

Biotic homogenization and changes in species diversity across human-modified ecosystems

Simon M. Smart^{1,2,*}, Ken Thompson³, Robert H. Marrs², Mike G. Le Duc²,
Lindsay C. Maskell¹ and Leslie G. Firbank¹

¹Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK

²Applied Vegetation Dynamics Laboratory, School of Biological Sciences, University of Liverpool, Liverpool L69 7ZB, UK

³Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

Changing land use and the spread of ‘winning’ native or exotic plants are expected to lead to biotic homogenization (BH), in which previously distinct plant communities become progressively more similar. In parallel, many ecosystems have recently seen increases in local species (α -) diversity, yet γ -diversity has continued to decline at larger scales. Using national ecological surveillance data for Great Britain, we quantify relationships between change in α -diversity and between-habitat homogenizations at two levels of organization: species composition and plant functional traits. Across Britain both increases and decreases in α -diversity were observed in small random sampling plots (10–200 m²) located within a national random sample of 1 km square regions. As α -diversity declined (spatially in 1978 or temporally between 1978 and 1998), plant communities became functionally more similar, but species-compositional similarity declined. Thus, different communities converged on a narrower range of winning trait syndromes, but species identities remained historically contingent, differentiating a mosaic of residual species-poor habitat patches within each 1 km square. The reverse trends in β -diversity occurred where α -diversity increased. When impacted by the same type and intensity of environmental change, directions of change in α -diversity are likely to depend upon differences in starting productivity and disturbance. This is one reason why local diversity change and BH across habitats are not likely to be consistently coupled.

Keywords: large scale; β -diversity; land use; global change; similarity; monitoring

1. INTRODUCTION

Terrestrial ecosystems are presently subjected to unprecedented rates of human-induced environmental change, yet the impact of these changes on species diversity and ecosystem function remains uncertain (Foley *et al.* 2005; Stokstad 2005). The concept of biotic homogenization (BH; McKinney & Lockwood 1999; Olden *et al.* 2004) offers a simple prediction of human impacts on the distribution of global biodiversity. Globalized transport mixes previously isolated biota, exposing more ecosystems to a greater number of potential colonists. In parallel, human impacts such as intensive farming, atmospheric pollution and urbanization decrease habitat suitability for a large number of species, but increase the suitability for a smaller number of ‘winners’. Human-induced environmental change may thus act as a non-random filter, selecting from a larger potential pool, for those species best able to survive within modified ecosystems. The consequence is predicted to be a more species-poor terrestrial biosphere, where local ecosystems and communities are also more similar from place to place as a result of the non-random turnover of species populations in response to human activity (McKinney & Lockwood 1999, 2001). Despite the simplicity of this basic scenario, a much larger number of outcomes appear theoretically possible or have been observed depending upon the scale of

observation (McKinney 2004a,b; Olden & Poff 2004), the species composition and relative abundance of the species pool from which new colonists are drawn (Olden & Poff 2003), variation in the competitive abilities of pool members (Davis 2003; MacDougall & Turkington 2005) and differences in the contribution of either extinction or invasion to homogenization patterns (McKinney & Lockwood 2001; Sax & Gaines 2003; Davis *et al.* 2005). For example, Olden & Poff (2003) described 14 scenarios, where impacts on between-community similarity varied widely depending upon the relative contributions of species invasion, local extinction and variation in the identity of the species concerned between impacted communities.

In practice, the BH concept has not been tested well across realistically large sampling domains comprising a mosaic of ecosystems that vary in productivity and land-use history (but see Olden *et al.* 2006). Also, while BH is usually understood to mean taxonomic convergence (i.e. increasing species-compositional similarity), it is also possible that communities may become functionally more similar (Olden *et al.* 2004), yet such functional convergence need not coincide with taxonomic convergence (Fukami *et al.* 2005; Olden & Rooney 2006). For example, increased dispersal of species that are functionally redundant with respect to trait syndromes favoured by human-induced environmental change, and that differ in their timing of invasion into abiotically similar patches, are expected to form multiple stable assemblages particularly under highly productive conditions (Samuels & Drake 1997; Chase 2003).

* Author and address for correspondence: Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK (ssma@cch.ac.uk).

It is also unclear whether observed changes in mean α - (i.e. local) diversity within habitat patches are correlated with the homogenization of species composition or trait values across larger regions (McKinney & Lockwood 2001; Scott & Helfman 2001; Lockwood 2004). Theoretical homogenization scenarios indicate that changes in α -diversity can be completely uncoupled from between-habitat homogenization (Olden & Poff 2003). For example, if species turnover in response to environmental change replaces locally distinctive assemblages with widespread species, this would reduce β -diversity, yet average α -diversity could remain the same. However, if environmental change favours a narrower range of trait syndromes, both β - and α -diversity of trait values would decline. Fukami *et al.* (2001) carried out a simulation analysis of the response of between-community similarity to changing mean α -diversity. To more realistically model species loss, they applied lognormal distributions to both the initial species pool and the extinction probability as mean α -diversity declined (Grime 2002). They showed that between-patch similarity tended to first increase then decrease. This follows because rare species disappeared first, initially lowering β -diversity because such species are by definition restricted in their distribution and survivors are biased towards more widely distributed species. At the turning point, subsequent declines in both α - and β -diversity appeared to be more consistent with a statistical 'variance-reduction' effect (Huston 1997). This simply predicts a lower probability of overlap in species composition between poorer samples randomly drawn from a common uniformly distributed species pool (Fukami *et al.* 2001). Since random probabilities of extinction or increase in population size are unrealistic assumptions for natural systems, tests against large-scale observational data could yield valuable insights into the form of these relationships at realistic scales (Kahmen *et al.* 2005).

We use national-scale, but fine-grained, ecological surveillance data for higher plants across Great Britain (GB) to address two predictions derived from the BH concept. First, is the change in trait variance positively correlated with the change in mean α -diversity within the habitats in a region? If true, this suggests that drivers of biodiversity loss also constitute a non-random filter on the values of key traits as expected if BH occurs (McKinney & Lockwood 1999; Suding *et al.* 2005). Second, as mean α -diversity declines, does the species composition of habitat patches become more similar in a region, suggesting that non-random species filtering favours a smaller number of residual species that increasingly occur in most habitats?

Hypotheses were tested on botanical records from small, fixed plots that comprise an unbiased sample of the mosaic of ecosystems that make up the British landscape in the last quarter of the twentieth century. This landscape represents a complete spatial gradient of α -diversity, initial productivity and disturbance (Smart *et al.* 2003a,b) that reflects centuries of human modification (principally agricultural intensification and human settlement; Ratcliffe 1984; Chamberlain *et al.* 2000) superimposed on a varied mosaic of upland and lowland ecosystems. Data were taken from national surveys carried out in 1978 and 1998 covering a period during which several key human impacts attained their

maximum prevalence and intensity. These included atmospheric nitrogen deposition, upland sheep grazing, upland afforestation, large-scale specialization and intensification of agriculture, abandonment of agriculturally marginal habitats and reduced disturbance on linear landscape features such as watercourse banks and road verges (Smart *et al.* 2005). During the 20-year period, substantial changes in α -diversity (both increases and decreases) and species composition occurred that have clearly favoured particular trait syndromes at the expense of others: in essence species that are tall, more nutrient demanding and largely either trees, shrubs or grasses have increased at the expense of native stress-tolerant forbs (Preston *et al.* 2002; Smart *et al.* 2005). GB surveillance data therefore allow a realistic test of the BH concept and its relationship to change in local diversity. Moreover, temperate and densely populated landscapes have received relatively less attention in BH studies even though impacts on biodiversity and ecosystem function are likely to be more evident as a result of demands on ecosystems imposed by large resident human populations.

2. MATERIAL AND METHODS

We tested both hypotheses by quantifying change in α -diversity through space and time in 1572 fixed plots located on a stratified, random basis within a representative, random sample of 238 1 km squares covering Britain (figure 1). Regression analysis was used to detect relationships between spatial and temporal changes in species richness within the fixed plots in each 1 km square versus regional change in the variance of key traits and pairwise species compositional similarity across each 1 km square. Traits analysed were based on a small number of simply measured attributes associated with the regenerative and established phases of higher plant growth, and were selected to be consistent with the established trait profiles of 'winners' and 'losers' in a human-dominated world (McKinney & Lockwood 1999).

(a) Survey design

Fine-grained data on plant species compositional change were taken from 238 1 km squares recorded as part of the Countryside Survey (CS) of Britain in 1978, 1990 and 1998 (Smart *et al.* 2003a). One kilometre squares (figure 1) were randomly sampled within 32 strata defined by an environmental classification of the GB land surface (Bunce *et al.* 1996). Botanical data were collected from fixed plots located inside each sample square and designed to sample linear landscape features (hedges, river, stream and ditch banks, and road verges) and areal features (fields and other enclosed or unenclosed areas of habitat such as woodland, heath, fen and bog). Full methods are given in Smart *et al.* (2003a).

(b) Sampling scales

Conclusions drawn from measurements of temporal and spatial change in species diversity can be weakened by failure to consider sampling scale (Huston 1999; Loreau 2000). In particular, large environmentally heterogeneous sample units confound assumptions that patterns result from local processes such as competition because many of the individuals enumerated may never have been able to



Figure 1. Map of Great Britain showing the location of the 238 1 km sample squares within which vegetation plots were recorded in 1978.

influence each other's resource consumption (Huston 1999). By using relatively small sampling plots (10–200 m²) nested within each 1 km square, we ensure that estimates of α -diversity and species composition target relatively homogenous stands sensitive to local processes of population sorting but where these translate into between-plot patterns within the regions defined by each biogeographically homogenous 1 km square.

We investigated patterns at two scales. Temporal changes in α -diversity were based on the analysis of Countryside Survey data for 1978 compared with 1998. To provide more information on the link between local species richness, local community similarity and cross-community trait variance national-scale spatial gradients were analysed in addition to the gradient of temporal change. In doing so, we assume that the spatial gradient reflects patterns of correlation formed cumulatively over a much longer time period. Although this is undoubtedly true, it remains a less direct test than the analysis of temporal change. Spatial associations were based on analysis of 1978 data because these data provided the longest gradient of species richness values against which species compositional similarity and trait variance could be correlated.

(c) Selection of trait data

Apart from specific leaf area (SLA) data, which is held by the Unit of Comparative Plant Ecology at the University of Sheffield, trait data were abstracted from published databases.

Two traits (seedbank longevity and probable dispersal vector) referred to the regenerative phase of higher plant growth. We estimated seedbank longevity using the index within the seedbank persistence database (Thompson *et al.* 1997). Information was available for 73% of species recorded. Dispersal vector information was extracted from two databases (Fitter & Peat 1994; Grime *et al.* 1995), and, where species were not included, dispersal vectors were attributed based on the presence of key morphological attributes (Hodgson & Grime 1990). Species could have more than one probable vector. Human dispersal was attributed to those species known to be actively sown for amenity or crops.

Two traits, SLA and canopy height (CH) referred to the established phase of plant growth. SLA was measured as leaf area per unit dry mass (Wilson *et al.* 1999). It has been verified experimentally as measuring a resilience versus resistance axis of primary higher plant specialization and as such, is also a consequence of adaptation to differing levels of nutrient availability (Weiher *et al.* 1999; Westoby *et al.* 2002; Díaz *et al.* 2004). CH is a key measure of competitive dominance and also tracks a second major axis of specialization among higher plants (Weiher *et al.* 1999; Westoby *et al.* 2002; Díaz *et al.* 2004). SLA data were available for 68% of the species recorded. CH data were available for all species recorded based on an ordinal scoring of the maximum attainable height of the leaf canopy of each species (Grime *et al.* 1995). Botanical data were only analysed where a trait value was available.

(d) Species-compositional similarity

Species-compositional similarity between fixed sample plots within each square in each year was calculated using the Jaccard coefficient (Kuo 1997; Olden & Rooney 2006) for presence data to generate a matrix of $1/2n^*(n-1)$ coefficients between all possible plot pairs in each year within each 1 km square.

(e) Trait variance

Variation in the range of trait values for each trait was expressed as the coefficient of variation for continuous and ordinal data, and the Gini coefficient for categorical data as follows (Engler *et al.* 2004):

$$G = \sum_{i=1}^n C_i(1 - C_i), \quad (2.1)$$

where C_i is the proportion of each category of trait value i to n over all the records of all plant species among all plots in each 1 km square. Coefficients were calculated across all plots in each 1 km square in each survey year giving one response variable per 1 km sample square.

(f) Analysis

Spatial and temporal correlations between change in mean pairwise similarity and trait variance versus change in mean α -diversity were initially explored using linear and quadratic regression, where mean α -diversity was the mean species richness across all fixed plots in each 1 km square each year.

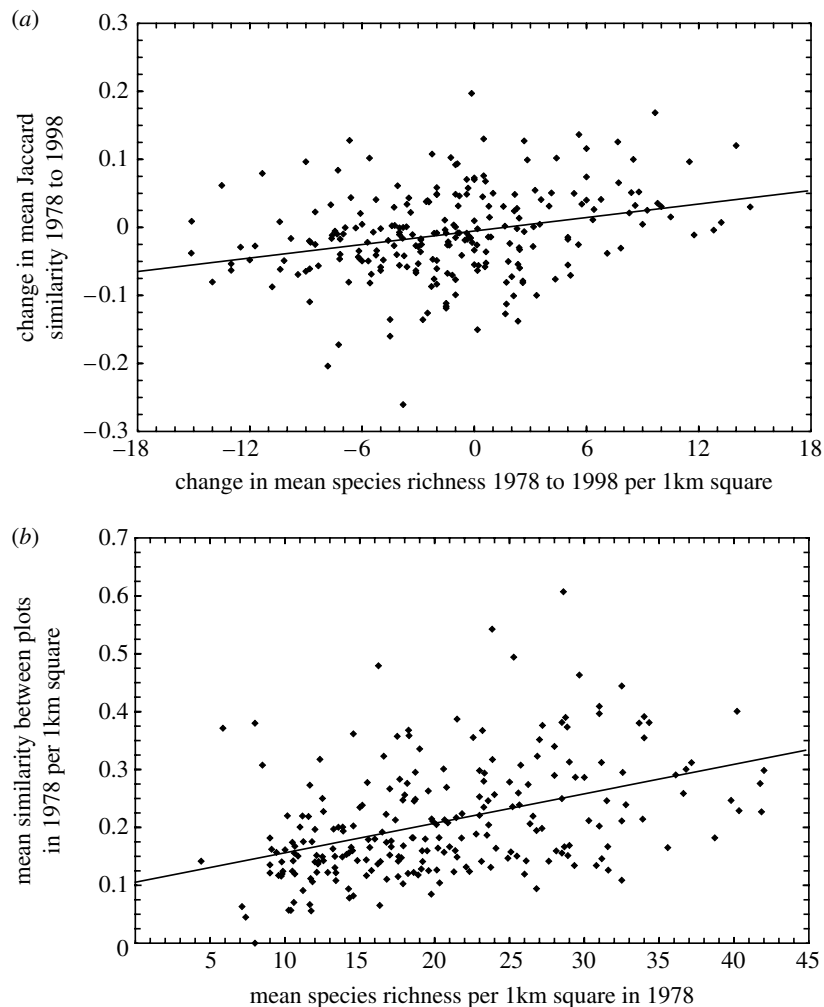


Figure 2. GB-wide spatial and temporal change in α -diversity and species-compositional similarity between local communities: (a) change in mean α -diversity per 1 km square between 1978 and 1998 versus difference in the mean similarity coefficient of the half-matrix of all plot pairs in each square in 1978 and 1998 ($n=238$, $r^2=8\%$, $p<0.001$); (b) mean α -diversity per 1 km square in 1978 versus the mean similarity coefficient of the half-matrix of all plot pairs in each square in 1978 ($n=238$, $r^2=18\%$, $p<0.001$).

Exploratory analyses were carried out using SAS Insight. We found that linear models best explained both temporal and spatial relationships between change in α - and β -diversity. Because the variance of the response variables changed with diversity, relationships were checked by comparing the observed Pearson correlation coefficient against 1000 such coefficients derived from randomized pairing of diversity, similarity and trait variance across all 1 km squares.

3. RESULTS

We found a positive correlation between change in mean α -diversity and both temporal (figure 2a) and spatial (figure 2b) changes in mean pair-wise species compositional similarity. Hence, as mean α -diversity declined, local communities became less similar in terms of their species composition. This pattern was found both for changes in α -diversity over time on the same plots (1978–1998), and for gradients of α -diversity across GB at the same point in time (1978 only).

Declining mean α -diversity was accompanied by declining trait variance, while increasing mean α -diversity saw greater variation in trait syndromes between habitats. Positive relationships were observed between temporal change in the variance of dispersal attributes and CH

and change in mean α -diversity across 1 km sample squares (table 1). Furthermore, positive spatial associations were observed between mean α -diversity and variance in all traits across 1 km squares in 1978 (table 1).

Variance explained was very low for all analyses. This is, however, typical for analyses of CS national-scale surveillance data, which generally have low signal to noise ratios (e.g. Petit *et al.* 2004; Smart *et al.* 2004) and where the appropriate goal is thus signal detection rather than explaining as much variation in the data as possible.

4. DISCUSSION

The positive association between species-compositional similarity and mean α -diversity across GB between 1978 and 1998 (figure 2a,b) indicates that, far from homogenizing species composition between local communities, reductions in local species richness resulted in species-compositional differentiation. Yet, trait variance declined alongside mean α -diversity, i.e. residual assemblages tended to increasingly share a common trait syndrome as habitat patches lost species in each 1 km square. Concurrent declines in trait variance, between-habitat species compositional similarity and mean α -diversity must therefore reflect the common ascendance of

Table 1. GB-wide spatial and temporal change in trait variance between local communities. ((a) Pearson correlation coefficients between change in mean α -diversity and change in trait variation between 1978 and 1998 in 238 1 km squares located randomly across Britain; (b) Pearson correlation coefficients between mean α -diversity in each 1 km square in 1978 and trait variation across each 1 km square in 1978. Mean α -diversity was based on the number of plant species recorded from a maximum of 13 stratified random vegetation sampling plots in each 1 km square. Trait variation was calculated across the total pool of plant species recorded in all plots in each square. Plots were fixed in permanent positions in 1978 and recorded again in 1990 and 1998. Pearson correlation coefficients are given with randomization p -value in brackets; emboldened where $p < 0.05$.)

plant trait	(a) temporal correlation (1978–1998)	(b) spatial correlation (1978 only)
seedbank longevity	0.087 (0.100)	0.107 (0.047)
dispersal attributes	0.242 (0.001)	0.420 (0.001)
canopy height	0.212 (0.001)	0.162 (0.005)
specific leaf area	0.178 (0.128)	0.367 (0.001)

successful trait syndromes among a small number of different community-specific specialists. Exactly, this process has recently been observed in experimental grassland communities (Fukami *et al.* 2005).

Given similar abiotic conditions among habitat patches, the combined effect of differences in invasion sequence and patch dominance are predicted to play a key role in increasing β -diversity between patches, but lowering α -diversity within patches (Chase 2003). However, where mean α -diversity and trait variance declined in British 1 km squares, land-use changes have tended to filter out subordinate species leaving pre-existing dominants to characterize the remaining habitat mosaic. Thus, in these situations, patch-level extinction has probably been more influential than the invasion and establishment of different winning species in generating observed diversity relationships (cf. Chase & Liebold 2002). Also, despite at least a century of increasingly intensive human exploitation, the vegetation plots within each 1 km square region in 1998 still reflect residual mosaics of different community types (Smart *et al.* 2003b). So, even though a number of traits homogenized across communities when α -diversity declined over time, differences in the identity of residual species were still likely to reflect persistent differences in, for example, soil moisture, soil pH, successional stage and type of land use (Smart *et al.* 2003b, 2005).

A remarkable feature of our results was that the correlations between α -diversity, trait variance and species composition applied across the entirety of the spatial and temporal α -diversity gradients (figure 2). Thus, many habitat patches saw increased α -diversity over time, and this was accompanied by increased variance of two out of four traits and increasing species-compositional similarity between habitats. Given the prevalence of drivers tending to reduce local diversity, why has richness of some communities increased? Increased plot occupancy by non-native species is unlikely to be responsible, since in the 86 1 km squares in which mean α -diversity increased between 1978 and 1998, there was a non-significant decrease in mean α -diversity of non-native species ($t = -1.08$, $p = 0.282$). There is evidence that local reductions in management intensity impacted two specific habitat types in the 20-year period: fertile grasslands were apparently subjected to deliberate, but highly localized, reductions in agricultural inputs (Potter & Lobley 1996), while around 10–20% of arable land was made fallow for varying periods as a result of the Europe-wide set-aside scheme first implemented in 1988 (Smart *et al.* 2005).

However, the weight of available evidence suggests that the effects of eutrophication and either intensive disturbance or abandonment were more prevalent across British ecosystems over the 20-year period (Smart *et al.* 2003a,b; 2005). Therefore, differences in the direction of change in α -diversity are more likely to reflect differences in initial habitat productivity and disturbance (Smart *et al.* 2003a). Thus, increases in richness have mainly occurred in communities that are (or were) still on the rising part of the unimodal biodiversity-fertility/disturbance curves or, more locally, where reduced land-use intensity impacted communities on the left of the mode. Our results therefore lead to the further prediction that initial abiotic conditions help control the extent to which species with losing and winning trait syndromes can coexist, albeit temporarily, and hence whether α -diversity initially increases or decreases in response to the same human-induced driving forces (Stohlgren *et al.* 1999; Wright & Jones 2004). Dependence upon starting conditions is therefore a further obvious reason why a consistent relationship between species diversity changes and biotic homogenization is unlikely.

Our analyses have focused specifically on the relationship between small-scale, within-community changes in α -diversity and their impact on β -diversity of species and traits across 1 km square regions. At these scales, the results suggest that the large-scale perturbation of temperate, terrestrial ecosystems may have an end-point not characterized by the supremacy of a small number of Darwinian demons that disperse everywhere and always outcompete neighbours (Rees 1993). Rather, human impacts could result in a mosaic of species-poor ecosystems, where subordinate species have been sieved out by environmental modification and the competitive effect of winning dominants that reflect local abiotic and climatic conditions (Grime 1998). If so, the eventual outcome would be analogous to industrial concentration, where a small number of different firms dominate within different market sectors, but share similar winning traits (Mueller 1986).

In Britain and elsewhere, these small-scale patterns exist within a larger-scale context of rare native species population declines and increased frequency of many new non-native species. However, detecting deletions and additions of these sparsely distributed, low abundance species typically requires a shift to larger sized recording units such as 10 km squares or counties (Walker 2003). Homogenization patterns attributable to these species are then inevitably expressed at these scales (e.g. McKinney 2004a) because

they are nearer optimal for detecting change in presence and absence in each unit and hence for quantifying gradients of β -diversity between units (Critchley & Poulton 1998). This raises the interesting possibility that a true characterization of homogenization patterns across large regions involves searching for the simultaneous operation of different theoretical homogenization scenarios (*sensu* Olden & Poff 2003) at different spatial scales.

We thank Michael Begon, Jason Fridley and Michael McKinney for their comments on a previous draft of this article. S.M.S. was supported by NERC and CEH funding during tenure at the University of Liverpool. K.T. was funded by the European Union LEDA project EVR1-CT-2002-40022.

REFERENCES

- Bunce, R. G. H., Barr, C. J., Clarke, R. T., Howard, D. C. & Lane, M. J. 1996 ITE Merlewood land classification of Great Britain. *J. Biogeogr.* **23**, 625–634.
- Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C. & Shrubbs, M. 2000 Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *J. Appl. Ecol.* **37**, 771–788. (doi:10.1046/j.1365-2664.2000.00548.x)
- Chase, J. M. 2003 Community assembly: when should history matter? *Oecologia* **136**, 489–498. (doi:10.1007/s00442-003-1311-7)
- Chase, J. M. & Liebold, M. A. 2002 Spatial scale dictates the productivity–diversity relationship. *Nature* **415**, 427–430. (doi:10.1038/416427a)
- Critchley, C. N. R. & Poulton, S. M. C. 1998 A method to optimise precision and scale in grassland monitoring. *J. Veg. Sci.* **9**, 837–846. (doi:10.2307/3237049)
- Davis, M. A. 2003 Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* **53**, 481–489.
- Davis, M. A., Thompson, K. & Grime, J. P. 2005 Invasibility: the local mechanism driving community assembly and species diversity. *Ecography* **28**, 696–704. (doi:10.1111/j.2005.0906-7590.04205.x)
- Diaz, S. *et al.* 2004 The plant traits that drive ecosystems: evidence from three continents. *J. Veg. Sci.* **15**, 295–304.
- Engler, R., Guisan, A. & Rechsteiner, L. 2004 An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *J. Appl. Ecol.* **41**, 263–274. (doi:10.1111/j.0021-8901.2004.00881.x)
- Fitter, A. H. & Peat, H. J. 1994 The ecological flora database. *J. Ecol.* **82**, 415–425.
- Foley, J. A. *et al.* 2005 Global consequences of land use. *Science* **309**, 570–574. (doi:10.1126/science.1111772)
- Fukami, T., Naeem, S. & Wardle, D. A. 2001 On similarity among local communities in biodiversity experiments. *Oikos* **95**, 340–348. (doi:10.1034/j.1600-0706.2001.950216.x)
- Fukami, T., Bezemer, T. M., Mortimer, S. R. & van der Putten, W. H. 2005 Species divergence and trait convergence in an experimental community assembly. *Ecol. Lett.* **8**, 1283–1290. (doi:10.1111/j.1461-0248.2005.00829.x)
- Grime, J. P. 1998 Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910. (doi:10.1046/j.1365-2745.1998.00306.x)
- Grime, J. P. 2002 Declining plant diversity: empty niches or functional shifts? *J. Veg. Sci.* **13**, 457–460.
- Grime, J. P., Hodgson, J. G., Hunt, R. & Thompson, K. 1995 *The electronic comparative plant ecology*. London, UK: Chapman & Hall.
- Hodgson, J. G. & Grime, J. P. 1990 The role of dispersal mechanisms, regenerative strategies and seed banks in the vegetation dynamics of the British landscape. In *Species dispersal in agricultural habitats* (ed. R. G. H. Bunce & D. C. Howard), pp. 65–81. London, UK: Belhaven Press.
- Huston, M. A. 1997 Hidden treatments in ecological experiments: re-evaluating the ecosystem function in biodiversity. *Oecologia* **110**, 449–460. (doi:10.1007/s004420050180)
- Huston, M. A. 1999 Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**, 393–401.
- Kahmen, A., Perner, J., Audorff, V., Weisser, W. & Buchmann, N. 2005 Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. *Oecologia* **142**, 606–615. (doi:10.1007/s00442-004-1749-2)
- Kuo, M. 1997 *The DISTANCE macro: preliminary documentation*, 2nd edn. Cary, NC: Multivariate & Numerical R&D application division, SAS Institute.
- Lockwood, J. L. 2004 How do biological invasions alter diversity patterns? In *Frontiers in biogeography* (ed. M. Lomolino & L. Heany), pp. 297–309. Sunderland, MA: Sinauer Press.
- Loreau, M. 2000 Are communities saturated? On the relationship between α , β and γ diversity. *Ecol. Lett.* **3**, 73–76. (doi:10.1046/j.1461-0248.2000.00127.x)
- MacDougall, A. S. & Turkington, R. 2005 Are invasive species the drivers or passengers in degraded ecosystems? *Ecology* **86**, 42–55.
- McKinney, M. L. 2004a Measuring floristic homogenization by non-native plants in North America. *Global Ecol. Biogeogr.* **13**, 47–53. (doi:10.1111/j.1466-882X.2004.00059.x)
- McKinney, M. L. 2004b Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biol. Invasions* **6**, 495–504. (doi:10.1023/B:BINV.0000041562.31023.42)
- McKinney, M. L. & Lockwood, J. L. 1999 Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **14**, 450–453. (doi:10.1016/S0169-5347(99)01679-1)
- McKinney, M. L. & Lockwood, J. L. 2001 Biotic homogenization: a sequential and selective process. In *Biotic homogenization* (ed. J. L. Lockwood & M. L. McKinney), pp. 1–17. New York, NY: Kluwer Academic Publishers.
- Mueller, D. C. 1986 *Profits in the long run*. New York, NY: Cambridge University Press.
- Olden, J. D. & Poff, N. L. 2003 Toward a mechanistic understanding and prediction of biotic homogenization. *Am. Nat.* **162**, 442–460. (doi:10.1086/378212)
- Olden, J. D. & Poff, N. L. 2004 Ecological mechanisms driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology* **85**, 1867–1875.
- Olden, J. D. & Rooney, T. P. 2006 On defining and quantifying biotic homogenization. *Global Ecol. Biogeogr.* **15**, 113–120. (doi:10.1111/j.1466-822X.2006.00214.x)
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E. & Fausch, K. D. 2004 Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* **19**, 18–24. (doi:10.1016/j.tree.2003.09.010)
- Olden, J. D., Poff, N. L. & McKinney, M. L. 2006 Forecasting faunal and floral homogenization associated with human population geography in North America. *Biol. Conserv.* **127**, 261–271. (doi:10.1016/j.biocon.2005.04.027)
- Petit, S., Griffiths, L., Smart, S. M., Smith, G. M., Stuart, R. C. & Wright, S. M. 2004 Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecol.* **19**, 463–471. (doi:10.1023/B:LAND.0000036141.30359.53)

- Potter, C. & Lobley, M. 1996. *Processes of countryside change in Britain*. Countryside survey 1990 series, vol. 7. London, UK: HMSO.
- Preston, C. D. *et al.* 2002 *The changing flora of the UK*. London, UK: Department of the Environment, Food and Rural Affairs.
- Ratcliffe, D. A. 1984 Post-medieval and recent changes in British vegetation: the culmination of human influence. *New Phytol.* **98**, 73–100. (doi:10.1111/j.1469-8137.1984.tb06099.x)
- Rees, M. 1993 Trade-offs among dispersal strategies in British plants. *Nature* **366**, 150–152. (doi:10.1038/366150a0)
- Samuels, C. L. & Drake, J. A. 1997 Divergent perspectives on community convergence. *Trends Ecol. Evol.* **12**, 427–432. (doi:10.1016/S0169-5347(97)01182-8)
- Sax, D. F. & Gaines, S. D. 2003 Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* **18**, 561–566. (doi:10.1016/S0169-5347(03)00224-6)
- Scott, M. C. & Helfman, G. S. 2001 Native invasions, homogenization and the mismeasure of integrity of fish assemblages. *Fisheries* **26**, 6–15. (doi:10.1577/1548-8446(2001)026<0006:NIHATM>2.0.CO;2)
- Smart, S. M., Clarke, R. T., van de Poll, H. M., Robertson, E. J., Shield, E. R., Bunce, R. G. H. & Maskell, L. C. 2003a National-scale vegetation change across Britain; an analysis of sample-based surveillance data from the Countryside Surveys of 1990 and 1998. *J. Environ. Manage.* **67**, 239–254. (doi:10.1016/S0301-4797(02)00177-9)
- Smart, S. M., Robinson, J. C., Shield, E. J. & van de Poll, H. M. 2003b Locating eutrophication effects across British vegetation between 1990 and 1998. *Global Change Biol.* **9**, 1763–1774. (doi:10.1046/j.1365-2486.2003.00707.x)
- Smart, S. M., Ashmore, M. R., Scott, W. A., Hornung, M. H., Dragosits, U., Fowler, D., Sutton, M. A., Famulari, D. & Howard, D. C. 2004 Detecting the large-scale signal of atmospheric N deposition across British ecosystems. *Water Air Soil Pollut.: Focus* **4**, 269–278. (doi:10.1007/s11267-004-3037-x)
- Smart, S. M., Bunce, R. G. H., Marrs, R., Le Duc, M., Firbank, L. G., Maskell, L. C., Scott, W. A., Thompson, K. & Walker, K. J. 2005 Large-scale changes in the abundance of common higher plant species across Britain between 1978, 1990 and 1998 as a consequence of human activity: tests of hypothesised changes in trait representation. *Biol. Conserv.* **124**, 355–371. (doi:10.1016/j.biocon.2004.12.013)
- Stohlgren, T. J. *et al.* 1999 Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* **69**, 25–46. (doi:10.2307/2657193)
- Stokstad, E. 2005 Ecology—taking the pulse of earth's life support systems. *Science* **308**, 41–43. (doi:10.1126/science.308.5718.41)
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G. & Pennings, S. 2005 Functional and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl Acad. Sci. USA* **102**, 4387–4392. (doi:10.1073/pnas.0408648102)
- Thompson, K., Bakker, J. P. & Bekker, R. M. 1997 *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge, UK: Cambridge University Press.
- Walker, K. J. 2003 One species lost every year? An evaluation of plant extinctions in selected British vice-counties since 1900. *Watsonia* **24**, 359–374.
- Weihner, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. 1999 Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.* **10**, 609–620. (doi:10.2307/3237076)
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. 2002 Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* **33**, 125–159. (doi:10.1146/annurev.ecolsys.33.010802.150452)
- Wilson, P. J., Thompson, K. & Hodgson, J. G. 1999 Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytol.* **143**, 155–162. (doi:10.1046/j.1469-8137.1999.00427.x)
- Wright, J. P. & Jones, C. G. 2004 Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* **85**, 2071–2081.