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

Alexandra D. Papanikolaou (iD) · **Ingolf Kühn** · **Mark Frenzel** · **Oliver Schweiger**

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.

A. D. Papanikolaou (✉) · I. Kühn · M. Frenzel · O. Schweiger
Department of Community Ecology, Helmholtz Centre for Environmental Research–UFZ, Theodor-Lieser-Straße 4, 06120 Halle, Germany
e-mail: alexandra.papanikolaou@ufz.de

I. Kühn
Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany

I. Kühn
German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

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 ($CV = σ/μ$) 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 × 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 (δAICc) 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	δAICc	Akaike weight	Cumulative weight
CV_{temp} × 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} × 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, *δAICc* 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	δAICc	Akaike weight	Cumulative weight
CV_{prec} × 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} × 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, *δAICc* 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; Kühsel 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
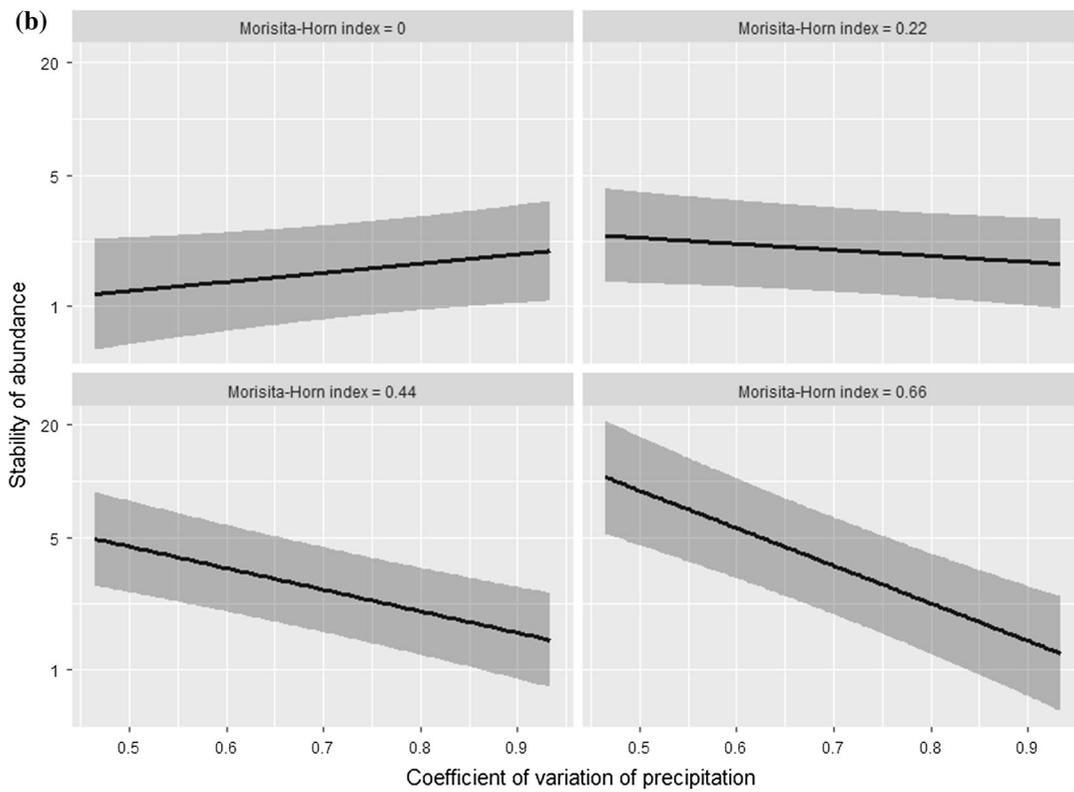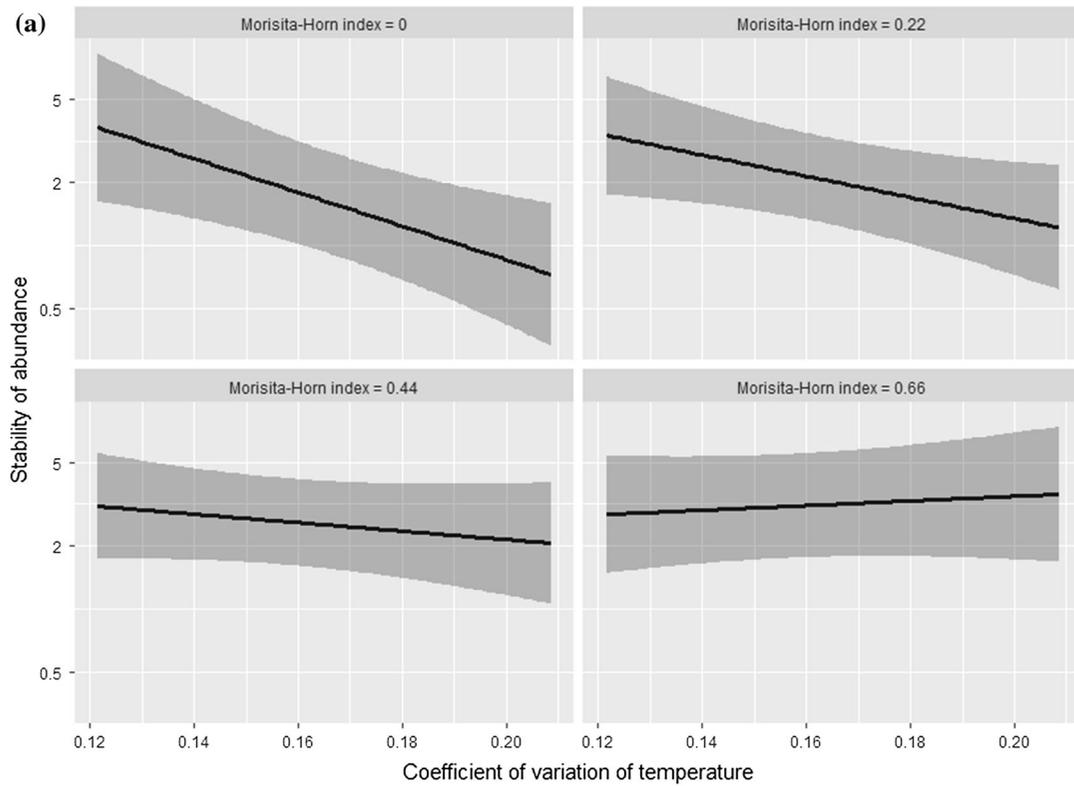
◄ **Fig. 1** Interactive effect of weather variability and landscape heterogeneity on the stability of wild bee abundance in Central Germany. The effect of **a** increasing temperature variability and of **b** increasing precipitation variability on stability of abundance (on log-scale) is displayed 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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