

Effects of rarity form on species' responses to land use

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Abstract

Anthropogenic land-use change causes substantial changes in local and global biodiversity. Rare and common species can differ in sensitivity to land-use change, with rare species expected to be more negatively affected. Rarity may be defined in terms of geographic range size, population density or breadth of habitat requirements. How these three forms of rarity interact in determining global responses to land use is yet to be assessed. Using global data representing 912 vertebrate species, we test for differences in the responses to land use of species characterised by different types of rarity. Species considered rare with respect to all three forms of rarity showed particularly strong declines in disturbed land uses (more than 40% of species and 30% of individuals in the most disturbed land uses). In contrast, species common both geographically and numerically, and with broad habitat requirements, showed strong increases (up to 90% increase in species and 40% in abundance in some land uses). Our results suggest that efforts to understand the vulnerability of species to environmental changes should account for different types of rarity where possible. Our results also have potentially important implications for ecosystem functioning, given that rare species may play unique roles within ecosystems.

Introduction

Habitat loss and fragmentation have been among the most important drivers of biodiversity change over the last century (Hoffmann et al. 2010; Laurance et al. 2012; Newbold et al. 2015), and over 75% of the land area has at some time experienced severe human impact or alteration (Ellis & Ramankutty 2008). The expansion of the area used for growing crops and grazing livestock is the

leading cause of habitat loss, and is likely to continue in future to meet the increasing food demands of a human population growing in both size and per-capita consumption levels (Tilman et al. 2011).

Extinctions (local and global) are non-random among species (Purvis et al. 2000a), and are related to species' rarity or commonness. Species typically have a higher extinction risk if they occur at low densities, have a small geographical range and are habitat specialists (Purvis et al. 2000b; González-Suárez et al. 2013). As a result of their increased vulnerability, rare species are often the focus of conservation efforts, while common species tend to be overlooked (Gaston & Fuller 2007; Gaston 2010). However, there are several different ways to define species rarity. One classic framework is that introduced by Rabinowitz (1981), which defines species rarity or commonness as a function of geographical range size, numerical abundance and habitat specialisation. These different forms of rarity may have individual and interacting effects on species' risk of extinction or sensitivity to land-use change, complicating efforts to identify the most vulnerable species.

Different types of rarity may influence species' sensitivity to environmental changes such as land-use change in different ways. Species that have narrower habitat requirements are expected to be lost more frequently as a result of land-use change compared with species with broader habitat affinities. Indeed, previous studies have shown much larger responses of natural forest specialist species compared with habitat generalists to land-use change and habitat fragmentation in tropical forests (Vetter et al. 2011; Newbold et al. 2013, 2014). Geographical rarity is generally associated with narrower ecological requirements (Harcourt et al. 2002), which in turn is associated with a high degree of sensitivity to land-use changes (Henle et al. 2004; Barbaro & van Halder 2009). A previous, global-scale study showed large losses of geographically rare species in disturbed land uses, compared with increases of widespread species (Newbold et al. 2018). The expectations with regard to numerical rarity are less clear. On one hand, species that typically exhibit low population density also have characteristics that likely make them sensitive to land-use and other environmental

changes, such as slow reproductive rates and greater susceptibility to demographic and environmental stochasticity (Davies et al. 2000; Purvis et al. 2000b; Barbaro & van Halder 2009; Newbold et al. 2013). On the other hand, these species are also likely to have larger body sizes, which shows a less clear relationship with sensitivity to land-use change (Newbold et al. 2013; González-Suárez et al. 2013), and may confer certain advantages through increased dispersal ability (Santini et al. 2013).

It is likely that the different forms of rarity, driven by the different underlying mechanisms, will interact with one another to determine sensitivity to land-use change. In general, we expect that species rare with respect to several forms of rarity will be more sensitive than species rare in just one way. Indeed, some local-scale studies have shown that geographical rarity and habitat specialism can interact to determine species sensitivity to land use (Thomas 1991; Kitahara & Sei 2001). However, global-scale studies investigating the combined effect of the three forms of rarity on species sensitivity to land-use change are lacking.

It is important to understand whether rare and common species respond differently to land-use changes in order to maximise the conservation of species. If human land-use consistently favours common species over rare species, then ecological communities will become more homogeneous spatially, and globally a small set of ubiquitous and generalist species will benefit at the expense of many rare and specialist species (McKinney & Lockwood 1999; Newbold et al. 2018; Cooke et al. 2019). There are also functional consequences of differences in land-use sensitivity with respect to rarity. Common species contribute substantially to the structure, energy turnover and biomass of ecosystems (Grime 1998; Smith & Knapp 2003), but very few species are common and the majority are rare according to at least one definition (Rabinowitz 1981; Gaston & Fuller 2007; Gaston 2010). Ecosystem structure, function and services can all be substantially affected by relatively small proportional declines in the abundance of common species, due to the large

absolute losses of individuals and biomass (Grime 1998). On the other hand, rare species have a unique combination of traits and thus may make a distinct contribution to ecosystem functioning if their functional role cannot be replaced (Mouillot et al. 2013). Rare species have been shown to play important roles in nutrient cycling and retention (Lyons et al. 2005), and in resistance to invasive species (Lyons & Schwartz 2001). They may also make an important contribution if environmental changes cause them to become more dominant (Lyons et al. 2005).

In this paper, we test whether responses of species richness and abundance to land use vary among groups of species characterised by different combinations of geographical rarity, population density and breadth of habitat requirements. We hypothesised that species rare in more than one way would be more sensitive to human land-use disturbance than species rare in just one way.

Methods

Data on land-use responses and rarity

We obtained data on responses of species to land use from the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) Project database (Hudson et al. 2016, 2017).

These data comprise 3,250,404 records of abundance and occurrence, from 666 different underlying studies, for over 47,044 species, at 26,114 sites in different land uses, representing 94 countries and all of the world's terrestrial biomes (Hudson et al. 2017). The database has a hierarchical structure:

1) individual source publications may contain one or more studies (designated as StudyID in the model formulations below), divided where different sampling methods are used; 2) studies may contain one or more spatial blocks (i.e. spatial clusters) of sampled locations (designated BlockID here); and 3) spatial blocks contain more than one sampled location (designated SiteID) (Hudson et

al. 2014). Records are categorised into 6 coarse types of land use: primary vegetation (undisturbed habitat with no record of prior destruction); secondary vegetation (natural habitat recovering after past destruction from human activities or extreme natural events); plantation forest (woody crops grown for human use); cropland (herbaceous crops); pasture (areas used to graze livestock); and urban (areas with human buildings or where the vegetation is managed for civic or personal amenity). For this analysis, we subset the PREDICTS database to include only data for amphibians, birds and mammals, giving a total of 450,843 records for 4,117 species at 7,881 sites.

Following Rabinowitz (1981), we characterised species rarity or commonness using estimates of their geographical range size, habitat specificity and average range-wide population density. We obtained estimates of species geographic ranges from the IUCN Red List (IUCN 2013) and Birdlife International (Birdlife International & NatureServe 2012). These estimates comprise polygons representing the extent of occurrence of species, derived based on a mixture of observed sightings and expert opinion. We estimated range area by projecting the original geographic range maps onto a Behrmann equal-area projection, and then summing the total area of all polygons for each species. We performed these operations using the 'Project' and 'CalculateAreas' functions in ArcMap Version 10.3 (ESRI 2015). Information on range area was available for 3,805 of the 4,117 non-reptile vertebrate species in the PREDICTS database.

We also obtained estimates of habitat specificity from the IUCN Red List (IUCN 2018), as the sum of the number of habitat types – Level 2 in the IUCN habitat classification, including both natural and artificial habitats – considered utilised by a species. We weighted this sum by the suitability and the importance of each habitat (a weight of 1 for suitable habitats of major importance, 0.5 for suitable habitats not of major importance, and 0.3 for marginal habitats). Estimates of habitat specificity were available for 3,349 of the 4,117 considered species.

Finally, we derived estimates of average population densities from the TetraDENSITY database (Santini et al. 2018a). This database contains 18,246 estimates of the population density of 2,439 vertebrate species across different locations (ranging from 1 to 408 locations; median = 2). For each species, we calculated the average \log_{10} -transformed population density across locations. The results were qualitatively very similar if we excluded estimates of population density from human land-use types (plantations, croplands, pastures or urban areas). Population density estimates were available for 1,036 of the 4,117 species in the original dataset.

The final PREDICTS dataset of species with estimates of all three types of rarity comprised 144,074 records for 912 species (3,165 birds, 563 mammals and 389 amphibians) at 7,005 sites (Figure 1; primary vegetation = 2,479; secondary vegetation = 1,478; plantation forest = 1,051; cropland = 917; pasture = 830; and urban = 183). We excluded urban sites from the final analysis owing to the small sample size.

Within each of the underlying datasets within PREDICTS, the total set of sampled species were divided around the medians of geographic range size, range-wide population density and habitat breadth, giving a total of eight groups of species with different combinations of rarity or commonness with respect to each of the three criteria. We then calculated site-level species richness and total organismal abundance for each category of rarity. The results were qualitatively similar when we defined species as being rare or common if their range sizes or population densities were in the top or bottom quartile rather than the bottom and top halves (results not shown). However, sample sizes were much reduced and so we do not pursue this alternative definition further here.

Statistical Analyses

We conducted all statistical analyses in R Version 3.3.2 (R Core Team 2016). We modelled species richness and total abundance as a function of land use using generalised linear mixed-effects models (GLMMs; Bolker et al. 2008). GLMMs were used to account for the hierarchical structure of the PREDICTS data, whereby each underlying dataset samples a different region and set of species, and uses different sampling methods and a different level of sampling effort (Purvis et al. 2018). We implemented GLMMs using the 'lme4' package Version 1.1-17 (Bates et al. 2015). We modelled species richness assuming a Poisson distribution of errors. We \log_e -transformed total abundance (adding values of 1 to correct zero values) prior to the analysis because abundance values were recorded on very different scales, and were often not integer values. All models included random intercepts describing study identity and spatial blocks of sites within studies. The model of species richness additionally included an observation-level random intercept (i.e., site identity) to control for over-dispersion (Rigby et al. 2008).

We tested whether interactions between different forms of rarity explained responses to land use better than the individual effects of different types of rarity, and whether including the effects of rarity was better than ignoring rarity altogether. To do so, we fitted three alternative sets of models of species richness and total abundance: 1) as a function of the full interaction between land use and all forms of rarity (i.e. Land Use \times Geographical Rarity \times Numerical Rarity \times Habitat Specificity); 2) as a function of the interaction between land use and each form of rarity individually (i.e. Land Use:Geographical Rarity + LandUse:Numerical Rarity + Land Use:Habitat Specificity); 3) as a function of land use alone. We also assessed the significance of land use in explaining responses of species richness and total abundance for each group of species separately. To do this, we compared for each species group: 1) models of abundance and species richness with land use as a single fixed effect

plus the random effects described above, with 2) null models including only random effects. We compared models using likelihood ratio tests.

Results

Responses of both species richness and total abundance to land use differed markedly across groups of species characterised by different forms of commonness or rarity (Tables 1 & 2; Figure 2). Models fitting the full set of interactions between land use and all different forms of rarity fit the data much better than models fitting two-way interactions between land use and each form of rarity separately ($\Delta\text{AIC} = -1,708$ for species richness and $-1,471$ for total abundance). These fully complex models were also much better fitting than models of land use alone, i.e. ignoring species' rarity altogether ($\Delta\text{AIC} = -2,800$ for species richness and $-2,228$ for total abundance). Species classified as being rare in all respects (geographical rarity, numerical rarity, and habitat specificity) declined substantially in all human-disturbed land uses compared with primary vegetation (Figure 2 a, e), with greater than 40% declines in areas converted for human use (plantation forests, croplands and pastures). Species rare with respect to two out of three types of rarity tended to decline in richness (but not in total abundance) in human-disturbed land uses compared with primary vegetation (Figure 2 b, f). Species that were rare in only one respect but common in other respects showed strongly contrasting responses to land use. Geographically rare species and species with narrow habitat requirements generally declined in disturbed land uses compared with primary vegetation, with declines of approximately 30-40% of species richness in the most disturbed land uses. In contrast, numerically rare but geographically common species with broader habitat requirements increased, by as much as 40% of species richness (Figure 2 c, g). Species common in all respects (i.e. that are geographically and numerically common, and have larger habitat specificity) increased strongly in most human-

disturbed land uses, by more than 90% in the most impacted land uses (Figure 2 d, h). The models generally conformed reasonably well to the assumptions of the statistical tests, although model residuals were somewhat leptokurtic (Figure S1 in Supporting Information).

Discussion

Overall, our results show that the response of species to land use depends strongly on the manner in which species are rare or common. These findings go beyond a previous global study that showed geographically rare species to be disproportionately sensitive to land-use change (Newbold et al. 2018), by considering the combinations of different forms of rarity and how they interact together. Being rare by all three forms of rarity is associated with strong negative responses to human land-use disturbance. Species characterised as rare by different types of rarity thus face multiple jeopardy from human dominated land uses, and the richness of these groups of species declined by more than 40% in the most disturbed land uses. Species rare with respect to two forms of rarity also tended to decline strongly in species richness, but interestingly not in total abundance. At the other extreme, species common by all definitions increased strongly in human-disturbed land uses. Species that are rare in just one way, but common in both other respects, showed mixed responses to land use. As expected, species characterised by geographical rarity or habitat specificity showed moderate declines in human land uses compared to natural habitat. Species that can tolerate only a very specific set of habitat conditions are likely to perform poorly with the very large changes to vegetation and habitat brought about by human land-use disturbance (Newbold et al. 2013). Geographically rare species tend to have narrower dietary and habitat requirements than more widespread species (Harcourt et al. 2002), which makes them more sensitive to land-use changes (Newbold et al. 2018). Surprisingly, while species characterised by either geographic rarity or narrow

habitat requirements declined in both species richness and total abundance, species characterised by both these forms of rarity declined only in species richness (Figure 2 b, f). Future studies should investigate the reasons for this unexpected result. Groups of species characterised only by numerical rarity increased in human-disturbed land uses compared to natural habitat. This result may occur because numerically rare species tend to be of large size, tending to disperse longer distances (Jenkins et al. 2007), and thus are less sensitive to land-use change (González-Suárez et al. 2013). We did not take into account here the effects of land-use intensity, which is associated with further differences in species richness (Newbold et al. 2015).

Our results support the idea that assessments of species' extinction risk or vulnerability to land-use change should where possible take into account the rarity of species in different dimensions (geographic range size, population density and habitat specificity) (Santini et al., in press). However, estimates of all forms of rarity are available only for a minority of species: even for the well-studied vertebrates represented in the PREDICTS database, we were able to obtain data on all three forms of rarity for less than one quarter of species. We show that interactions between different forms of rarity often determine species' sensitivity to human land use. It is therefore important to understand how sensitivity to land use, as a function of different types of rarity or commonness, translates into extinction risk. Another crucial question is whether interactions between types of rarity similarly affects species sensitivity to other major pressures, such as hunting, climate change, or invasive species (Maxwell et al. 2016).

Interacting effects of different forms of rarity on species' sensitivity to land use will also complicate efforts to understand the implications of biodiversity loss for ecosystem functioning. Common species play a disproportionately large role in many ecosystem functions and services (Grime 1998; Smith & Knapp 2003; Gaston 2010). On the other hand, both numerical and geographical rarity are associated with distinct ecological characteristics, and thus presumably with a

distinct contribution to ecosystem functioning (Mouillot et al. 2013). Furthermore, numerically rare species often make important contributions to nutrient cycling and to invasion resistance of communities (Lyons & Schwartz 2001; Lyons et al. 2005). Understanding the contributions that different types of rare and common species make to functions and services is therefore a topic of great importance.

There are a number of reasons why we may under-estimate declines in species richness in human-disturbed land uses (Purvis et al. 2018). First, there are almost no truly pristine reference habitats in the modern world. Second, ecologists sampling biodiversity in disturbed habitats tend to sample the more natural features within those habitats (i.e. tending not to sample the centres of agricultural fields or fully built-up city centres). Third, it is likely that species from natural habitats will have spread into nearby disturbed habitats even if they could not persist there in the absence of immigration (Purvis et al. 2018). There are also a few limitations specific to this study, principally deriving from our estimates of range size, average population density and habitat specificity. There is likely to be substantial intraspecific variation in population density and habitat specificity (Brown et al. 1995; Violle et al. 2012). For example, population density can vary across two orders of magnitude across species' ranges (Santini et al. 2018a). However, there are insufficient data to allow the inclusion of such intra-specific variation into global-scale studies. Furthermore, many of the estimates of average population density of species were based on estimates of local population density at just one or two locations, and thus may be somewhat sensitive to sampling artefacts (but see Santini et al. 2018b). Finally, estimates of geographic range size are subject to considerable uncertainty, although a previous study focusing on geographical range size and land-use sensitivity found that results were generally very robust in the face of this uncertainty (Newbold et al. 2018). Despite these uncertainties, the rarity measures that we use should be able to capture coarse differences among species, and so should be adequate for our purposes. These measures are, to the

best of our knowledge, the most complete and comprehensive currently available. Another limitation of this study is that classifications of all three forms of rarity are available for only 912 species, out of a total of 4,117 non-reptile terrestrial vertebrate species in the PREDICTS database and over 25,000 terrestrial vertebrate species globally. We thus assume that this sample of 912 species is representative of all vertebrate species, but our analysis should be repeated in future as more complete data on species' rarity becomes available.

In summary, we show that different forms of rarity interact to determine species' sensitivity to land-use change. Being common in many ways makes species particularly robust to habitat disturbance. In contrast, species rare in all respects are highly sensitive. The results are important for understanding which species are most at risk in an era of rapid land-use changes. Both climate change and overexploitation are likely to add a further layer of complexity, since species' sensitivity to these other pressures will also likely be non-random with respect to rarity. A disproportionate sensitivity of species rare in several ways may also affect ecosystem functioning, given that rare species appear to play unique roles within ecosystems.

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Supporting Information

The data (DOI: 10.6084/m9.figshare.8040146 and code (<https://github.com/timnewbold/RarityStudyPublic>) needed to run the analyses are published.

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Figure legends

Figure 1. Sites included in the analysis. Points show the sites sampled for vertebrate species in the PREDICTS database, and for which at least some species in the sampled assemblage had complete estimates of geographical range size, average population density and degree of habitat specificity. Points are translucent so darker areas indicate overlapping points.

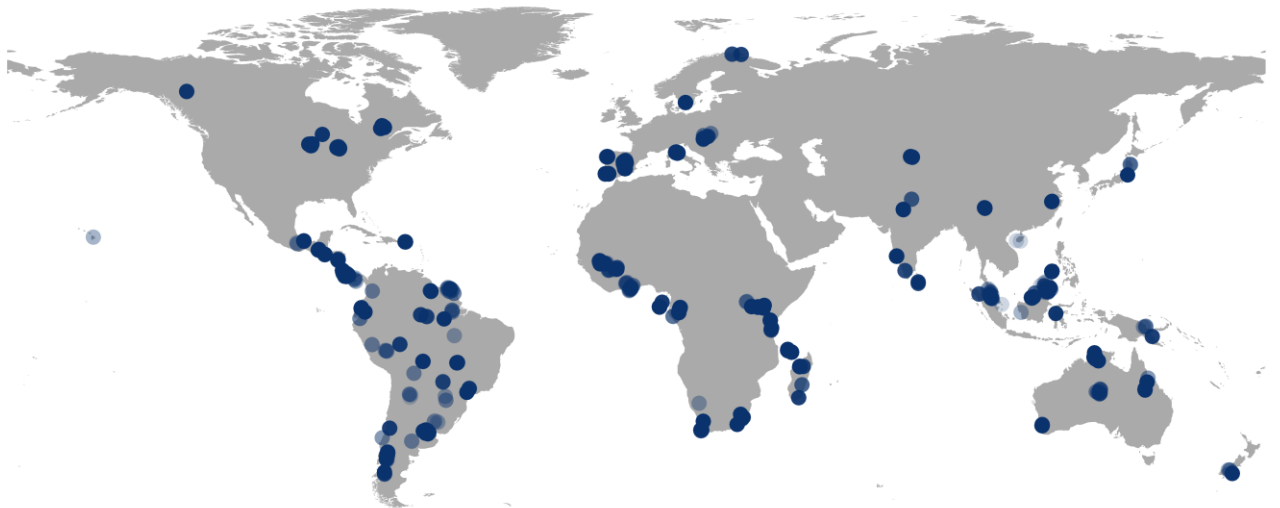
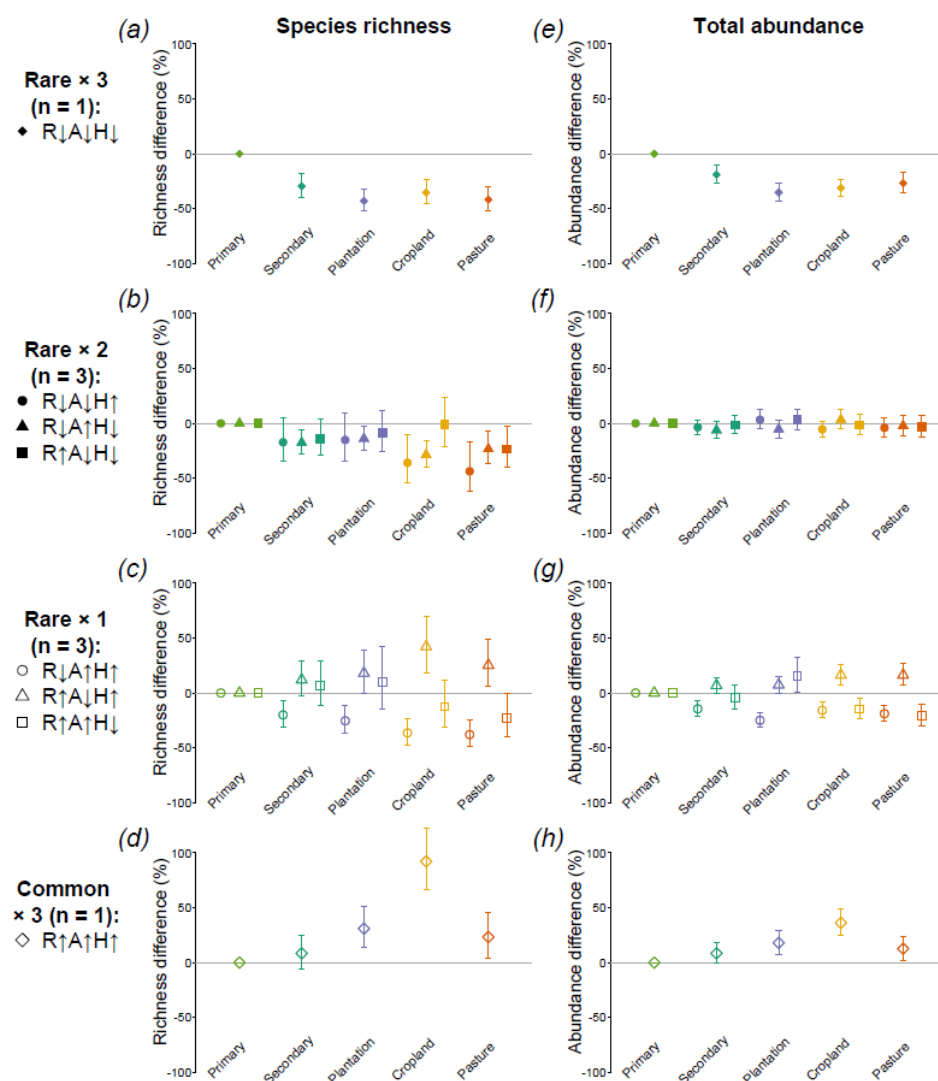


Figure 2. Responses to land use of groups of species characterised by different combinations of types of rarity. In the legends, rare species are denoted with downward-facing arrows and common species with upward-facing arrows (Geographical rarity = R; Numerical rarity = A; habitat specificity = H). We considered responses both of species richness (a, b, c, d) and of total abundance (e, f, g, h). Species could be characterised as being rare in all three respects (a, e), in just one respect (b, f), in two of three respects (c, g), or as being common in all respects (d, h). Land use was classified as primary vegetation (Primary), secondary vegetation (Secondary), plantation forest (Plantation), cropland or pasture. Error bars show 95% confidence intervals.



Tables

Table 1. Statistical results describing the response to land use of the species richness of groups of species characterised by different combinations of types of rarity. For each group of species, the significance of the response to land use was tested by comparing a model including land use with a null model (i.e. random effects only), using a likelihood-ratio test. χ^2 and P values are provided. The letters denoting different types of rarity (R = range size; A = numerical abundance; H = habitat specificity) and the arrows (\downarrow = rare or narrow habitat requirements; \uparrow = common or broad habitat requirements) correspond with the letters and symbols used in the legend of Figure 2.

Geographical rarity (R)	Numerical rarity (A)	Habitat Specificity (H)	Number of rarity forms	χ^2 (DF = 4,8)	P
Rare (\downarrow)	Rare (\downarrow)	Narrow (\downarrow)	3	62.5	< 0.001
Rare (\downarrow)	Rare (\downarrow)	Broad (\uparrow)	2	10.0	0.04
Rare (\downarrow)	Common (\uparrow)	Narrow (\downarrow)	2	16.8	0.002
Common (\uparrow)	Rare (\downarrow)	Narrow (\downarrow)	2	5.98	0.20
Common (\uparrow)	Common (\uparrow)	Narrow (\downarrow)	1	7.63	0.11
Common (\uparrow)	Rare (\downarrow)	Broad (\uparrow)	1	14.14	0.007
Rare (\downarrow)	Common (\uparrow)	Broad (\uparrow)	1	32.7	< 0.001
Common (\uparrow)	Common (\uparrow)	Broad (\uparrow)	0	88.4	< 0.001

Table 2. Statistical results describing the response to land use of the total abundance of groups of species characterised by different combinations of types of rarity. For each group of species, the significance of the response to land use was tested by comparing a model including land use with a random-effects-only model, using a likelihood ratio test. χ^2 and P values are provided. The letters denoting different types of rarity (R = range size; A = numerical abundance; H = habitat specificity) and the arrows (\downarrow = rare or narrow habitat requirements; \uparrow = common or broad habitat requirements) correspond with the letters and symbols used in the legend of Figure 1.

Geographical rarity (R)	Numerical rarity (A)	Habitat Specificity (H)	Number of rarity forms	χ^2 (DF = 4,8)	P
Rare (\downarrow)	Rare (\downarrow)	Narrow (\downarrow)	3	71.7	< 0.001
Rare (\downarrow)	Rare (\downarrow)	Broad (\uparrow)	2	3.25	0.52
Rare (\downarrow)	Common (\uparrow)	Narrow (\downarrow)	2	6.38	0.17
Common (\uparrow)	Rare (\downarrow)	Narrow (\downarrow)	2	1.41	0.84
Common (\uparrow)	Common (\uparrow)	Narrow (\downarrow)	1	26.5	< 0.001
Common (\uparrow)	Rare (\downarrow)	Broad (\uparrow)	1	156	0.004
Rare (\downarrow)	Common (\uparrow)	Broad (\uparrow)	1	43.6	< 0.001
Common (\uparrow)	Common (\uparrow)	Broad (\uparrow)	0	57.2	< 0.001