

Contrasting responses of bee communities to coffee flowering at different spatial scales

Dorthe Veddeler, Alexandra-Maria Klein and Teja Tschardtke

Veddeler, D., Klein, A.-M. and Tschardtke, T. 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. – *Oikos* 112: 594–601.

While investigating biodiversity patterns on different spatial scales, ecological processes determining these patterns have been rarely analysed. Flower visitation by bees is an important ecological process that is related to floral resource availability. However, little is known about whether responses of bee communities to floral resource availability change at different spatial scales. We studied density and species richness of flower-visiting bees in relation to floral resource availability, provided by coffee, in traditional agroforestry systems on a field, shrub, and branch scale. On a field scale, mean bee density per shrub increased with decreasing proportion of flowering coffee shrubs per site, showing a dilution effect. Conversely, on shrub and branch scales bee density per shrub, or shrub part, increased with increasing number of inflorescences, showing a concentration effect. Additionally, bee density per shrub was higher on those that were only partly, rather than totally surrounded by other flowering coffee shrubs. Species richness of flower-visiting bees was positively affected by high resource availability on a shrub and a branch scale, expressed by a high number of inflorescences, but at the field scale the proportion of flowering shrubs per site did not have any effect on species richness. Our results show contrasting responses of the community of flower-visiting bees to floral resource availability, depending on the spatial scale considered. We conclude that patterns of flower-visiting bee communities of only one spatial scale can not be generalized, since the number of pollinators may be limited on a field scale, but not on smaller scales.

D. Veddeler, A.-M. Klein and T. Tschardtke, Agroecology, Univ. of Göttingen, Waldweg 26, DE-37073 Göttingen, Germany (dveddel@gwdg.de).

Biodiversity patterns vary across different spatial scales (Wagner et al. 2000, Gering and Christ 2002, Willis and Whittaker 2002, Summerville et al. 2003). Factors driving biodiversity are known to be scale-delimited such that variables accounting for species richness on a smaller scale may operate differently on broader scales (Crawley and Harral 2001, Steffan-Dewenter et al. 2001, Willis and Whittaker 2002, Tylianakis et al. 2005). Investigations of communities on different spatial scales have mainly paid attention to gradients from local fields to landscapes, regions or even larger geographical scales (latitudes, continents). Examples include studies on birds (Lennon et al. 2001, Rahbek and Graves 2001), bees (Steffan-Dewenter et al. 2001, 2002), butterflies

(Summerville et al. 2003) or herbivory and parasitism rates (Thies et al. 2003). Only few studies included community patterns on scales within single sites, like patches or quadrats for comparing plant diversity (Wagner et al. 2000, Crawley and Harral 2001) or even single plant individuals and seedheads for analyzing parasitoid density (Norowi et al. 2000). Moreover, the majority of studies on scale dependence of biodiversity failed to analyse the ecological processes determining these patterns (Huston 1999, Wagner et al. 2000, Crawley and Harral 2001). Combining community structures and ecological processes on small scales below the local (field) scale may contribute to the assessment of large-scale biodiversity patterns, providing a better

Accepted 29 August 2005

Copyright © OIKOS 2006
ISSN 0030-1299

understanding of the ecological factors driving these patterns.

The distribution of bee communities is of particular interest. As pollen vectors, bees provide important ecosystem services (Daily et al. 1997) and thus not only contribute to the maintenance of plant diversity but also encourage crop production (Free 1993, Roubik 1995, Buchmann and Nabhan 1996, Daily et al. 1997, Allen-Wardell et al. 1998, Kremen et al. 2002, de Marco and Coelho 2004, Ricketts et al. 2004). A high species richness and abundance of pollinating bees can provide high pollination success, even in self-pollinated plants such as the highland coffee, *Coffea arabica* L. (Rubiaceae), a tropical cash crop (Raw and Free 1977, Roubik 2002, Klein et al. 2003, Ricketts et al. 2004). Even though some investigations have already produced insights into the scale dependence of bees and their foraging behaviour on a landscape scale (Steffan-Dewenter et al. 2002, Westphal et al. 2003), to our knowledge, a comparison of bee distributions at smaller scales, from habitat level down to single plant species or individuals, is still missing.

Foraging behaviour may change in response to the factors that operate at different scales (Crist and Wiens 1994). In particular, floral resource availability, the quantity of flowers but also floral reward structure (nectar and pollen) affects the foraging behaviour of flower visitors (Stone 1994, Steffan-Dewenter and Tscharrntke 2000, Klein et al. 2004, Potts et al. 2004). Patterns of floral supply may differ between and within scales. On a field scale, synchronous flowering of a single plant species provides a high number of flowers, which is supposed to attract a large number of pollinators, thereby enhancing cross pollination (Sakai 2002, Forsyth 2003). On smaller scales, within a habitat, plant arrangement and the number of flowers on single plants respectively may influence foraging behaviour and flower or plant constancy of bees (Kunin and Iwasa 1996). On the smallest scale, the distribution of flowers on a plant may affect patterns of flower visitors on a single plant. In the case of coffee, inflorescences develop predominantly on the new shoots at the end of a branch or the upper part of the coffee shrub. Additionally, pollinators may prefer certain flower positions on a single plant (Hambäck 2001) and differences in pollen deposition at different heights have also been found (Lortie and Aarsen 1999). An investigation of bee communities over different spatial scales may provide new insights into bee foraging behaviour and thus bear implications for the management of crop cultivars with the aim of successful pollination.

We studied the responses of flower-visiting bees on coffee to floral resource availability at three different scales, a field, a shrub and a branch scale, considering the following questions on each scale respectively:

Field scale. How does synchronous flowering of coffee shrubs in a single coffee field influence the distribution of bee communities?

Shrub scale. Does the degree of floral resource availability on and around a single coffee shrub have an impact on foraging behaviour of bees?

Branch scale. Do flower visitors prefer certain spatially oriented flower patches on a coffee shrub?

Methods

Study area

The study was carried out from October to December 2003 in the cantons Jipijapa, Pajan, and Noboa in Manabi, coastal Ecuador. The study area is situated at an altitude of 100–550 m (17 N546800 m, E 9849274 m) with an annual rainfall of 1500 to 1700 mm, and a mean annual temperature of 25°C. Seasonality is very distinctive; the dry season lasts approximately from June until the end of December, with hardly any rainfall. Coffee (*Coffea arabica*) is cultivated in traditional agroforestry systems, planted under a canopy of various shade trees. The tree canopy is comprised of Leguminosae (*Inga* sp.), forest remnant trees, or trees that provide products for local or market subsistence, (e.g. fruits, construction materials or timber). Low-density or mono-specific shade coffee or sun coffee scarcely occur in this region and thus were not included. Certified organic as well as non-organic coffee agroforestry systems exist, but the latter generally also lack agrochemical inputs. Weeds are cut once per year, just before the final ripening of coffee fruits in June/July, to facilitate harvest. In this region, coffee flowers only once per year in the dry season, with buds generally opening eight days after a single heavy rainfall. Coffee flowered at different times in different sites, due to temporal variation in rainfall between different parts of the study region.

For an investigation of coffee flower-visiting bees, we chose 22 agroforestry sites (Fig. 1). In most sites, more than 50 percent of coffee shrubs flowered synchronously within 1–2 days. In four sites we watered eight to ten randomly chosen shrubs, because buds had already started to dry out. Accordingly there was a gradient in the proportion of flowering coffee shrubs along sites.

Bee observations

For the observation of flower-visiting bees we chose four coffee shrubs per site. Shrubs were about the same height of 1.6–1.8 m, and approximately reached about the same age. Shrubs were situated in the middle of a field to avoid edge effects. Flower-visiting bees were observed 15 min on each of the four coffee shrubs (divided into five minute intervals) between 8:00 and 14:00 when bees were

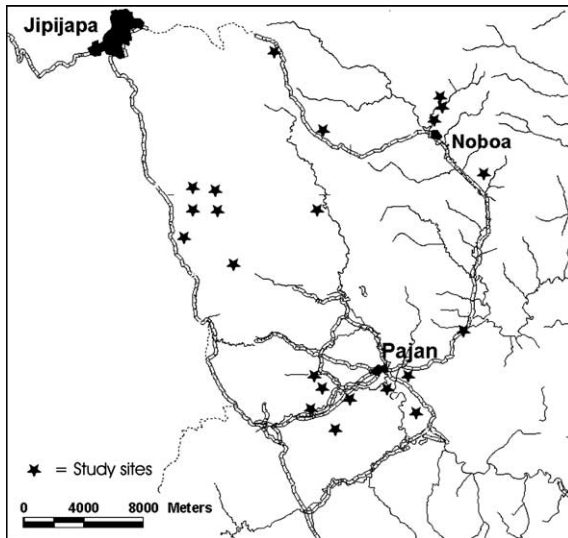


Fig. 1. Map of the study region with study sites.

active. Each flower visitor was recorded and identified. After observations, bees were caught by sweep-netting for further identification. Short flowering times combined with a low number of individuals inhibited sampling of some of the observed morphospecies, so that only eight could be identified to genus or species level. Spatial distribution of the flower-visiting community foraging on coffee shrub was analysed on a total of 18 extra shrubs in three sites, chosen after the same criteria as the four shrubs per site. We defined the shrub parts as the half of the height of the shrub (excluding the branchless stem) for top/bottom ($n=9$) and the half of each branch for outside/inside ($n=9$). We observed bees on each shrub part for 15 min.

Floral resource availability and biotic and abiotic habitat parameters

Field level

The flower availability per site was calculated as the proportion of all flowering coffee shrubs relative to all shrubs found in one site. Additionally the percent cover of all non-coffee flowering plants (of which all were herbs) was estimated.

Habitat characteristics of the 22 agroforestry sites were quantified to test for possible relations with species richness or density of bees. Percentage incident light was measured with a luxmeter (digital light-gauge with four scopes from 0–1999 $W\ m^{-2}$, Mavoloux, Gossen) and canopy cover was estimated using a densitometer (Spherical crown densitometer, Forestry Suppliers). Vegetation was sampled in nine quadrats per site. In $2.5 \times 2.5\ m$ quadrats for herbs and $10 \times 10\ m$ quadrats for shrubs and trees the number of morphospecies and

the respective number of individuals were recorded. Height of trees was measured to calculate the coefficient of variation in tree height as an indicator of structural habitat diversity. Because some tree species were represented by only one or few individuals in a site, we calculated the Shannon-Wiener diversity index as a measurement for canopy tree diversity.

Shrub and branch scale

Floral resource availability per shrub was estimated by counting all flower inflorescences on the observed shrub. Here an inflorescence consisted of a collar in the leaf axils, comprising 10–20 flowers. Additionally we noted whether shrubs were totally surrounded by other flowering coffee shrubs, (all neighbouring shrubs flowered, 4–6 shrubs) or only partly surrounded by flowering shrubs (1–3 shrubs). During bee observations, we measured temperature and humidity on each observed shrub in five minutes intervals between observation periods to calculate mean values, and recorded the time by starting the observations. We classified shrubs into the three groups sunny, half-shaded, and shaded shrubs.

On each of the 18 extra observed shrubs we counted inflorescences and estimated their proportion at branches at the top and at the bottom, and outside and inside of the respective shrubs.

Statistical analyses

All data were transformed to meet conditions of normality if necessary. Percentages were arcsin-square-root-transformed (Sokal and Rohlf 1995). Statistical analyses were performed using the software Statgraphic Plus 3.0 for Windows (Manugistics 1997) and Statistica 6.1 (StatSoft 2003).

For analyses at the field scale we calculated the mean value of the four observed shrubs for the number of individuals thereby yielding the mean bee density (number of individuals per shrub) per shrub but we used the total number of species found in a site. For analyses on the shrub scale we took the density per shrub and the actual species number per shrub. Similarly, we used the density and species richness per shrub part for branch scale analyses. To investigate relations with the biotic and abiotic habitat parameters on a field scale we conducted multiple regressions using backward selection until only significant variables were left. To show that sites were independent from each other we tested for spatial autocorrelation. We related the residuals from the results of the multiple regressions with either bee density or bee species richness to the geographic distances between sites with the Mantel statistics based on Spearman's rank correlations with 1000 permutations and Euclidian distances as similarity indices (Legendre and Legendre 1998). This method

allows excluding the variation explained by the habitat parameters rather than arbitrarily pooling them. For the analyses we used the statistics program R (R development Core Team 2004). The results showed that there was no spatial autocorrelation in the data, neither for bee density nor for bee species richness (bee density: $r = -0.11$, $p = 0.94$, bee species richness: $r = -0.08$, $p = 0.86$). Because the four shrubs of one site were not independent of each other, we used a mixed effects model for analyzing the relation of floral resources or light conditions to bee density or species richness on a single shrub. With this model we were able to exclude within-site variation by using "site" as a random factor in the model (Crawley 2002, p. 35), thereby accounting for spatial autocorrelation on a shrub scale. Differences between shrub parts were analysed with one-way ANOVAs. We estimated total species richness of bees using the abundance-based coverage estimator ACE of the program EstimateS (Colwell and Coddington 2000), using 100 randomizations, and calculated saturation values of the recorded species numbers.

Results

We identified 29 morphospecies of flower-visiting bees on coffee in 22 sites including 19 morphospecies of social bees (2743 individuals) and ten solitary bee species (only 29 individuals). The bee community in a single site was dominated by one or two species, the Africanized honeybee *Apis mellifera scutellata* (Lepelletier) (10 to 67%, mean: 41.83 ± 19) and/or the stingless bee *Partamona peckolti* (Friese) (2 to 66%, mean: 23.3 ± 18.4). Further significant visitors were the stingless bee species *Nannotrigona mellaria* (Smith), *Nannotrigona perilampoides* (Cresson), *Cephalotrigona capitata* (Smith), *Tetragonisca angustula* (Latreille), *Trigona almathea* (Vachal), and *Melipona mimetica* (Cockerell). The number of morphospecies observed was highly correlated with the estimated species number ($r = 0.91$, $n = 22$, $p < 0.0001$). The mean saturation value was $84.39 \pm 14.5\%$ of the estimated species number. Because observed species richness revealed the pattern of estimated species richness we used the observed species number for further analyses.

Field scale

Density of flower-visiting bees did not correlate with species richness. Bee density (mean number of individuals per shrub) increased significantly with decreasing proportion of flowering shrubs per site (Fig. 2), but was not related to the percent cover of non-coffee flowering plants (average of $7.7 \pm 12.13\%$), nor to any of the habitat parameters. The number of bee species was not related to the percentage of flowering coffee shrubs per

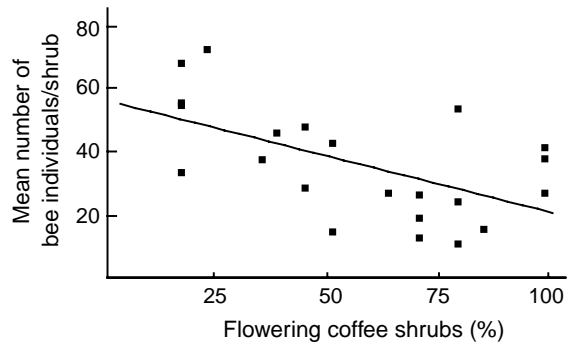


Fig. 2. Mean density of flower-visiting bees per shrub (observed within 15 min per shrub) in relation to the proportion of flowering coffee shrubs per agroforestry site. $F_{1,20} = 8.09$, $r^2 = 0.32$, $p < 0.05$, $\log(y) = 2.32 - 0.32 \times \arcsin(\sqrt{x/100})$.

site or to the percent cover of non-coffee flowering plants, but it was positively correlated with the diversity of canopy trees (simple regression: $F_{1,20} = 9.21$, $r^2 = 0.32$, $p < 0.01$, $y = 3.31 + 5.73 \times x$).

Shrub scale

Both density and species richness of bees on a shrub were significantly positively correlated with the number of inflorescences per shrub (Fig. 3A, 3B). Additionally, bee density was significantly higher on shrubs that were

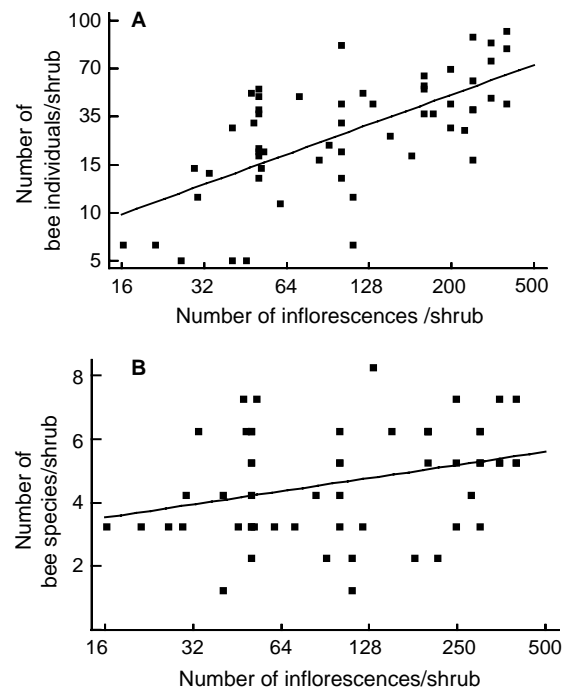


Fig. 3. Density (A) and species number (B) of flower-visiting bees per shrub (observed within 15 min per shrub) in relation to number of flower inflorescences per shrub. Mixed effects model: (A) bee density: $F_{1,53} = 38.1$, $r^2 = 0.34$, $p < 0.0001$; (B) bee species richness: $F_{1,53} = 7.45$, $r^2 = 0.09$, $p < 0.01$.

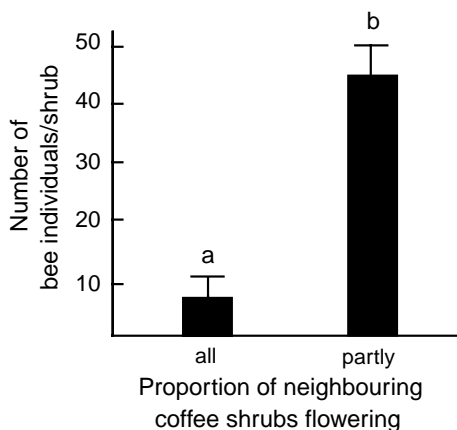


Fig. 4. Density of flower-visiting bees on shrubs being totally or only partly surrounded by other flowering coffee shrubs (observed within 15 min per shrub). Arithmetic mean and standard error are given. Mixed effects model: $F_{1,53} = 10.35$, $r^2 = 0.09$, $p < 0.01$.

only partly rather than totally surrounded by other flowering coffee shrubs (Fig. 4).

More species were observed on sunny and half-shaded than on shaded shrubs ($F_{2,52} = 8.70$, $r^2 = 0.23$, $p < 0.001$). Species richness similarly increased with temperature, which was positively related with time and differed between the three shade categories of the shrubs (correlation matrix, Table 1).

Branch scale

The proportion of inflorescences on a coffee shrub was significantly higher on branches at the top of a shrub than at the bottom (one-way ANOVA: $F_{1,17} = 46.49$, $p < 0.0001$) and significantly higher at the outer than at the inner part of a shrub (one-way ANOVA: $F_{1,14} = 10.22$, $p < 0.01$). The same pattern was revealed for both bee density (Fig. 5A, 5B) and bee species number (Fig. 6A, 6B), indicating that both corresponded to relative dense flower patches on a coffee shrub. When the proportion of inflorescences was included as a covariable in the analyses, differences in species number or density between the different parts of a shrub were no longer significant.

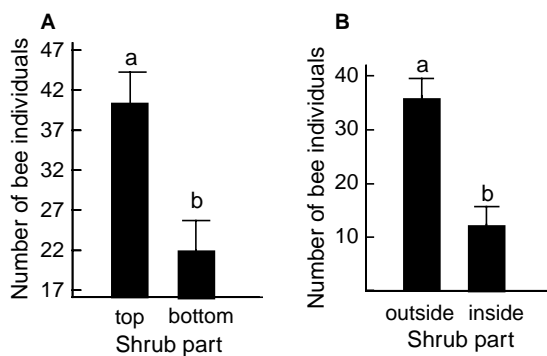


Fig. 5. Density of flower-visiting bees at (A) the top and at the bottom and (B) outside and inside of a coffee shrub (observed within 15 min per shrub part). One-way ANOVA: (A) $F_{1,16} = 10.81$, $p < 0.01$, (B) $F_{1,16} = 20.39$, $p < 0.001$.

Discussion

Our results show that the density of flower-visiting bees on coffee responded contrastingly to the availability of floral resources at three different spatial scales. On the field scale, bee density increased with decreasing proportion of flowering shrubs per site, whereas on a shrub scale bee density increased with increasing number of inflorescences per shrub, but was higher on shrubs that were only partly, rather than totally surrounded by other flowering shrubs. On a branch scale, density of bees corresponded to dense flower patches at different parts of a coffee shrub. Bee species richness was positively affected by high resource availability on a branch and on a shrub scale, but not on a field scale.

Accordingly, on a branch and on a shrub scale, bee density was positively influenced by a high number of inflorescences, whereas at the field scale relative high floral resource availability due to a high proportion of shrubs flowering influenced bee density negatively. When all shrubs flowered synchronously, the number of bees per shrub was reduced, resulting in a dilution effect. Additionally, the reduced number of bees on shrubs that were completely surrounded by other flowering coffee shrubs also implies a dilution of bee density. However, when only few shrubs flowered in a site, the number of bee visitors per shrub increased, resulting in a concentration effect. The density of flower visitors seemed to increase proportionally with increasing resource avail-

Table 1. Correlation^a matrix of the abiotic shrub parameters and species number and density of flower visiting bees per shrub^b.

	Temperature	Time of day	Species number	Bee density
Humidity	-0.8169****	-0.7327****	-0.3700**	0.1606
Temperature		0.7160****	0.3848**	-0.1215
Time of day			0.1659	-0.2499
Species number				0.5136****

^aPearson correlation coefficient

^bSignificance, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$; $n = 64$ shrubs

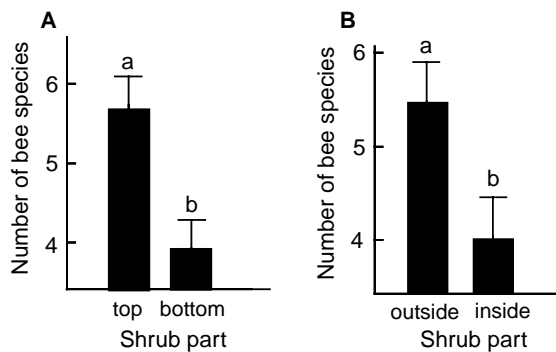


Fig. 6. Species number of flower-visiting bees at (A) the top and the bottom and (B) the outer and the inner part of a coffee shrub (observed within 15 min per shrub part). One-way ANOVA: (A) $F_{1,16}=11.08$, $p < 0.01$, (B) $F_{1,16}=5.16$, $p < 0.05$.

ability only to a certain degree. That is in accordance with the suggestion that the pool of available pollinators might be saturated below the maximum flower density (Tøtland and Matthews 1998). However, these results do not support the assertion that synchronized flowering may increase activity of flower visitors through immigration and population growth (Sakai 2002). In contrast, on a smaller scale (i.e. shrub and branch scale), a high number of flowers enhanced the number of flower-visiting bees. This was in accordance with a previous study that found an increase in the density of flower visitors with increasing flower density on a shrub (Klein et al. 2002).

On the basis of these contrasting effects of high resource levels on different spatial scales, we conclude that the number of flower visitors seems to increase with a high number of flowers available but only as long as there still exists a pool of pollinators. This implies that the number of flower visitors in a site is constant but bee density per observation unit may decrease after saturation of floral resources is reached. In this study the relatively small number of non-coffee flowering plants did not have an impact on flower visitors observed on coffee plants. In the dry-season, flowering herbs are very sparse so the high number of coffee flowers may be the more attractive food source for bees. Furthermore, the heterogeneity of flower-visiting bee communities on a single plant was related to a similarly heterogeneous distribution of flower inflorescences. Flower visitors on a single plant seemed to be attracted by flower patches on a shrub with a relatively high number of flowers. Finally, floral reward structure, as the ultimate attractant of flower visitors (Bosch et al. 1997), might have influenced foraging behaviour of bees on this smallest scale. Flower visitors are known to prefer high quality nectar (Stone 1994, Skyhoff and Bucheli 1995) and flowers at the top and outside of a shrub might have offered more favourable floral reward conditions. However flower visitors did not have apparent preferences concerning

the spatial position of flowers per se. Hence, from this point of view we can not confirm the idea of a spatially heterogeneous bee community on single plants, suggested by Hambäck (2001).

Species richness on a field scale showed no response to floral resource availability. On a shrub and branch scale it increased, similarly to bee density, with the number of inflorescences per shrub or shrub part. Dense flower patches seem to be the more attractive resource for many different bee species at smaller spatial scales. Furthermore, on a field scale, bee species richness increased with the diversity of shade trees, underlining the results found by Klein et al. (2002), who observed an increase in social bee species richness on coffee flowers with decreasing land-use intensity. Additionally, on a shrub scale, species richness of flower-visiting bees was higher at sunny and half-shaded coffee shrubs than at shaded ones, showing a preference for high light intensity in flower-visiting bees. Foraging behaviour of bees is known to be temperature dependent (Roubik 1989, Herrera 1995), and we also found a positive relationship between species number and temperature. At cold ambient temperatures, bees may prefer to visit sunny flowers to raise their body temperature (Roubik 1989). Consequently microclimate might also have had an effect on the distribution of foraging bees on the branch scale. Flowers at the top and outside of a shrub may be more exposed to sun light than those at the bottom and inside a shrub. Furthermore flowers in direct sunlight secrete nectar earlier and at a higher rate (Roubik 1989), increasing the availability of floral rewards and thereby attracting more visitors (Stone 1994, Skyhoff 1995).

Our results on smaller than landscape scales affirm the suggestion that factors which are responsible for either biodiversity or community patterns are scale-dependent (Clarke and Lidgard 2000, Crawley and Harrol 2001) and reflect results of studies on broader scales, which show scale-specific dependences on different variables of communities. For example, Rahbek and Graves (2001) demonstrated that birds responded in a varied manner to a suite of environmental variables on different spatial scales in South America. Furthermore, de Vries et al. (1997) and de Vries and Walla (1999) found that butterfly communities are affected by scale-dependent factors such as forest strata and forest type. Here we show that even on smaller scales below the local one, species richness can be related to different variables, depending on the respective scale considered. In addition, our results demonstrate that a single variable can even have reversed effects on the same community at different scales, as revealed by the contrasting responses of flower-visiting bee communities to resource availability from a field to a branch scale. Varying patterns of resource-density dependence at different scales are not unlikely. For example Norowi et al. (2000) found reverse parasitism rates for a single parasitoid–host relationship

comparing the finest scale, represented by seed heads, with the intermediate scale, represented by plant individuals.

We conclude that community patterns such as the relation of flower-visiting bee communities to floral resource availability can not be generalized but have to be considered separately for each single scale, assuming that the number of bees may be limited in a site. From an applied perspective this may be taken into account in management schemes to reach optimal coffee productivity, by encouraging successively rather than synchronously flowering coffee shrubs, thereby enabling concentration rather than dilution effects on flower visitation by bees.

Acknowledgements – We like to thank Dr David W. Roubik, who kindly identified most of the bee species and Dr Giovanni Onore for the use of the bee collection at the Universidad Católica in Quito. We are grateful to Free de Koning, Roland Olschewski and Betty Pico Diaz of the project BIO-SYS (Evaluation of biological diversity of land-use systems in a mega-diverse region of Ecuador) for their support and help and to Tannya Lozada for the help with the collection of vegetation data. Dennis Hansen, Taylor Ricketts, Stacy Philpott and Jason Tylanakis provided helpful comments on the manuscript. We are thankful to Cesar Calderon, Angel Chóez and Jesus Lino from COFENAC (Consejo Cafetalero Nacional) for their great help with the field work, to Anne Richter for help with bee observations, and to all Ecuadorian smallholders in and around Jipijapa for their permission to work in their “cafetales”. We like to thank the GTZ (Deutsche Gesellschaft für technische Zusammenarbeit) for their cooperation and the German Ministry of Education and Research (BMBF) for the financial support.

References

- Allen-Wardell, G., Bernhardt, P., Bitner, R. et al. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. – *Conserv. Biol.* 12: 8–17.
- Bosch, J., Retana, J. and Cerdá, X. 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. – *Oecologia* 109: 583–591.
- Buchmann, S. and Nabhan, G. 1996. *The forgotten pollinators*. – Island Press.
- Clarke, A. and Lidgard, S. 2000. Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. – *J. Anim. Ecol.* 69: 799–814.
- Colwell, R. K. and Coddington J. A. 2000. EstimateS: statistical estimation of species richness and shared species from samples. Version 5. User's guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>.
- Crawley, M. J. 2002. *Statistical computing: an introduction to data analysis using S-Plus*. – John Wiley & Sons Ltd.
- Crawley, M. J. and Harral, J. E. 2001. Scale dependence in plant diversity. – *Science* 291: 864–868.
- Crist, T. and Wiens, J. A. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. – *Oikos* 69: 37–46.
- Daily, G. C., Alexander, S., Ehrlich, P. et al. 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. – *Issues Ecol.* 2.
- De Marco, P. and Coelho, F. M. 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. – *Biodiv. Conserv.* 13: 1245–1255.
- De Vries, P. J. and Walla, T. R. 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. – *Biol. J. Linn. Soc.* 68: 333–353.
- De Vries, P. V., Murray, D.M. and Lande, R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. – *Biol. J. Linn. Soc.* 62: 343–364.
- Forsyth, S. A. 2003. Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. – *Oecologia* 136: 551–557.
- Free, J. B. 1993. *Insect pollination of crops*. – Academic Press.
- Gering, J. C. and Christ, T. O. 2002. The alpha-beta regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. – *Ecol. Lett.* 5: 433–444.
- Hambäck, P. A. 2001. Direct and indirect effects of herbivory: feeding by spittlebugs affects pollinator visitation rates and seedset of *Rudbeckia hirta*. – *Ecoscience* 8: 45–50.
- Herrera, C. M. 1995. Floral biology, microclimate, and pollination by ectothermic bees in an early blooming herb. – *Ecology* 76: 218–228.
- Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. – *Oikos* 86: 393–401.
- Klein, A. M., Steffan-Dewenter, I., Buchori, D. et al. 2002. Effects on land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. – *Conserv. Biol.* 14: 1226–1228.
- Klein, A. M., Steffan-Dewenter, I. and Tschardt, T. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. – *Proc. R. Soc. B* 270: 955–961.
- Klein, A. M., Steffan-Dewenter, I. and Tschardt, T. 2004. Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. – *J. Anim. Ecol.* 73: 517–525.
- Kremen, C., Williams, N. M. and Thorp, R. W. 2002. Crop pollination from native bees at risk from agricultural intensification. – *Proc. Natl Acad. Sci. USA* 99: 16812–16816.
- Kunin, B. and Iwasa, Y. 1996. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. – *Theor. Popul. Biol.* 49: 232–263.
- Legendre, P. and Legendre, L. 1998. *Developments in environmental modelling*. – Elsevier.
- Lennon, J. L., Koleff, P., Greenwood, J. J. D. et al. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. – *J. Anim. Ecol.* 70: 966–979.
- Lortie, C. J. and Aarsen, L. W. 1999. The advantage of being tall: higher flowers receive more pollen in *Verbascum thapsus* (Scrophulariaceae). – *Ecoscience* 6: 68–71.
- Manugistics 1997. *Statgraphics plus for Windows, Version 1, User manual*. – Manugistics Inc.
- Norowi, H. M., Perry, I. N., Powell, P. et al. 2000. The effect of spatial scale on interactions between to weevils and their parasitoid. – *Ecol. Entomol.* 25: 188–196.
- Potts, S. G., Vulliamy, B., Roberts, S. et al. 2004. Nectar resource diversity organises flower-visitor community structure. – *Entomol. Exp. Appl.* 113: 103–107.
- R Development Core Team 2004. *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Rahbek, C. and Graves, G. R. 2001. Multiscale assessment of pattern of avian species richness. – *Proc. Natl Acad. Sci. USA* 98: 4534–4539.
- Raw, A. and Free, J. B. 1977. The pollination of coffee (*Coffea arabica*) by honeybees. – *Tropical Agric.* 54: 365–370.

- Ricketts, T. H., Daily, G. C., Ehrlich, P. R. et al. 2004. Economic value of tropical forest to coffee production. – *Proc. Natl Acad. Sci. USA.* 101: 12579–12582.
- Roubik, D. W. 1989. Ecology and natural history of tropical bees. – Cambridge Univ. Press.
- Roubik, D. W. 1995. Pollination of cultivated plants in the tropics. – Food and Agric. Org., Rome, Italy.
- Roubik, D. W. 2002. Feral African bees augment Neotropical coffee yield. – In: Kevan, P. G. and Imperatriz-Fonseca, V. L. (eds), *Proc. Int. Symp. on pollination*, Cardiff, Wales, 1998. Proceedings. IBRA (International Bee Research Association).
- Sakai, S. 2002. General flowering in lowland mixed dipterocarp forests of southeast Asia. – *Biol. J. Linn. Soc.* 75: 233–247.
- Skyhöff, J. A. and Bucheli, E. 1995. Pollinator visitation pattern, floral rewards and the probability of transmission of *Microbotryum violaceum*, a venereal disease of plants. – *J. Ecol.* 83: 189–198.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry, the principles and practice of statistics in biological research.* – Freeman.
- StatSoft 2003. *Statistica for Windows 6.1.* Statsoft Inc.
- Steffan-Dewenter, I. and Tschardtke, T. 2000. Resource overlap and possible competition between honeybees and wild bees in central Europe. – *Oecologia* 122: 288–296.
- Steffan-Dewenter, I., Münzenberg, U. and Tschardtke, T. 2001. Pollination seed set and seed predation on a landscape scale. – *Proc. R. Soc. B* 268: 1685–1690.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, Chr. et al. 2002. Scale dependent effects of landscape context on three pollinator guilds. – *Ecology* 83: 1421–1432.
- Stone, G. N. 1994. Activity patterns of females of the solitary bee *Anthophora plumipes* in relation to temperature, nectar supplies and body size. – *Ecol. Entomol.* 19: 177–189.
- Summerville, K. S., Boulware, M. J., Veech, J. A. et al. 2003. Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. – *Conserv. Biol.* 17: 1045–1057.
- Thies, C., Steffan-Dewenter, I. and Tschardtke, T. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. – *Oikos* 101: 18–25.
- Tøtland, Ö. and Matthews, I. 1998. Determinants of pollinator activity and flower preference in the early spring blooming *Crocus verus*. – *Acta Oecol.* 19: 155–165.
- Tylianakis, J., Klein, A. M. and Tschardtke, T. 2005. Spatio-temporal variation in the diversity of Hymenoptera across a tropical habitat gradient. – *Ecology* 86: 3296–3302.
- Wagner, H. H., Wildi, O. and Ewald, K. C. 2000. Additive partitioning of plant species diversity in an agricultural mosaic landscape. – *Landscape Ecol.* 15: 219–227.
- Westphal, C., Steffan-Dewenter, I. and Tschardtke, T. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. – *Ecol. Lett.* 6: 961–965.
- Willis, K. J. and Whittaker, R. J. 2002. Species diversity-scale matters. – *Science* 295: 1245–1248.

Subject Editor: Jane Memmott