eigenvalue of the Jacobian matrix resulted in a clear positive relationship between interaction specialisation and resilience (see also Benadi *et al.*, 2012b), both in general plant-animal mutualisms and in pollination systems. For the resilience criterion, the risk of extinction of a specialised species as a result of decreased abundance of its mutualistic partner is not relevant as long as the coexistence equilibrium is qualitatively stable. Therefore, if the equilibrium is at all stable, as indicated by the positive value of $1 - |\hat{\lambda}|$, the speed of return following an infinitely small perturbation only depends on the magnitude of plant and animal growth rates at that moment. In order to rapidly recover from a perturbation, populations with a density higher than their equilibrium size must show a steep decline, while those below their equilibrium density should increase correspondingly. Our results show that specialisation of mutualistic system promotes this behaviour. However, due to the complexity of the model equations the mechanistic link between S and $\hat{\lambda}$ cannot be easily understood.

Whereas in the classical Lotka-Volterra model of interspecific competition a locally stable coexistence equilibrium is also globally stable (Mitra *et al.*, 1992), this is not necessarily the case for our mutualistic system: Even if the coexistence equilibrium is locally stable, the abundance of each population can only be reduced to a certain threshold density below which the species will fail to return to the coexistence equilibrium, and become extinct. Therefore, another measure of the stability of species coexistence in this system is the domain of attraction that encompasses all combinations of initial population densities leading to the coexistence equilibrium. The size of the domain of attraction depends on the severity of the birth rate reduction experienced by a population when it becomes rare. As previously mentioned, in plant-animal mutualisms in general a rare species disadvantage only exists with specialised interactions, whereas in plant-pollinator systems with limited pollen carryover both generalised and specialised interactions put rare species at a disadvantage. In the simulations presented here, with pollen carryover restricted to directly consecutive flower visits ($B = 1$) the combined effects of both types of disadvantages produce a nonlinear relationship between interaction specialisation and stability, with the smallest domains of attraction at an intermediate degree of specialisation. On the other hand, without the restriction of pollen carryover, coexistence is globally stable for almost all parameter combinations where it is locally stable, except for highly specialised interactions in combination with a relatively high degree of plant niche overlap. Note that the small size of domains of attraction at levels of specialisation just above zero in Fig. 4.2 is a methodological artefact: Here, the dynamics of the system was so slow that in nearly all simulation runs the coexistence equilibrium could not be reached within the maximum number of simulated time steps ($5 \cdot 10^{10}$).

A closer look at the shape of single domains of attraction shows that the propensity to return to the coexistence equilibrium is mainly determined by the relative initial abundances of plant and animal species ($\frac{P_1}{P_1+P_2}$ and $\frac{A_1}{A_1+A_2}$, respectively). As might be expected, ratios close to 0.5, the ratio at the coexistence equilibrium, tend to lead to coexistence, whereas ratios considerably below or above 0.5 do not. Surprisingly however, certain combinations of relative densities far below or above 0.5 can lead to coexistence. These are combinations where a rare species is rescued by its abundant preferred mutualistic partner. Obviously, this kind of rescue effect cannot occur in completely generalised systems, because with generalised interactions the identity of mutualistic partners does not matter.

In contrast to the attractor domain criterion, under the persistence criterion generalised mutualistic systems exhibit high stability even with the most restricted pollen carryover. Systems with $S = 0$, in which both animal species are identical in all respects, are not stable in a strict mathematical sense, as they do not return to the same equilibrium state following a small disturbance. Instead, these systems possess an infinite number of equilibrium states, i.e., their dynamics is neutral. Which of these equilibrium states is attained depends on the starting conditions. Systems with a degree of specialisation slightly above $S = 0$ possess only a limited number of equilibrium states, but their dynamics is so slow that often no equilibrium state is reached within an ecologically relevant time period. Thus, even though with unlimited time one or more populations would eventually become extinct, for all practical purposes a system can be considered stable if the species maintain large enough populations on an ecologically relevant time scale.

When the criterion for stability is preservation of the mutualistic service for both plant species, the range of parameter combinations that appear globally stable is again extended compared to the previous stability measure. This is due to the fact that for relatively generalised mutualistic interactions a further equilibrium state exists at which both plant species and one animal have densities above zero. Since the remaining animal species prefers one plant species over the other, different equilibrium densities are reached by the two plant species at this three-species equilibrium state. Under the ecosystem function criterion, the notion of a specialised species being at higher risk of extinction is certainly true: The higher the degree of specialisation of mutualistic plant-animal interactions, the lower the chance that both plant species will survive if one of the animal species becomes extinct. On the other hand, a certain degree of plant specialisation with respect to abiotic resources is necessary to allow coexistence of the two plant species despite the preference of the remaining animal species for one of them.

With these four criteria leading to different conclusions regarding the relationship between specialisation and stability of plant-animal mutualistic systems, the question arises which of these measures is the most appropriate for a specific purpose. In order to determine whether a species assemblage can coexist indefinitely in the absence of external influences such as fluctuating environmental conditions or immigration, the mathematical concept of qualitative stability of an equilibrium state, defined by the leading eigenvalue of the Jacobian matrix $\hat{\lambda}$, is still very useful. The magnitude of $1 - |\hat{\lambda}|$ provides additional information on resilience, the rate of return after a small disturbance. Ideally, the resilience of a system at equilibrium should always be considered together with its domain of attraction. A high rate of return to the equilibrium after an infinitely small perturbation has little practical relevance if the domain of attraction of that equilibrium is so narrow that the system would not return to the equilibrium under realistically variable environmental conditions. For conservation biologists and practitioners faced with the task of identifying the most fragile ecological systems, the persistence criterion is probably the most relevant, while policy makers and managers interested in maintaining a certain ecosystem service such as pollination may choose the ecosystem function criterion. Often the time needed to reach an equilibrium state is so long that the equilibrium is unlikely to be observed in natural ecosystems that are subject to frequent perturbations. Moreover, even if a system approaches an equilibrium state in the long term, its dynamics may at first amplify the effect of a perturbation and bring one or more populations to the brink of extinction (Neubert & Caswell, 1997). Hence, an adequate measure of stability should consider the transient dynamics of a system, not only its behaviour near the equilibria (Hastings, 2004). The last two measures of ecological stability fulfil this criterion. For these measures, empirical data on the magnitude and frequency of disturbances can be helpful to determine the range of starting conditions and the appropriate time scale.

Although the model used in this study contains a fair amount of mechanistic detail, it still makes a number of simplifying assumptions that may impact the results of our analyses. In the following, we discuss potential caveats and limitations of our modelling approach, and suggest directions for future research. First, the results presented in this paper to some degree depend on the choice of parameter values for numerical simulations, specifically on the assumption of an equal number of plant and animal individuals in the system at equilibrium. Choosing a lower animal-plant ratio results in a narrower range of specialisation and niche overlap values allowing qualitative stability of the coexistence equilibrium, while a higher animal-plant ratio extends that region (see Benadi *et al.*, 2012b). However, a different animal-plant ratio does not qualitatively affect the patterns presented in this study for the region allowing stable coexistence. As discussed in Benadi *et al.* (2012b), the few available empirical studies indicate that the amount of floral resources needed to sustain one animal varies widely, but at least for pollination mutualisms it seems that the ratio of animal to plant individuals is usually below one. On related terms, the choice of equal competition coefficients for both plant species, constant sums of trait matching values for all mutualistic interactions and equal values for all other parameters in this study was made in order to concentrate on the effects of community-wide specialisation. Since real mutualistic systems always deviate from the perfect symmetry assumed in this study, future work should explore the consequences of asymmetric interaction strengths and demographic parameters. For example, it would be interesting to study the consequences of a trade-off in plant competitive ability with respect to abiotic resources and attractiveness towards pollinators. Furthermore, future research should target larger mutualistic communities containing a mixture of various degrees of specialisation, and elucidate the effect of different distributions of specialisation levels on community stability. Some attempts in this direction have already been made (see e.g. Okuyama & Holland, 2008; Bastolla *et al.*, 2009), but much remains to be understood.

The current study is to some extent a theoretical exercise whose predictions are difficult to test in the field. Its main result, the finding that no single relationship between specialisation and stability of mutualistic systems exists, is bad news for conservationists and managers in search of rules of thumb for assessing the fragility of ecological systems. In order to strengthen the link between theory and application, future theoretical studies could employ stochastic models of larger communities and use easily measurable stability metrics such as the rate of species turnover and the coefficient of variation of population densities (Nilsson & Grelsson, 1995). For now, the present study highlights the need to account for the effects of disturbances on mutualistic and competitive interactions, and the special properties of plant-pollinator systems in this respect.

5

THE IMPORTANCE OF BEING SYNCHRONOUS: SPECIALIZATION AND PHENOLOGICAL SYNCHRONY OF PLANT-POLLINATOR INTERACTIONS ALONG AN ALTITUDINAL GRADIENT[1]

5.1 ABSTRACT

One of the most noticeable effects of anthropogenic climate change is the shift in timing of seasonal events towards earlier occurrence. The high degree of variation in species' phenological shifts has raised concerns about the temporal decoupling of interspecific interactions, but the extent and implications of this effect are largely unknown. In the case of plant-pollinator systems, specialist species are predicted to be particularly threatened, but until now most studies have focussed on generalists. In this paper, we studied phenology and interactions of plant and pollinator communities along an altitudinal gradient in the Alps as a model for the possible effects of climate change in time. Our results show that even relatively specialised pollinators were much more flexible in their use of plant species as floral resources than their local flower visitation suggested. We found no relationship between local specialisation of pollinators and the consistency of their visitation patterns across sites, and also no relationship between specialisation and phenological synchrony of pollinators with particular plants. Thus, in contrast to the conclusions of a recent simulation study, our results suggest that most pollinator species included in this study are not threatened by phenological decoupling from specific flowering plants. However, the flexibility of many rarely observed pollinator species remains unknown. Moreover, the observed flexibility of plant-pollinator interactions likely depends on a high degree of functional redundancy in the plant community, which may not exist in less diverse systems.

5.2 INTRODUCTION

Climate change generally advances the timing of phenological events in temperate regions of the world, but the magnitude

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[1] Article by G. Benadi, T. Hovestadt, H.-J. Poethke and N. Blüthgen
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of shifts in phenology varies greatly among species (Fitter & Fitter, 2002; Parmesan, 2006). As a result, previously existing species interactions may be disrupted when the species involved respond differently to changing environmental conditions (Stenseth & Mysterud, 2002). While a small number of such phenological desynchronisations have been documented (Visser & Holleman, 2001; Edwards & Richardson, 2004; Winder & Schindler, 2004; Both *et al.*, 2006), for most systems observations detailed enough to detect the existence and consequences of phenological mismatches are lacking (Miller-Rushing *et al.*, 2010). Mutualistic systems are expected to be particularly vulnerable to phenological desynchronisation, since in these systems both partners benefit from the interaction and are likely to be negatively affected by its loss (Bartomeus *et al.*, 2011). For plant-pollinator systems, one of the most common mutualistic interactions in terrestrial ecosystems (Ollerton *et al.*, 2011), it is currently uncertain whether phenological desynchronisation constitutes a major threat (Hegland *et al.*, 2009b; Willmer, 2012). Of the limited number of studies available, some report similar rates of advance of flowering phenology and pollinator appearance (Bartomeus *et al.*, 2011), while others suggest that either flower-visiting insects (Gordo & Sanz, 2005) or flowering plants (Forrest & Thomson, 2011) respond more strongly to climate change. However, even if mean rates of phenological shifts of plant and pollinator communities do not differ substantially, a critical question is to what extent each species depends on the availability of particular mutualists (Willmer, 2012). Phenological synchrony with one or a few species of mutualists should be important for species that are specialised in the sense that their performance (rate of survival and/or reproduction) is much higher in the presence of these particular mutualists compared to others. While most plant-pollinator networks exhibit a moderate degree of specialisation at the community level (Blüthgen *et al.*, 2007), species-level specialisation can vary considerably even within the same network, ranging from entirely opportunistic behaviour to highly specific associations (Vazquez & Aizen, 2003; Waser & Ollerton, 2006). Until now, studies of the effects of climate change on pollination mutualisms have mostly focussed on a limited number of generalist pollinators, providing a somewhat incomplete and possibly biased picture (Bartomeus *et al.*, 2011; Forrest & Thomson, 2011; Willmer, 2012). An exception is the simulation study by Memmott *et al.* (2007) which covered a large pollination network and predicted reduced availability of floral resources for up to 50% of all flower visitor species under simulated climate change scenarios. However, these simulations were based on the assumption that each pollinator species can only visit plant species that it has been previously observed to visit. For many rarely observed pollinators, this approach underestimates the true range of interaction partners (Blüthgen, 2010). Moreover, many species may be able to use new floral resources when they become available through phenological shifts. Thus, it is likely that Memmott *et al.* (2007) overestimated the negative effects of climate change on pollinators.

In the current study, we examined data on phenology and interactions of plant and pollinator communities to assess the extent of phenological synchrony with particular plant species among pollinators of different degrees of specialisation. Since sufficiently long time series of plant and pollinator phenology in combination with recordings of their interactions are currently unavailable, we used data collected at six sites along an altitudinal gradient in the Alps as a space-for-time substitution. Provided that the results are interpreted with some caution, the climatic changes along altitudinal gradients can serve as a useful model for the effects of climate change in time (Fukami & Wardle, 2005). For the current study, we monitored flowering phenology of insect-pollinated plants and insect flower visitation at each site weekly over the course of a season. We expected to observe changes along the altitudinal gradient that are at least qualitatively similar to the effects of climate change in time: An overall shift of plant and pollinator phenology towards earlier occurrence and an increase in the length of the season with decreasing altitude.

In our analyses, we took the perspective of the insects, since we assumed that flower-visiting insects are more vulnerable to changes in availability of their mutualistic partners compared to plants. Most insect-pollinated plant species are buffered against fluctuations in pollination success by a variety of traits such as self-pollination, vegetative reproduction, seed banks and iteroparity (Bond, 1994). By contrast, obligate flower visitors, particularly bees, but also numerous species of butterflies and flies, depend on the availability of nectar and/or pollen for survival (and reproduction in the case of bees) on a shorter time scale. Consequently, the selection pressure on insects to synchronize with the phenology of their floral resources should be stronger than the reciprocal pressure on plants, although long-term reductions in pollinator availability are likely to be detrimental to most plant species as well.

Our main aim in this study was to test the hypothesis that specialised flower visitors show a higher degree of phenological synchrony with the plant species they visit than generalised visitors. At a given time and location, a specialised pollinator should use a relatively small fraction of all available flowering plant species. Moreover, the sets of plant species visited by a specialised pollinator at different sites should be similar. Thus, we expected to be able to identify specialists both by their local specialisation and the consistency of their visitation patterns across sites. Regarding phenology, according to our hypothesis a specialised pollinator should show a high degree of phenological overlap with the plant species it depends on at a given site. In addition, if the specialist occurs at more than one altitude, its phenology should closely track the phenological shift of the relevant plant species from one site to the next. In summary, we expected to find a positive relationship between local and inter-site specialisation and phenological synchrony.

5.3 METHODS

5.3.1 *Data collection*

The data used in this paper were recorded in the National Park Berchtesgaden in the German part of the Alps (47 °32′ N, 12 °53′ E). Six grasslands in the central valley of the Park ("Wimbachtal") at altitudes between 950 m and 2020 m a.s.l. were selected for data collection. These sites were neither mown nor grazed by cattle during the period of data collection. Only after the flowering season the three lowest sites were grazed extensively. Hence, the flowering phenologies recorded in this study are not influenced by human land use. At each of the six sites, five rectangular transects of 30 x 4 m were established. Transect locations were chosen so as to cover a representative sample of the local vegetation. Data collection at the lowest site took place from 8 May until 2 September 2010. Sampling at higher sites began as soon as they were free of snow and the first plants started to flower. Whenever possible, each site was visited once a week during dry weather to record open flowers and visiting insects. However, due to long-lasting rain and bouts of snowfall at higher altitudes, this was not always possible. As a result, between 13 (site 1: 950 m) and 9 (site 6: 2020 m) censuses were taken at each site over the course of the season.

When visiting a site, all open flowers of insect-pollinated species (excluding grasses) were counted in 5 quadrats of 2 m^2that were placed at equal distances along each transect. Thus, quadrats covered 5 x 2 m^2x 5 = 50 m^2or 1/12 of the total area of all transects at a site. Flowers of rarer plant species that were not found in at least one of the quadrats were counted separately. Diameters of flowers of all plant species found at a site were measured in the lab with a digital calliper to the nearest 0.1 mm, and converted to flower area by assuming a circular shape. Between 1 and 10 flowers per species were measured (mean: 7.1 flowers), and the mean of their diameters taken as a basis for the calculation of flower areas. For zygomorphic flowers, the mean of length and width of a flower was used as diameter of the circle. Strongly compact inflorescences (e.g. those of Asteraceae) were treated as single flowering units both in counting and measurement of diameters. For each plant species, the total flower area per site was calculated by multiplying the number of counted flowers in quadrats by the average area of a single flower or flowering unit, and by extrapolating from the quadrat samples to the total area covered by all transects at a site (600 m^2).

In addition to the monitoring of open flowers, transect walks were carried out for five to seven hours (mean: 6:12 h) between 9 a.m. and 6 p.m. at each sampling date. During transect walks, the observer walked along the middle line of the long side of a transect, and recorded flower-visiting insects within two meters to the left and to the right of this line. Only taxonomic groups comprising obligate flower visitors were included in insect sampling: Bees (Hymenoptera: Apidae), flies (Diptera: Brachycera), and butterflies and moths (Lepidoptera). Except for a few very common and easily identifiable species (e.g. *Apis mellifera*, *Episyrphus balteatus*), all recorded flower visitors were caught with a sweepnet and kept in individually labelled test tubes for later identification. Fly specimens were killed and preserved in 70% alcohol, while bees and lepidopterans were killed with ethyl acetate and stored in dry tubes. All captured insect specimens were later identified to species level with the help of taxonomists (see Acknowledgements).

To examine the relationship between specialisation and floral morphology, we took measurements of the length of the floral tube from the same flowers used to determine flower areas (see above). The procedure was identical to the one described by Stang *et al.* (2006).

5.3.2 *Statistical analyses*

5.3.2.1 *Phenological estimator*

For all statistical analyses of insect and plant phenology, we used the weighted mean day of occurrence (WMD) as a phenological estimator. The WMD is the arithmetic mean of all dates on which the species in question was observed, weighted by its abundance on each date. In a simulation study comparing ten phenological estimators, Moussus *et al.* (2010) found that WMD and a second estimator based on Generalized Additive Modelling were the most accurate, unbiased and robust measures of phenophase, while commonly employed metrics such as first appearance dates performed poorly. In our analyses, abundances of insect and plant species were quantified as counts of individuals per hour of observation and flower area (m^2) per m^2 transect area, respectively.

5.3.2.2 *Overall phenological shift*

To describe the overall shift of plant and insect phenology with increasing altitude, we used a linear mixed-effects model with WMD per species and site as response variable, and altitude and guild ("plant" or "insect") as explanatory variables. To account for the non-independence of data points of the same species at multiple sites, species identity was included as a random factor. In a first step, a choice was made between a model without the random factor, a model with random intercepts and a model with random intercepts and slopes for each species. The best model of this choice was then subjected to model selection of the fixed effects. In both cases, we selected the best model based on Akaike's Information Criterion (AIC). Diagnostic plots were examined to check for heteroscedacity and normality of errors. We used the R statistical software version 2.14 (R Development Core Team, 2011b) for all data analyses and production of graphs. For linear mixed-effects models, we used the "lme" function included in the R package "nlme" (Pinheiro *et al.*, 2011).

5.3.2.3 *Local specialisation*

In order to quantify the degree of specialisation of insect species on flowering plants at a given date and site, we calculated the d′ index for species-level specialisation in bipartite interaction networks (Blüthgen *et al.*, 2006, 2008). This metric describes the deviation of the observed flower visits of a focal pollinator species from the expected distribution of visits based on resource availability. Its value ranges from zero (most generalised) to one (most specialised). While a number of other metrics of specialisation at the species level have been proposed (Dormann, 2011; Poisot *et al.*, 2012), the d′ index has two advantages over alternative indices: It considers the visitation pattern of a species in relation to resource availability and is robust to differences in numbers of observations per species (Blüthgen *et al.*, 2006). Thus, singleton observations do not automatically count as maximum specialisation, when in fact the sample size is too low to judge the range of resources used by a species.

For the calculation of d′, the relative availability of floral resources of different plant species can be assessed in two ways: Either the distribution of total visitor numbers on plant species can be taken as estimates of resource availability, or a measure of floral abundance such as flower area may be used instead (Dormann, 2011). While external flower abundances have the advantage of being independent of the overall visitation patterns of the pollinator community, using the plant abundance distribution as a null expectation for the distribution of flower visits may lead to unrealistic assumptions. For example, the theoretical maximum of specialisation is reached when all visits of a pollinator species are to the least abundant plant species in the community, but for a highly abundant pollinator it is unrealistic to assume that all individuals could visit a plant with only one or two flowers at the site. For our calculations of d′, we used the total number of visits to each plant as a null expectation, because in our opinion, these visitation totals give a better estimate of resource availability or floral attractiveness. For 60 out of 66 date-site combinations, flower areas and total numbers of visits per plant species were significantly positively correlated (mean of Kendall's τ: 0.49).

In a first step, we compiled separate interaction networks for all date-site combinations, and calculated d′ values for all insect species in each network. In this way, we avoided the problem of impossible interactions ("forbidden links") in aggregated networks due to separation of species in time or space. To obtain one overall specialisation value for each insect species, we then calculated the mean of all d′ values of a species weighted by number of observations. Index values based on single observations of a species were excluded. For comparison with other studies of mutualistic networks, we also calculated the H2′ index for specialisation at the network level (Blüthgen *et al.*, 2006). Both d′ and H2′ were calculated using the "bipartite" package for R (Dormann *et al.*, 2008).

We conducted a simple ANOVA followed by Tukey's posthoc test for pairwise comparisons to test for a difference in specialisation between taxonomic groups (bees, flies and butterflies and moths). The analysis of the relationship between specialisation and tube length of flowers visited by each insect species was split into two parts. For each insect species, we calculated the mean floral tube length of all plant species visited, with plant species weighted by numbers of visits. Since there was a high number of zero values in the data set (i.e., insect species visiting only flowers with openly accessible nectar), we first applied a Generalized Linear Model (GLM) to tube length as a binary variable (zero / nonzero values) with local specialisation (weighted mean d') and insect group as explanatory variables. We then performed a second analysis on the subset of data with nonzero tube lengths, this time treating tube length as a continuous variable. As the subsets of data of the three taxonomic groups showed different distributions and normality could not be achieved by applying a transformation to the whole data set, we fitted separate linear models to the data of each insect group, and applied log-transformation only to the fly data.

5.3.2.4 *Consistency of flower visitation across altitudes*

To assess the similarity of groups of plant species visited by an insect species at two altitudes (hereafter termed "visitation consistency"), we used the Bray-Curtis index of community similarity (Bray & Curtis, 1957; Legendre & Legendre, 1998). Given two vectors of standardized species abundances X_j and X_k with elements x_{ij} and x_{ik} for species *i* at site *j* and *k*, respectively, the Bray-Curtis similarity S is calculated as

$$S = \frac{2\sum_{i=1}^{N} \min(x_{ij}, x_{ik})}{\sum_{i=1}^{N} x_{ij} + \sum_{i=1}^{N} x_{ik}}$$

where N is the number of species. The index ranges between zero (no overlap in species occurring at the two sites) and one (all species with identical relative abundances). To compare the flower choices at two sites, we used the relative frequency of visits of the focal insect species to each plant species instead of the abundances X_j and X_k in the calculation of S. For this purpose, all observations of the focal insect from different dates were pooled. Depending on the number of sites at which each insect species was found, one to fifteen comparisons of plant species visited by an insect species at two sites could be made. However, in order to avoid pseudoreplication due to non-independence of pairwise comparisons, we only included comparisons between the lowest site at which a species occurred and all other sites in the analyses. Thus, one to five comparisons per insect species were made. Using only comparisons between neighbouring sites produced qualitatively and quantitatively similar results. Visitation consistency was calculated for all 56 insect species that were found at two or more sites with at least five individuals per site.

In order to test whether a value of S as high or higher than the observed value could have occurred by chance, we performed randomization tests. For this purpose, we drew random samples from all plant species available to the focal insect at each site. In a first step, samples were taken separately for each date at which the insect species was observed. The sample size was equal to the number of flower visits of the insect species observed at that date, while the probability of choosing a certain plant species equalled the proportion of visits of all insects to this plant species at that date and site. In a second step, all plant visitation samples of the separate days were summed to obtain an overall sample of flower visits as large as the total number of visits of the focal insect observed at the site. The similarity of these overall plant visitation samples of the two sites was assessed in the same way as for the real visitation data. The procedure was repeated 1000 times. A p-value was then calculated as the proportion of all similarity values as high or higher than the observed value (i.e., the value obtained from real visitation data). Following (Manly, 2007), the observed value of S was included in both the numerator and the denominator of the proportion. Significance was assessed at the 5% level in all randomization tests.

As in the case of floral tube lengths, due to an excess of zero values the statistical analysis relating visitation consistency to local specialisation (d′) and taxonomic group was divided into two stages. First, consistency was analysed as a binary variable (zero / non-zero consistency). In addition to d′ and order, we included the mean consistency of random plant samples (mean of 1000 replicates) and sample size (minimum number of observations at the two sites) as covariates in the model. We then built a second model including only non-zero consistency values, this time treating consistency as a continuous variable. In both cases, we first compared the fit of a mixed-effects model with species as a random factor to a (G)LM with only fixed effects. Since for the continuous data the mixed model did not perform significantly better in a likelihood ratio test, we proceeded with a linear model, whereas for the binary data a GLMM was used. The GLMM was fitted using the function "lmer" included in the R package "lme4" (Bates *et al.*, 2012).

5.3.2.5 *Phenological synchrony*

For flower visitors that depend on particular sets of plant species for survival and/or reproduction, we expected that the WMD of each flower visitor should be close to the WMD of the plant species it uses. Therefore, we used the absolute difference between the WMD of an insect species and the collective WMD of the plant species it visited as a measure of phenological asynchrony at one site. However, one could argue that a close match between weighted mean occurrences of insects and plants is of less importance if the flowering phase of the plant species is long. Hence, we also calculated a z-score (absolute difference in WMD divided by the standard deviation of the plant phenology) as an alternative measure of phenological asynchrony. All insect-site combinations with at least five observations were included in the analysis. Overall, the data set comprised 286 asynchrony values of 138 insect species. Since a mixed model with species identity as a random factor did not result in a better fit, we employed a linear model to test for an effect of local specialisation (d′) and taxonomic group.

For insect species that occurred at more than one site, we examined the shift of WMD between sites in relation to the shift of the group of plant species visited by the insect at one of the two sites (Fig. 5.1). Using the higher altitude as a reference, we considered the phenology of all plant species that were visited by the insect at the reference site and also occurred at the lower site. Phenological asynchrony was defined as the absolute difference between the insect's and plants' shifts. The higher altitude was chosen as a reference since a shift from high to low altitude corresponds to the direction of climate change. However, using the lower site as a reference did not qualitatively change the results of the analyses. The procedure for statistical tests of asynchrony of shifts in phenology in relation to insect specialisation and order was the same as for synchrony at one site. As in the case of visitation consistency (see above), we calculated phenological shifts between the lowest site at which each insect species occurred and all other sites. Using combinations of neighbouring sites instead yielded qualitatively similar results. All combinations of insect species and pairs of sites with at least five observations of the insect were included in the analysis, resulting in 138 data points of 54 insect species.

5.3.2.6 *Effects of environmental variation and observer identity on pollinator abundance*

Visitor numbers at flowers tend to fluctuate with current environmental conditions and may therefore not always reflect actual population densities. Although all our observations were carried out under dry and relatively warm conditions (at least 12 °C), it is likely that some of the observed variation in in-

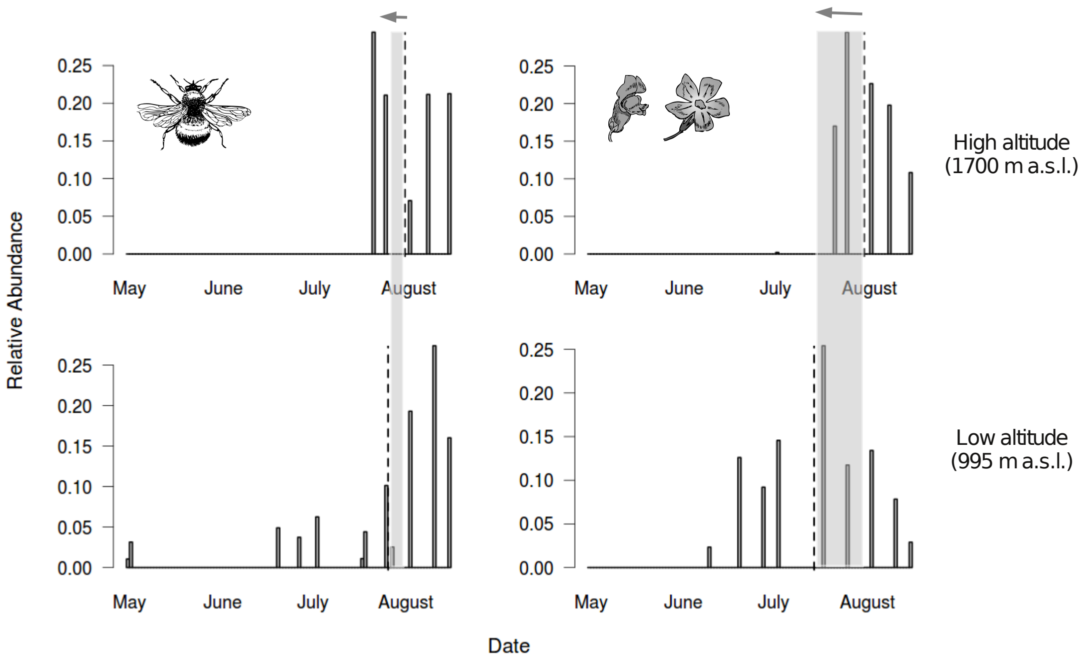

Figure 5.1: Synchrony of the phenological shift of an insect species (Bombus pascuorum) and the flowering plants it visited. Barplots show the relative abundance of the bumblebee (left) and the flowers (right) over time. The flowering phenology comprises all plant species that were visited by the bumblebee at the higher altitude and occurred at both altitudes. Dashed lines mark the weighted mean day of occurrence (WMD) of the bumblebee and plant species, respectively. Grey rectangles indicate the magnitude and arrows the direction of shifts in phenology between the two sites.

sect abundance was due to the weather being more or less favourable for flower visitation. Moreover, since data collection for this study was carried out by three different observers, recorded visitor numbers may have been affected by inter-observer differences in rates of detecting and catching insects from flowers. To examine the influence of environmental conditions and observer identity on visitor numbers per day (all species combined) we employed a Poisson GLM with mean daily temperature (°C) and humidity (%), observation time (hours), total flower area (m^2 / m^2 transect area), altitude (m a.s.l.) and observer as explanatory variables. Since exploratory data analyses suggested a nonlinear relationship between flower area and visitor number, flower area was log-transformed to linearise the relationship. In addition, a quadratic effect of altitude was included in the model. The final model showed significant positive effects of humidity and flower area, a marginally significant positive effect of observation time and a significant hump-shaped relationship with altitude (Table 5.2). Since one of the three observers recorded significantly lower individual numbers compared to the other two, we multiplied all visitor numbers by a correction factor to account for this inter-observer difference and repeated the analyses presented in this paper. Using the correction did not qualitatively change the results of the analyses.

5.4 RESULTS

5.4.1 *Overall patterns*

In total, we observed 10504 interactions between 166 flowering plant species and 444 insect species. Flower-visiting insects included 326 species of flies, 45 bees and 73 butterflies and moths. The data set comprised 67 interaction networks, of which 59 were significantly specialised (mean H2′ = 0.554, SD = 0.149).

5.4.2 *Local specialisation*

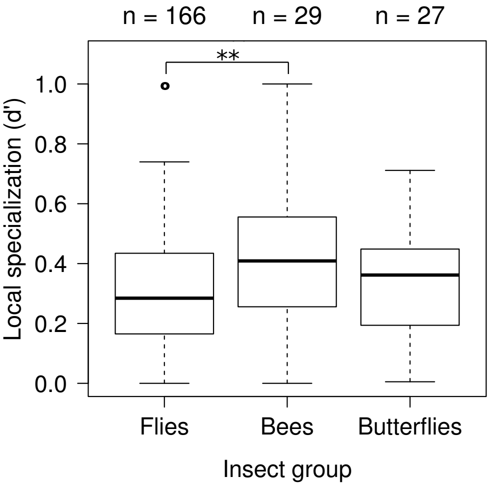

Figure 5.2: Local specialisation of insect taxonomic groups. Sample sizes given above each box are species numbers. Each data point is the mean d′ value over all networks in which a species was observed weighted by number of observations. Single observations were excluded from the calculation. Overall effect of taxonomic group: $F_{2,219} = 4.399$, $p = 0.013$. Asterisks indicate a significant difference ($p < 0.01$) determined by Tukey's post-hoc test for pairwise comparisons.

At the species level, flower visitors were on average moderately specialised (overall mean of species' weighted mean d′ values = 0.332, SD = 0.208). Bees were significantly more specialised than flies, with lepidopterans at an intermediate level of specialisation (Fig. 5.2). The average number of plant species visited by an insect species (all sites and dates pooled, singletons excluded) was 6.53 (flies: 6.62, bees: 7.62, butterflies and moths: 4.77).

Mean tube length of flowers used was generally positively related to local specialisation of insects, but we found differences between insect groups. In the analysis of tube length as a binary variable (flowers without or with tubes), the proportion of species visiting flowers with non-zero tube lengths was highest for lepidopterans (100%, n = 27), followed by bees (92.8%, n = 28) and flies (69.3%, n = 166). Both the effects of taxonomic group ($p < 0.001$, estimate on the logit scale: Flies 0.207 (s. e. 0.293), bees 1.541 (0.761), butterflies and moths 17.732 (0)) and of d′ (estimate: 2.104 (s. e. 0.876), $p = 0.012$) on the probability of visiting flowers with tube lengths greater than zero were significant, with no significant interaction between the two variables. With tube length as a continuous variable (flowers with openly accessible nectar excluded), mean floral tube lengths increased strongly with insect specialisation for bees and to a lesser extent for flies, but not for butterflies and moths (Fig. 5.3).

5.4.3 *Visitation consistency*

In addition to the local specialisation of insects on flowering plants at a given date and site, we calculated the Bray-Curtis similarity of sets of plant species visited by each insect species at two sites (its visitation consistency) to assess the degree of dependence of insect species on particular plant species. For 51 out of 148 insect-altitude combinations, we found that the plant species visited were significantly more similar than expected by chance. Thus, the proportion of significant tests was much higher (34.4%) than expected if the null hypothesis were true in all cases (5%). In the analysis of visitation consistency as a binary variable (consistency equal to zero or higher than zero), significant effects of taxonomic group ($p < 0.001$, estimates on logit scale: Flies -6.648 (s. e. 1.550), bees 1.164 (2.060), lepidopterans -7.088 (2.018)) and of the mean similarity of random plant samples (square-root transformed, 29.965 (6.354), $p < 0.001$) were found. The effect of local specialisation (d′) on visitation consistency was not significant. On the other hand, when visitation consistency was treated as a continuous variable (zero values excluded), only the mean similarity of random plant samples had a significant effect (Fig. 5.4). Moreover, the within-species variation in visitation consistency was high

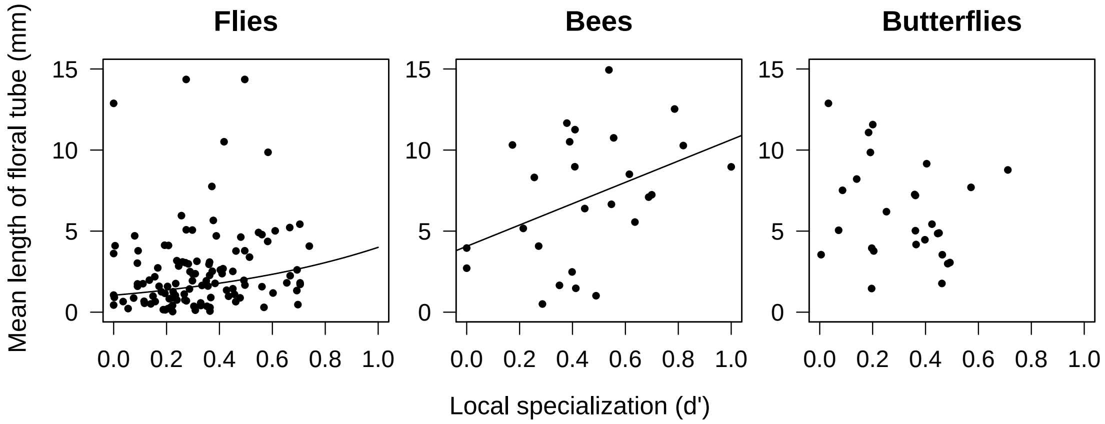

Figure 5.3: Relationship between pollinator specialisation and mean tube length of flowers visited. Tube lengths are means of flowers visited by an insect species weighted by number of visits. Lines indicate the prediction of linear regressions: Flies: $\log(y) = 1.342\ x + 0.044$, $p = 0.015$, $R^2 = 0.04$; Bees: $y = 6.578\ x + 4.061$, $p = 0.045$, $R^2 = 0.12$. The regression for butterflies and moths was not significant ($p = 0.25$).

in relation to the between-species variation. Specifically, the average standard deviation of consistency values of the same insect species was approximately 1.5 times as large (0.232) as the standard deviation of all species means (0.15).

5.4.4 *Phenological shifts and asynchrony*

When assessing the overall shift in phenology with increasing altitude, model selection resulted in a linear mixed-effects model of WMD against altitude and guild without an interaction between the two explanatory variables (Fig. 5.5). Thus, the population-level estimate of the mean shift of WMD with increasing altitude was the same for plants and insects (estimate ± s. e.: 1.34 ± 0.16 days / 100 m, $p < 0.001$). The estimated mean WMD of insect species was approximately six days later than the plants' mean (5.91 ± 2.09 days, $p = 0.005$).

The average difference in WMDs of insects and the plant species they visited at one site was 11±9.5 days (median: 8.4 days). We found no significant effect of local specialisation and no difference between insect groups regarding the degree of phenological asynchrony at one altitude (Fig. 6, panels a) and b), Table 5.1). The same was true for synchrony of shifts in phenology of insect species and the plants they visited (Fig. 6, panels c) and d), Table 5.1).

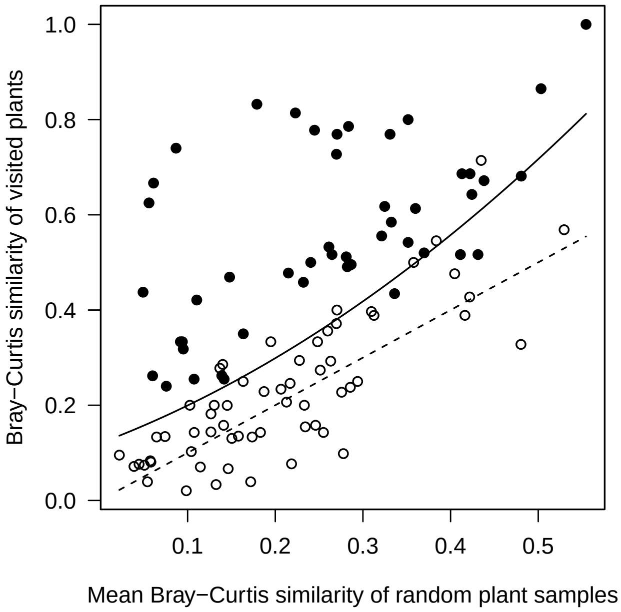

Figure 5.4: Similarity of flower selection across sites. The Bray-Curtis similarity of plant species visited by an insect species at two altitudes is plotted against the mean similarity of random samples of all flowering plants available to the insect at the two sites. The dashed diagonal line marks the expected similarity of visited plant species under the null hypothesis of random selection of flowers. Filled circles indicate significantly higher similarity of visited plants than expected by chance, as determined in randomization tests. Open circles indicate nonsignificant tests. The solid line is the prediction of a linear regression: $\text{sqrt}(y) = 1.167\, x + 0.336$, $p < 0.001$, $F_{1,105} = 51.28$, $R^2 = 0.32$.

5.5 DISCUSSION

In order to be able to predict the effects of climate change on plant-pollinator interactions via shifts in phenology, it is important to understand to what extent pollinator species depend on phenological synchrony with specific plant species as floral resources. The current study sheds light on this question by considering the relationship between pollinator specialisation and phenological synchrony with flowering plants along an altitudinal gradient. Contrary to our expectation, we found that specialised pollinators did not show a closer phenological match with the plant species they visited than generalised pollinators. Moreover, the similarity of plant species visited by the same pollinator species at different altitudes ("visitation consistency") was highly variable within species and showed no

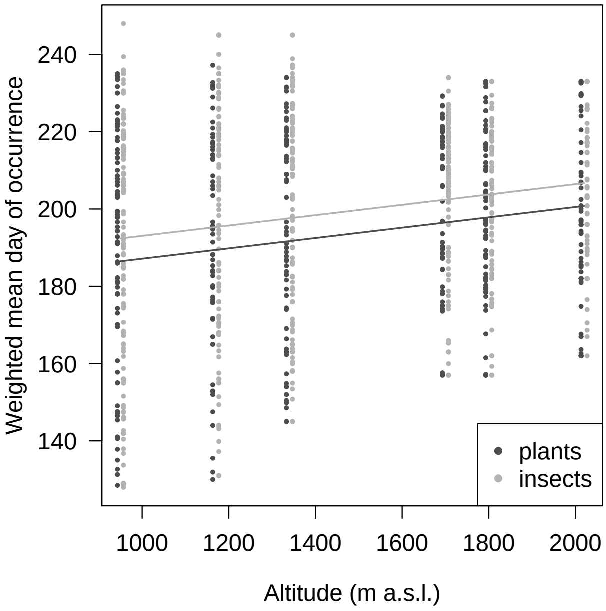

Figure 5.5: Shift of flowering phenology and flower visitor occurrence with increasing altitude. For each species at each site, the weighted mean day of occurrence (WMD) is plotted against the site's altitude. Day 1 refers to 1 January 2010. Sampling at the lowest altitude began on 8 May (day 128). For clarity, plant data have been plotted 7 m below their true altitude, insect data 7 m above. The straight lines indicate the population-level prediction of a linear mixed-effects model of weighted mean day against altitude and guild ("plant" or "insect"), with species as a random factor.

relationship with local specificity of flower visitation at a given time and location.

As always when a statistical test fails to reject the null hypothesis, there are several alternative explanations. One possibility is that the proposed relationship is truly absent, but the data used may also simply be inadequate to evaluate the hypothesis in question, or the effect may be weak, highly nonlinear, or confounded with other factors. Below, we explore some of the possible explanations for the lack of a relationship between the two aspects of specialisation and between specialisation and phenological synchrony in greater detail.

5.5.1 *Why did we not find a positive relationship between local specialisation and visitation consistency?*

Highly specialised pollinators should always visit the same flowering plant species, and thus appear specialised under both cri-

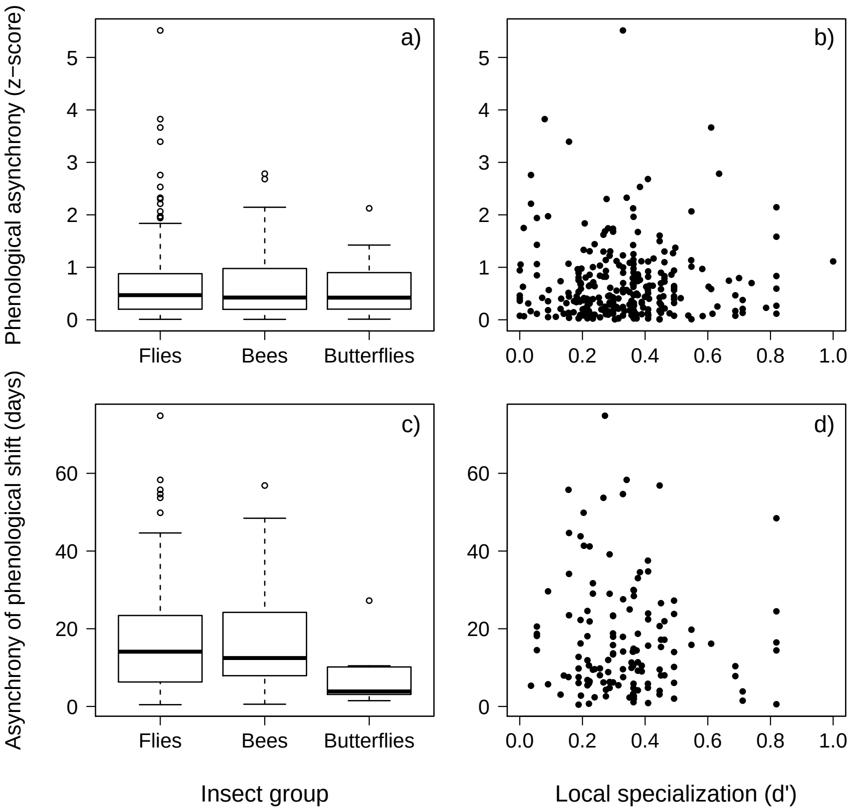

Figure 5.6: Phenological asynchrony of insects and the plants they visited. Boxplots in panels a) and c) display the relationship between phenological asynchrony and taxonomic groups of insects, scatterplots in b) and d) the relationship with local specialisation of insect species. In a) and b), asynchrony is measured as the absolute difference of the weighted mean days of occurrence (WMD) of insects and plants at one site divided by the standard deviation of the plant WMD. Panels c) and d) show the asynchrony of shifts in WMD of insects and the plants they visited with changing altitude. See Table 5.2 for results of the statistical analyses.

teria. However, since the measure of local specialisation used in this study (d′) is based on a comparison of observed and expected distributions of flower visits among plant species, it is not well suited to detect specialisation on abundant and frequently visited plant species. Other measures may indicate a high degree of specialisation even if all visits of a pollinator species are to the most abundant plant species, but this detection ability comes at the cost of many false positives – pollinators without any preference for specific plant species are treated as specialists, simply because their visitation patterns follow the skewed abundance distribution of the plant community and only a subset of their interactions have been sampled (Blüthgen

Table 5.1: Results of linear models of phenological asynchrony at one altitude and asynchrony of phenological shifts between altitudes as a function of degree of local specialisation (d′) and taxonomic group (insect order).

RESPONSE VARIABLE	EXPLANATORY VARIABLE(S)	D.F.	F	P
Asynchrony at one site	Taxonomic group	2, 280	0.16	0.851
	Specialization	1, 280	0.35	0.557
	Taxonomic group × Specialization	2, 280	0.76	0.471
Asynchrony of shifts between sites	Taxonomic group	2, 132	1.96	0.145
	Specialization	1, 132	0.05	0.831
	Taxonomic group × Specialization	2, 132	0.22	0.802

et al., 2006; Dormann, 2011). Therefore, we preferred to use a conservative measure of specialisation such as d′, which admittedly fails to detect true specialists under some circumstances.

Of the three insect groups included in this study, the flower visitation patterns of bees have received the most attention in the literature. Traditionally, bee species have been classified as either oligolectic or polylectic, depending on whether they collect pollen from flowers of one or more plant families. Most bee species included in the current study are classified as polylectic in the literature (Westrich, 1989). Of the oligolectic species, *Bombus gerstaeckeri* (specialised on flowers of monkshood, genus *Aconitum*) had a high mean d′ value (0.79), while *Chelostoma florisomne* (a specialist on the genus *Ranunculus*) and *Panurginus montanus* (a specialist on Asteraceae, particularly the subfamily Cichorioideae) scored low on the d′ scale, because the flowers they visited were common and visited by many other insect species, particularly by flies who constituted by far the most abundant visitor group. Hence, it is likely that several other insect species were wrongly classified as generalists by our approach. On the other hand, several bee species known as polylectic in the literature received high d′ values in our study. The fact that d′ was positively related to floral tube length suggests that many insect species classified as specialised based on d′ visited flowers of multiple plant species, but were selective with respect to the floral traits of the species they visited.

This would explain the high degree of intraspecific variation in visitation consistency. For example, for *Bombus wurflenii*, a bumblebee species with a high mean d′ value (0.82) that occurred at all six sites, seven out of fifteen pairwise comparisons of visited plant species showed significant visitation consistency, while in the remaining eight cases the similarity of plant species visited by the bumblebee was even lower than the mean of randomly chosen plant samples. Yet the species consistently selected flowers with mean tube lengths greater than the average at all six sites (Fig. 5.7). Thus, it seems that *Bombus wurflenii* is a specialist with respect to certain floral traits, and that the bumblebee did not visit the same plant species throughout its altitudinal range because the traits it prefers were present in multiple plant species of which a subset occurred at each site.

5.5.2 *Why did we not find a positive relationship between specialisation and phenological synchrony?*

Regarding the synchrony of phenological shifts of flower visitors and the plants they visited, one possible explanation for the lack of a relationship with specialisation is that those species that were both unable to shift their phenology in synchrony with the relevant flowering plants and not flexible enough to use other floral resources simply did not occur at more than one altitude. Since only 56 out of 444 flower visitor species were found at more than one site in sufficient numbers to be included in the analysis, this argument does not seem unreasonable. If highly specialised species have trouble adjusting to the conditions at different altitudes, we would expect that species occurring at more than one altitude should on average be less specialised than single site species, or at least have a lower variance of degrees of specialisation. While the mean degree of specialisation did not differ significantly between the two groups (Generalized Least Squares; estimates ± s. e.: single site 0.312 ± 0.022, n=119; multiple sites 0.334 ± 0.027, n=103; p = 0.407), insects found at a single site did indeed show a higher variance of d′ compared to species found at multiple sites (Fligner-Killeen test of homogeneity of variances; single site variance: 0.056; multiple sites variance: 0.028; $p < 0.001$). However, this difference in variances may simply be due to a sampling effect, since the average number of observations per species was significantly lower for species that occurred only at one site (Generalized Least Squares; estimates ± s. e.: single site 3.296 ± 0.210; multiple sites 6.050 ± 0.050; p = 0.005). On the other hand, as discussed above, some specialised species almost certainly remained undetected by our approach. Thus, the possibility that less flexible pollinator species did not occur at more than one site cannot be ruled out based on our data.

5.5.3 *Limitations of the study design*

As in any non-manipulative study, it is difficult to assess to what degree the results presented in this paper were affected by the specific conditions under which the study was carried out. For example, it is possible that the phenological patterns of 2010 were exceptional, and many pollinator species whose occurrence in the season would normally closely match the flowering phase of the plant species relevant to them were out of synchrony in this particular year. To be sure of the generality of the patterns described here, data should be collected over several seasons.

Furthermore, since our estimates of pollinator phenology were based on observations of insects on flowers, a certain degree of phenological synchrony is a necessary consequence of the sampling design. To date, few data sets of pollinator phenology independent of flowering phenology have been collected (Forrest and Thomson, 2011). Even with this constraint in sampling design, the degree of phenological synchrony of insects and flowers may vary considerably, depending on the abundance distribution of each species over time. However, our study design did not allow to detect early appearance of pollinators in spring before the first flowers, or late occurrence in autumn after the end of flowering. It is possible that synchronous peaks in abundance are less fitness-relevant for pollinators than synchrony in first appearance. Unfortunately, estimates of first appearance dates of insects from field data are usually very inaccurate due to detection issues (Moussus *et al.*, 2010). One solution to this problem is to record emergence dates of adult insects, for example by using trap nests for bees or ground traps for flies (Forrest & Thomson, 2011). However, such studies can usually only cover a small subset of the pollinator community.

Finally, as mentioned in the introduction, some caution is needed when drawing conclusion about the effects of climate change in time based on data from altitudinal gradients (Fukami & Wardle, 2005). Whereas plant phenology in alpine habitats is primarily affected by local conditions, pollinators experience resource availability and abiotic conditions at a larger spatial scale (Hegland *et al.*, 2009a). Hence, it is possible that some of the more mobile insect species were able to relocate their foraging ranges along the altitudinal gradient according to resource availability, and did not need to synchronize their flight period with the flowering phenology of plants at only one altitude.

5.5.4 *Conclusion*

Whereas previous work predicted that, as a consequence of climate change, many pollinator species would suffer from reduced availability of floral resources due to phenological asynchrony with the flowering plants they were previously visiting (Memmott *et al.*, 2007), the current study suggests that for most pollinators phenological synchrony with specific sets of plant species is not important. Despite the fact that many pollinator species showed nonrandom patterns of flower visitation, we found no evidence that insect species that were more selective with regard to the flowers they visited synchronized their flight period with the flowering phase of particular plants. Thus, as Willmer (2012) suggested, plant-pollinator interactions seem to be buffered against climate change by their flexibility in the choice of interaction partners.

A possible explanation for the lack of a positive relationship between pollinator specialisation and phenological synchrony lies in the finding that specialised pollinators visited plant species with longer floral tubes than generalists. Since the morphological traits (and possibly other traits such as flower colour and scent) that these specialists preferred were present in multiple plant species of which a subset occurred at each altitude, they did not need to track the phenological shifts of particular plant species. This interpretation highlights the importance of understanding the mechanisms behind ecological specialisation. Until now, specialisation of plant-pollinator interactions has predominantly been studied from the plants' perspective (Aigner, 2001; Fenster *et al.*, 2004). While a number of studies have examined pollinator preferences for single floral traits (morphology: Stang *et al.* (2007), scent: Junker *et al.* (2010), colour: Lunau & Maier (1995)), the study of combinations of multiple traits has only just begun (Junker *et al.*, 2012). Furthermore, the costs and benefits of specialisation for pollinators are still not fully understood. For example, specialisation may be an adaptation to increase the efficiency of exploiting particular resources (Waser *et al.*, 1996; Goulson, 2003), a constraint imposed by chemical protection of pollen by plants (Praz *et al.*, 2008), or a reaction to the presence of competitors. Progress in these areas of basic ecological research will allow more accurate predictions regarding the effects of anthropogenic disturbances on natural pollination systems.

While our results indicate that at least for the most abundant pollinator species in our study system phenological synchrony is not an issue, we cannot be certain about the generality of these findings. Further investigations are needed to assess the importance of phenological synchrony for the many species of pollinators that were observed too infrequently to be included in the analyses. Since samples of insect communities always contain a large number of singleton observations, this issue can only be addressed by focussing sampling efforts on a small number of species. Likewise, the community approach to estimating specialisation employed in this study very likely underestimates the dependence of pollinator species specialised on common and frequently visited plants. Here again, species-level studies are needed to elucidate the effects of shifts in phenology on extreme specialists such as the oligolectic bee species mentioned above. Finally, the exceptionally high diversity of plant species found at our study sites may in itself explain the absence of phenological synchrony of pollinators with specific plant species. As mentioned above, it appears that even pollinator species with strong preferences for certain floral traits had no need to synchronize with particular plants because the high degree of functional redundancy (Rosenfeld, 2002) in the plant community allowed them to visit different plant species at different sites. If this is true, phenological synchrony should be much more important for pollinator species in less diverse systems. Hence, biodiversity may be the best buffer against climate change.

5.6 APPENDIX

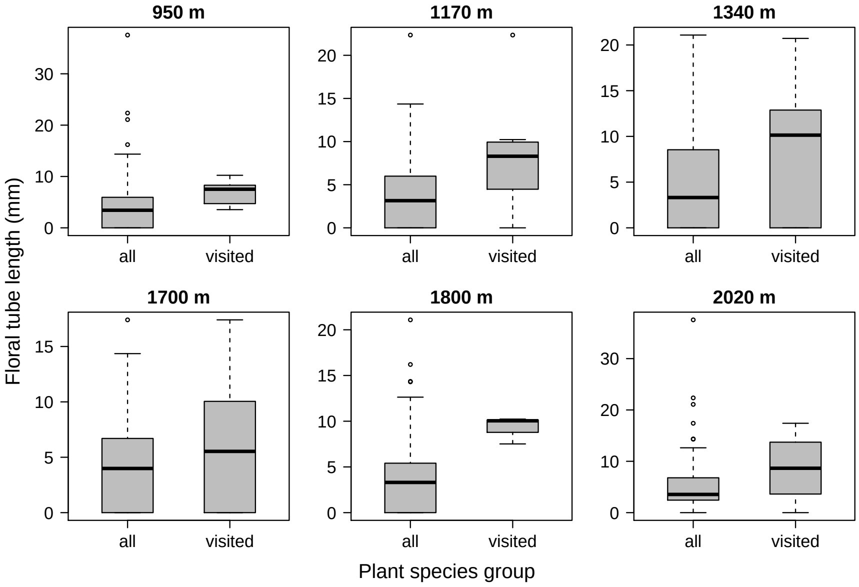

Figure 5.7: Floral tube lengths of plant species visited by *Bombus wurflenii* (Hymenoptera: Apidae) compared to tube lengths of all available flowering plants. For each altitude, boxplots show the distribution of tube lengths of all plant species that flowered on the dates on which the bumblebee was observed ("all") and the tube lengths of plant species visited by the bumblebee ("visited"). Note that floral tube lengths are not weighted by abundance.

Table 5.2: Results of the best model explaining insect abundance (number of individuals of all insect species combined per day). Since we detected overdispersion in the data, the standard errors were corrected by using a quasi-Poisson GLM.

EXPLANATORY VARIABLE	D.F.	F	P
Altitude	1, 63	2.399	0.127
$(\text{Altitude})^2$	1, 63	8.482	0.005
Observer	2, 63	50.272	< 0.001
Observation time	1, 63	3.233	0.078
Humidity	1, 63	20.207	< 0.001
Flower cover (log-transformed)	1, 63	12.679	< 0.001

6

SYNTHESIS

The previous four chapters of this thesis examined specific questions concerning diversity maintenance in animal-pollinated plant communities and stability of plant-pollinator networks against disturbances caused by climate change. In this final chapter, I look at these issues from a larger perspective to place our findings in the context of their respective fields. For both topics, I provide an overview of current knowledge and highlight questions to be answered by future research.

6.1 MECHANISMS OF DIVERSITY MAINTENANCE IN ANIMAL-POLLINATED PLANT COMMUNITIES

Based on theoretical considerations (Levin & Anderson, 1970; chapter 2), it is clear that pollination by animals makes plant species coexistence more difficult, since it puts less abundant plants at a disadvantage. Whereas in perfectly specialised plant-pollinator systems rare plant species receive a lower quantity of pollinator visits, generalised pollination results in equal visitation rates, but lower visit quality (amount of pollen transferred per visit) for rarer plants. In chapter 2, we studied the effects of a possible stabilising mechanism, niche differentiation with respect to abiotic resources, that may counteract the destabilising tendency of pollination. Surprisingly, we found that under certain conditions interactions with pollinators can increase the resilience of a plant community, allowing faster recovery from a small disturbance. As shown in chapter 3, in a plant community stabilised by niche differentiation it is theoretically possible that interactions with pollinators increase the maximum number of coexisting plant species, but the conditions under which this effect occurs are much more restricted than suggested by a previous study (Bastolla *et al.*, 2009).

Niche differentiation is only one of several possible mechanisms that may contribute to species coexistence in animal-pollinated plant communities. Other possibilities are scattered over the literature, but a comprehensive overview is lacking (but see Palmer *et al.*, 2003). Here, I attempt to give such an overview. Following Chesson (2000), I distinguish between equalising and stabilising mechanisms, with a focus on specific features of plant-pollinator systems. The possibility of positive (facilitative) interactions between plant species is considered separately. For each mechanism, I try to answer the following questions: Is it theoretically plausible? What is the empirical evidence that the mechanism is important for diversity maintenance in real plant communities? I conclude this section with a discussion of open questions.

6.1.1 *Equalising mechanisms*

As mentioned in chapter 1, equalising mechanisms contribute to species coexistence by reducing fitness differences between community members. Numerous trade-offs may equalise the fitness of flowering plants with different strategies, for example, a trade-off between allocation of resources to pollinator attraction and production of ovules (Haig & Westoby, 1988), but these do not affect the fitness disadvantage of plant species with low relative abundance. In the following, I discuss the effects of behavioural traits of pollinators and the spatial structure of plant communities that may decrease the difference in the quality and/or quantity of pollinator visits received by rare and abundant plant species.

Flower constancy, the specialisation of individual pollinators on particular flowering plants, reduces loss of pollen to heterospecific flowers and clogging of stigmas with pollen of other plant species (Levin & Anderson, 1970; Straw, 1972; Goulson, 1994; Montgomery, 2009). The effect on plant reproduction is essentially the same as for specialisation at the species level. However, whether pollinator constancy really reduces the difference in reproductive success between rare and common plant species depends on the relative numbers of pollinators specialising on each plant species and their visitation rates. Obviously, specialisation on a rare plant species can only be profitable for a pollinator if the reward per time it receives is at least as high as for specialisation on a more common plant species. Since pollinators foraging on rare plant species have higher costs of travelling than those foraging on more abundant plants, the only way to achieve equal rewards per time is if rare plant specialists receive a higher reward per flower visited. In a game-theoretic model of pollinator foraging behaviour, Kunin & Iwasa (1996) explored the conditions for equal profitability of specialisation on a rare and a common plant species, respectively, and the consequences for plant reproductive success. Assuming that both plant species produce nectar at identical rates, they found that the rarer plant species always received disproportionately fewer pollinator visits compared to the common plant. However, the difference in reproductive success of the two plants was lower than in the case of generalist foraging behaviour. Thus, it seems that flower constancy can alleviate the fitness difference between rare and common plant species, but constancy alone is not sufficient to ensure species coexistence. Flower constancy is particularly well studied in bees, but it has been reported to occur in all other major groups of pollinators as well (reviewed by Amaya-Marquez, 2009). Several hypotheses have been suggested to explain why pollinators exhibit this behaviour (Chittka *et al.*, 1999). Just like specialisation at the species level, constancy can be viewed as an adaptation to maximise resource intake while minimising the costs of learning to recognise and handle different types of flowers. Thus, constancy is expected to be common when co-occurring plant species differ strongly in floral traits, the energetic reward per flower is large and the costs of travelling are low.

Another mechanism that has been proposed to contribute to coexistence of plant species sharing pollinators is pollen carryover, that is, pollen carriage over non-consecutive flower visits. In the simplest case, carryover is modelled as the maximum number of flower visits between pollen removal and deposition (Feldman *et al.* 2004; chapter 2). An increase in this number indeed results in slower competitive exclusion of rare plant species. As the maximum number of flower visits between pollen removal and deposition approaches infinity, pollen receipt is completely equalised because every flower visit results in pollination regardless of a plant species' relative abundance. However, in a more detailed model incorporating a trade-off between the degree of pollen carryover and the amount of pollen delivered per visit, Montgomery (2009) showed that under certain conditions pollen carryover may even have a detrimental effect on the reproductive success of rare plants, particularly in combination with flower constancy of pollinators and the requirement of a threshold quantity of pollen for successful pollination. Such a trade-off probably exists for the majority of plant species, although some species, for example many orchids, are able to minimise pollen loss in intervening visits by precisely positioning packages of pollen on the pollinator's body (Johnson & Edwards, 2000). In general, the distribution of pollen of a donor plant in a sequence of flower visits depends on floral traits as well as on morphology and behaviour of pollinators (Harder & Johnson, 2008). Thus, species-specific traits need to be considered to determine whether pollen carryover contributes to plant species coexistence in each case.

In one of the earliest theoretical papers on plant competition for pollination, Levin & Anderson (1970) already pointed to the important role of the spatial distribution of plant species for plant and pollinator fitness, but to my knowledge only Campbell (1986) explicitly incorporated small-scale spatial structure into her model of plant reproduction. Nonspatial models such as the one presented in chapter 2 usually assume a homogeneous landscape with random distribution of plant species and "blindly searching" pollinators. Deviations from these patterns can contribute to species coexistence in several ways. Spatial autocorrelation of conspecific plants may minimise pollen loss to heterospecific flowers and shorten travelling times of specialised pollinators, assuming that pollinators move primarily between neighbouring flowers. Thus, the destabilising effects of both generalised and specialised plant-pollinator interactions can be mitigated. Since most natural plant communities show some degree of spatial autocorrelation of conspecifics due to dispersal limitations (Crawley, 2009), this mechanism is likely to be important. Whether it is sufficient to completely equalise the reproductive success of plant species with different relative abundances merits further investigation. In addition, since competition for water, light and nutrients is strongest among direct neighbours, spatial aggregation of conspecifics can reduce the relative strength of interspecific competition for abiotic resources in plant communities (Stoll & Prati, 2001; Bolker *et al.*, 2003).

6.1.2 *Stabilising mechanisms*

Given the destabilising properties of plant-pollinator interactions, are there intrinsic mechanisms that actually contribute to stable coexistence of animal-pollinated plant species? Behavioural flexibility of foraging pollinators could in principle have a stabilising effect if pollinators preferentially target rare plant species. Whereas good theoretical support and empirical evidence for negative frequency-dependent pollination of rewardless flowers exist (Smithson & MacNair, 1997; Gigord *et al.*, 2001), pollinators visiting rewarding flowers are generally expected to exhibit positive frequency-dependence to maximise their foraging success (Eckhart *et al.*, 2006, and references therein). However, if the most efficient or common pollinator species preferentially visits the most abundant plant, other pollinators may benefit from focusing on less common plant species (Possingham, 1992). This phenomenon has been reported for visitors to two colour morphs of *Clarkia xantiana*

(Eckhart *et al.*, 2006). Yet even if this mechanism should be widespread, the fact that only relatively inefficient or infrequent pollinators are expected to exhibit negative frequency-dependence reinforces the competitive disadvantage of rare plant species. Thus, it seems highly unlikely that negative frequency-dependence of pollinators can account for diversity maintenance in animal-pollinated plant communities.

In addition to the potential equalising effect of small-scale spatial structure of plant communities, spatial structure at a larger scale may act as a stabilising mechanism. Whereas in our model of plant-pollinator systems (chapter 2) in the absence of niche differentiation slight disturbances lead to competitive exclusion of all but the most abundant plant species in a given location, different species may be favoured by chance in different local communities. In this manner, diversity could be maintained at a regional scale. Moreover, if dispersal between local populations is sufficiently strong, declining populations may be rescued by immigration from patches where the species dominate ("mass effect": Leibold *et al.*, 2004, and references therein). Since a mass effect results in a higher per-capita "birth rate" (i.e., births plus immigrants) when a species becomes rare, it fulfils the criterion for a stabilising mechanism. How important this mechanism is for diversity maintenance in real plant communities is currently uncertain, due to a lack of both data and models. Mutualistic metacommunities have been modelled by Prakash & de Roos (2004) and Fortuna & Bascompte (2006), but these studies did not account for competitive interactions within plant and animal communities. In general, diversity can be maintained through a mass effect if local communities are sufficiently separated to have diverging dynamics, but sufficiently connected by dispersal to prevent competitive exclusion of declining species. The classical mass effect is based on spatial heterogeneity of the environment that favours different species in different locations (Leibold *et al.*, 2004), but in the case of animal-pollinated plants dominance of one species in a given location may be the result of incidental higher initial abundance, which would then be amplified by its higher pollination success. Further research is needed to assess the importance of mass effects for coexistence of animal-pollinated plants, but at least for plant species that are generally rare alternative mechanisms need to be considered.

Another potential stabilising mechanism also involves structured plant populations, but here the structure is temporal rather than spatial. Clearly, temporal segregation of flowering phenologies reduces interspecific competition for pollination. In line with this idea, several earlier studies attempted to demonstrate that the temporal distribution of flowering phenologies within a plant community minimises overlap, but found it difficult to distinguish the hypothesized pattern from randomness (e.g. Fleming & Partridge, 1984). On the other hand, in a more recent study, Bolmgren *et al.* (2003) showed that phenologies of wind-pollinated species are generally less segregated in time than phenologies of biotically pollinated plants. The potential of reduced overlap of flowering phenologies as a stabilising mechanism was explored by Ishii & Higashi (2001). Using a model of two annual plant species competing for pollinators as well as space, they showed that under certain conditions the inferior species in competition for space can invade a habitat occupied by the superior competitor by temporarily exceeding the superior species in the number of simultaneously open flowers. However, in their model coexistence is only possible if pollen limitation prevents the superior competitor from occupying all available habitat. Without further investigations, the importance of limited phenological overlap as a stabilising mechanism remains uncertain.

All further stabilising mechanisms that may counterbalance the reproductive disadvantage of rare plant species in plant-pollinator systems are not limited to this type of interaction, but can contribute to species coexistence in various ecological communities. Among these mechanisms are niche differentiation (chapters 2 and 3), positive frequency-dependence of predators, parasites or pathogens, and several fluctuation-dependent mechanisms such as the storage effect (Chesson, 2000; chapter 1). While the general importance of these mechanisms for diversity maintenance has been discussed elsewhere (e.g. Levine & HilleRisLambers, 2009), it is important to note that unless fitness differences between rare and common plant species are reduced by equalising mechanisms, a stronger stabilising effect is required to maintain diversity in animal-pollinated plant assemblages compared to plant communities with other modes of reproduction (see chapter 2).

6.1.3 *Facilitation*

Finally, it should be mentioned that interactions between co-occurring plant species do not have to be competitive under all possible circumstances. Several empirical studies have demonstrated that facilitative interactions between neighbouring plant species with shared pollinators can occur (e.g. Moeller, 2004; Molina-Montenegro *et al.*, 2008; Hegland *et al.*, 2009a). This seems to be primarily a phenomenon of small plant populations that can attract more pollinators to a local patch if another attractive plant is flowering nearby. However, whereas the per-capita number of visits received may increase in the presence of other plant species, pollen loss to heterospecific flowers and interspecific competition for other resources remain. Taking these factors into account, Feldman *et al.* (2004) constructed a model of the population dynamics of two coexisting plant species. They predicted that a positive effect of at least one plant species on the growth rate of the second species required an initially accelerating response of pollinator visits to the combined densities of the two plant species. Empirical evidence for the occurrence of such a response is sparse, and it is likely that the conditions required for true facilitation between plant species sharing pollinators are rarely fulfilled in natural ecosystems.

6.1.4 *Conclusions and outlook*

Whereas the theoretical possibilities for diversity maintenance in animal-pollinated plant communities are comparatively well understood, the relative contributions of specific mechanisms to species coexistence in natural plant communities remain uncertain. A key question is whether declining plant populations generally experience increasing pollen limitation. If equalising mechanisms are sufficiently strong, plant species could become relatively rare without a noticeable negative effect on their pollination success, but below a certain threshold density pollination rates might suddenly drop. For conservation purposes, it would then be important to identify these thresholds. While several empirical studies have addressed reduced pollination success of plant species that are rare in absolute terms (i.e., an Allee effect: Hackney & McGraw, 2001; Forsyth, 2003), the consequences of low relative abundance have received comparatively little attention (but see Kunin, 1993). Often, species are rare in both respects. In this case, carefully designed experiments are required to separate the effects of both aspects of rarity. More such experiments in conjunction with field observations are needed to understand the role of particular diversity-maintaining mechanisms. Ideally, experiments should be conducted that allow direct manipulation of the strength of a mechanism and examine its effect on all aspects of plant fitness. While the design of such experiments is undoubtedly a challenging task, it does not seem altogether unachievable and would greatly improve our understanding of the basis of plant diversity.

6.2 STABILITY OF POLLINATION NETWORKS IN THE FACE OF CLIMATE CHANGE

6.2.1 *General effects of climate change on biological populations*

Today, anthropogenic climate change is widely regarded as one of the greatest threats to biodiversity (Thomas *et al.*, 2004; Pereira *et al.*, 2012). Hence, a considerable proportion of ecological research is aimed at evaluating the effects of climatic changes in recent decades and predicting future impacts on ecosystems. Climate change itself has two aspects which may be equally important: A rise in mean global surface temperature (0.74 °C from 1906 to 2005, with increases of up to 1.5 °C at high northern latitudes), and an increase in the frequency and intensity of extreme climatic events such as heat waves, heavy rainfall or drought (IPCC, 2007). The direct effects of the first aspect, rising mean temperature, on plant and animal populations are reasonably well understood (reviewed by Parmesan, 2006). Many species respond by shifting their ranges towards higher latitudes and higher elevation in mountainous areas. At a given latitude and altitude, species' phenologies generally shift towards earlier occurrence in the season, and especially ectothermic species complete their life cycle in a shorter amount of time. Responses of organisms adapting to changing environmental conditions in a given location may involve ecological changes within the range of phenotypic plasticity, genetic changes mediated by natural selection, or a mixture of both. By comparison, the indirect effects of climate warming on organisms through changes in biotic interactions are less well studied. Since the magnitude and direction of direct responses vary considerably between species (Fitter & Fitter, 2002; Parmesan, 2006), climate change may lead to increased or reduced strength of interactions such as predation, competition and mutualism, and to changes in the availability of particular interaction partners. Asynchronous shifts of ranges or phenology may disrupt previously existing interactions, with possible negative effects especially for specialised species that depend on the availability of particular species as resources, hosts or mutualistic partners (van Asch & Visser, 2007; Miller-Rushing *et al.*, 2010).

Until now, the second aspect of climate change, increased frequency and intensity of climate extremes, has been less intensively studied. Generally, increased environmental variation causes stronger fluctuations of population sizes and growth rates over time. Since a population's long-term average growth rate is the geometric mean of short-term (e.g. annual) growth rates, stronger fluctuations are generally expected to slow down the growth of a population, although under certain conditions they may also accelerate long-term growth (Drake, 2005). Moreover, stronger fluctuations in population sizes generally increase the risk of extinction especially for small populations (McLaughlin *et al.*, 2002). Just as the increase of average global temperature, extreme climatic events may have direct and indirect effects on each species' population dynamics. Species may be affected indirectly if the population densities of the species they interact with, such as competitors or mutualists, increase or decrease as a result of climate extremes. As in the case of other types of disturbances (see chapter 1), specialists are thought to be more susceptible to such indirect effects of extreme events than generalists (WallisDeVries *et al.*, 2011).

6.2.2 *Phenological asynchrony of plants and pollinators: Causes and consequences*

The mechanisms that determine the timing of flowering in plants and the seasonal occurrence of flower-visiting insects are quite complex (reviewed by Forrest & Thomson, 2011). While phenology certainly has a genetically fixed component, environmental cues also play an important role. For plants, both photoperiod and temperature seem to be of primary importance. Some species do not produce buds before a certain day length is exceeded, others require short days for bud formation (Glover, 2007). In many cases, degree days (the cumulative sum of temperatures above a certain threshold) are a good predictor of flowering phenology. Since climate change affects only temperature, but not photoperiod, plant species may differ in their responses to a changing climate depending on the relative importance of each cue in determining their flowering phenology. To complicate matters, some plant species additionally require a period of chilling (vernalisation) to trigger the onset of flowering. Especially for plants growing at higher altitudes and latitudes, the timing of snow melt also plays a role, at least by setting a lower limit to the beginning of flowering. Thus, depending on the changes in temperature and precipitation in a given location, climate change may advance or delay the onset of flowering. The emergence of adult insects from metamorphosis or overwintering is primarily triggered by temperature. As for plants, degree days are often a good predictor of insect phenology, but the thresholds above which accumulated temperature sums count seem to be generally higher than for flowering in plants (Forrest & Thomson, 2011, and references therein). In addition, some insects have a vernalisation requirement analogous to that of plants.

Although the factors determining flowering phenology of plants and emergence of insects are quite similar, this does not necessarily imply that plants and pollinators respond to climate change in the same way, because their specific temperature requirements (thresholds, accumulated degree days and days of chilling) may differ. Recent studies provide mixed evidence concerning rates of advance of plant and pollinator phenology. While some found no difference between the two groups (Bartomeus *et al.*, 2011), others suggested that either flowering plants (Forrest & Thomson, 2011) or flower-visiting insects (reviewed by Hegland *et al.*, 2009b) show a stronger average response to climate warming. Based on the fact that flowering phenology is not only triggered by temperature, but also by photoperiod, insects may be expected to exhibit a stronger phenological shift with increasing temperature, but further studies are needed to confirm this hypothesis. Meanwhile, it is clear that both plants and pollinators show considerable interspecific variation in their responses to global warming (Memmott *et al.*, 2007, and references therein). Generally, early-flowering plants and pollinators emerging early in the season seem to react most strongly to climatic changes (Hegland *et al.*, 2009b).

If it is true that insect phenology responds more strongly to climate change, the first pollinators may emerge before the onset of flowering of the earliest plants. To my knowledge, until now no case of such a general mismatch between the two groups has been reported, but this may be due to the fact that pollinators are usually observed while visiting flowers. Obviously, data of pollinator abundances based on flower visits are not suitable to detect a general mismatch (Forrest & Thomson, 2011, see also chapter 5). Theoretically, a similar mismatch may occur at the end of the season, if either flowering or pollinator activity continue in the absence of mutualistic partners.

In addition to the possibility of a general mismatch, climate change may result in phenological desynchronisation of particular pairs of plant and pollinator species. This type of mismatch has been reported for bumblebee-pollinated spring ephemerals in Japan whose early flowering before the emergence of bumblebee queens resulted in reduced seed set, while other early-flowering species pollinated by flies remained unaffected (Kudo *et al.*, 2004). As noted by Willmer (2012), the consequences of asynchronous shifts of specific plants and pollinators largely depend on the degree of dependence of each species on the availability of particular mutualists. Since species using a restricted range of resources are generally thought to be less flexible in their interactions (see chapter 1), specialist plants and pollinators are expected to be most vulnerable to phenological desynchronisation. Following this idea, in chapter 5 we used data on phenology and interactions of plants and pollinators along an elevation gradient to evaluate the importance of phenological synchrony with particular plant species for pollinators of different degrees of specialisation. Contrary to our expectation, we found that even locally specialised pollinator species did not depend on synchrony with the flowering phenology of particular plants, but were flexible in their use of floral resources at different altitudes. This result is in agreement with studies of the temporal dynamics of plant-pollinator networks which report a high degree of flexibility in the structure of interactions from year to year due to variation in species' phenology and abundance (Alarcon *et al.*, 2008; Burkle & Alarcon, 2011). Thus, although some interactions may be lost through asynchronous shifts in phenology, even relatively specialised species seem to be flexible enough to interact with new mutualistic partners when they become available.

If a species' response to climate change results in a strongly maladaptive phenology (e.g. desynchronisation of a plant's flowering phase with its only pollinator), the species may be rescued from extinction by rapid evolution of the traits that determine its response to environmental cues such as photoperiod and temperature (Miller-Rushing *et al.*, 2010; Gilman *et al.*, 2012). In general, such an evolutionary response is possible if the population is genetically diverse and the selection pressure sufficiently strong. However, the availability of mutualistic partners is not the only factor influencing the evolution of phenology. For plants as well as insects, abiotic factors and biotic interactions with competitors, predators or herbivores, parasites and pathogens may affect the optimal timing of flowering or emergence (Elzinga *et al.*, 2007; Miller-Rushing *et al.*, 2010). Thus, it remains uncertain whether species that are not flexible enough to switch to new interaction partners can be rescued from phenological mismatches by a rapid evolutionary response.

6.2.3 *Effects of extreme climatic events on plant-pollinator systems*

Compared to the effects of rising mean temperature, the consequences of extreme climatic events on plant-pollinator systems remain largely unstudied. The general lack of research on this subject may be due to the fact that the change in the frequency and intensity of extreme weather events has only recently been recognized or the difficulty of precisely defining what constitutes an extreme event (Jentsch *et al.*, 2007; Smith, 2011). Nevertheless, in addition to the general consequences of increased population fluctuations discussed above (section 6.2.1), some inferences can be drawn from the literature examining the effects of various other types of disturbances on plant-pollinator systems. The direct effects of disturbances caused by extreme weather are likely to be most severe for plant and pollinator species whose populations are already small and fragmented (e.g. Steffan-Dewenter & Tscharntke, 2002). Moreover, the thermal tolerance of organisms influences their robustness to climatic extremes. Therefore, tropical species may be especially vulnerable, despite the fact that the absolute effect of climate change in the tropics is comparatively weak (Deutsch *et al.*, 2008). In addition to these direct effects of extreme events, plants and pollinators may be indirectly affected through changes in the availability of mutualistic partners. For reasons outlined in chapter 1, specialised species and communities are generally assumed to be most susceptible to indirect effects of disturbances, but empirical evidence is not unequivocal (see discussion in chapter 4). However, since nearly all of the empirical studies on disturbance effects on plant-pollinator systems examined long-lasting disturbances such as habitat fragmentation (Aguilar *et al.*, 2006), grazing (Vazquez & Simberloff, 2002) or general land use change (Biesmeijer *et al.*, 2006), their results may be of limited relevance to the study of the effects of climate extremes that are characterised by their short duration, either in absolute terms or, as suggested by Jentsch *et al.* (2007), in relation to the life span of the organisms considered. Thus, the possibility of recovery is an important aspect of extreme events (Smith, 2011). Our study of the relationship between specialisation and stability of model systems of plants and pollinators (chapter 4), although admittedly rather abstract, provides some clues regarding robustness of plant-pollinator systems to temporary disturbances. From our results, it seems that the interplay between the contrasting effects of specialisation – increased risk of coextinction, but decreased risk of competitive exclusion – may lead to different specialisation-stability relationships, depending on which effect is more important in a given situation. This prediction results from the fact that changes in the relative abundances of plant or pollinator populations affect species coexistence via changes in plant pollination success (see section 6.1). As previously noted, further studies are needed to clarify how strongly the relative abundances of natural plant populations affect their pollination success, and to test whether the predictions of our modelling exercise can explain different specialisation-stability relationships observed in the field.

6.2.4 *Conclusions and outlook*

Although climate change is currently perhaps the most widely studied topic in ecological research, the number of unanswered questions regarding its effects on ecosystems in general and plant-pollinator systems in particular is probably sufficient to keep ecologists busy for decades to come. For example, what factors other than early occurrence in the season are good predictors of the strength and direction of species' phenological responses to climate warming? For community-wide studies, it would be highly useful if phenological shifts could be predicted based on taxonomic groups or species traits that are more easily determined than phenology. Furthermore, the potential for rapid evolution as a means of escaping the detrimental effects of climate change is largely unexplored. If at least some extreme specialists are threatened by loosing their mutualistic partners as a result of phenological desynchronisation, is it more likely that their traits related to specialisation or the traits affecting phenology will be modified by natural selection? If population fluctuations increase as a result of extreme climatic effects, will animal-pollinated plant species develop traits that reduce the negative effects of low relative abundance on pollination success? The answers to these questions may not only help in predicting and mitigating the effects of climate change, but improve our understanding of general issues in ecology and evolution.

Based on current knowledge, it seems that by themselves neither asynchronous phenological shifts nor extreme events threaten the existence of the majority of plant-pollinator systems, although some particularly fragile species will almost certainly be lost. However, in conjunction with other anthropogenic changes that lead to decreased functional redundancy in ecological communities (see chapter 5) and smaller and more fragmented populations, climate change may well prove fatal for a significant fraction of species. The combination of factors imposing pressure on ecosystems is probably the key difference between previous rapid changes of the earth's climate and the situation today. It can only be hoped that the stability of ecological systems is such that they can withstand and recover from this unprecedented strain.

SUMMARY

For most angiosperm plant species, pollination by animals is an essential service that enhances both the quality and quantity of offspring produced. The degree of dependence on animal pollination varies between plant species, with some species completely relying on this service, while others possess additional means of reproduction. Since flowering plants account for the bulk of primary production in all terrestrial ecosystems, the integrity of these ecosystems depends on the pollination services of animals. Moreover, pollination by animals is an important ecosystem service for human agriculture, with an overall economic value of at least €153 billion per year (Gallai *et al.*, 2009).

While some plants are pollinated by only one or a few species, others are literally visited by hundreds of different pollinators, with the majority of flowering plant species in between these two extremes. Likewise, most pollinators visit multiple plant species, but visitation patterns range from specialisation on a single plant to extreme generalisation. The complex relationships between often highly diverse communities of plants and pollinators can be described as ecological networks, in which each link between a plant and pollinator species symbolises an interaction.

In this dissertation, I examine the relationship between specialisation and stability of plant-pollinator networks, with a focus on two issues: Diversity maintenance in animal-pollinated plant communities and robustness of plant-pollinator systems against disturbances such as those caused by anthropogenic climate change. Chapter 1 of this thesis provides a general introduction to the concepts of ecological stability and specialisation with a focus on plant-pollinator systems, and a brief outline of the following chapters. Chapters 2-5 each consist of a research article addressing a specific question. While chapters 2 and 3 deal with different aspects of diversity maintenance in animal-pollinated plant communities, chapters 4 and 5 are concerned with the consequences of climate change in the form of temporary disturbances caused by extreme climatic events (chapter 4) and shifts in phenology of plants and pollinators (chapter 5). From a methodological perspective, the first three articles (chapter 2-4) can be grouped together as they all employ mathematical models of plant-pollinator systems, whereas chapter 5 describes an empirical study of plant-pollinator interactions

along an altitudinal gradient in the Alps. The final chapter (6) provides a review of current knowledge on each of the two main themes of this thesis and places the findings of the four research articles in the context of related studies.

A fundamental question in ecology is how multiple species that compete for resources are able to coexist. In chapter 2, we examine this question for the case of plant species that compete for abiotic resources as well as for pollination by animals. Previous studies demonstrated the existence of a minority disadvantage with respect to pollination success that results in extinction of all but the most abundant plant species in a model community of plants sharing a generalist pollinator (e.g., Levin & Anderson, 1970). In spite of this prediction, real communities of animal-pollinated plants are often remarkably species-rich. To resolve this apparent paradox, we developed a mechanistic model of plant and pollinator population dynamics and introduced a classical stabilising mechanism, niche differentiation of plant species with respect to abiotic resources, to overcome the destabilising influence of pollination. Our results show that without a sufficient degree of niche differentiation, pollination is indeed destabilising, regardless of the degree of specialisation of plant-pollinator interactions. However, when niche differentiation is strong enough to counteract the destabilising tendency, interactions with pollinators may even increase the stability of plant coexistence measured as resilience – the speed of return to the equilibrium state after a small disturbance. Thus, this study not only offers an explanation for the existence of species-rich communities of plants pollinated by animals, but it also shows that under certain conditions interactions with pollinators may enhance the stability of plant coexistence.

In contrast to the destabilising effect of pollination proposed by Levin & Anderson (1970), a recent study suggested that interactions with pollinators can promote plant diversity by increasing the maximum number of coexisting plant species (Bastolla *et al.*, 2009). However, Bastolla *et al.* (2009) used a generic model of mutualism that did not account for the specific mechanisms of plant-pollinator interactions. Moreover, in their model the positive effect of interactions with pollinators on plant diversity arises from an increase in the total population size of the plant community, which may not be possible if the plant community already fills all available habitat in the absence of animal pollinators. To elucidate the conditions under which interactions with pollinators can promote plant diversity, the study presented in chapter 3 uses a slightly modified version of the model of plant and pollinator population dynamics developed in chapter 2. Our analyses show that, when accounting for the specific mechanisms of plant-pollinator interactions and the existence of a habitat capacity that limits the growth of the overall plant population, the conditions allowing a positive effect of the presence of pollinators on plant diversity become much more restricted than proposed by Bastolla *et al.* (2009). Indeed, our results suggest that plant diversity is more likely to be negatively affected by interactions with pollinators due to the minority disadvantage discussed in chapter 2. Based on these results, it seems unlikely that the loss of pollinators would result in decreased species richness of plant communities with alternative means of reproduction beside animal pollination. However, while the population dynamics of these plants may remain unaffected by the loss of pollinators, the negative effects of reduced outcrossing on the fitness of plant offspring can be severe.

Beside its utility in understanding the mechanisms of diversity maintenance, the concept of ecological stability can be used to investigate the robustness of ecological systems to various disturbances. In the study presented in chapter 4, we examined the relationship between specialisation of plant-pollinator interactions in model communities with two species in each group and stability of these systems against temporary disturbances such as those caused by extreme climatic events. Since the frequency and intensity of extreme events are predicted to increase with climate change (Jentsch *et al.*, 2007), studying their effects on communities of organisms has become a priority for ecological research. Although specialisation is generally assumed to destabilise plant and pollinator communities by increasing the risk of coextinction, it may also have a stabilising effect by reducing the likelihood of competitive exclusion. The results of our study reflect this dual role of specialisation. Depending on the strength of a temporary disturbance and the criterion for stability, positive, negative and unimodal specialisation-stability relationships are possible in our model system. These results show that specialisation does not necessarily destabilise mutualistic systems. Further research is needed to assess the relative importance of direct effects of disturbances and indirect effects via competitors and mutualists on natural plant and pollinator populations.

Another well-documented effect of anthropogenic climate change is the shift in species' phenologies with increasing global mean temperature. While most seasonal events shift towards earlier occurrence in the season, the high degree of interspecific variation in the direction and magnitude of phenological shifts has raised concerns about the possibility of phenological desynchronisation of interacting species. In the case of mutualistic interactions between plants and pollinators, specialised species are predicted to be especially vulnerable to the effects of phenological desynchronisation, but until now most studies of this issue have focused on generalists. In the study presented in chapter 5, we used data on phenology and interactions of plants and pollinators from six sites along an altitudinal gradient in the Alps to examine the degree of phenological synchrony with particular plant species among pollinators of different degrees of specialisation. Thus, the altitudinal gradient serves as a model for the effects of climate change in time. Contrary to our expectation, we found no relationship between specialisation and phenological synchrony of pollinators with particular plant species. Moreover, there was no relationship between local specialisation of pollinators and the consistency of their flower visitation across sites. However, for flies and bees we found a positive relationship between specialisation on plant species and the mean tube length of flowers visited. These results suggest that even relatively specialised pollinator species are flexible in their use of plant species and do not need to synchronise with the flowering phenology of specific plants. However, since our analysis was limited to the most abundant pollinator species at the sites, we do not know whether our results hold for less common pollinators. Furthermore, our data suggest that many pollinators specialise on particular functional types of flowers rather than on single plant species. If this is the case, the observed flexibility of plant-pollinator interactions is contingent on the existence of diverse plant communities that contain a relatively high number of functionally redundant species.

Taken together, these four research articles highlight the complex consequences of specialisation of plant-pollinator interactions for various aspects of community stability. In the last chapter, I take a broader perspective on the two main topics covered by this thesis. The first part of chapter 6 provides a general overview of possible mechanisms of diversity maintenance in animal-pollinated plant communities. Following Chesson (2000), I distinguish between equalising mechanisms, which reduce fitness differences between species, and stabilising mechanisms, which increase the fitness of rare species in a community. An additional section covers the possibility of facilitation between plant species sharing pollinators. The second part of chapter 6 reviews current knowledge on the effects of climate change on plant-pollinator systems, particularly the consequences of phenological shifts and increased frequency and intensity of extreme climatic events. In both parts of chapter 6, I identify gaps in our knowledge of the respective issues and provide suggestions for future research.

ZUSAMMENFASSUNG

Für die meisten angiospermen Pflanzenarten ist die Bestäubung durch Tiere eine wichtige Dienstleistung, die sowohl die Zahl als auch die Qualität der Nachkommen positiv beeinflusst. Der Grad der Abhängigkeit von Tierbestäubung variiert zwischen Pflanzenarten, so dass einige Arten völlig auf diese Dienstleistung angewiesen sind, während andere sich zusätzlich auf anderem Wege reproduzieren können. Da Blütenpflanzen für den Großteil der Primärproduktion in allen terrestrischen Ökosystemen verantwortlich sind, hängt die Integrität dieser Ökosysteme von der von Tieren erbrachten Bestäubungsleistung ab. Darüber hinaus ist die Bestäubung durch Tiere eine wichtige Ökosystemdienstleistung für die Landwirtschaft, die einen wirtschaftlichen Gesamtwert von mindestens 153 Milliarden Euro pro Jahr besitzt (Gallai *et al.*, 2009).

Während einige Pflanzen nur von einer oder wenigen Arten bestäubt werden, werden andere buchstäblich von Hunderten verschiedener Bestäuber besucht. Die Mehrheit der Pflanzenarten findet sich zwischen diesen beiden Extremen wieder. Desgleichen besuchen die meisten Bestäuber mehrere Pflanzenarten, aber die Bandbreite der Bütenbesuchsmuster reicht von Spezialisierung auf eine einzige Pflanzenart zu extremer Generalisierung. Die komplexen Beziehungen zwischen oft sehr artenreichen Pflanzen- und Bestäubergemeinschaften können als ökologische Netzwerke beschrieben werden, in denen jeder "Link" zwischen einer Pflanzen- und einer Bestäuberart eine Interaktion repräsentiert.

In dieser Dissertation untersuche ich den Zusammenhang zwischen Spezialisierung und Stabilität von Pflanzen-Bestäuber-Netzwerken. Dabei konzentriere ich mich speziell auf zwei Themengebiete: Die Erhaltung der Diversität in Pflanzengemeinschaften, die durch Tiere bestäubt werden, und die Widerstandsfähigkeit von Pflanzen-Bestäuber-Systemen gegenüber Störungen, wie sie durch den anthropogenen Klimawandel hervorgerufen werden. Kapitel 1 dieser Arbeit gibt eine allgemeine Einführung zu den Konzepten der ökologischen Stabilität und der Spezialisierung mit einem Schwerpunkt auf Pflanzen-Bestäuber-Systemen, und einen kurzen Überblick über die folgenden Kapitel der Arbeit. Kapitel 2-5 bestehen jeweils aus einem wissenschaftlichen Artikel, der eine spezifische Fragestellung untersucht. Während Kapitel 2 und 3 sich mit verschiedenen Aspek-

ten der Erhaltung der Diversität in tierbestäubten Pflanzengemeinschaften befassen, beschäftigen sich Kapitel 4 und 5 mit den Auswirkungen des Klimawandels in Form von temporären Störungen verursacht durch klimatische Extremereignisse (Kapitel 4) und zeitlichen Verschiebungen der Phänologie von Pflanzen und Bestäubern (Kapitel 5). Aus methodologischer Sicht bilden die ersten drei Artikel eine Einheit, da sie alle mathematische Modelle der Populationsdynamik von Pflanzen und Bestäubern verwenden, während Kapitel 5 eine empirische Studie über Pflanzen-Bestäuber-Interaktionen entlang eines Höhengradienten in den Alpen beschreibt. Das letzte Kapitel (6) gibt einen Überblick über den Wissensstand in den beiden zentralen Themengebieten dieser Arbeit und bettet die Ergebnisse der vier Artikel in den Kontext verwandter wissenschaftlicher Arbeiten ein.

Eine grundlegende Frage in der Ökologie ist, wie mehrere Arten koexistieren können, die miteinander um Ressourcen konkurrieren. In Kapitel 2 untersuchen wir diese Frage für den Fall von Pflanzenarten, die sowohl um abiotische Ressourcen als auch um Bestäubung durch Tiere konkurrieren. Frühere Untersuchungen ergaben, dass in solchen Pflanzengemeinschaften seltene Arten bezüglich des Bestäbungserfolges im Nachteil sind, so dass in einer Modellgemeinschaft von Pflanzen, die von einem generalistischen Bestäuber besucht werden, alle Arten außer der häufigsten aussterben (z. B. Levin & Anderson, 1970). Trotz dieser Modellvorhersage sind reale Pflanzengemeinschaften, die von Tieren bestäubt werden, oft bemerkenswert artenreich. Um diesen scheinbaren Widerspruch aufzulösen, entwickelten wir ein mechanistisches Modell der Populationsdynamik von Pflanzen und Bestäubern und führten einen klassischen stabilisierenden Mechanismus ein, Nischenpartitionierung der Pflanzenarten in der Konkurrenz um abiotische Ressourcen, um die destabilisierende Wirkung der Bestäubung zu überwinden. Unsere Ergebnisse zeigen, dass ohne eine genügende Nischenpartitionierung die Bestäubung durch Tiere in der Tat destabilisierend wirkt, unabhängig davon, wie stark die Pflanzen-Bestäuber-Interaktionen spezialisiert sind. Wenn die Nischendifferenzierung jedoch groß genug ist, um den destabilisierenden Einfluss der Bestäubung aufzuheben, können Interaktionen mit Bestäubern die Stabilität der Koexistenz von Pflanzen sogar erhöhen. Stabilität wird hier als Resilienz gemessen, d.h. als Geschwindigkeit der Rückkehr zum Gleichgewicht nach einer kleinen Störung. Diese Untersuchung bietet nicht nur eine Erklärung für die Existenz artenreicher Pflanzengemeinschaften, die durch Tiere bestäubt werden, sie zeigt auch, dass unter bestimmten Bedingungen Interaktionen mit Bestäubern die Stabilität der pflanzlichen Koexistenz erhöhen können.

Im Gegensatz zu dem von Levin & Anderson (1970) vorhergesagten destabilisierenden Effekt von Bestäubung legte eine neuere Untersuchung nahe, dass Interaktionen mit Bestäubern die Diversität von Pflanzen fördern, indem sie die maximale Zahl koexistierender Pflanzenarten erhöhen (Bastolla *et al.*, 2009). Allerdings verwendeten Bastolla *et al.* (2009) ein allgemeines Modell mutualistischer Systeme, das die spezifischen Mechanismen von Pflanzen-Bestäuber-Interaktionen nicht berücksichtigt. Darüber hinaus entsteht der positive Effekt von Interaktionen mit Bestäubern auf die Pflanzendiversität in ihrem Modell durch eine Zunahme der Gesamt-Populationsgröße aller Pflanzenarten. Dies ist aber nicht möglich, wenn die Pflanzengemeinschaft bereits in Abwesenheit von Bestäubern das gesamte verfügbare Habitat ausfüllt. Um zur Aufklärung der Bedingungen beizutragen, unter denen Interaktionen mit Bestäubern die Pflanzendiversität fördern können, verwendet die in Kapitel 3 vorgestellte Studie eine leicht modifizierte Form des in Kapitel 2 entwickelten Modells der Populationsdynamik von Pflanzen und Bestäubern. Unsere Analysen zeigen, dass, wenn man die spezifischen Mechanismen von Pflanzen-Bestäuber-Interaktionen und die Existenz einer Habitatkapazität berücksichtigt, die das Wachstum der gesamten Pflanzenpopulation begrenzt, die Bedingungen, die einen positiven Effekt der Anwesenheit von Bestäubern auf die Pflanzendiversität erlauben, sehr viel eingeschränkter sind als von Bastolla *et al.* (2009) angenommen. Tatsächlich legen unsere Ergebnisse nahe, dass die Pflanzendiversität aufgrund des in Kapitel 2 diskutierten Nachteils für Minderheiten mit höherer Wahrscheinlichkeit von Interaktionen mit Bestäubern negativ beeinflusst wird. Ausgehend von diesen Ergebnissen erscheint es unwahrscheinlich, dass der Verlust von Bestäubern zu geringerem Artenreichtum in Pflanzengemeinschaften mit alternativen Reproduktionsmechanismen führen würde. Während die Populationsdynamik dieser Pflanzen durch den Verlust von Bestäubern wohl wenig beeinflusst wird, können allerdings die negativen Auswirkungen geringerer Auskreuzung für die Fitness der Nachkommen von Pflanzen gravierend sein.

Neben seiner Nützlichkeit für das Verständnis von Mechanismen zur Erhaltung der Diversität kann das Konzept der ökologischen Stabilität dabei helfen, die Widerstandsfähigkeit ökologischer Systeme gegenüber verschiedenen Störungen zu untersuchen. In der in Kapitel 4 vorgestellten Studie untersuchten wir den Zusammenhang zwischen Spezialisierung von Pflanzen-Bestäuber-Interaktionen in Modellgemeinschaften mit je zwei Arten pro Gruppe und der Stabilität dieser Systeme gegenüber temporären Störungen, wie sie durch klimatische Extremereignisse hervorgerufen werden. Da vorhergesagt wurde, dass die Häufigkeit und Intensität von Extremereignissen durch den Klimawandel zunehmen werden (Jentsch *et al.*, 2007), ist die Untersuchung der Auswirkungen dieser Störungen zu einer Priorität in der ökologischen Forschung geworden. Obwohl allgemein angenommen wird, dass Spezialisierung Pflanzen- und Bestäubergemeinschaften destabilisiert, da sie das Risiko von Koextinktionen erhöht, kann Spezialisierung auch stabilisierend wirken, indem sie das Risiko des Konkurrenzausschlusses von Arten verringert. Die Ergebnisse unserer Studie spiegeln diese zweifache Rolle der Spezialisierung wider. Je nachdem, wie stark die temporäre Störung ist, und welches Kriterium für Stabilität angelegt wird, sind in unserem Modellsystem positive, negative oder unimodale Beziehungen zwischen Spezialisierung und Stabilität möglich. Diese Ergebnisse verdeutlichen, dass Spezialisierung nicht zu einer Destabilisierung mutualistischer Systeme führen muss. Weitere Untersuchungen sind nötig, um die relative Bedeutung der direkten Auswirkungen von Störungen und indirekter Effekte durch Konkurrenten und Mutualisten abzuschätzen.

Ein anderer gut dokumentierter Effekt des anthropogenen Klimawandels ist die Verschiebung der Phänologie von Arten mit der Zunahme der globalen mittleren Temperatur. Während die meisten saisonalen Ereignisse sich hin zu früherem Auftreten in der Saison verschieben, hat die beträchtliche interspezifische Varianz in der Richtung und Stärke der phänologischen Verschiebungen zu der Sorge geführt, dass das zeitliche Auftreten interagierender Arten entkoppelt werden könnte. Im Fall von mutualistischen Interaktionen zwischen Pflanzen und Bestäubern gelten spezialisierte Arten als besonders gefährdet, aber bisher haben sich die meisten Untersuchungen zu diesem Thema auf generalistische Arten konzentriert. In der in Kapitel 5 präsentierten Studie verwendeten wir Daten über Phänologie und Interaktionen von Pflanzen und Bestäubern auf sechs Flächen entlang eines Höhengradienten in den Alpen, um den Grad der Synchronität von unterschiedlich stark spezialisierten Bestäubern mit der Blühphänologie bestimmter Pflanzen zu untersuchen. Mithin dient hier der Höhengradient als Modell für die Auswirkungen des Klimawandels im Laufe der Zeit. Entgegen unserer Erwartung fanden wir keinen Zusammenhang zwischen Spezialisierung und phänologischer Synchronität von

Bestäubern mit bestimmten Pflanzenarten. Weiterhin gab es keinen Zusammenhang zwischen dem lokalen Spezialisierungsgrad von Bestäubern und der Konsistenz ihrer Blütenbesuchsmuster auf verschiedenen Flächen. Jedoch fanden wir einen positiven Zusammenhang zwischen dem Spezialisierungsgrad von Bestäubern und der mittleren Länge der Blütenkelche der von ihnen besuchten Pflanzenarten. Diese Ergebnisse legen nahe, dass selbst relativ spezialisierte Bestäuberarten flexibel in der Nutzung von Pflanzenarten sind und daher nicht mit der Blühphänologie einzelner Pflanzen synchronisiert sein müssen. Allerdings wissen wir nicht, ob diese Ergebnisse auch auf seltenere Bestäuberarten zutreffen, da unsere Analyse auf die auf den Flächen am häufigsten auftretenden Arten beschränkt war. Darüber hinaus weisen unsere Daten darauf hin, dass viele Bestäuberarten sich nicht auf einzelne Pflanzenarten spezialisieren, wohl aber auf bestimmte funktionelle Typen von Blüten. Wenn dem so ist, ist die beobachtete Flexibilität von Pflanzen-Bestäuber-Interaktionen nur bei genügend großem Artenreichtum der Pflanzengemeinschaft möglich, da artenreiche Gemeinschaften mehr funktionell redundante Arten enthalten.

Insgesamt veranschaulichen diese vier Artikel die komplexen Auswirkungen der Spezialisierung von Pflanzen-Bestäuber-Interaktionen auf verschiedene Aspekte der Stabilität der Gemeinschaften. Im letzten Kapitel betrachte ich die beiden Haupt-Themen dieser Arbeit aus einem weiteren Blickwinkel. Der erste Teil von Kapitel 6 gibt einen generellen Überblick über mögliche Mechanismen der Erhaltung der Diversität in Pflanzengemeinschaften, die von Tieren bestäubt werden. In Anlehnung an Chesson (2000) unterscheide ich zwischen dämpfenden Mechanismen, die Fitnessunterschiede zwischen Arten verringern, und stabilisierenden Mechanismen, welche die Fitness seltener Arten in einer Gemeinschaft erhöhen. Ein weiterer Abschnitt ist der Möglichkeit von "Facilitation" (positiven Wechselwirkungen) zwischen Pflanzenarten mit gemeinsamen Bestäubern gewidmet. Der zweite Teil von Kapitel 6 fasst den aktuellen Wissensstand zu den Auswirkungen des Klimawandels auf Pflanzen-Bestäuber-Systeme zusammen, wobei der Schwerpunkt auf den Konsequenzen phänologischer Verschiebungen und erhöhter Häufigkeit und Intensität von klimatischen Extremereignissen liegt. In beiden Teilen von Kapitel 6 weise ich auf Lücken im heutigen Wissensstand hin und mache Vorschläge für zukünftige Forschungsarbeiten.

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LIST OF PUBLICATIONS

Benadi, G., Hovestadt, T., Poethke, H.-J. & Blüthgen, N. (2013). The importance of being synchronous: specialization and phenological synchrony of plant-pollinator interactions along an altitudinal gradient. In prep.

Benadi, G., Blüthgen, N., Hovestadt, T. & Poethke, H.-J. (2013). Contrasting specialization-stability relationships in plant-animal mutualistic systems. Submitted to *Ecological Modelling*.

Benadi, G., Blüthgen, N., Hovestadt, T. & Poethke, H.-J. (2013). Can plant-pollinator interactions promote plant diversity? Submitted to *American Naturalist*.

Benadi, G., Blüthgen, N., Hovestadt, T. & Poethke, H.-J. (2012). Population dynamics of plant and pollinator communities: stability reconsidered. *American Naturalist*, 179, 157-168

Benadi G., Fichtel C. & Kappeler P. (2008) Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Primatology*, 70, 956-965

LIST OF CONFERENCE CONTRIBUTIONS

Endangered synchrony: phenology and interaction patterns of plants and pollinators along an altitudinal gradient. Oral presentation at the 42nd Annual Meeting of the Gesellschaft für Ökologie (GfÖ), Lüneburg, Germany, 2012.

Can plant-pollinator mutualisms increase the diversity of plant communities? Oral presentation at the 12th Congress of the European Ecological Federation, Ávila, Spain, 2011.

Specialization of plant-pollinator systems and community stability. Oral presentation at the 41st Annual Meeting of the Gesellschaft für Ökologie (GfÖ), Oldenburg, Germany, 2011.

Specialization of plant-pollinator systems and community stability. Oral presentation at the 6th Workshop of the Young Modellers in Ecology, Wallenfels, Germany, 2011.

Population dynamics of interacting plant and pollinator communities: stability revisited. Oral presentation at the 24th Annual Meeting of the Scandinavian Association for Pollination Ecologists (SCAPE), Tovetorp, Sweden, 2010.

Gefährdung von Pflanzen-Bestäuber-Netzwerken durch klimatischen Wandel und Extremereignisse. Oral presentation at the workshop "Klimafolgenforschung im Nationalpark Berchtesgaden", Berchtesgaden, Germany, 2010.

Population dynamics of plant and pollinator communities: How stable are mutualistic systems in the face of disturbances? Poster presentation at the 39th Annual Meeting of the Gesellschaft für Ökologie (GfÖ), Bayreuth, Germany, 2009.

Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). Poster presentation at the 6th Göttinger Freilandtage, Göttingen, Germany, 2007.

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