SPATIOTEMPORAL VARIATION IN THE DIVERSITY OF HYMENOPTERA ACROSS A TROPICAL HABITAT GRADIENT

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Abstract. Understanding global biodiversity patterns requires analyses at multiple spatial and temporal scales, across a variety of different habitat types. We used a highly replicated study in coastal Ecuador to examine simultaneously for the first time spatial and temporal species turnover and the contribution of five different habitat types (rice, pasture, coffee agroforests, abandoned coffee agroforests, and native forest fragments) to regional diversity in the tropics, using the experimental placement of standardized nesting structures for bees and wasps. There was notable overlap in the communities of different habitat types, indicating that even intensively managed land can provide a valuable contribution to the overall biodiversity of the landscape mosaic. Importantly, there was a significant effect of habitat type on temporal variation in diversity. While intensive cropping systems such as rice and pasture exhibited higher diversity in certain months, greater species turnover through time in the abandoned coffee and forest plots accounted for the higher overall diversity in these habitats. Overall, spatial and temporal turnover explained 38.6% and 23.1%, respectively, of partitioned regional species richness. A quantitative analysis revealed that the relative habitat specificity of Hymenoptera decreased with increasing habitat disturbance.

Key words: additive partitioning; bee; Ecuador; temporal scale; trap nest; wasp.

INTRODUCTION

Global biodiversity is declining at an alarming rate, and the impending loss of important ecosystem services (Luck et al. 2003) has made this one of the most pressing issues facing ecologists today. The realization that set-aside conservation areas are no longer sufficient to slow this decline has led to an increased focus on managed land for conservation (Perfecto et al. 1996, Hughes et al. 2002, Bawa et al. 2004); however, the importance of such anthropogenic habitats remains somewhat ambiguous and a more complete understanding requires analyses at multiple spatial and temporal scales (Ricklefs and Schluter 1993, May 1994).

While the partitioning of spatial components of species turnover to determine local–regional diversity patterns has attracted considerable attention recently (Gering and Crist 2002, Gaston 2004), temporal variation in biodiversity patterns, such as the contribution of temporal regimes (abiotic, biotic, or anthropogenic) in different habitat types to overall landscape diversity is a neglected issue. Some studies have shown that increased management intensity leads to decreased diversity of a variety of taxa (Steffan-Dewenter et al. 2002, Mas and Dietsch 2003, Schulze et al. 2004, Shahabuddin et al. 2005), whereas others have demonstrated higher species richness in disturbed habitats (e.g., DeVries et al. 1997, Lawton et al. 1998, DeVries

and Walla 2001, Klein et al. 2002; J. M. Tylianakis, A.-M. Klein, T. Lozada, and T. Tscharntke, *unpublished manuscript*). The temporally changing importance of habitat type for overall biodiversity may partly explain the contradicting results of these studies; however, this has not yet been examined over a range of different habitats. Temporal heterogeneity in the biodiversity of different habitat types may occur when important resources become available at different times (Wolda 1978, 1988), e.g., during periods of mast flowering or anthropogenic sowing/harvesting. Species may therefore move from one habitat to another, exploiting the availability of predictable, ephemeral resources (Wissinger 1997, Bambaradeniya et al. 2004). If there is strong temporal heterogeneity in habitat biodiversity, the time scale of sampling could lead to a serious over- or underestimation of diversity within a given habitat type (Summerville and Crist 2005), or an unbalanced comparison of diversity between different habitats (Roubik 2001). This is especially pertinent to tropical regions, where relatively little seasonal variation in temperature means that biodiversity sampling is often carried out over short time scales and assumed to be representative of general patterns (e.g., Hughes et al. 2002, Shahabuddin et al. 2005, but see DeVries et al. 1997).

Here, we use a highly replicated study to examine simultaneously for the first time spatial and temporal species turnover and the contribution of different habitat types to regional diversity in the tropics. We assess the contribution of five different habitats to the bio-

PLATE 1.   (Left) An example of a pasture site in Manabi, Ecuador. (Right) A ''trap nest,'' a standardized nesting resource for cavity-nesting bees and wasps. Photo credit: J. Tylianakis.

diversity of a guild of bees and wasps. This variety of habitats is necessary, as many past studies examining the importance of different habitat types for biodiversity deal only with differing management intensities or disturbance levels of a single habitat type (or group of closely related habitats), and therefore cannot give accurate estimates of the overall contribution of managed land to regional biodiversity (but see Schulze et al. 2004, Shahabuddin et al. 2005). More importantly, we examine whether there is temporal variation in the spatial partitioning of biodiversity. Specifically, we ask (1) does partitioned biodiversity in the region show temporal variation, and is this variation consistent across habitats, (2) do the different habitat types show complementarity in partitioned biodiversity, (3) is there a seasonal shift of species between habitats, and (4) are there significant differences in the specific species composition of each habitat, such that species may be specific to just one type? Specificity is often given a cursory mention in biodiversity studies, as it is intuitively obvious that high diversity of cosmopolitan species is not preferable to slightly lower diversity of rare habitat specialists when global biodiversity decline is considered. Nevertheless, specificity is seldom quantified further than anecdotal observations that a species was only found in one habitat and must therefore be specific to that habitat (for exceptions see McGeoch and Chown 1998, Wagner and Edwards 2001, and references within).

For this study, we use the guild of trap-nesting Hymenoptera, as they comprise an important group of pollinators and potential natural enemies of insect pests (Klein et al. 2002, 2004). The diversity of these communities is highly correlated with total bee and wasp diversity (Tscharntke et al. 1998). Therefore, our results have implications not only for the study and management of biodiversity, but also for the timing and availability of ecosystem services, such as crop pollination or pest population reduction, provided by these

species. The habitat types we consider (rice, pasture, coffee agroforests, abandoned coffee agroforests and native forest fragments), represent a gradient of decreasing anthropogenic disturbance, and the predominant habitat types found in Southwest Ecuador.

MATERIALS AND METHODS

Study region

The 48 study plots are spread across three cantons; Jipijapa (1°19′60″ S, 80°34′60″ W, 259 m above sea level), Pajan (1°34′00″ S, 80°25′00″ W, 142 m above sea level), and 24 de Mayo (largest town, Noboa; 1°24′00″ S, 80°23′00″ W, 260 m above sea level) within the province of Manabi, Southwest Ecuador (see Supplement for site details). The region falls within the semiarid tropics and is largely dominated by agriculture. There are a variety of different crops cultivated in this area; however, we consider only the dominant ones: an arable crop (rice), pasture (see Plate 1), and agroforestry (coffee). The structure of coffee agroforests can vary greatly with individual management. Therefore, an effort was made to select plots that had been in cultivation for over 8 yr, used no chemical fertilizers, and had a similar degree of shade tree cover (60–80%). Many coffee agroforests have been abandoned by owners due to low economic returns. As these abandoned agroforests occupy a large proportion of the landscape, we included abandoned coffee as a natural intermediate between cultivated coffee and forest. There is no primary rainforest remaining in the zone, so for this study we used the most ''natural'' systems available (which were partly disturbed forest fragments). Coffee is the most abundant land-use type within the landscape (54.8% of the study zone), followed by forest (including disturbed forest and abandoned agroforests) (17.2%), pasture (16.2%), and arable crops (1.9%) (Segarra 2004). Twelve replicates of each managed habitat type were sampled in the study, as well

as six abandoned coffee agroforests (abandoned for 10–15 yr and now resembling secondary forest) and six forest fragments.

The study plots were generally clustered in groups of three or more different habitat types so as to avoid spatial autocorrelation resulting from several plots of one habitat type being clustered together.

Trap nests

Nine trap nests were positioned (in a 3×3 grid, 25 m between adjacent traps) in the center of each of the 48 plots. Trap nests were constructed according to the methodology of Tscharntke et al. (1998). A PVC tube with a length of 22 cm and a diameter of 15 cm formed the outer case of the nest. Internodes of reeds *Arundo donax* L. (Poaceae) with varying diameter (2–20 mm) and a length of 20 cm 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; Tanglefoot Company, Grand Rapids, Michigan, USA) 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, Propineb 21 g/L, Cymoxanil 1.8 g/L; Bayer Crop Science S. A., Bayer del Ecuador, Quito, Ecuador) that is not toxic to Hymenoptera was applied to each trap with a hand sprayer every month.

Sampling period

Each trap was evaluated every month from June 2003 to May 2004 (temperature and rainfall for this region are presented in the Appendix), 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 morphospecies (hereafter referred to simply as "species"). Data from each of the nine traps were pooled for each plot. Parasitoids and cleptoparasites were excluded from analyses, as their diversity is partially dependent on available host species.

Data analyses

We carried out all statistical analyses using Statistica 6.1 (StatSoft, Tulsa, Oklahoma, USA). The effect of habitat type on overall diversity and abundance per plot was analysed with ANOVA and post hoc Tukey's pairwise comparisons on data with normally distributed model residuals. Analyses of seasonal effects of habitat type on species richness, Shannon index, and abundance were conducted using repeated-measures ANOVA.

The effects of habitat area and time in cultivation (plot age) on diversity were tested simultaneously using general linear models with habitat type as a fixed factor.

To determine temporal species turnover, we used additive partitioning of species diversity (Lande 1996), a technique that is insensitive to differences in sampling effort among replicates, and therefore does not require rarefaction of data prior to analyses (Veech et al. 2002, Crist et al. 2003). Alpha diversity (α) was defined as the mean number of morphospecies per plot per month. The temporal turnover in species richness between months was calculated for each plot (β_{TPlot}) within a given habitat type as: the total number of morphospecies found within that plot (over the entire year) minus the mean number of morphospecies per month for that plot (α). Overall β_T was calculated as the mean β_{TPlot} for a given habitat type. Spatial turnover (β_S) was calculated as the total number of morphospecies found within a habitat type over the entire year minus the mean number of morphospecies per plot of that habitat type (over the entire year). Therefore, the overall diversity of a habitat type can be described as $\gamma = \alpha + \beta_T + \beta_S$. As α and β_{TPlot} were replicated across plots, they were analyzed as a proportion of γ (arcsine square-root transformed), and treated as multivariate responses in a mixed effects model with habitat type as a fixed factor.

We estimated a habitat specificity index for each species by comparing observed and expected numbers of each species in each habitat type. Some published specificity measures (e.g., McGeoch and Chown 1998) are useful for within-habitat comparisons of species, but are biased by differences in sample size between habitats. We therefore calculated the expected number of individuals of species i for plot j as $E_{ij} = N_i \times P_j$, where N_i is the total number of individuals of species i across all habitats, and P_j is the proportion of the total individuals sampled (of all species across all habitats) that were found in plot j. E_{ij} therefore represents the number of individuals of species i that we would expect in plot j if this species showed no preference for any habitat type and distributed itself randomly across habitats proportionately to the relative abundance of all species in each habitat. We then used $\log_{10}([O_{ij}/E_{ij}] + 1)$, where O_{ij} is the observed number of individuals of species i in plot j, as a measure of specificity, i.e., the deviation of species i from the expected random distribution. The specificity measures for every species were compared across habitats using a nonparametric Friedman ANOVA by ranks, to determine whether the species had on average higher specificity in one or more habitats. Post hoc pairwise comparisons were then made with Wilcoxon matched-pairs tests.

RESULTS

Seasonal analyses

In total, 15 047 individuals of 31 species (Hymenoptera: Apidae, Eumenidae, Megachilidae, Mutilidae, Pompilidae, and Sphecidae) were collected from the 432 trap nests. Species richness was not significantly
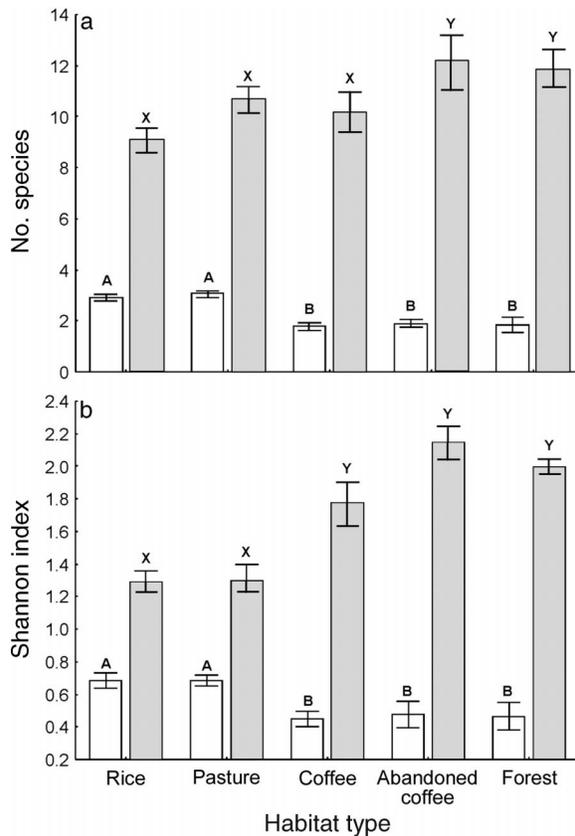
FIG. 1. Mean ($\pm$ SE) (a) number of species and (b) Shannon index per plot per month (open bars) and per plot over the entire year (shaded bars) in each of the five habitat types: rice, pasture, coffee agroforest, abandoned coffee agroforest, and forest fragment. Different letters represent significant differences ($P < 0.05$) between means in a post hoc Fisher LSD test.

correlated with individual abundance (Spearman rank correlation, $r = -0.15$, $N = 48$, $P > 0.1$).

Season had a strong effect on species richness ($F_{11, 473} = 7.30$, $P < 0.0001$) and Shannon index ($F_{11, 473} = 6.83$, $P < 0.0001$) in the different habitat types, as did the habitat type itself ($F_{4,43} > 5.54$, $P \leq 0.001$ for richness and Shannon). Season and habitat interacted significantly on species richness, such that seasonal effects were different in the different habitat types $F_{44, 473} = 2.25$, $P < 0.0001$. On average per month, species richness and Shannon index were highest in the most intensive systems (Fig. 1). At the beginning of the dry season (June–August 2003), rice and pasture had significantly higher alpha diversity than other habitat types ($F_{4,43} > 9.97$, $P < 0.0001$ in each month). Rice and pasture were also highest in October 2003 and January–February 2004, although the effect was weaker in these months ($F_{4,43} > 2.72$, $P < 0.05$ in each month). Abundance of individuals was also affected by season ($F_{11, 473} = 13.61$, $P < 0.0001$) and habitat type ($F_{4, 473} = 18.93$, $P < 0.0001$), and these variables interacted significantly ($F_{44, 473} = 6.97$, $P < 0.0001$).

In a comparison of the rainy vs. dry season (see Appendix A), the mean number of species per plot was higher in the rainy season ($F_{1,43} = 9.90$, $P < 0.005$), and this effect did not differ significantly among habitat types (interaction effect, $F_{4,43} = 9.90$, $P > 0.05$). There were eight out of 31 species that were found in the rainy season and not in the dry season (and eight species that showed the reverse pattern), across all habitat types.

Effects of habitat on overall diversity and abundance

When data for the entire year were pooled for each plot, habitat type significantly affected the number of individuals ($F_{4,43} = 18.69$, $P < 0.0001$), which was highest in rice and pasture plots. Species richness ($F_{4,43} = 2.58$, $P = 0.050$) and Shannon index ($F_{4,43} = 11.09$, $P < 0.0001$) were also significantly affected by habitat type. However, despite having lower abundance of individuals, and lower diversity per month, forest and abandoned coffee showed the highest richness and Shannon index per plot over the entire year, and coffee showed an equally high Shannon index (Fig. 1). In total, across all plots and months, rice contained 21 species, managed coffee contained 24, and the remaining habitat types contained 25 species each.

Habitat area and time in cultivation did not significantly affect species richness ($F_{1,41} < 0.71$, $P > 0.40$ for both age and area) or Shannon index ($F_{1,41} < 0.19$, $P > 0.66$ for both age and area) of trap nesting Hymenoptera.

Partitioning of species diversity across spatiotemporal scales

The different habitat types showed substantial differences in the relative partitioning of diversity across space and time (Fig. 2). The most intensive systems (rice and pasture) had proportionately higher diversity per plot (α/γ) ($F_{4,43} = 18.16$, $P < 0.0001$), and relatively high species turnover across plots (β_S); however, temporal species turnover (β_T) was low in these systems. Conversely, abandoned coffee and forest had a significantly larger proportion of γ explained by β_{TPlot} than did the other systems ($F_{4,43} = 3.27$, $P < 0.02$), and they also had relatively low α and β_S diversity (Fig. 2). Overall, at the level of sampling conducted, α diversity comprised 6.9% of the total diversity of our study region (31 species). Temporal and spatial turnover comprised 23.1% and 38.6%, respectively, of total diversity and the remaining 31.4% represented turnover in species between the different habitat types.

Specificity analyses

Although there was some variation in species composition across habitat types, overall specificity was relatively low. Abandoned coffee had no entirely specific species, forest had two (forest and abandoned coffee combined had an additional one) and each of the remaining habitats contained one species that was spe-

cific to that type. Specificity (as measured by the specificity index) varied significantly across habitats ($\chi^2 = 11.63$, $N = 33$, df $= 4$, $P = 0.020$), with rice and pasture showing significantly lower specificity (below expected values), than coffee, abandoned coffee, or forest (Wilcoxon matched-pairs tests, valid $N = 33$, $Z > 2.6$, $P < 0.0078$ in significantly different pairs), which had median observed values that were higher than those expected by random distribution of individuals among habitats in proportion to sample size (Fig. 3).

DISCUSSION

Diversity varied greatly among habitat types and seasons. If we had only carried out a ''snapshot'' comparison of habitat types at the beginning of the dry season (June–August 2003), we would have falsely concluded that the most intensive cropping systems (rice and pasture) contained the highest diversity of trap-nesting bees and wasps in this study system (as found by Klein et al. 2002; J. M. Tylianakis, A.-M. Klein, T. Lozada, and T. Tscharntke, *unpublished manuscript*). However, when we analyzed data for the entire year, we found that the less-disturbed habitats (forests and abandoned coffee agroforests) had higher temporal species turnover, which led to greater overall diversity. These highly contradictory outcomes demonstrate the necessity for adequate sampling regimes that incorporate the temporal component of variation in biodiversity, and may help to explain the varied responses of diversity to disturbance intensity that have been observed in previous, single season studies (e.g., Schulze et al. 2004, Shahabuddin et al. 2005; J. M. Tylianakis, A.-M. Klein, T. Lozada, and T. Tscharntke, *unpublished manuscript*). This is particularly important for mobile species with short generation times such as insects.

Surprisingly, coffee agroforests did not maintain significantly higher overall species richness than did the more intensively managed crops, although the Shannon index was significantly higher. This more marginal role of agroforestry is consistent with the results of Shahabuddin et al. (2005), and contrasts with the perception that shade coffee agroforests may be a potentially important refuge for biodiversity (e.g., Perfecto et al. 1996, Moguel and Toledo 1999). However, we found that agroforests that had been abandoned for 10–15 yr were not significantly different from forest fragments in their associated diversity of Hymenoptera, and that both productive and abandoned coffee showed high habitat specificity scores. This may imply that decreases in biodiversity are more ephemeral in agroforests compared with more destructive annual crops; however, studies are needed that compare several crop types that have been abandoned for the same period. Coffee also showed relatively high spatial and temporal turnover in diversity (Fig. 2), indicating that there may be great variation among different plots due to variation in management practices.
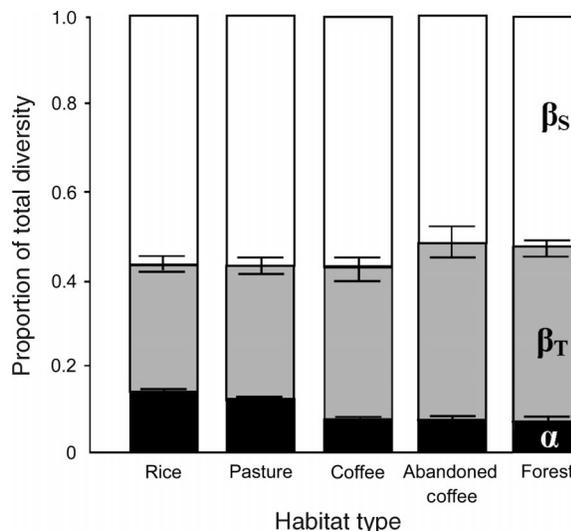

FIG. 2. Proportion of total (γ) diversity partitioned into α diversity and temporal (β_T) and spatial (β_S) turnover. The mean number of species per plot, per month is represented by α diversity. Error bars show $\pm$SE among plots.

The increase in Hymenoptera diversity per plot that we observed in the rainy season was concomitant with higher herb diversity per plot at this time (T. Lozada, *unpublished data*). This is in accordance with the broad pattern of high trap-nesting bee and wasp diversity in areas of high flowering herb diversity (Klein et al. 2002; J. M. Tylianakis, A.-M. Klein, T. Lozada, and T. Tscharntke, *unpublished manuscript*).

Contrary to expectations, there was not a great degree of habitat specificity in communities of trap-nesting bees and wasps. All habitat types had one or two species specific to that type, but there was considerable overlap in community composition between habitats, rather than high complementarity. Coffee, abandoned coffee, and forest fragments had the highest specificity scores, indicating that the proportion of habitat specialists (like overall diversity) declines with increasing habitat disturbance.

Total regional species richness did not show great variation between the dry and rainy seasons (23 species in each season); however, species composition changed dramatically (ca. 30% turnover in species identity between the two seasons; see Supplement), as did the distribution of species richness among the different habitat types. We found no direct evidence of seasonal movement between different habitat types, although there were a total of 16 species that we only observed in either the rainy or dry season. Whether these taxa migrate from outside the region, are present year-round at low densities, or spend part of the year in a larval or pupal stage is unclear. Metapopulation studies of individual species will be necessary to ascertain whether movement between different habitat types actually occurs. Furthermore, in order for the ecosystem ser-
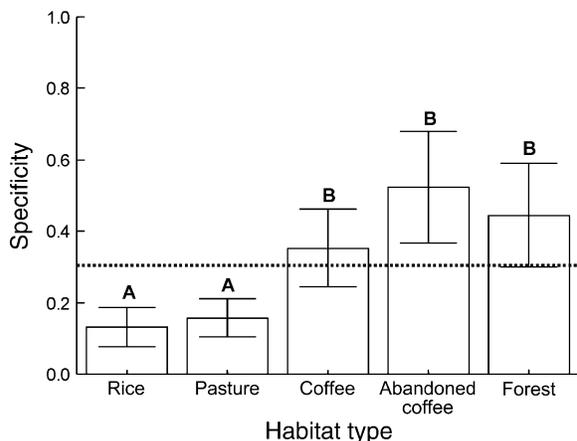
FIG. 3. Specificity ($\log_{10}$[(observed/expected) + 1]) number of individuals per species) (median and 95% CI) in the five different habitat types. Different letters show significant differences ($P < 0.05$) based on pairwise comparisons using Wilcoxon matched-pairs tests. The dotted line represents observed values equal to expected values, i.e., distribution among habitats in proportion to sample size.

vices of different species to be utilized, the time at which they occur requires careful consideration. For example, Sperber et al. (2004) found that populations of beneficial parasitoids emigrated from Brazilian cacao agroforests to nearby forest remnants in winter, yet high tree diversity encouraged a greater diversity of parasitoid families in spring and summer.

In conclusion, although we found the highest overall biodiversity and specificity in the more natural systems (abandoned coffee and forest fragments), the diversity of Hymenoptera within each habitat type showed great temporal variability. This emphasizes that temporal, as well as spatial, dynamics are integral to the distribution of biodiversity, and even studies conducted in the tropics must consider temporal variation when partitioning components of regional species diversity. Although our results indicate that temporal variation in biodiversity is very important, we realize that one year is, ecologically speaking, a relatively short time, and interannual temporal turnover may also explain a significant portion of overall species richness. All habitat types contributed to between 60% and 70% of the total regional diversity observed in our study. Therefore, our results show that even intensively managed land can provide a valuable contribution to the overall biodiversity of the landscape mosaic.

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APPENDIX

A table showing monthly temperature (°C) and rainfall (mm) in Pajan, Ecuador, within our study region in 2003 is available in ESA's Electronic Data Archive: *Ecological Archives* E086-180-A1.

SUPPLEMENT

Details of site location, age, and area with corresponding abundance and diversity measures of trap-nesting Hymenoptera and a list of morphospecies found in each habitat type at each sampling date are available in ESA's Electronic Data Archive: *Ecological Archives* E086-180-S1.