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

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(A)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 one 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

51 functional richness.

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53 Key words: agriculture, agro-ecosystem, bees, biodiversity, crop, ecosystem

54 function, functional richness, functional traits, land-use change, pollination.

55

(A) 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).

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 colonisation 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?

(A) Methods

105 (B) *Land-use types*

106 Six replicates of each of four land-use types (i.e. 24 sites) were sampled in the
107 Canterbury plains region, on the South Island of New Zealand. The sites were
108 positioned within four different land-use types (named in decreasing order of
109 intensity): rotational cropping, dairy farms, blackcurrant orchards and New Zealand
110 native gardens (Fig. S1; see Appendix S1 and S2 in Supporting Information for
111 details about site selection). The order of intensity was based on qualitative
112 information gained from farmer consultation concerning the frequency and depth of
113 soil disturbance, biomass removal, and use of external inputs (i.e. fertilizer,
114 herbicide), which, in turn, impacted vegetation complexity and the proportion of
115 exotic species (Table S1; see Appendix S1). All land-use types were embedded
116 within a highly modified agricultural landscape in the Canterbury region of New
117 Zealand.

118 (B) *Insect pollinator sampling*

119 We selected a focal sampling area (5 m x 5 m) at each replicate site, in which to trap
120 insect pollinators. Pollinators were trapped for five days each month from November
121 2008 to 2009 using flight intercept and pan traps. Insect traps were placed within a
122 field boundary nearest to the centre of a given farm of a given land-use type. At each
123 site, four yellow flight intercept/pan traps (Howlett *et al.*, 2009) were positioned 2 m
124 apart on stakes at a height of 1.2 m. Each trap consisted of a pan trap measuring 22
125 cm x 35 cm x 6 cm attached to two vertical panes (flight intercept) that were
126 arranged perpendicular to each other (Fig. S2; see Appendix S1 for more details on
127 sampling). Two traps contained a mixture of water and detergent and two traps
128 contained clear acetate sheets (22 cm x 30 cm) lined with Tanglefoot paste (The

Tanglefoot Company, Minnesota, 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.

(B) 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. inter-tegula 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) (10) nesting behaviour: central nest (i.e. foraging is focused around nest location); no nest (foraging is not centered 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 are also likely to influence responses to disturbance (Lavorel & Garnier, 2002; Larsen *et al.*, 2005).

(B) Richness analyses

We tested how species richness responded to our land-use intensity gradient in order 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 among 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 among sites (Gotelli & Colwell, 2001). We tested for spatial autocorrelation of both data and model residuals using the Moran 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 among land-use types, with species richness as the response variable and land-use type as the predictor.

(B) Nestedness and functional diversity analyses

To test whether pollinator communities were nested among 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 presences 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 if 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; Elmqvist *et al.*, 2003; Laliberté *et al.*, 2010). We used linear models to compare each of the two functional diversity metrics among 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 if changes in functional richness simply reflected changes in species richness, or if 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 standardised deviations of functional richness in each site from the null expectation and compared these deviations among land-use types using linear models (Ingram & Shurin, 2009; Mason *et al.*, 2012; Laliberté *et al.*, 2013).

(B) 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 among land-use types, and non-parametric 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 among 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 among 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).

(A) Results

We collected 23,509 pollinator individuals over one 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 (Fig. 1 and 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 to 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 behavior, 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 behavior, 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).

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305 Functional richness declined by 83% from the least intensive gardens to the most
306 intensive rotational cropping. Although functional richness of gardens was
307 significantly higher than that of dairy and cropping (Table S4; See Appendix S1),
308 overall, this decline was not significantly different from that expected according to a
309 random loss of species at most sites as determined by the null model (Fig. S3; see
310 Appendix S1). However, sites within each land use showed different patterns in
311 relation to the null model, as evidenced by significant differences ($P = 0.03$) in
312 standardised deviations among land-use types. Standardised deviations of observed
313 functional richness from the null expectation were positive (i.e. greater-than-
314 expected) for the less intensive land-use types (blackcurrant: 0.36; native garden:
315 0.41) and negative (i.e. lower-than-expected) for the more intensive land-use types
316 (crop: -0.11; dairy: -0.64). Functional dispersion, however, did not differ significantly
317 among land-use types (Fig. 2; Table S4; See Appendix S1).

318

319 Abundance-weighted community composition differed significantly among land-use
320 types (PERMANOVA, $R^2 = 0.23$; $P = 0.041$; Fig. S6). For example, among the
321 common species, *L. sordidum* comprised 58% and 53% of the individuals in
322 blackcurrant and rotational cropping, while only 35% and 17% in garden and dairy,
323 respectively (Table S6; See Appendix S1). The community-level weighted trait
324 means showed that communities in different land uses were characterized by
325 different traits (Figs. S4, S5; Table S5; See Appendix S1). For example, pollinators in
326 rotational cropping had a greater proportion of species that foraged on many plant
327 species than those in gardens, such as *A. mellifera* and *B. terrestris*, (Table S4; Fig.
328 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 among 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 among land-use types (PERMANOVA, $R^2 = 0.37$, $P = 0.005$; Fig. S7). However, functional dispersion among 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).

(A) Discussion

(B) 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 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.

(B) 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 management (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; Howlett, 2012; Rader *et al.*, 2013b).

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 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.

404

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416 **(A) References**

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620 **Biosketch**

621 Romina Rader is interested in plant–animal interactions. Her current research

622 focuses on the potential impacts of land-use change upon pollinator communities

623 and the provision of ecosystem services by unmanaged pollinator taxa.

624

625 **Supporting Information**

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

627 Appendix S1 { Supplementary information relating to site selection and results }

628 Appendix S2 { Supplementary information relating to methods and analyses }

629 Appendix S3 { Supplementary information concerning trait correlation matrix }

630 Figure S1 { Location of study sites }

631 Figure S2 { Flight-intercept trap design and measurements }

632 Figure S3 { Results of null model analyses }

633 Figure S4 { Changes in continuous functional traits with land-use type }

634 Figure S5 { Changes in discrete functional traits with land-use type }

635 Figure S6 { Differences in taxonomic composition with land-use type }

636 Figure S7 { Differences in functional composition with land-use type }

637 Table S1 { Features of land-use types }

638 Table S2 { Insect functional traits used in this study }

639 Table S3 { Species list }

640 Table S4 { Model estimates for diversity indices }

641 Table S5 { Model estimates for Community Weighted Means }

642 Table S6 { Dominance of common species }

643

644 Figure captions:

645

646 Fig. 1: Matrix of species composition and land-use intensity showing nested pattern

647 (sites with fewer species contain a subset of the species in more diverse sites)

648 derived from the analyses of nestedness. Grey-shaded squares represent species

649 presence and un-shaded represents species absence at each site. Note that garden

650 and blackcurrant sites predominately occupy upper matrix, indicating higher

651 richness. Crop and dairy sites contain a subset of the species found in richer sites.

652 The curve delineates the condition in which perfect nestedness would occur, i.e.

653 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.

Fig. 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 to other habitats; see table S4 for further details.

Fig. 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 if 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 $P \leq 0.01$): A. abundance (log transformed), B. body length, C. sociality, D. larval feeding behaviour, E. visitation duration, F. diversity of pollen carried. Refer to Table S7 in Appendix S1 for further details.

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