Spatial scale of observation affects $\alpha$, $\beta$ and $\gamma$ diversity of cavity-nesting bees and wasps across a tropical land-use gradient

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**ABSTRACT**

**Aim** Anthropogenic changes in land use may have major consequences for global biodiversity. However, species diversity is determined by a suite of factors that may affect species differently at different spatial scales. We tested the combined effects of land use and spatial scale on $\alpha$, $\beta$ and $\gamma$ diversity in the tropics using experimental communities of cavity-nesting bees and wasps (Hymenoptera: Aculeata). We aimed to determine whether: (1) land-use intensity negatively affects species richness of cavity-nesting Hymenoptera, (2) $\beta$ diversity, both within and between plots, is higher in more natural systems, (3) species richness of flowering herbs correlates positively with species richness of Hymenoptera within and across habitats, (4) richness of cavity-nesting Hymenoptera in highly modified habitats declines with increasing distance from natural or semi-natural habitats, (5) the effects of land use, herb diversity and forest distance on Hymenoptera $\alpha$ and $\beta$ diversity vary at different spatial scales, and (6) bees and wasps respond to land use in a similar way.

**Location** Manabi, south-west Ecuador.

**Methods** We examined diversity (species richness) within 48 plots of five habitat types that comprised a gradient of decreasing agricultural intensity from rice and pasture to coffee agroforests, unmanaged abandoned agroforests and forest fragments, using standardized nesting resources for reproducing communities of cavity-nesting bees and wasps.

**Results** (1) Land use significantly affected $\alpha$ diversity of trap-nesting bees and wasps at the subplot (per trap) scale, but not subplot $\beta$ diversity or plot-scale species richness ($\gamma$ diversity). (2) Beta diversity was surprisingly higher between plots within a land-use type than between land-use types. (3) Species richness of bees and wasps increased with diversity of flowering herbs at the subplot (trap) scale only. (4) Forest distance correlated positively with bee species richness at the plot scale only. (5) Land use, herb diversity and forest distance each showed significant correlations with bee and wasp diversity at only one spatial scale. (6) Despite differences in life history, bees and wasps responded to land-use intensity in a similar way.

**Main conclusions** The effects of land use on species richness were highly dependent on spatial scale. Subplot-scale analyses showed that rice and pasture contained the highest species diversity, whereas plot-scale analyses showed no significant difference in the diversity of different land-use types. We emphasize caution in the estimation of biodiversity at only one spatial scale, and highlight the surprisingly large contribution of managed land to the regional biodiversity of these species.

**Keywords** Agriculture, biodiversity, Ecuador, habitat selection, managed land, multiple scales, spatial scale, trap nest.
INTRODUCTION

Tropical ecosystems are the greatest contributors to global biodiversity (Myers et al., 2000), and these regions are heavily reliant on managed land for biodiversity conservation (Perfecto et al., 1996; Bawa et al., 2004). The contribution of different land-use systems to tropical biodiversity requires thorough assessment, but past studies on the effects of land-use intensity on biodiversity have frequently measured diversity at only one spatial scale (e.g. Klein et al., 2002). This may mask subtle differences in species diversity, because the factors that determine diversity may not scale up or down across different spatial and temporal scales (Whittaker et al., 2001; Koleff & Gaston, 2002; Willis & Whittaker, 2002; Zanette et al., 2005). On a landscape scale, species richness can be affected by factors such as fragmentation (Didham et al., 1996; Cane, 2001); matrix composition (Ricketts, 2001; Dauber et al., 2003); landscape diversity (Steffan-Dewenter et al., 2002; Dauber et al., 2003; Krauss et al., 2003; Kruess, 2003); urbanization (Zanette et al., 2005); or climate (James & Shine, 2000; Opdam & Wascher, 2004). At smaller spatial scales, factors such as habitat type (Kruess, 2003; Weibull et al., 2003); habitat area (Ritchie & Olff, 1999; James & Shine, 2000; Krauss et al., 2003; Summerville & Crist, 2004); management intensity (Klein et al., 2002; Perfecto et al., 2003); and inter- or intraspecific interactions (Veech et al., 2003) become more important in determining species distributions. Therefore the spatial scale selected for the study may inadvertently determine the outcome, for instance if species turnover is low within plots, but high between plots (Summerville et al., 2003).

The challenge of assessing diversity at multiple scales can be met by partitioning diversity between different levels of a nested spatial hierarchy (Hughes et al., 1999; Willis & Whittaker, 2002), thereby determining the spatial scale across which the highest β diversity occurs. This multi-scale approach was used by Summerville et al. (2003) to evaluate lepidopteran diversity in temperate forests in Ohio, USA; and Wagner et al. (2000) used this technique to examine the plant species diversity of different land-use systems in an agricultural landscape on the Swiss Plateau.

Many studies on the effects of land use on biodiversity consider only a few related management systems, such as different intensities of coffee or cacao management (Perfecto et al., 2003; but see Ricketts et al., 2001). While this work can provide valuable guidelines for conservation and management of the systems concerned, it fails to assess the overall contribution of managed land to regional biodiversity.

Here we use a highly replicated field study to examine the effects of the five predominant land-use types (rice, pasture, coffee, abandoned coffee and forest fragments) on the diversity of trap-nesting bees and wasps (Hymenoptera: Aculeata). Experimental communities of trap-nesting Hymenoptera make useful tools for investigations of biodiversity, due to their ease of physical manipulation, trophic complexity and species diversity (Tscharntke et al., 1998). In terms of ecosystem services (sensu Costanza et al., 1997; Luck et al., 2003), communities of trap-nesting Hymenoptera are particularly salient as many species are important pollinators of both crops and wild plants (Klein et al., 2003). Moreover, many predacious or parasitic trap-nesting species may act as biological control agents (Klein et al., 2004).

We use additive partitioning of β diversity at multiple spatial scales to assess the land-use types in which the greatest β diversity occurs. Finally, we examine possible drivers of observed variation in species richness by assessing the effects of distance from forest remnants and of vegetation diversity on the diversity of trap-nesting Hymenoptera, and how these effects manifest themselves at different spatial scales. Such drivers are often absent from studies of human impacts on hymenopteran diversity, and this can lead to broad, questionable generalizations (Cane, 2001). The spatial scales we define are the subplot scale, which comprises variation between traps of a particular plot; the plot scale, which examines variation between different plots of a given land-use type; and the regional scale, which examines variation between land-use types.

Specifically, we test the following predictions regarding the effects of land use on diversity of trap-nesting Hymenoptera at different spatial scales.

1. Land-use intensity negatively affects the diversity of trap-nesting Hymenoptera. In general, more natural habitats tend to exhibit higher biodiversity of a variety of insect taxa (Mas & Dietsch, 2003; Shahabuddin et al., 2005). However, trap-nesting Hymenoptera may be able to exploit resources such as crop plants and their herbivore communities, and they have been shown to benefit from increased intensity of agroforest management (Klein et al., 2002). Nevertheless, agroforests comprise a relatively natural habitat compared with arable crops. We therefore aim to determine how different land-use types, rather than management intensity of a single type, affect diversity of this guild of bees and wasps.

2. Beta diversity, both within and between plots, is higher in more natural systems. Natural systems are more heterogeneous than intensely managed land-use types, and therefore provide a greater array of niches. We expect this will lead to higher β diversity in unmanaged systems than in the agricultural land-use types (Clausnitzer, 2003).

3. Species richness of herbs is positively correlated with species richness of Hymenoptera within and across habitats. Plants may provide flower resources for bees and wasps, and herbivore prey for wasps; herb diversity has been shown to correlate positively with Hymenoptera diversity within coffee agroforests (Klein et al., 2003). However, the robustness of this effect across different land-use types remains to be tested.

4. Diversity of trap-nesting Hymenoptera in highly modified habitats declines with increasing distance from natural or semi-natural habitats. Klein et al. (2003) found a negative
effect of forest distance on the diversity of social bees, but not solitary species such as those that occupy trap nests. Natural habitats may act as source populations for trap-nesting species, leading to higher diversity in traps or plots that are proximate to such habitats.

5. The effects of land use, herb diversity and forest distance on Hymenoptera α and β diversity are not consistent at all spatial scales. Land use has been shown to affect plant diversity differently at different spatial scales (Wagner et al., 2000), and the same may occur for bee and wasp communities. Herb diversity and forest distance have been examined previously at only one spatial scale (Klein et al., 2003); however, these effects cannot always be linearly scaled up across space and time (Hamer & Hill, 2000; Loreau, 2000; Willis & Whittaker, 2002).

6. Bees and wasps respond similarly to habitat modification. Bees and wasps have different food requirements, and previous studies within a habitat type have shown that these taxa can respond differently to abiotic parameters (Gathmann et al., 1994; Zanette et al., 2005). However, both taxa require nesting materials, and extreme management intensity may create habitats that are too hostile for either taxon.

### MATERIALS AND METHODS

#### Study plots

The study plots are located in the province of Manabi, southwest Ecuador. They comprise private farms spread across three cantons: Jipijapa (17N 546800 m, E 9849274 m alt. 259 m), Pajan (17N 563969, E 9828342 m alt. 142 m) and 24 de Mayo (largest town: Noboa 17N 567374 m, E 9844106 alt. 260 m) (Fig. 1; for individual plot location details and a full description of the region see Tylianakis et al., 2005). The region falls within the semi-arid tropics, and has a mean (± SD) annual temperature of 25.7 (± 0.22) °C and mean rainfall per month of 16.9 (± 13.0) mm in the dry season (June–November) and 215.1 (± 109.2) mm in the rainy season (December–May). The natural vegetation of the zone is semi-deciduous forest, but the region is now largely dominated by agriculture, therefore the effects of agricultural intensification are directly relevant to this region.

There are a variety of different crops cultivated in this area; in this study we consider the dominant ones, an arable crop (rice), pasture and agroforestry (coffee). Coffee agroforests can vary

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**Figure 1** Map of study region showing distribution of plots in relation to the major towns: Jipijapa (17N 546800 m, E 9849274 m alt. 259 m), Pajan (17N 563969, E 9828342 m alt. 142 m) and Noboa (17N 567374 m, E 9844106 alt. 260 m). Circles with number at top right indicate clusters of plots within a village or two adjacent villages.
Table 1 Area (ha) and percentage of total canton area occupied by each of the land-use types in this study (Segarra, 2004)

<table>
<thead>
<tr>
<th>Land-use type</th>
<th>Area</th>
<th>Percentage of study zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agroforestry, predominantly coffee</td>
<td>59,347</td>
<td>54.8</td>
</tr>
<tr>
<td>Forests and partially intervenient natural vegetation, including abandoned agroforests</td>
<td>18,660</td>
<td>17.2</td>
</tr>
<tr>
<td>Seasonal, permanent and partly overgrown pastures</td>
<td>17,570</td>
<td>16.2</td>
</tr>
<tr>
<td>Rice and other annual crops</td>
<td>2030</td>
<td>1.9</td>
</tr>
<tr>
<td>Total area of zone</td>
<td>108,241</td>
<td>100.0</td>
</tr>
</tbody>
</table>

greatly with individual management, so an effort was made to select plots that had been in cultivation for over 8 years, used no chemical fertilizers and had a similar degree of shade tree cover (60–80%). As there is no pristine rain forest remaining in the zone (only a few secondary and fragmented forest remnants), we used the most ‘natural’ systems available, abandoned coffee agroforests and forest fragments, and these two types were treated separately in analyses. These land-use types represent a gradient of decreasing management intensity. Their relative abundance and the total area within the study region are presented in Table 1. Twelve replicates of each managed land-use type were sampled in the study, as were six abandoned coffee agroforests (abandoned for 10–15 years and now resembling secondary forest) and six forest fragments.

The study plots were generally clustered in groups of three or more different land-use types (Fig. 1) to reduce the common problem of spatial autocorrelation resulting from several plots of one land-use type being clustered together. By clustering plots in this way, overall similarity between plots of a cluster would be maximized, and any differences between them are more likely to be due to their differences in management, rather than possible location-specific effects. The land-use types in which we set up the plots had received the same management regime for at least 5 years and, on average, there was no significant difference in the area of plots from each land-use type, except for two forest plots that were made at opposite ends of a 25-ha forest fragment (the exact age and area of plots can be found in the electronic supplement to Tylianakis et al., 2005). Percentage forest cover and habitat diversity within a 1-km radius of each plot did not differ significantly between land-use types (data not presented).

Trap nests

Nine trap nests were positioned (in a 3 × 3 grid, 25 m between adjacent traps) in the centre of each of the 48 plots, to provide nesting sites for naturally occurring bee and wasp communities. Analyses at each of these traps are referred to here as the ‘subplot scale’, and all nine traps within a plot combined as the ‘plot scale’. Exposure of standardized trap nests is similar to the exposure of other resources (e.g. phytometer plants), but because the guild of above-ground cavity-nesting species reproduces in these traps, the problem of species appearing as ‘tourists’ in samples is eliminated. It may be argued that in open habitats, where fewer natural nesting sites are available, these trap nests will attract Hymenoptera more than in wooded habitats; however, this has been shown not to be the case. Rather, cavity-nesting species are restricted-range foragers (Gaimari & Martins, 1996) and usually build nests very close to the nesting site from which they pupated, and trap nests give an accurate representation of the community normally occurring in a particular habitat (Tscharntke et al., 1998 and references therein). Trap nests were constructed according to the methodology of Tscharntke et al. (1998). A PVC tube 22 cm long, 15 cm diameter formed the outer case of the nest. Approximately 75 internodes of reeds *Arundo donax* L. (Poaceae) with varying diameter (2–20 mm), 20 cm long, were inserted into this tube and provided the nesting sites for bees and wasps. Trap nests were hung from trees in shaded (coffee, abandoned coffee and forest) systems, and suspended from wooden posts in open (rice and pasture) systems. Sticky glue (tanglefoot) was applied to the post or attachment point to deter ants. All traps were positioned 1.5 m above the ground.

A broad-spectrum fungicide, Fitoraz® 76 PM (Bayer Crop Science SA: propineb 21 g L⁻¹, cymoxanil 1.8 g L⁻¹), which is not toxic to Hymenoptera, was applied to each trap with a hand sprayer every month.

Each trap was evaluated every month during the dry season (June–December 2003), and all reed internodes that were occupied by Hymenoptera were removed and replaced with new internodes of the same diameter. Occupied reeds were opened and the larvae were reared to maturity for positive identification to subfamily level. Genera and species were identified where possible by D.W. Roubik, J. Gusenleitner and the authors, using keys and reference collections from the Pontificia Universidad Católica del Ecuador. Remaining species were identified as morphospecies. A list of bee and wasp species, the months and land-use types in which they are found, and the number of nests and individuals found in each type are presented in Table S1 in Supplementary Material. Species-richness data from the six evaluations were pooled for each trap. Parasitoids and cleptoparasites were excluded from analyses, as their diversity is dependent partially on available host species.

Plant surveys

Plant surveys were conducted in 2.5 × 2.5-m quadrats below each of the traps in shaded systems or adjacent to the wooden posts in open systems. Two surveys were conducted (in May/June and September/October 2003) in order to estimate herb diversity at the beginning and end of the dry season. We sampled all vascular herbaceous species (including ferns), and gathered voucher specimens for identification. Specimens were identified by experts at Quito (QCA) and Guayaquil (GUAY) herbaria in Ecuador. Voucher specimens were deposited at QCA and GUAY. The total species richness from the two

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surveys combined was used in the analyses. Tree diversity (number of species) was also recorded in 10 × 10-m quadrats around each trap in the shaded land-use types (coffee, abandoned coffee and forest).

**Forest distance**

The distance to the nearest possible hymenopteran source population (‘forest distance’) was measured for each trap in the open systems. This constituted the distance from each trap to the border of the nearest forested habitat type: forest fragment, agroforest or abandoned agroforest. This parameter could not be assessed meaningfully for the remaining land-use systems, as the border between one agroforest and another was often based arbitrarily on ownership rather than any biological significance, and all plots would essentially have zero values for this parameter. Distances up to 100 m were measured with a tape measure and greater distances were measured using a GPS (Etrex Venture – Garmin: mean error for measurements, 12.4 ± 4.36 m). For analysis, forest distance was partitioned into the distance from forest to plot (plot scale), and the distance from the edge of the plot to each trap (subplot scale).

**α, β and γ diversity**

Beta diversity is a measure of the proportion of total species diversity that is not present in each sample unit. We used additive partitioning (Lande, 1996) to calculate this value such that regional species diversity, γ, is the sum of α diversity (the average within-sample diversity) and β diversity (species turnover). The benefit of this technique is that α, β and γ diversity can be defined according to a hierarchy of spatial scales, so that γ diversity at one scale becomes α diversity for the next scale. Thus in our study, if α_{sub} is defined as the mean species richness at the subplot scale, that is, the average number of species in each trap within a plot, β_{sub} is β at the subplot scale and α_plot (= γ_{sub}) is the total species richness for a plot, then: α_{sub} = α_plot − β_{sub}.

At the next scale of the hierarchy, mean α_plot for a land-use type = α_{typ} − β_plot where α_{typ} (= γ_plot) is the total number of species within a land-use type. Finally, mean α_{typ} = γ_{typ} − β_{typ} where γ_{typ} is the total number of species across all land-use types within the study region. In order to compare α and β diversity meaningfully between different land-use types, we compared them as a proportion of the total diversity for the land-use type (arc sine square-root transformed). As α and β are correlated with each other, we treated them as a multivariate response variable when making comparisons between land-use types. We also included plot cluster (Fig. 1) as a random effect to control for variation due to spatial autocorrelation (see below).

**Statistical analyses**

A preliminary Mantel test, based on Pearson’s product-moment correlation conducted in r (R Development Core Team, 2004), using x and y GPS coordinates to create the distance matrix, found that our plots were spatially autocorrelated (Mantel statistic, r = 0.2124, P = 0.005). Although the majority of this autocorrelation was between plots of different land-use types, to be conservative we nevertheless grouped our plots into 12 clusters (Fig. 1) and included this ‘plot cluster’ as a random effect in all analyses. Any plots within 2 km of each other were grouped into a cluster. This distance was conservative, as a study and review of solitary bee foraging ranges (Gathmann & Tscharntke, 2002) found a maximum dispersal range of 1200 m in large solitary bees, and cavity-nesting species are known to restrict foraging to the proximity of the nesting site (Gaimari & Martins, 1996).

To measure whether our samples were close to species saturation, we calculated the abundance-based coverage estimator (ACE) and Chao1 estimates of species richness using the ESTIMATES software ver. 5 (Colwell, 1997). Sampled species richness was then divided by each estimator for each plot to calculate the percentage species saturation. Remaining analyses were conducted in STATISTICA 6.0 (StatSoft Inc., 2003).

Model residuals were tested for adherence to a normal distribution before this was assumed in analyses. Non-normal count data were square-root transformed when necessary, and proportion data were arcsine square-root transformed. The effect of land use on (square root) subplot species richness was calculated using a linear mixed effects model (Crawley, 2002), with diversity of individual traps as the response variable, grouped with plot and plot cluster as random effects. Grouping per-trap diversity using ‘plot’ as a random effect overcomes the problem of individual traps within a plot being non-independent, while avoiding the loss of within-plot variation associated with averaging of data (Crawley, 2002). Similarly, grouping plots by using plot cluster as a random effect overcomes the non-independence of spatially autocorrelated plots.

Plot-scale effects of land use on species richness were tested in a linear mixed effects model, with plot cluster as a random effect and land-use type as a fixed effect. Abundance was also included as a covariable in both analyses to ensure that differences in richness were not artefacts of differences in sample size. Mixed effects models, under the Variance Components module of STATISTICA, calculate error degrees of freedom (d.f.) using Satterthwaite’s method of denominator synthesis (Satterthwaite, 1946) and can yield non-integer d.f. values.

Correlations between tree and herb diversity, and bee and wasp species richness at the plot scale were tested with a linear mixed effects model, using land use as a fixed effect, plot cluster as a random effect, and tree or herb diversity as continuous predictors. At the subplot scale, traps were also grouped into plots (random effect). Correlations with tree diversity were analysed only in the shaded systems (rice and pasture were excluded as they had few, if any, trees).

In rice and pasture plots, the correlation between forest distance and species richness was tested in a general linear model. Distance from forest to plot (plot scale) and distance
from each trap to the plot edge closest to the forest (subplot scale) were analysed as separate predictor variables, to determine whether traps within a plot that were closer to a forested habitat had higher diversity (e.g. through edge effects). Land-use type was included as a fixed effect, traps were nested in plots (random effect), and plots were nested in plot clusters (random effect). Subplot- and plot-scale forest distances were included as continuous predictors, and an interaction effect between the two was included to determine whether subplot correlations only occur when the plot is close to the forest. The correlations between plot age and area and plot-scale richness were also tested using a mixed effects model with land-use type and plot cluster as fixed and random effects, respectively.

**RESULTS**

A total of 10,006 individuals from 22 morphospecies (Hymenoptera: Apidae, Eumenidae, Megachilidae, Pompilidae and Sphecidae) (Table S1) were collected from the 432 trap nests. Generally, there was little specialization in land-use selection by the bees and wasps, as there was a great overlap in the species that constituted the communities of each land-use type. Pasture, rice and coffee each had one species specific to only that type, and a further bee species was specific to coffee and abandoned coffee. The mean species saturation per study plot ($n = 48$) was $96.3 \pm 0.85\%$ according to ACE and $97.7 \pm 0.86\%$ according to Chao1 estimators. Percentage species saturation according to the estimators did not vary significantly between land-use types (one-way ANOVA: $F < 1$, $P > 0.5$ in both cases), so we made further direct comparisons with original species richness data rather than estimated values.

**Effects of land use on species richness**

At the subplot scale, land use strongly affected species richness of bees ($F_{(4,408)} = 18.76$, $P < 0.0001$) and wasps ($F_{(4,408)} = 10.43$, $P < 0.0001$) (Fig. 2a). However, at the plot scale there was no significant effect of land-use type on species richness (bees: $F_{(4,423.5)} = 2.14$, $P = 0.107$; wasps: $F_{(4,423.5)} = 0.37$, $P = 0.827$) (Fig. 2b).

**Partitioning of species diversity across spatial scales**

In general, $\alpha$ diversity accounted for proportionately low levels of the total species richness (a mean of 10.7% of $\gamma_{\text{typ}}$ for bees, 14.7% for wasps), and the highest proportions of $\alpha_{\text{typ}}$ and $\gamma_{\text{typ}}$ were accounted for by species turnover between plots of each land-use type, $\beta_{\text{plot}}$ (Fig. 3). Alpha diversity, as a proportion of total plot diversity ($\alpha_{\text{plot}}/\alpha_{\text{plot}}$) was affected significantly by land-use type (bees, $F_{(4,32)} = 22.97$, $P < 0.00001$; wasps, $F_{(4,32)} = 13.39$, $P < 0.00001$), but relative $\beta$ diversity within plots ($\beta_{\text{plot}}/\gamma_{\text{plot}}$) was unaffected (bees, $F_{(4,32)} = 1.29$, $P = 0.295$; wasps, $F_{(4,32)} = 0.83$, $P = 0.502$) (Fig. 3). Both $\alpha$ and $\beta$ as a proportion of plot diversity were significantly affected by plot cluster ($F_{(22,62)} > 1.74$, $P < 0.05$ in both cases), indicating that communities were partly affected by geographical location.

**Correlations between plant diversity and abiotic variables on species richness**

At the subplot scale, herb richness was significantly correlated with species richness of trap-nesting bees ($F_{(1,77.6)} = 23.09$, $P < 0.0001$, $r^2 = 0.303$) and wasps ($F_{(1,67.0)} = 10.46$, $P = 0.002$, $r^2 = 0.053$) (Fig. 4); however, this correlation was not apparent at the plot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$). Tree richness in the shaded plots did not correlate significantly with hymenopteran species richness at the subplot scale (bees, $F_{(1,26.5)} = 0.07$, $P = 0.793$; wasps, $F_{(1,23.6)} = 0.00$, $P = 0.954$).
did not interact ($F_{1,104} = 1.33$, $P = 0.251$) (Fig. 5). Furthermore, proximity of the plot to forest patches significantly affected variation between traps within a plot, such that subplot scale forest distance began to have a positive effect in plots that were close to forest (subplot $\times$ plot-scale forest distance interaction effect: $F_{1,104} = 5.18$, $P = 0.025$, $r^2 = 0.050$). Forest distance had no correlation with wasp species richness at either scale, and the effects at each scale did not interact ($F_{1,104} < 1.44$, $P > 0.233$ in all cases).

DISCUSSION

Land use significantly affected species richness of trap-nesting Hymenoptera at the subplot ($\alpha_{sub}$) scale, yet we found no effect on species richness at the plot ($\alpha_{plot}$) scale. This apparently contradictory result can be explained by differences in the proportionate $\alpha$ and $\beta$ diversity of the different land-use types. Alpha diversity explained a larger proportion of the total diversity in rice and pasture than in the other land-use types, and this manifested itself as significantly higher per-trap ($\beta_{sub}$) diversity. However, plot-scale diversity ($\alpha_{plot}$) and $\beta_{sub}$ as a proportion of total diversity, did not vary significantly between land-use types (Fig. 3). This illustrates that land use does affect diversity (prediction 1); however, $\alpha$ and $\beta$ diversity must be considered at multiple spatial scales in order to gain a full understanding of community structure (prediction 5).

Trap-scale ($\alpha_{sub}$) diversity in our traps accounted for c. 11% of the total bee and wasp species richness for the study region. On average, a high percentage of the total species for a given land-use type were not present in each plot (average $\beta_{plot}$ was 30.6% of the total richness for a land-use type for bees, 45.6% for wasps), a greater proportion than $\beta$ between land-use types (Fig. 3, total). This contradicts the suggestion that within-taxon $\beta$ diversity should increase with environmental dissimilarity between plots (Harrison et al., 1992), such as between different land-use types. Our results also support the contention that human impacts reduce $\beta$ relative to $\alpha$ diversity (prediction 2; see also Thomas, 1991), as the proportion of overall diversity explained by $\alpha$ increased in the most intensively impacted
systems, with a concomitant decrease in the proportion explained by $\beta$ diversity.

The increased species richness we observed at the subplot scale in more intensively managed systems is in general accordance with Klein et al. (2002), who found higher diversity of trap-nesting Hymenoptera in more intensively managed agroforestry systems. This is also congruent with the results of DeVries and colleagues (DeVries et al., 1997; DeVries & Walla, 1999), who found higher diversity of butterflies in more disturbed forests in eastern Ecuador. However, we found this result across a variety of land-use types, not simply across different management or disturbance intensities of a single type. These results contradict the common perception that managed land is depauperate in biodiversity, and show that it can be a very valuable contributor to regional conservation of cavity-nesting Hymenoptera.

High herb diversity was correlated with high diversity of bees and wasps at the subplot scale, supporting prediction 3. This was consistent with the results of Klein et al. (2003), who found that diversity of solitary bees increased with increasing blossom cover in coffee agroforests in Indonesia. Floral resource subsidies have been shown to cause aggregation and increased reproduction in parasitic Hymenoptera (Tylianakis et al., 2004), and one of these mechanisms may have led to the higher diversity that we observed. However, plot-scale herb diversity did not correlate with diversity of Hymenoptera. This suggests that floral resources are important for attraction of individual bees within plots, but (perhaps due to their ephemeral nature) are not primary determinants of community diversity at larger spatial scales (prediction 5).

In open (rice and pasture) systems, bee species richness was higher in plots that were more distant from forest, the reverse pattern to that of prediction 4. However, within a plot, traps that were closer to forest did not differ significantly in species richness from traps that were further from forest, although this subplot forest distance interacted with the plot-scale correlation. That forest distance had a significant correlation only with bee and wasp richness on larger spatial scales again supports prediction 5. It is commonly assumed that natural habitats act as a kind of source population for many species within agriculturally intensified landscapes. For example, Klein et al. (2003) found a decrease in the number of social bee species in coffee agroforests with increasing forest distance, and Ricketts (2004) found that higher bee diversity at close proximity to forest led to improved pollination and fruit quality of coffee in Costa Rica. This would not be surprising if intensity of production does, in fact, go hand-in-hand with reduced biodiversity. However, the pattern found by Klein et al. (2003) did not hold for solitary species, such as those in our study, and Krauss et al. (2003) found no effect of habitat isolation on butterfly diversity. Species richness of solitary wild bees has been shown to correlate positively with the percentage of semi-natural habitats at scales of up to 750 m (Steffan-Dewenter et al., 2002). If ‘natural’ habitats were to act as a source population for trap-nesting Hymenoptera, how then could we rationalize the contrary pattern of reduced diversity we observed in plots and patches that are proximate to forest-like habitats? It is possible that, in regions that are heavily dominated by agriculture, where natural forest systems have been heavily fragmented and disturbed (such as in our study region), forest-specializing species cannot survive easily, and that open, disturbed habitat specialists proliferate. In this sense, many trap-nesting species, such as the bees of our study, may represent a special case of species that actually benefit from agricultural intensification, perhaps through a greater abundance of flowering weeds. A similar phenomenon occurs in some tropical butterflies that benefit from feeding on flowering weeds in disturbed forest habitats (DeVries et al., 1997). This would explain the positive correlation with increasing forest distance we observed in open, more disturbed systems, and suggest that determinants of diversity in landscapes depend on the taxa concerned, and possibly on the predominant land use in the region (in our study region, agriculture).

Surprisingly, forest distance was the only variable tested to which bees and wasps responded differently. In general, bees and wasps showed the same correlations with herb diversity, and the same effects of land use on $\alpha$ and $\gamma$ diversity, indicating that anthropogenic modification may have similar effects on these taxa (prediction 6).

In summary, the significance of herb diversity at the subplot scale only, and the surprising correlation with forest distance at the plot scale, highlight the importance of testing driving factors for differences in biodiversity at different spatial scales. Moreover, the effects of land use on species richness were highly dependent on spatial scale. If diversity estimates in our study region were based only on subplot-scale analyses, it would appear that rice and pasture contain the highest species diversity, and therefore merit the greatest attention. Conversely, a plot-scale analysis would give no indication of which land-use system contains the most species. We emphasize caution in the estimation of biodiversity at only one spatial scale, as the selection of different scales for an investigation may result in completely disparate conclusions.

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REFERENCES


SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from http://www.Blackwell-Synergy.com:

Table S1 Excel spreadsheet of bee and wasp species, the months and land-use types in which they are found, and the number of nests and individuals found in each land-use type.

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