

**Spatiotemporal response of pollinators to drivers of global change
at landscape scale**

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Summary

Wild bees constitute one of the most important groups of animal pollinators, contributing to the reproduction of both wild plants and crops, while obtaining resources such as food. For this reason, wild bees and insect-pollinated plants are closely interdependent. Diverse and stable wild bee communities promote the continuous delivery of pollination services. Reduction in habitat area and richness imperil the diversity of both flowering plants and pollination services in agricultural landscapes. Nevertheless, potential indirect effects of the landscape on the diversity of wild bees and flowering plants, mediated by the interdependence between the two groups, have not been thoroughly assessed. Additionally, climate change related alterations in weather patterns, i.e. changes in the mean, variation and extremes of temperature and precipitation, are expected to further affect wild bees. However, the actual effect of such alterations on the diversity and stability of wild bee communities has yet to be assessed. Drivers such as land-use and climate change act simultaneously on biotic communities, enabling interactive effects. Despite the assumption that land-use and climate change interactively affect wild bees and despite the arising risks and opportunities, no evidence in this direction has been provided so far.

In the present thesis, I investigated how landscape properties and weather conditions interactively affect the diversity of wild bee communities in agricultural landscapes, as well as the stability of wild bee abundance in space and time. Additionally, I aimed to disentangle how landscape properties indirectly affect the diversity of wild bees and plants via the interdependence between the two groups.

To this end, I used data from two wild bee monitoring schemes. The first set of monitoring data was collected in six agriculturally-dominated landscapes in central Germany with six samplings every year starting from 2010. The wild bee data were accompanied by landscape and weather data for each sampling period. The second data set included wild bee data from 24 sites in seven European countries. In addition, data on plant records and landscape structure were available for each site. Using the German data set, I first investigated the interactive effects of landscape structure (composition, configuration, diversity) and weather (temperature, precipitation) on wild bee species richness and total abundance. Furthermore, with the same data I assessed whether landscape heterogeneity alters the

effect of intra-annual weather variability on the stability of wild bee abundance in space and time. Finally, I used the European data set to investigate how the effect of landscape on wild bee and flowering plant diversity is influenced by the interdependence between the two species groups.

Wild bee species richness and abundance was negatively affected by increasing temperature, but the impact was mitigated as the area covered by semi-natural habitats increased. Similarly, the stability of wild bee abundance was negatively affected by highly varying temperature only in homogeneous landscapes. Nevertheless, landscape heterogeneity did not suffice to buffer the negative effect of highly varying precipitation conditions. Lastly, habitat richness enhanced wild bee diversity, while arable land cover restricted flowering plant diversity. Wild bee diversity was found to be strongly interconnected with the diversity of insect-pollinated plants, resulting in additional indirect effects of habitat richness on plants mediated by bees and indirect effects of arable land cover on bees mediated by plants.

According to my findings, the combination of land use and climate change can have a negative impact on wild bee communities. I demonstrated that the consequences of different aspects of climate change on wild bee diversity and stability have to be considered. Yet, the present thesis provides intriguing insights on potential protection measures for wild bees in agricultural landscapes and offers opportunities for biodiversity conservation in a changing world. Namely, proper landscape management could not only promptly benefit pollinators, but could also contribute to the mitigation of the detrimental effects of climate change on their community composition and richness. Furthermore, my findings highlight the importance of considering the relationship between interacting species groups when studying the effects of abiotic factors on their diversity. In particular, the results presented here indicate strong, bidirectional links between wild bee and flowering plant diversity, which also lead to indirect effects of landscape properties. Consequently, it is advisable to take their interdependence into account in conservation decision making, in order to achieve more realistic and successful plans for habitat management and nature conservation under climate change.

CHAPTER 1

General Introduction

Animal-mediated pollination

Pollination is a fundamental plant-animal interaction. Cross-pollination involves two flowers located on two different individuals of the same plant species and consists in the transfer of pollen from the anther of one flower to the stigma of the other flower (Willmer 2011). Although cross-pollination can be achieved by abiotic means such as wind and water, biotic pollination is reportedly more common (Renner 1998) and more effective (Willmer 2011). The majority of angiosperms, which constitute one sixth of all described species, reproduce with the mediation of animal pollinators (Willmer 2011). The investigation of the benefits arising from cross-pollination started already in the 19th century, when Charles Darwin examined the mechanisms promoting cross- over self-pollination (Darwin 1876, Barrett 2010). Since then, inbreeding depression has been recognised as a key determinant of the rate of cross- and self- pollination (Charlesworth and Charlesworth 1987, Husband and Schemske 1996), while exclusive self-pollination is considered unlikely even for predominantly selfing species (Barrett 2010).

The interaction between a plant and its pollinator is of mutualistic character, yielding benefits for both organisms. As a consequence of the interaction, the plant is ideally fertilised by the pollen of another individual, while the pollinator receives rewards, usually in the form of food (pollen, nectar, tissues), but potentially also nest-building material, fragrances used in mating or places suitable for oviposition, shelter, warmth provision and meeting opportunities (Renner 2006). However, the plant-pollinator interactions also involve costs for the two partners (Thomson 2003, Lucas-Barbosa 2016) and the interplay between costs and benefits is crucial for determining the level of generalisation or specialisation of plant-pollinator interactions (Blüthgen et al. 2007, Mitchell et al. 2009).

Between 130,000 and 300,000 animal species visit flowers regularly and potentially act as pollinators (Buchmann and Nabhan 1997, Kearns et al. 1998). Although a wide range of animals, including birds, mammals, and even lizards, can contribute to pollination, insects are the most abundant group of pollinators (Potts et al. 2016). Namely, 90% of angiosperms are adapted to pollination by insects (Renner 1998) and insects contribute to the pollination of commodity crops to a considerably greater degree compared to vertebrate pollinators (Klein et al. 2007). Insect pollinators include representatives from the orders Hymenoptera

(bees, wasps, ants), Diptera (flies), Lepidoptera (butterflies, moths) and Coleoptera (beetles) (Potts et al. 2016, Rader et al. 2016). Given that the variety in morphology and behaviour among different insect pollinator taxa results in complementary use of resources (and hence niche differentiation), diverse communities of insect pollinators enhance the provided pollination services (Blüthgen and Klein 2011, Albrecht et al. 2012, Garibaldi et al. 2015). For example, different pollinators visit flowers in different parts of trees, improving the overall pollination services and continuing their provision even under inclement weather conditions, such as high speed winds (Brittain et al. 2013a). Nevertheless, despite the importance of diverse pollinator assemblages, bees in particular are considered primary pollinators of most wild plants and crops (Potts et al. 2016). All bee species are obligate flower visitors and often the most important pollinators of certain habitats (Willmer 2011).

The most widespread bee pollinator species is the honeybee (*Apis mellifera* Linnaeus, 1758). Honeybee colonies are installed and managed worldwide to achieve greater crop pollination (Rucker et al. 2012). However, dependence on a single species is a perilous strategy, which increases the vulnerability of the provided pollination services to predators and pathogens as well as temporal and spatial variation in abundance (Winfree et al. 2007b, Potts et al. 2010a, Bommarco et al. 2013). Furthermore, honeybees are not a suitable substitute for wild pollinators, since they do not maximise pollination and cannot entirely compensate for the service provided by diverse wild insect communities (Garibaldi et al. 2013, Mallinger and Gratton 2015). The risks arising from relying solely on one species become more pronounced as honeybees have been experiencing severe declines in Europe (Potts et al. 2010b) and North America (van Engelsdorp et al. 2008) during the last decades.

Wild bees have been demonstrated to be more efficient pollinators than honeybees (Garibaldi et al. 2013), suggesting that they may be able to compensate for honeybee losses (Tylianakis 2013). Wild bee species differ in a series of traits, such as habitat specialisation, lecty (i.e. diet breadth), nesting requirements, body size or sociality (Winfree et al. 2011). Such traits influence the efficiency of individual bee species as pollinators (de Bello et al. 2010) and define their response to environmental pressures (Murray et al. 2009, Roulston and Goodell 2010). Trait diversity within wild bee communities determines the level of functional complementarity among species, which promotes the successful pollination of a broader variety of plants (Fründ et al. 2013).

Pollination as an ecosystem service

Animal pollinators provide a key ecosystem service (Vanbergen and the Insect Pollinators Initiative 2013), yielding substantial benefits to humans. Overall, almost 90% of flowering plants depend at least to some extent on animal-mediated pollination (Ollerton et al. 2011). Apart from natural plant communities, animal pollinators contribute to the pollination of 75% of world crops (Klein et al. 2007), therefore, being of high economic interest (Gallai et al. 2009, Lautenbach et al. 2012). In particular, wild bees contribute to the provision of enhanced pollination services to crops (Greenleaf and Kremen 2006, Brittain et al. 2013b, Mallinger and Gratton 2015). The economic contribution of wild bees to crop production has been found to be equivalent to those of honeybees (Kleijn et al. 2015). Pollination services, measured by surrogates, such as flower visitation rate, seed set or fruit set, have been associated to the abundance (Kleijn et al. 2015, Winfree et al. 2015), species richness (Rogers et al. 2014, Mallinger and Gratton 2015) and functional diversity of wild bee communities (Hoehn et al. 2008, Fründ et al. 2013, Martins et al. 2015).

Still, it is an established fact that the majority of staple crops do not depend on animal-mediated pollination (Ghazoul 2005). For instance, almost 50% of the world caloric intake is derived from cereals (Dave et al. 2016), which are not pollinated by animals. Nevertheless, essential micronutrients are to a large extent acquired from animal-pollinated crops (Eilers et al. 2011) and their insufficient production overlaps with global malnutrition patterns (Chaplin-Kramer et al. 2014), highlighting the contribution of animal pollination to a balanced human diet. Apart from the nutrition aspect, animal-pollinated plants are involved in the supply of fibres, construction materials, biofuels, medicines, arts, crafts and recreation activities (Jha et al. 2013, Potts et al. 2016).

As the demand for pollinator-dependent crops increases globally (Aizen et al. 2008), greater areas of agricultural land will have to be employed further contributing to global land-use change patterns (Aizen et al. 2009). Considering the lower growth and yield stability levels of pollinator-dependent crops, concerns regarding future effects on global agricultural production and human welfare have been raised (Garibaldi et al. 2011a). The continuous provision of pollination ecosystem services requires stable presence of pollinators in space

and time. Highly variable abundance of wild bees across the flowering season could compromise the successful pollination of insect-pollinated crops, affecting pollen deposition patterns and leading to reduced or unstable crop yield (Klein 2009, Garibaldi et al. 2011a). When pollination is characterised by high spatial or temporal variability, plants in particular locations or during certain periods may not be successfully fertilised (Garibaldi et al. 2011b). Such shortcomings could jeopardise food security by affecting the quality and quantity of agricultural production (Jha et al. 2013). The resilience of ecosystem services, i.e. their resistance to environmental perturbations or their ability to recover fast, is crucial, especially in the face of global environmental changes (Oliver et al. 2015a). Within this context, the maintenance of diverse wild bee communities displaying stable abundances in space and time can contribute to sustaining the pollination ecosystem services. However, studies on the spatiotemporal stability of wild bee abundance are scarce.

Wild bees under threat

Besides belonging to the most important pollinators, wild bees are one of the most sensitive pollinator groups and have even been used as bioindicator taxa (Schindler et al. 2013). To date, about 20,000 bee species have been described worldwide (Michez et al. 2012, Danforth et al. 2013), with Europe hosting 10% of them (1965 species - Nieto et al. 2014). Lack of data impedes an extensive evaluation of the status of wild bee species. Nieto et al. (2014) demonstrated that extinction risk and population trends for 56.7% and 79% of European bee species, respectively, could not be evaluated due to data deficiency.

The majority of evidence pointing to large-scale declines, species loss, and range contractions of wild bees is focused on the subgroup of bumblebees (genus *Bombus*) and limited to Europe and North America (e.g. Goulson et al. 2008, Gixti et al. 2009, Cameron et al. 2011, Kerr et al. 2015). However, bumblebee declines and species loss have also been reported in other parts of the world (Japan - Inoue et al. 2008, China - Xie et al. 2008, South America - Schmid-Hempel et al. 2014). Although data are scarce for the remaining wild bee species, declines have been described in parts of Europe and North America. For instance, in Illinois (USA) 50% of wild bee species were lost over a period of 120 years (Burkle et al. 2013). Additionally, wild bee diversity has decreased in northwest Europe during the 20th

century, although the decline seems less pronounced or even reversed in some regions after 1990 (Biesmeijer et al. 2006, Carvalheiro et al. 2013). Syntheses of local studies demonstrate patterns of decline in species richness and abundance as a result of anthropogenic disturbance (Ricketts et al. 2008, Winfree et al. 2009) and, therefore, could be indirect evidence of a widespread wild bee loss (Potts et al. 2010a). Nevertheless, those patterns should be interpreted with caution given that regionally-based responses of wild bee diversity to disturbance may vary largely (De Palma et al. 2016).

Such declines can be caused by a series of threats that wild bees face worldwide (Winfree 2010, Goulson et al. 2015, Brown et al. 2016, Potts et al. 2016), including land-use change (Hendrickx et al. 2007, Winfree et al. 2009), climate change (Williams et al. 2007, Hegland et al. 2009), introduction of alien species (Moroń et al. 2009, Stout and Morales 2009), application of pesticides (Woodcock et al. 2016) and spread of pathogens (Cameron et al. 2011). The current thesis aims to investigate land-use change, as it has been indicated as the main trigger for bee declines (Brown & Paxton 2009), and climate change, as it is expected to further amplify the effects of other stressors (Winfree 2010, Goulson et al. 2015, Brown et al. 2016, Potts et al. 2016).

Land-use change involves the loss, fragmentation and degradation of (semi-)natural habitats, leading to altered landscape composition, landscape configuration and habitat diversity. Anthropogenic land-use change impacts bee diversity through the diminution of foraging and nesting resources (Biesmeijer et al. 2006, Scheper et al. 2014, Baude et al. 2016), affecting abundance, diversity, and community structure (Senapathi et al. 2015). Increasing area of arable land decreases the abundance and diversity of bees and the density of insect-pollinated plants (Clough et al. 2014). Meta-analyses support the notion that bee diversity is negatively affected by habitat loss and fragmentation (Ricketts et al. 2008, Winfree et al. 2009), but also display different patterns among different geographical areas and taxonomic groups (De Palma et al. 2016). Agriculture and urbanisation have been found to even benefit certain bee guilds as well as bee richness and abundance in general (Winfree et al. 2007a, Carré et al. 2009, Baldock et al. 2015, Theodorou et al. 2016). Such positive effects can be related to the fact that bees require a variety of food, nesting and overwintering resources often relying on multiple different habitats (Westrich 1996). Thus, bees may benefit from intermediate disturbance levels, if the availability of such resources

is promoted in disturbed habitats (Winfree 2010). Furthermore, wild bees are more strongly affected by land-use in contrast to honeybees or other insect pollinators because of their higher dependency on semi-natural habitats (Rader et al. 2016).

Apart from the long-term gradual changes in average weather conditions, climate change involves changes in the frequency and/or strength of extreme weather events (Cubasch et al. 2013) and is considered a major threat to biodiversity, including pollinators' diversity (Goulson et al. 2015, Potts et al. 2016). Climate change likely causes differential shifts in the distributional ranges and phenology of pollinators and their animal-pollinated plants, resulting in potential spatial and temporal mismatches (Memmott et al. 2007, Hegland et al. 2009, Schweiger et al. 2010). The disruption of phenological synchrony between plants and bees due to temporal mismatch may have less pronounced impact than feared (Willmer 2012), given that flowering and bee emergence seem to advance in similar rates (Bartomeus et al. 2011) and bee species with complementary activity periods and differential responses to warming safeguard phenological matching in diverse communities (Bartomeus et al. 2013b). Nevertheless, there is some indication for potential spatial mismatches between plants and different pollinator taxa (Schweiger et al. 2008, Polce et al. 2014). Additionally, important pollinators, such as bumblebees, experience range contractions at their southern range limits and fail to track climate change at their northern range limits (Kerr et al. 2015), while also shifting their elevational ranges as response to warming (Ploquin et al. 2013). The narrower thermal niches of wild bees and their lower thermal niche complementarity in comparison to other pollinators, such as other hymenopterans, flies and beetles (Kühnel and Blüthgen 2015), may also increase their vulnerability to climate change (Buckley and Kingsolver 2012, Huey et al. 2012). Apart from warming, other aspects of climate change, such as the increasing frequency of extreme weather events, are also expected to influence bee communities (Goulson et al. 2015).

The response of wild bee communities to stressors, such as land-use and climate change, depends on ecological traits of individual species. Climate change is expected to affect specialist species more intensely, allowing for higher representation of generalist species in the arising novel communities (Schweiger et al. 2010). For instance, species with large body size, narrow dietary and phenological breadth were found more likely to experience climate change-related declines in relative abundance (Bartomeus et al. 2013a). Traits similarly

modify the response of bees to habitat loss and fragmentation (Bommarco et al. 2010, Hopfenmuller et al. 2014, De Palma et al. 2015, Carrié et al. 2016). Bee species with specific dietary (Winfree et al. 2011) or nesting (Williams et al. 2010) requirements appear to be more sensitive to landscape alteration. Such trait-specific responses may result in non-random losses and biotic homogenisation of insect communities (Gámez-Virués et al. 2015).

Changes in species richness and functional diversity of wild bees are often attributed to the availability of floral resources (e.g. Le Féon et al. 2010, Geslin et al. 2016). In this context, the impact of land-use change on both wild bees and bee-pollinated plants could be exacerbated by the interdependence between those two groups of organisms. Nonetheless, indirect effects of land-use change on bee and plant diversity have been scarcely studied and the underlying mechanisms causing declines in bee diversity still remain uncertain.

Interactions among stressors

The observed declines of wild bees cannot be attributed to one single cause (Vanbergen and the Insect Pollinators Initiative 2013, Goulson et al. 2015), but are rather the outcome of multiple stressors acting simultaneously. The fact that each of them acts at different spatiotemporal scales and levels of biological organisation renders their combined effects more complex. Such effects of multiple pressures could be non-additive, i.e. their overall impact is not equal to the addition of their single effects. In that case, their combination could be of synergistic or antagonistic character, denoting amplification or buffering of the effects of single stressors, respectively (Coors and De Meester 2008, Oliver and Morecroft 2014).

Despite the importance of combined effects for understanding pollinator declines, different pressures are commonly assessed in isolation (Gonzalez-Varo et al. 2013). Thus, our current understanding is limited and mostly focused on certain combinations of stressors (e.g. pesticides-pathogens, pesticides-malnutrition) as well as on certain species groups (e.g. honeybee, bumblebees). For instance, several studies have found synergistic effects of pesticides and pathogens on honeybees and bumblebees (e.g. Alaux et al. 2010, Fauser-Misslin et al. 2014, Doublet et al. 2015). Furthermore, there is evidence for interactive effects on wild bees between land-use change and agricultural intensification (farming

practice - Rundlöf et al. 2008, application of pesticides - Park et al. 2015), as well as between land-use change and alien species (Morales and Aizen 2002, Williams et al. 2011). However, a more thorough evaluation of interactive effects of multiple stressors on wild bees is still lacking (Vanbergen and the Insect Pollinators Initiative 2013).

In general, the interactive effect of climate and land-use change on biodiversity is scarcely studied, because the underlying mechanisms are poorly understood and relevant data are limited (Oliver and Morecroft 2014). Although proper management in the face of future global changes requires understanding of the interactions among drivers (Brook et al. 2008, Tylianakis et al. 2008), few studies have assessed such interactions, mostly focusing on taxa with higher data availability. A global meta-analysis regarding the diversity of a range of taxa demonstrated more pronounced effects of habitat loss in areas with higher maximum temperatures and decreasing precipitation over time (Mantyka-Pringle et al. 2012). Additionally, the impact of land-use change on species richness has been found to increase by up to 43% for birds and 24% for mammals because of the interaction between climate and land-use change (Mantyka-Pringle et al. 2015).

Recent studies have approached the question of combined effects of climate and land-use change on biodiversity by investigating how different taxa are jointly affected by landscape context and weather conditions. Still, only certain taxa, such as birds or butterflies, have been the focus of studies that follow such an approach. For example, it has been demonstrated that when a larger area of an appropriate habitat is available, species richness of birds is less affected by extreme drought (Nimmo et al. 2016) and their populations are more resistant to weather-mediated declines (Newson et al. 2014). Additionally, the percentage of available habitat in the landscape has been shown to modify the effect of temperature on bird productivity (Cox et al. 2013). As far as pollinators are concerned, the existing studies are restricted to butterflies. Namely, habitat fragmentation has been found to limit the ability of butterfly populations to resist and recover after extreme drought events (Piessens et al. 2009, Oliver et al. 2013, Oliver et al. 2015b). On the contrary, the combined effect of climate change and land-use change on wild bees has been assessed rarely and with a focus on single plant species only (Parsche et al. 2011, Hoover et al. 2012), preventing generalisations across whole communities.

Climate change and land-use change are expected to synergistically affect pollinators (Gonzalez-Varo et al. 2013), e.g. by increasing the spatial and temporal mismatches between plants and their pollinators (Burkle et al. 2013). Low availability and connectivity of suitable habitats could prevent species migration and, thus, limit their ability of tracking suitable climatic conditions (Williams and Osborne 2009). Habitat specialists with low dispersal ability are more likely to be affected, leading to species-poor and homogenised pollinator communities (Vanbergen and the Insect Pollinators Initiative 2013). Nevertheless, the combined effects of climate and land-use change on wild bees have not been assessed so far.

Objectives and thesis outline

As presented above, despite the extensive research on pollinators, several issues remain unresolved. The negative impact of land-use change on wild bees in agricultural landscapes has been well-studied, but few studies have assessed the effect of climate change on this group. The response of wild bee communities to changes such as warming or increasing variability in weather conditions has yet to be assessed. Additionally and to the best of my knowledge, no studies have evaluated the combined effects of changes in weather conditions and landscape structure on wild bees. In the present thesis, I aim to bridge this knowledge gap, by analysing the interaction effect between weather and landscape on wild bees and making inferences about potential combined effects of climate and land-use change. Furthermore, when studying the effects of landscape structure on bee communities, the relationship between the diversity of bees and insect-pollinated plants has often been neglected. Hence, this thesis aims to improve our understanding of the response of wild bee communities to global changes. Specifically, I address the following research questions:

- How do landscape structure and weather conditions interactively affect the diversity and spatiotemporal stability of wild bee communities in agricultural landscapes?
- Does the interdependence between wild bees and insect-pollinated plants lead to indirect effects of landscape properties on the diversity of both species groups?

I use two data sets covering different temporal and spatial scales to approach these research questions. All the wild bee data used in the current thesis are derived from pollinator monitoring schemes in agricultural landscapes. Long-term monitoring of pollinators at national and international level is essential for assessing current status and future trends of wild bee populations (Potts et al. 2016) and, thus, it can be used as a tool for informing management practices (Goulson et al. 2015).

The first data set was compiled in the context of an ongoing wild bee monitoring scheme in Saxony-Anhalt, Germany. The monitoring takes place in six sites of the Terrestrial Environmental Observatories network (TERENO, www.tereno.net – Figure 1), which belongs to the German and European Long-Term Ecological Research Network and its main aim is the long-term integrated monitoring of impacts of global changes at a regional scale (Zacharias et al. 2011). The data used in the current thesis were collected during the period of 2010-2013 (Chapter 2: 2010-2012, Chapter 3: 2010-2013). The second data set comprises wild bee and plant data collected in the context of the EU Framework Programme 5 project GREENVEINS (www.greenveins.nl). In that case, the data represent short-term monitoring (summer-autumn 2001, spring 2002) in larger spatial scale (24 sites in seven European countries). The two data sets were used as the basis of the analyses presented in Chapters 2, 3 and 4 to answer the above-mentioned research questions.

In Chapter 2, I assess the combined effects of landscape structure and weather conditions on the diversity of wild bees, using monitoring data from Central Germany. Specifically, I investigate whether species richness and total abundance of wild bees can be explained by weather and landscape predictors and whether the response to weather conditions can be modified by the landscape structure.

In Chapter 3, I focus on the stability of wild bee abundance in space and time and, in particular, on how it is affected by changes in temperature and precipitation variability. I further investigate the role of landscape heterogeneity, assessing whether it can contribute to ensuring stability of wild bee abundance under varying weather conditions.

The analysis in Chapter 4 is conducted at a larger scale, as it is based on data from seven European countries. Here, I focus on the effect of the landscape on both wild bees and insect-pollinated plants. Taking into account species richness and functional diversity, I

investigate the relationship between plant and pollinator diversity and assess potential indirect effects of the landscape on both groups mediated by their interdependence.



Figure 1: The six landscapes where the long term bee monitoring takes place. The yellow pins indicate the location of the installed flight traps within each site. (a) Friedeburg; (b) Greifenhagen; (c) Harsleben (d) Siptenfelde; (e) Schafstaedt; (f) Wanzleben

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CHAPTER 2

Semi-natural habitats mitigate the effects of temperature rise on wild bees

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Semi-natural habitats mitigate the effects of temperature rise on wild bees

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Summary

1. The effect of climate change on wild bee communities is of major concern since the decline of bee species could imperil the provision of pollination services. Additionally, habitat loss and fragmentation are major threats to wild bee populations, but improvements to the landscape structure could also improve the general conditions for wild bees. However, potential interactive effects of climate change and landscape structure on wild bee communities remain unknown.

2. In this study, we assessed the potential of semi-natural areas to maintain robust communities under changing weather conditions. We used bee monitoring data from six 4 × 4 km field sites across Germany. Almost 30 000 bee specimens were collected from 2010 to 2012 in 16 local communities per site at six sampling occasions per year. Following a multimodel inference approach, we identified the most important weather and landscape variables as well as interaction terms that affect wild bee species richness and total abundance.

3. Correcting for overall phenology, we found a strong negative relationship between bee species richness and temperature, indicating that future increasing temperatures will lead to a decrease in species richness. However, a high proportion of semi-natural habitats can considerably decrease the detrimental effect of warmer temperatures on bee species richness and abundance.

4. *Synthesis and applications.* Semi-natural areas and green infrastructure elements within agricultural landscapes become even more important under changing temperature conditions to mitigate the negative effects of increasing temperatures on wild bee species richness and total abundance. This has important implications for conservation decision making, suggesting that maintaining or restoring a fair amount of semi-natural areas could serve as a countermeasure against climate change for wild bees.

Key-words: climate change, climate warming, ecosystem service, global changes, green infrastructure, mitigation, pollination decline, pollinator decline, semi-natural areas, wild bees

Introduction

Pollinators provide a key ecosystem service, contributing to the maintenance of wild plant communities as well as crop production (Potts *et al.* 2010). Almost 90% of the angiosperm plant species depend at least partially on animal pollination (Ollerton, Winfree & Tarrant 2011), which is mostly performed by insects and especially by bees (Kearns, Inouye & Waser 1998). Additionally, about 70% of the most important global crops that constitute 35% of the

global food production rely to some extent on animal pollination (Klein *et al.* 2007). Although domesticated honeybees are often used for pollinating crops such as rape, wild bees have been found to be more efficient pollinators in agricultural landscapes (Garibaldi *et al.* 2013; Mallinger & Gratton 2015). Furthermore, the stability of the pollination service in time is dependent on bee species richness (Kremen, Williams & Thorp 2002) and abundance (Winfree *et al.* 2015). In this context, the role of species-rich and abundant communities of wild bees in agricultural landscapes is of paramount importance to protect biodiversity and to maintain human welfare.

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Wild bees face several threats world-wide: among the major pressures to pollinators are climate change and land-use change (Potts *et al.* 2010; Winfree 2010; Goulson *et al.* 2015). Climate change is expected to differentially impact the abundance, distribution and phenology of bees and their host plants, for example causing spatial and temporal mismatches between them (Schweiger *et al.* 2010; Polce *et al.* 2014). Land-use change, involving the processes of habitat loss and habitat fragmentation, may lead to the limitation of food and nesting resources for wild bees, decrease in abundances, isolation of populations and altered biotic interactions (Aizen & Feinsinger 2003).

However, the above-mentioned pressures do not act in isolation but simultaneously upon pollinator communities. The combination of multiple stressors can cause synergistic or antagonistic effects (Gonzalez-Varo *et al.* 2013), exacerbating the spatial and temporal mismatches between pollinators and pollinated plants (Burkle, Marlin & Knight 2013). Recent studies have investigated the interactive effects between weather and landscape on organisms, focusing mostly on how the landscape context could mediate the consequences of extreme weather events on different taxa (e.g. Oliver, Brereton & Roy 2013; Newson *et al.* 2014; Nimmo *et al.* 2015). For example, Nimmo *et al.* (2015) showed that increasing the area of appropriate habitat increased the resistance of woodland bird species richness to extreme drought, while Oliver, Brereton & Roy (2013) showed that butterfly sensitivity to drought decreased and population recovery increased in the presence of a large amount of well-connected habitats.

In this context, pollinator communities in differentially structured landscapes may respond differentially to climate change, so that detrimental effects (e.g. temperature rise) may be aggravated or mitigated. For example, bee species that will have to shift their ranges to track suitable climatic conditions may be further limited in fragmented landscapes with a small proportion of favourable habitat and a large degree of isolation, while the implementation of green infrastructure elements might mitigate impacts of climate change by rendering the landscape more permeable (EEA 2011). Yet, management decisions that ignore such interactive effects may turn out to be

perilous and undermine conservation efforts (Gonzalez-Varo *et al.* 2013; Oliver & Morecroft 2014). Measures that aim to tackle climate change without considering the landscape structure could be proven as a less efficient use of resources. So far little is known on the combined effect of climate and land-use change on wild bees.

In the present study, we tested the hypothesis that the response of bee species richness and total abundance (jointly termed 'bee diversity' hereafter, where appropriate) to changing weather conditions can be modulated by landscape structure. For this purpose, we used data from a monitoring programme of bee communities in central Germany in order to test how landscape modification and changes in temperature and precipitation synergistically affect wild bees. The data were collected in six agriculturally dominated landscapes for three consecutive years (2010–2012) with multiple samplings within each year, enabling us to take into account weather variability within and among the sampling years and differences in landscape structure among the landscapes. Focusing on the interaction between weather and landscape, we explore whether the effects of changes in weather conditions are buffered by landscape structure. Given that climate is intertwined with weather and climate change is identified on the basis of changes in weather over time (Le Treut *et al.* 2007), we also consider the long-term implications of changing weather conditions on wild bee communities.

Materials and methods

BEE MONITORING DATA

The bee monitoring data were collected in six sites across the federal state of Saxony-Anhalt in Germany. The study sites are monitored as part of the TERENO project (Terrestrial Environmental Observatories; www.tereno.net; Zacharias *et al.* 2011) and of the German and European LTER (Long-Term Ecological Research) network (Müller *et al.* 2010).

The six sites where the bee monitoring took place are representative of the agricultural land use in a wider region and largely differ in terms of landscape structure, altitude and climatic conditions (Table 1). The monitoring took place for three consecutive years (2010–2012), extending from May to September in two periods: early (May–June) and late (August–September) summer.

Table 1. Coordinates of site centroids and mean values (\pm one standard deviation) of environmental variables and species richness for the six study sites. Mean temperature and precipitation were calculated using daily data from 6 years (2001–2002, 2010–2013). Landscape composition: percentage cover of semi-natural areas, landscape configuration: mean area-weighted proximity index of semi-natural areas

| Site | Latitude | Longitude | Elevation | Temperature (°C) | Precipitation (mm) | Landscape composition | Landscape configuration | Habitat richness | Species Richness |
|--------------|------------|------------|-----------------|--------------------|--------------------|-----------------------|-------------------------|------------------|------------------|
| Friedeburg | 51-6177° N | 11-7096° E | 122 (\pm 31) | 9.66 (\pm 0.69) | 592 (\pm 128) | 16.91 | 7476 | 24 | 129 (\pm 3) |
| Greifenhagen | 51-6329° N | 11-4340° E | 270 (\pm 27) | 9.27 (\pm 0.89) | 606 (\pm 118) | 10.48 | 2823 | 24 | 104 (\pm 10) |
| Harsleben | 51-8423° N | 11-0753° E | 143 (\pm 14) | 9.56 (\pm 0.74) | 581 (\pm 176) | 16.30 | 259 943 | 18 | 121 (\pm 11) |
| Siptenfelde | 51-6491° N | 11-0526° E | 423 (\pm 31) | 7.43 (\pm 0.76) | 646 (\pm 117) | 15.89 | 56 589 | 19 | 73 (\pm 6) |
| Schafstaedt | 51-3770° N | 11-7224° E | 177 (\pm 11) | 8.83 (\pm 0.82) | 580 (\pm 101) | 1.65 | 898 | 18 | 101 (\pm 5) |
| Wanzleben | 52-0803° N | 11-4518° E | 113 (\pm 10) | 9.68 (\pm 0.69) | 591 (\pm 130) | 10.26 | 63 332 | 21 | 101 (\pm 16) |

Each of the TERENO sites measured 4×4 km and was divided into 16 squares of 1 km^2 . One combined flight trap (a combination of yellow funnel and window panel; Duelli, Obrist & Schmatz 1999) was arbitrarily placed within each square at ecotones (i.e. transition area between two habitat types, usually between a semi-natural habitat and an agricultural field). Although the colour of the traps might impact the captured species composition depending on the predominant flower colour in the area, yellow has been suggested as the most effective one (Duelli, Obrist & Schmatz 1999) and our combination of a very large diameter and the window panel (more details in Schweiger *et al.* 2005) proved an extremely high trapping efficiency as confirmed by local experts (Frank Burger and Frank Creutzburg). Traps were active for 2 weeks before being emptied. Then, the trapped insects were collected and, subsequently, all wild bees were identified to species level. This sampling procedure was repeated for three fortnightly sampling intervals per period. Species richness and total abundance were determined for each trap and sampling interval as the number of species and the total number of individuals identified, respectively. Honeybees were excluded from the analyses to eliminate the possible anthropogenic effect caused by honeybee management.

LANDSCAPE DATA

Digitized habitat maps of the six sites were derived from orthorectified photographs at a resolution of 20 cm. Habitats were classified to the third level of the EUNIS classification system, and the classification was verified by on spot observations (see Frenzel, Everaars & Schweiger 2015).

Three different aspects of the landscape were taken into account: composition, configuration and diversity. The landscape metrics were calculated at the level of the 4×4 km sites. Landscape composition was assessed as the percentage of semi-natural habitats per study site. The total number of EUNIS habitats identified at a site was used as a proxy for habitat richness, while the area-weighted mean proximity index of semi-natural habitat patches was used as a measure of landscape configuration at the site level. The proximity index (Gustafson & Parker 1992) describes the geographical distance between habitat patches weighted by patch size; thus, the index takes higher values in landscapes with large patches situated close to each other and lower values for small patches far from each other. A search radius of 200 m was specified for the calculation of the proximity index. A wide variety of habitats, including woodland, urban areas and even agricultural land, can provide resources to wild bees. However, for the above-mentioned calculations we focused on what would be considered as typical bee habitat in an agricultural land, that is grasslands, hedgerows, shrublands. A full list of the semi-natural habitat types is provided in Appendix S1 (Supporting Information). The calculation of the landscape metrics was performed in FRAGSTATS v4.2 (McGarigal, Cushman & Ene 2012).

WEATHER DATA

Data on air temperature and precipitation were obtained from DWD (German Meteorological Service) weather stations in the vicinity of each of the six sites. Mean daily temperature and total daily precipitation were available at site level throughout the years 2001–2002 and 2010–2013.

Two different aggregation levels of weather variable sets were incorporated in our analyses. The first variable set describes the short-term weather conditions during each fortnightly sampling interval by mean temperature and total precipitation. The second variable set comprises two longer-term weather variables, which were employed to account for systematic differences among the six sites (caused by altitude, topography, etc.). To this end, mean annual temperature and total annual precipitation per site and year were computed for each of the 6 years we had available weather data and, subsequently, the mean across all years was calculated for both temperature and precipitation. For simplicity, the two resulting variables are referred to below as 'longer-term temperature' and 'longer-term precipitation'.

STATISTICAL ANALYSES

Although species richness and total abundance were highly positively correlated (Pearson's $r = 0.8$, $P < 0.001$), we analysed them separately following the same procedure, since they are by no means perfectly correlated and, therefore, are not necessarily expected to give the same results.

First, we accounted for the effects of phenology, since bee species abundance and richness usually peaks during the early (cooler) monitoring period and levels off during the late (warmer) period. To make the response of bee species richness to fluctuations in weather conditions independent from general phenological patterns (i.e. emergence in spring, peak abundance, levelling off towards autumn) and, thus, from corresponding annual temperature cycles, we built a generalized additive mixed-effects model (GAMM) with logarithmic link function for species richness using a third-order polynomial (including first- and second-order terms) of the Julian day as an explanatory variable (the central Julian day of each sampling interval was taken as reference point). Local species richness data at trap level were averaged per site and used as response variable. Site was included in the analyses as a random effect. The GAMM explained 78.3% of the variation in the data (proportion of null deviance explained). The outcome of the GAMM was one phenology curve representing the expected changes in species richness along a year within the entire region of the study (Fig. 1; see Fig. S1 for raw data). The fitted model values were an estimation of the expected richness for the sampling intervals based on their positions within the year. The same approach was followed for total abundance, with the GAMM explaining 63% of the data variation in that case (see Fig. S2 for phenology curve and Figs S3 and S4 for the residuals of the two models plotted per site).

Secondly, to examine whether the effect of weather on bee species richness depends on the landscape structure, generalized linear mixed-effects models (GLMMs) were applied. Since the species richness and abundance data were overdispersed, a negative binomial error distribution with a log link function was used. The random structure of the model included two crossed random intercepts: the trap nested within site and the sampling interval nested within year. The expected species richness value for each sampling interval according to overall phenology patterns (as previously calculated by the GAMM) was added to the model as an offset (Schmucki *et al.* 2016). This approach enabled us to assess anomalies in the relationship between particular weather conditions (e.g. overly hot or cold) and species richness (i.e. being independent of the general effects of annual weather cycles on the phenology of bees). Thus, using the expected species richness as

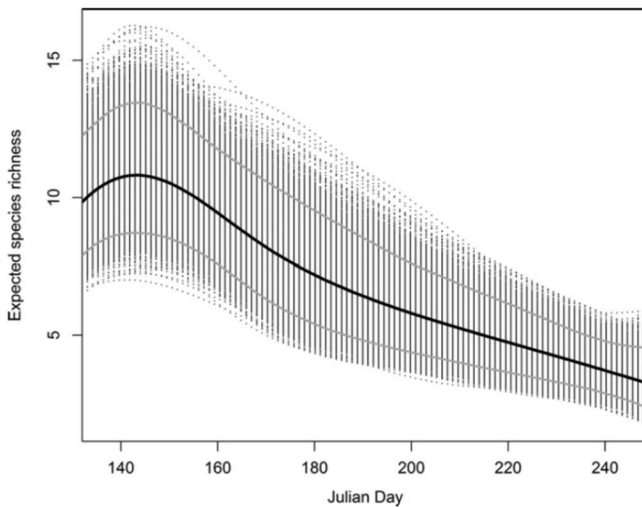


Fig. 1. Phenology curve displaying the expected species richness per trap along the total monitoring period within a year (black curve). The dark-grey lines represent the 95% prediction intervals based on predictions from the posterior distribution with 10 000 replicates per Julian day (black dots).

an offset, we assess deviations from the expected phenology curve and investigate whether they can be attributed to changes in weather conditions. Including that term prevented from misinterpreting mere phenological patterns as responses of species richness to weather anomalies.

All variables intended to be included in our main model were tested for collinearity. To this end, Pearson's correlation coefficients were estimated for each pair of explanatory variables and a threshold of 0.7 was set as an indicator of high collinearity that could distort model estimation (Dormann *et al.* 2013). None of the pairwise comparisons resulted in a higher correlation value, apart from the two negatively correlated longer-term weather variables ($r = -0.82$). To select which one to include in the main model, two additional models were built. The two models had species richness as dependent variable and the random structure and offset of the main model but only longer-term temperature or precipitation as explanatory variable. The two models were compared based on second-order Akaike Information Criterion (AICc; corrected for sample size). Longer-term precipitation resulted in the model with the lowest AICc value and, thus, was retained for the main model.

Subsequently, we followed a multimodel inference approach (Burnham & Anderson 2002). This circumvents problems with null hypothesis testing of complex GLMMs, such as inflated type I error (Ives 2015). To begin with, global models were fitted for species richness and abundance. The initial explanatory variables were temperature and precipitation for each sampling interval and their quadratic terms, the three landscape variables and the interactions between each one of the weather and landscape variables (two weather variables \times three landscape variables = six interaction terms). Furthermore, longer-term precipitation was added to the set of explanatory variables. All explanatory variables were standardized to zero mean and unit standard deviation to obtain comparable coefficient estimates (Quinn & Keough 2002). The model residuals were checked for spatial autocorrelation by computing Moran's I correlograms (Moran 1950), but none was detected. Additionally, all usual diagnostics were conducted and the statistical assumptions for GLMMs were met.

The amount of variance explained was estimated by calculating the Nagelkerke pseudo R^2 for the global models. More specifically, two values were calculated using the intercept-only model

once with and once without the random structure of our main model in order to describe the variance explained by the fixed effects only and by both the fixed and random effects, respectively.

Subsequently, all plausible candidate models including up to four explanatory variables were developed and AICc values and relative weights were calculated. The model with the lowest AICc value was considered the best model. The models were compared in terms of their difference in AICc value (δAICc) from the best model, as well as their evidence ratio. The evidence ratio is calculated as the weight of the best model divided by the weight of each one of the other models and represents the likelihood of a model to be the best one relative to each of the others (Burnham & Anderson 2002). A subset of models was derived from the list of all candidate models for calculating relative variable importance and model averaging. The cut-off value for model inclusion was an evidence ratio smaller than eight (Burnham & Anderson 2002). The relative importance of each variable in the selected set was calculated as the sum of weights of all models in which the specific variable occurs.

All analyses were implemented in the statistical software R v3.1.2 (R Core Team 2014). The data analysed can be found in Table S1. The GAMM was built with the package mgcv version 1.8-3 (Wood 2011), while the packages glmmADMB version 0.8.0 (Skaug *et al.* 2014) and MuMIn version 1.12.1 (Barton 2014) were used for the GLMM and the multimodel inference, respectively.

Results

During the 3 years of monitoring, more than 28 000 individual bees of 261 bee species were collected.

The global GLMM testing weather and landscape effects on species richness explained 51.1% of the data variation, of which 6% was explained by the fixed component represented by all the weather and landscape variables and their interactions. In the context of multimodel inference, 126 models were compared. Our set of three selected models based on the evidence ratio had a cumulative weight of 65.1% and δAICc not exceeding four

(Table 2a). The variables included in this set were mean temperature of the sampling interval, longer-term precipitation, percentage of semi-natural areas in the landscape, number of habitats, proximity index and the interaction of percentage of semi-natural areas with mean temperature (Table 2b).

The percentage of semi-natural habitats occurred in all the selected models and had the highest relative importance, followed by mean temperature and the interaction between these two variables. Longer-term precipitation also occurred in two models. The number of habitats and the proximity index were of lesser importance, both of them occurring in just one model.

The three selected models were supported to different extent by our data (Table 2a). Based on the evidence ratios, it seems that the first model is the one that best represents the data compared to the second and the third one.

Comparing the predictions of the model averaging of the selected model set to those of the best model, no important differences were observed ($R^2 = 0.99$; additionally, the remainder of subtracting the predictions of the averaged model from the predictions of the best model is not different from zero, Wilcoxon signed rank test $P = 0.93$). As a result and taking into account the simplicity of the model, the best model is presented hereafter.

According to the best model, phenology-independent species richness increased with percentage of semi-natural areas, but decreased with mean temperature of the sampling interval (Table 2b). However, the positive interaction between the two variables suggests that the effect of temperature depends on the proportion of semi-natural habitats within a site in a way that higher proportion of semi-natural habitats decreases the negative effects of

higher temperatures (see Fig. 2 for the interactive effect of temperature and landscape composition on bee species richness and Fig. S5 for the relationship between temperature and species richness in each study site). In addition, longer-term precipitation also negatively affected species richness (Table 2b).

The global GLMM for total abundance explained 52.1% of the data variation, of which 5.7% was explained by the fixed effects. Our selected model set consisted of six models with a cumulative weight of 98.7% and δAICc not exceeding four (Table 3a). According to the relative importance index, the most important terms included in the set were mean temperature of the sampling interval, percentage of semi-natural habitats in the landscape and their interaction, while five other terms were of lesser importance (Table 3b). Like for species richness, temperature had a negative effect on abundance, while the impact of semi-natural areas was positive. Also similar to species richness, we found a positive interaction between mean temperature and percentage of semi-natural areas, but this effect was stronger for abundance than for species richness (Fig. S6).

Discussion

We found that suitable habitat area is the most important factor affecting local bee diversity (see relative importance index, Tables 2b and 3b). The importance of a high proportion of favourable habitats has been previously supported by studies performed in the same area almost a decade ago (Hendrickx *et al.* 2007) or elsewhere (e.g. Kremen, Williams & Thorp 2002; Steffan-Dewenter *et al.* 2002; Klein *et al.* 2012). However, we also found that bee diversity (i.e. richness and abundance) is highly sensitive

Table 2. Selected set of models explaining species richness: (a) Statistics for model comparison; AICc, Akaike Information Criterion corrected for small sample size; δ , difference to best model. (b) Variables included in each model and their relative importance based on the whole set of models. Parameter estimates and their standard errors are displayed for each model; landscape composition: percentage cover of semi-natural areas, mean temperature: mean temperature of the 2-week sampling interval, interaction: interaction between cover of semi-natural areas and mean temperature, habitat richness: number of habitats, landscape configuration: mean area-weighted proximity index of semi-natural areas

| (a) | | | | | |
|-------|--------|---------------------|---------------|-------------------|----------------|
| Model | AICc | δAICc | Akaike weight | Cumulative weight | Evidence ratio |
| A | 9049.8 | 0.00 | 0.434 | 0.434 | 1.00 |
| B | 9052.4 | 2.56 | 0.121 | 0.554 | 3.60 |
| C | 9052.8 | 3.00 | 0.097 | 0.651 | 4.47 |

| (b) | | | | | | |
|---------------------|-----------------------|----------------------|---------------------|---------------------------|----------------------|-------------------------|
| Model | Landscape composition | Mean temperature | Interaction | Longer-term precipitation | Habitat richness | Landscape configuration |
| A | 0.12 (± 0.07) | -0.05 (± 0.03) | 0.04 (± 0.01) | -0.20 (± 0.07) | | |
| B | 0.40 (± 0.08) | | | -0.37 (± 0.06) | -0.23 (± 0.07) | -0.37 (± 0.09) |
| C | 0.05 (± 0.1) | -0.05 (± 0.03) | 0.04 (± 0.01) | | | |
| Relative importance | 0.88 | 0.81 | 0.68 | 0.68 | 0.23 | 0.21 |

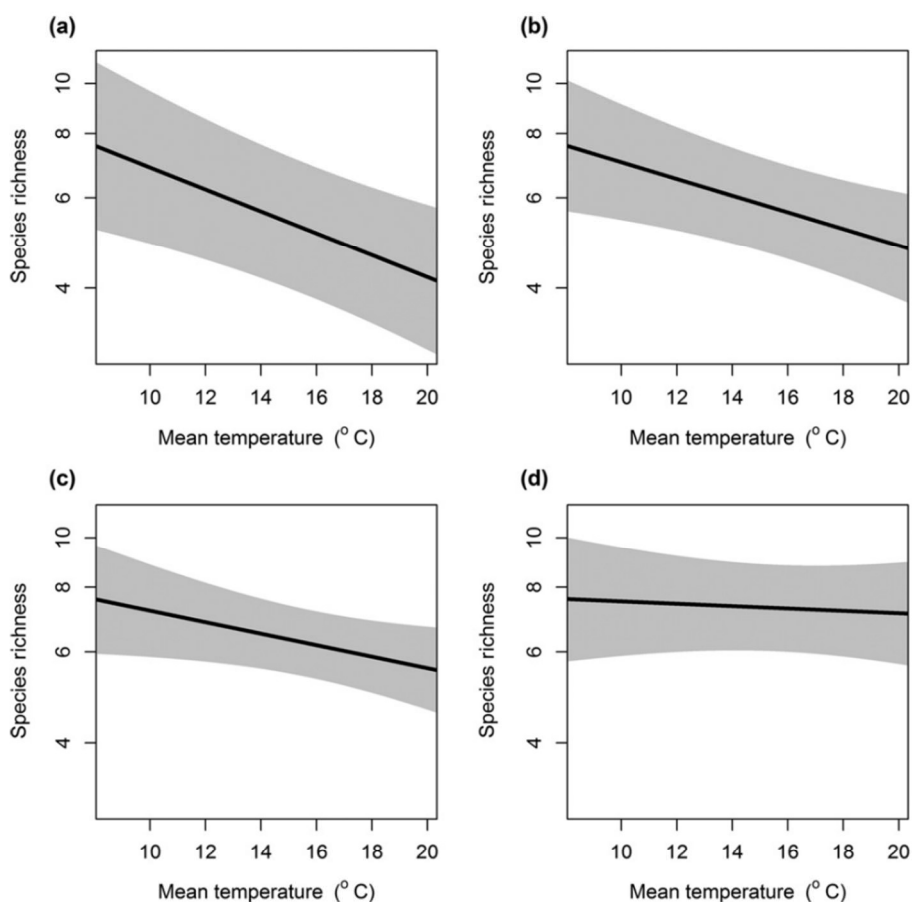


Fig. 2. Interactive effect of temperature and landscape composition on bee species richness. The effect of temperature increase on species richness is displayed for four different levels of percentage of semi-natural areas: (a) 2%, (b) 6%, (c) 10%, (d) 17%. The cover range in the plot starts from the minimum cover of semi-natural areas in our study sites (i.e., 2%) and reaches the maximum coverage observed (i.e. 17%). We, additionally, used 10% (as a representative value for two of our sites) and 6% (as the mean value between 2 and 10% to cover the whole range). The y -axis is displayed on the logit scale. Grey bands indicate 95% confidence intervals.

to temperature. More specifically, an increase in temperature leads to a decline in bee diversity, even when corrected for the effect of phenology, corroborating the worrisome reports about the potential negative effects of climate warming on wild bees (Potts *et al.* 2010; Winfree 2010). Such a decline has been observed in studies assessing the effect of climate change on wild bees with use of long-term data (Biesmeijer *et al.* 2006; Bartomeus *et al.* 2013) and can be inferred from range contractions of bumblebees in Europe and North America especially at their warm (southern) range margins (Kerr *et al.* 2015).

The variable 'longer-term precipitation' turned out to be an important parameter, negatively affecting bee diversity. This variable was highly negatively correlated with the variable 'longer-term temperature'. This indicates that drier and hotter sites tended to have higher bee diversity, in accordance with the species richness–energy hypothesis (e.g. Currie *et al.* 2004). On the contrary, increases in the short-term temperature (i.e. of the fortnightly sampling interval) had a negative impact on bee diversity.

Temperature has a direct impact on development, survival, range and abundance of bees (Bale *et al.* 2002) and is the main determinant of pollinator activity (Kühnel & Blüthgen 2015). The activity patterns of different species are expected to be differentially affected by climate warming (Rader *et al.* 2013), while the narrower thermal niches of bees compared to other pollinators could render them more susceptible to climate change effects (Kühnel & Blüthgen 2015). Such divergent responses may lead to a decline in bee diversity with temperature increase as we observe here, especially when a threshold of high temperature is surpassed. Our results on temperature further reflect that short-term and longer-term weather may have different, even opposing, effects on bee diversity. One possible explanation might be that organisms can locally adapt to local climate conditions, yet higher temperature deviations around this longer-term mean might drive rapid declines. Indeed, a recent review showed that the effects caused on population growth by changes in mean temperature can be altered or even reversed by variance in temperature

Table 3. Selected set of models explaining total abundance: (a) Statistics for model comparison; AICc, Akaike Information Criterion corrected for small sample size; δ , difference to best model. (b) Variables included in each model and their relative importance based on the whole set of models. Parameter estimates and their standard errors are displayed for each model; mean temperature: mean temperature of the 2-week sampling interval, landscape composition: percentage cover of semi-natural areas, interaction: interaction between cover of semi-natural areas and mean temperature, habitat richness: number of habitats, landscape configuration: mean area-weighted proximity index, total precipitation: total precipitation during the 2-week sampling interval

| (a) | | | | | | | | |
|-------|----------|---------------|--|---------------|-------------------|--|----------------|--|
| Model | AICc | δ AICc | | Akaike weight | Cumulative weight | | Evidence ratio | |
| A | 11845.67 | 0.00 | | 0.391 | 0.391 | | 1.00 | |
| B | 11846.69 | 1.02 | | 0.235 | 0.627 | | 1.66 | |
| C | 11848.49 | 2.82 | | 0.096 | 0.722 | | 4.10 | |
| D | 11848.61 | 2.94 | | 0.090 | 0.812 | | 4.35 | |
| E | 11848.63 | 2.96 | | 0.089 | 0.901 | | 4.39 | |
| F | 11848.71 | 3.04 | | 0.086 | 0.987 | | 4.57 | |

| (b) | | | | | | | | |
|---------------------|---------------------|-----------------------|--------------------|---------------------------|------------------|---------------------------------|-------------------------|---------------------|
| Model | Mean temperature | Landscape composition | Interaction | Longer-term precipitation | Habitat richness | (Mean temperature) ² | Landscape configuration | Total precipitation |
| A | -0.09 (\pm 0.05) | 0.16 (\pm 0.14) | 0.10 (\pm 0.02) | -0.28 (\pm 0.14) | | | | |
| B | -0.08 (\pm 0.06) | 0.05 (\pm 0.17) | 0.10 (\pm 0.02) | | | | | |
| C | -0.09 (\pm 0.06) | 0.05 (\pm 0.17) | 0.10 (\pm 0.02) | -0.01 (\pm 0.03) | | | | |
| D | -0.08 (\pm 0.06) | 0.04 (\pm 0.17) | 0.10 (\pm 0.02) | 0.05 (\pm 0.17) | | | | |
| E | -0.08 (\pm 0.06) | 0.08 (\pm 0.19) | 0.10 (\pm 0.02) | -0.06 (\pm 0.19) | | | | |
| F | -0.08 (\pm 0.06) | 0.05 (\pm 0.17) | 0.10 (\pm 0.02) | 0.004 (\pm 0.04) | | | | |
| Relative importance | 1.00 | 0.99 | 0.99 | 0.40 | 0.10 | 0.10 | 0.09 | 0.09 |

(Lawson *et al.* 2015). Additionally, Vasseur *et al.* (2014) found that whereas higher mean temperatures favoured invertebrate ectotherms, simultaneous changes in mean and variance resulted in diverse responses, leading temperate species to performance declines.

Yet, our most interesting finding is the interactive effect of temperature and landscape composition. Increasing temperatures can have severe effects on bee diversity in landscapes largely dominated by agricultural areas, while agricultural landscapes with higher amount of habitats suitable for bees (coverage of around 17%) are much less affected. Thus, increasing agricultural area on the cost of semi-natural habitats does not only decrease overall bee species richness (Kormann *et al.* 2015), but also makes the remaining species more vulnerable to rising temperatures. The presence of semi-natural habitats provides a larger variety of floral resources and nesting habitats to wild bees, likely making them less vulnerable to changes in weather conditions. Additionally, suitable habitats in a matrix of exposed agricultural land can serve as refuges to ectotherms, like bees, offering them an opportunity to cool down when they reach extreme body temperatures (Sunday *et al.* 2014). Such resources are limited in the agriculturally dominated landscapes, permitting only the survival of the nearby living species or the more mobile species.

In the context of climate warming, the high sensitivity of wild bees to increasing temperatures, as observed in our study, could imply a threat to their communities given the temperature rise predicted by climate change

scenarios. More specifically, RCP (Representative Concentration Pathways) scenarios for summer temperature predict a median increase between 4 and 6 °C in Central Europe by 2100 (IPCC 2013). Such an increase in summer temperature is likely to cause a decrease in the diversity of local bee communities by 20–30% in landscapes with extremely low cover of semi-natural areas, for example 2% in our case (Fig. 2). Semi-natural areas are found to be highly beneficial in terms of preserving bee diversity according to our study, but also averting population collapse of single, sensitive species (Oliver *et al.* 2015). For our calculations, potentially new species are not considered, but a recent study showed that northwards range expansions of pollinators, such as bumblebees, are surprisingly limited (Kerr *et al.* 2015).

In addition to a long-term climate change perspective, the positive effect of semi-natural areas on the temperature sensitivity of wild bees is also relevant in a short-term weather variability perspective. Although pollination of many crops is dominated by few common species (Kleijn *et al.* 2015) and their abundance (Winfrey *et al.* 2015), species-rich pollinator communities can still enhance crop pollination (Garibaldi *et al.* 2014) and, moreover, increase the resilience of the provided service against climate warming (Rader *et al.* 2013) and environmental disturbances (Brittain, Kremen & Klein 2013). Thus, temperature-driven variability in wild bee diversity might signal a risk for the provision of pollination especially in landscapes with low cover of bee habitats. Yet, yield deficits

are the result of the cumulative actions of pollinators across the key flowering seasons. Bees may be less apparent during hot spells, but they may as well be more active for the rest of the year to compensate for the temporary lack of activity, ultimately resulting only in a somewhat lower overall impact on pollination service. How well such a potential compensation mechanism may work under future, warmer climates, however, still needs to be resolved. Therefore, some implications for current pollination services may arise from our results, but such conclusions should be drawn with care.

The interactive effect of temperature and landscape composition on bee diversity could give rise to ground-breaking applications in conservation. Pollinators have been found to benefit from the implementation of agri-environmental schemes in croplands located in simple landscapes covered by 1–20% of semi-natural habitats (Scheper *et al.* 2013) and especially in intensive agricultural areas where foraging habitats are scarce (Carvell *et al.* 2011). Our findings further highlight that the proportion of semi-natural habitats and green infrastructure elements within agricultural landscapes becomes even more important under the prism of climate change. Nevertheless, landscape configuration does not seem to have a large impact on bee diversity (at least at the scale of our study), although increasing landscape connectivity is included in the main goals of many climate change management plans. In any case, weak or no effect of landscape configuration on bees has been found in several studies testing different scales (e.g. Kennedy *et al.* 2013; Steckel *et al.* 2014).

SYNTHESIS AND APPLICATIONS

According to our findings, some regulations of the EU Common Agricultural Policy (CAP) and the EU strategy for Green Infrastructure could be beneficial for the conservation of bees. The article 46 of the EU Regulation 1307/2013 (EC 2013) focuses on the greening of agricultural areas establishing a threshold of arable land that should be designated as Ecological Focus Areas (EFAs). In particular, the EFAs should cover 5% by 2015 and 7% later. The EFAs include what was classified as semi-natural habitat in the present study (hedgerows, field margins, fallows, etc.). Consequently, the proposed measure in combination with semi-natural areas in the landscape matrix (e.g. grasslands, shrublands) could contribute to limiting the dependence of bee diversity on climatic conditions and function as a protective shield against future temperature increase. Still, the amount proposed by EU regulations is far too small and is recommended to increase to about 17%. Note, however, that our study measures differences in bee diversity among sites with different landscape structure, which we use to infer the effects of changes in the habitat at a given site through time. This approach, although reasonable and commonly used, carries assumptions that might be important from a

management perspective, for example there could be a substantial time-lag (Jackson & Sax 2010) before species richness increases to the level predicted by the model.

Our results are promising regarding the potential measures that can be taken to mitigate the detrimental effects of climate change. Considering that in the context of our study, the highest percentage of semi-natural areas was around 17%, it becomes apparent that a reasonable increase in the amount of semi-natural areas within agricultural areas could yield important results. Hedgerows, field strips and other human-made constructions of green infrastructure are also regarded as semi-natural habitats, making it more realistic to reach the aim of creation and maintenance of these structures. Increasing and maintaining this amount of semi-natural habitat can have a two-fold function: namely, such a change can buffer the effects of both intra-annual weather variability and climate warming. Therefore, it could at the same time secure the short-term income of farmers as well as the long-term food security for humans.

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Conflict of interest

The authors have no conflict of interests to declare.

Data accessibility

All data have been uploaded as online supporting information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Phenology curve displaying the expected species richness per trap with raw data overlaid.

Fig. S2. Phenology curve displaying the expected abundance per trap along the total monitoring period.

Fig. S3. Residuals of the GAMM for species richness plotted per site.

Fig. S4. Residuals of the GAMM for total abundance plotted per site.

Fig. S5. Effect of temperature on bee species richness for each site with raw data overlaid.

Fig. S6. Interactive effect of temperature and landscape composition on total abundance.

Appendix S1. List of EUNIS habitat types that were considered semi-natural in our analyses.

Table S1. Monitoring, landscape and weather data used for the analysis.

Supplementary Material

Appendix S1: List of EUNIS habitat types that were considered semi-natural in our analyses

EUNIS code and description

C2G Grassy margins of temporary and running waters
D50 Sedge and reedbeds, normally without freestanding water
E10 Dry grasslands
E20 Mesic grasslands
E30 Seasonally wet and wet grasslands
E50 Woodland fringes and clearings and tall forb habitats
F30 Temperate and mediterraneo-montane scrub habitats
F40 Temperate shrub heathland
F90 Riverine and fen scrubs
FAB Broadleaved deciduous hedgerows
G1D Fruit and nut tree orchards
G57 Coppice and early-stage plantations
GLB Lines of broadleaved deciduous trees
GLC Lines of coniferous trees
H30 Inland cliffs, rock pavements and outcrops
I1F Long term fallow arable land
I1G Grassy field margin
J30 Extractive industrial sites
J4V Grassy road verges
J4W Transport network for wind turbines

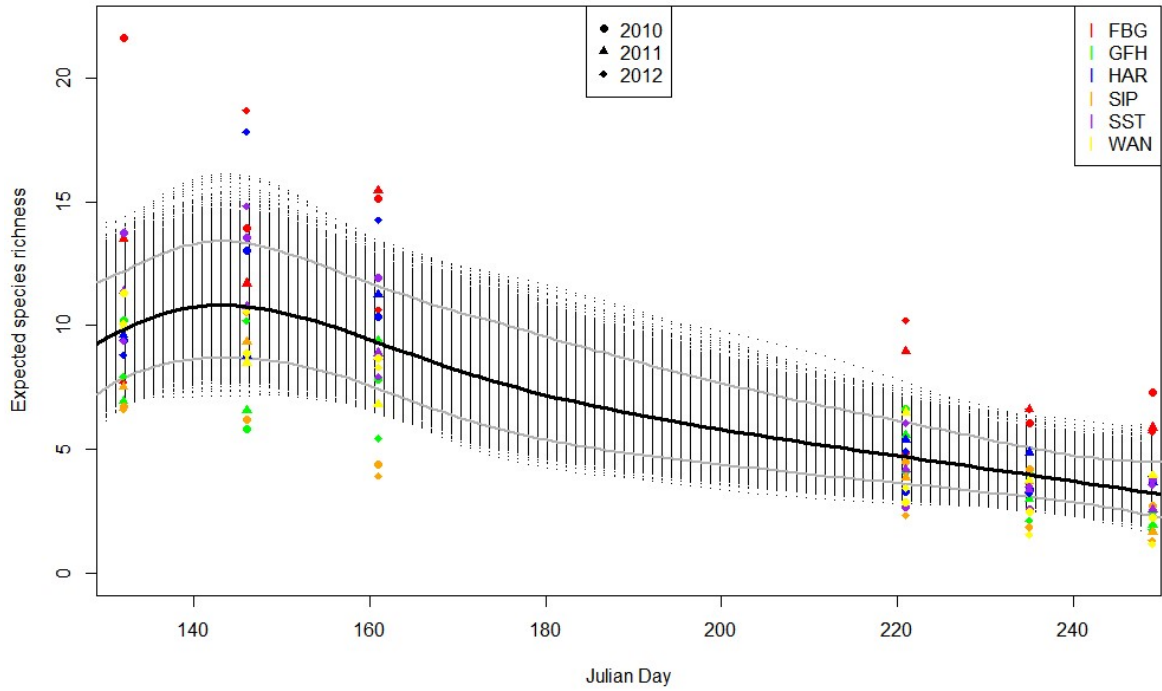


Fig. S1: Phenology curve displaying the expected species richness per trap with raw data overlaid.

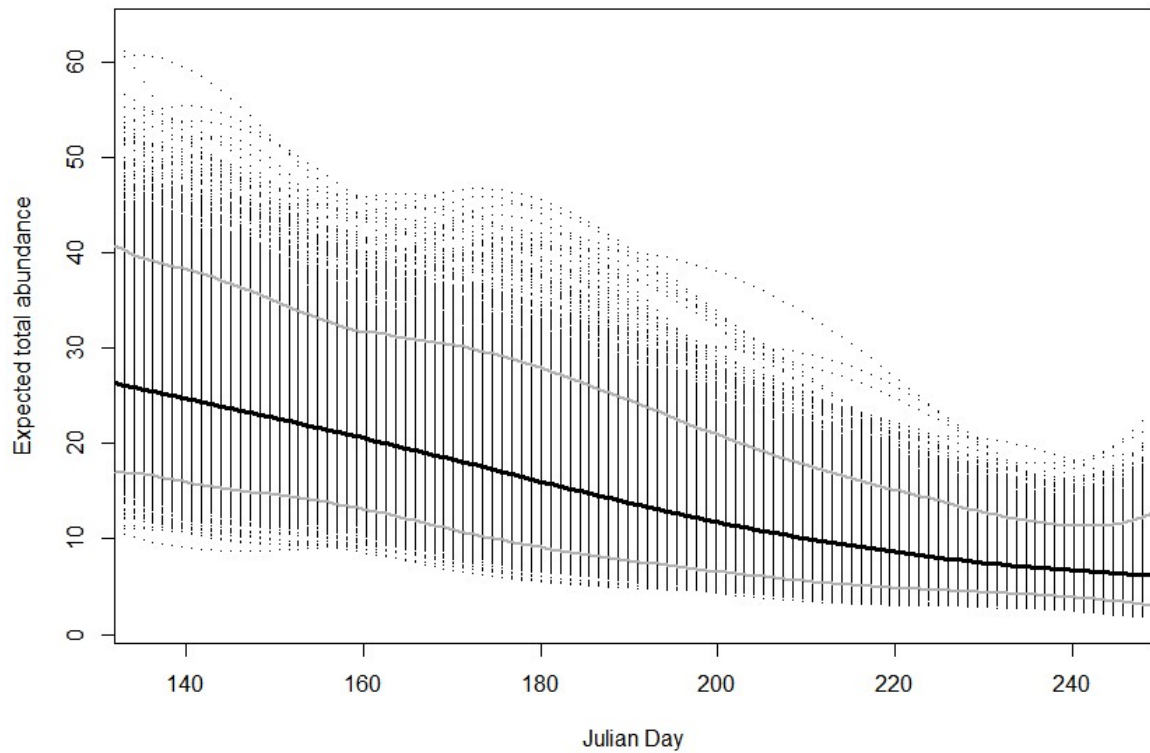


Fig. S2: Phenology curve displaying the expected abundance per trap along the total monitoring period.

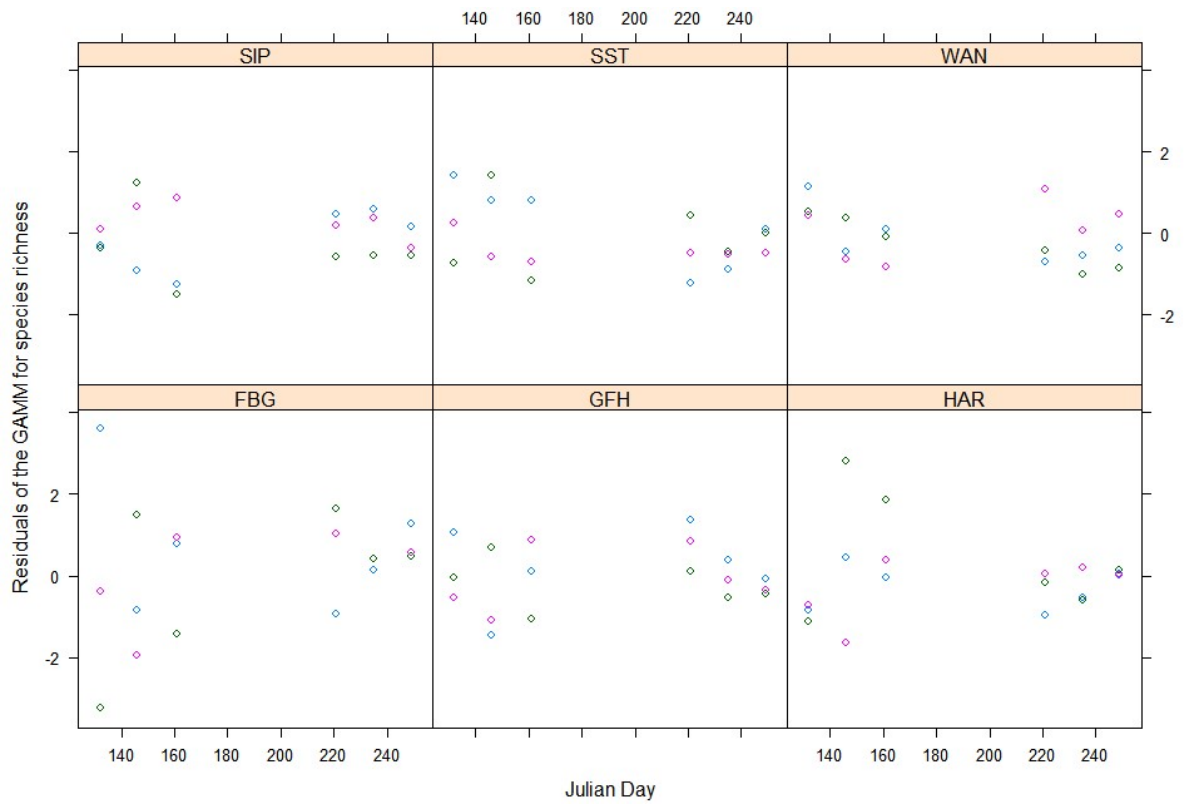


Fig. S3: Residuals of the GAMM for species richness plotted per site. The colours represent different years.

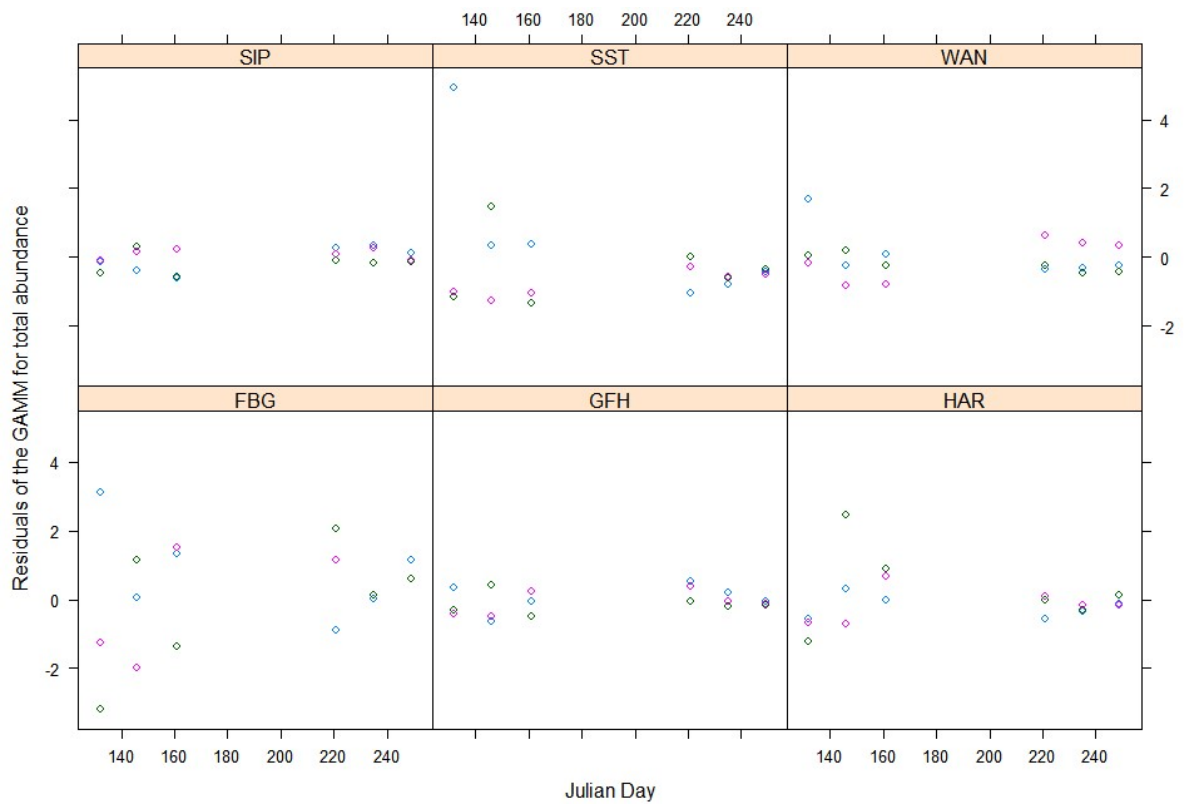


Fig. S4: Residuals of the GAMM for total abundance plotted per site. The colours represent different years.

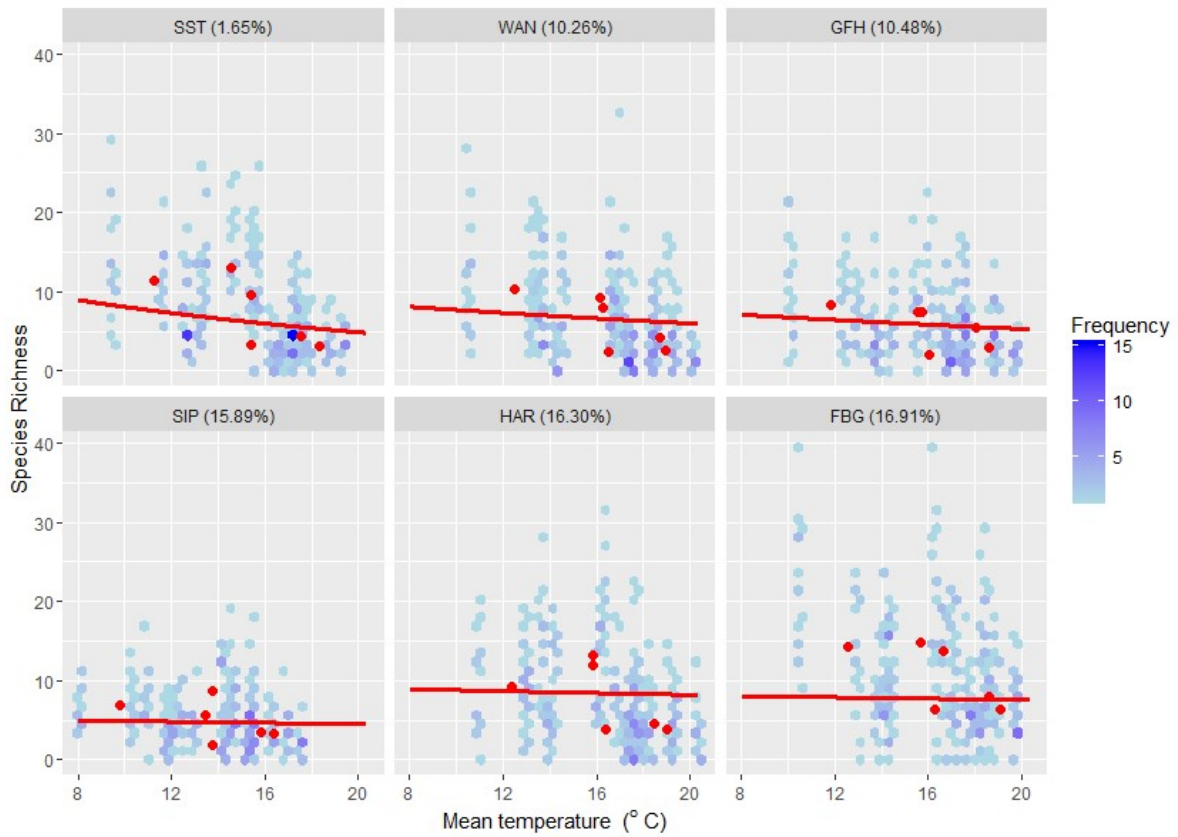


Fig. S5: Effect of temperature on bee species richness for each site with raw data overlaid. The six panels display the relationship between species richness and temperature for each one of our study sites, which are ordered in ascending percentage of semi-natural habitats. The exact percentage cover of semi-natural areas is displayed on the panel labels. The raw data of species richness per trap are overlaid. We use different shades of blue to present the densities of overlapping points, with darker colour indicating more points overlaid. To remove the variation already explained by our random structure, we aggregated the data per period across years and traps, resulting in six red-coloured points per site. The regression lines derived from our model for each site are also presented in red.

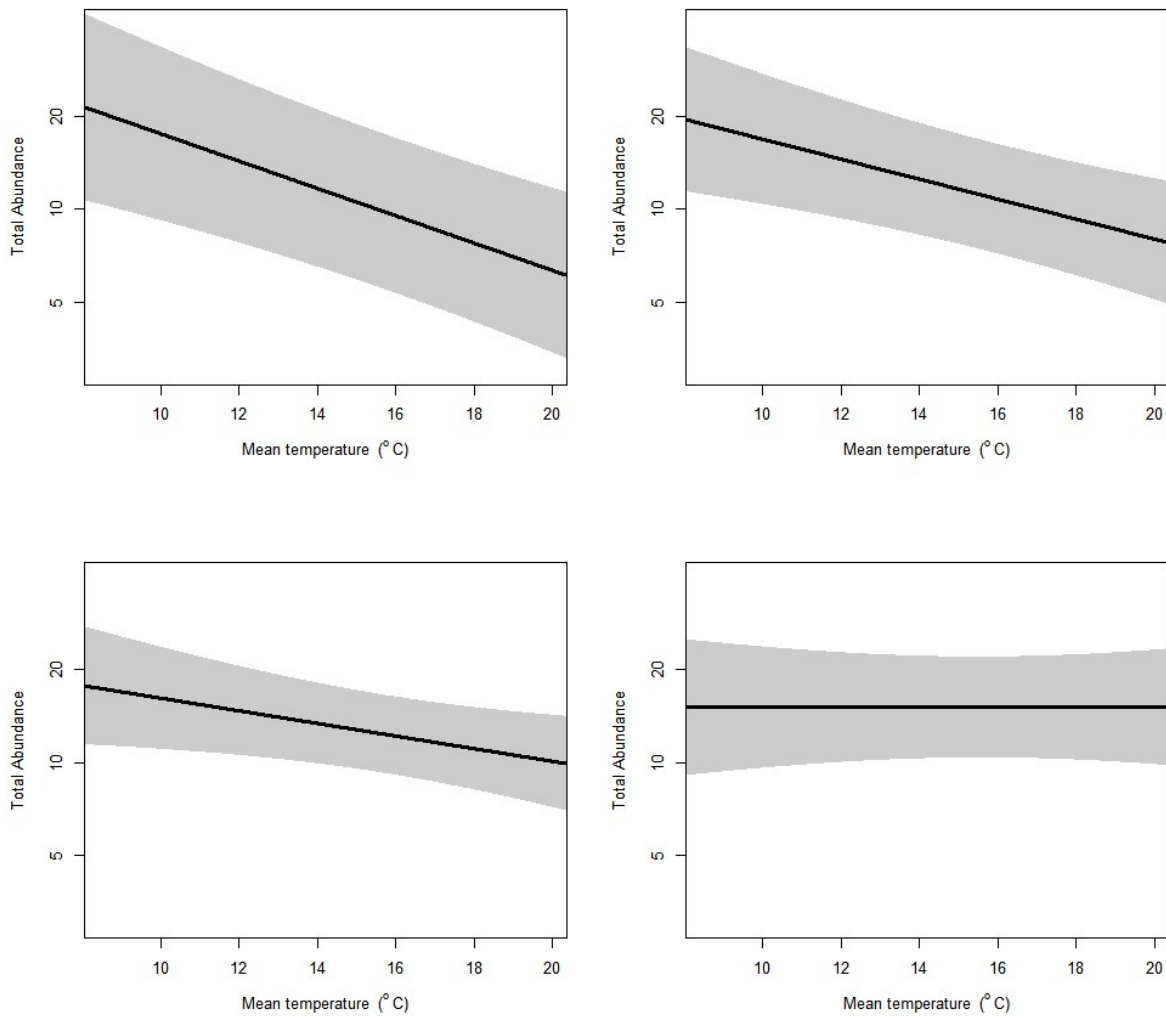


Fig. S6: Interactive effect of temperature and landscape composition on total abundance. The effect of temperature increase on species richness is displayed for four different levels of percentage of semi-natural areas: (a) 2%; (b) 6%; (c) 10%; (d) 17%). The cover range in the plot starts from the minimum cover of semi-natural areas in our study sites (i.e., 2%) and reaches the maximum coverage observed (i.e. 17%). We, additionally, used 10% (as a representative value for two of our sites) and 6% (as the mean value between 2 and 10% to cover the whole range). The y-axis is displayed on the logit scale. Grey bands indicate 95% confidence intervals.

Table S1 can be found online following the link below:

<http://onlinelibrary.wiley.com/store/10.1111/1365-2664.12763/asset/supinfo/jpe12763-sup-0008-TableS1.txt?v=1&s=62bf1eaecd9d66adaed174ae3cbf2af88479e3a3>


CHAPTER 3

Landscape heterogeneity enhances stability of
wild bee abundance under highly varying
temperature, but not under highly varying
precipitation

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Landscape heterogeneity enhances stability of wild bee abundance under highly varying temperature, but not under highly varying precipitation

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Abstract

Context The abundance of important providers of ecosystem services such as wild bees likely increases with landscape heterogeneity, but may also fluctuate across the flowering season following varying weather conditions.

Objectives In the present study, we investigated the combined effect of landscape heterogeneity and intra-annual variability in temperature and precipitation on the spatial and temporal stability of wild bee abundance.

Methods We used bee monitoring data from six 4 km × 4 km sites in central Germany and 16 local

communities per site. The data were collected six times per year from 2010 to 2013. Following a multimodel inference approach, we identified the importance of landscape heterogeneity, weather variability and their interaction to the stability of wild bee abundance.

Results We found that the stability of wild bee abundance increased with landscape heterogeneity, but decreased with increasing intra-annual variability in both temperature and precipitation. However, our key finding was a buffering mechanism enabling high abundance stability in heterogeneous landscapes even under highly variable temperature conditions. Interestingly, the same mechanism did not apply for high variability in precipitation.

Conclusions Our findings suggest that increasing landscape heterogeneity is beneficial for protecting wild bees against the projected increase in temperature variability until the end of the twenty first century, although we cannot make inferences for extreme events such as heatwaves. Nevertheless, our results equally highlight that landscape heterogeneity should not be treated as a one-size-fits-all solution and the need remains for developing alternative strategies to mitigate the effect of increasing variability in precipitation.

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Keywords Climate change · Ecosystem service ·
Landscape heterogeneity · Landscape management ·
Mitigation · Spatiotemporal stability · Weather
variability · Wild bee abundance

Introduction

Animal pollinators, mainly bees, contribute to the agricultural production of about 70% of leading crop species worldwide through the provision of the ecosystem service of pollination (Klein et al. 2007). The total economic value of insect pollination was found to exceed €150 billion (Gallai et al. 2009), while Kleijn et al. (2015), using data from 53 studies, estimated the service provided by wild bees to be worth a mean of \$3251 per hectare of agricultural land, a value exceeding the respective service provided by managed honey bees. Additionally, wild bees have been shown to pollinate crops more effectively than honey bees (Garibaldi et al. 2013; Mallinger et al. 2015), while the fluctuation in the abundance of common species, and not species richness, is the main factor determining successful pollination (Winfree et al. 2015).

Within this context, maintaining stability of wild bee abundance in time and space is crucial to sustain the continuous provision of the desired service. Two of the factors that may alter the stability of wild bee abundance are landscape heterogeneity and weather conditions. Landscape heterogeneity has been found to positively affect species richness and total abundance of pollinators (Rundlöf et al. 2008; Aguirre-Gutiérrez et al. 2015; Winfree et al. 2015). Additionally, it has been shown that landscape heterogeneity contributes to maintaining population stability of other insects like butterflies (Oliver et al. 2010) and crickets (Kindvall 1996). At the same time, bees respond to changes in weather conditions and several studies report alarming messages regarding the response of insect pollinators to climate change (e.g. Biesmeijer et al. 2006; Bartomeus et al. 2013a; Kerr et al. 2015). Long-term changes as well as short-term fluctuations in temperature and precipitation can affect bees by impeding foraging (Blüthgen and Klein 2011) or by altering the provided floral rewards in time and space, resulting in reduced abundance of wild bees (Jha et al. 2013).

Reduced or variable abundance of wild bees could jeopardise the provisioning of the pollination service across the flowering period of insect-pollinated crops, resulting in low or irregular pollen deposition, which could consequently lead to reduced or unstable crop yield (Klein 2009; Garibaldi et al. 2011a). Spatial and temporal variability in pollination could translate into

unsuccessful fertilisation at particular locations and periods, respectively (Garibaldi et al. 2011b). Considering the predicted reduction in the production of leading crops (Lobell et al. 2011) and the increasing preference for pollinator-dependent crops (Aizen et al. 2008), disruptions in pollination could further compromise the quality and quantity of agricultural production posing a threat to food security (Jha et al. 2013). Thus, the importance of strategies to safeguard the stability of abundant pollinator communities under weather variability becomes critical.

Pollinators and animal-mediated pollination are currently under pressure of several global change drivers, with climate change and landscape alteration among the most important ones (Gonzalez-Varo et al. 2013). These drivers could synergistically affect pollination. For example, the impact of climate change (including warming, changes in precipitation patterns) is expected to be higher in homogeneous landscapes and lower in heterogeneous ones (Oliver and Morecroft 2014). Nevertheless, only few studies have been carried out on insects (e.g. Piessens et al. 2009; Oliver et al. 2013, 2015) and, consecutively, little is still known about interactive effects of different drivers on wild bees.

In the present study, we investigated whether landscape heterogeneity and intra-annual weather variability interactively affect the stability of wild bee abundance. We expected that highly varying weather conditions would detrimentally affect stability of wild bee abundance, but landscape heterogeneity would counterbalance this effect, supporting stable wild bee abundance across the flowering period. We assessed two aspects of stability (temporal, spatial) and, subsequently, combined them into one index. First, we assumed overall spatial stability to be beneficial (unrelated to temporal aspects). Less variation in bee abundance across space should lead to a constant level of pollination while high variation may lead to spatially varying pollination success. Second, we assume temporal stability to be beneficial (unrelated to spatial aspects), given that highly variable pollen deposition leads to reduced yield (Klein 2009; Garibaldi et al. 2011a). Third, stability in terms of both the temporal and the spatial aspect would be the most beneficial situation. For our analysis, we used data from a monitoring scheme in central Germany in order to assess how the stability of abundance is affected by different levels of intra-annual weather variability in

different landscapes. Six agriculturally dominated sites and sixteen locations within each one of them were sampled six times per year from 2010 to 2013. Our analysis focused on the potential interactive effect between landscape heterogeneity and variability in temperature and precipitation on the combination of spatial and temporal abundance stability. Taking into account the projected future increase in weather variability and in frequency of extreme weather events (Seneviratne et al. 2012), we assessed the potential to maintain stable wild bee communities and, by extension, we discussed possible consequences on agricultural production.

Materials and methods

Bee monitoring data collection

Our six study sites are located in the federal state of Saxony-Anhalt in Germany and they form part of the Terrestrial Environmental Observatories network (TERENO www.tereno.net, Zacharias et al. 2011). The TERENO network is linked with the German and European Long-Term Ecological Research Network (Müller et al. 2010) and its main aim is the long-term integrated monitoring of impacts of global changes at the regional scale (Zacharias et al. 2011).

The land use of the wider region is well represented in the six selected sites, which differ in terms of landscape structure, altitude and climatic conditions (Table 1). Each site measures 4 km × 4 km and is divided into 16 squares of 1 km². Within each square, a yellow pan-trap was arbitrarily placed at transitional areas between semi-natural habitat and agricultural land. The data spanned 4 years (2010–2013; Frenzel et al. 2016a, b, c, d) with the monitoring season extending from May to September being divided into two periods: early (May–June) and late (August–September). The sampling took place six times per year, i.e. three times in the early and three times in the late period. Between the two periods, there was a summer break of 6 weeks. On each sampling date, the traps were emptied after being active for 2 weeks. The trapped bees were collected, counted and identified to species level. Bee abundance was calculated for each trap at each sampling date as the number of wild bee individuals captured. Honey bees were not taken into account in the analyses.

In total, more than 41,000 individuals of wild bees were collected across all sites and years of monitoring, with abundance varying among traps, sites, samplings and years.

Stability calculation

In ecological studies, stability has been defined as the opposite of variability (Lehman and Tilman 2000; Garibaldi et al. 2011b). In this context, a commonly used measure of stability is the inverse of the coefficient of variation CV^{-1} (e.g. Tilman et al. 2006; Ebeling et al. 2008; Isbell et al. 2009; Haddad et al. 2011), calculated as the mean μ divided by the standard deviation σ . The specified metric has several advantages (see Lehman and Tilman 2000), including that its value increases with increasing stability, while the coefficient of variation ($CV = \sigma/\mu$) approaches zero as stability increases (Isbell et al. 2009).

In the present study, we regarded temporal stability as low within year variability and spatial stability as low within site variability. Our data are organized in two levels in time (years, samplings) and two levels in space (sites, traps). Our aim was to calculate the within site spatial stability for each year and the within year temporal stability for each site and, then, to combine them in order to assess the overall stability per year and site. In order to assess spatial stability, we ignored the sampling date, i.e. we obtained one aggregated abundance value per trap and year by adding up the abundance recorded in that trap during the six samplings of this year. On this basis, we calculated the CV^{-1} per site and year. As a result, our spatial stability measure does not explicitly measure synchrony across space. Higher spatial stability means that all traps of a particular site displayed high abundances per year ignoring any temporal variation. The temporal aspect was captured by a temporal stability measure. Therefore, we ignored the trap, i.e. we obtained one aggregated abundance value per sampling date and site by adding up the abundance recorded in all the traps per site during this specific sampling date. Using these aggregated values, we then calculated CV^{-1} . In a final step, we calculated a combined stability index by multiplying the indices of spatial and temporal stability. By combining the spatial and the temporal aspects of stability, we were able to analyse the impact and interaction of habitat heterogeneity and variability in weather conditions on

Table 1 Mean values (± 1 SD) of environmental variables and mean wild bee abundance per year for the six study sites in Central Germany

| Site | Elevation | Mean annual temperature | Mean annual precipitation | Habitat heterogeneity | Wild bee abundance |
|--------------|------------------|-------------------------|---------------------------|-----------------------|--------------------|
| Friedeburg | 122 (± 31) | 9.66 (± 0.69) | 592 (± 128) | 0.35 | 2730 (± 418) |
| Greifenhagen | 270 (± 27) | 9.27 (± 0.89) | 606 (± 118) | 0.24 | 1014 (± 282) |
| Harsleben | 143 (± 14) | 9.56 (± 0.74) | 581 (± 176) | 0.34 | 1652 (± 296) |
| Siptenfelde | 423 (± 31) | 7.43 (± 0.76) | 646 (± 117) | 0.67 | 1254 (± 948) |
| Schafstaedt | 177 (± 11) | 8.83 (± 0.82) | 580 (± 101) | 0.00 | 2318 (± 708) |
| Wanzleben | 113 (± 10) | 9.68 (± 0.69) | 591 (± 130) | 0.45 | 1322 (± 133) |

overall stability of wild bee abundance. Our combined index of stability in space and time does not explicitly measure synchrony, but asynchrony will lead to higher values of the index (for a hypothetical example see Appendix S1).

Landscape data

We used orthorectified aerial photos of the six study sites at a resolution of 20 cm. These photos were converted into digitized habitat maps. The habitat classification followed the EUNIS system up to level 3. More details are provided by Frenzel et al. (2015).

As a first step, the area of each EUNIS habitat type was measured in circles of 200 m radius around each trap. Then, based on the habitat types' area, we calculated the pairwise dissimilarity among all trap pairs within the same site using the Morisita–Horn dissimilarity index (Horn 1966). Finally, in order to assess habitat heterogeneity at site level, we calculated the mean of the obtained dissimilarity matrix of each site. Higher values of the calculated habitat heterogeneity entail larger variety and higher amount of habitat types within a site, while lower values represent homogeneous agricultural landscapes.

Weather data

Data on mean daily air temperature and on total daily precipitation were acquired by weather stations of the German Meteorological Service in the vicinity of each one of the six sites. The official weather stations are on average 11.5 km away from the centre of the 4 km \times 4 km study sites (range between 6 and 25 km). These data were available throughout the years 2010–2013. Mean temperature and total

precipitation were calculated for each two-week sampling interval. Then, the coefficient of variation of temperature (CV_{temp}) and the coefficient of variation of precipitation (CV_{prec}) were calculated for each site and year. These variables represent the within year weather variation.

Statistical analyses

We investigated the combined effect of variation in weather conditions and habitat heterogeneity on the stability of wild bee abundance. To this end, we built two generalized linear mixed effects models (GLMM) with a Gaussian error distribution and a log link function. The use of simple linear mixed effect models was ruled out due to the fact that a logarithmic link function was necessary to properly analyse our continuous and non-negative response variable. The response variable in both models was the stability of wild bee abundance, while random intercepts were allowed for site and year to avoid potential problems of pseudoreplication. The fixed component of the first model included habitat heterogeneity, CV_{temp} and their interaction, while the fixed effects of the second model were habitat heterogeneity, CV_{prec} and their interaction. The observed variability in precipitation was much higher in comparison to the variability in temperature; CV_{temp} ranged from 0.12 to 0.21, while CV_{prec} from 0.47 to 0.93 (plus an excluded outlier of 1.24). However, all explanatory variables were standardized and centred (mean = 0, SD = 1) to obtain coefficient estimates comparable in terms of importance (Quinn and Keough 2002).

Prior to inclusion in the model, the explanatory variables were tested for collinearity by calculating the

Pearson's correlation coefficient for each pair of variables. No high correlation was detected in any case (habitat heterogeneity– CV_{temp} : $r = -0.05$; habitat heterogeneity– CV_{prec} : $r = 0.07$; CV_{temp} – CV_{prec} : $r = -0.12$; all $p > 0.05$) with the obtained Pearson's r values being much lower than the recommended thresholds of 0.4 or 0.7 (Dormann et al. 2013).

Despite the fact that CV_{temp} and CV_{prec} were not correlated, we opted for two separate general models instead of including both variables in one, because of an outlier of CV_{prec} . In one site (Siptenfelde) an exceptionally high value of CV_{prec} was observed in 2012 (see Appendix S2). Applying Grubbs' test (Grubbs 1950), this point was identified as an outlier ($p = 0.02$) and its exclusion altered the observed relationship. Therefore, this data point was removed from the data set that was used for the development of the model with CV_{prec} . The choice of using two separate models allowed us to maintain this data point in the analysis of CV_{temp} . As a consequence, the data sets used for the models with CV_{temp} and CV_{prec} included 24 and 23 data points, respectively.

Following an extension of Johnson (2014) to a method suggested by Nakagawa et al. (2013), we calculated R^2 values in order to assess the amount of data variance explained by each global model. The marginal R^2 ($R^2_{GLMM(m)}$) represents the variance explained by the fixed effects only, while the conditional R^2 ($R^2_{GLMM(c)}$) describes the amount of variance explained by both the fixed and random effects.

Subsequently, a multimodel inference approach (Burnham and Anderson 2002) was followed separately for the two global models. The random intercepts for site and year were maintained in all the compared models in order to reflect our experimental design and avoid pseudoreplication. Each one of them was compared with simpler nested models based on second-order Akaike Information Criterion (AICc; corrected for small sample size). In both cases the model with the lowest AICc value was considered the best model and all the models were compared in terms of their difference in AICc value ($\delta AICc$) from the best model.

The residuals of our models were checked for spatial autocorrelation by computing Moran's I correlograms (Moran 1950), but none was detected. Additionally, all statistical assumptions for GLMMs were met. All analyses were performed in the

statistical software R v3.2.2 (R Core Team 2015). The packages lme4 version 1.1-9 (Bates et al. 2015) and MuMIn version 1.15.1 (Barton 2015) were used for the GLMM and the multimodel inference respectively.

Results

Our results involve two separate sets of candidate models, each one derived from one of the two previously described global models. Thus, the first set includes the global model with the CV_{temp} and four models that are nested submodels of this global model (Table 2), while the second set contains the model with the CV_{prec} and its four nested submodels (Table 3).

Regarding the temperature model set, the full model including the interaction between CV_{temp} and habitat heterogeneity was better supported by our data compared to the simpler models based on their AICc values and model weights (Table 2). This model explained 34.9% of the variance ($R^2_{GLMM(c)}$), of which 18.5% was explained by the fixed component ($R^2_{GLMM(m)}$). Extracting the variance components of the random effects, we found that site and year explained 4.7 and 15.4% of the total variation, respectively. According to this model, increasing CV_{temp} decreased the stability of abundance while increasing habitat heterogeneity favoured it. The positive interaction between the two variables indicated that the stability of abundance was particularly negatively affected by varying temperature conditions in homogeneous landscapes, while this effect became less pronounced as landscape heterogeneity increased and finally disappeared in the most heterogeneous landscapes (Fig. 1a).

Regarding the second (i.e., precipitation) model set, the full model with the interaction between CV_{prec} and habitat heterogeneity was markedly better supported by our data compared to the simpler models (Table 3). This model explained 45.3% of the variance ($R^2_{GLMM(c)}$), of which 25.3% was explained by the fixed component of the model ($R^2_{GLMM(m)}$). The extraction of the variance components showed that site explains 5.7%, while year 21.1% of the total variation. According to this model, the stability of

Table 2 Model set containing CV_{temp} : (a) Statistics for model comparison, (b) model estimates and standard errors for the variables in the each model explaining bee abundance in six locations in Central Germany

| (a) | | | | |
|--|---------------------|----------------------|-----------------------|---|
| Model | AICc | $\delta AICc$ | Akaike weight | Cumulative weight |
| $CV_{temp} \times$ habitat heterogeneity | 81.83 | 0.00 | 0.823 | 0.823 |
| Habitat heterogeneity | 85.73 | 3.90 | 0.117 | 0.940 |
| Null model (intercept only) | 88.27 | 6.44 | 0.033 | 0.973 |
| $CV_{temp} +$ habitat heterogeneity | 89.22 | 7.39 | 0.020 | 0.993 |
| CV_{temp} | 91.45 | 9.62 | 0.007 | 1.000 |
| (b) | | | | |
| Model | Intercept | CV_{temp} | Habitat heterogeneity | Interaction between CV_{temp} and habitat heterogeneity |
| $CV_{temp} \times$ habitat heterogeneity | 0.83 (± 0.24) | -0.19 (± 0.12) | 0.2 (± 0.1) | 0.16 (± 0.04) |
| Habitat heterogeneity | 0.89 (± 0.21) | - | 0.28 (± 0.08) | - |
| Null model (intercept only) | 0.88 (± 0.24) | - | - | - |
| $CV_{temp} +$ habitat heterogeneity | 0.89 (± 0.21) | 0.04 (± 0.14) | 0.28 (± 0.08) | - |
| CV_{temp} | 0.83 (± 0.24) | -0.02 (± 0.12) | - | - |

AICc Akaike Information Criterion corrected for small sample size, $\delta AICc$ difference to best model

Table 3 Model set containing CV_{prec} : (a) Statistics for model comparison, (b) model estimates and standard errors for the variables in the each model explaining bee abundance in six locations in Central Germany

| (a) | | | | |
|--|---------------------|----------------------|-----------------------|---|
| Model | AICc | $\delta AICc$ | Akaike weight | Cumulative weight |
| $CV_{prec} \times$ habitat heterogeneity | 66.14 | 0.00 | 0.999 | 0.999 |
| $CV_{prec} +$ habitat heterogeneity | 80.57 | 14.43 | 0.001 | 0.999 |
| CV_{prec} | 81.33 | 15.19 | 0.001 | 1.000 |
| Habitat heterogeneity | 84.03 | 17.89 | 0.000 | 1.000 |
| Null model (intercept only) | 86.49 | 20.35 | 0.000 | 1.000 |
| (b) | | | | |
| Model | Intercept | CV_{prec} | Habitat heterogeneity | Interaction between CV_{prec} and habitat heterogeneity |
| $CV_{prec} \times$ habitat heterogeneity | 0.73 (± 0.26) | -0.29 (± 0.08) | 0.14 (± 0.09) | -0.29 (± 0.05) |
| $CV_{prec} +$ habitat heterogeneity | 0.84 (± 0.22) | -0.22 (± 0.08) | 0.24 (± 0.09) | - |
| CV_{prec} | 0.83 (± 0.26) | -0.25 (± 0.08) | - | - |
| Habitat heterogeneity | 0.89 (± 0.21) | - | 0.29 (± 0.09) | - |
| Null model (intercept only) | 0.89 (± 0.25) | - | - | - |

AICc Akaike Information Criterion corrected for small sample size, $\delta AICc$ difference to best model

abundance was also negatively affected by increasing CV_{prec} and positively affected by increasing habitat heterogeneity. However, in this case the interaction term between CV_{prec} and habitat heterogeneity was strongly negative. In heterogeneous landscapes, the

stability of abundance was affected by varying precipitation, whereby low variability in precipitation favoured the stability of abundance. However, as habitat heterogeneity decreased, the profit of stable precipitation conditions became lower and

finally, in homogeneous landscapes, abundance stability was consistently low irrespective of the CV_{prec} (Fig. 1b).

Please note that the difference in scale of the y-axis between the plots in Fig. 1a, b is caused by the fact that the plotted values are model predictions obtained by two different models which actually differ in the number of data points used for model parameterization (one outlier excluded for the precipitation model). Further, the high upper range of 20 for stability of bee abundance on the y-axis of plots in Fig. 1b is needed to depict the larger values of uncertainty (95% CI) in cases of low variation in precipitation and high values of heterogeneity at the logarithmic axis scale (upper left panel in Fig. 1).

Discussion

In the present study, we have demonstrated that landscape heterogeneity increased the stability of wild bee abundance. Additionally, increasing variability in weather conditions led to decreased stability of wild bee abundance. However, we also found strong evidence for interacting effects, suggesting that the impact of weather variability on stability of abundance depended on the landscape structure. This is an indication of synergistic effects between two major effects of global change, namely land use change and increasing weather variability. In this context, our expectation that landscape heterogeneity buffers against increasing weather variability was met for temperature. The impact of increased temperature variability on abundance stability was high in homogeneous landscapes, while it was buffered in heterogeneous ones. Nevertheless, our expectation was not met for precipitation. The impact of changes in precipitation variability on abundance stability was higher in heterogeneous landscapes, while there was no effect in homogeneous landscapes, where bee abundance stability was always low and seemingly limited by other factors than precipitation variability.

According to our findings, the stability of wild bee abundance was negatively affected by high variability in both temperature and precipitation conditions. Temperature and precipitation affect both wild bees and their host plants. More specifically, temperature is a key factor determining the activity of bees (Willmer and Stone 2004; Kühnel and Blüthgen 2015). At the

same time, temperature has an effect on pollination-related plant traits, such as the production of nectar and pollen (Scaven and Rafferty 2013). For instance, nectar secretion and nectar sugar content have been found to have a hump-shaped relationship with temperature (Petanidou and Smets 1996; Takkis et al. 2015). Thus, varying temperature conditions lead to alterations in nectar production, composition and concentration (Pacini et al. 2003), which in turn have a negative impact on pollinator activity (Kudo and Harder 2005). The altered nectar production may prove insufficient, especially for small pollinators, to counterbalance the increase in metabolic rates and energy demands caused by higher temperatures (Schweiger et al. 2010). Additionally, bee activity is affected by precipitation (Willmer and Stone 2004). Water stress can limit the performance of insects (Huberty and Denno 2004), while during light and heavy rainfall events, bees are affected to different extents depending on the species (Tuell and Isaacs 2010). Simultaneously, plant availability, plant growth and traits related to pollinator attraction are affected by water availability (Burkle and Runyon 2016). For example, nectar secretion in different plant species has been shown to be reduced under drought conditions (Petanidou and Smets 1996; Carroll et al. 2001; Halpern et al. 2010), while intermediate levels of soil moisture have been linked to maximal nectar production (Gillespie et al. 2015). Therefore, the high variability in temperature and precipitation alter the activity patterns of wild bees and the provided floral rewards by the plants, resulting into less stable wild bee abundance over time.

In addition, we found that landscape heterogeneity positively affected stability of wild bee abundance. Landscape heterogeneity is considered beneficial for wild bee abundance and richness (Rundlöf et al. 2008; Steckel et al. 2014). Moreover, heterogeneous landscapes have been found to promote the stability of insect populations (Kindvall 1996; Oliver et al. 2010). Here, we further demonstrated that habitat heterogeneity buffers the detrimental effect of temperature variability on the stability of wild bee abundance. A possible mechanism could be that habitat heterogeneity provides a variety of resources and microclimates that buffer weather variability and promote population stability (Oliver et al. 2010). Homogeneous landscapes provide more similar resources in space, limiting the choices of wild bees when the temperature

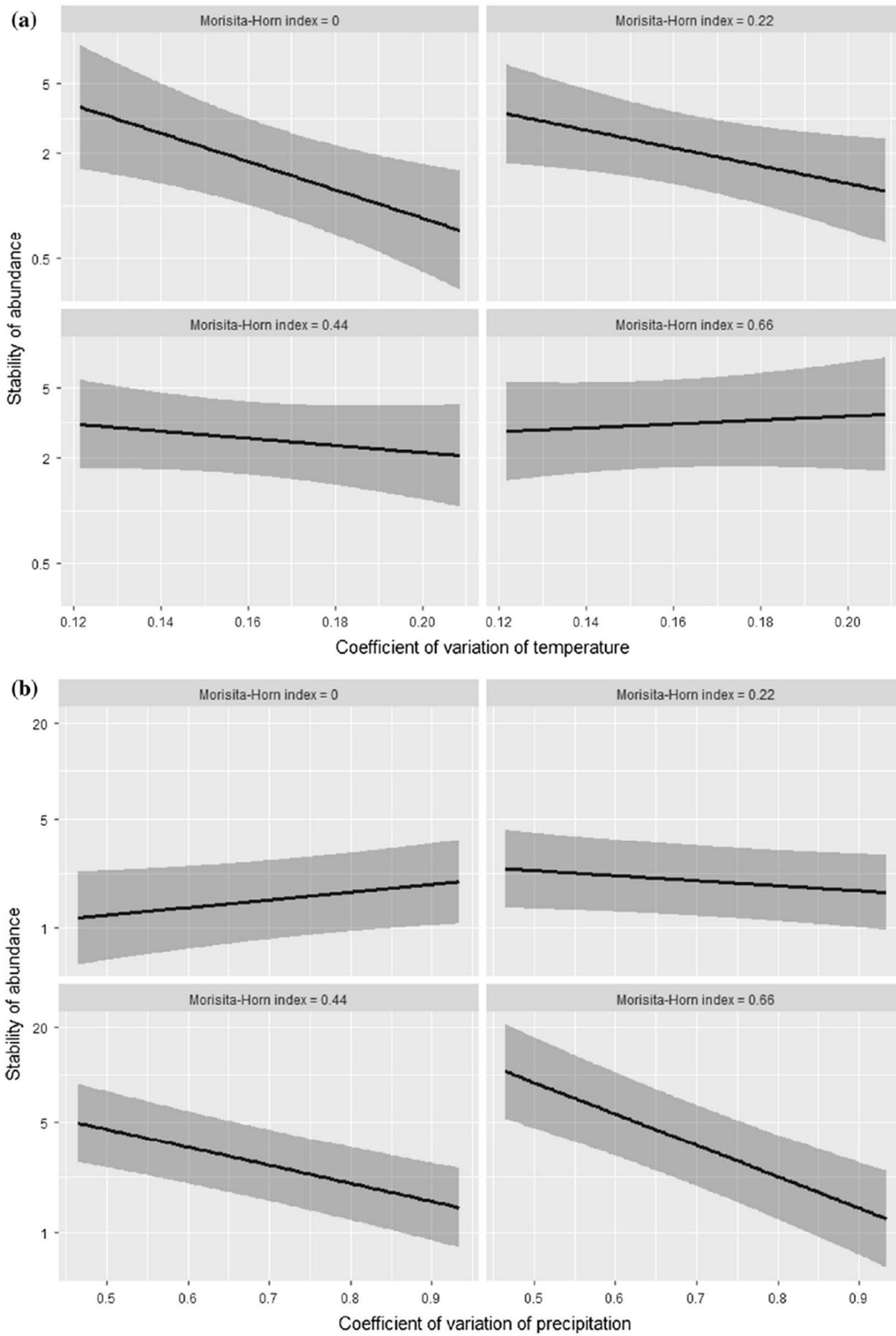


Fig. 1 Interactive effect of weather variability and landscape heterogeneity on the stability of wild bee abundance in Central Germany. The effect of **a** increasing temperature variability and of **b** increasing precipitation variability on stability of abundance (on log-scale) is displayed for four different levels of landscape heterogeneity (mean Morisita–Horn index as a proxy for landscape heterogeneity). Grey bands indicate 95% confidence intervals that represent the confidence in the estimate. Random variation is already accounted for by the random effects

conditions are unfavourable. On the contrary, habitat heterogeneity allows for the utilisation of different resources in space and time, enabling wild bees to forage according to their thermal requirements and increasing the chances of successful breeding. Furthermore, heterogeneous landscapes support functionally diverse plant (Rader et al. 2014) and insect (Gamez-Virues et al. 2015) communities, which might favour the stability of wild bee abundance according to the biodiversity insurance hypothesis (Yachi and Loreau 1999; Valone and Barber 2008). This hypothesis suggests that in changing environments high levels of biodiversity and corresponding high levels of variability in the responses of species to changes or high levels of functional redundancy safeguard ecosystem functioning, such as pollination and synchrony among plants and pollinators (Bartomeus et al. 2013b).

A similar buffering mechanism could be expected to apply to precipitation, as well. Resource heterogeneity of plants and nesting sites in heterogeneous landscapes could contribute to the mitigation of the detrimental effects of highly varying precipitation conditions on wild bee abundance. Nevertheless, this is not the case according to our findings. Presumably, the negative effects of extreme and prolonged dry conditions on both insects (Huberty and Denno 2004) and pollen and nectar plants (e.g. Halpern et al. 2010) might be so strong that landscape heterogeneity cannot act as an adequate buffer. It should also be taken into account that during extreme rainfalls (which would be another cause of increased variability in precipitation in addition to days with prolonged rain) most bees are unable to fly and are bound to stay in their nests (Willmer and Stone 2004). Thus, it is probable that even landscape heterogeneity cannot reverse the situation. At the same time, we demonstrate that the stability of wild bee abundance in homogeneous landscapes seems to be constantly low and unaffected

by the variation in precipitation. This finding suggests that in such landscapes the stability of abundance could possibly be limited by other factors such as high levels of population synchronicity (Powney et al. 2010) or highly temporally limited availability of nectar and pollen resources, e.g. as in landscapes dominated by oilseed rape fields (Westphal et al. 2009).

Our findings could have remarkable implications for agricultural production. The fast growing rate of human population requires reliable provision of agricultural goods (Tilman et al. 2011). Animal-pollinated crops are a vital source of micronutrients and pollination decline could further exacerbate malnutrition issues globally (Eilers et al. 2011; Chaplin-Kramer et al. 2014). Increasing pollinator dependence of crops has been linked with decreasing mean and stability of yield and yield growth, suggesting that pollen limitation might disrupt stable agricultural production (Garibaldi et al. 2011a). Spatial and temporal variation in pollination may have as a consequence failed fertilisation in particular locations and in different periods, respectively (Garibaldi et al. 2011b). Furthermore, the yielding fruit set of pollinator-dependent crops has been found to increase with increasing visitation rate of wild bees (Garibaldi et al. 2013), which is, in turn, strongly positively associated with wild bee abundance (Ricketts et al. 2004). In the present study, we showed that the stability of wild bee abundance in space and time depends on the variability of weather conditions. Taking into account the links established above, stable wild bee abundance can be related to stable visitation rate and, thus, to stable agricultural production of pollinator dependent crops. In light of this, we raise concern regarding the stability of crop production and its consequences for prices, security and diversity of food, since pollinator loss could lead to alterations in several aspects of food production, e.g. quantity, quality, availability, nutritional content (Jha et al. 2013).

Additionally, our findings are of great relevance to the imminent impact of climate change on pollinators. Despite the fact that climate change is expected to have an impact on weather means, variability and extremes (Rummukainen 2012), most of the studies that investigate potential impacts of climate change on biodiversity focus only on changes in mean conditions. Nevertheless, recent studies have shown that changes in climatic variability, although understudied,

could affect both plants (Reyer et al. 2013) and insects (Vasseur et al. 2014). In Central Europe the warm days have increased since 1950 and their frequency and intensity is predicted to further increase until the end of the twenty first century (Seneviratne et al. 2012). These changes could alter the observed patterns of temperature variability, posing dangers to wild bees, especially in homogeneous landscapes.

The positive aspects of our findings are the noteworthy management opportunities that arise. Given that agricultural landscapes can be manipulated (e.g. by creating new habitat patches) or conservation priority can be given to already heterogeneous landscapes (i.e. by focusing protection efforts on them), our findings provide a straightforward way to address the problems caused to pollinators by the imminent increase in temperature variability. In this context, it would be beneficial to promote the goal of increasing landscape heterogeneity of agricultural landscapes in policies such as the Common Agricultural Policy and the Green Infrastructure Strategy of the European Union and other national conservation strategies. However, please note that our data support the finding that heterogeneity can buffer effects of increasing variability in temperature only up to a certain extent. The reason for this limitation lies in the difference between the range of CV_{temp} and CV_{prec} . In the context of our study we observed high precipitation variability, but this was not the case for temperature variability that only ranged from low to moderate. Therefore, we cannot infer from our results whether landscape heterogeneity would also be beneficial under extremely varying temperature conditions and whether it could actually buffer effects of extreme events like heatwaves.

On the other hand, our study highlights a worrisome prospect about wild bees under changing precipitation patterns. Although there is more uncertainty in the projections of the precipitation models than in those of the temperature models (Flato et al. 2013), heavy precipitation and drought events are considered to have increased in parts of central Europe since 1950 and they are projected to further increase during the twenty first century (Seneviratne et al. 2012). Such alternations between extreme conditions could result in higher variability in precipitation along a year, which, as shown here, could be detrimental to the stability of wild bee abundance irrespective of the landscape structure. Increasing frequency of drought

events could be perilous for the resilience of pollinators in agricultural landscapes, potentially threatening the production of bee-pollinated crops. Thus, although heterogeneous landscapes still support stability of wild bee abundance under less variable precipitation conditions, landscape heterogeneity should not be considered a one-size-fits-all solution. The role of precipitation should not be neglected, especially since Straka et al. (2014) demonstrated that the life span of bees is more strongly affected by precipitation than by temperature. Thus, there is a need to develop alternative measures in order to moderate the consequences of increasing precipitation variability on wild bees and promote stable wild bee populations.

Here, we showed that landscape heterogeneity counterbalances the decrease in wild bee abundance stability caused by high temperature variability. Furthermore, heterogeneous landscapes, in contrast to homogeneous ones, enhance wild bee abundance stability in years with low precipitation variability. The abovementioned findings highlight that increasing and/or maintaining landscape heterogeneity is an appealing conservation measure that could benefit pollinator populations and possibly safeguard agricultural production especially under climate change. Nevertheless, we also demonstrated that although heterogeneous landscapes are more likely to maintain stable abundance of wild bees during years with low variability in precipitation compared to homogeneous ones, increasing landscape heterogeneity is not useful as a mitigation action against highly varying precipitation. Given the alarming reports about the imminent increase in precipitation variability and the effect of precipitation on pollinator survival and activity, the need to develop alternatives to the commonly suggested measure of increase in landscape heterogeneity becomes imperative.

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Supplementary Material

Appendix S1: Example of calculation of abundance stability. We use a simplified structure of four traps per site and four samplings per year to compare the calculation of stability between five sites.

| Site A | Trap A1 | Trap A2 | Trap A3 | Trap A4 | Total per sampling |
|----------------|---------|---------|---------|---------|--------------------|
| Sampling 1 | 2 | 2 | 5 | 2 | 11 |
| Sampling 2 | 1 | 1 | 4 | 1 | 7 |
| Sampling 3 | 1 | 1 | 4 | 1 | 7 |
| Sampling 4 | 1 | 1 | 4 | 1 | 7 |
| Total per trap | 5 | 5 | 17 | 5 | |

Calculation of spatial stability

The figures that are used for the calculation are in the column Total per sampling.

- Total abundance across traps = 32
- Mean abundance across traps = 8
- Standard deviation of abundance among traps = 2
- Spatial $CV^{-1} = 4$

Calculation of temporal stability

The figures that are used for the calculation are in the row Total per trap.

- Total abundance across samplings = 32
- Mean abundance across samplings = 8
- Standard deviation of abundance among samplings = 6
- Temporal $CV^{-1} = 1.33$

Overall stability

- Spatial $CV^{-1} * \text{Temporal } CV^{-1} = 5.32$

| Site B | Trap A1 | Trap A2 | Trap A3 | Trap A4 | Total per sampling |
|----------------|---------|---------|---------|---------|--------------------|
| Sampling 1 | 2 | 2 | 5 | 2 | 11 |
| Sampling 2 | 1 | 4 | 1 | 1 | 7 |
| Sampling 3 | 1 | 1 | 1 | 4 | 7 |
| Sampling 4 | 1 | 1 | 4 | 1 | 7 |
| Total per trap | 5 | 8 | 11 | 8 | |

Calculation of spatial stability

- Total abundance across traps = 32
- Mean abundance across traps = 8
- Standard deviation of abundance among traps = 2
- Spatial $CV^{-1} = 4$

Calculation of temporal stability

- Total abundance across samplings = 32
- Mean abundance across samplings = 8
- Standard deviation of abundance among samplings = 2.45
- Temporal $CV^{-1} = 3.27$

Overall stability

- Spatial $CV^{-1} * \text{Temporal } CV^{-1} = 13.08$

Site C

| | Trap A1 | Trap A2 | Trap A3 | Trap A4 | Total per sampling |
|----------------|---------|---------|---------|---------|--------------------|
| Sampling 1 | 22 | 22 | 25 | 22 | 51 |
| Sampling 2 | 21 | 24 | 21 | 21 | 47 |
| Sampling 3 | 21 | 21 | 21 | 24 | 47 |
| Sampling 4 | 21 | 21 | 24 | 21 | 47 |
| Total per trap | 45 | 48 | 51 | 48 | |

Calculation of spatial stability

- Total abundance across traps = 192
- Mean abundance across traps = 48
- Standard deviation of abundance among traps = 2
- Spatial $CV^{-1} = 24$

Calculation of temporal stability

- Total abundance across samplings = 192
- Mean abundance across samplings = 48
- Standard deviation of abundance among samplings = 2.45
- Temporal $CV^{-1} = 19.59$

Overall stability

- Spatial $CV^{-1} * \text{Temporal } CV^{-1} = 470.16$

Site D

| | Trap A1 | Trap A2 | Trap A3 | Trap A4 | Total per sampling |
|----------------|---------|---------|---------|---------|--------------------|
| Sampling 1 | 1 | 45 | 45 | 1 | 92 |
| Sampling 2 | 1 | 1 | 1 | 1 | 4 |
| Sampling 3 | 1 | 45 | 45 | 1 | 92 |
| Sampling 4 | 1 | 1 | 1 | 1 | 4 |
| Total per trap | 4 | 92 | 92 | 4 | |

Calculation of spatial stability

- Total abundance across traps = 192
- Mean abundance across traps = 48
- Standard deviation of abundance among traps = 50.81
- Spatial $CV^{-1} = 0.94$

Calculation of temporal stability

- Total abundance across samplings = 192
- Mean abundance across samplings = 48
- Standard deviation of abundance among samplings = 50.81
- Temporal $CV^{-1} = 0.94$

Overall stability

- Spatial $CV^{-1} * \text{Temporal } CV^{-1} = 0.88$

Site E

| | Trap A1 | Trap A2 | Trap A3 | Trap A4 | Total per sampling |
|----------------|---------|---------|---------|---------|--------------------|
| Sampling 1 | 22 | 23 | 24 | 23 | 92 |
| Sampling 2 | 1 | 1 | 1 | 1 | 4 |
| Sampling 3 | 23 | 23 | 23 | 23 | 92 |
| Sampling 4 | 1 | 1 | 1 | 1 | 4 |
| Total per trap | 47 | 48 | 49 | 48 | |

Calculation of spatial stability

- Total abundance across traps = 192
- Mean abundance across traps = 48
- Standard deviation of abundance among traps = 0.82
- Spatial $CV^{-1} = 58.54$

Calculation of temporal stability

- Total abundance across samplings = 192

- Mean abundance across samplings = 48
- Standard deviation of abundance among samplings = 50.81
- Temporal $CV^{-1} = 0.94$

Overall stability

- Spatial $CV^{-1} * \text{Temporal } CV^{-1} = 55.03$

Conclusions

The comparison of the five sites provides useful insight into the properties of the stability index we used, displaying the advantage of combining the spatial and temporal stability in one common index.

Site A (synchrony) and Site B (asynchrony) have the same total abundance and the same abundance for each sampling. This results into identical values for spatial stability. However, because of the different synchrony patterns, the temporal stability in Site B is higher, leading to a higher combined value of stability. Therefore, for a specified value of total abundance, our index favours asynchrony, taking lower values when synchrony increases.

Site B (constantly low abundances) and Site C (constantly high abundance) follow the same patterns of change and have the same standard deviation among traps and the same standard deviation among samplings. However, the higher abundances in Site C lead to much higher values of temporal, spatial and overall stability.

Sites C, D and E have the same total abundance, but the even distribution of abundance across all traps and samplings in site C, which likely safeguards the provision of pollination services over space and time, results in higher overall stability compared to sites D and E.

Sites D and E have equally low values of temporal stability, but the abundance is differently distributed among traps in the samplings of high abundance. Therefore, Site E with an even distribution of abundance among traps has a higher value of spatial and overall stability in comparison to Site D that is characterised by very high abundance in specific traps and samplings and very low abundance in all other cases. In practice, in a landscape like the one of Site D it is unlikely that the increased abundances in few locations or times can

compensate the potential losses in the low-abundances fields - especially if they belong to different farmers.

Appendix S2

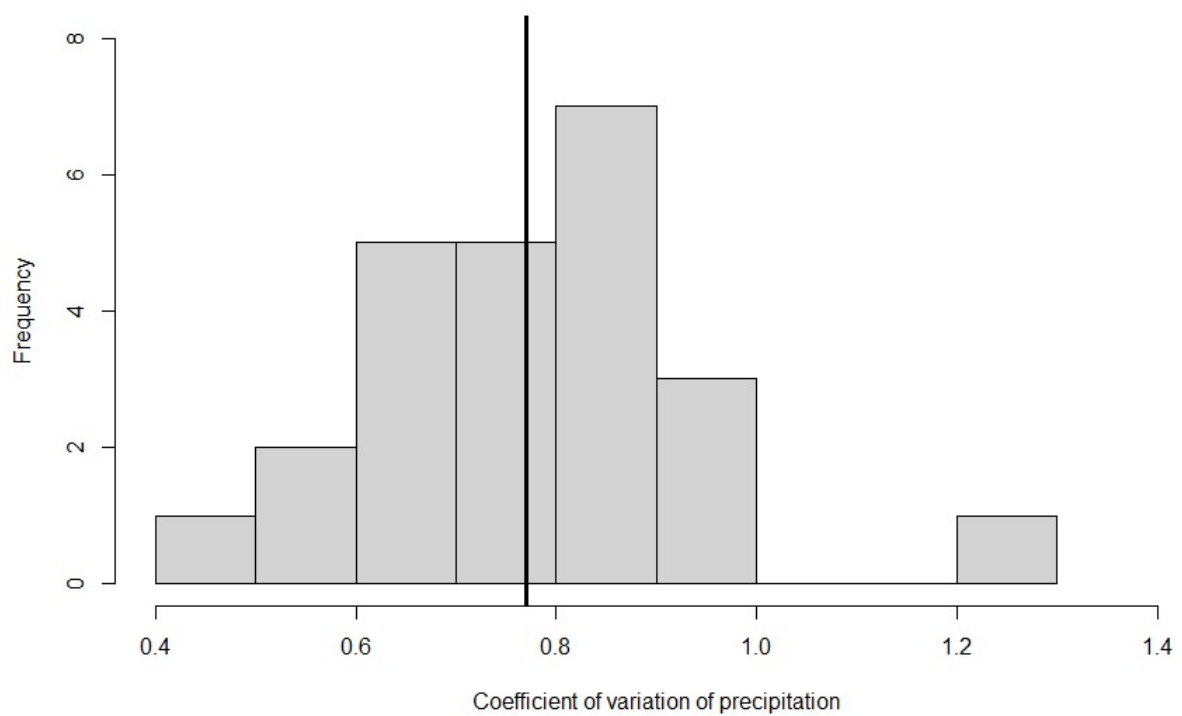


Fig. S7: Distribution of CV_{prec} across the whole data set of six locations in Central Germany. The vertical black line indicates the mean CV.

CHAPTER 4

Wild bee and floral diversity co-vary in
response to the direct and indirect impacts of
land use

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Abstract

Loss of habitat area and diversity poses a threat to communities of wild pollinators and flowering plants in agricultural landscapes. Pollinators, such as wild bees, and insect-pollinated plants are two groups of organisms that closely interact. Nevertheless, it is still not clear how species richness and functional diversity, in terms of pollination-relevant traits, of these two groups influence each other and how they respond to land-use change. In the present study, we used data from 24 agricultural landscapes in seven European countries to investigate the effect of landscape composition and habitat richness on species richness and functional diversity of wild bees and insect-pollinated plants. We characterized the relationships between the diversity of bees and flowering plants and identified indirect effects of landscape on bees and plants mediated by these relationships. We found that increasing cover of arable land negatively affected flowering plant species richness. While increasing habitat richness and plant species richness, both positively affected species richness and functional diversity of bees. In contrast, pollination-related plant functional diversity (when corrected for species richness) was unaffected by landscape composition, and habitat richness showed little relation to bee functional diversity. The relationships between flowering plant and bee diversity were modulated by indirect effects of landscape characteristics on the biotic communities. In conclusion, our findings demonstrate that landscape properties affect plant and bee communities in both direct and indirect ways. The interconnection between the diversities of wild bees and insect-pollinated plants increases the risk for parallel declines, extinctions and functional depletion. Our study highlights the necessity of considering the interplay between interacting species groups when assessing the response of entire communities to land-use changes.

Keywords: wild bees; flowering plants; pollination; species richness; functional diversity; land use; arable land cover; habitat richness; piecewise structural equation models

Introduction

Land cover change is a major threat to biodiversity and ecosystems leading to changes in species richness, abundance and composition (Sala et al. 2000, Millennium Ecosystem Assessment 2005, Newbold et al. 2015). Species diversity is commonly linked to ecosystem processes, but it is still unclear how its decline may affect ecosystem function and the provided ecosystem services (Loreau et al. 2001, Tylianakis et al. 2007). However, biodiversity plays a crucial role in long-term resilience of ecosystem services (Oliver et al. 2015) and its loss due to intensified land use could impair ecosystem functioning (Allan et al. 2015). Additionally, diversity at multiple trophic levels has been found to support the maintenance of ecosystem services and to affect ecosystem services as much as abiotic factors (Soliveres et al. 2016).

One of the ecosystem services anticipated to be affected by changes in land use is animal-mediated pollination, which is of high economic interest (Gallai et al. 2009, Lautenbach et al. 2012, Klatt et al. 2014). Almost 90% of flowering plants in wild communities and crops depend, at least to some extent, on animal-mediated pollination (Ollerton et al. 2011) and plant reproductive success benefits from diverse communities of pollinators (Albrecht et al. 2012). Several species from different taxa contribute to pollination (Rader et al. 2016), but bees are considered the principal groups of pollinators for both wild and crop plants (Potts et al. 2016). As a consequence, recent declines in bee diversity observed at large geographic extent (Biesmeijer et al. 2006, Kerr et al. 2015) result in increasing concern regarding potential detrimental effects on pollination service.

Habitat loss and degradation, following agricultural intensification, have a negative impact on the diversity of pollinators and flowering plants in agricultural landscapes. By contrast, habitat-rich agricultural landscapes that provide a wide range of resources promote more diverse communities of pollinators and insect-pollinated plants (Billeter et al. 2008). Therefore, habitat diversity promotes higher bee species richness (Aguirre-Gutiérrez et al. 2015). Increasing distance from semi-natural areas has been found to decrease species richness and abundance of several pollinator groups (Krewenka et al. 2011, Ekroos et al. 2013) and the visitation rate and reproductive output of commercial crops (Ricketts et al. 2008, Garibaldi et al. 2011). Additionally, decreasing cover of semi-natural areas leads to

declines in wild bee species richness and abundance (Steffan-Dewenter et al. 2002, Le Féon et al. 2010, Papanikolaou et al. 2016) and to reduced wild bee visitation rates and fruit set of different crops (e.g. Holzschuh et al. 2012, Klein et al. 2012). Although less is known regarding the effect of semi-natural areas on native plant diversity and pollination success, increased cover of semi-natural habitats was shown to be associated with higher plant species richness (Billeter et al. 2008) and increased visitation rates of native plants (Steffan-Dewenter et al. 2001), while increasing proximity to semi-natural areas has been found to increase seed production of native plants (Schmucki and de Blois 2009, Jakobsson and Agren 2014) with potential positive effects on wild plant communities.

Recent studies demonstrate that pollinator species richness alone is not the determining factor for pollination success (Kleijn et al. 2015, Winfree et al. 2015), since not all potential pollinators contribute equally to pollination (Kwak et al. 1998). Therefore, functional diversity seems to play a key role. For instance, increasing functional diversity of bee communities has been found to increase seed production of crops (Hoehn et al. 2008, Martins et al. 2015) and wild plants (Fründ et al. 2013), highlighting the importance of functional complementarity. In any case, the presence of, and vicinity to, semi-natural habitats seem to benefit wild bee functional diversity (Martins et al. 2015, Geslin et al. 2016), while high diversity of land cover types in the landscape can reduce functional homogenization of communities (Gamez-Virues et al. 2015). However, species richness and functional diversity of wild bees have also been shown to respond differentially to land use (Forrest et al. 2015).

Previous studies have established a relationship between the diversity of plant and pollinator communities (e.g. Potts et al. 2003). In an experimental study, Ebeling et al. (2008) demonstrated a positive effect of plant species richness on species richness of bumble bees, solitary bees and other pollinators. Furthermore, bee diversity was found to increase with higher plant diversity in meadows (Fründ et al. 2010) and apple orchards (Rosa García and Miñarro 2014). Additionally, functional diversity of both plants and pollinators seems to benefit plant recruitment, promoting the persistence of plant communities (Fontaine et al. 2006). Such relationships indicate that changes in plant and pollinator communities could be interconnected. In fact, Biesmeijer et al. (2006) found parallel declines of bees and insect-pollinated plants in Britain and the Netherlands, while

Weiner et al. (2014) demonstrated that the effects of land use on plant-pollinator networks are accelerated by the mutual dependence of plants and pollinators that results in interdependent losses.

Plant-pollinator networks are usually structured in such a way that they comprise more animal than plant species. Having such an arrangement, those networks are more vulnerable to loss of bee species and more protected against plant species losses (Memmott et al. 2004, Schleuning et al. 2016). In addition to this, the often observed redundancy of pollinators (Schleuning et al. 2015) and the development of alternative regeneration methods such as clonal propagation, self-pollination and soil seed bank (Brodie et al. 2014) may reduce the level of dependence of plants on pollinators. Based on the above, the relationship between plants and wild bees seems more likely to be bottom-up (i.e. from plants to bees) instead of top-down.

In the present study, we investigate the relationship between wild flowering plant and wild bee diversity. In this case, we expect that due to its trophic level bee diversity is highly dependent on plant diversity rather than *vice versa*. Additionally, we focus on the effect of landscape composition on species richness and functional diversity of insect-pollinated plants and wild bees. Taking into account the interdependence of flowering plants and their pollinators, we expect that landscape composition and habitat diversity have both direct and indirect effects on plant and bee diversity, i.e. changes in plant diversity caused by altered landscape properties (direct effect) may subsequently cause changes in bee diversity (indirect effect) or the other way round.

Methods

Study sites

Twenty-four study sites in agricultural landscapes distributed over seven European countries originally being part of the EU FP 5 project GREENVEINS were selected for our analysis: Belgium (four sites), Czech Republic (two), Estonia (four), France (three), Germany (four), the Netherlands (four) and Switzerland (three). The sites measured 4 × 4 km² each and

covered a large gradient in landscape composition and structure, i.e. ranging from 43 to 96% arable land and from 18 to 34 distinct habitat types (Bailey et al. 2007, Billeter et al. 2008).

Digitized habitat maps derived from aerial photographs and updated by field observations were used to obtain landscape metrics. The percentage cover of arable land per site was calculated to assess landscape composition, while the number of EUNIS habitats (<http://eunis.eea.europa.eu>) was used as a proxy of habitat richness. We used a modified EUNIS classification scheme which allowed us to measure and classify linear elements such as grassy field or road margins, hedgerows or lines of trees in addition to the usually patchy elements (Appendix S1).

Biodiversity sampling

The plant data were collected based on a stratified random sampling scheme. Between 79 and 314 plots of $2 \times 2 \text{ m}^2$ were sampled per site, with a constant ratio of 1:4:5 among plots distributed in agricultural, patches of semi-natural and linear semi-natural elements across all sites (for classification see Appendix S1). The average percentage cover of each plant species within all plots of the same site was used as a proxy for abundance. Only plant species specified as insect-pollinated in the TRY database (Durka 2002, Poschlod et al. 2003, Diaz et al. 2004, Kühn et al. 2004, Green 2009, Kattge et al. 2011) were considered in the analyses.

Flight traps combining the properties of window and yellow pan traps (Duelli et al. 1999) were used for wild bee sampling. Each study site was divided into 16 squares of 1 km^2 and a trap set, comprising two combined flight traps located between 25 and 50 m apart from each other, was placed within each square at a randomly chosen transition zone between a semi-natural habitat and an agricultural field. Therefore, 32 combined flight traps, grouped into 16 trap sets, were installed per site. Taking into account the differences in climatic conditions and, thus, phenological properties among countries, the full bloom of *Taraxacum officinale* Wiggers was used as a reference point to initiate sampling at two periods. The first part of the sampling took place in late summer 2001 starting 15 weeks after the full bloom of *T. officinale* and the second part took place in spring 2002 at full bloom. Over all countries the traps were kept open for seven weeks in late summer and five weeks in spring and

emptied weekly. However, only the samples with most specimens were retained in the analyses, namely 4 weeks in autumn and 3 weeks in spring. The samples of each trap set were merged and the specimens were identified to the species level.

Biodiversity metrics

Two metrics of diversity were assessed at the site level: species richness and abundance-weighted functional diversity.

Species richness was calculated as the total number of species found in a site across all samples, corrected with rarefaction curves (from now on SR) (Chao et al. 2014), as the number of vegetation plots surveyed and trapped bee specimens was quite different among the countries. For flowering plants (SR_{plant}), percentage cover was translated to presence/absence data per plot and plot-based rarefaction curves were generated. We used a threshold of three times the smallest number of plots per site to cut or extrapolate the rarefaction curves (Colwell et al. 2004). For richness estimates of bee communities (SR_{bee}), we used abundance-based rarefaction based on accumulated specimen numbers per site. Here we also truncated or extrapolated rarefaction curves at a threshold of three times the smallest number of overall bee abundance per site.

To calculate functional diversity, nine pollination-related traits were derived from the TRY database (Kattge et al. 2011) for flowering plants (Table 1a) and six relevant traits were obtained from a database hosted at the University of Reading for wild bees (Table 1b).

In total, we obtained trait data for 673 flowering plant (out of 1,321 species in total – including plants that do not depend on pollination by insects) and all 181 bee species occurring at our study sites. However, not all traits were available for the mentioned species with the problem being especially pronounced for plants. In a preliminary step we excluded all plant species with missing values for at least four traits, retaining 603 species. Consecutively, the trait data table was dummy coded and the missing data were imputed using a regularized iterative principal component analysis (PCA) algorithm (Josse and Husson 2012). We first attributed the mean value of each variable to the missing values of the

Table 1: Description of the functional traits used in this study for calculation of functional diversity. (a) Traits related to pollination derived from the TRY database (Kattge et al. 2011) for 673 insect-pollinated plants. (b) Traits for 181 wild bees derived from a database hosted at the University of Reading and updated ITD measures by Michael Kuhlmann.

| (a) | Trait | Description | References ¹ |
|-----|--|---|-------------------------|
| | UV light reflectance of flower centre | percentage | 1,2 |
| | UV light reflectance of flower periphery | percentage | 1,2 |
| | UV reflectance pattern | presence/absence | 1,2 |
| | flower colour | four categories blue-violet, red-pink, white-green, yellow-orange | 1,2,3 |
| | flower type | ten categories bell-shaped flowers, brush flowers, disk flowers, ray flowers, ray and disk flowers, flag blossom, flower heads, funnel flowers, lip flowers, pollen flowers, spike flowers | 1,2 |
| | nectar availability | five categories no nectar, open nectar, partly hidden nectar, totally hidden nectar, nectar present with no information about accessibility | 1,2 |
| | self-compatibility | self-compatible/self-incompatible | 1,2 |
| | insemination | three categories allogamous, autogamous, mixed mating | 1,2 |
| | sex timing | three categories homogamous, protandrous, protogynous | 1,2 |
| (b) | Trait | Description | |
| | sociality | five categories solitary, communal, primitively eusocial, cleptoparasite, social parasite | |
| | pollen transfer to nest | five categories legs, legs and body, underside of abdomen, crop, accidental transfer only | |
| | lecty | three categories oligolectic, polylectic | |
| | preferred flower morphology | three categories open, restricted, open and restricted access to nectar or pollen | |
| | activity period | overall expected presence/absence as dummy coded variable for each month from March till October | |
| | body size | intertegular distance (mm) | |

¹ References for TRY data: 1) Kühn et al. (2004); 2) Durka (2002); 3) Green (2009)

variable and then performed a PCA on the complete dataset. Using cross-validation criteria, we specified the number of components to be retained. Finally, the missing values were imputed with the fitted matrix of the regularized scores and loadings of the PCA. The procedure was performed with the functions `estim_ncpPCA` and `imputePCA` from the R package `missMDA` (Josse and Husson 2016). A PCA was then performed on the imputed dataset. For the sake of consistency, we repeated the same procedure for the bee trait data, although only few values were missing and no bee species had to be excluded from the analysis. The factor loadings of all axes cumulatively explaining 70% of the data variation were retained for the calculation of functional diversity, namely 13 axes for plants and 7 for bees. Functional diversity (from now on FD; flowering plant FD: FD_{plant} ; bee FD: FD_{bee}) was calculated as abundance-weighted Rao's quadratic entropy (Botta-Dukát 2005). The reason for following this approach is that calculating FD using directly the selected traits resulted in FD values very close to each other (extremely low range), as it can often happen when calculating FD across many traits simultaneously.

Abundance-weighted FD is often confounded by species richness. In order to obtain an unbiased metric, we applied a null model approach by randomizing the trait matrix and recalculating Rao's Q (Gotelli and Graves 1996). After 999 repetitions, the standardized effect size (Gotelli and McCabe 2002) of functional diversity (from now on SESFD; flowering plant SESFD: $SESFD_{\text{plant}}$; bee SESFD: $SESFD_{\text{bee}}$) was calculated by subtracting the mean randomized Rao's Q from the observed one and dividing the resulting number by the standard deviation of the randomized Rao's Q.

Data analysis

First, we wanted to identify the biotic and abiotic variables affecting each biodiversity metric. To this end, we developed a linear mixed effects model for each biodiversity metric (SR_{plant} , FD_{plant} , SR_{bee} , FD_{bee}), obtaining in this way four global models. The landscape metrics habitat richness and percentage cover of arable land were included as fixed effects in all four models and country was specified as random effect in all models to avoid potential bias caused by systematic differences among countries (e.g. different climate). Additionally, each model fitted to a flowering plant biodiversity metric included the bee biodiversity metrics as

predictors and *vice versa*. Therefore, SR_{plant} and FD_{plant} were modelled as functions of the two landscape metrics, SR_{bee} and FD_{bee} , while SR_{bee} and FD_{bee} were modelled as functions of the two landscape metrics, SR_{plant} and FD_{plant} . The same procedure was repeated by replacing FD_{plant} with $SESF_{\text{plant}}$ and FD_{bee} with $SESF_{\text{bee}}$ and, thus, obtaining four additional global models. All variables were standardized to zero mean and unit standard deviation to obtain comparable coefficient estimates (Quinn and Keough 2002). Additionally, all explanatory variables were tested for collinearity by estimating pairwise Pearson's correlation coefficient and checking whether its absolute value exceeds the commonly used threshold of 0.7 (Dormann et al. 2013). No pair demonstrated such a high correlation value.

Subsequently, we followed a multi-model inference approach (Burnham and Anderson 2002) to identify relevant predictors for each metric. For each one of the eight global models all candidate models were developed and compared in terms of the second-order Akaike Information Criterion corrected for sample size (AICc). The best model was defined as the one with the lowest AICc value and the remaining models were compared to it based on their difference in AICc value (δAICc). All models with a δAICc lower than two were considered equivalent to the best model and the explanatory variables included in the set of equivalent models were seen as the most important factors affecting the modelled metric in each case.

The outcome of the multi-model inference was used to construct piecewise structural equation models (piecewise SEMs). In the context of piecewise SEMs paths are first estimated in individual models and then assembled to the full SEM (Shipley 2000). Fisher's C statistic was used for evaluating the fit of piecewise SEM (Shipley 2009). The statistic is calculated based on the significance of all missing paths and a χ^2 test on it determines whether the model has a good fit (the model is not rejected when $p > 0.05$). Direct and indirect effects can be specified in piecewise SEMs. The strength of a direct effect is equivalent to the coefficient estimate of the link connecting the two variables, while the strength of an indirect effect is calculated by multiplying the coefficient estimates of all the relationships included in the path connecting the two variables. The total effect of one variable on another can be specified by adding up the direct effect and the indirect effects obtained by all paths between them.

In our analysis, the relationships that were selected during the multi-model inference procedure were represented as arrows in the SEMs. The arrows were directed from each one of the factors found to be important for a specific biodiversity metric towards the biodiversity metric. Two piecewise SEMs were constructed. The first one included all the SR and FD metrics, while the second included the SR and SESFD metrics. Taking into account the correlation between SR and abundance-weighted FD, we specified correlated errors between SR_{plant} and FD_{plant} and between SR_{bee} and FD_{bee} in the first model. No correlated errors were specified in the second SEM. Bi-directional relationships are not allowed in SEMs; therefore, when the direction of an arrow could not be clearly deduced from the multimodel inference results, we created different versions of the same model. In those cases, separate SEMs were created changing the arrow direction while keeping everything else unchanged. Afterwards, SEMs were compared using Fisher's C and AIC in order to assess which directionality of the relationship provides a better fit.

Results

Direct effects of landscape on the diversity of bees and insect-pollinated plants

We found a strong positive effect of habitat richness on bee diversity (bee species richness SR_{bee} : Tables 2b, 2f; bee functional diversity FD_{bee} : Table 2d; standardized effect size of bee functional diversity $SESFD_{\text{bee}}$: Table 2h) and on FD_{plant} (plant functional diversity; Table 2c), but not on $SESFD_{\text{plant}}$ (standardized effect size of plant functional diversity), which was not affected by either of the landscape variables (Table 2g). The percentage of arable land directly negatively affected only SR_{plant} (plant species richness; Tables 2a, 2e).

It is noteworthy that the intercept-only model occasionally ranked high in the model selection procedure (fourth-best, best and second-best for FD_{bee} , $SESFD_{\text{plant}}$ and $SESFD_{\text{bee}}$, respectively) indicating that the selected direct effects are probably not very strong in those cases.

Table 2: Selected models for each biodiversity variable. Eight global models were built and a multi-model inference approach was followed to compare all submodels and select those that provided the best fit. The selection threshold in all cases was $\delta AICc < 2$. Two landscape variables (habitat richness, percentage cover of arable land) were included as fixed effects in all the global models. (a) Flowering plant species richness (SR_{plant}) modelled with landscape, bee species richness (SR_{bee}) and abundance-weighted bee functional diversity (FD_{bee}); (b) SR_{bee} modelled with landscape, SR_{plant} and abundance-weighted flowering plant functional diversity (FD_{plant}); (c) FD_{plant} modelled with landscape, SR_{bee} and FD_{bee} ; (d) FD_{bee} modelled with landscape, SR_{plant} and FD_{plant} ; (e) SR_{plant} modelled with landscape, SR_{bee} and abundance-weighted bee functional diversity corrected for species richness ($SESFD_{bee}$); (f) SR_{bee} modelled with landscape, SR_{plant} and abundance-weighted flowering plant functional diversity corrected for species richness ($SESFD_{plant}$); (g) $SESFD_{plant}$ modelled with landscape, SR_{bee} and $SESFD_{bee}$; (h) $SESFD_{bee}$ modelled with landscape, SR_{plant} and $SESFD_{plant}$.

(a) SR_{plant} (with FD metrics)

| Intercept | % arable | SR_{bee} | AICc | $\delta AICc$ | Weight |
|-----------|----------|------------|--------|---------------|--------|
| 172.40 | -1.37 | 1.79 | 213.25 | 0.00 | 0.62 |

(b) SR_{bee} (with FD metrics)

| Intercept | Habitat richness | SR_{plant} | AICc | $\delta AICc$ | Weight |
|-----------|------------------|--------------|--------|---------------|--------|
| 9.10 | - | 0.20 | 166.15 | 0.00 | 0.35 |
| 0.47 | 0.74 | 0.13 | 166.85 | 0.70 | 0.24 |

(c) FD_{plant}

| Intercept | Habitat richness | AICc | $\delta AICc$ | Weight |
|-----------|------------------|-------|---------------|--------|
| 8.23 | 0.10 | 67.51 | 0.00 | 0.34 |

(d) FD_{bee}

| Intercept | Habitat richness | SR_{plant} | AICc | $\delta AICc$ | Weight |
|-----------|------------------|--------------|-------|---------------|--------|
| 0.75 | 0.11 | - | 73.81 | 0.00 | 0.25 |
| 1.80 | - | 0.01 | 74.42 | 0.62 | 0.19 |
| 0.26 | 0.08 | 0.01 | 75.37 | 1.57 | 0.12 |
| 3.92 | - | - | 75.64 | 1.84 | 0.10 |

(e) SR_{plant} (with SESFD metrics)

| Intercept | % arable | SR_{bee} | AICc | $\delta AICc$ | Weight |
|-----------|----------|------------|--------|---------------|--------|
| 172.40 | -1.37 | 1.79 | 213.25 | 0.00 | 0.63 |

(f) SR_{bee} (with SESFD metrics)

| Intercept | Habitat richness | SR_{plant} | AICc | $\delta AICc$ | Weight |
|-----------|------------------|--------------|--------|---------------|--------|
| 9.10 | - | 0.20 | 166.15 | 0.00 | 0.34 |
| 0.47 | 0.74 | 0.13 | 166.85 | 0.70 | 0.24 |

(g) $SESFD_{plant}$

| Intercept | $SESFD_{bee}$ | AICc | $\delta AICc$ | Weight |
|-----------|---------------|-------|---------------|--------|
| -0.70 | - | 33.31 | 0.00 | 0.36 |
| -0.49 | 0.20 | 35.10 | 1.80 | 0.15 |

(h) $SESFD_{bee}$

| Intercept | Habitat richness | SR_{plant} | $SESFD_{plant}$ | AICc | $\delta AICc$ | Weight |
|-----------|------------------|--------------|-----------------|-------|---------------|--------|
| -2.07 | 0.04 | - | - | 32.88 | 0.00 | 0.23 |
| -1.02 | - | - | - | 33.00 | 0.12 | 0.22 |
| -1.67 | - | 0.004 | - | 34.22 | 1.34 | 0.12 |
| -0.89 | - | - | 0.19 | 34.86 | 1.98 | 0.09 |

Interdependencies of flowering plant and bee diversity aspects

Our results indicate strong positive relationships between bee and flowering plant diversity. SR_{plant} and SR_{bee} were strongly interconnected (Tables 2a, 2b, 2e, 2f). The directionality of their relationship, that had to be tested by comparing different versions of piecewise SEMs, was not well resolved. However, the versions of the piecewise SEMs that included arrows pointing from SR_{bee} towards SR_{plant} (SEM 1 Version 2, SEM 2 Version 2) provided better fit than the respective versions with arrows from SR_{plant} towards SR_{bee} (Table 3). The better performance of that model was clear when using the SESFD metrics, but the δAICc between the two model versions only marginally exceeded the threshold of 2 when using the FD metrics. Additionally, bee functional diversity (both FD_{bee} and $\text{SESFD}_{\text{bee}}$) was positively affected by increasing SR_{plant} (Tables 2d, 2h).

Table 3: Fit evaluation for the different versions of the two piecewise SEMs; SEM 1 includes SR and FD metrics, while SEM 2 includes SR and SESFD metrics. The relationships of the SEMs were specified based on the results of the multimodel inference. When the directionality of the relationship was unclear, two different versions of the SEM were created by changing the direction of the relationship in question while keeping everything else unchanged. The different versions were subsequently compared in terms of AIC to identify the version that provides a better fit. SR_{plant} : flowering plant species richness; SR_{bee} : bee species richness; $\text{SESFD}_{\text{plant}}$: abundance-weighted flowering plant functional diversity corrected for species richness; $\text{SESFD}_{\text{bee}}$: abundance-weighted bee functional diversity corrected for species richness.

| Model | Version | Arrow direction | Fisher's C | p value | AICc |
|--------------------------|---|---|------------|---------|--------|
| SEM 1 (FD metrics) | 1 | $SR_{\text{plant}} \rightarrow SR_{\text{bee}}$ | 10.73 | 0.55 | 183.53 |
| | 2 | $SR_{\text{bee}} \rightarrow SR_{\text{plant}}$ | 8.68 | 0.73 | 181.48 |
| SEM 2 (SESFD metrics) | 1 | $SR_{\text{plant}} \rightarrow SR_{\text{bee}}$ | 10.24 | 0.60 | 100.24 |
| | | $\text{SESFD}_{\text{plant}} \rightarrow \text{SESFD}_{\text{bee}}$ | | | |
| | 2 | $SR_{\text{bee}} \rightarrow SR_{\text{plant}}$ | 6.33 | 0.90 | 96.33 |
| | | $\text{SESFD}_{\text{plant}} \rightarrow \text{SESFD}_{\text{bee}}$ | | | |
| 3 | $SR_{\text{plant}} \rightarrow SR_{\text{bee}}$ | 11.37 | 0.79 | 184.17 | |
| | $\text{SESFD}_{\text{bee}} \rightarrow \text{SESFD}_{\text{plant}}$ | | | | |
| 4 | $SR_{\text{bee}} \rightarrow SR_{\text{plant}}$ | 8.49 | 0.93 | 181.29 | |
| | $\text{SESFD}_{\text{bee}} \rightarrow \text{SESFD}_{\text{plant}}$ | | | | |

The corrected functional diversity metrics $\text{SESFD}_{\text{plant}}$ and $\text{SESFD}_{\text{bee}}$ were also related (Tables 2h, 2g). In that case, when comparing piecewise SEMs to decide on the directionality of the relationship, it is evident that the model versions 1 and 2 with the relationship directed from $\text{SESFD}_{\text{plant}}$ to $\text{SESFD}_{\text{bee}}$ performed much better than the other two, with version 2 (arrow from SR_{bee} to SR_{plant}) being the best (Table 3). Thus, when using functional diversity metrics independent of richness, $\text{SESFD}_{\text{bee}}$ depends on $\text{SESFD}_{\text{plant}}$.

Indirect effects of landscape on the diversity of bees and insect-pollinated plants

The interdependence between bee and flowering plant diversity resulted in indirect effects of the landscape on both species groups (Figs 1, 2). The indirect effects and their strengths differed among the model versions (Table 4).

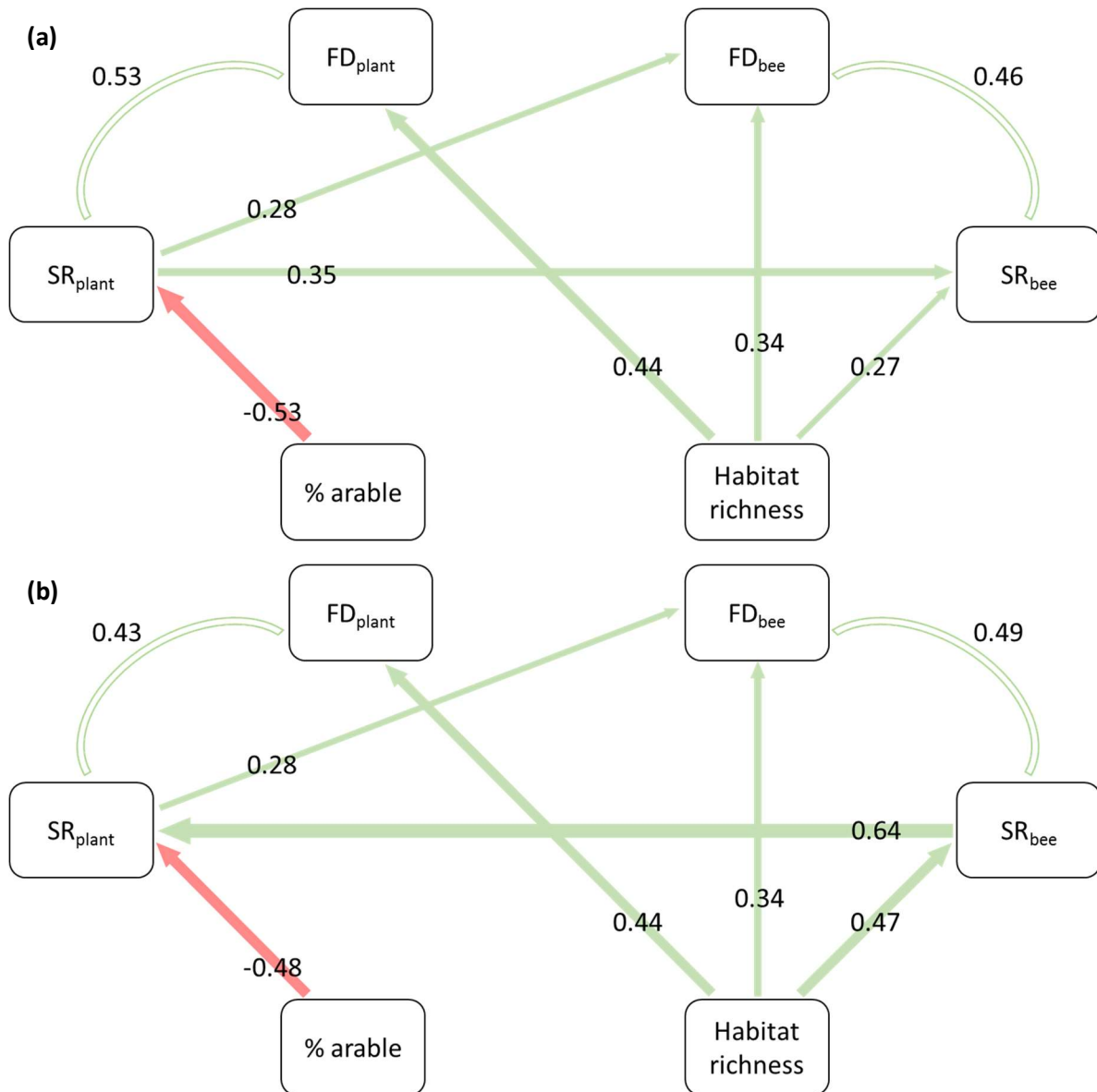


Fig. 1: Representation of the two versions of SEM with FD metrics. The green and red arrows indicate positive and negative relationships, respectively. The links without arrowheads indicate correlated errors. The numbers represent the coefficient estimates that correspond to each relationship and the arrow width is weighted to indicate the strength of the relationships. (a) Model version 1: $SR_{plant} \rightarrow SR_{bee}$ (b) Model version 2: $SR_{bee} \rightarrow SR_{plant}$. % arable: percentage cover of arable land in the landscape; Habitat richness: number of habitats; SR_{plant} : flowering plant species richness; SR_{bee} : bee species richness; FD_{plant} : abundance-weighted flowering plant functional diversity; FD_{bee} : abundance-weighted bee functional diversity.

All the models included a negative indirect effect of percentage of arable land on bee functional diversity (either FD_{bee} or $SESF_{D_{bee}}$) mediated by SR_{plant} . Both model versions with

the best fit (SEM 1 Version 2, SEM 2 Version 2) indicated positive indirect effects of habitat richness on SR_{plant} mediated by SR_{bee} and on $FD_{\text{bee}}/SESFD_{\text{bee}}$ mediated by SR_{bee} and SR_{plant} . Finally, we also found a negative indirect effect of percentage of arable land on SR_{bee} mediated by SR_{plant} in the SEM 1 Version 1 (Table 4a), the fit of which not much worse than that of best model version.

Table 4: Direct and indirect effects of landscape variables on biodiversity metrics derived from (a) the two versions of the SEM with FD metrics and (b) the best version of the SEM with SESFD metrics. SR_{plant} : flowering plant species richness; SR_{bee} : bee species richness; FD_{plant} : abundance-weighted flowering plant functional diversity; FD_{bee} : abundance weighted bee functional diversity; $SESFD_{\text{plant}}$: abundance-weighted flowering plant functional diversity corrected for species richness; $SESFD_{\text{bee}}$: abundance-weighted bee functional diversity corrected for species richness.

(a) FD metrics

| Model Version | Cause | Effect on | Direct | Indirect | Total | | |
|---|---------------------|---------------------|---------------------|-----------------------|-------|-------|-------|
| 1: $SR_{\text{plant}} \rightarrow SR_{\text{bee}}$ | % arable | SR_{plant} | -0.53 | | 0 | -0.53 | |
| | | SR_{bee} | 0 | -0.19 (-0.53*0.35) | | -0.19 | |
| | | FD_{plant} | 0 | | 0 | 0 | |
| | | FD_{bee} | 0 | -0.15 (-0.53*0.28) | | -0.15 | |
| | Habitat Richness | SR_{plant} | 0 | | 0 | 0 | |
| | | SR_{bee} | 0.27 | | 0 | 0.27 | |
| | | FD_{plant} | 0.44 | | 0 | 0.44 | |
| | | FD_{bee} | 0.34 | | 0 | 0.34 | |
| | | % arable | SR_{plant} | -0.48 | | 0 | -0.48 |
| | | | SR_{bee} | 0 | | 0 | 0 |
| FD_{plant} | 0 | | | 0 | 0 | | |
| FD_{bee} | 0 | | -0.13 (-0.48*0.28) | | -0.13 | | |
| 2: $SR_{\text{bee}} \rightarrow SR_{\text{plant}}$ | Habitat Richness | SR_{plant} | 0 | 0.30 (0.47*0.64) | | 0.30 | |
| | | SR_{bee} | 0.47 | | 0 | 0.47 | |
| | % arable | FD_{plant} | 0.44 | | 0 | 0.44 | |
| | | FD_{bee} | 0.34 | 0.08 (0.47*0.64*0.28) | | 0.42 | |

(b) SESFD metrics

| Model Version | Cause | Effect on | Direct | Indirect | Total | | |
|--|---------------------|------------------------|--------|-----------------------|------------------|-------|------|
| 2: $SR_{\text{bee}} \rightarrow SR_{\text{plant}}$ $SESFD_{\text{plant}} \rightarrow SESFD_{\text{bee}}$ | % arable | SR_{plant} | -0.48 | | 0 | -0.48 | |
| | | SR_{bee} | 0 | | 0 | 0 | |
| | | $SESFD_{\text{plant}}$ | 0 | | 0 | 0 | |
| | | $SESFD_{\text{bee}}$ | 0 | -0.08 (-0.48*0.16) | | -0.08 | |
| | Habitat Richness | SR_{plant} | 0 | | 0.30 (0.47*0.64) | | 0.30 |
| | | SR_{bee} | 0.47 | | 0 | 0.47 | |
| | | $SESFD_{\text{plant}}$ | 0 | | 0 | 0 | |
| | | $SESFD_{\text{bee}}$ | 0.23 | 0.05 (0.47*0.64*0.16) | | 0.28 | |

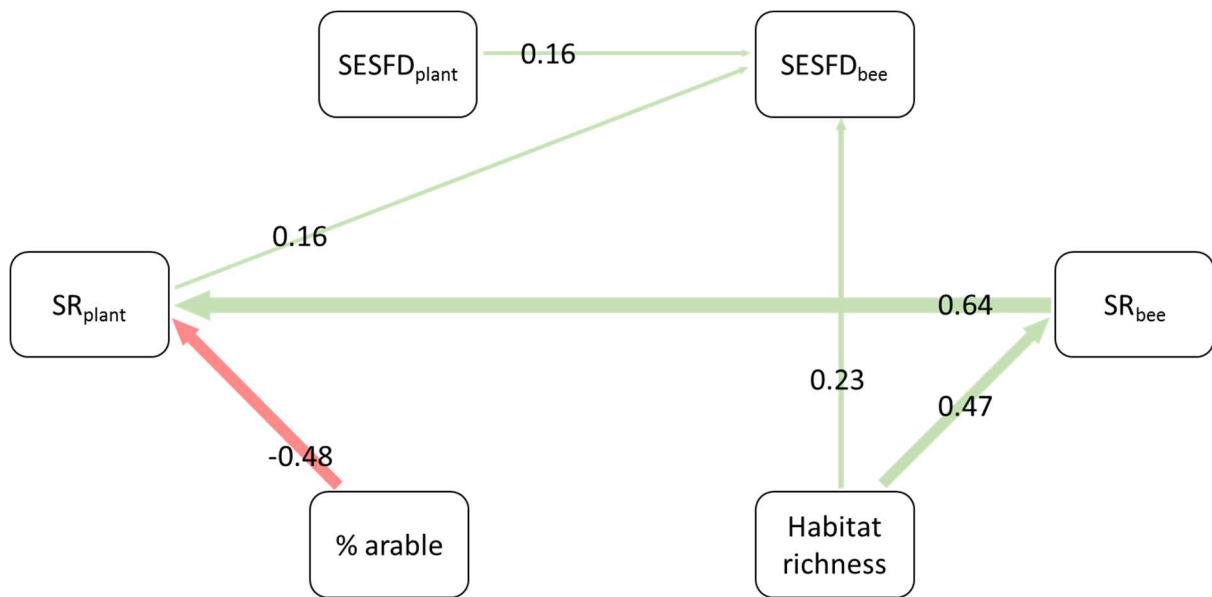


Fig. 2: Representation of the version of SEM with SESFD metrics that demonstrated the best fit (Model version 2: $SR_{bee} \rightarrow SR_{plant}$, $SESFD_{plant} \rightarrow SESFD_{bee}$). The green and red arrows indicate positive and negative relationships, respectively. The numbers represent the coefficient estimates that correspond to each relationship and the arrow width is weighted to indicate the strength of the relationships. % arable: percentage cover of arable land in the landscape; Habitat richness: number of habitats; SR_{plant} : flowering plant species richness; SR_{bee} : bee species richness; $SESFD_{plant}$: abundance-weighted flowering plant functional diversity corrected for species richness; $SESFD_{bee}$: abundance-weighted bee functional diversity corrected for species richness.

Discussion

We found strong relationships between insect-pollinated plant and wild bee diversity; although there are indications for both bottom-up and top-down effects, which was contrary to our expectations that the effect of flowering plants on bees would be more pronounced than *vice versa*. Overall, we found not only direct effects of landscape structure on wild bees and insect-pollinated plants but also indirect ones, resulting from the interdependence of these two groups.

The effects of landscape on the diversity of bees and flowering plants is in line with other studies demonstrating the detrimental effects of habitat loss on communities in agricultural landscapes (e.g. Billeter et al. 2008, Gamez-Virues et al. 2015). However, the indirect effects we found may indicate that some of the impacts reported in those studies are actually indirect influences related to species interactions. For instance, the positive relationship between percentage cover of semi-natural areas and bee diversity, which is often encountered in literature (Steffan-Dewenter et al. 2002, Le Féon et al. 2010, Papanikolaou

et al. 2016), would be translated in our study as a negative relationship between percentage cover of arable land and bee diversity (Russo et al. 2015). All our models included such a negative relationship between arable land cover and at least one of the two bee diversity metrics, but this relationship was always an indirect one mediated by plant species richness. The diversity, quantity and quality of floral resources (nectar, pollen) affect bee community composition (Potts et al. 2003) and the lack of floral resources in landscapes devoid of semi-natural habitats was considered a possible mechanism behind the decline of bee diversity in such landscapes. Our findings provide evidence for this mechanism, since bee species richness and functional diversity declined with decreasing number of insect-pollinated plant species. However, wild bees depend on diverse habitats for nesting and food resources and, thus, they are directly affected by habitat richness. Since the impact of percentage cover of arable land was much stronger, we did not find a direct effect of habitat richness on plant species richness but plant richness can indirectly benefit from positive effects of linear and patchy habitat diversity on bee species richness (Poschlod and Braun-Reichert 2016).

Investigating plant-pollinator networks, Weiner et al. (2014) demonstrated linked losses in plants and pollinators with increasing grassland management, assessed through three variables: fertilization, mowing and grazing intensity. According to their findings, land-use intensification causes a direct decline in plant diversity which in turn precipitates non-random extinctions of pollinators mediated by limited resources. Although they did not find direct effects of land use on pollinators in the context of their study, they claim that such effects are possible especially for more specialized pollinators such as bees. Our findings support their conclusions about plant-mediated effects of landscape on bee diversity and further demonstrate the possibility of bee-mediated effects of landscape on flowering plant diversity. Biesmeijer et al. (2006) found a relationship between bee and plant diversity, but they were unable to point to which direction it was operating. In our case, we identified bottom-up effects (from plant species richness to bee functional diversity) in accordance with our expectations. However, our results further highlight the possibility of top-down (from bee to plant species richness) effects, given that the directionality of the strong relationship between plant and bee species richness was unclear. This finding may be explained by the fact that some plants need specific pollinators and therefore cannot produce seed set in a site where their pollinator does not occur (Steffan-Dewenter and

Tscharntke 1999). More surprisingly, there was stronger evidence to a certain extent for an effect directed from bee to plant species richness. This result supports the idea of a more complex structure where individuals of multiple plant and pollinator species interact and indirectly affect each other (Carvalho et al. 2014).

It is worth noting that the factors affecting flowering plant functional diversity change when using the corrected and non-corrected metric. The uncorrected FD_{plant} is strongly positively affected by habitat richness, but the corrected $SESFD_{\text{plant}}$ was neither affected by percentage cover of arable land nor by habitat richness. Thus, it can be inferred that the effect of habitat richness on FD_{plant} is mainly caused by the correlation with plant species richness. Additionally, we did not find a relationship between FD_{plant} and FD_{bee} , which might be caused by the fact that the effect of species richness is stronger. However, when functional diversity was corrected for species richness, there was a relationship between $SESFD_{\text{plant}}$ and $SESFD_{\text{bee}}$. Therefore, it is possible that high species richness correlated with high abundances means quite many and diverse resources allowing the coexistence of different bees species. The explanation for the independency of the corrected plant functional diversity to landscape variables lies within the traits used. All the selected plant traits are pollination-related. Therefore, those traits determine the effect of plants on the ecosystem function of pollination, but they do not directly respond to environmental changes and disturbances (Lavorel and Garnier 2002). Nevertheless, land use is likely to act on functional diversity via changes in plant and pollinator diversity, although such effects were not detected in our study.

Our study mainly found strong relationships between the diversity of bees and insect-pollinated plants. Several other studies have report that bee species richness increases with increasing plant species richness (Steffan-Dewenter et al. 2001, Holzschuh et al. 2007, Ebeling et al. 2008), while others highlight the importance of bee diversity for the persistence of the plant community (Fontaine et al. 2006) or just identify the positive correlation between the diversity of flowers and flower visitors (Fründ et al. 2010). In our study, the relationship between bee and flowering plant species richness was strongly positive. Our results are not conclusive regarding the directionality of the relationship, although there seems to be slightly more support for a direction from bee to plant species richness. The support is clearer when using functional diversity as $SESFD$ metrics, but the

difference is only marginal in the models with FD metrics. This result corroborates the mutual dependence between these two groups of organisms which may result into linked species losses and secondary extinctions as response to disturbance (Kaiser-Bunbury et al. 2010).

Furthermore, our models show increasing flowering plant species richness causes an increase in bee functional diversity (either FD_{bee} or $SESFD_{bee}$), suggesting that species impoverished plant communities can lead to a decline in functional diversity of the bee community. The decrease in the number of flowering plant species seems to have a filtering effect on the wild bee community, limiting the variety of flowering resources and leading to trait convergence (i.e. lower values of Rao's Q). We also found that increasing plant functional diversity leads to increasing bee functional diversity, as well (when using the $SESFD$ metrics), denoting that parallel declines in functionality occur and trait convergence of the insect-pollinated plant community results in more homogeneous communities also for wild bees. Even bee species that are considered generalists (e.g. most bumblebees) tend to prefer specific plant families and species (Fontaine et al. 2006, Fründ et al. 2010, Fründ et al. 2013). Fründ et al. (2010) suggested this higher than expected specialization, which is not affected by flower diversity, to be a possible mechanism promoting species coexistence and allowing higher pollinator diversity when plant diversity increases. Such a mechanism could explain the positive effect of flowering plant diversity on bee functional diversity found in our study. Another possible explanation could be that higher plant species richness promotes niche complementarity (Venjakob et al. 2016), since bees are able to shift their floral niches in order to avoid interspecific competition (Fründ et al. 2013). Plant communities with more species differing in their pollination-related functional traits can support a more diverse wild bee species community, comprising species with different preferences that display increased niche complementarity, meaning that trait divergence in the plant community leads to a more functionally diverse bee community.

To conclude, we demonstrate that landscape composition and habitat richness affect flowering plant and pollinator communities in both direct and indirect ways. The diversity of wild bees and insect-pollinated plants in agricultural landscapes is strongly interconnected, increasing the risks for parallel declines, extinctions and functional depletion. Therefore, it would be imperative to consider in environmental policy indirect effects mediated by

species interactions. Agri-environmental schemes that aim to facilitate pollinators often focus on enhancing the quality of semi-natural elements, such as flower strips. Here, however, we show the importance of additionally including the indirect effects via the plant species richness that is affected by the amount of agricultural area. Overall, our study emphasizes the necessity of considering the interplay between interacting species groups when assessing their response to disturbances.

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Supplementary material

Appendix S1: The table lists the EUNIS classes described in the study sites. Linear semi-natural features were transformed into areas by multiplying their length with standard widths (see the respective column).

| EUNIS Class | EUNIS | Classification | Type | Standard width (m) |
|---|-------|----------------|---------|--------------------|
| Surface Standing Water | C10 | other | polygon | - |
| Surface and Temporary Running Water >2m | C2B | other | polygon | - |
| Grassy Margins of Surface and Temporary Running Water | C2G | semi-natural | line | 2 |
| Surface and Temporary Running Water >1m and <2m | C2S | other | polygon | - |
| Littoral Zone of Inland Surface Water Bodies | C30 | semi-natural | line | 2 |
| Raised and blanket bogs | D10 | semi-natural | polygon | - |
| Valley mires, poor fens and transition mires | D20 | semi-natural | polygon | - |
| Base-rich fens | D40 | semi-natural | polygon | - |
| Sedge and reed beds, normally without free standing water | D50 | semi-natural | polygon | - |
| Inland saline and brackish marshes and reed beds | D60 | semi-natural | polygon | - |
| Dry grassland | E10 | semi-natural | polygon | - |
| Mesic grasslands | E20 | semi-natural | polygon | - |
| Seasonally wet and wet grasslands | E30 | semi-natural | polygon | - |
| Woodland fringes and clearings and tall forb habitats | E50 | semi-natural | polygon | - |
| Inland saline grass and herb dominated habitats | E60 | semi-natural | polygon | - |
| Temperate and mediterraneo-montane scrub habitats | F30 | semi-natural | polygon | - |
| Scrubby woodland edge | F3M | semi-natural | line | 3 |
| Temperate shrub heathlands | F40 | semi-natural | polygon | - |
| Riverine and fen scrubs | F90 | semi-natural | polygon | - |
| Broadleaved Hedgerows | FAB | semi-natural | line | 5 |
| Coniferous Hedgerows | FAC | semi-natural | line | 5 |
| Mixed deciduous and coniferous hedgerows | FAM | semi-natural | line | 5 |

continued on next page

| EUNIS Class | EUNIS | Classification | Type | Standard width (m) |
|---|--------------|-----------------------|-------------|---------------------------|
| Shrub plantations | FB0 | agricultural | polygon | - |
| Broadleaved deciduous woodlands | G10 | semi-natural | polygon | - |
| Fruit and nut orchards | G1D | semi-natural | polygon | - |
| Coniferous woodlands | G30 | semi-natural | polygon | - |
| Mixed deciduous and coniferous woodlands | G40 | semi-natural | polygon | - |
| Small broadleaved deciduous woodlands | G52 | semi-natural | polygon | - |
| Small coniferous woodlands | G54 | semi-natural | polygon | - |
| Small mixed deciduous and coniferous woodlands | G55 | semi-natural | polygon | - |
| Line of broad-leaved trees | GLB | semi-natural | line | 5 |
| Line of coniferous trees | GLC | semi-natural | line | 5 |
| Mixed line of broad-leaved and coniferous trees | GLM | semi-natural | line | 5 |
| Inland habitats with sparse or no vegetation | H00 | semi-natural | polygon | - |
| Inland cliffs, rock pavements and outcrops | H30 | semi-natural | polygon | - |
| Arable land and market gardens | I10 | agricultural | polygon | - |
| Long term fallow on arable land | I1F | semi-natural | polygon | - |
| Grassy field margins | I1G | semi-natural | line | 2 |
| Buildings of cities, towns and villages | J10 | other | polygon | - |
| Low density buildings | J20 | other | polygon | - |
| Extractive industrial sites | J30 | other | polygon | - |
| Grassy Margins of extractive industrial sites | J3M | semi-natural | line | 2 |
| Transport networks (hard-surfaced) | J4B | other | polygon | - |
| Transport networks (soft-surfaced) | J4S | other | polygon | - |
| Grassy road verges | J4V | semi-natural | line | 2 |
| Waste Deposits | J60 | other | polygon | - |

CHAPTER 5

Synthesis

Key results

This thesis aimed to investigate (i) the interactive effects of landscape and weather on wild bees and (ii) the indirect effects of landscape on wild bee diversity, mediated by the strong links between bees and plants. By analysing long-term monitoring data with restricted spatial extent and short-term monitoring data with large spatial extent, the acquired results provide intriguing insights into the interaction effects between weather and landscape and into the interdependence between the diversity of pollinators and flowering plants. The key results are as follows:

- Chapters 2 and 3 provide the first evidence of interactive effects between landscape properties and weather conditions on the diversity and stability of wild bee communities. Increasing cover of semi-natural habitats in agricultural landscapes mitigated the negative effect of temperature increase on wild bee richness and abundance, while landscape heterogeneity prevented the spatiotemporal stability of wild bee abundance from declining under highly varying temperature conditions. Nevertheless, heterogeneous landscapes sustained stable wild bee abundance only under low precipitation variability and abundance stability was negatively affected by highly varying precipitation regardless of the landscape structure.
- Chapter 4 demonstrates how biotic factors (i.e. the interdependence between interacting species groups) interfere with the effect of abiotic factors (i.e. landscape properties) on the diversity of these groups. Surprisingly, apart from the bottom-up effects from flowering plants to pollinators, the results additionally indicate top-down effects from pollinators to plants, thereby highlighting the strong interdependence between the diversity of wild bees and the diversity of insect-pollinated plants. This interdependence resulted in indirect effects of landscape properties on the two interacting groups. Arable land cover indirectly affected bee diversity via its direct effect on plant species richness, while habitat richness was found to have an indirect effect on plant species richness, mediated by bee species richness.

Effect of landscape on wild bees and insect-pollinated plants

Wild bee diversity was negatively affected by unfavourable landscape properties, such as reduced area of semi-natural habitats and low habitat richness. The results in Chapter 2 are in line with a series of studies (e.g. Steffan-Dewenter et al. 2002, Le Féon et al. 2010, Krewenka et al. 2011, Ekroos et al. 2013), which demonstrate the positive effect of increasing area and proximity of semi-natural habitats on wild bee richness and abundance. Analysing landscape data from a broader geographical area, the number of different habitat types available in the landscape was also demonstrated to positively affect species richness and functional diversity of wild bees (Chapter 4), as in Billeter et al. (2008) and Aguirre-Gutiérrez et al. (2015).

Semi-natural habitats in agricultural landscapes are widely used by wild bees for foraging and nesting (Westrich 1996) and, thus, their decrease can deprive wild bees of indispensable resources. Clough et al. (2014) have demonstrated that increase in semi-natural habitat cover leads to parallel increases in flowering plant density and bee diversity, while Orford et al. (2016) have shown that increasing plant species richness in grasslands promotes bee diversity and the provided pollination services. The lack of diverse floral resources has often been suggested as the potential mechanism behind the link of semi-natural habitat cover and bee diversity (see e.g. Le Féon et al. 2010, Martins et al. 2015, Geslin et al. 2016). Chapter 4 corroborates this idea, indicating that increasing arable land cover (i.e. inversely related to semi-natural habitat cover in the study sites) negatively influences flowering plant species richness, which in turn affects wild bee species richness and functional diversity. Therefore, the positive effect of semi-natural habitat cover on wild bee diversity (Chapter 2) is mediated by flowering plant diversity (Chapter 4).

Apart from its effect on diversity, landscape structure was additionally found to affect stability of wild bee abundance in space and time. Landscape heterogeneity has been associated with more stable population dynamics in insects (crickets: Kindvall 1996, butterflies: Oliver et al. 2010). In Chapter 3, I demonstrated that temporal and spatial fluctuations in wild bee abundance were more likely to occur in homogeneous landscapes, while heterogeneous landscapes maintained more stable wild bee abundance across the entire landscape and during the whole monitoring period. Intense variation of wild bee

abundance as a result of varying weather conditions and suboptimal landscape structures could result in pollinator deficiency in certain periods or places with detrimental effects on pollination services for wild plants and pollinator-dependent crops.

Effect of weather on wild bees and implications in the context of climate change

In the present thesis, I have also demonstrated that weather conditions and their variability affect the diversity and stability of wild bee communities. Species richness and total abundance of wild bees decreased with increasing temperature, but were not affected by precipitation (Chapter 2). In contrast, the stability of wild bee abundance in space and time decreased with increasing intra-annual variability in both temperature and precipitation (Chapter 3). These findings are particularly noteworthy, considering the alterations in temperature and precipitation patterns which occur in the context of climate change.

Climate change is expected to impact means, variability, and extremes of weather variables (Rummukainen 2012). In particular, warm days, heavy precipitation events, and droughts have increased in Central Europe since 1950 and are projected to further increase in frequency and intensity until the end of the 21st century (Seneviratne et al. 2012). A recent review (Brown et al. 2016) described the climate change-related increase in frequency of heatwaves and droughts as one of the six high priority issues for pollinators and pollination in the near future. The results presented in this thesis caution that such climatically dependent changes in weather conditions can negatively influence the persistence and diversity of wild bees in agricultural landscapes. For instance, an increase in warm days could lead to a decrease in bee species richness and abundance, while the simultaneous increase in frequency of heavy rainfalls and droughts would result in higher precipitation variability with detrimental consequences for bee abundance stability and the resulting pollination services.

Long-term data have indicated wild bee species losses (Bartomeus et al. 2013), also in parallel with declines in species richness of insect-pollinated plants (Biesmeijer et al. 2006), contributing to the degradation of plant-pollinator networks (Burkle et al. 2013).

Additionally, bumblebees, an important group of wild bees, have experienced range contractions and demonstrated inability to track warming by northern range margin expansion (Kerr et al. 2015). Therefore, the already documented responses, along with the results presented here, delineate alarming prospects for wild bees in the face of climate change.

Combined effect of landscape and weather on wild bees

Although global change drivers, such as climate and land-use change, are speculated to have interactive effects on pollinators (Gonzalez-Varo et al. 2013, Brown et al. 2016, Potts et al. 2016), such interactions have been scarcely studied (Oliver and Morecroft 2014). Therefore, the most novel aspect of Chapters 2 and 3 is the finding that landscape and weather interactively affect wild bee diversity and stability, although the interaction with the landscape differs for temperature and precipitation. No study had evaluated these interactive effects on wild bees before, yet there is some support of such interactions for other species groups.

Bird communities in landscapes with low cover of suitable habitat showed higher vulnerability to temperature-mediated population declines and lower ability to recover after declines (Newson et al. 2014), while bird and butterfly communities in intensively managed landscapes demonstrated limited capacity to reorganise during warming (Oliver et al. 2017). In the present thesis, the response of wild bees to warming and increased temperature variability displayed similar patterns, with favourable landscape conditions (i.e. high cover of semi-natural habitats, landscape heterogeneity) mitigating the detrimental effects of temperature-related changes on species richness, abundance, and stability of wild bee communities (Chapters 2 and 3).

Regarding precipitation, evidence from butterflies indicated that landscape heterogeneity promoted population persistence and recovery after extreme droughts (Oliver et al. 2015b), while also limiting the population declines of vulnerable species and buffering community shifts towards generalist species (De Palma et al. 2016). The results presented in Chapter 3 align to a certain extent with those studies. Landscape heterogeneity promoted stability of wild bee abundance when intra-annual precipitation variability was low, but was no longer

advantageous under highly varying precipitation conditions. Thus, landscape heterogeneity may not suffice for maintaining stable wild bee abundances when extreme fluctuations in precipitation occur within a year. In this context, Oliver et al. (2015b) suggested that the persistence of drought-sensitive butterflies would require major emission reductions in addition to decreasing habitat fragmentation. Nevertheless, the results can be cautiously interpreted in a positive way on the basis of using landscape management to help mitigating the negative impact of climate change and hint at potential appropriate measures (see next section).

Implications for wild bee conservation

Appealing opportunities for conservation arise from the results presented here. Chapters 2 and 3 suggest that proper landscape management not only mitigates the impact of loss of wild bee habitat and food resources, but it additionally provides the opportunity to tackle to a certain extent the consequences of climate change. Chapter 4 further highlights that considering the links between interacting species groups is essential when making landscape management decisions.

Landscape management of agricultural landscapes has been linked to climate change adaptation and mitigation (Locatelli et al. 2015), but prior to this thesis no studies had actually demonstrated the efficiency of the approach for wild bees. Although proper landscape management has been reported to be beneficial against other stressors, e.g. pesticides (Park et al. 2015), here, for the first time, I provide evidence for the possibility to jointly handle the detrimental effects of land-use and climate change on wild bees.

Proper landscape management in agricultural landscapes has been suggested as an essential measure to reduce the impact of land-use change on pollinators and on the provided pollination services. A pollinator-friendly change in landscape management would combine ecological intensification, diversified farming systems, and enhancing ecological infrastructure (Potts et al. 2016). The results presented in this thesis corroborate that such management actions would be beneficial for both wild bees and flowering plants and would additionally safeguard wild bee diversity and stability against climate change. These findings should further prompt the implementation of policies aiming to improve environmental

conditions in agricultural landscapes, such as the Greening of the European Common Agricultural Policy and the European Strategy on Green Infrastructure. Improvements of those strategies in the direction of enhancing biodiversity (Pe'er et al. 2016) would be beneficial for wild bees.

Furthermore, given the complexity of species interactions, incorporating the underlying mechanisms in conservation decision making can result in joint benefits for the diversity of closely interacting groups, such as wild bees and flowering plants. The present thesis demonstrates that limiting the area covered by arable land would promote species-rich communities of flowering plants and, by extension, wild bees. Moreover, the increase in the number of available habitat types would benefit wild bee species richness directly and species richness of flowering plants indirectly. The maintenance of species-rich flower strips has been suggested and implemented as a conservation measure for supporting pollinator diversity in agricultural landscapes (Winfree 2010, Scheper et al. 2015). Such actions are based on bottom-up effects (i.e. plant diversity affecting bee diversity) that are commonly identified in studies of plant-pollinators interactions (Holzschuh et al. 2007, Ebeling et al. 2008, Weiner et al. 2014) and were also found in Chapter 4. Nevertheless, the strong effects in the opposite direction (top-down), which were also demonstrated here, indicate a more complex structure of interdependence between plants and their pollinators, i.e. the dependence of plants being pollinated as well as the dependence of pollinators on the food resources. Being aware of such relationships between the diversity of interdependent organisms can allow more informed and cost-efficient conservation decisions.

Concluding remarks

During the last centuries, global biodiversity of both vertebrates and invertebrates has undergone declines, triggered by human activities, at alarming rates (Dirzo et al. 2014). International targets to prevent further biodiversity loss have been set, but the implementation of measures towards their achievement has been proven problematic so far (Butchart et al. 2010, Pe'er et al. 2014, Tittensor et al. 2014). Biodiversity loss is acting as a driver of ecosystem change, leading to declines in functions such as productivity and decomposition (Hooper et al. 2012) and altering ecosystem stability (Hautier et al. 2015). In

this context, biodiversity conservation may contribute to the long-term resilience of ecosystem functions and related services (Oliver et al. 2015a). Alike, the conservation of pollinator biodiversity, bees included, can safeguard ecosystem resilience against environmental changes (Senapathi et al. 2015). Despite the fact that the contribution of wild bees to crop pollination and the subsequent financial benefits are often used as an argument for their conservation, such reasoning disregards that the majority of wild bee species do not contribute considerably to crop production (Kleijn et al. 2015). Instead, moving beyond ecosystem-service-based arguments and employing aesthetic (Breeze et al. 2015) or moral (Kleijn et al. 2015) arguments might better promote conservation of wild bee diversity.

In conclusion, I have demonstrated that applying conservation measures that collectively tackle different stressors and harness the links between interacting organisms could benefit wild bee biodiversity in agricultural landscapes. Nevertheless, even such measures may be insufficient in case of drastic changes (e.g. extreme fluctuation of precipitation across a year) and they should be combined with measures to slow down climate change, such as emission reductions (Oliver et al. 2015b).

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Appendix

Curriculum vitae

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EDUCATION

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04/2011-03/2013 Master’s Degree in Ecological Design, Sustainable Development and
Management of Protected Areas
Aristotle University of Thessaloniki, Greece
Mark: 9.8/10 (Excellent, ECTS Scale A)
MSc Thesis: “Studying the effect of land use change on the connectiv-
ity of the European network of protected areas Natura 2000” (Mark:
10/10)

09/2006-03/2011 Bachelor’s Degree in Biology
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BSc Thesis: “Potential changes of plant species richness under differ-
ent pressures: an example of Mediterranean-type ecosystems”
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OCCUPATIONAL COMPETENCES

| | |
|-----------------|---|
| 03/2013 | Research Assistant Aristotle University of Thessaloniki Project: SCALES – Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal and Ecological Scales (EU FP 7, Integrated Project) |
| 09/2012-10/2012 | Research Assistant Aristotle University of Thessaloniki Project: Spatial patterns and ecological processes at a landscape level, Management Body of Ecodevelopment Area of Karla-Mavrovouni-Kefalovriso-Velestino" (Greek Ministry of Environment, Energy and Climate Change) |
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List of publications

Publications of this thesis

Papanikolaou A.D., Kühn I., Frenzel M. & Schweiger O., 2017. Semi-natural habitats mitigate the effects of temperature rise on wild bees. *Journal of Applied Ecology*, 54: 527–536

Papanikolaou A.D., Kühn I., Frenzel M., Schweiger O., 2017. Landscape heterogeneity enhances stability of wild bee abundance under highly varying temperature, but not under highly varying precipitation. *Landscape Ecology*, 32: 581–593

Papanikolaou A.D., Kühn I., Frenzel M., Kuhlmann M., Poschlod P., Potts S.G., Roberts S.P.M., Schweiger O. Wild bee and floral diversity co-vary in response to the direct and indirect impacts of land use (Under review in *Ecological Monographs*)

Other publications by the author

Mazaris A.D., **Papanikolaou A.D.**, Barbet-Massin M., Kallimanis A.S., Jiguet F., Schmeller D.S., Pantis J.D., 2013. Evaluating the connectivity of a protected areas' network under the prism of global change. *Plos One*, 8 (3), e59640

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Klenke R., Mertzanis Y., **Papanikolaou A.D.**, Arponen A., Mazaris A.D., 2014. Stay in contact: practical assessment, maintenance, and re-establishment of regional connectivity. In: Henle K., Potts S.G., Kunin W.E., Matsinos Y.G., Similä J., Pantis J.D., Grobelnik V., Penev L., Settele J., (eds.) *Scaling in ecology and biodiversity conservation*. Pensoft, Sofia, 167-172

Conference Contributions

Papanikolaou A.D., Kühn I, Frenzel M., Schweiger O. Landscape structure alters the response of wild bee communities to changes in weather conditions (Oral presentation) 46th Annual Conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 5-9 September 2016, Marburg, Germany.

Papanikolaou A.D., Schweiger O., Frenzel M, Kühn I. Bee richness response to warming can be modified by landscape structure (Oral presentation) 27th International Congress for Conservation Biology - 4th European Congress for Conservation Biology, 2-6 August 2015, Montpellier, France.

Papanikolaou A.D., Schweiger O., Kühn I. How green infrastructure can mitigate the consequences of climate change? (Poster presentation) 43rd Annual Conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ), 9-13 September 2013, Potsdam, Germany.

Papanikolaou A.D., Almpantidou V., Mazaris A.D., Pantis J.D. Applying graph theory to explore the properties of the Natura2000 conservation network. (Poster presentation) 3rd European Congress of Society of Conservation Biology, 28 August-1 September 2012, Glasgow, UK.

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit mit dem Titel „Spatiotemporal response of pollinators to drivers of global change at landscape scale“ bisher weder bei der Naturwissenschaftlichen Fakultät I - Biowissenschaften - der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), 06.04.2017

Alexandra Papanikolaou