

Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity

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Summary

1. Carabid beetles are important functional components of many terrestrial ecosystems. Here, we describe the first long-term, wide-scale and quantitative assessment of temporal changes in UK carabid communities, to inform nationwide management aimed at their conservation.

2. Multivariate and mixed models were used to assess temporal trends over a 15-year period, across eleven sites in the UK Environmental Change Network. Sites covered pasture, field margins, chalk downland, woodland and hedgerows in the lowlands, moorland and pasture in the uplands, and grassland, heaths and bogs in montane locations.

3. We found substantial overall declines in carabid biodiversity. Three-quarters of the species studied declined, half of which were estimated to be undergoing population reductions of > 30%, when averaged over 10-year periods. Declines of this magnitude are recognized to be of conservation concern. They are comparable to those reported for butterflies and moths and increase the evidence base showing that insects are undergoing serious and widespread biodiversity losses.

4. Overall trends masked differences between regions and habitats. Carabid population declines (10-year trend, averaged across species) were estimated to be 52% in montane sites, 31% in northern moorland sites and 28% in western pasture sites (with at least 80% of species declining in each case). Conversely, populations in our southern downland site had 10-year increases of 48% on average. Overall, biodiversity was maintained in upland pasture, and populations were mostly stable in woodland and hedgerow sites.

5. *Synthesis and applications.* Our results highlight the need to assess trends for carabids, and probably other widespread and ubiquitous taxa, across regions and habitats to fully understand losses in biodiversity. Land management should be underpinned by a consideration of how wide-scale environmental drivers interact with habitat structure. The stability of population trends in woodlands and hedgerows of species that are declining elsewhere puts these habitats at the fore-front of integrated landscape management aimed at preserving their ecosystem services.

Key-words: biodiversity declines, community ecology, ecosystem services, environmental change, functional traits, insect conservation, population trends, UK Environmental Change Network

Introduction

Global biodiversity declines have serious repercussions for human health and well-being (Hanski *et al.* 2012). How-

ever, declines remain unabated and concerns are increasing that attempts to diminish the strength of their drivers have largely failed (Butchart *et al.* 2010). Such biodiversity losses can disrupt the functioning of ecosystems and delivery of their services (Balvanera *et al.* 2006). Finding management strategies to conserve such services will, however, require substantial improvements in our

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understanding of the mechanisms controlling losses of functionally important taxa (Purvis & Hector 2000). Currently, fundamental understanding of how species respond to environmental change suggests that such advances will be dependent on unravelling complex biotic interactions (Gilman *et al.* 2010). For example, changes in climate can alter trophic links between species (Tylianakis *et al.* 2008), and studying species in isolation is unlikely to deliver a holistic understanding of the mechanisms driving their populations because their responses are linked to networks of interacting taxa (Magurran *et al.* 2010). Furthermore, theoretical approaches to modelling wide-scale changes in biodiversity recognize that species responses are rarely equivalent over time and space (Magurran *et al.* 2010). Scaling studies up to the level of communities of functionally important taxa, therefore provides a powerful way to detect emergent patterns and processes (Ferrier & Guisan 2006). Indeed, understanding the spatial and temporal dynamics of species-rich communities is critical to understanding how environmental change will affect biodiversity (McCann 2007). Central to these endeavours will be an increased knowledge of how effects of potential drivers vary across habitats and regions (Parmesan & Yohe 2003). Models that assess geographical variation in the trends of multiple species and their interactions with habitats are therefore urgently required to bridge gaps in our understanding of biodiversity declines (Magurran & McGill 2010).

Studies of insects have revealed strong declines for some groups, suggesting that biodiversity losses are disproportionately high for this class (Thomas & Clarke 2004). This is of concern because insects are important for the functioning of ecosystems, and their declines are likely to cause serious disruptions to natural processes (Walpole *et al.* 2009). However, there is a lack of information on population trends of many key insect groups with roles critical to the viability of ecosystems (Butchart *et al.* 2010). Carabid beetles are suitable for such investigations because they are a species-rich group of insects that are ubiquitous to the majority of terrestrial ecosystems (Thiele 1977). This success has been aided by the high biological diversity of carabid species, which have numerous dispersal, feeding, breeding and temperature regulation strategies adapting them to a wide range of environmental conditions (Thiele 1977). This has enabled widespread success in terrestrial ecosystems where they have important functional roles because of their voracious predation of other invertebrates and granivorous feeding on plants (Lövei & Sunderland 1996). For example, in agricultural food webs, these functions provide important ecosystem services because carabids feed on numerous economically damaging pest species (Lövei & Sunderland 1996) and provide national-scale regulation of weed seeds in arable fields (Bohan *et al.* 2011). These services are particularly pertinent given increasing concerns about food security and the need to enhance ecological services to maintain productivity under decreasing chemical inputs (Glendinning

et al. 2009). Thus, given the urgent need to determine which habitats and regions are most vulnerable to losses of functionally important taxa (Sutherland *et al.* 2009), wide-scale quantification of carabid population trends represents a strategic research priority.

Since 1993, carabids have been intensively monitored within a range of habitats across the United Kingdom (UK), in close unison with numerous climatic and physiochemical variables, as part of the Environmental Change Network (ECN) (Morecroft *et al.* 2009). These data therefore provide an opportunity to advance understanding of the mechanisms controlling biodiversity. Studies of carabids in north-west, mainland Europe have demonstrated contractions in species distributions, most probably resulting from anthropogenic disturbance and climatic variation (Hengeveld 1985; Kotze & O'Hara 2003). However, the lack of consistently collected and quantitative data in these studies has hampered accurate modelling of population trends (Desender *et al.* 2010). The ECN overcomes these problems by using standardized population surveys that are comparable across time and regions. Here, we use these data to test three hypotheses investigating how carabid communities have changed over time. First, we test the hypothesis that an overall change in community composition has occurred. In doing this, we test whether trends for a mostly predatory group of insects are commensurate with the large declines observed for herbivores and pollinators in this class (Thomas & Clarke 2004; Conrad *et al.* 2006). Second, we test the hypothesis that community trends diverge between habitats and regions. This is because patterns of carabid distributional change can differ at this spatial scale (Kotze & O'Hara 2003). Third, we test the hypothesis that community trends not only have broad spatial divergence, but are unique to specific combinations of habitats and regions. This hypothesis is invoked because species responses to environmental change may be highly specific to the habitats occupied (Forister *et al.* 2010), and trends can be nonlinear and have strong geographical variation (Stenseth *et al.* 2002). The results of these tests are used to guide models estimating population changes, to validate our findings and assess how the biodiversity of a functionally important group is changing over time in relation to UK regions and habitats.

Materials and methods

SURVEYING OF CARABIDS

The ECN consists of twelve terrestrial sites, covering a range of habitats, regions and climatic variation in the UK, of which eleven have viable carabid data (Fig. 1). The upland sites are cooler and have higher rainfall, western lowland sites at Hillsborough and North Wyke have atypically wet maritime climates, while the remaining lowland sites are relatively warm and dry (Morecroft *et al.* 2009). Three transects were used to sample carabids at each site, each consisting of ten pitfall traps placed at 10-m intervals.



Fig. 1. Site locations and the division of their three transects between region by habitat groups: filled circle = all western pasture, open circle = two western pasture and one woodland and southern hedgerow, open diamond = all southern downland, filled star = all southern open (grass field margins), filled crosses = all woodland and southern hedgerow, open cross = two woodland and southern hedgerow and one southern open (extensive grassland), filled upright triangles = two northern moorland and one northern pasture, and open upright triangles = all montane.

Transects were either located within one, or divided between two, broad habitat types at each site (Fig. 1). Within sites, the areas of each of these habitats range from *c.*15 to 1100 ha. Individual transects at each site were separated by *c.*10–1400 m when in the same habitat, or by at least *c.*500 m when in different habitats (see Table S1 in Supporting Information for detailed transect descriptions).

Pitfall traps consisted of 7.5 cm diameter polypropylene cups filled with ethylene glycol preservative, placed with the top flush with the soil surface. The number of sampling rounds and their dates were synchronized across all sites and years. Surveys were conducted continuously from the beginning of May until early November, as this period covers nearly all carabid activity. During this time, traps were recovered every 2 weeks and all carabid species were counted and identified. Here, we analyse data within a 15-year time series between 1994 and 2008 for all sites, except Snowdon and Cairngorms that were considered separately because their trapping commenced in 1999. Data points in our analyses comprised of annual pooled totals of the traps within each transect. Carabids predominantly have single annual activity peaks and univoltine life cycles (Thiele 1977), and multiple samples, each comprising of captures from at least five pitfall traps and spanning periods of major activity, provide good estimates of localized carabid population abundance (Luff 1996). Transects were replicated across sites, habitats and regions. Therefore, variability between transects and their repeated counts across years was accounted for before estimating their combined effects over habitats and regions. Where up to three traps within a transect

were missing during sampling periods, totals were adjusted to the count expected for ten traps (by multiplying the count by 10/number of traps retrieved). In limited instances where more traps were missing, a transect by year value was calculated from the slope of the temporal trend across that transect remaining years. Around half of the species had zero values for > 75% of their transect by year counts. Such species represented < 1% of total captures, of which two-thirds had counts of < 20 individuals. Preliminary investigations revealed data were too sparse to estimate reliable trends for these species and they were removed from further analyses.

COMMUNITY TIME-SERIES MODELS

Changes in community composition were investigated with partial redundancy analyses (pRDA) (Ter Braak 1995). A model building process was used to simplify temporal trends amongst individual transects to their most parsimonious region (*R*) by habitat (*H*) descriptors (here-after, '*RH*' groups) (see Appendix S1 for methods). These factors were then used to test three hypotheses describing alternative ways that communities could change over time. Tests employed nonparametric Monte Carlo permutation procedures within pRDAs to assess combined effects of years, after removing the variance associated with individual transects and their repeated counts across years. This was performed by permuting years as split-plots within whole plots represented by transects (Ter Braak & Šmilauer 2002). First, the hypothesis that an overall change in community composition has occurred over time across the network was tested by evaluating the effects of time *T*, after accounting for transect, region and habitat effects. If significant, such a test would demonstrate not only that community composition has changed, but that such change is dominated by a single strong, uni-directional trend that is unbiased by habitats or regions. Second, the hypothesis that temporal trends have different magnitudes or directions between regions and habitats was tested by evaluating interaction terms between *T* and all *RH* groups, after accounting for the overall effects of time and transects. If significant, such a test would show that trends between single *RH* groups, or clusters of them, can have strong deviations from any overall trend owing to their interaction terms representing noticeably different responses to those predominating across the network. Third, the hypothesis that *RH* groups have unique community trends was tested by evaluating the interaction between *T* and each *RH* term, after accounting for all other interaction terms between *T* and the remaining *RH* groups. If significant for any *RH* group, this test would demonstrate that such a group has independent effects, not just from any overall trend, but from all other individual trends within each *RH* group. See Table S2 for the detailed structure of pRDA models. Tests of the last hypothesis were complemented by investigating trajectories of community change over time, to assess whether trends were nonlinear and if so, whether such effects were unique within *RH* groups because of their rates of change varying at different times. This was carried out for each *RH* group by extending their linearly constrained responses in pRDAs to nonlinear trajectories of community change over time using principal response curve (PRC) analysis (Van den Brink & Ter Braak 1999). Generalized additive models (GAMs) were used to assess nonlinear trends in the PRCs, by fitting progressively more complex models until the shape of any response curve was described adequately. The least complex model required to do this was found by selecting the first model with an Akaike information criteria (AIC) value not

greater than 15% of the next more complex model. Temporal trends for Snowdon and Cairngorms were assessed in a separate pRDA reduced to years 1999–2008. The CANOCO V4.5 program (Ter Braak & Šmilauer 2002) was used for all community modelling.

Tests of the last hypothesis were further informed by multiple linear regression models investigating the relationship between temporal trends and species ecological traits, such as breeding period, size, dispersal power and microclimatic preferences for light and moisture (see Table S3 for trait details). Linear trends were derived for this relationship, and the interactive effect of *RH* factors on these trends parameterized. Nonlinear responses were investigated where any significant linear effects were found by fitting higher order terms.

ESTIMATING POPULATION TRENDS

The results of the community modelling guided species level analyses to clarify and aid inferences about changing carabid biodiversity. Species population trends were estimated using linear mixed models fitted using residual maximum likelihood (REML; Patterson & Thompson 1971). For each analysis, the full random model had three components. First, it allowed for the years-within-transects repeated measures (split-plot) structure of the data. Second, transect effects were assumed to be independent and possible temporal correlation within them to have a first order autoregressive (AR1) structure. Third, cubic smoothing spline terms were fitted to detect nonlinear responses. When more than one *RH* group was involved in the analysis, splines were either allowed to vary or forced to be common, across groups. A parsimonious random model (with all fixed terms fitted) was initially selected. The need for the autocorrelation term was assessed first and then the appropriate spline model was determined. Once an appropriate random model had been selected, the fixed terms were assessed. The full fixed model included 'year' as an explanatory variate; for species with counts in multiple region by habitat groups, an *RH* factor identified by multivariate modelling and the year by *RH* interaction. Overall changes in populations were

tested by fitting a single temporal trend, after allowing for *RH* grouping. For species in multiple *RH* groups, differences in the trends between such groups were investigated by a sequence of increasingly complex fixed models, representing: (a) lines for each *RH* group with a common slope and intercept, (b) lines with a common slope but different intercepts and (c) lines with different slopes and intercepts. From these, a parsimonious fixed model was determined, and the final overall model was fitted and summarized. Similar analyses were completed for total carabid abundance. Mixed model analyses were conducted in GenStat (12th Edition: Payne *et al.* 2009).

Results

GENERAL TRENDS ACROSS THE NETWORK

We found an alarming overall decline in the biodiversity of carabid beetles amongst our network of study sites. The main temporal trend across the whole carabid community, after allowing for transect differences, was highly significant in the pRDA model ($F = 11.59$; $P = 0.002$; Model M2 in Table S2), with examination of the associated biplot, and species scores on the relevant axis, confirming the negative effect of time on most species. This supports our first hypothesis that there is a directional change in carabid community composition over time and demonstrates that this change results in a loss in biodiversity. There were also significant reductions in total carabid counts (Fig. 2a), but more worryingly, population models revealed that around three-quarters of species had declined, half of which underwent significant reductions in their abundance, at rates estimated to exceed 30% when averaged over 10-year periods (Tables 1, S4a, Fig. 2b). Such rates are of concern because under International Union for Conservation of Nature (IUCN) criteria, they represent a threshold at which species are considered to

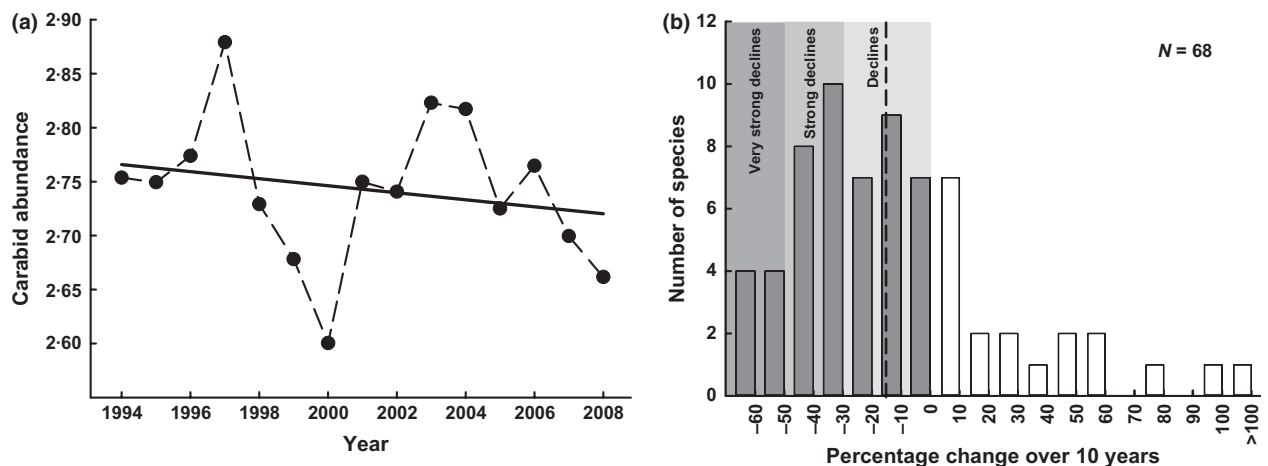


Fig. 2. Overall population trends across the network: (a) changes in total carabid abundance over time represented by the \log_{10} transformed mean count for each transect per year; in mixed models, this trend represents a significant decline of 15.8% and (b) frequency distribution of species 10-year percentage population changes, where N = the number of species analysed; the dashed line shows the median 10-year change; and shaded areas for very strong and strong declines correspond with IUCN endangered and vulnerable classifications, respectively (see Table 1 for species represented by each bar and Table S4a for their population models).

Table 1. Species overall trends ordered by estimates of their average 10-year percentage population change. The predominating trends across the network are given, with any regional or habitat biases removed by aggregating data from 27 equally weighted transects and allowing for their individual repeated year effects. Larger species (>10 mm) are shown in bold. Species in each trend bracket represent taxa within individual bars in Fig. 2b; their authorities and full models are given in Table S4a

Trend strength	Species
>–70 <–60	Carabus arvensis , Pterostichus adstrictus , <i>Demetrias atricapillus</i> , <i>Pterostichus rhaeticus</i>
>–60 <–50	<i>Agonum emarginatum</i> , <i>Leistus terminatus</i> , <i>Bembidion biguttatum</i> , <i>Trechus obtusus</i>
>–50 <–40	<i>Bembidion aeneum</i> , <i>Bembidion properans</i> , <i>Calathus micropterus</i> , <i>Calathus melanocephalus</i> , <i>Bembidion lunulatum</i> , <i>Leistus fulvibarbis</i> , <i>Microlestes maurus</i> , <i>Bradycellus ruficollis</i>
>–40 <–30	<i>Pterostichus vernalis</i> , <i>Anchomenus dorsalis</i> , <i>Panagaeus bipustulatus</i> , <i>Bradycellus harpalinus</i> , <i>Bembidion quadrimaculatum</i> , <i>Agonum muelleri</i> , <i>Clivina fossor</i> , <i>Bembidion lampros</i> , <i>Leistus rufomarginatus</i> , <i>Harpalus latus</i>
>–30 <–20	<i>Leistus ferrugineus</i> , <i>Ophonus rufibarbis</i> , <i>Amara plebeja</i> , <i>Loricera pilicornis</i> , <i>Patrobus assimilis</i> , <i>Bembidion obtusum</i> , <i>Amara lunicollis</i>
>–20 <–10	<i>Bembidion guttula</i> , Carabus violaceus , Nebria salina , <i>Pterostichus diligens</i> , Pterostichus macer , <i>Pterostichus strenuus</i> , <i>Pterostichus nigrita</i> , <i>Amara communis</i> , Pterostichus melanarius
>–10 <0	Carabus problematicus , <i>Stomis pumicatus</i> , <i>Oxytetranychus obscurus</i> , Pterostichus niger , Poecilus cupreus , <i>Trechus quadristriatus</i> , <i>Badister bullatus</i>
>0 <10	Cychrus caraboides , Carabus glabratus , Pterostichus madidus , <i>Notiophilus biguttatus</i> , <i>Notiophilus aquaticus</i> , <i>Patrobus atrorufus</i> , Carabus nemoralis
>10 <20	Nebria brevicollis , Calathus rotundicollis
>20 <30	<i>Syntomus obscuroguttatus</i> , Abax parallelepipedus
>30 <40	<i>Leistus spinibarbis</i>
>40 <50	Licinus depressus , Calathus fuscipes
>50 <60	<i>Agonum fuliginosum</i> , Harpalus rufipes
>70 <80	Carabus nitens
>90 <100	<i>Notiophilus germyini</i>
>100	Laemostenus terricola

have threatened populations (Gärdenfors *et al.* 2001). Therefore, if representative of any wider trends outside the ECN, such rates would be regarded as serious for carabids. There was also a general trend for greater declines amongst spring breeding, dispersive, diurnal and smaller carabids (Tables 1, S3).

TRENDS AMONGST HABITATS AND REGIONS

The model building exercise reduced descriptors of major temporal variation to six regions by habitat groups (Fig. 1). Upland transects in northern regions were grouped according to whether they were in heather moorland (northern moorland) or grazed grassland (northern pasture). Lowland transects were grouped into pasture habitats in the west (western pasture), open, extensively managed grass-

land in the south (southern open), chalk downland in the south (southern downland), or woodlands anywhere, plus hedgerows which only had southern transects (woodland and southern hedgerows). The significance of the pRDA model testing differences in the temporal trends of carabid communities amongst these groups ($F = 12.72$; $P = 0.002$; Model M3 in Table S2) validates our hypothesis that the magnitude and direction of species changes over time varies between regions and habitats (Fig. S1a, b). These differences were supported by significant interactions between the region by habitat trends for total carabid counts, with median 10-year trends varying from 48.4% declines in our northern moorland and western pasture sites, to 50% increases in our southern downland site (Fig. 3). Trends across species, however, revealed even greater contrasts between regions and habitats (Fig. 4). Losses were especially serious in our northern moorland and western pasture sites, where around 80% of species declined (more than half declining at more than 30% over 10-year periods), with median cross-species 10-year declines of 30.7% and 27.8%, respectively (Fig. 4). Declines also predominated in open southern habitats, where two-thirds of species underwent reductions, and the median 10-year change rate was a 14.9% decline (Fig. 4). Trends were noticeably different for our southern downland transects, however, where two-thirds of species had increasing populations and the median change over 10 years was a 47.5% increase (Fig. 4). Populations were much more stable in woodland and southern hedgerow transects, where only one-fifth of species underwent significant changes, and the median 10-year change was a 6.2% increase (Table S4a, Fig. 4). Furthermore, over two-thirds of species in this group had 10-year change rates below 30%, regardless of trend direction (Fig. 4). Most species in our northern pasture sites had significant trends, but with equal numbers increasing or decreasing, leading to a median 10-year change rate close to zero (Fig. 4).

Over their 10-year surveys, montane sites had similar trends to upland moorland habitats in our analyses, but their rates of decline were even greater (Table S4b, Fig. S1c), with a significant 10-year reduction in total carabid numbers of 63.6% (Fig. 5a). The median 10-year change rate represented a 51.8% decline, and declines for over half the species were large enough for them to be classified as endangered under IUCN criteria (Gärdenfors *et al.* 2001; Fig. 5b), if such trends proved representative of the whole habitat.

TRENDS WITHIN HABITATS AND REGIONS

Community trends within each region by habitat group were significantly different from those in all other groups in pRDA models, confirming our hypothesis that assemblages are changing in ways that are unique to their regions and habitats (Models M4–9 in Table S2, Fig. 6). This was attributed to differences in both the responses of species and the times when those responses occurred. First, intraspecific responses mostly differed between

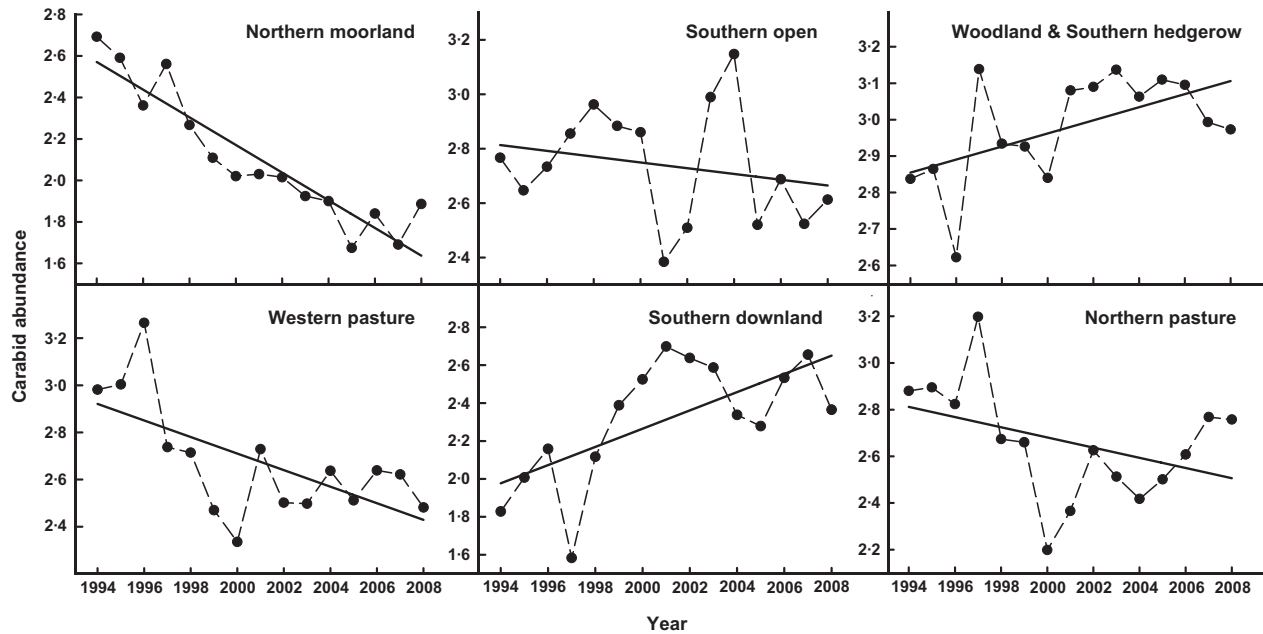


Fig. 3. Changes in total carabid numbers within region by habitat groups (see Fig. 2a for figure formatting). In mixed models, these trends represent significant declines of 48% in northern moorland, 33% in western pasture and 22% in northern pasture, non-significant declines of 12% in southern open habitats, and significant increases of 57% in southern downland and 16% in woodland and southern hedgerow. In mixed models, trends were significantly different between these groups ($F = 25.09_{(5, 90.4)}$, $P < 0.001$).

groups, usually because of noticeable changes in the strength of trends, but also because the direction of trends often changed as well (Table S4a). In population models, this was supported by two-thirds of species in multiple groups requiring different slopes to represent their contrasting trends between regions and habitats (Table S4a). For example, many of the species declining at our northern moorland sites, typified by the large species *Pterostichus niger* (Schaller), *Carabus problematicus* L. and *C. violaceus* L., had dissimilar trends in geographically proximal northern pasture habitats (Table S4a). Also, woodland and southern hedgerow communities were sufficiently similar to those in other habitats to allow analysis of 90% of their taxa in other groups. This showed that although such taxa were usually stable in woodland and southern hedgerow transects, they were often declining elsewhere (Table S4a). Second, species often had contrasting functional responses between regions and habitats, according to their size, and their microclimatic preferences for shade and moisture (Table S3, Fig. 6). Declining species in our northern moorland sites were mostly xerophilous, whereas in western pasture transects they were mostly hygrophilous, covering, in particular, *Bembidion* Latreille., spp. (Tables S3, S4a, Fig. 6). Species requiring less shade increased at our southern downland site, whereas in northern pasture transects, larger species with a preference for more shady microhabitats prospered (Table S3, Fig. 6). These habitat differences were exemplified by divergent trends between large, shade tolerant *Carabus* L., spp. and a smaller species of more open countryside, *Calathus fuscipes* (Goeze)

(Table S4a). Third, the times and rates at which the observed changes in communities occurred differed between groups (Fig. 6). For example, declines in northern moorland transects were consistent over time, whereas in western pasture transects, changes were more rapid and occurred earlier, with precipitous losses in biodiversity after 1996 (Fig. 6). At our southern downland site, changes mostly occurred between 1998 and 2001, whereas in our woodland and southern hedgerow transects, rates of change were much lower between years and lacked a trend in any one direction, indicating that communities were comparatively stable in this habitat (Fig. 6).

Discussion

Our analyses revealed substantial declines in carabids (Figs 2, 4). These declines are comparable to trends for other insect groups, thereby contributing to growing evidence that this class is suffering especially serious biodiversity losses (Thomas & Clarke 2004; Conrad *et al.* 2006). Concerns are exacerbated for carabids because they have wide-ranging roles within food webs (Lövei & Sunderland 1996). Although the widespread repercussions of a depletion in such roles for the functioning of ecosystems are unknown (Koivula 2011), carabid declines raise concerns for the production of food because their services are particularly valuable to agriculture (Bohan *et al.* 2011).

Our results support contentions that to fully understand biodiversity losses and manage them at the landscape level, trends should be assessed at scales sufficient to capture regional and habitat variation (Magurran *et al.* 2010).

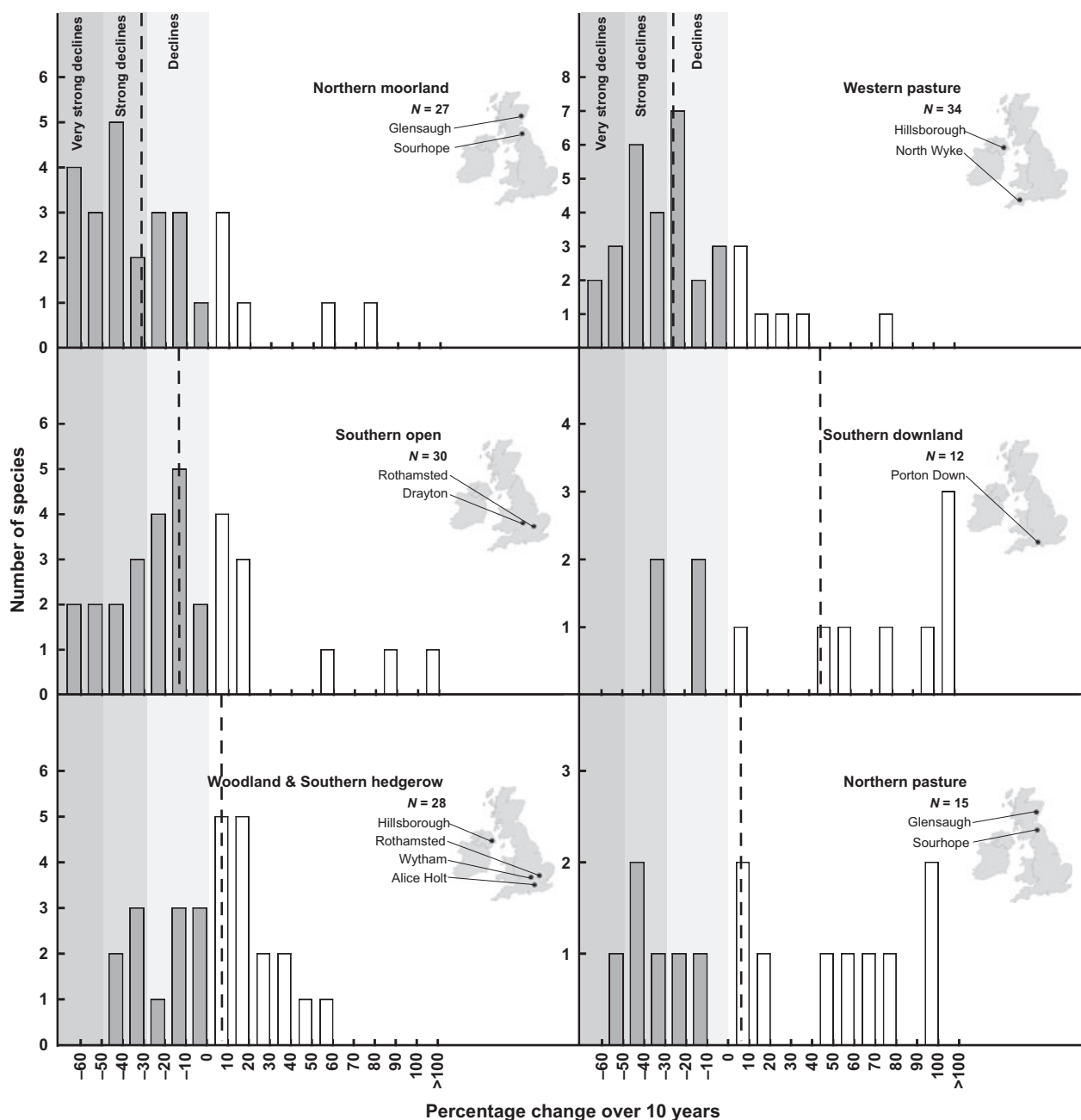


Fig. 4. Frequency distribution of species percentage population changes over 10-year periods within region by habitat groups (see Fig. 2b for figure formatting). The locations of transects representing each group are shown. See Table S4c for the species represented by the bars in each plot.

Given that the trends in carabid biodiversity are mostly downward, it would be tempting to ascribe one dominant driver of change. However, responses varied significantly between regions and habitats, suggesting more complex interactions between local population drivers and wider-scale factors. We found wide-scale inconsistencies in the ways that communities responded in moorland in the north, and pastoral farmland in the west, which may be due to regional differences in the effects of climatic change. For instance, increases in winter temperature have been disproportionately greater in upland habitats, with concomitant

reductions in their snow cover (Holden & Rose 2011). This may be increasing soil moisture, adversely affecting the xerophilic species that are declining most in the uplands. Conversely, hygrophilous and spring breeding species dominated assemblages and declines in western pasture. Their responses were early and rapid, possibly reflecting deleterious effects of freezing on the wetter soils of these sites during a particular cold and dry winter in 1995–1996, linked to the North Atlantic Oscillation (NAO) (Ottersen *et al.* 2001). Carabids have an intolerance to freezing (Rossolimo 1997), the effects of which could be exacerbated

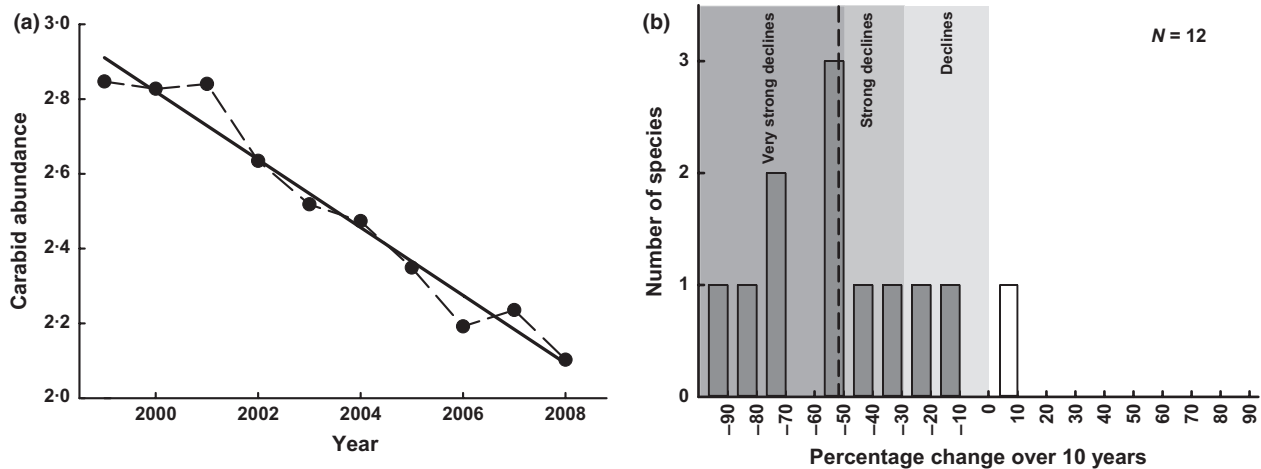


Fig. 5. Population trends in montane habitats: (a) changes in total carabid numbers; in mixed models, this trend represents a significant decline of 63.6%, and (b) frequency distribution of species percentage population changes over the 10-year time series (see Fig. 2 for formatting of graphs).

for overwintering, spring breeding adults if they were unable to burrow into frozen soils to escape temperature extremities, and conditions remained adversely dry and cold early in their breeding season.

Despite such regional differences, our results suggest localized changes in habitats are just as important as wider-scale factors and may even over-ride them in some cases. For example, heather moorland and upland pasture probably experience similar macro-climatic conditions because of their geographical proximity, yet the grassland communities avoided dramatic declines. This may be attributable to pasture management, as the trait responses found in upland pasture accord with previously observed changes in carabid assemblages when sward height and complexity increase under less intense management and grazing (Cole *et al.* 2010). However, trait-based responses in chalk downland were the reverse of those in northern pasture, probably reflecting shorter sward heights caused by increased rabbit grazing (S.J. Corbett, pers. comm.; Eyre *et al.* 1989). Such results accord with carabids perceiving their environment at fine-scales of microhabitat variation and selecting niches accordingly (Niemelä *et al.* 1992), increasing evidence that management of microhabitats is a key tool for manipulating and conserving ecosystem functioning. For example, changes in sward height can alter thermal conditions at rates above those predicted by climate change scenarios, allowing insects to conserve their populations by moving to suitable microclimates (Suggitt *et al.* 2011). Indeed, losses in microhabitat heterogeneity are unquantified, but are thought more detrimental to insects than larger-scale changes in landscape diversity (Hanski 2005). In this respect, our study pinpoints woodland and hedgerows as worthy of further research. These habitats are already known to be important feeding and overwintering refuges for many generalist carabids moving between a variety of habitats (Lee & Landis 2002). However, woodland and hedgerows also

have particularly stable microclimates (Geiger 1957), which may buffer wider-scale perturbations and explain why their carabid communities were stable in this study. If proved correct, this presents exciting opportunities to manage these habitats in ways that will increase their value as refuges in the landscape, thereby conserving taxa during periods of adverse environmental change.

It is also likely that community composition will need to be considered in tandem with microclimatic requirements to maximize habitat management. For example, communities in western pasture are rich in hygrophilous carabid taxa which are thought to coexist in finely separated niches along moisture gradients (Andersen 1971). However, cold winters, linked for example to the NAO, can reduce such microclimatic heterogeneity (Crozier 2004), which may have contributed to biodiversity declines in these taxa. Indeed, carabid declines are often more pronounced when species are adapted to either very dry or wet conditions (Kotze *et al.* 2011). Established theory also predicts that larger, less mobile and fecund taxa are more prone to extinction under adverse disturbance (Lawton 1995). Our results, however, show that the populations of smaller, and often more dispersive, species can also be susceptible to declines. Successful strategies for coping with environmental adversity may, therefore, be more complex than originally thought. For example, dispersive butterfly species have recently been found to be just as prone to range contractions as those that are more sedentary (Forister *et al.* 2010). Furthermore, although higher fecundity and mobility are thought to increase resistance to disturbance in carabids, lower fecundity and mobility are traits often associated with smaller but more stable and persistent carabid populations that are less sensitive to macro-environmental change (Den Boer 1985). Thus, careful management of habitat architecture could influence population stability, but only when designed around the species traits most influencing community structure.

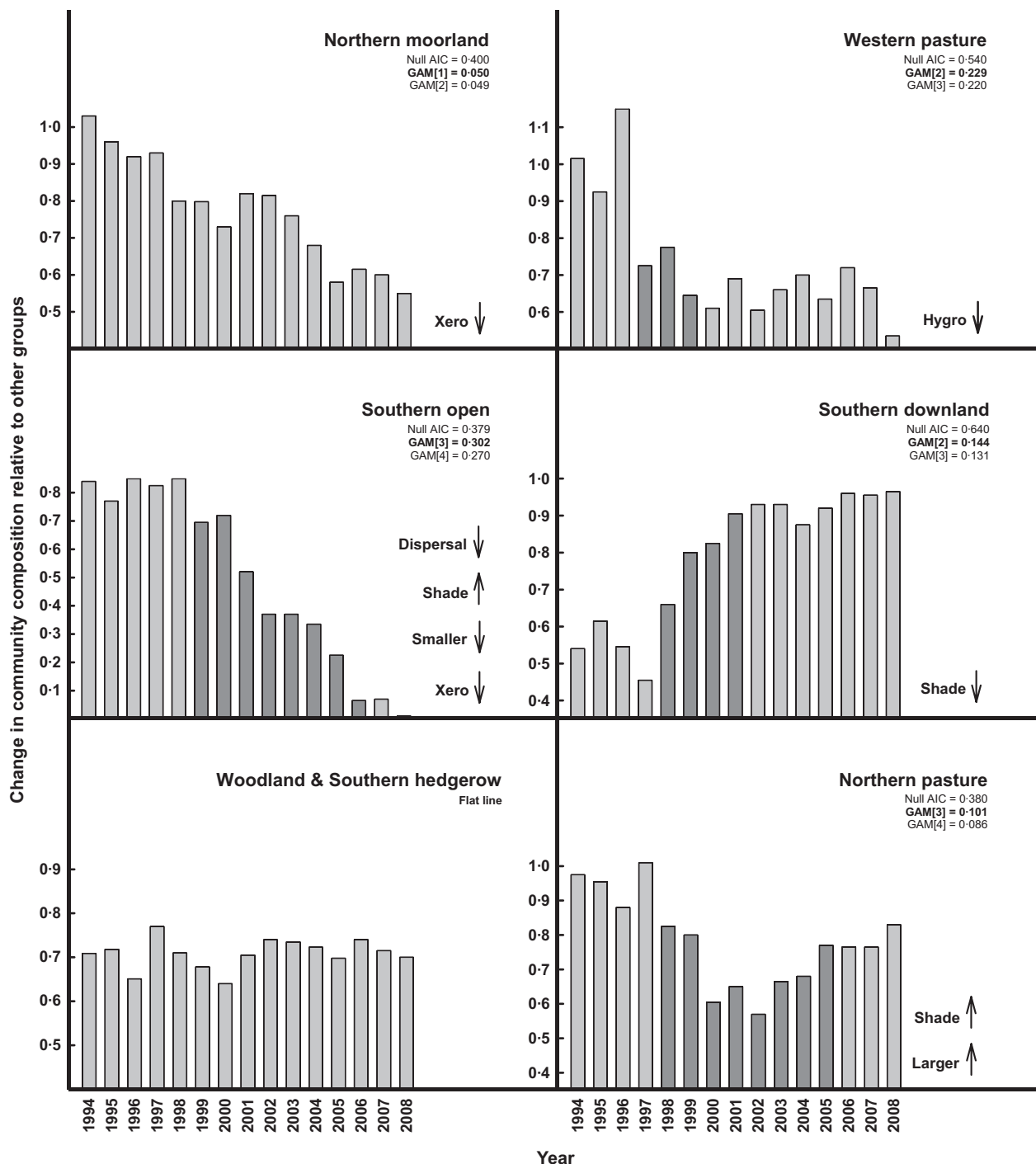


Fig. 6. Change in community composition within each region by habitat group, where changes are relative to those in other groups in a PRC analysis. Arrows show directions of significant trends in trait-based responses, where Xero, xerophilous spp., and Hygro, hygrophilous spp., describing preferences for drier or wetter conditions, respectively; Shade = increasing preference for shade; Dispersal = increasing dispersal power; and Smaller or Larger = trends for beetle size (see Table S3). Figures under group labels show AIC values for generalized additive models of that groups trend, with increasing complexity from a null model (null), to; first order, linear trend [1]; second order, nonlinear quadratic trend [2]; third order, nonlinear cubic trend [3]; and fourth order, complex nonlinear trend [4]. The model in bold is the one best describing the trend shown by the bars. Woodland and southern hedgerow had no significant deviation from a linear flat line trend. Dark bars show years when changes are occurring at relatively high rates.

Environmental data are often insufficient to explain insect trends (Thomas 2005). The ECN, however, circumvents these problems by linking comprehensive environmental data with carabid surveys, which are often

accompanied by variables describing vegetation changes (Morecroft *et al.* 2009). However, unravelling links between changing environmental conditions and plant communities, and their interactive effects on carabid

populations, will require careful consideration. For example, moorland carabid biodiversity is significantly greater in early successional stages in the cycle of growth and burning of heather used to conserve Red Grouse populations (Gimingham 1985). Thus, management aimed at preserving more open vegetation may be of greater long-term importance to carabid biodiversity than climate. However, the growth of heather, and other plants, is also strongly affected by climate (Caughley & Lawton 1981). Similarly, moisture changes affecting hygrophilous carabids are also likely to affect vegetation, which could have knock-on effects on the microclimate. Our results will be useful for guiding the development of more complex models aimed at disentangling the effects of these population drivers. In achieving this target, it will be critical that models forge strong links between the mechanisms driving species trends and changes in habitat structure. This will enable close alignment between land management practices and the conservation of ecosystem services.

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Supporting Information

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

Appendix S1. Model building methodology.

Table S1. Transect locations and habitat details.

Table S2. Full parameterization of pRDA models.

Table S3. Multiple regression models of trait-based responses.

Table S4. Full parameterization of mixed population models for: (a) the main 15-year time series, (b) the shortened time series for upland sites and (c) an overall summary of species trends in these models.

Fig. S1. Biplots for pRDA models for: (a) first and second axes, (b) second and third axes, in the 15-year time series and (c) pRDA for the 10-year upland time series.

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