



The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity

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ABSTRACT

Aim Pollination services are at risk from land use change and intensification, but responses of individual pollinator species are often variable, making it difficult to detect and understand community-level impacts on pollination. We investigated changes in community composition and functional diversity of insect pollinator communities under land use change in a highly modified landscape.

Location Canterbury region, South Island, New Zealand.

Methods We trapped insect pollinators every month for 1 year at 24 sites across four land use types of increasing intensity in New Zealand: gardens with native vegetation, blackcurrant orchards, dairy farms, and rotational cropping farms. We investigated changes in pollinator species and functional richness and differences in species and functional composition.

Results Under increasing land use intensity, both species and functional richness declined markedly. Changes in functional richness, however, were overall not significantly different than expected based on the observed declines in species richness. Nevertheless, there was a significant trend towards greater than expected functional richness within less-intensive land use types and lower than expected functional richness within intensive land use types. The order of species loss under increasing land use intensity was non-random, as pollinators with a narrow diet breadth, large body size, solitary behaviour and a preference for non-floral larval food resources were lost first.

Main conclusions Our study shows that pollinator species bearing particular trait attributes are susceptible to differences in land use. Our study suggests that pollination services may be more vulnerable to environmental changes and disturbances in more intensive land use types as a result of lower pollinator functional richness.

Keywords

Agriculture, agro-ecosystem, bees, biodiversity, crop, ecosystem function, functional richness, functional traits, land use change, pollination.

INTRODUCTION

Land use change is frequently associated with biodiversity loss and altered species composition (Tylianakis *et al.*, 2005; Kremen *et al.*, 2007). This has functional consequences, because species with particular functional traits appear to

be especially vulnerable to decline (Henle *et al.*, 2004; Bartomeus *et al.*, 2013b; Newbold *et al.*, 2013). As species' traits determine their contribution to ecosystem processes, loss of particular traits may translate to changes in ecosystem functioning and services (Kleijn *et al.*, 2004; Larsen *et al.*, 2005; Cardinale *et al.*, 2012).

The consequences of land use change are particularly important for insect pollinators, which provide pollination services for between 78 and 94% of all flowering plants and 75% of the leading global food crops (Klein *et al.*, 2007; Ollerton *et al.*, 2011; Winfree *et al.*, 2011). Yet, while the benefits of pollinator biodiversity are known to depend on functional trait diversity (Hoehn *et al.*, 2008; Albrecht *et al.*, 2012), studies on pollinator responses to land use have largely focused on metrics relating to species richness and/or abundance (e.g. Hatfield, 2007; reviewed in Winfree *et al.*, 2011). The full impact of disturbance (e.g. land use intensity) on communities includes changes to the identity and functional roles of species (e.g. Bracken & Low, 2012). For example, social bee species have been shown to be more strongly affected by isolation from natural habitat and pesticides than are solitary bee species (Williams *et al.*, 2010), and small-bodied generalists tend to be more strongly affected by habitat loss, compared with small-bodied specialists (Bommarco *et al.*, 2010).

Non-random species losses occur because of specific trait–environment relationships and may reflect differential extinction or colonization rates, differences in dispersal ability and/or differential habitat quality (Loo *et al.*, 2002; Hylander *et al.*, 2005). These factors may result in communities that show a nested composition pattern, whereby species in disturbed habitats are a subset of those present in less disturbed habitats (Ulrich, 2009; Aizen *et al.*, 2012; Sasaki *et al.*, 2012). Nestedness has thus been used as a tool to identify the functional and compositional consequences of land use change and non-random patterns of species loss (Patterson & Atmar, 1986; Ulrich *et al.*, 2009; Selmants *et al.*, 2012).

In this study, we use a novel approach to investigate pollinator community response to changes in land use type by investigating functional diversity and community nestedness in four anthropogenic habitats with differing land use intensity. We base our analyses on 10 pollinator morphological, behavioural and life history traits that contribute to pollination functions and are likely to influence responses to disturbance.

Specifically, we ask the following questions:

1. How do pollinator richness and composition differ among land use types and do these changes translate to altered functional diversity among land use types?
2. Are losses of functional diversity predictable from losses of species diversity?
3. Which functional traits are favoured in different land use types?

METHODS

Land use types

Six replicates of each of four land use types (i.e. 24 sites) were sampled in the Canterbury plains region, on the South Island of New Zealand. The sites were positioned within four different land use types (named in decreasing order of intensity): rotational cropping, dairy farms, blackcurrant orchards

and New Zealand native gardens (Fig. S1; see Appendix S1 and S2 in Supporting Information for details about site selection). The order of intensity was based on qualitative information gained from farmer consultation concerning the frequency and depth of soil disturbance, biomass removal and use of external inputs (i.e. fertilizer, herbicide), which, in turn, impacted vegetation complexity and the proportion of exotic species (Table S1; see Appendix S1). All land use types were embedded within a highly modified agricultural landscape in the Canterbury region of New Zealand.

Insect pollinator sampling

We selected a focal sampling area (5 m × 5 m) at each replicate site, in which to trap insect pollinators. Pollinators were trapped for 5 days each month from November 2008 to 2009 using flight intercept and pan traps. Insect traps were placed within a field boundary nearest to the centre of a given farm of a given land use type. At each site, four yellow flight intercept/pan traps (Howlett *et al.*, 2009) were positioned 2 m apart on stakes at a height of 1.2 m. Each trap consisted of a pan trap measuring 22 cm × 35 cm × 6 cm attached to two vertical panes (flight intercept) that were arranged perpendicular to each other (Fig. S2; see Appendix S1 for more details on sampling). Two traps contained a mixture of water and detergent and two traps contained clear acetate sheets (22 cm × 30 cm) lined with Tanglefoot paste (The Tanglefoot Company, Grand Rapids, MI, USA). Tanglefoot was applied as a thin film to the entire surface area of each acetate sheet to ensure maximum insect capture. We applied Tanglefoot as a thin film such that pollen was retained on insect bodies and not lost in drops of excess Tanglefoot; preliminary trials were conducted in commercial *Brassica rapa* fields to perfect this method. The two trapping methods were used to maximize the diversity and sample size of insects captured. All traps were replaced daily. All insects captured were transported back to the laboratory and stored in a freezer (−80 °C) until further processing. Insects were sorted to species using existing collections, identification keys (Donovan, 2007; Landcare Research, 2013) and assistance from expert taxonomists. Potential pollinators were separated from non-pollinators on the basis of the proportion of individuals carrying pollen and the mean amount of pollen carried. In this dataset, some taxa comprised numerous individuals that carried no pollen at all and a few that carried 1 or 2 pollen grains, arriving at a mean of 0 or 1 pollen grain/s. We did not consider these to be pollinators. The remaining species carried a minimum mean pollen load of five or more pollen grains. These were considered potential pollinators. Although we did not measure viability of pollen, the transfer and adherence of pollen to the pollinator was deemed a potential pollination event. The number of pollen species carried by pollinators was identified using a pollen library of plant specimens collected at each site at the time of sampling. Voucher specimens are located at the New Zealand Institute for Plant and Food Research in Lincoln, New Zealand.

Pollinator traits

Pollinator traits were compiled using field observations and existing published and unpublished datasets (Table S2; See Appendix S1) from the Canterbury region. For each pollinator species, we compiled information for the following 10 traits: (1) body width, measured as distance between the base of the wings in mm (i.e. intertegula span in bees); (2) body depth (mm); (3) body length (mm); (4) pollen carrying structure: scopa, corbicula, none; (5) larval feeding type: decaying vegetation, parasite, predator of other insect, dung, carrion, nectar or pollen; (6) behaviour: social, solitary; (7) foraging preference: nectar or pollen; (8) mean duration of flower visitation; (9) richness of pollen carried (i.e. the number of plant species carried by the pollinator species); and (10) nesting behaviour: central nest (i.e. foraging is focused around nest location), no nest (foraging is not centred around a nest location). Morphological trait values (e.g. body length, width and depth) were derived by obtaining the mean dimensions of ten representative specimens (Table S2, Appendix S1). Traits related to foraging preferences and flower visitation were measured in mass flowering *Brassica rapa* fields as part of another study (Rader *et al.*, 2009). All species were scored for all traits; hence, all species have the same number of traits recorded and each trait has a number of values for continuous traits and a number of levels for categorical traits (See Appendix S1 for summary statistics of traits).

The traits selected were intended to capture characteristics known to be important for the quantity and quality of pollination services. For example, body size correlates with pollination efficiency (Larsen *et al.*, 2005), foraging duration (Stone & Willmer, 1989; Stone, 1994), foraging distance in some bees (Greenleaf *et al.*, 2007) and susceptibility to land use change (Larsen *et al.*, 2005; Winfree *et al.*, 2009; Williams *et al.*, 2010). Although the response-effect functional trait framework suggests assignment of traits to two groups (i.e. 'effect' traits influence ecosystem functioning, while 'response' traits influence how species respond to disturbance Naeem & Wright, 2003; Hooper *et al.*, 2005; Violle & Jiang, 2009), most traits in our dataset not only contribute to pollination functions, but also are likely to influence responses to disturbance (Lavorel & Garnier, 2002; Larsen *et al.*, 2005).

Richness analyses

We tested how species richness responded to our land use intensity gradient to provide baseline information against which to compare changes in functional diversity. Data were pooled across trap types (sticky and flight intercept traps) and time (i.e. monthly trap collections for 1 year). Even though sampling effort was standardized, species abundances differed between sites, which can strongly influence species richness estimates (Gotelli & Colwell, 2001). We therefore calculated rarefied richness to the lowest sample size ($n = 193$ individuals) to test whether observed richness was affected by differences in abundances between sites (Gotelli

& Colwell, 2001). We tested for spatial autocorrelation of both data and model residuals using Moran's index in the 'spdep' package (Bivand *et al.*, 2012) in the R environment (R Development Core Team, 2012). Spatial autocorrelation was not significant, as indicated by low and non-significant Moran values (range -0.05 to 0.03 ; $P > 0.2$) and hence was not taken into account in further analysis. We used linear models to compare species richness between land use types, with species richness as the response variable and land use type as the predictor.

Nestedness and functional diversity analyses

To test whether pollinator communities were nested between land use types (i.e. if species from sites with lower species richness were a subset of the species found at sites with higher richness), nestedness was calculated using NODF (Almeida-Neto *et al.*, 2008) and tested for significance against 100 null matrices using the null model described in Patterson & Atmar (1986). This analysis determines the order in which species are lost or colonize a system and calculates the rank of sites by taking into account the percentage overlap of presence for each pair of columns (i.e. species) and for each pair of rows (i.e. sites) in a matrix ordered to maximize nestedness; hence, both columns and rows are included in the analyses (Ulrich & Gotelli, 2007; Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009). To determine which traits were lost first, we used the rank of each species on the nested configuration as a measure of species loss order (Ulrich & Gotelli, 2007; Ulrich, 2009; Sasaki *et al.*, 2012) using the 'vegan' package in R (Oksanen *et al.*, 2011). A more nested system indicates that species loss is non-random.

This rank was then used as a response variable in a linear model with species abundance and individual species traits as predictors. We performed stepwise model selection using AIC in the 'MASS' package (Venables & Ripley, 2002) in R to select the best model. As five species were represented at all sites, their rank was considered to be the same; hence, we attributed the rank value of one to all five species. Body depth was excluded as it was highly correlated with body width.

Just as diversity is different to composition in taxonomic diversity studies, we explored both functional diversity and functional community composition to better understand community response to different land use types. Functional diversity indices (functional richness and functional dispersion) were calculated using the 'FD' package in R (Laliberté & Legendre, 2010). Functional richness and dispersion are important metrics to understand the impacts of land use change upon functional diversity as they can be used to indicate whether species within a given habitat are performing similar (i.e. redundant) or different (i.e. complementary) roles for a given function or service (Walker, 1992; Elmquist *et al.*, 2003; Laliberté *et al.*, 2010). We used linear models to compare each of the two functional diversity metrics between land use types, with functional richness and functional dispersion indices as response variables. Details of the methods used to calculate these metrics are described in Appendix S2 of the

Supporting Information. We used a null model to distinguish whether the observed change in functional richness was higher or lower than expected given the species richness observed (Petchey, 2004). We used a simulation approach to create a random (null) distribution of functional richness values for a given number of species. Holding species richness constant for each land use type, we randomly selected species from the species pool (the total number of species in the study) to calculate a null functional richness for each richness level. We repeated this 1000 times to produce a distribution of null values and tested whether the actual functional richness for each community was significantly higher or lower than the mean of the null functional richness distribution, at $\alpha = 0.05$.

This approach permitted us to determine whether changes in functional richness simply reflected changes in species richness or whether species loss and trait diversity responded differently to land use management. As sites within each land use type showed different patterns in relation to the null model, we also calculated standardized deviations of functional richness in each site from the null expectation and compared these deviations between land use types using linear models (Ingram & Shurin, 2009; Mason *et al.*, 2012; Laliberté *et al.*, 2013).

Community-weighted mean and functional trait composition

To further explore which particular traits drive the changes observed in functional diversity, we obtained the community-weighted trait means (CWM) of all traits for each site (Garnier *et al.*, 2004) as measures of functional composition. We used permutational analysis of variance (PERMANOVA) and permutational analysis of dispersion tests (PERMDISP) based on Gower distance (to enable inclusion of discrete variables) to compare CWMs between land use types and nonparametric multidimensional scaling (NMDS) to visualize functional composition of the CWM indices. We used a Procrustes test (Peres-Neto & Jackson, 2001) to test whether sites with similar species composition exhibited similar functional composition. This method compares two distance matrices using permutation tests to calculate the statistical significance of matrix resemblance (Alarcón *et al.*, 2008; Burkle and Irwin, 2009; Alarcón, 2010) and has been shown to be more robust than the classic Mantel test (Peres-Neto & Jackson, 2001).

To test for differences in community composition between land use types, we used PERMANOVA on a Bray–Curtis distance matrix between sites using the ‘vegan’ package in R (Oksanen *et al.*, 2011). Differences in beta diversity between land uses were assessed using the PERMDISP test. To visualize patterns in species composition, we used NMDS.

All statistical analyses in this study were conducted using R software (R Development Core Team, 2012).

RESULTS

We collected 23,509 pollinator individuals more than 1 year (mean: 2439 individuals/month) and recorded 25 different

pollinator species, the most abundant of which were bees and flies (Table S3; See Appendix S1). All taxa in this study were unmanaged and assemblages comprised both native (14 species) and introduced (11 species) taxa. Even though we recorded *Apis mellifera* at study sites, it is likely this taxon was unmanaged, as managed hives were >1.2 km away from our study sites and feral honey bees existed in this region at the time of this study.

Observed species richness in gardens was significantly higher than in crops (Figs 1 & 2; Table S4; See Appendix S1) and this pattern matched that of rarefied species richness (Fig. 2; Table S4; See Appendix S1). Less species-rich communities contained a subset of the species found in more species-rich communities (Fig. 1, NODF nestedness = 79.01, compared with 100 simulations of the null model: Mean = 59.81, $Z = 13.12$, $P = 0.01$). The core pollinator species present at most sites included two introduced social (*Apis mellifera* and *Bombus terrestris*, Apidae) and one native solitary bee (*Lasioglossum sordidum*, Halictidae) and two common flies (*Delia platura*, Anthomyiidae and *Pollenia pseudorudis*, Calliphoridae, Fig. 1).

The species that were less common, with a large body size, solitary behaviour, larval feeding preferences other than nectar/pollen (i.e. decaying vegetation, parasitic, etc.) and foragers of few plant species were lost first with increasing land use intensity (Fig. 3). These species were present in less-intensive, species-rich sites, representative of garden and blackcurrant land uses (Fig. 3). In contrast, common species with a small body size, social behaviour, preference for nectar/pollen and generalist foragers of many plant species were associated with less diverse sites, including cropping and dairy land uses (Fig. 3; Table S7; See Appendix S1).

Functional richness declined by 83% from the least intensive gardens to the most intensive rotational cropping. Although functional richness of gardens was significantly higher than that of dairy and cropping (Table S4; See Appendix S1), overall, this decline was not significantly different from that expected according to a random loss of species at most sites as determined by the null model (Fig. S3; see Appendix S1). However, sites within each land use showed different patterns in relation to the null model, as evidenced by significant differences ($P = 0.03$) in standardized deviations between land use types. Standardized deviations of observed functional richness from the null expectation were positive (i.e. greater than expected) for the less-intensive land use types (blackcurrant: 0.36; native garden: 0.41) and negative (i.e. lower than expected) for the more intensive land use types (crop: -0.11 ; dairy: -0.64). Functional dispersion, however, did not differ significantly between land use types (Fig. 2; Table S4; See Appendix S1).

Abundance-weighted community composition differed significantly between land use types (PERMANOVA, $R^2 = 0.23$; $P = 0.041$; Fig. S6). For example, among the common species, *L. sordidum* comprised 58% and 53% of the individuals in blackcurrant and rotational cropping while only 35% and 17% in garden and dairy, respectively (Table S6; See Appen-

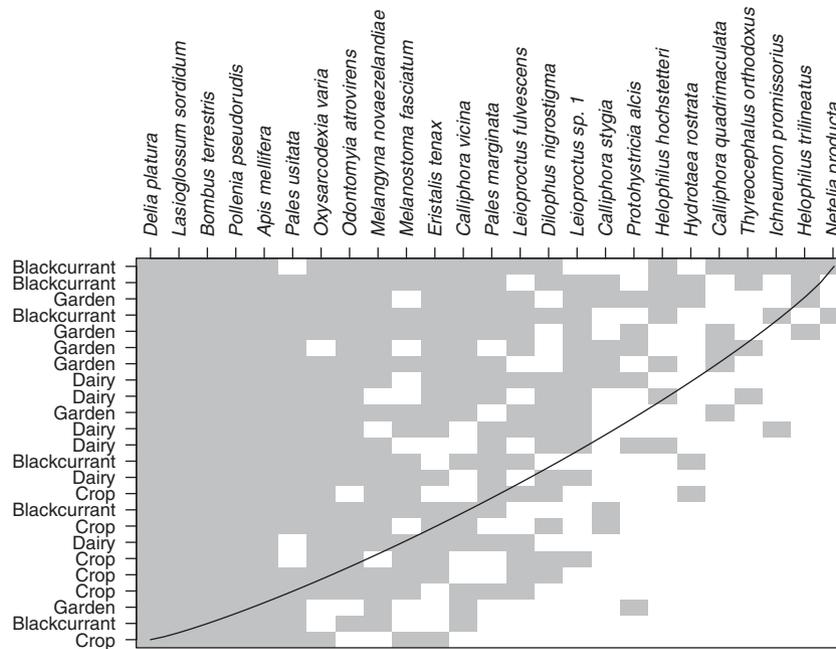


Figure 1 Matrix of species composition and land use intensity showing nested pattern (sites with fewer species contain a subset of the species in more diverse sites) derived from the analyses of nestedness. Grey-shaded squares represent species presence and unshaded represents species absence at each site. Note that garden and blackcurrant sites predominately occupy upper matrix, indicating higher richness. Crop and dairy sites contain a subset of the species found in richer sites. The curve delineates the condition in which perfect nestedness would occur, that is, whereby species on the far right of the figure are only found at few sites and those species on the far left are found at all sites. A perfectly nested community would thus be represented by grey shading of all cells above the line and empty white cells below the line.

dix S1). The community-level weighted trait means showed that communities in different land uses were characterized by different traits (Figs. S4, S5; Table S5; See Appendix S1). For example, pollinators in rotational cropping had a greater proportion of species that foraged on many plant species than those in gardens, such as *A. mellifera* and *B. terrestris*, (Table S4; Fig. S4; see Appendix S1). All land uses (with the exception of two sites) were dominated by solitary species and pollinator body size did not differ between land use types ($F_{3,20} = 1.25$, $P = 0.31$; Table S5; see Appendix S1).

Congruent with the species composition results, mean trait composition differed significantly between land use types (PERMANOVA, $R^2 = 0.37$, $P = 0.005$; Fig. S7). However, functional dispersion between land uses was not significantly different (PERMDISP, $F_{3,20} = 1.60$, $P = 0.22$). Not surprisingly, though, communities that were more similar in species composition tended to be more functionally similar, but this pattern was not statistically significant (Procrustes test; correlation: 0.42, P -value = 0.09; based on 1000 permutations).

DISCUSSION

Land use change and the preferential loss of particular species

Land use change is driving rapid declines in global species diversity (Sala *et al.*, 2000), but taxa do not all respond in the

same way. Differences in sensitivity to land use intensity are largely a result of the traits species possess and species responses to landscape change and associated changes in environmental factors (Kleijn *et al.*, 2004; Larsen *et al.*, 2005).

Vegetation loss and fragmentation in anthropogenic habitats is frequently associated with declines in pollinator species richness (Garibaldi *et al.*, 2011; Winfree *et al.*, 2011), yet few studies have determined the extent to which changes in composition accompany changes in species richness. For example, the identification of compositional shifts will enable detection of whether specialist species are being replaced with more common generalist species (Tylianakis *et al.*, 2005; Aizen *et al.*, 2012). In our study, large-bodied taxa, solitary bees and taxa with non-floral larval food requirements were the most likely to be lost with increasing land use intensity. Solitary taxa commonly nest in the ground resulting in sensitivity to changes in agricultural management associated with intensification (Williams *et al.*, 2010; Jauker *et al.*, 2013). The loss of large-bodied taxa concurs with larger-scale trends reported for pollinators (Bartomeus *et al.*, 2013a) and the preferential loss of specialist, parasitic and cavity-nesting pollinators (Williams *et al.*, 2010; Burkle *et al.*, 2013).

Sociality and diet alone do not, however, mitigate a negative response to land use intensification. Other traits, such as body size, may mediate or exacerbate land use change impacts. For example, Jauker *et al.* (2013) demonstrated

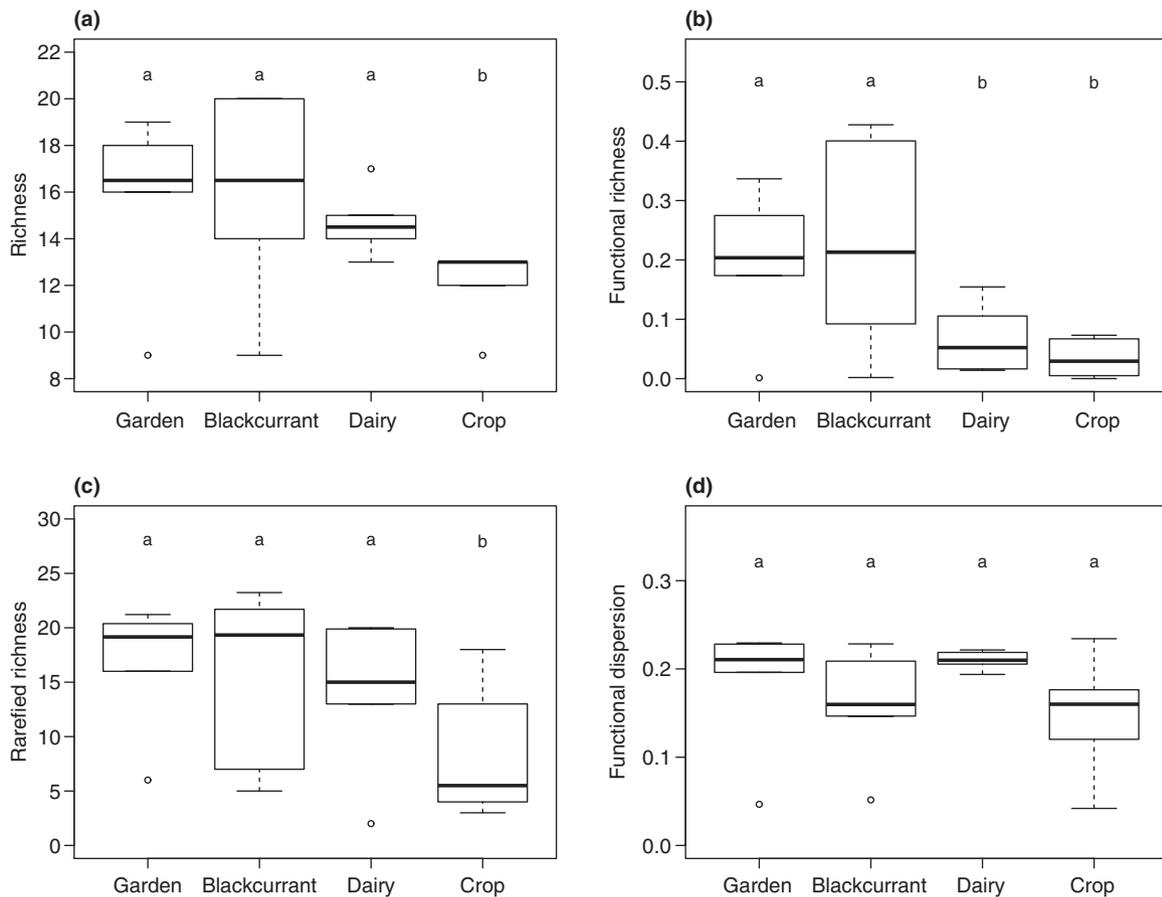


Figure 2 Species and functional diversity metrics across different land use types in the Canterbury region, New Zealand: (a) Species richness, (b) functional richness, (c) rarefied richness, (d) functional dispersion. Significant differences indicated by letters that relate to garden as the baseline habitat for comparison with other habitats; see Table S4 for further details.

that although solitary reproduction resulted in species being particularly vulnerable to habitat loss, this response was mediated by body size. Small-bodied social bees within the family Halictidae were susceptible to land use change, whereas large-bodied bumblebees were not. Furthermore, Bommarco *et al.* (2010) demonstrated that large-bodied generalist pollinators were less affected by land use change than were small-bodied generalists. In our study, the two generalist, social bee species, *Apis mellifera* and *Bombus terrestris*, were present across all study sites and hence were not sensitive to changes in land use. Declines in large-bodied taxa in this dataset are thus largely represented by Diptera, solitary bees (*Leioproctus sp.*) and non-bee hymenopteran taxa.

The implications of pollinator loss

The dominance of common species, most often exotic in our dataset, is a common feature of modified or disturbed habitats (Dukes & Mooney, 1999; Tylianakis *et al.*, 2005; Didham *et al.*, 2007), yet its functional consequences are less obvious. This is because the non-dominant functional groups that appear to be susceptible to differences in land use manage-

ment (e.g. solitary taxa with non-floral larval food requirements) are important pollination service providers to many New Zealand native plants and some commercial mass flowering crops (Primack, 1983; Newstrom & Robertson, 2005; Rader *et al.*, 2009, 2013b; Howlett, 2012).

Determination of the full magnitude of impact of these losses would thus require an assessment of the changes in pollination function associated with land use intensification. Irrespective of this knowledge gap, the losses of particular functional groups will likely reduce the insurance value provided by functionally-dissimilar communities (Loreau *et al.*, 2001; Bartomeus *et al.*, 2013a), as resilience is conferred to diverse assemblages by the provision of a range of ecological responses to environmental change (Elmqvist *et al.*, 2003; Norberg, 2004; Laliberté *et al.*, 2010; Rader *et al.*, 2013a).

In conclusion, our study shows that species bearing particular trait attributes (i.e. large body size, solitary behaviour and non-floral larval food resources) are more susceptible to changes in land use than species without. While particular trait attributes are being selected in response to intensification, intensification is not currently affecting the breadth of functional diversity (i.e. functional dispersion showed little

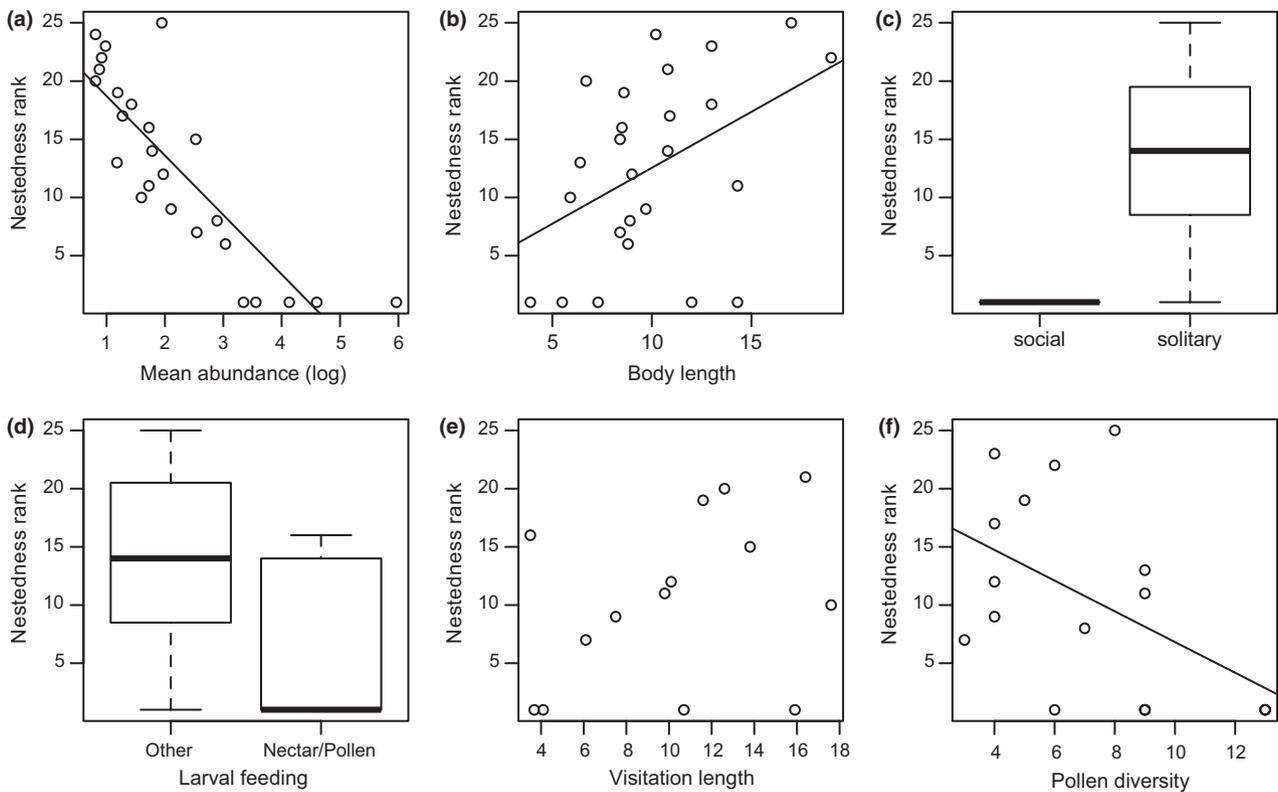


Figure 3 The relationship between species nestedness rank and pollinator abundance and traits retained in the best model. Nestedness rank was obtained using the order in which each site is listed in the nestedness matrix illustrated in Fig. 1. A higher ranking represents species that are present in most sites. This ranking was used as a response variable in analyses to determine whether rarer species are lost first, and which traits are lost first with increasing intensification. For simplicity, the slopes of the univariate relationships were plotted for the predictors that were retained in the full multivariate model. Significance indicated by asterisk (all $P \geq 0.01$): (a) abundance (log-transformed), (b) body length, (c) sociality, (d) larval feeding behaviour, (e) visitation duration, and (f) diversity of pollen carried. Refer to Table S7 in Appendix S1 for further details.

difference across land use types). Nonetheless, the capacity to cope with future change may be reduced as a result of lower functional richness in more intensive land use types.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary information relating to site selection and results.

Figure S1 Location of study sites.

Figure S2 Flight intercept trap design and measurements.

Figure S3 Results of null model analyses.

Figure S4 Changes in continuous functional traits with land use type.

Figure S5 Changes in discrete functional traits with land use type.

Figure S6 Differences in taxonomic composition with land use type.

Figure S7 Differences in functional composition with land use type

Table S1 Features of land use types.

Table S2 Insect functional traits used in this study.

Table S3 Species list.

Table S4 Model estimates for diversity indices.

Table S5 Model estimates for Community-weighted means.

Table S6 Dominance of common species.

Table S7 Model estimates resulting from linear model of species ranked nestedness.

Appendix S2 Supplementary information relating to methods and analyses.

Appendix S3 Supplementary information concerning trait correlation matrix.

BIOSKETCH

Romina Rader is interested in plant–animal interactions. Her current research focuses on the potential impacts of land use change upon pollinator communities and the provision of ecosystem services by unmanaged pollinator taxa.

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