

Effects of anthropogenic habitat disturbance on local pollinator diversity and species turnover across a precipitation gradient

Carolina Quintero · Carolina Laura Morales · Marcelo Adrián Aizen

Received: 11 February 2009 / Accepted: 22 September 2009 / Published online: 24 October 2009
© Springer Science+Business Media B.V. 2009

Abstract Anthropogenic habitat disturbance can have profound effects on multiple components of forest biotas including pollinator assemblages. We assessed the effect of small-scale disturbance on local richness, abundance, diversity and evenness of insect pollinator fauna; and how habitat disturbance affected species turnover across the landscape and overall diversity along a precipitation gradient in NW Patagonia (Argentina). We evaluated the effect of disturbance on overall pollinator fauna and then separately for bees (i.e. Apoidea) and non-bee pollinators. Locally, disturbed habitats had significantly higher pollinator species richness and abundances than undisturbed habitats for the whole pollinator assemblage, but not for bees or non-bees separately. However, significant differences in species richness between habitats vanished after accounting for differences in abundance between habitat types. At a local scale Shannon–Weaver diversity and evenness did not vary with disturbance. A β diversity index indicated that, across forest types, species turnover was lower between disturbed habitats than between undisturbed habitats. In addition, rarefaction curves showed that disturbed habitats as a whole accumulated fewer species than undisturbed habitats at equivalent sample sizes. We concluded that small patches of disturbed habitat have a negligible effect on local pollinator diversity; however, habitat disturbance reduced β diversity through a homogenization of the pollinator fauna (in particular of bees) across the landscape.

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-009-9720-5](https://doi.org/10.1007/s10531-009-9720-5)) contains supplementary material, which is available to authorized users.

C. Quintero · C. L. Morales · M. A. Aizen

Laboratorio Ecotono, Instituto de Investigaciones en Biodiversidad y Medio Ambiente, Universidad Nacional del Comahue - CONICET, Quintral 1250, 8400 Bariloche, Río Negro, Argentina

C. L. Morales

e-mail: cmorales@crub.uncoma.edu.ar

M. A. Aizen

e-mail: marcelo.aizen@crub.uncoma.edu.ar

C. Quintero (✉)

Department of Ecology and Evolutionary Biology, University of Colorado, Campus Box 334, Boulder, CO 80309-0260, USA

e-mail: carolina.quintero@colorado.edu

Keywords α Diversity · Bees · β Diversity · Habitat alteration · Homogenization · Landscape · Pollinators · Rarefaction

Introduction

Pollinators represent a significant portion of insect biodiversity and their function is essential to ecosystem integrity and biodiversity maintenance by being involved in the sexual reproduction of about 90% of angiosperm species (Kearns et al. 1998; Potts et al. 2003). Despite the key role played by insect pollinators in angiosperm reproduction, our knowledge of how human-induced habitat disturbance affects their abundance, diversity and composition is still fragmentary (Sao Paulo Declaration on Pollinators 1999; Aizen and Vázquez 2006). Although several studies have looked at the effects of forest fragmentation on plant–pollinator interactions and pollinator faunas (reviewed in Murcia 1996; Cane 2001; Aizen and Feinsinger 2003; Aguilar et al. 2006; Winfree et al. 2009), assessment of how insect pollinator faunas change in relation to other types of anthropogenic disturbance has received much less attention (Aizen et al. 2002; Aizen and Feinsinger 2003; Winfree et al. 2009). Furthermore, a recent review (Winfree et al. 2009) concluded that responses of bee richness and abundance may vary among disturbance types, stressing the need of more studies on anthropogenic disturbances, other than fragmentation, on pollinator faunas. In addition, our knowledge regarding the impacts of anthropogenic disturbance on pollinator biotas is mostly based on patterns observed in tropical ecosystems (e.g. Tylianakis et al. 2005, 2006; Brosi et al. 2007); while similar data from temperate forest ecosystems are comparatively scarce (Steffan-Dewenter et al. 2002).

Anthropogenic habitat disturbance is one of the most important drivers of biodiversity changes, which operates at multiple spatial scales (Tylianakis et al. 2005, 2006). In forest habitats, small-scale disturbances like clear-cutting, fire or small human settlements, involve profound alterations of the vertical and horizontal structure of the forest (Vázquez and Simberloff 2004; Echeverria et al. 2007; Dumbrell et al. 2008) as well as of the plant community composition (Potts et al. 2003). Thus, the resulting configuration of various disturbed patches enclosed within a mostly homogeneous forest matrix can lead to changes in the mechanisms driving diversity at a local scale (mostly community-structuring processes like competition) as well as at a landscape scale (mostly meta-community processes like species turnover).

At the local scale, species richness and composition of insect pollinators can be affected by species interactions and availability of food and nesting sites. Because these requirements can be spatially redistributed through disturbance (Bronstein 1995; Tschamtket et al. 2005), it is expected that pollinator assemblages may change accordingly. Yet, the direction and magnitude of the change are difficult to predict as habitat disturbance has been associated with both increased as well as decreased abundance and richness (Tylianakis et al. 2005; Aizen 2007; Winfree et al. 2009).

At a larger spatial scale, disturbance dynamics may create diverse successional landscape mosaics in which both habitat heterogeneity and species diversity and composition may be greater than in undisturbed mature stages (Potts et al. 2003). Alternatively, a spatial succession of small patches of disturbed habitat may reduce landscape heterogeneity, leading to impoverished meta-communities (e.g. Paritsis and Aizen 2008) due to reduced species turnover. This effect may be especially detrimental in highly heterogeneous landscapes such as those occurring along strong environmental gradients.

Because both patch (local) and landscape processes influence diversity (Graham and Blake 2001; Collinge et al. 2003; Fleishman et al. 2003), understanding the scale at which habitat disturbance modifies biodiversity is essential (Hamer and Hill 2000; Hill and Hamer 2004; Tylianakis et al. 2006; Dumbrell et al. 2008). Thus, assessing simultaneously changes in α and β diversity due to anthropogenic habitat modification may help to define the right scale at which conservation measures for highly mobile taxa like insect pollinators are soundest (Hatfield and LeBuhn 2007; Kremen et al. 2007; Dumbrell et al. 2008).

Here we asked whether small-scale habitat disturbance in a mostly woody landscape affects local (α) diversity, richness, abundance and evenness of diurnal insect pollinators and whether this succession of disturbed patches affects species turnover (β diversity) across the landscape, and the overall (γ) diversity along a precipitation gradient in NW Patagonia, Argentina. To address these questions, we compared disturbed and nearby undisturbed habitats in terms of overall insect pollinator fauna as well as of bee and non-bee pollinators separately. Because bees (superfamily Apoidea, Hymenoptera) are a key pollinator group (Michener 1979; Cane 2001) and strongly rely on flower resources during their entire life cycle (Goulson 2003), we expected them to be more sensitive to disturbance-mediated changes than more facultative flower-visiting taxa.

Materials and methods

Study sites

We carried out field work in Nahuel Huapi National Park, Patagonia, Argentina (41° S 71° W) during the 2000–2001 austral flowering season (September–February). Nahuel Huapi National Park lies at the eastern limit of the Austral temperate forest and is bound by the Patagonian steppe towards the east (Dimitri 1962). We selected four different study sites (“Puerto Blest”, PB; “Llao Llao”, LL; “Cerro Otto”, CO; and “Challhuaco”, CH), which were located along a W–E transect of approximately 50 km, beginning at the Andean continental divide and ending at the forest-steppe ecotone towards the east (Fig. 1). Along this transect, mean annual precipitation decreases from more than 3,000 mm to ca. 700 mm, leading to a steep gradient of diverse vegetation types within a limited geographic area. Each site represents a unique combination of forest type and habitat disturbance: PB, Valdivian temperate rain forest, road opening and small-scale human settlement; LL, mixed *Nothofagus dombeyi*-*Austrocedrus chilensis* forest, abandoned orchard; CO, pure *Austrocedrus chilensis* forest, clear cutting and nearby human settlement; CH, pure *Nothofagus pumilio* high altitude forest, forest-fire and occasional grazing by feral cattle.

We chose sites separated by at least 10 km (maximum site separation 50 km), (see Fig. 1). At each site, we set up two sampling plots of ca. 2 ha each, located nearly 200 m from each other and characterized by contrasting intensities of anthropogenic habitat disturbance; one plot in a highly disturbed habitat and the other plot in an undisturbed or less disturbed habitat. Disturbances (i.e. events causing a rapid loss of a large fraction of the standing biomass of an area; Sutherland 1998) were characterized by an opening of at least 2 ha in the forest canopy due to human activities. Thus, in this study, changes at the local scale refer to variation in species richness, diversity, abundance and evenness within a few hectares; whereas changes at the landscape scale refer to variation in species richness, diversity, abundance and species turnover across the four sites covering an area of approx. 10,000 ha. All patches of disturbed habitat had on average higher sun irradiance

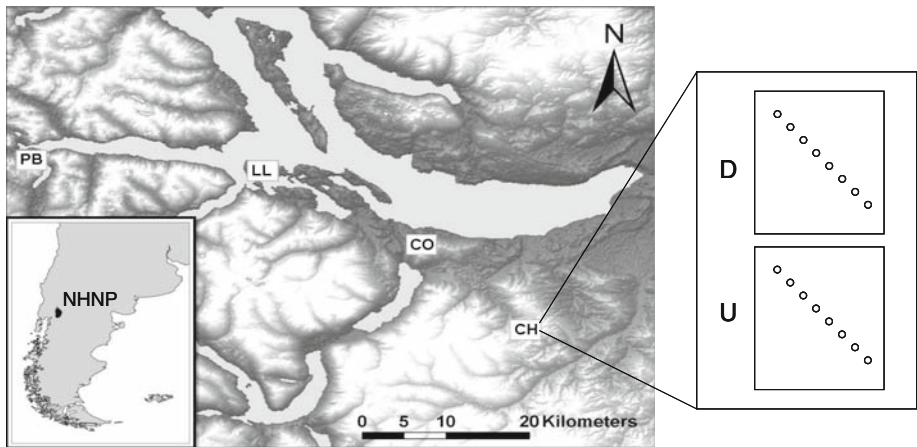


Fig. 1 Location of the study sites in Nahuel Huapi National Park (NHNP) and sampling design. Sites represent four forest types along a precipitation gradient, from west to east: PB = Pto. Blest, LL = Llao Llao, CO = Co. Otto, and CH = Challhuaco. Within each site paired Disturbed (D) and Undisturbed (U) plots were selected and eight pan traps were set along a transect

than nearby undisturbed forest (Morales 2006). Regardless of the history of use and type of disturbance, all disturbed plots were characterized by a higher richness and abundance of alien flowering plant species than their paired undisturbed plots (Morales and Aizen 2002, Morales 2006). A more detailed description of the sites and types of human disturbances occurring at each site can be found in Morales and Aizen (2002, 2006).

Sampling method

To sample pollinators, we used yellow plastic pan traps 21 cm in diameter, filled with water mixed with few drops of detergent to break water surface tension. Although these pan traps may provide taxonomically biased estimates of the local pollinator fauna due to differences in attraction to the traps and capturability among flying insect taxa (Cane and Tepedino 2001; Roulston et al. 2007), and/or ecological biases in relation to floral resource availability (Cane et al. 2000), they are an adequate and straightforward method for comparative purposes that provide similar effect sizes of abundance and diversity of many flying insect taxa when compared to other methods (Kearns and Inouye 1993; Aizen and Feinsinger 1994).

In each plot, we set out eight pan traps on the ground at regular distances from each other (ca. 50–80 m depending on the shape of the site) along a transect located at least 100 m from the habitat edge, from 0900 to 1800 h, the period of highest activity of diurnal pollinators (see Fig. 1 for sampling design). At 1800 h, traps were collected and all insects were transferred to plastic tubes and preserved in 70% ethanol. We set traps simultaneously in both disturbed and undisturbed plots within the same site; and sampled different sites on contiguous days. Each plot was sampled three times over the flowering season (from late October to mid February), every 35–45 days. In addition, in order to obtain a rapid characterization of resource availability at the plot level, we recorded the number of entomophilous flowering species blooming within a maximum distance of 2 m at both sides of the transects during the three sampling dates.

Insects that were known to visit and presumably pollinate flowers because of their taxonomic affiliation or from previous work in Nahuel Huapi NP (Aizen et al. 2002, 2008; Morales and Aizen 2002, 2006; Vázquez and Simberloff 2002) were separated and identified to the lowest possible taxonomic level. Those specimens that could not be identified to species level were assigned to different morphospecies. In spite of the importance of authoritative identification in order to define some ecological attributes (Cane 2001), identification through morphotyping is useful for the purpose of characterizing and quantifying pollinator faunas in comparative studies (see also Memmott and Godfray 1993). We recorded the total number of individuals and species/morphospecies at each plot and sampling date. Voucher specimens are deposited at Laboratorio Ecotono, Universidad Nacional del Comahue (Bariloche, Argentina), and at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina).

Data analysis

We pooled specimens from the eight traps from each plot per sampling date for analysis to avoid pseudoreplication (Aizen and Feinsinger 1994). We estimated species richness, abundance and the Shannon–Weaver H Diversity Index (Weaver and Shannon 1949) per plot. In addition, we estimated the Pielou’s E Evenness index, as a measure of the extent to which individuals are evenly distributed among species in a community, calculated as the ratio of observed diversity to maximum diversity ($E = H/H_{\max}$, where H_{\max} was calculated as the natural log of richness; Pielou 1966).

We compared changes in (log-transformed) species richness and abundance throughout the flowering season between habitat types using repeated-measures ANOVA, with sampling date (early-, mid- and late- summer) as the within-subject factor and habitat type (disturbed vs. undisturbed) as the between-subject factor. In a second step, abundance was included as a covariate in the analysis of richness in order to account for differences between habitat types and sites in the number of sampled individuals. In addition, overall differences in total species richness, abundance, Shannon–Weaver H index and Evenness between habitat types over the entire flowering season were analyzed by paired *t*-tests, pooling samples of the three sampling dates from each plot. Because of the small number of replicates (i.e., four pairs of sites), the statistical power of our analyses was rather low. Thus, we used a critical probability level of $\alpha = 0.1$ for all paired *t*-tests to avoid a high probability of committing Type II error (e.g. Vázquez and Simberloff 2004). In all cases, we performed separate analyses for the overall pollinator fauna, as well as for bees and non-bees separately.

To assess potential differences in flowering-plant richness between habitat types we used repeated-measures ANOVA. In addition, the relation between flowering plant species richness and insect pollinator, bee and non-bee richness at the sampling date level were evaluated through Spearman-rank correlation.

To compare changes in community composition across forest types and between disturbed and undisturbed habitat units we estimated the β_{sim} diversity index (Lennon et al. 2001) for all pairs of plots for total pollinators, and for bee and non-bee pollinators. This indicator of species turnover has three main advantages: it is not influenced by differences in abundance, it is very sensitive to species replacement, and it assesses replacement independently of any species richness gradient (Koleff et al. 2003).

The β_{sim} diversity index was calculated as: $1 - (a/[\min(b,c) + a])$, where *a* is the total number of species present in both plots, *b* is the number of species present in the neighboring plot but not in the focal one, and *c* is the number of species present in the focal plot but not in the neighboring one (Lennon et al. 2001). We calculated all possible β_{sim} for all

paired combinations of the eight plots, i.e. a total of 28 β_{sim} values. Four out of the 28 β_{sim} values corresponded to species turnover between paired plots within each site (i.e., between-habitats comparison D–U), six to species turnover between pairs of disturbed plots (D–D) and six to species turnover between pairs of undisturbed plots (U–U) from different sites. The remaining 12 β_{sim} values corresponded to species turnover between pairs of disturbed and undisturbed plots from different sites. Mean β_{sim} values (D–D, U–U and D–U) were compared with the 2.5 and 97.5% percentiles of mean β_{sim} obtained from random subsamples of equal size ($N = 4$, $N = 6$ and $N = 6$, respectively) from the 28 β_{sim} , with replacement. The undisturbed plot in site Llao Llao was dropped for the calculation and analysis of β_{sim} for bees because no bee species were captured in that plot. Thus, mean β_{sim} between undisturbed plots (U–U) and between habitats (D–U) and the corresponding randomization, are based on $N = 3$ each.

Since β_{sim} values are estimated in a pairwise manner, values from the same site are not independent. However, the main advantage of randomization tests, such as the one used here, is their validity as the non-independence structure of the data is at least partially incorporated into the test (Manly 1991). The randomization was run with Resampling Stats (Simon 1992).

We used rarefaction curves to assess the effect of habitat disturbance on overall species richness within each site and across the landscape (Gotelli and Graves 1996; Vázquez and Simberloff 2002). We constructed individual-based rarefaction curves (Gotelli and Colwell 2001) for each disturbed and undisturbed pair of plots separately, and from pooled samples of each habitat type from the four sites. Rarefaction curves were calculated using the software Ecosim V. 6.0 (Gotelli and Entsminger 2001).

Finally, we integrated the local and landscape scale, calculating additive partitioning of species diversity (Lande 1996; Veech et al. 2002) to describe the relative importance of different components of diversity across space and time in disturbed and undisturbed habitats (Tylianakis et al. 2005). Total species diversity (γ) in a given habitat type can be partitioned into additive components representing alpha diversity and spatial and temporal species turnover such that $\gamma = \alpha + \beta_T + \beta_S$. We calculated α , β_T , and β_S following Tylianakis et al. (2005) procedure. Alpha diversity (α) for each plot was calculated as the average number of species per sampling date. Temporal turnover (β_T) was calculated as the average β_T plot for disturbed and undisturbed habitat units, where β_T plot is the total number of species found in a given plot over the entire flowering season minus the mean number of species per census for that plot. Spatial turnover (β_S) was calculated as the cumulative total number of species found within a given habitat type (i.e., disturbed or undisturbed) over the entire flowering season minus the mean number of species per plot of that habitat type over the entire flowering season.

Results

Local richness, abundance and diversity of pollinators

We collected a total of 1009 individual insects belonging to 55 pollinator species including 467 bees (i.e. Apoidea) belonging to 18 species (Appendix A in Supplementary Materials). In total, 96% of all pollinator insects captured in the traps were identified to family, almost 40% to genus and 19% to species. Among bees, 94% of all individuals were identified to genus and almost 40% to species. Bees accounted for 43% and 47% of pollinator richness and abundance, respectively, in disturbed habitats, and 37% and 36% in undisturbed habitats. We recorded five bee families in trap samples, Andrenidae, Halictidae, Colletidae,

Apidae, and Megachilidae, in decreasing order of abundance. With the exception of a single individual belonging to the Megachilidae (*Anthidium gayi*), all bee families were present in at least three of the four forest types. Among the non-bee pollinators, Syrphidae (Diptera) was the most diverse family, and Diptera and Coleoptera were the most diverse orders. Lepidoptera and Thysanoptera were represented by a single species each (see Appendix A in Supplementary Materials).

Species richness and abundance vary considerably between habitat types as well as among forest types (see Table 1). Repeated-measures ANOVA showed that habitat disturbance significantly affected local pollinator richness ($F_{1,6} = 9.15, P < 0.05$) and abundance ($F_{1,6} = 15.83, P < 0.01$) but failed to detect significant differences between habitat types for bee and non-bee pollinator richness separately (Table 2), probably due to the low number of specimens captured per category (see Table 1). Thus, disturbed plots hosted on average a more abundant and specious pollinator fauna than undisturbed plots. In addition, time during the flowering season had a strong effect on overall local pollinator, bee, and non-bee richness ($F_{2,12} = 15.16, P < 0.001; F_{2,12} = 10.78, P < 0.01$ and $F_{2,12} = 8.74, P < 0.01$ respectively), and abundance ($F_{2,12} = 33.85, P < 0.001; F_{2,12} = 14.62, P < 0.01$ and $F_{2,12} = 24.08, P < 0.01$, respectively). The seasonal effect on pollinator richness and abundance was consistent across habitats as reflected by the lack of significant Time \times Habitat interaction (Table 2). In all cases, total richness and abundance reached their maximum peak at the middle of the flowering season, in early summer ($F_{1,6} = 54.16, P < 0.0001; F_{1,6} = 31.34, P < 0.001$ respectively). Differences in pollinator richness between disturbed and undisturbed habitats vanished when we accounted for differences in abundance among plots (repeated measures ANCOVA, $F_{1,3} = 0.07, P = 0.81$). When data for the entire flowering season were pooled for each plot, paired *t*-tests revealed only statistically marginal ($P < 0.1$) differences between disturbed and

Table 1 Species richness, abundance, diversity (H = Shannon–Weaver Index of diversity) and evenness for all pollinators, bee and non-bee pollinator communities at the four paired sites (D = disturbed and U = undisturbed)

| | Challhuaco | | Co. Otto | | Llao Llao | | Pto. Blest | |
|------------------|------------|------|----------|------|-----------|------|------------|------|
| | U | D | U | D | U | D | U | D |
| Richness | | | | | | | | |
| Non-bees | 5 | 4 | 7 | 13 | 6 | 19 | 8 | 8 |
| Bees | 6 | 10 | 5 | 5 | 0 | 7 | 4 | 12 |
| Total | 11 | 14 | 12 | 18 | 6 | 26 | 12 | 20 |
| Abundance | | | | | | | | |
| Non-bees | 11 | 44 | 54 | 93 | 14 | 292 | 9 | 25 |
| Bees | 16 | 250 | 5 | 8 | 0 | 55 | 29 | 104 |
| Total | 27 | 294 | 59 | 101 | 14 | 347 | 38 | 129 |
| H | | | | | | | | |
| Non-bees | 1.39 | 0.46 | 1.08 | 1.31 | 1.47 | 1.3 | 2.04 | 1.87 |
| Bees | 1.44 | 1.23 | 1.61 | 1.49 | – | 0.94 | 0.95 | 1.9 |
| Total | 2.1 | 1.5 | 1.4 | 1.6 | 1.5 | 1.7 | 1.8 | 2.4 |
| Evenness | | | | | | | | |
| Non-bees | 0.86 | 0.33 | 0.56 | 0.51 | 0.82 | 0.44 | 0.98 | 0.90 |
| Bees | 0.80 | 0.53 | 1.00 | 0.93 | – | 0.48 | 0.69 | 0.76 |
| Total | 0.88 | 0.57 | 0.56 | 0.55 | 0.84 | 0.52 | 0.72 | 0.80 |

Table 2 Results of repeated-measurement ANOVAs of log-transformed (a) richness and (b) abundance of total pollinators, bee and non-bee pollinators by means of pan trap samples

| (a) | df | Pollinator richness | | Bee richness | | Non-bee richness | |
|------------------|----|----------------------|----------|---------------|---------|-------------------|----------|
| | | SS | F | SS | F | SS | F |
| Between-subjects | | | | | | | |
| Habitat | 1 | .499 | 9.15* | .431 | 2.93 | .227 | 3.36 |
| Error | 6 | .328 | | .883 | | .405 | |
| Within-subjects | | | | | | | |
| Time | 2 | .523 | 15.16*** | .398 | 10.78** | .318 | 8.74** |
| Time × Habitat | 2 | .030 | .865 | .083 | 2.24 | .098 | 2.69 |
| Error | 12 | .207 | | .221 | | .218 | |
| (b) | df | Pollinator abundance | | Bee abundance | | Non-bee abundance | |
| | | SS | F | SS | F | SS | F |
| Between-subjects | | | | | | | |
| Habitat | 1 | 2.384 | 15.83** | 2.312 | 3.89 | 1.102 | 3.45 |
| Error | 6 | .903 | | 3.560 | | 1.914 | |
| Within-subjects | | | | | | | |
| Time | 2 | 4.098 | 33.85*** | 2.223 | 14.62** | 3.173 | 24.08*** |
| Time × Habitat | 2 | .108 | .435 | .391 | .118 | .503 | 3.82 |
| Error | 12 | .726 | | .913 | | .791 | |

* $P < .05$, ** $P < .01$, *** $P < .001$

undisturbed habitats for total pollinators richness and abundances, as well as for bee richness (Fig. 2a,b). In addition, Shannon–Weaver H and Evenness did not vary significantly between habitat types for any category (Fig. 2c,d).

Rarefaction curves of the individuals sampled at each plot reflected the striking difference in pollinator abundance between habitat types and the consistently higher species richness in disturbed habitats (Fig. 3). In accordance with the repeated-measures ANCOVA, rarefaction analysis indicated that when differences in abundances between habitats are accounted for, no differences in species richness between habitat types can be observed (i.e. overlapping curves and confidence intervals, except in the site Challhuaco). In addition, with the exception of the disturbed plot in Challhuaco, none of the curves reach an asymptote, indicating the need for more sampling in order to capture the actual species richness, in particular in undisturbed habitats (Fig. 3).

Repeated-measures ANOVA did not detect significant differences between habitats in (log transformed) flowering species richness ($F_{1,12} = 0.974$, $P = 0.362$). However, Spearman rank correlations showed that total pollinator as well as non-bee pollinator richness significantly correlated with flowering species richness ($r_s = 0.43$, $P = 0.036$, $N = 24$), whereas, although positive, the correlation between bee and flowering species richness was not significant ($r_s = 0.29$, $P = 0.16$, $N = 24$).

Species diversity, composition and turnover across the landscape

Comparisons of the β_{sim} diversity index across sites revealed that, between pairs of disturbed plots (D–D), β_{sim} was not different than expected by chance, for all pollinators

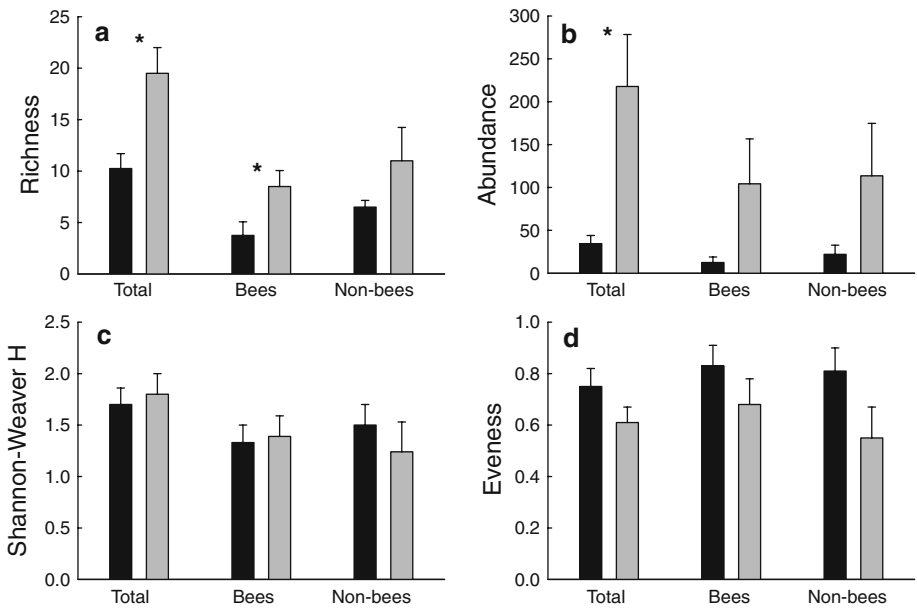


Fig. 2 Species richness, abundance, diversity and evenness for total pollinator fauna, bee and non-bee pollinators (mean of four paired sites \pm 1SE) pooling data for the entire flowering season in disturbed (gray) and undisturbed (black) habitats. Asterisks denote statistical differences between habitats at a $P < 0.1$ according to results of paired t -tests

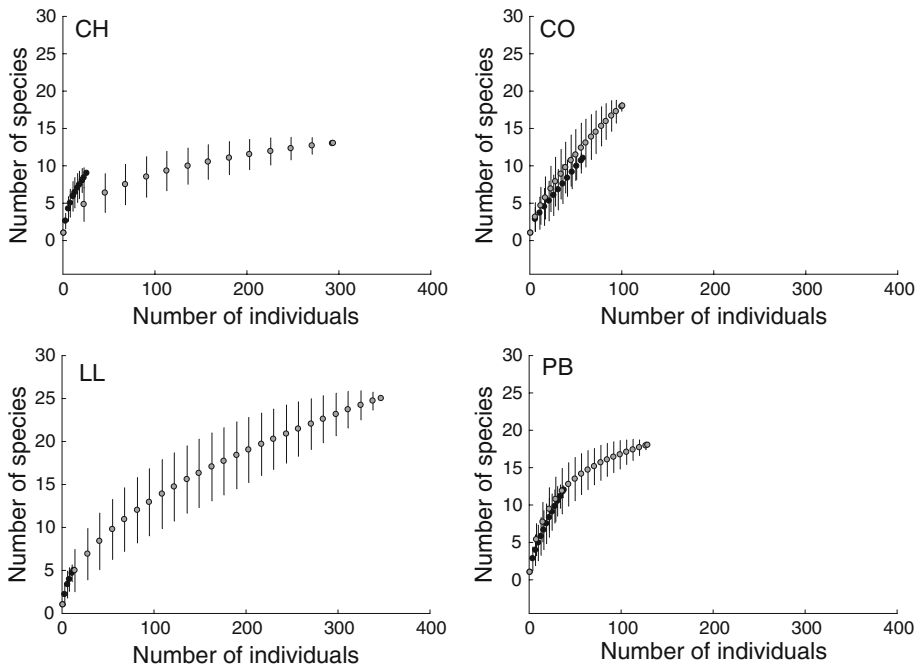


Fig. 3 Individual-based rarefaction curves for all pollinators captured during the flowering season in the four pairs of disturbed (gray) and undisturbed (black) habitat types. See site abbreviations in Fig. 1

(Fig. 4a) and non-bee pollinators (Fig. 4c), whereas bees showed significantly less turnover than expected by chance (Fig. 4b). On the contrary, between pairs of undisturbed plots (U–U), average β_{sim} for all pollinators and bees showed significantly more turnover than expected by chance (Fig. 4a,b), whereas differences beyond random expectations were not detected for non-bee pollinators (Fig. 4c). Mean β_{sim} was consistently lower for the three groups (all pollinators, bees and non-bees) between disturbed pairs of plots than between undisturbed pairs of plots. Thus, at the landscape scale spatial turnover of overall pollinator species, and particularly of bees, was lower between disturbed than undisturbed habitats. In addition, species turnover between paired disturbed and undisturbed plots (i.e. within the same site) was not significantly different from random (Fig. 4), indicating that despite changes in species abundance and concomitant changes in species richness, habitat disturbance did not lead to major changes in local species composition.

At the landscape scale, total species richness and abundance (all plots pooled) varied considerably between disturbed and undisturbed habitats. The rarefaction curve for the pool of undisturbed habitats, in contrast to the curve for the disturbed habitats, was far from reaching an asymptote, indicating that our sampling did not capture the actual species richness of this system in undisturbed habitats (Fig. 5). More interestingly, the rarefaction curve for undisturbed habitats was steeper than the curve for disturbed habitats. As a result, disturbed plots accumulated a lower number of species than undisturbed plots for the same number of individuals sampled, as reflected by the non-overlapping confidence intervals (Fig. 5).

The partitioning of species diversity across spatiotemporal scales

Figure 6 shows the relative partitioning of total species diversity across spatiotemporal scales for disturbed and undisturbed habitats. Patterns of species partitioning were very similar regardless of habitat type. Nevertheless, α diversity appears to represent a comparatively higher portion of γ diversity in disturbed than in undisturbed habitats, whereas spatial turnover (β_s) represents a comparatively higher portion of γ diversity in undisturbed habitats. These patterns are consistent with those found for local richness (Figs. 2 and 3) and spatial species turnover (Fig. 4).

Considering the whole study area, disturbed habitats contributed proportionally more to pollinator abundance than to richness. Disturbed plots together accounted for 86.2% of total abundance, while undisturbed plots accounted for the remaining 14%. Nevertheless, differences in term of richness were considerably lower: 82% of all species sampled were recorded in disturbed plots, whereas 59% were recorded in undisturbed plots. Overall, α diversity comprised 11.5% of the total diversity at the landscape level, whereas temporal and spatial turnover comprised 15.5% and 42.05%, respectively. The remaining 30.91% represented turnover in species between the habitat types.

Discussion

Local habitat disturbance affected pollinator richness, abundance and species turnover across the strong environmental gradient represented by the temperate forests of NW Patagonia. At the local scale, insect pollinators reached higher richness and abundance in disturbed than in undisturbed habitats. However, variation in species richness between plots was mainly driven by the strong variation in the number of sampled insects. Thus, the difference in richness between habitats vanished when the number of sampled individuals was accounted for, as reflected by ANCOVA and rarefaction curves (Fig. 3). Thus, higher

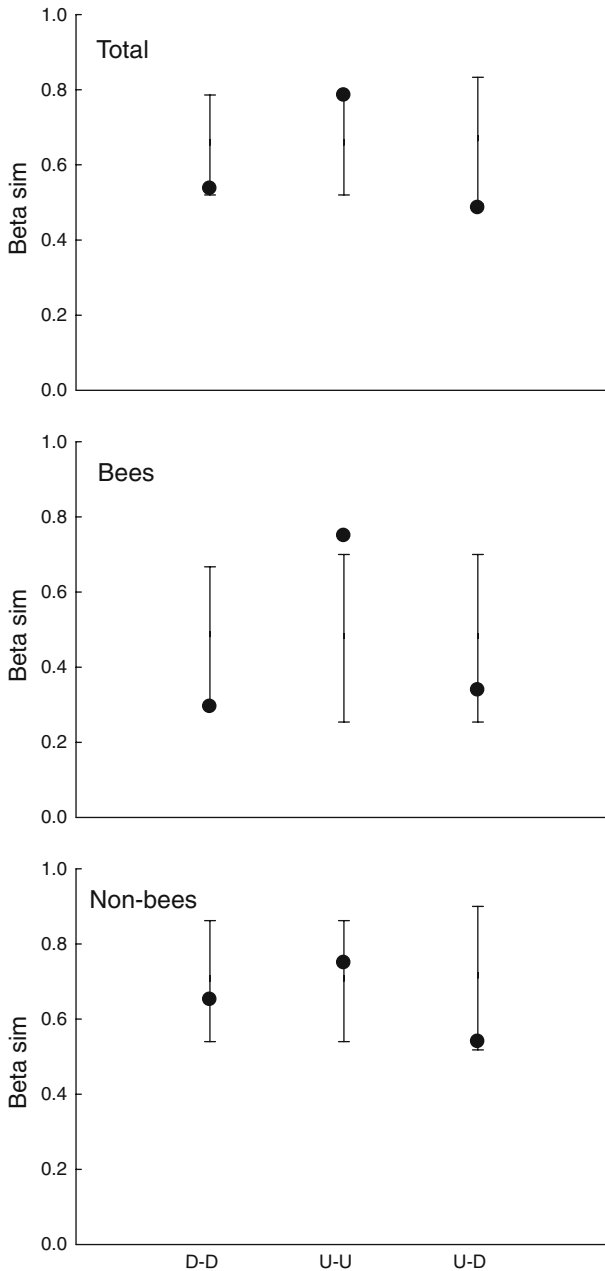


Fig. 4 Mean β_{sim} diversity index for total pollinators (a), bees (b), and non-bees (c) between pairs of undisturbed habitats across sites, between pairs of disturbed habitats across sites, and between undisturbed and disturbed paired habitats within the same site. Bars indicate the randomly generated 95% confidence intervals

local species richness associated with disturbance could be, at least in part, an artifact of limited sampling in the undisturbed forest. Accordingly, local pollinator diversity (as measured by Shannon–Weaver H) and evenness did not vary between habitats. In turn, at

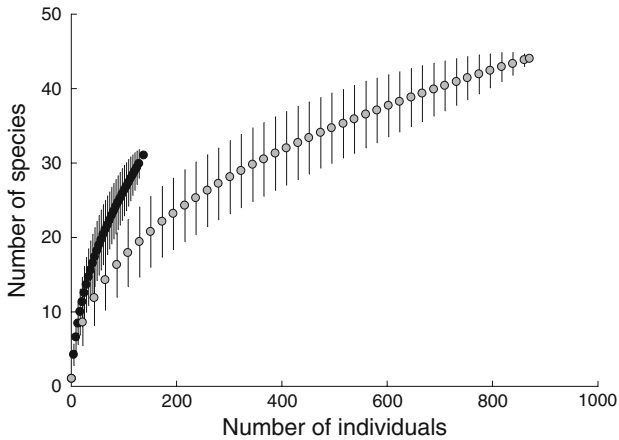


Fig. 5 Individual-based rarefaction curves for all the pollinators captured during the flowering season in the pooled disturbed (*gray*) vs. undisturbed (*black*) habitat types

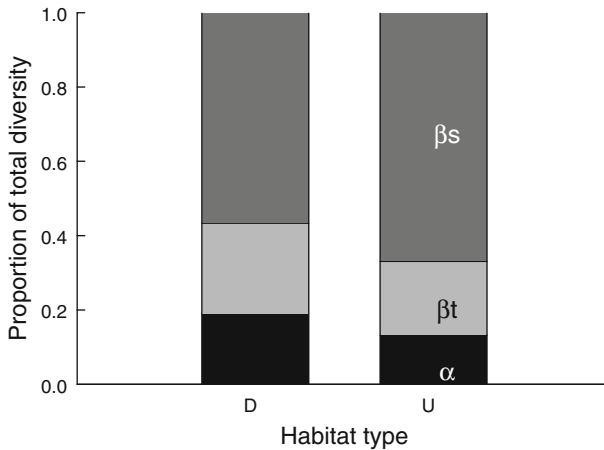


Fig. 6 Proportion of total (γ) diversity partitioned into α diversity (α), temporal turnover (β_t), and spatial turnover (β_s)

the landscape scale, the presence of patches of disturbed habitat within a mostly continuous undisturbed forest was associated with a reduced spatial species turnover (β_{sim} and β_s). Thus homogenization of the pollinator fauna across the landscape led to a reduction in the expected overall diversity (γ diversity), as suggested by the composite rarefaction curve (Fig. 5). Finally, and supporting our initial contention, bee composition more strongly reflected habitat changes caused by anthropogenic disturbance at the landscape scale than more facultative non-bee flower visitors. Although the findings reported here might be specific to the particular group of insect pollinators that are well represented in the pan traps, they resemble results of disturbance-driven homogenization of pollinator assemblages sampled at flowers in subtropical forests (Aizen and Feinsinger 1994; Chacoff and Aizen 2006).

Locally, the higher pollinator richness in disturbed habitats seems to be explained by higher pollinator abundance in these habitat types, which increases the chances of sampling more species. Similar responses to small-sized disturbance have also been documented for fruit feeding butterflies (Lewis 2001), and bees (Romey et al. 2007). A meta-analysis conducted by Winfree et al. (2009) also found positive effects (despite non significance and very large variation in effect size) of disturbance by fire and grazing on bee richness and abundance, suggesting that bee abundance might be especially favoured by small disturbed patches.

This increase in abundance, and concomitantly in richness, may be explained by increased population growth of resident species of disturbed habitats. However, given the small size of the disturbed patches, this pattern may be also explained by temporary (day time) or permanent migration of pollinators from nearby mature forests. Both increased local populations and spill-over from undisturbed forest to disturbed forest gaps can be associated with several abiotic and biotic characteristics common to disturbed habitats such as higher light availability, increased temperature and more abundant flower resources (e.g. Feinsinger et al. 1988).

Higher insolation in forest gaps has been shown to increase pollinator activity, particularly of small-sized bees (Herrera 1995), which may lead to increasing local abundance and richness, at least during the day time. In addition, higher insolation in forest gaps can increase flower resources and therefore sustain higher pollinator abundance. Increased flower density has been significantly associated with augmented pollinator diversity and activity (Thompson 2000; Hegland and Boeke 2006). Thus, disturbed forest areas might act as oases of concentrated floral resources (e.g. Romey et al. 2007).

In our study, despite the dissimilar disturbance types analyzed, all disturbed habitats were characterized by the opening of the forest canopy and an increase in the richness and abundance of flowering plants, particularly of exotic plant species (Morales and Aizen 2002). In accordance with this, both bee richness and abundance were marginally related to average light irradiance per sampling date ($r_s = 0.34$, $P = 0.09$, and $r_s = 0.39$, $P = 0.06$, $N = 24$, respectively) and Spearman correlations demonstrated a significant association of flowering-plants richness with richness of pollinator biota. Thus, although further research is needed to carefully identify the possible drivers of the observed variation in richness and abundance, the pattern reported by this study at the local scale appears to be driven by flower resources and abiotic characteristics, such as light irradiance, common to all disturbed plots.

Interestingly, the four sites showed a similar response (increased richness and abundance) to habitat disturbance. This outcome was somewhat unexpected since each site represented a different forest type and experienced a dissimilar disturbance type, which are thought to result in different responses of the pollinator community (Winfree et al. 2009). Despite the lack of replicates for forest types or for disturbance types, our study suggests that the response of the diurnal insect pollinator fauna of forested habitats to small-scale disturbances varies little, regardless of forest and disturbance type. However, since species richness is not only dependent on the scale of observation (Lennon et al. 2001; Rahbeck 2005), but also on the spatial scale of the disturbance, our results should not be extrapolated to large-scale disturbances, like extensive and/or long-term forest clearances and widespread forest fires where more negative effects have been observed (Spagarino et al. 2001; Diaz et al. 2005; Moretti et al. 2006; Echeverria et al. 2007). In fact, the apparent contradictory evidence of the effect of habitat disturbance on insect diversity might be partly explained not only by differences in the sampled spatial scale among studies, as exemplified by Hamer and Hill (2000), but also by the contrasting sizes of disturbed areas

examined among empirical studies (e.g., Lewis 2001; Beck et al. 2002; Gray et al. 2007; Romey et al. 2007; Winfree et al. 2007; Noske et al. 2008).

In turn, at the landscape scale, our results indicated that habitat disturbance appears to be associated with a reduced species turnover, in particular of the bee fauna, across the landscape (Fig. 4). At a scale of 10 km, Lennon et al. (2001) found, for British birds, high species turnover associated with low species richness, once local gradients in species richness had been filtered out. Under the untested assumption that such a pattern is also valid for smaller spatial scales, the higher than expected average β_{sim} values of the bee fauna recorded between pairs of undisturbed plots (U–U) could be interpreted as the result of lower local richness (i.e. without taking abundance into account) detected in undisturbed habitats. Nevertheless, the strong similarity between β_{sim} values for the D–D and U–D comparisons suggests that the observed pattern is not an artifact of differences in richness between habitat types. Thus, our results suggest that the typical assemblages of diurnal insect pollinators associated with the different forest types in this study have been partially replaced by a more homogeneous pollinator fauna, particularly among bees, occupying altered habitats.

This study adds to the growing literature providing evidence of taxonomic homogenization under habitat disturbance of arthropod faunas in general (Holway et al. 2002 and references therein) and pollinators in particular (Aizen and Feinsinger 1994; Chacoff and Aizen 2006 for bees; Ghazoul 2002 for butterflies). In addition, this study goes a step further and demonstrates that even habitats experiencing dissimilar disturbance types and with varying times since disturbance converge to a more similar pollinator fauna due to homogenization. Nonetheless, further research is required to examine whether this pattern holds true under the possible scenario of higher disturbance frequency or increased disturbance area.

Taxonomic homogenization implies an increase in the compositional similarity among communities, mainly by the successful invasion of “winner” and the extirpation of “loser” species (McKinney and Lokwood 1999). In particular, human disturbance may shift plant-pollinator interactions by affecting the abundance and species composition of flower assemblages (Feinsinger et al. 1987). In this study, canopy opening associated with habitat disturbance fostered a massive recruitment of a few highly invasive flowering plants with conspicuous flowering, such as *Cytisus scoparius*, *Rosa rubiginosa*, *Carduus nutans*, *Cirsium vulgare* and *Lupinus polyphyllus* (Morales and Aizen 2002). As most of these species have successfully colonized different forest types, pollinators associated with those invasive plants might be favored over other species in undisturbed habitats. For example, the halictid bee *Ruizantheda mutabilis* was the second most dominant species in disturbed habitats (Appendix A in Supplementary Materials), supporting previous observations of high preference for alien flowering plants by this native species (Morales and Aizen 2006). Similarly, *Heterosarus* sp. has been observed as a frequent flower visitor of alien *Rosa rubiginosa* (Morales, unpublished data) as well as a species showing positive responses to other anthropogenic disturbances in the area such as cattle grazing (Vázquez and Simberloff 2002). Thus, a possible mechanism underlying homogenization among disturbed areas can be the ability of some native generalist pollinator species to take advantage of massive flowering events of alien species across different forest types. From a plant perspective, whereas pollination and reproduction of alien plants may benefit by massive recruitment of “weedy” pollinators, sexual reproduction of at least some native plant species remaining in disturbed habitats may be impaired by a loss of interactions with more specialized pollinators (Vázquez and Simberloff 2004; Aizen et al. 2008), which may be more forest-dependent than more generalist species (Morales 2006).

Management and conservation implications

Our results show that small-scale habitat disturbances, like those exemplified in this study, can increase local pollinator abundance, without having a major effect on local diversity, once abundance has been taken into account. From this pattern, we might conclude that the presence of small patches of disturbed habitats should not be considered a major threat to local biodiversity. On the contrary, they may provide floral resources that contribute to sustaining populations of some pollinator species that inhabit the undisturbed matrix. However, disturbed habitats may provide poor nesting habitats for some of these species, and thus their dependence on undisturbed forest patches may still be high (Kremer et al. 2004). More importantly, the apparent overall benefits of disturbance mosaics may obscure the simple fact that it may be only the late successional species within the disturbance mosaic that are rare, threatened and in need of protection (Sutherland 1998). Thus, the idea of habitat disturbance increasing local abundance and richness should be taken as cautionary and not extrapolated to disturbances of larger extent.

At the landscape scale, small patches of disturbed habitat increased the homogeneity of pollinator fauna. If the goal of protected natural areas is to preserve representative samples of the different habitats present in the region (Sutherland 1998), conserving the uniqueness of each community (i.e. maximizing species turnover) in relatively large undisturbed areas should be a priority. In addition, if small-scale disturbances are viewed as initial stages in the process of fragmentation, our results suggest that even early fragmentation can lead to impoverishment of otherwise rich pollinator meta-communities. Because anthropogenic habitat disturbance such as fragmentation, fire, and agriculture are causing not only precipitous declines in wild pollinators, but also they are thereby threatening ecosystem services (Pimentel and Wilson 1997; Kremen et al. 2002, 2007), studies reporting biodiversity decay at early stages of fragmentation are critical. Furthermore, our study was unable to detect differences in pollinator responses to the various classes of disturbances or time since the origin of the perturbation. This result may imply that human-induced forest fires, clear-cutting and urbanization may generate somewhat similar behavioral responses in diurnal insect pollinators. However, before this pattern can be generalized, we suggest a long-term monitoring of pollinator biotas in relation to disturbance with, if existing, adequate replication of classes of human-induced disturbances.

South American temperate forests are of special conservation concern due to their highly endemic flora and fauna (Heywood 1995; Armesto et al. 1996) and the occurrence of unique plant–animal mutualisms (Aizen and Ezcurra 1998; Amico and Aizen 2000). Currently, the combination of human-induced forest fires, clear-cutting and urbanization represent some of the most important regional threats. Despite the importance of these disturbances in the area, few studies have addressed their effects on native pollinator communities, either in Chile or in Argentina. Because the frequency and intensity of fire and clear-cutting can increase considerably in the near future due to economic pressures and climate change, assessment of how the native pollinator biota reacts to the environmental changes generated by these disturbances at larger spatial scales has become critical for policy makers. This study suggests that habitat disturbances may affect the uniqueness of each forest type leading to homogenization of the pollinator fauna, especially of the bee community, even at an early stage when patches of disturbances are infrequent and limited in extent.

Acknowledgments We are indebted to A. Roig and G. Clapps for help on bee identification and for valuable bibliography on Diptera identification. We thank C. Nufio, Y. Linhart, M. D. Bowers, and two

anonymous reviewers for their useful comments on an earlier version of this paper, and J. Paritsis for designing the map used in Fig. 1. We also thank the National Park Administration for authorizing field work in the Nahuel Huapi NP. Funding was provided by The Canon National Park Science Scholars Program for the Americas. CLM and MAA are members of Research Career of the National Research Council of Argentina (CONICET).

References

- Aguilar R, Ashworth L, Galetto L et al (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol Lett* 9:968–980
- Aizen MA (2007) Enfoques en el estudio de la reproducción sexual de las plantas en ambientes alterados: limitaciones y perspectivas. *Aust Ecol* 17:7–19
- Aizen MA, Ezcurra C (1998) High incidence of plant-animal mutualisms in the woody flora of the temperate forest of South America: biogeographical origin and present ecological significance. *Aust Ecol* 8: 217–236
- Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine “Chaco Serrano”. *Ecol Appl* 4:378–392
- Aizen MA, Feinsinger P (2003) Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. In: Bradshaw G, Marquet P, Mooney HA (eds) *How landscapes change: human disturbance and ecosystem disruption in the Americas*. Springer-Verlag, New York, pp 111–129
- Aizen MA, Vázquez DP (2006) Flower performance in human-altered habitats. In: Harder LD, Barrett SCH (eds) *Ecology and evolution of flowers*. Oxford University Press, Oxford, pp 159–179
- Aizen MA, Vázquez DP, Smith-Ramirez C (2002) Natural history and conservation of plant-animal mutualisms in the temperate forest of southern South America. *Rev Chil Hist Nat* 75:79–97
- Aizen MA, Morales CL, Morales JM (2008) Invasive mutualists erode native pollination webs. *PLoS Biol* 6(2):e31. doi:10.1371/journal.pbio.0060031
- Amico G, Aizen MA (2000) Ecology- mistletoe seed dispersal by a marsupial. *Nature* 408:929–930
- Armesto JJ, Rozzi R, Smith-Ramirez C et al (1996) Conservation targets in South American temperate forests. *Science* 282:1271–1272
- Beck J, Schulze CH, Linsenmair KE et al (2002) From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *J Trop Ecol* 18:33–51
- Bronstein JJ (1995) The plant-pollinator landscape. In: Hansson L, Fahrig L, Merriam G (eds) *Mosaic landscapes and ecological processes*. Chapman and Hall, London, pp 256–288
- Brosi BJ, Daily GC, Ehrlich PR (2007) Bee community shifts with landscape context in a tropical countryside. *Ecol Appl* 17:418–430
- Cane J (2001) Habitat fragmentation and native bees: a premature verdict? *Conserv Ecol* 5: 3 [online] URL: <http://www.consecol.org/vol5/iss1/art3>
- Cane JH, Tepedino VJ (2001) Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conserv Ecol* 5:1
- Cane JH, Minckley RL, Kervin LJ (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *J Kans Entomol Soc* 73:225–231
- Chacoff N, Aizen MA (2006) Edge effects on flower-visiting insects in grapefruit plantations bordering premontane sub-tropical forest. *J Appl Ecol* 43:18–27
- Collinge S, Prudic K, Oliver J (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conserv Biol* 17:178–187
- Diaz IA, Armesto JJ, Reid S et al (2005) Linking forest structure and composition: avian diversity in successional forests of Chiloe Island, Chile. *Biol Conserv* 123:91–101
- Dimitri MJ (1962) La flora andino-patagónica. *Anales de Parques Nacionales (Buenos Aires)* 9:1–115
- Dumbrell AJ, Clark EJ, Frost GA et al (2008) Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. *J Appl Ecol* 45:1531–1539
- Echeverría C, Newton AC, Lara A et al (2007) Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecol Biogeogr* 16:426–439
- Feinsinger P, Beach JH, Linhart YB et al (1987) Disturbance, pollinator predictability, and pollination success among Costa Rica cloud forest plants. *Ecology* 68:1294–1305
- Feinsinger P, Busby WH, Murray KG et al (1988) Mixed support for spatial heterogeneity in species interactions: hummingbirds in a tropical disturbance mosaic. *Am Nat* 131:33–57
- Fleishman E, Betrus CJ, Blair RB (2003) Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin, USA. *Landsc Ecol* 18:675–685

- Ghazoul J (2002) Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodivers Conserv* 11:521–541
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Gotelli NJ, Entsminger GL (2001) Ecosim: Null Models Software for Ecology, Version 6.0. Acquired Intelligence Inc. and Kesity-Bear. <http://homepages.together.net/gentsmin/ecosim.htm>
- Gotelli NJ, Graves RG (1996) Null models in ecology. Smithsonian Institution, Washington, DC
- Goulson D (2003) Bumblebees, behaviour and ecology. Oxford University Press, NY
- Graham C, Blake L (2001) Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscape. *Ecol Appl* 11:1709–1721
- Gray MA, Baldauf SL, Mayhew PJ et al (2007) The response of avian feeding guilds to tropical forest disturbance. *Conserv Biol* 21:133–141
- Hamer KC, Hill JK (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conserv Biol* 14:1435–1440
- Hatfield RG, LeBuhn G (2007) Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biol Conserv* 139:150–158
- Hegland SJ, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecol Entomol* 31:532–538
- Herrera CM (1995) Microclimate and individual variation in pollinators: flowering plants are more than their flowers. *Ecology* 76:1516–1524
- Heywood VH (1995) Global diversity assessment. Cambridge University Press, Cambridge
- Hill JK, Hamer KC (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *J Appl Ecol* 41:744–754
- Holway DA, Lach L, Suarez AV et al (2002) The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–233
- Kearns CA, Inouye DW (1993) Techniques for pollination biologists. University of Colorado Press, Colorado
- Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annu Rev Ecol Syst* 29:83–112
- Koleff P, Lennon JJ, Gaston KJ (2003) Are there latitudinal gradients in species turnover? *Global Ecol Biogeogr* 12:483–498
- Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc Natl Acad Sci USA* 99:16812–16816
- Kremen C, Williams NM, Aizen MA et al (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett* 10:299–314
- Kremer C, Williams NM, Bugg RL et al (2004) The area required of an ecosystem service: crop pollination by native bee communities in California. *Ecol Lett* 7:1109–1119
- Lande R (1996) Statistics and partitioning of species diversity and similarity among multiple communities. *Oikos* 76:5–13
- Lennon JJ, Koleff P, Greenwood JJD et al (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J Anim Ecol* 70:966–979
- Lewis OT (2001) Effect of experimental selective logging on tropical butterflies. *Conserv Biol* 15:389–400
- Manly BFJ (1991) Randomization, Bootstrap and Monte Carlo methods in biology. Chapman & Hall/CRC, London
- McKinney ML, Lokwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14:450–453
- Memmitt J, Godfray H CJ (1993) Parasitoid webs. In: Lasalle J, Gould ID (eds) Hymenoptera and biodiversity. C.A.B. International, Wallingford, pp 217–234
- Michener CD (1979) Biogeography of the bees. *Annals of the Missouri Botanical Garden* 66:277–347
- Morales CL (2006) Alteración del hábitat e interacciones entre especies nativas y exóticas a través de la polinización en Bosques Templados de Sudamérica Austral. Tesis Doctoral. Universidad Nacional del Comahue, Bariloche, Argentina
- Morales CL, Aizen MA (2002) Does the invasion of alien plants promote invasion of alien flower visitors? A case study from the temperate forests of southern Andes. *Biol Invasions* 4:87–100
- Morales CL, Aizen MA (2006) Invasive mutualisms and the structure of plant–pollinator interactions in the temperate forests of north-west Patagonia, Argentina. *J Ecol* 94:171–180
- Moretti M, Duelli P, Obrist MK (2006) Biodiversity and resilience of arthropod communities after fire disturbance in temperate forests. *Oecologia* 149:312–327
- Murcia C (1996) Forest fragmentation and the pollination of neotropical plants. In: Schelhas J, Greenberg R (eds) Forest patches in tropical landscapes. Island Press, Washington, DC, pp 19–36

- Noske NM, Hilt N, Werner FA et al (2008) Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. *Basic Appl Ecol* 9:4–12
- Paritsis J, Aizen MA (2008) Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. *For Ecol Manage* 255:1575–1583
- Pielou EC (1966) The measurement of diversity in different types of biological collections. *J Theor Biol* 13:131–144
- Pimentel D, Wilson C (1997) Economic and environmental benefits of biodiversity. *Bioscience* 47:112–117
- Potts SG, Vulliamy B, Dafni A et al (2003) Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101:103–112
- Rahbeck C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol Lett* 8:224–239
- Romey WL, Ascher JS, Powell DA et al (2007) Impacts of logging on midsummer diversity of native bees (Apoidea) in a northern hardwood forest. *J Kans Entomol Soc* 80:327–338
- Roulston TH, Smith SA, Brewster (2007) A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *J Kans Entomol Soc* 80:179–181
- Sao Paulo Declaration on Pollinators (1999) Report on the recommendations of the workshop on the conservation and sustainable use of pollinators in agriculture with emphasis on bees. Brazilian Ministry of the Environment, Brazilia
- Simon JL (1992) Resampling stats. IBM Version 3:13
- Spagarino C, Martinez Pastur G, Peri PL (2001) Changes in *Nothofagus pumilio* forest biodiversity during the forest management cycle. 1. Insects. *Biodivers Conserv* 10:2077–2092
- Steffan-Dewenter I, Munzenberg U, Burger C et al (2002) Scale dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421–1432
- Sutherland WJ (1998) Conservation science and action. Blackwell Science Ltd., London, UK
- Thompson JD (2000) How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia* 126:386–394
- Tscharntke T, Klein AM, Kruess A et al (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874
- Tylianakis JM, Klein AM, Tscharntke T (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology* 86:3296–3302
- Tylianakis JM, Klein AM, Lozada T et al (2006) Spatial scale of observation affects α , β and γ diversity of cavity-nesting bees and wasps across a tropical land-use gradient. *J Biogeogr* 33:1295–1304
- Vázquez DP, Simberloff D (2002) Ecological specialization and susceptibility to disturbance: conjectures and refutations. *Am Nat* 159:606–623
- Vázquez DP, Simberloff D (2004) Indirect effects of an introduced ungulate on pollination and plant reproduction. *Ecol Monogr* 74:281–308
- Veech JA, Summerville KS, Crist TO et al (2002) The additive partitioning of diversity: recent revival of an old idea. *Oikos* 99:3–9
- Weaver W, Shannon CE (1949) The mathematical theory of communication. University of Illinois, Urbana, Illinois
- Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conserv Biol* 21:213–222
- Winfree R, Aguilar R, Vázquez DP et al (2009) How do bees respond to anthropogenic disturbance? A synthesis and meta-analysis. *Ecology* 90:2068–2076