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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 (± 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 (±31)	9·66 (±0·69)	592 (±128)	16·91	7476	24	129 (±3)
Greifenhagen	51·6329° N	11·4340° E	270 (±27)	9·27 (±0·89)	606 (±118)	10·48	2823	24	104 (±10)
Harsleben	51·8423° N	11·0753° E	143 (±14)	9·56 (±0·74)	581 (±176)	16·30	259 943	18	121 (±11)
Siptenfelde	51·6491° N	11·0526° E	423 (±31)	7·43 (±0·76)	646 (±117)	15·89	56 589	19	73 (±6)
Schafstaedt	51·3770° N	11·7224° E	177 (±11)	8·83 (±0·82)	580 (±101)	1·65	898	18	101 (±5)
Wanzleben	52·0803° N	11·4518° E	113 (±10)	9·68 (±0·69)	591 (±130)	10·26	63 332	21	101 (±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) proofed 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 fortnight 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 $r = 0{\cdot}8$, $P < 0{\cdot}001$), 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

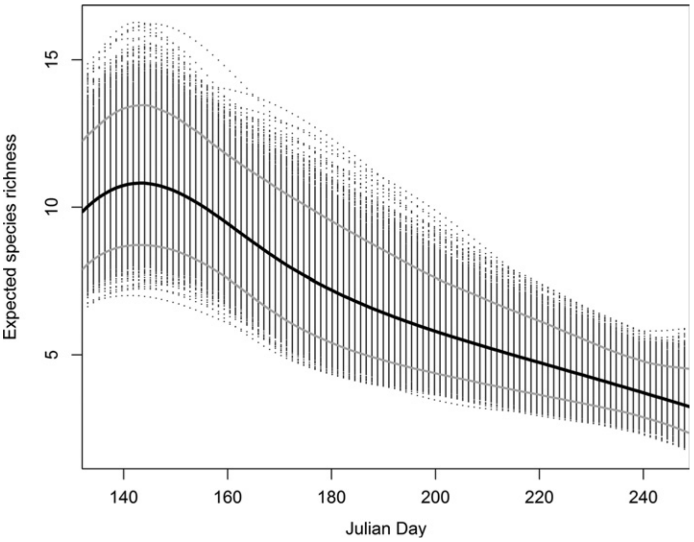

Fig. 1. Phenology curve displaying the expected species richness per trap along the total monitoring period within a year (black curve). The dark-grey lines represent the 95% prediction intervals based on predictions from the posterior distribution with 10 000 replicates per Julian day (black dots).

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 ($r = -0{\cdot}82$). 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 × 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 ($R^2 = 0{\cdot}99$; 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 $P = 0{\cdot}93$). 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

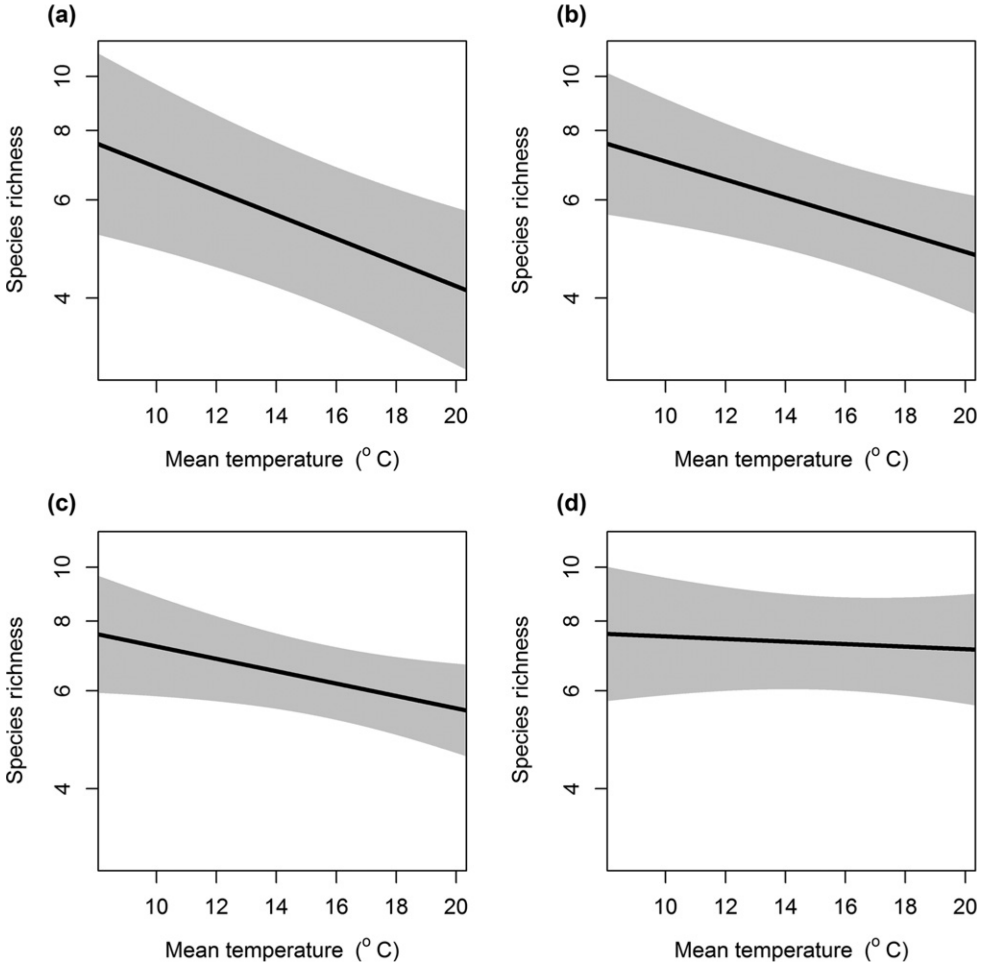

Fig. 2. Interactive effect of temperature and landscape composition on bee species richness. The effect of temperature increase on species richness is displayed for four different levels of percentage of semi-natural areas: (a) 2%, (b) 6%, (c) 10%, (d) 17%. The cover range in the plot starts from the 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 (Kühsel & 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 (Kühsel & 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	δAICc	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 (±0·05)	0·16 (±0·14)	0·10 (±0·02)	−0·28 (±0·14)				
B	−0·08 (±0·06)	0·05 (±0·17)	0·10 (±0·02)					
C	−0·09 (±0·06)	0·05 (±0·17)	0·10 (±0·02)			−0·01 (±0·03)		
D	−0·08 (±0·06)	0·04 (±0·17)	0·10 (±0·02)		0·05 (±0·17)			
E	−0·08 (±0·06)	0·08 (±0·19)	0·10 (±0·02)				−0·06 (±0·19)	
F	−0·08 (±0·06)	0·05 (±0·17)	0·10 (±0·02)					0·004 (±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 (Winfree *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 (hedges, 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 twofold 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.