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Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination

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ABSTRACT

Global change may substantially affect biodiversity and ecosystem functioning but little is known about its effects on essential biotic interactions. Since different environmental drivers rarely act in isolation it is important to consider interactive effects. Here, we focus on how two key drivers of anthropogenic environmental change, climate change and the introduction of alien species, affect plant–pollinator interactions. Based on a literature survey we identify climatically sensitive aspects of species interactions, assess potential effects of climate change on these mechanisms, and derive hypotheses that may form the basis of future research. We find that both climate change and alien species will ultimately lead to the creation of novel communities. In these communities certain interactions may no longer occur while there will also be potential for the emergence of new relationships. Alien species can both partly compensate for the often negative effects of climate change but also amplify them in some cases. Since potential positive effects are often restricted to generalist interactions among species, climate change and alien species in combination can result in significant threats to more specialist interactions involving native species.

Key words: biological invasions, competition, ecosystem functions, ecosystem services, global change, higher order effects, multiple drivers, pollination, species interactions.

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I. INTRODUCTION

It is well established that ongoing global change may significantly impact biodiversity (Vitousek *et al.*, 1997; Dukes & Mooney, 1999; Sala *et al.*, 2000) and may lead to the generation of novel communities (Ohlemüller *et al.*, 2006; Hobbs *et al.*, 2006; Williams & Jackson, 2007). While separate effects of the main drivers of global change, such as climate change, habitat loss, nitrogen deposition and biological invasions are increasingly well documented (Millennium Ecosystem Assessment, 2005), much less is known about their consequences when acting in combination (Sala *et al.*, 2000). This may result in flawed conclusions since multiple pressures can act in a non-additive manner on biodiversity (Stevens, 2006). In addition, studies on the effects of global change have largely focused on responses in organism physiology, population size or on community metrics such as species richness, but knowledge about their effects on conditions for biotic interactions in the novel communities is scarce (Tylianakis *et al.*, 2008). Yet, biotic interactions form an indispensable basis for the functioning of ecosystems and the provision of ecosystem services. Thus, the consideration of the effects of multiple interacting drivers of global change on biotic interactions (Ibáñez *et al.*, 2006; Elzinga *et al.*, 2007) represents a significant challenge for predicting the future consequences of global change (Tylianakis *et al.*, 2008).

The effects of drivers acting in combination on biotic interactions can be highly complex and impact trophic levels or species groups differently (Walther, 2010). To deal with the complexities of multiple interactions in diverse species communities, and to obtain a high level of detail, we focus on two major drivers of global change, climate change and alien species, and their interactive effects on pollination. Species-specific responses to various components of climate change have the potential to cause temporal, spatial, or functional shifts in the composition of species assemblages that affect species interactions (Harrington, Woiwod & Sparks, 1999; Traveset & Richardson, 2006; Menéndez *et al.*, 2008; Schweiger *et al.*, 2008).

We define alien species as taxa that are new to a region and have established self-maintaining populations in the wild as a result of their introduction *via* direct human activities (cf. Richardson *et al.*, 2000; Pyšek *et al.*, 2004). They can thereby impact ecological interactions that have established over evolutionary time scales, cause the loss of biodiversity, and alter the structure and function of whole ecosystems (Levine *et al.*, 2003; MacDougall & Turkington, 2005; Vilà *et al.*, 2010). In addition, the colonisation, establishment and survival of alien species can be modified by climate change (Walther *et al.*, 2009). This may subsequently alter the network of existing species interactions which may lead to unanticipated effects on ecosystems (Tylianakis *et al.*, 2008). It is therefore crucial to consider the impact of biological invasions in the light of climate change.

In this review, we focus on pollination since it is a key ecosystem function and a basis for the maintenance of biodiversity (Kremen, 2005; Balvanera, Kremen & Martinez-Ramos, 2005). In addition, pollination is one of the best-studied ecosystem services in terms of understanding qualitative links between provider and beneficiary and this facilitates the investigation of interactive impacts of invasions and climate change. An estimated 60–80% of wild plants and 35% of global crop production depends on animal pollination (Kearns, Inouye & Waser, 1998; Ashman *et al.*, 2004; Klein *et al.*, 2007). However, concerns about the loss of pollinators have grown (Kearns *et al.*, 1998; Steffan-Dewenter, Potts & Packer, 2005), and parallel declines in bee species richness and insect-pollinated plants indicate a potential reduction in pollination services and/or in available flower resources for flower-visiting insects (Biesmeijer *et al.*, 2006). While reviews have attempted to assess the separate impacts of climate change (Hegland *et al.*, 2009) and species invasions

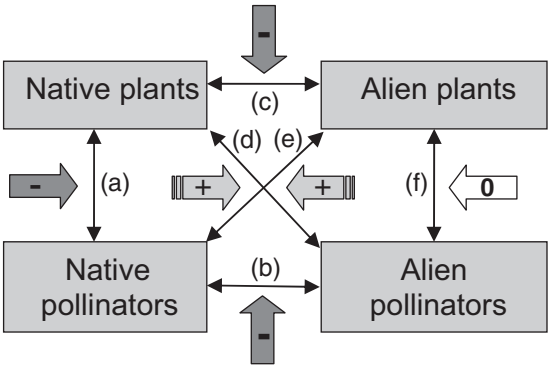

Fig. 1. Indirect effects of climate change (thick arrows) on interactions (thin arrows a-f) within a simplified pollination network of alien and native plants and pollinators. Dark grey arrows, negative effects; light grey arrows, positive effects; white arrow, no effects.

(Bjerknes *et al.*, 2007; Morales & Traveset, 2009) on native plant–pollinator networks, relatively little is known about the potential combined effects of these two environmental drivers (Tylianakis *et al.*, 2008).

Here we propose a framework for the assessment of how these two drivers interact to affect plant–pollinator interactions (Fig. 1). In particular we identify climate-change-sensitive mechanisms for different pairwise interactions. We start with interaction mechanisms of native plants and pollinators (arrow a in Fig. 1), followed by a review of effects of alien species within trophic levels (arrows b and c in Fig. 1) and across trophic levels (arrows d and e in Fig. 1). We then condense knowledge about more complex indirect interactions across corresponding trophic levels (i.e. plant-pollinator-plant, arrows e-a in Fig. 1; and pollinator-plant-pollinator, arrows d-a in Fig. 1), and finally we investigate interactions between alien plants and pollinators (arrow f in Fig. 1). For all these mechanisms of interactions we assess potential effects of climate change and derive hypotheses that may form the basis of future research (Tables 1–4).

II. CLIMATE-CHANGE EFFECTS ON PLANT–POLLINATOR INTERACTIONS

Recent global warming is known to have altered existing species interactions by either addition or loss of species from local plant and animal assemblages (Parmesan, 2006; Hegland *et al.*, 2009). The consequences for pollination mutualisms are complex but one clear expectation is the disruption of ecological matches such as spatial and temporal synchronicity of occurrence (Parmesan, 2006; Memmott *et al.*, 2007; Hegland *et al.*, 2009), or morphological and physiological interdependencies (Bond, 1994; Corbet, 2000).

Temporal mismatches are increasingly well documented for species interactions in general (Parmesan, 2006) and for plant–insect interactions in particular (Visser & Both, 2005; Memmott *et al.*, 2007; Both *et al.*, 2009) and have recently been reviewed by Hegland *et al.* (2009). Under climate warming, flowering periods (e.g. Fitter & Fitter, 2002; Badeck *et al.*, 2004; Menzel *et al.*, 2006) and/or flight times may initiate earlier and/or last longer (e.g. Roy & Sparks, 2000) but plant and insect phenology may respond to different environmental cues or different thresholds of the same cue and thus may not respond equally to climate change (Visser & Both, 2005; Both *et al.*, 2009). Although many plant–insect interactions have a long evolutionary history and have been maintained through a range of natural climate cycles in the past, synchrony may be lost due to the relative speed of anthropogenic climate change (Yurk & Powell, 2009). For plant–herbivore systems, the general pattern seems to be that insect phenologies advance more than plant phenologies (Visser & Both, 2005; Both *et al.*, 2009). This was also observed for two pollinator species (*Apis mellifera* L. and *Pieris rapae* L.) and their preferred forage plants on the Iberian Peninsula (Gordo & Sanz, 2005; reviewed in Hegland *et al.*, 2009). The occurrence of *A. mellifera* changed from about 10 days later than the flowering of crucial host plants to about 25 days earlier during the last 30 years, while the advancement was not so drastic for *P. rapae* (5 days later compared to 15 days earlier; Table 1).

Climate change may also affect co-occurrences of plant and pollinator species in space. Range shifts in plants (e.g. Thuiller *et al.*, 2008; Lenoir *et al.*, 2008; Pompe *et al.*, 2008) and pollinators (e.g. Parmesan, 1996; Parmesan *et al.*, 1999; Menéndez *et al.*, 2007; Wilson *et al.*, 2007; Settele *et al.*, 2008) are documented and projected, but it is likely that current species distribution overlaps will not remain the same (Table 1). Schweiger *et al.* (2008), for instance, modelled the climatic niche for the butterfly *Boloria titania* Esper and its larval host plant *Polygonum bistorta* L. and found that the overlap of their climatic niches will be considerably reduced under future projected climate change scenarios. These local disruptions of rather basic trophic interactions may well apply to other more complex interactions such as pollination.

Climate change may also affect morphological and physiological matching of plant and pollinator species. Successful pollination of a particular plant is often determined by the appropriateness of pollinator morphological characteristics, e.g. tongue length, while a particular pollinator can forage profitably only on plants that offer adequate and accessible rewards, e.g. pollen or nectar (Corbet, 2000). Consequently, associations between pollinator body size and plant functional type have been reported (Bond, 1994; Corbet, 2000). Such size-dependencies are a likely result of pollinator-mediated selection processes (Steiner, Whitehead & Johnson, 1994; Johnson & Steiner, 1997). Species-specific flower size, for instance, has been shown to increase along an elevation gradient (Malo & Baonza, 2002; Herrera, 2005) and is correlated with the average body size of the pollinator community (Malo & Baonza, 2002). Malo & Baonza (2002) argue that Bergman's rule applies to insect pollinators with larger body sizes at higher altitudes and latitudes as a response to lower temperatures (but see Hawkins, 1995; Hawkins & DeVries,

Table 1. Climate-change effects on species and communities, potential consequences for plant–pollinator interactions, and derived hypotheses. For potentially contradicting evidence see text. Indication provides evidence from literature given as superscripts

Climate change affects:	Indication	Consequences	Indication	Hypothesis
phenology of plants and pollinators	Phenological changes reported[1]	Disrupted temporal matching	Phenologies of pollinators advance more than plant phenologies[2]	Partial or full uncoupling of pollinator flight period and flower blooming
spatial distribution of plants and pollinators	Distributional changes reported[1]	Disrupted spatial matching	Potential co-occurrence of a butterfly and its larval host plant is projected to be reduced[3]	Increased or full mismatching in pollinator and plant ranges
pollinator body size distribution	Bergman's rule may apply to insect pollinators[4]	Disrupted morphological matching	Associations between pollinator body size and plant functional type[5,6]	Pollen limitation because of mismatching in (size-dependent) pollinator and plant morphology
nectar quantity and quality	Sucrose content changes with temperature[7]	Disrupted energetic matching	Pollinator behaviour is affected by sucrose content[8]	Pollen limitation because of lowered nectar quantity and quality
pollinator energy demand	Metabolic rates increase with temperature[9]	Disrupted energetic matching	Sucrose content changes with temperature[7]	Increased energy demands of small pollinators can not be fully compensated by nectar production in increasingly hotter and dryer regions
	Flight metabolic rate decreases with increasing temperature[10]	Eased energetic matching	Crop loading and foraging behaviour affected by temperature[10]	Large pollinators can spend more time on foraging when cooler regions get warmer
plant community structure	Changes reported[1]	Conditions of competition for pollinators change	Decreased pollinator availability for a particular plant[11]	Pollen limitation because of decreased plant attractiveness
		Facilitative structure changes	Increased pollinator availability for a particular plant[12,13]	Decreased pollen limitation because of increased pollinator availability
pollinator community structure	Changes reported[1]	Pollination effectiveness changes	Plant species richness depends on functional diversity and complementarity of pollinators[14,15]	Pollen limitation when functional diversity or complementarity of pollinators is decreased

References: 1, Parmesan (2006); 2, Gordo & Sanz (2005); 3, Schweiger *et al.* (2008); 4, Malo & Baonza (2002); 5, Bond (1994); 6, Corbet (2000); 7, Petanidou & Smets (1996); 8, Golubov *et al.* (1999); 9, Gillooly *et al.* (2001); 10, Afik & Shafir (2007); 11, Palmer *et al.* (2003); 12, Moeller (2004); 13, Molina-Montenegro *et al.*(2008); 14, Fontaine *et al.* (2006); 15, Fleming *et al.* (2001).

1996). These large-bodied pollinators may in turn select for large flowers. Furthermore, Johnson, Delph & Elderkin (1995) demonstrated decreased pollination success when petal size of *Campanula americana* L. was artificially reduced indicating high interrelation of flower size and a given pollinator community. These evolutionary relationships are not always so straightforward. Mayfield, Waser & Price (2001) demonstrated that *Ipomopsis aggregata* (Pursh) V. Grant is seemingly adapted to hummingbirds while the most efficient but less reliable pollinators are long-tongued bumblebees. They conclude that an optimally specialised floral morphology is not always achievable and that particular constraints favour at least some degree of generalisation. However, global-warming-induced shifts in the body size distributions of local pollinator communities to smaller sizes, according to Bergman's rule, may lead in many cases to a mismatch in pollinator and plant morphology and reduced pollination. This will particularly apply to plant species with specialised flower morphologies that restrict the body-size ranges of potential pollinators (Table 1).

There is no corresponding evidence that flower size will be influenced directly by changes in climate but the adequacy and accessibility of nectar reward may change considerably with changing temperature and water supply (Willmer & Corbet, 1981). Nectar secretion can be reduced by water stress, and analysis of the percentage of sucrose in the nectar of the Mediterranean plant *Thymus capitatus* (L.) Hoffmanns. & Link revealed a hump-shaped relationship

Table 2. Direct effects of alien species within trophic levels in response to climate change, potential consequences, and derived hypotheses. For potentially contradicting evidence see text. Indication provides evidence from literature given as superscripts

Climate change affects:	Indication	Consequence	Indication	Hypothesis
domesticated alien pollinators less than native specialists	Domesticated alien pollinators are generalists with broad niches[1] and effects of climate change may be diminished[2]	Relative competitive ability of domesticated alien pollinators may increase	Range of generalist butterfly species increased during climate change while specialists decreased[3]	Impact of domesticated alien pollinators will increase
some alien plants less than native specialists or even favours alien plants	Invasive alien plants are highly competitive[4] and effects of climate change may be diminished[5]	Relative competitive ability of alien plants may increase	Some alien plants are successful in novel communities and novel climates[6]	Impact of some alien plants will increase
distributional potential of domesticated alien pollinators	Climatic conditions halt the recent rapid spread of Africanized honeybees[7,8]	Introgression of invasive genes into local gene pools	Hybridisation and replacement of European honeybees by Africanised honeybees[9]	Subspecies of native pollinators go extinct
distribution of alien plants	Distributional changes reported[10]	Introgression of invasive genes into local gene pools	Hybridisation between native and alien plants[11]	Subspecies of native plants go extinct
distribution of pathogens and their vectors	Translocation of honeybees discussed as sources of new pathogens[12]	Transmission of pathogens to native pollinators	Honeybee viruses easily expand to multiple hosts[13]	Native pollinators suffer more from (alien) pathogens than the alien hosts
virulence of pathogens	Virulence depends on temperature[14,15]	Altered transmission of parasites and diseases to native pollinators	Honeybee viruses easily expand to multiple hosts[13]	Pathogen pressure will be regionally lowered or increased

References: 1, Goulson (2003); 2, Lodge (1993); 3, Warren *et al.* (2001); 4, Vilà & Weiner (2004); 5, Baker (1974); 6, Vetaas (2002); 7, Sheppard *et al.* (1991); 8, Diniz *et al.* (2003); 9, Kraus *et al.* (2007); 10, Walther *et al.* (2009); 11, Daehler & Carino (2001); 12, Cox-Foster *et al.* (2008); 13, Eyer *et al.* (2009); 14, Martín-Hernández *et al.* (2009); 15, García-Fernández *et al.* (1995).

with temperature; an initial increase until 32.5°C with a sharp decrease above 38°C (Petanidou & Smets, 1996). Although average temperatures may reach such a threshold only under the most severe climate-change scenario (Christensen *et al.*, 2007), increasing frequencies and amplitudes of climatic extremes, which can easily go far beyond this threshold, could be of particular concern (Easterling *et al.*, 2000). Sugar concentration and the resulting viscosity of nectar (Vogel, 1983) impact the energy intake rate of pollinators, which is optimal at intermediate concentration levels (Borrell, 2007), and thus affect pollinator behaviour such as visitation frequency and time spent foraging (Golubov *et al.*, 1999). After a potential initial positive effect of increasing temperatures on sucrose content in the nectar, overly hot and arid conditions in the Mediterranean may shift nectar volume and viscosity to sub-optimal levels for nectar-feeding pollinators which can in turn impact pollination success (Table 1).

Climate change may also affect thermal budgets, energy demands and water balance of the pollinators. Large and dark-coloured bees warm up (and cool down) faster than small and light-coloured bees (Pereboom & Biesmeijer, 2003). This results in differences in resource exploitation and might lead to shifts in pollinator assemblages with increasing temperatures (Pereboom & Biesmeijer, 2003). Metabolic rates of exothermic species usually increase with temperature (Gillooly *et al.*, 2001). In addition, an insect's water balance has been shown to be important for pollination (Willmer, 1988). The combination of higher metabolic rates leading to greater pollinator water demands and more viscous nectar will thus pose significant constraints on the foraging time of small pollinators (Table 1). By contrast, flight metabolic rate of larger endothermic insects, such as honeybees, decreases with increasing temperature (Afik & Shafir, 2007; Table 1). Thus in cooler regions, such species may be able to spend more time foraging when temperatures are rising (Table 1).

III. INDIRECT EFFECTS OF CLIMATE CHANGE: THE EMERGENCE OF NOVEL COMMUNITIES

Individualistic responses by plants and pollinators to climate change both spatially and temporally as well as the local extinction of native species (Section II) and the introduction of alien species (Sections IV, V, VI) will ultimately lead to the generation of novel biotic communities (Ohlemüller *et al.*, 2006; Hobbs *et al.*, 2006; Williams & Jackson, 2007). Palaeological records of late-glacial plant and insect communities show that this has already been the case (Williams & Jackson, 2007), and considerations about dissimilarities between current and future climates indicate high potential for novel climates (Williams, Jackson & Kutzbacht, 2007) and thus novel

Table 3. Direct effects of alien species across trophic levels, potential consequences, and derived hypotheses with respect to climate change. For potentially contradicting effects see text. Indication provides evidence from literature given as superscripts

Alien species affect:	Indication	Consequence	Indication	Hypothesis
functional pollinator community composition	Domesticated alien pollinators integrate into native plant–pollinator communities[1]	Increased compensatory ability	Domesticated alien pollinators augment or rescue pollination services in habitat fragments[2,3]	Alien pollinators partly compensate and sustain pollination services
		Decreased compensatory ability	Domesticated alien pollinators could lack specialist morphology[4]	Alien pollinators may not compensate for morphological and behavioural mismatches
			Domesticated alien pollinators favour highly rewarding plant populations[5,6]	Alien pollinators may not compensate for energetic mismatches
		Altered pollination mode and success	Domesticated alien pollinators may stay longer at inflorescences[7] but also move frequently between different species[8]	Increased proportion of alien pollinators increases the probability of selfing and/or hybridisation
functional plant community composition	Enthomophilous alien plants integrate into native plant–pollinator communities[9]	Increased compensatory ability	Alien plant *Impatiens glandulifera* facilitates short- and long-term survival of native bumblebees when native nectar sources are scarce[10,11]	Alien plants partly compensate and sustain resource availability

References: 1, Goulson (2003); 2, Dick (2001); 3, Gross (2001); 4, Vaughton (1996); 5, Eickwort & Ginsberg (1980); 6, Sowig (1989); 7, Dupont *et al.* (2004); 8, Brown & Mitchell (2001); 9, Bartomeus, Vilà & Santamaría (2008); 10, Starý & Tkalcù (1998); 11, Kleijn & Raemakers (2008).

communities in the future (Ohlemüller *et al.*, 2006; Williams & Jackson, 2007; Walther, 2010). These novel communities may be characterised by a lack of potentially co-evolved interactions but also by the potential for new interactions (Fig. 2). Given the fundamental niche of a species, potential interactions are restricted to cases of overlap with the fundamental niches of other species. Not all of these interactions can be realised under the given climatic conditions, i.e. the overlap of the fundamental niches of two species may lie outside the current climate. But when climate changes, these former potential interactions can become possible while others may vanish (Fig. 2A,B). The long-term ecological consequences of such community changes for plant–pollinator interactions are still hard to predict. For instance, changes in plant community composition can decrease pollinator availability for a particular plant species *via* changed conditions for competition (Section VI.3; Campbell, 1985; reviewed in Palmer, Stanton & Young, 2003; Table 1).

On the other hand, changes in plant community structure under climate change may also have beneficial effects on pollinator availability *via* facilitation among co-occurring plant species (Table 1). Although we are not aware of studies on the effects of climate change on facilitation, there are several that indicate facilitative effects in changed communities (Section VI.3). Moeller (2004) showed that the number of visiting bees increased and pollen limitation decreased when the annual herb, *Clarkia xantiana* Gray ssp. *xantiana*, occurred together with ecologically similar congeners. Molina-Montenegro, Badano & Cavieres (2008) confirmed that both pollinator visitation rates and seed output of a less attractive plant (*Carduus pycnocephalus* L.) increased when grown together with a more attractive plant (*Lupinus arboreus* L.).

Antagonistic species, such as herbivores or seed predators, may shift under climate warming with potential ecological and evolutionary consequences (Section VII) for the mutualistic plant–pollinator interactions (Toräng, Ehrlén & Agren, 2008). In a study on the perennial bumblebee-pollinated alpine herb *Polemonium viscosum* Nutt. at different altitudes, Galen & Cuba (2001) demonstrated shifts in floral shape at lower altitudes where flower-damaging ants are present. Such changes in antagonistic and mutualistic interactions may have consequences for the reproductive success of the pollinated plants as well as for the pollinating bumblebees. Although difficult to predict, it is important to recognise that climate warming can lead to systemic shifts in antagonistic and mutualistic interactions.

Table 4. Indirect effects of alien species across trophic levels, potential consequences, and derived hypotheses with respect to climate change. For potentially contradicting effects see text. Indication provides evidence from literature given as superscripts

Alien species affect:	Indication	Consequence	Indication	Hypothesis
floral resource availability	High level of resource overlap between domesticated alien and native pollinators[1,2]	Increased competition	Reduced reproductive success and body size of native pollinators[3,4]	Reduced plant diversity increases resource competition among alien and native pollinators
pollinator availability	High attractiveness of many enthomophilous alien plants[5]	Increased competition	Reduced pollinator visitation rate and seed set[6,7]	Reduced pollinator diversity increases competition for pollinators and pollen limitation
		Increased facilitation	Magnet species attract additional pollinators[5,8]	Increased diversity of alien plants increases visitation rates and decreases risk of pollen limitation
			Competition and facilitation effects are density dependent[9]	Indirect effects of alien plants vary regionally
pollen deposition	Alien plants increase deposition of heterospecific pollen[10]	Stigma clogging	Reduced seed set in spite of increased visitation rates[10]	Increased diversity and abundance of alien plants increases pollen limitation

References: 1, Thomson (2006); 2, Matsumura *et al.* (2004); 3, Thomson (2004); 4, Goulson & Sparrow (2009); 5, Lopezaraiza-Mikel *et al.* (2007); 6, Chittka & Schürkens (2001); 7, Brown *et al.* (2002); 8, Molina-Montenegro *et al.* (2008), 9, Muñoz & Cavieres (2008); 10, Grabas & Laverty (1999).

Changes in the pollinator community in the course of climate change also might affect pollination effectiveness in some plant species (Section VI.3). In a recent consensus of current knowledge, Hooper *et al.* (2005) agreed that species' functional characteristics strongly influence ecosystem properties, and Lavorel *et al.* (1997) suggest that the effects of changes in pollinator communities might be more related to changes in functional groups than to species composition. Fontaine *et al.* (2006) experimentally demonstrated a positive relationship between the functional diversity of pollinators and plant species richness and highlight the importance of functional diversity for the maintenance of pollination. Furthermore, even if pollination of a particular plant is provided by several species and/or functional groups, pollination can be affected by the loss of single species, as can be expected under climate change, when these species act in a complementary rather than in a compensatory way (Fleming *et al.*, 2001; Table 1).

Novel communities will not be random assemblages of species since generalist species tend to be less affected or may even profit from climate change or the presence of novel species, while many specialists may suffer (Section IV; Warren *et al.*, 2001; Menéndez *et al.*, 2006; Pompe *et al.*, 2008; Settele *et al.*, 2008). In addition to a simple reduction of climatically suitable area, the likelihood of ecological mismatches will increase with increasing specialisation of interaction between plant and pollinator (Fig. 2C,D). This is supported by studies on plants (Thuiller *et al.*, 2005; Broennimann *et al.*, 2006) as well as on pollinators (Kotiaho *et al.*, 2005; Williams, Araujo & Rasmont, 2007) which found increased vulnerability of species with narrow niches to climate change. These pronounced differences between specialist and generalist species in their response to climate change, and the likelihood that novel communities will be mainly dominated by generalist species (Warren *et al.*, 2001), is of particular importance to understanding impacts of climate change and alien species on pollination.

IV. ALIEN *VS.* NATIVE POLLINATORS: DIFFERENCES IN SPECIES TRAITS AND RESPONSE TO CLIMATE

Climate change will affect both the relative performance of already established alien pollinators and the establishment of new taxa both of which may play important roles in future communities (Memmott *et al.*, 2007). While 90% of alien invertebrates in Europe were introduced unintentionally, most introductions of alien pollinators were by intention (Roques *et al.*, 2009). Most accounts of alien pollinators involve domesticated bees (Goulson, 2003), whilst other non-commercially used alien pollinators are little studied. Thus, for this review we will focus on the former group of domesticated alien pollinators which is comprised mainly by colony-forming social bees (the honeybee *Apis mellifera;* European bumblebees: *Bombus terrestris* L., *B. ruderatus* Fabricius, *B. hortorum* L.) but also

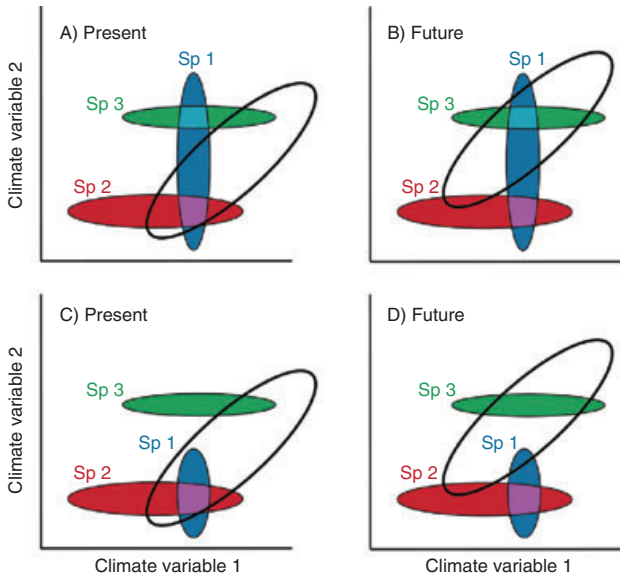

Fig. 2. Schematic diagram showing how community changes in the course of climate change may lead to disruptions of existing and generation of novel species interactions. The fundamental niches of three species (Sp 1–3) in a two-dimensional niche space are shown as coloured ellipses. Present (A,C) and future (B,D) climatic conditions are represented as open ellipses. Present-day interactions are restricted to cases where the fundamental niches of two species overlap and where these overlaps are realised within the current environmental conditions (Sp 1 and 2 in A). When climatic conditions change, current interactions can be disrupted but potentially new ones can be realised (Sp and 3 in B). These patterns will depend on the degree of specialisation. The likelihood of novel interactions will be larger for generalist species with large fundamental niches (Sp 1 in A,B) compared to specialist species with restricted fundamental niches (Sp 1 in C,D). Modified after Williams & Jackson (2007).

by some solitary bees (e.g. *Megachile rotundata* Fabricius and *Nomia melanderi* Cockerell; see Goulson, 2003). This group represents a non-random sample of pollinators with a set of common traits which generally facilitate commercial use and might thus also characterise common responses to climate change.

In particular, domesticated alien pollinators tend to be both social and generalist species with broad niches (Goulson, 2003) and thus may not be sensitive to climate change and resulting ecological mismatches (Fig. 2A,B). There is no reason to assume that alien social generalist species are superior to native social generalists under climate change. However, their importance lies in the comparison with the multitude of native specialist and/or solitary species which might be more affected by climate change (Fig. 2C,D). Thus, potential negative effects of alien pollinators are not necessarily a consequence of their alien status but can rather be attributed to their generalist and social lifestyle. In the following we will discuss effects of alien pollinators within the frame of differential response of social and generalist *vs.* solitary and specialist species.

At least three consequences of climate change may provide social and generalist pollinators (such as *Apis* spp. and *Bombus* spp.) with an advantage in inter-specific competition with solitary or specialised pollinators. Firstly, social domesticated pollinators, notably *Apis mellifera*, are widespread, have long foraging seasons and are likely to be phenologically more flexible than some solitary, especially univoltine, species, which are often restricted to narrow activity windows (Wcislo & Cane, 1996). Consequently, social generalists may suffer less from temporal mismatches and so can extend their active season and build up and maintain populations more easily than solitary and more specialised pollinators. Secondly, social and generalist pollinators often have broader diets due to extended flight season and range of worker body sizes (e.g. *Bombus* spp.; Goulson, 2003) and hence are less likely to experience complete temporal and spatial mismatches with their food plants than diet specialists. Thirdly, *Apis* and *Bombus* species tend to do relatively well in environments with spatially variable resource patches as longer flight ranges (Greenleaf *et al.*, 2007) and recruitment behaviour (*Apis* spp.) allow much more efficient exploitation of forage (Steffan-Dewenter & Kuhn, 2003; Westphal, Steffan-Dewenter & Tscharntke, 2006). In addition, the large amount of workers of social bee colonies enables optimisation of egg production and food intake (Stevens, Hogendoorn & Schwarz, 2007). Taken together, efficient forage, predictable food intake and parental care enhances reproductive fitness of social bees compared to solitary insects (e.g. Smith, Weislo & O'Donnell, 2003). Further, the ability to store food reserves allows the colony to survive periods of inclement weather or periods of sparse floral reward availability. Consequently, climate change and the predicted increased variability in precipitation and evapotranspiration (Christensen *et al.*, 2007) will affect domesticated social generalist bees and thus most alien pollinators much less than most of the solitary specialist predominantly native pollinators (Table 2).

V. ALIEN *VS.* NATIVE PLANTS: DIFFERENCES IN SPECIES TRAITS AND RESPONSE TO CLIMATE

Similar to domesticated alien pollinators, alien plants also represent a non-random sample of plant species, and common traits related to their invasion success may be relevant when it comes to the assemblage of future novel communities. Superior competitive ability is one of the most common mechanisms invoked to explain why alien plant species increase in local abundance at the expense of native plant assemblages (Vilà & Weiner, 2004; but see Daehler, 2003), and these interactions are potentially influenced by climate change (Brooker, 2006; Walther *et al.*, 2009; Table 2). Traits that can confer an advantage under any type of climate change are also related to high alien species invasiveness and include (1) high growth rate, (2) wide climatic or environmental tolerance, (3) high dispersal ability, and (4) increased potential for rapid microevolutionary changes and corresponding adaptation to

changing conditions (e.g. Kolar & Lodge, 2001; Grotkopp, Rejmánek & Rost, 2002; Kühn, Brandenburg & Klotz, 2004*a*; Pyšek & Richardson, 2007).

Increasing temperature and decreasing precipitation have already increased the colonisation potential of some alien plant species *via* increased growth rate. For example, the alien grass *Poa pratensis* L. has colonised Antarctica due to higher survival and growth rate as a response to lengthening of the growing season; it was recorded for the first time in 1944 (Smith, 1996).

Tolerance to a wide range of climates and long-lived seed banks are an advantage in an ecosystem with increasing probability of climatic extremes but as yet there is no evidence that alien species exhibit these traits any more than native species (Vilà *et al.*, 2006). It is intuitive that where alien plants are currently strongly constrained by climate (e.g. by frost sensitivity) that they may benefit from rising average temperatures (e.g. Hanspach *et al.*, 2008; several examples in Walther *et al.*, 2009). In northern temperate regions, many alien species come from warmer areas (Pyšek *et al.*, 2003; Walther *et al.*, 2007; Hulme, 2009) and thus may be particularly sensitive to low temperatures but also predisposed to surviving increasing temperatures and drought. Established alien species have been shown to benefit more from singular drought periods when they are more resilient to limited water availability or suboptimal environmental conditions (Vilà *et al.*, 2006). Yet such pre-adaptation to warmer environments may be less significant in the dynamics of the species than their response to land-use change and eutrophication (Hulme, 2009).

Possession of an efficient dispersal mechanism is an advantage where species must keep up with any spatial changes to their optimal climate space (Ohlemüller *et al.*, 2006; Thuiller *et al.*, 2008). However, in a recent study on the ability of nine plant species to achieve long-distance colonisation of a remote arctic archipelago, Alsos *et al.* (2007) found that wind and drifting sea ice repeatedly transported propagules from several source regions across large distances. They conclude that long-distance dispersal is quite frequent and that establishment limits distribution more than dispersal, at least in the Arctic and in the long term. However, the short-term nature of current climate change might increase the importance of high dispersal capacities. Widespread alien species often possess efficient dispersal mechanisms either using wind or animals to spread seed over long distances (Lloret *et al.*, 2005; Pyšek & Richardson, 2007; Dawson, Burslem & Hulme, 2009). Moreover, a recent study by Niggemann *et al.* (2009) found that alien species benefit more from human dispersal than native species, showing that better natural dispersal ability of alien species may further be amplified by humans, making them more efficient in tracking climate change. Potential sources for spread of alien species are cities which tend to have a warmer climate than surrounding regions (Landsberg, 1981) and are generally rich in alien species (Pyšek, 1998; Kühn, Brandl & Klotz, 2004*b*). Yet the available evidence indicates rather limited spread of alien species from urban areas in the UK over the last 20 years (Botham *et al.*, 2009).

An increased potential for rapid microevolutionary adaptation (see Section VII) may also increase competitive ability of alien plants. For instance, data by Barney, Whitlow and DiTommaso (2009) suggest that since its introduction to North America, *Artemisia vulgaris* L. has evolved a more competitive invasive phenotype, allowing establishment and subsequent dominance in dense stands of existing vegetation. One may expect that potential native competitors, when they are not able to adapt so fast, will either suffer increasingly from changed conditions or even become locally extinct.

In addition to the possible differential impact of climate change on interactions between alien and native plants, the performance of native and alien plant species also depends on community-level processes. Climate change has the potential to shift functional and species dominances in ecosystems (see Section III). Thus, even ecosystems with a currently minor alien component might be converted, under future climate change, to a system dominated by the functional make-up of the alien species already present while competitive hierarchies may be altered (Brooker, 2006).

VI. ALIEN SPECIES: THREAT OR BUFFER WHEN CLIMATE CHANGES?

Effects of alien species may be disentangled into (1) direct effects within trophic levels (plant–plant, pollinator–pollinator; arrows b and c in Fig. 1), (2) direct effects across trophic levels (plant–pollinator and *vice versa*; arrows d and e in Fig. 1), and (3) indirect effects *via* the corresponding trophic level (plant–pollinator–plant, pollinator–plant–pollinator; arrows e-a and d-a in Fig. 1). Their relevance for plant–pollinator interactions will differ markedly.

(1) Direct effects within trophic levels

Besides altered community structure and competitive conditions, other mechanisms of interaction are likely to alter due to climate change. For instance, species introduction and range expansion can result in the introgression of alien genes into local gene pools, which can lead to the extinction of local (sub-) species (Table 2). Studies on dilution of local gene pools and gene replacement in native pollinator populations are scarce. However, the impact of the invasive Africanized honeybee in South America (introduced in the 1950s in Brazil), which has now largely replaced feral and managed European honeybees (repeatedly introduced since the 1500s; Kraus, Franck & Vandame, 2007), may serve as an example. Africanized honeybees have expanded rapidly since first introductions but seem to have come to a halt due to climatic constraints (Sheppard *et al.*, 1991; Diniz *et al.*, 2003). However, they can be expected to expand further as a result of climate warming.

Hybridisation has been shown to be an important mechanism of evolution of invasive plant species (Abbott, 1992; Vilà, Weber & D'Antonio, 2000; Ellstrand & Schierenbeck, 2000) and many widespread and successful invaders are recently formed allopolyploid hybrids (Lee, 2002). Invasive plants may evolve by interspecific hybridisation in the introduced range that creates novel genotypes (Bossdorf *et al.*, 2005). Hybridization often has a positive effect on alien species, but also a strong negative impact on natives. Genetic hazard to native populations results from hybridization between alien and native species, which has been demonstrated to affect the genetic composition of the latter (Love & Feigen, 1978; Daehler & Carino, 2001; Table 2).

Alien pollinators may also spread parasites and diseases to native (sub-)species where they may cause serious declines. Translocations of honeybees and therewith also of pathogens are currently debated as one of the reasons for the recently observed honeybee colony collapse disorder (Watanabe, 2008; Anderson & East, 2008; Cox-Foster *et al.*, 2008). However, little is known about the potential for inter- and intra-specific transfer of pathogens in bee communities, though evidence is accumulating that the extent and role of shared pathogens has been underestimated (Woolhouse, Taylor & Haydon, 2001). It seems that honeybee viruses easily expand to multiple hosts (e.g. Eyer *et al.*, 2009) and are thus likely to infect native bees (Gilliam, Lorenz & Buchmann, 1994; Stout & Morales, 2009; Table 2).

As with honeybee colony collapse disorder, where no particular pathogen or driver of mortality can be identified as responsible (Cox-Foster *et al.*, 2007), a virulent interaction of transferred pests, diseases and other environmental threats such as climate change may also have serious consequences for native bees. Climate change may, for instance, alter pathogen virulence (Table 2). The two microsporidian bee pathogens *Nosema apis* Zander and *N. ceranae* Fries *et al.* have their temperature optimum at 33°C while their virulence is markedly reduced at lower (25°C) and higher (37°C) temperatures (Martín-Hernández *et al.*, 2009). Further, the reproductive biology of the ectoparasitic, virus-transmitting mite *Varroa destructor* Anderson and Trueman also depends on ambient temperature and phenology of the vegetation. García-Fernández, Rodriguez and Orantesbermejo (1995) reported that population growth is faster in the Mediterranean climate (Spain) compared to temperate climate and that infestation rates are increased with a prolonged flowering period. Climate warming may thus affect the distribution, seasonality and severity of diseases (Le Conte & Navajas, 2008) and therewith the potential for intra- and inter-specific transfer (Table 2).

(2) Direct effects across trophic levels

Across trophic levels, alien species can generally be considered as additional resources having the potential to compensate for ecological mismatches in the course of climate change. Generalist alien pollinators often integrate into native plant–pollinator networks and they can improve pollination services to native plant species, especially in species-poor islands (Goulson, 2003). Thus, alien pollinators might be able partly to compensate climate-change-induced spatial and temporal mismatches within native plant–pollinator networks and therefore sustain pollination services (Table 3).

However, such compensatory effects are probably not evenly distributed across species, environments and pollination networks and will not guarantee pollination success for all plant species. For instance, morphological mismatching is not likely to be compensated for by domesticated alien pollinators since generalist alien pollinators could lack specialist pollinator morphology (e.g. tongue length) or behaviour (e.g. buzz pollination) and are thus less efficient at pollinating plants with more complex morphologies than specialised native Pollinators (Vaughton, 1996; Hansen, Olesen & Jones, 2002; Table 3). Also, constraints due to reduced energetic reward or energetic mismatching might not be compensated for by domesticated alien pollinators, since they often have strong preferences for large, mass-flowering and highly rewarding food plant populations (Eickwort & Ginsberg, 1980; Sowig, 1989; Table 3).

In addition, an increasing proportion of alien pollinators could promote alterations in the genetic structure of food plant communities. Domesticated alien pollinators may stay longer at a particular inflorescence and thus can promote higher rates of self-pollination (Dupont *et al.*, 2004; Table 3). Furthermore, most domesticated alien pollinators are generally quite loyal to the plant species they visit at any one time, but nevertheless the observed frequent movements between different plant species can produce mixed-species pollen loads (Brown & Mitchell, 2001). This might interfere with native pollen deposition onto the stigma and is suggested to facilitate hybridisation with native plant congeners (Brown, Mitchell & Graham, 2002; Table 3).

Similar to alien pollinators, there is empirical evidence that enthomophilous alien plants are readily integrated into native plant–pollinator networks (Memmott & Waser, 2002; Lopezaraiza-Mikel *et al.*, 2007; Stout, 2007; Bartomeus, Vilà & Santamaría, 2008), and might receive more visits from more pollinator species than any native plant species in the community (Vilà *et al.*, 2009). Although reproductive traits such as clonal growth and abiotic pollination were positively related to alien plant invasion (Milbau & Stout, 2008), native pollinators can be of crucial importance, especially to obligate animal-pollinated plants with less attractive flowers. For instance, a study on the rapid-spreading alien shrub *Cytisus scoparius* L. in North America revealed a high impact of pollen limitation on seed-set (Parker, 1997). In a follow up study, Parker & Haubensak (2002) compared visitation rates and fruit production of *C. scoparius* and the closely related, co-occurring alien shrub *Genista monspessulana* (L.) L. Johnson. *Genista monspessulana* produced fewer pollen grains than *C. scoparius* (the only reward for insect visitors in both cases), and received fewer visitations. However, these differences in visitation rates were not reflected in differences

of fruit set although pollen limitation was evident for both plants. The importance of potential pollen limitation of alien plants is also supported by the finding that alien plants with longer flowering periods are more successful invaders (Lloret *et al.*, 2005; Pyšek & Richardson, 2007; Küster *et al.*, 2008). Thus, the speed of invasion of highly rewarding alien species that profit from climate change could be increased if also facilitated by native pollinators.

As with alien pollinators, alien plants may compensate for spatial and temporal mismatching in native plant–pollinator networks in the course of climate change by providing additional resources for native pollinators. Several studies have shown that pollinators are sensitive to the distribution of resources and are attracted to areas of high floral rewards (Nielsen & Ims, 2000; Potts *et al.*, 2003; Westphal, Steffan-Dewenter & Tscharntke, 2003). Therefore, alien plants that produce showy floral displays and/or large rewards decrease the dependence of native pollinators on native plants and could make an invaded area able to sustain larger pollinator populations. Given that a significant proportion of alien plants are ornamental species selected for long flowering season, appealing scent or showy flowers (Lambdon, Lloret & Hulme, 2008*a*; Lambdon *et al.*, 2008*b*) these facilitative interactions with native pollinators may be quite frequent (Table 3).

(3) Indirect effects *via* the corresponding trophic level

Most evidence of indirect effects of domesticated alien pollinators on native pollinators mediated *via* plants reflects resource competition rather than facilitation. A high level of resource overlap among domesticated alien pollinators and many native pollinators [up to 90% for *Apis mellifera* in California, USA (Thomson, 2006); up to 70% for *Bombus terrestris* in Hokkaido, Japan (Matsumura, Yokoyama & Washitani, 2004)] indicates high potential for competition. Yet, whether competition actually occurs and impacts population viability of native pollinators remains controversial. Several studies show no support for negative effects of domesticated alien pollinators (Steffan-Dewenter & Tscharntke, 2000; Roubik & Wolda, 2001; Paini, Williams & Roberts, 2005). However, such studies often rely on easily measured proxies such as niche overlap or correlations in abundance rather than more difficult but superior direct measures of reproductive success or population dynamics that can reveal otherwise undetected effects of competition (Thomson, 2006). Thomson (2004), for instance, found that proximity to experimentally introduced honeybee hives in North America reduced reproductive success of the native *Bombus occidentalis* Greene and suggests nectar scarcity as a potential reason. Similarly, in Scotland, Goulson & Sparrow (2009) found reduced body sizes of workers of four different native bumblebee species in areas with honeybees present. They further argue that reduced worker size is likely to have implications for bumblebee colony success, since smaller workers collect less food than their larger sisters leading to restrictions in food supply for the whole colony and thus to reduced performance and reproductive success (Table 4).

In the context of climate change it is interesting that the level of competition, measured as resource overlap, seems to increase when floral resources are scarce (Thomson, 2006). Thus, if climate change leads to reduced plant diversity (Thuiller *et al.*, 2005; Pompe *et al.*, 2008) or potentially to reduced floral rewards (e.g. Petanidou & Smets, 1996; see Section II), negative effects of domesticated alien pollinators on native pollinators may increase *via* increased competition for floral resources (Table 4).

Positive, negative and neutral effects of alien plants on native plant–pollinator interactions and thus native plant pollination have been found (Bjerknes *et al.*, 2007; Table 4). Although negative effects seem to dominate, especially when flower colour and symmetry are similar between alien and native plant species (Morales & Traveset, 2009). The strength and direction of these effects are likely to be density-dependent (Morales & Traveset, 2009). It has been shown that low densities of the alien plant *Taraxacum officinale* group in the Andes act as a magnet to native pollinators that otherwise would not have visited patches of native species. On the other hand, high densities of the alien plant reduced pollinator visitation rates and seed output of neighbouring native species (Muñoz & Cavieres, 2008).

Reduced visitation rates are one source of pollen limitation of native plants, while another is the deposition of heterospecific pollen on native stigmas which may interfere with legitimate pollen transfer and fertilization success and, subsequently, reduce seed set (Bjerknes *et al.*, 2007; Table 4). Even when the presence of the alien plant *Lythrum salicaria* L. increased visitation rates of the native plant *Eupatorium maculatum* L. in North American wetlands, the seed set of *E. maculatum* decreased as a potential consequence of increased deposition of alien pollen (Grabas & Laverty, 1999). However, in most cases, even at high alien plant densities, alien pollen loads deposited on native stigmas by shared pollinators are too low to reduce reproduction by stigma clogging or saturation of stigmatic surfaces (Bartomeus, Bosch & Vilà, 2008; Tscheulin *et al.*, 2009).

Consequently, the effect of climate change on such indirect interactions seems to be context-dependent and can be expected to differ regionally. In regions where alien plant species are phenotypically similar to native plant species and dominate the provision of resources, the effects on native plant–pollinator interactions will be detrimental while in regions with little contribution of alien species native plant–pollinator communities may even profit from alien plants (Table 4).

(4) More complex interactions

Actually, interactions of native and alien plants and pollinators in the context of climate change are rather complex and involve feedback loops (Fig. 3). Most studies only address particular aspects, but the Himalayan annual plant *Impatiens glandulifera* Royle, alien to Europe, may serve

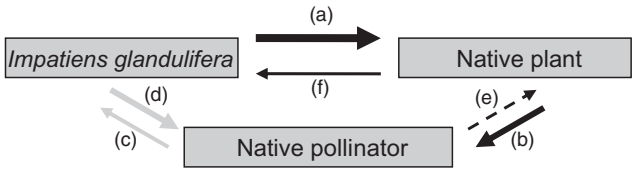

Fig. 3. Simplified interactions among the alien plant *Impatiens glandulifera*, native plants and native pollinators. Arrows indicate the consequences after invasion. Dark grey arrows, negative effects; light grey arrows, positive effects; dashed arrow, both positive and negative effects reported. Arrow thickness indicates the intensity of the effects. (a) *Impatiens glandulifera* invades and replaces native riparian plants. (b) Decreased plant diversity decreases pollinator diversity (potential loss of specialists). (c) *I. glandulifera* is self-compatible but still high visitation rates by generalist pollinators enhance seed set. (d) *I. glandulifera* represents an additional nectar source and may improve short- and long-term survival of generalist pollinators. (e) High attraction of *I. glandulifera* impedes pollination of native plants (potentially density dependent). (f) Native community impedes *I. glandulifera* invasion but to a much lesser extent than it is itself impacted through competition.

as a well-studied example with contrasting impacts on native plants and pollinators and their interactions (Fig. 3).

The direct effect of *I. glandulifera* on native vegetation is primarily through competition for microsites, soil resources and light that results in lower species richness (Hulme & Bremner, 2006) and altered plant community structure (Hejda & Pyšek, 2006; a in Fig. 3). These direct effects on the native vegetation are accompanied by indirect effects *via* pollinators (Fig. 3). *Impatiens glandulifera* was widely introduced as a nectar resource by beekeepers and has particularly high nectar secretion rates ($\sim$1.0 mg sugar h^{-1}) and as the nectar accumulates in the flowers, it is highly attractive to pollinators (Burquez & Corbet, 1991; Titze, 2000; Nienhuis, Dietzsch & Stout, 2009). Thus, *I. glandulifera* can act as an additional energy source and may facilitate short- and long-term survival of at least some generalist pollinators such as bumblebees (Starý & Tkalců, 1998; Kleijn & Raemakers, 2008). As a result, the richness of the pollinator fauna visiting native plants was increased when vegetation was invaded by *I. glandulifera* and native pollen transfer was higher for some taxa (Lopezaraiza-Mikel *et al.*, 2007). However, while *I. glandulifera* may benefit species that almost exclusively utilise the nectar only, this may not be the case for species that require pollen sources (Titze, 2000). Besides positive effects on some pollinators, indirect negative effects of *I. glandulifera* on co-occurring native plants are also evident. For instance, pollinator visitation rates and subsequent seed set in the native *Stachys palustris* L. was reduced in the presence of *I. glandulifera* (Chittka & Schürkens, 2001). However, it is unclear how important a reduction in seed set will be for a self-compatible perennial plant, such as *S. palustris*, that is capable of vegetative reproduction and has a persistent seed bank (Hulme, 1996). As a species with particularly low nectar secretion rates (Comba *et al.*, 1999) the response by *S. palustris* may also not be reflective of the flora as a whole.

How might climate change alter this scenario? Currently, there is no evidence that *Impatiens glandulifera* will perform any better or worse than other riparian species, but its annual habit, early germination, high leaf area index, reasonable tolerance of both light and shade, good seed dispersal, high fecundity, and potential for rapid adaptation to local environments may represent advantageous traits under changing conditions so as to maintain its high competitive ability. The species also benefits from long-distance dispersal through movement by humans of seeds for horticulture (Walker, Hulme & Hoelzel, 2009). Additionally, its extraordinarily high rate of sugar production may make *I. glandulifera* still a preferred nectar source and magnet to pollinators when drier conditions decrease general nectar production levels and drive some plants to suboptimal levels. Thus, the most parsimonious prediction is that the future performance of *I. glandulifera* will differ regionally, due to its high dependence on temperature (Willis & Hulme, 2002) and its particular sensitivity to drought (Beerling & Perrins, 1993). Thus while the northern range of this species may expand as it is released from the constraints of low temperatures, its southern range may contract as seasonal water deficits become more common. In regions where it is neither temperature nor water limited, the impact of *I. glandulifera* on the plant community will primarily be through direct replacement of native plant species rather than changes in plant–pollinator interactions. It will however play an important direct role in the foraging and survival of nectar-feeding pollinators but there is little evidence that the population dynamics of native riparian vegetation would become more pollinator-limited (Nienhuis *et al.*, 2009).

(5) Invader complexes

Although alien pollinators often visit a wide range of plant species, they tend to preferentially visit alien plants (Stimec, ScottDupree & McAndrews, 1997; Olesen, Eskildsen & Venkatasamy, 2002; Goulson & Hanley, 2004), potentially forming ''invader complexes'' (Morales & Aizen, 2006). Alien pollinators can be important for the pollination of alien plant species (e.g. Stout, Kells & Goulson, 2002). These alien plants could, in turn, support alien pollinators by providing a food resource. This may result in positive feedback, enhancing and facilitating the invasion of both alien plants and pollinators.

All forms of mismatching quoted for native plant–pollinator interactions may in principle apply to these invader complexes too. On the other hand, since the effects of climate change may be diminished for both alien plants and pollinators (Baker, 1974; Lodge, 1993), such ''invader complexes'' may provide a buffer against ecological mismatches when communities are restructured. For instance, longer growing seasons will affect diapause and voltinism in some taxa, supporting additional generations of alien insects (Walther *et al.*, 2009). This could increase the potential for alien pollinators to pollinate alien plants in periods when native pollinators are not active, e.g.

during winter in temperate areas, or in late summer when many native species have already finished flowering and alien plant species have filled that niche (Kato *et al.*, 1999; Celesti-Grapow, Di Marzio & Blasi, 2003; Küster *et al.*, 2009).

VII. RAPID EVOLUTION AS A POTENTIAL BUFFER

Species may have the potential to adapt to changing environmental conditions. However, current and predicted climate changes are expected to be rapid, therefore necessitating equally fast and matched evolutionary adaptations. Rapid evolution has been increasingly acknowledged as an ecological process acting at relevant time scales (Thompson, 1998; Parmesan, 2006). Thompson (1998) reported on interspecific specialists interactions that coevolved over only a few decades implying that ecologically significant evolutionary responses of plants and pollinators can accompany both climate change and the generation of novel communities.

(1) Microevolutionary response to climate change

Disruptions of ecological matches such as spatial and temporal synchronicity (Section II) will lead to selection. However, the degree to which particular plants and pollinators may adapt to changing conditions and therewith maintain interactions is unclear. For plant–herbivore interactions, there is evidence that phenological mismatches might be reversed by rapid evolution. For instance, *Operophtera brumata* L. (winter moth) egg hatch date has advanced more than the bud burst date of its larval food plant *Quercus robur* L. (pedunculate oak) over the past two decades. Van Asch *et al.* (2007) demonstrated that crucial prerequisites for rapid adaptation (sufficient genetic variation, heritable reaction norm, severe fitness consequences) exist for *O. brumata* and predict, based on climate change scenarios, a rapid response to selection pressures and a restoration of synchrony of egg hatch with *Q. robur* bud opening. However, in spite of the potential for rapid adaptation, the reasons for currently observed asynchrony remain unclear. Still, genetic preconditions for adaptation and response mechanisms differ among the species involved in different interactions (Holt, 1990). According to such variation, we can also expect variation in the importance of rapid adaptation to lessen or restore asynchrony.

Spatial mismatches could potentially be counterbalanced when both species involved retain their current geographical distribution by adapting to previously unsuitable climates. However, there is little experimental or theoretical support that a particular species will be able sufficiently to evolve absolute climatic tolerances (reviewed in Parmesan, 2006). Even if this happens, it seems unlikely that the evolutionary potential of an interacting species would allow for similar adaptations. In fact, evolution will rather complement and modulate than replace projected ecological changes (Parmesan, 2006). In the context of plant–pollinator interactions it is interesting that such modulations may result in unexpected alterations of the level of specialisation. For the European butterfly *Aricia agestis* Schiffermüller it has been shown that diet breadth was climatically controlled at the northern range margins. The species was specialised on the host genus, *Helianthemum*, which grows in warmer microclimates. In the course of climate warming, *A. agestis* shifted its host and could additionally feed on native *Geranium* ssp., which grow in comparably cooler microclimates. This local diet evolution promoted further expansion to northern areas where the original host, *Helianthemum*, was absent and thus enabled this species to move ahead of changing climates (Thomas *et al.*, 2001).

Specialisation on resources that mitigate the effects of extreme climate has been repeatedly reported (Nylin, 1988; Thomas *et al.*, 2001) and is also likely for pollinators. Consequently, observed effects of diet evolution in plant-herbivore systems may well be transferred to plant–pollinator interactions. One consequence would be that even if a pollinator is (locally) highly specialised on particular pollen resources and strong trade-offs between climate tolerance and resource preferences exist, relaxation from climate control at poleward range boundaries could enable a formerly specialised pollinator to expand its dietary niche. This in turn could also increase the frequency and number of pollinator species visiting plants with flower morphologies or microhabitat requirements that would, under cooler conditions, not especially attract many pollinators (e.g. by lowering dependence on warmth-rewarding plants; Kudo, 1995; Luzar, 2001). But there are limits to such rapid changes, e.g. due to constraints imposed by phylogenetic histories of the involved species. Thus, shifts in pollinator specialisation may be restricted to a small subset of the available resource plants (Thompson, 1998).

(2) Microevolutionary response to novel communities

In novel communities, both conditions of competition and resource supply are changed (Section II), while rapid evolution might allow for adaptive responses that may facilitate coexistence. The potential for evolutionary response has been particularly documented for communities invaded by alien species (Thompson, 1998; Strauss, Lau & Carroll, 2006; Vellend *et al.*, 2007). Alien plants might impose disruptive selection within populations of native plants when they compete for pollinators. This kind of asymmetric selection might favour traits that can reduce the negative effects of competition (Palmer *et al.*, 2003) including traits that increase the effectiveness of infrequent pollinator visits (Medan & Basilio, 2001; Medan, 2003) or that facilitate self-fertilisation (Fishman & Wyatt, 1999; Kudo & Kasagi, 2005; van Kleunen *et al.*, 2008).

For pollinators, resource partitioning is suggested as a widespread mechanism that minimises interspecific competition (Heinrich, 1976; Palmer *et al.*, 2003). In novel

communities, competition with novel species could then be avoided by evolutionary shifts in spatial, temporal or floral forage patterns. However, novel communities tend to be dominated by generalist species with broad ecological niches, and thus subordinate pollinators may frequently be restricted to suboptimal flower species. This is supported by evidence for hierarchical competitive displacement rather than fixed preferences. Kato *et al.* (1999) found that native bees were rarer and visited a narrower range of available flowers on pacific islands dominated by the alien honeybee compared to uninvaded islands.

However, even though rapid evolution may represent a potential buffer against effects of climate change and the restructuring of communities, it will not 'rescue' endangered species in equal measure (Skelly *et al.*, 2007). Whether a species is capable of responding evolutionarily to adverse selection will depend on its genetic preconditions and, due to their complex nature, predictions for a particular species are still hard to make (Holt, 1990; Parmesan, 2006). In some cases, a species will fail to evolve or otherwise adapt, and local or global extinction will result. In other cases, adaptive change may diminish impacts of climate change and potentially promote coexistence in novel communities (Strauss *et al.*, 2006).

VIII. PLANT–POLLINATOR NETWORK ARCHITECTURE AS A POTENTIAL BUFFER

The intrinsic structure of plant–pollinator networks may act as a buffer against cascading effects of climate change (Hegland *et al.*, 2009), species extinction (Memmot, Waser & Price, 2004) and species introductions (Vilà *et al.*, 2009). Plant–pollinator interactions are often highly asymmetric and plant–pollinator networks have been shown to display a nested structure (Fortuna & Bascompte, 2006). This means that a core set of generalist species, both plants and pollinators, play key roles, with specialist plants and pollinators interacting with generalist pollinators and plants, respectively (Jordano, Bascompte & Olesen, 2003; Petanidou & Potts, 2006). The core of generalist species are often less vulnerable to environmental change, therefore they may partly sustain network structure under altered environmental conditions. These network structural properties are suggested to confer robustness to loss of species and interactions due to the high level of redundancy and flexibility within the systems (Memmott *et al.*, 2004; Fortuna & Bascompte, 2006; Petanidou *et al.*, 2008; Alarcón, Waser & Ollerton, 2008; Hegland *et al.*, 2009). There is empirical evidence that although the introduction of single alien plants changes pairwise native plant–pollinator interactions, it does not change the general structure of the network (Vilà *et al.*, 2009).

Another intrinsic property of plant–pollinator networks is their plasticity with respect to species composition and interaction identity. Several studies have shown that plant–pollinator networks are not static, but highly variable through time. Olesen *et al.* (2008) showed in a study system on Greenland that one-fifth of the pollinator species and two-thirds of all links were only observed in one of the two years they studied. Petanidou *et al.* (2008) found similar results in a Greek pollination network studied over four consecutive years. The high degree of generalisation within plant–pollinator networks can by itself confer robustness to alien species and climate change, as few species depend solely on one particular interaction partner.

The assumed buffering capacities of plant–pollinator networks, providing a potential 'safety net' for overall pollination function, may be weakened, however, when changing environmental conditions also affect the pathways and strengths of interactions (Lopezaraiza-Mikel *et al.*, 2007; Tylianakis *et al.*, 2008). For instance, Memmott *et al.* (2007) simulated phenological shifts in plant–pollinator networks and found that the resulting temporal mismatches reduced resource availability and thus diet breadth for the pollinators. They also showed that this again could lead to extinction of pollinators and their interactions, initiating an interaction vortex ultimately also affecting the plants. The authors simulated extinctions by removing pollinators at random, systematically from least-linked (most specialised) to most-linked (most generalised), and systematically from most- to least-linked. Even under the worst-case scenario, removing the most generalised pollinators first, the decrease in plant species was only linear, as opposed to catastrophic species declines reported from standard food-webs. They argue again that intrinsic properties of the plant–pollinator networks, such as the nested structure, are responsible for the relative tolerance to extinctions.

However, the presence of invader complexes can change the native plant–pollinator network transferring links from specialist or generalist native species to super-generalist invading species (e.g. Memmott & Waser, 2002; Aizen, Morales & Morales, 2008). Thus in the course of climate change and generation of novel plant–pollinator systems, the robust structure of the networks may not suffice and the system might reach a tipping point and collapse under severe pressures from multiple factors (Memmott *et al.*, 2004; Fortuna & Bascompte, 2006).

IX. CONCLUSIONS

(1) The combined effects of climate change and alien species on species performance and interactions (Fig. 1) will lead to the generation of novel communities. Within these novel communities established interactions may be disrupted while in turn new interactions will be possible (Fig. 2). It is hard to judge whether this will have a net negative effect on biodiversity and ecosystem function (Fig. 3). What can be expected though is that generalist species are more likely to profit while specialists will rather not. And as a consequence, novel communities might be

increasingly dominated by generalists as global change proceeds.

(2) Climate change in particular is likely to impact native plant–pollinator interactions negatively by altering or disrupting temporal, spatial, behavioural, morphological or energetic matching and changing conditions of competition (arrow a in Fig. 1; Table 1).

(3) Similar to climate change, alien species are also commonly viewed as having a negative effect on native species (Table 2). While the weight of evidence suggests that this is true for competition within the same trophic level (arrows b and c in Fig. 1; Table 4), such effects may actually result in positive interactions when mutualists such as pollinators or nectar and pollen resources are facilitated (arrows d and e in Fig. 1; Table 3).

(4) Net effects of direct and indirect interactions among native and alien species are hard to predict because of complex feedback loops (Fig. 3). But generalist species may profit more from potential positive compensatory effects of alien species than specialists (Table 3).

(5) The effects of alien species, no matter if positive or negative, might be enhanced by the fact that alien plants and alien pollinators tend to form invader complexes (arrow f in Fig. 1). Invader complexes, often consisting of super-generalists, have so far been little affected by climate change and may sustain or even enhance, perhaps increasingly competitive and dominant, alien populations *via* positive feedback mechanisms.

(6) Several buffer mechanisms may come into play: alien species can compensate for lost interactions (Table 3), rapid evolution enables adaptation, and plant–pollinator network architecture, redundancy and flexibility might impede cascading extinctions. However, all these buffer capacities are not unlimited and although they may well modulate the responses to climate change and alien species, they will not necessarily circumvent severe changes in plant–pollinator interactions and the consequent species extinctions.

(7) The complex interplay of negative and positive effects of multiple drivers, acting directly or *via* indirect feedback loops on a set of species interactions, as described in this review, highlights the importance of considering both multiple drivers and species interactions in concert. To predict reliably the consequences of global change for biodiversity, ecosystem functioning and the provision of ecosystem services, a great challenge for future research will be to assess net effects of multiple drivers.

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