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# Distinguishing between turnover and nestedness in the quantification of biotic homogenization

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**Abstract**

Compositional changes through local extinction and colonization are inherent to natural communities, but human activities are increasingly influencing the rate and nature of the species being lost and gained. Biotic homogenization refers to the process by which the compositional similarity of communities increases over time through a non-random reshuffling of species. Despite the extensive conceptual development of the homogenization framework, approaches to quantify patterns of homogenization are scarcely developed. Most studies have used classical dissimilarity indices that actually quantify two components of compositional variation: turnover and nestedness. Here we demonstrate that a method that partitions those two components reveals patterns of homogenization that are otherwise obscured using traditional techniques. The forest understorey vegetation of an unmanaged reserve was recorded in permanent plots in 1979 and 2009. In only thirty years, the local species richness significantly decreased and the variation in the species composition from site to site shifted towards a structure with reduced true species turnover and increased dissimilarity due to nestedness. A classic analysis masked those patterns. In summary, we illustrated the need to move beyond the simple quantification of homogenization using classical indices and advocate integration of the multitude of ways to quantify community similarity into the homogenization framework.

**Keywords** vegetation resurvey - permanent plot - forest understorey - beta diversity - global changes - succession

**Introduction**

The diversity and composition of species in local communities are fundamentally shaped by the colonization of species from the regional species pool versus the extinction of resident species through drift and selection (Vellend 2010). Continuous compositional changes are thus inherent to communities, but human activities are increasingly influencing species colonization and extinction and therefore also the patterns of biodiversity. In human dominated habitats, the loss of resident species is often accompanied by the colonization of a relatively small set of native and alien species that thrive in the human-altered environments (McKinney and Lockwood 1999; Clavel et al. 2011). Besides its evident impact on the local species diversity, such a non-random reshuffling of communities also alters the compositional differentiation between communities. The replacement of resident species with a restricted set of already common species can cause substantial increases in the compositional similarity among communities over time, called biotic homogenization (definitions in McKinney and Lockwood 1999, Olden and Rooney 2006). An increasing number of conceptual models describe the mechanisms and ecological, functional and evolutionary consequences of biotic homogenization (Olden and Poff 2003; Olden et al. 2004; Clavel et al. 2011), but there has not been as much effort in the development of different approaches to quantify homogenization.

Taxonomic homogenization, i.e., based on taxonomic similarity rather than genetic or functional, is generally quantified as the difference in the mean pairwise similarity among communities between two time periods (Olden and Rooney 2006). This approach is largely equivalent to the variation concept of β diversity (Vellend 2001; Anderson et al. 2011): the among-community variation in species composition within a certain area is calculated from similarities between pairs of sites. A reduction of the β diversity between two time periods basically expresses the degree of homogenization. Developing sound procedures to quantify homogenization therefore largely comes down to integrating existing concepts and measures of β diversity into homogenization studies. However few studies on homogenization have used measures other than classical Jaccard and Bray-Curtis dissimilarity (e.g., Van Calster et al. 2007; Vellend et al. 2007; Naaf and Wulf 2010; reviewed in Olden and Rooney 2006). The lack of exploration of the multitude of ways to quantify β diversity in homogenization literature thus deserves more attention.

One disadvantage of classical dissimilarity indices (e.g., Jaccard, Sørensen) is that they actually quantify two different phenomena: turnover and dissimilarity due to nestedness (Baselga et al. 2007; Baselga 2010). Turnover refers to the replacement of some species by other species from site to site, independent of potential differences in species richness between the sites (e.g., Koleff et al. 2003; Baselga 2010; Chase et al. 2011). The nestedness component accounts for the differences in composition when no species is replaced from one site to the other. These differences are derived from differences in species richness between nested assemblages, i.e., the species composition of the poorest site is a subset of that of the richest site. Classical indices in homogenization studies therefore do not distinguish different changes in among-community structure over time that nonetheless result in a comparable level of homogenization (Fig. 1). The two processes that underlie homogenization, i.e., species loss and non-random species replacements (Olden and Poff 2003), also generate the patterns of nestedness and turnover (Baselga 2010). Distinguishing between nestedness and turnover would therefore be very informative in homogenization studies. Baselga (2010) theoretically developed an additive partitioning of the total dissimilarity among sites into a turnover and nestedness component. Here we integrate this partitioning into the study of a resurvey

vegetation dataset to demonstrate its ingenuity for unravelling the patterns of taxonomic homogenization. We examined among- and within-plot (temporal) variation in community structure on a set of 35 permanent vegetation plots in an unmanaged forest reserve that were recorded in 1979 and 2009. By showing that classical indices may obscure the different patterns resulting from species loss and replacement, we aim to break a lance for moving beyond the conventional approaches to quantify this central aspect of the biodiversity crisis.

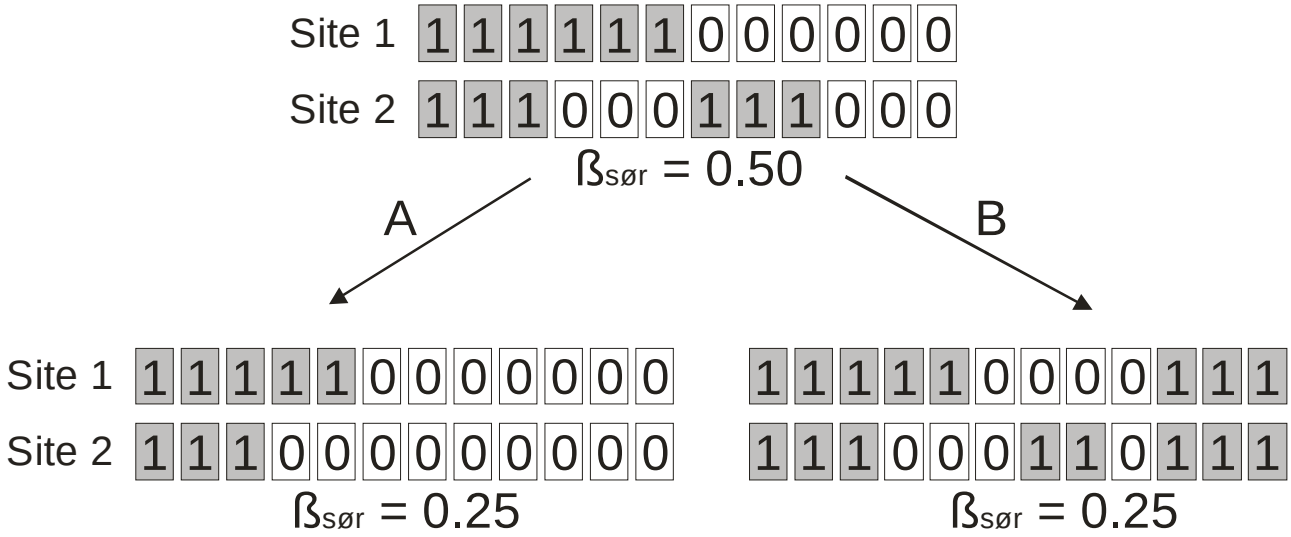


**Fig. 1** Hypothetical example of the presences '1' and absences '0' of twelve species in two sites. The sites share three species and three species are unique to Site 1 and 2, so species richness is equal and Sørensen dissimilarity βsor = 0.50. Two different trajectories of change in species composition result in an equal decrease in the dissimilarity to 0.25. (A) Species loss in both sites, e.g., species that differentiated between Site 1 and Site 2 disappeared, results in a perfectly nested structure. (B) The loss of a differentiating species in Site 1 and Site 2 is accompanied by the gain of three species in both sites. Species richness between the sites remains equal and the trajectory only leads to changes in the turnover.

## Methods

*Study site and understorey vegetation survey*

The 35 ha forest reserve of Lady Park Wood is an ancient, semi-natural woodland, which forms part of the 1400 ha Highmeadow Woods situated in the Lower Wye Valley along the border between England and Wales (N 51° 49.6', W 2° 39.6'). Soils vary from relatively acidic soils developed in old red sandstone to alkaline (colluvial) loam, clay loams and clay. The main canopy trees include beech (Fagus sylvatica), sessile oak (Quercus petraea), ash (Fraxinus excelsior), small-leaved lime (Tilia cordata) and birches (Betula pendula, B. pubescens) and the subcanopy further includes hazel (Corylus avellana), yew (Taxus baccata), field maple (Acer campestre) and holly (Ilex aquifolium). An extensive description of the soil and vegetation can be found in Peterken and Jones (1987). The forest stands were managed as coppice-with-standards for centuries until the last coppicing in 1870. Currently, the forest basically comprises two age classes (Peterken and Mountford 1998): (1) 'old growth' forest, which was merely thinned since 1870 and has not been cut since at least the 1930s;

(2) ‘young growth’ forest which was largely cut in 1943-1944, and was left to spontaneous development afterwards. In 1944, part of the forest was designated as an unmanaged nature reserve. The stands are thus unmanaged for over six decades, which is quite exceptional for Western-Europe. In addition to the forest development following the abandonment of management, deer grazing has also profoundly affected the vegetation in Lady Park Wood over the past decades (Peterken and Jones 1989).

In 1979, Vanessa Williams established 72 permanent vegetation plots in the forest, 60 of which were actually located within the unmanaged forest reserve. The plots were set out in a stratified random way in order to cover most of the variation in soil conditions and management history. Plots were 14 m □ 14 m and contained four 2 m □ 4 m subplots in each corner. In each plot, the trees and shrubs were positioned, measured and recorded on detailed tree maps. The subplots were used to record the ground flora. All species of the ground layer vegetation were recorded together with their estimated percentage cover and frequency. The frequency was recorded using 8 grid cells of 1 m □ 1 m in each subplot. This survey was performed between May and August. In 2009, 35 of the Williams plots could be relocated using the permanent corner posts of the plots and the detailed tree maps. The 35 plots were all located in the unmanaged part and selected to represent the variation in topography, soil types and management histories (old growth N = 11 plots, young growth N = 24 plots) of the forest reserve. The herb layer was recorded again using the same methodology in May and August 2009. Before statistical analysis, the vegetation data were converted into presence-absence data and pooled to the plot level, i.e., combining the species occurrences in the four respective subplots.

*Analysis of biotic homogenization and compositional change*

The data were analysed in two different ways, beginning with the change in among-plot taxonomic similarity between the two surveys as a measure of homogenization. Second, we looked at within-plot compositional shifts over time to determine the plot-level patterns of change that contributed to the homogenisation. The Sørensen dissimilarity index is one of the most commonly used indices to quantify taxonomic homogenization using presence-absence data. The index is closely related to other indices such as the Jaccard dissimilarity (see Koleff et al. 2003). For each pair of sites, the dissimilarity is calculated as:

$$\beta_{sor} = \frac{b + c}{2a + b + c} \qquad (1)$$

where a is the number of species shared by both sites, b is the number of species that only occur in the first site and c is the number of species unique to the second site. Koleff et al. (2003) showed that the Sørensen index not only expresses true turnover, but is also sensitive to differences in species richness among sites. A second dissimilarity measure that exclusively expresses turnover, i.e., it is not confounded by differences in species richness, is the Simpson index (Simpson 1943; Lennon et al. 2001; Koleff et al. 2003):

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)} \qquad (2)$$

Baselga (2010) showed that the difference between the βsor and the βsim index expresses the nestedness component of the compositional differentiation between a pair of sites:

$$\beta_{nes} = \beta_{sor} - \beta_{sim} \quad (3)$$

$$\beta_{nes} = \frac{\max(b,c) - \min(b,c)}{2a + \min(b,c) + \max(b,c)} \times \frac{a}{a + \min(b,c)} \quad (4)$$

The first term of this product is a measure of the difference in species richness between the sites. The second term is needed to separate differences in richness caused by nestedness patterns from other differences in richness. For instance, two sites that share no species (i.e., a = 0) may differ in species richness, but they are obviously not nested. For consistency of terminology, it is important to notice here that βnes does not measure the perfectness of the nested patterns (as would for instance the NODF or 'nestedness metric based on overlap and decreasing fill', Almeida-Neto et al. 2008), but quantifies the fraction of total dissimilarity that is derived from nestedness patterns (see Baselga 2010 for more details). In this way, the commonly used Sørensen dissimilarity measure in homogenization studies can be easily decomposed into its turnover and nestedness component.

To quantify biotic homogenization, we first need to calculate the β diversity as among-plot variation in 1979 and in 2009. This implies calculating the dispersion of the plots in multivariate space (Anderson et al. 2006, 2011): as average interplot dissimilarities, as the sum of squared interplot dissimilarities or as the average distance-to-centroid of all the plots. The dominant approach in homogenization literature is to calculate the simple average interplot dissimilarities (e.g., Rooney et al. 2004; Van Calster et al. 2007; Vellend et al. 2007; Naaf and Wulf 2010) and we will do the same. For a plot i, the mean of the pairwise dissimilarities against all other plots measures that plot's compositional differentiation (e.g., βsor, i, βsim, i and βnes, i). The level of taxonomic homogenization based on Sørensen dissimilarity and the contribution of changes in turnover and nestedness was tested by comparing the mean βsor, βsim and βnes, respectively, between 1979 and 2009 with a t-test. The mean number of species per plot, i.e., a measure of α diversity, was also compared between both surveys with a paired t-test.

Nonmetric multidimensional scaling analyses (NMDS) on the full data matrix (i.e., 1979 and 2009 data) were used to visualise plot-level compositional shifts over time. The three dissimilarity measures produced three dissimilarity matrices, which were used for ordination with the metaMDS function in the vegan library of R 2.11.1 (Oksanen et al. 2010; R Development Core Team 2010). The metaMDS function uses several random starts to find a stable solution. Based on scree plots of dimensionality versus stress, we used a two (βsor, βsim) and a one dimensional (βnes) NMDS solution. The solution was rotated so that the largest variance of site scores is on the first axis and half-change scaling was applied (see documentation Oksanen et al. 2010). Finally, using a permutational multivariate analysis of variance (PERMANOVA; adonis function) we tested whether the observed compositional changes over time were significant (Anderson 2001). The significance of the factor year (1979 versus 2009) was tested with 2000 permutations.

**Results**

The total ground flora species pool of the plots contained 97 different taxa, 57 of which occurred both in 1979 and 2009. A total of 36 species were only found in 1979, whereas only four species were unique to the 2009 survey. The mean species richness per plot significantly decreased from 21.3 species in 1979 to 15.5 species per plot in 2009 ($t = 6.74$, $P < 0.001$). The species that were lost between the surveys but still occurred in several plots in 1979 included Hypericum pulchrum (number of plots in 1979 N = 11), Lysimachia nemorum (N = 9), Rosa canina (N = 7), Lamium galeobdolon (N = 7) and Epilobium angustifolium (N = 7) (see Electronic Supplementary Material). On the other hand, 14 out of the 36 species that were lost between 1979 and 2009 only occurred in one plot in the first survey. The four new species in the 2009 survey were only found in one (Viburnum opulus, Vicia sepium, Neottia nidus-avis) or two plots (Epilobium parviflorum).

The mean Sørensen dissimilarity did not significantly change between 1979 and 2009 ($t = 1.74$, $P = 0.087$, Fig 2a). A plot's compositional differentiation against all other plots in terms of Sørensen dissimilarity did thus not change over time. The turnover and nestedness components of compositional differentiation did change, but in opposite directions. The Simpson dissimilarity, which expresses turnover in species composition between a pair of plots, significantly decreased from 0.34 in 1979 to 0.28 in 2009 ($t = 4.00$, $P < 0.001$, Fig. 2b). In effect, going from one plot to another, a smaller number of species is actually replaced by other species. In contrast, the nestedness-resultant dissimilarity, which expresses the difference in species richness derived from nestedness patterns, increased significantly from 0.09 to 0.13 ($t = -3.77$, $P < 0.001$, Fig. 2c), indicating that plots with lower species richness became to a larger extend subsets of the more species rich plots.

The NMDS ordination of plots based on Sørensen dissimilarity indicated clear plot-level directional changes in species composition between 1979 and 2009 (Fig. 3a; PERMANOVA $F = 5.70$, $P < 0.001$). The species turnover between plot pairs was much lower (Fig. 3b; $F = 0.97$, $P = 0.99$), which illustrates the low number of species replacements at the plot level over 30 years. The strong dissimilarities between plot pairs based on βnes (Fig. 3c; $F = 22.42$, $P < 0.001$) similarly express species losses without compensatory species gains in the permanent plots, i.e., the 2009 community composition in a plot is largely a subset of the 1979 community.

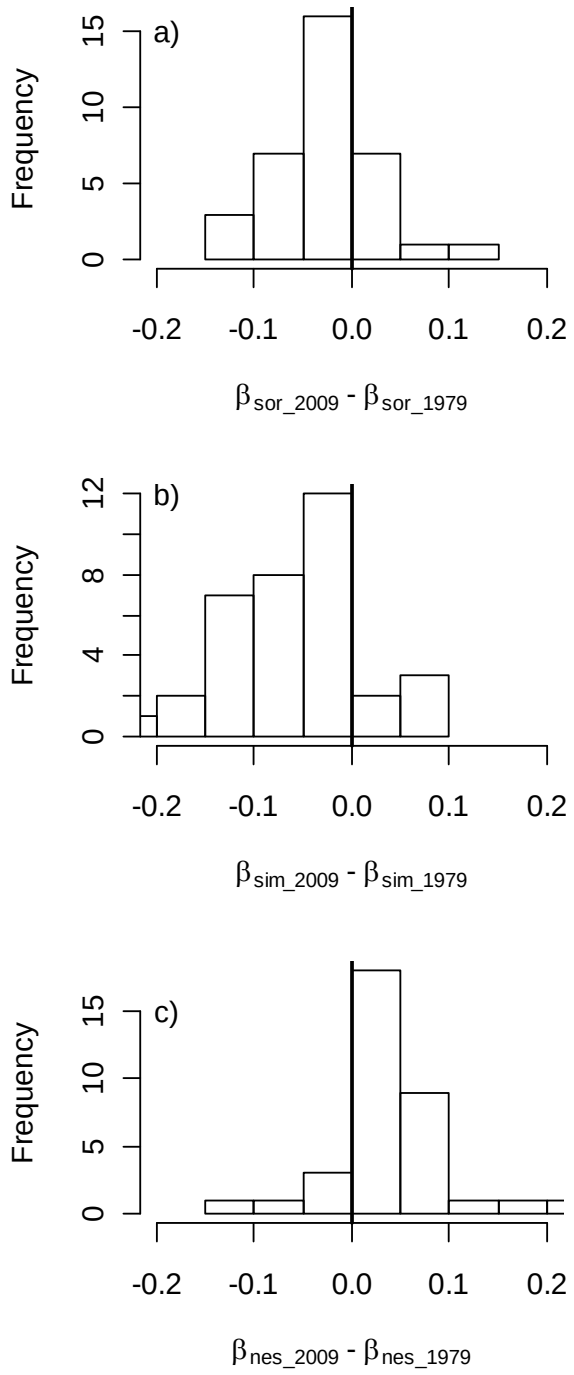


**Fig. 2** Histograms of plot level differences in (a) the mean Sørensen dissimilarity βsor, (b) the mean Simpson dissimilarity βsim, which expresses true species turnover, and (c) the mean nestedness component of the β diversity βnes (see methods for details). Negative values indicate lower values in 2009 compared to 1979.

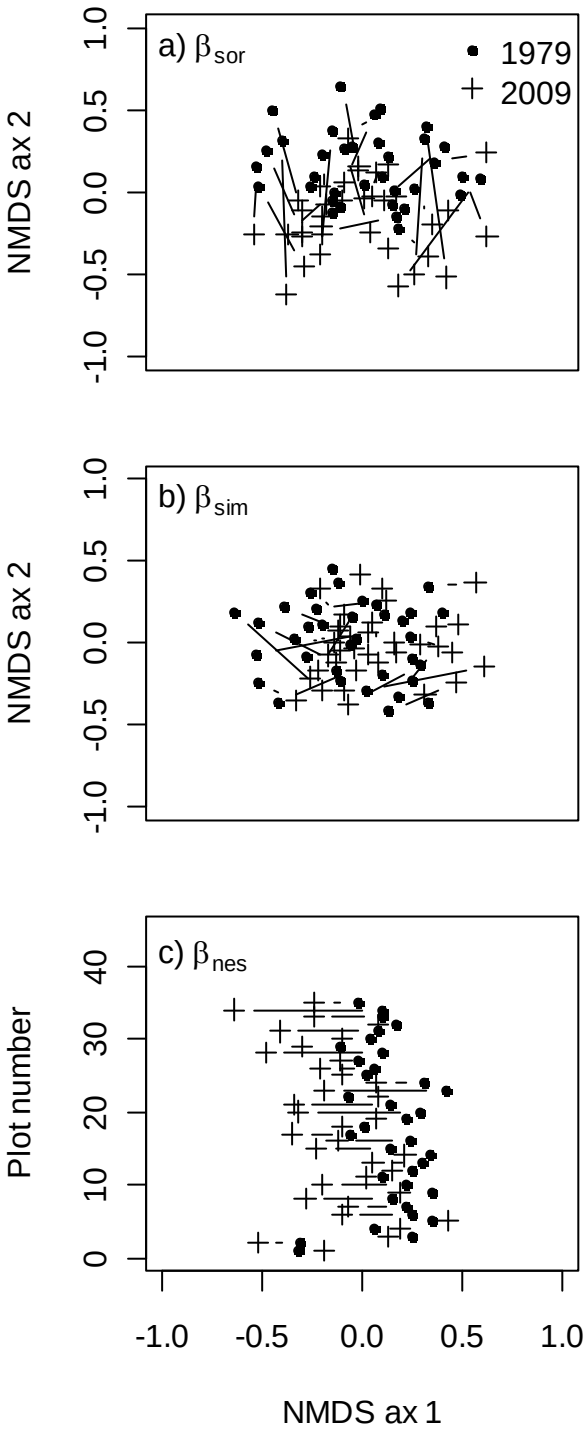


**Fig. 3** Nonmetric multidimensional scaling of the herb layer community composition of the Lady Park Wood permanent plots in 1979 and 2009. The three configurations show plot dissimilarities based on three different indices: βsor, βsim and βnes (see methods for details). Lines connect the two vegetation surveys for each individual permanent plot and visualise temporal plot-level shifts. Because the ordination of the βnes-based dissimilarities was performed in one dimension, the second axis was replaced by a plot number.

**Discussion**

The biotic homogenization of communities has emerged as an important component of the current biodiversity crisis during the past several years. As the study of the causes and consequences of homogenization are so fundamental for conservation (Olden et al. 2004; Clavel et al. 2011), its proper quantification is of more than philosophical importance. The patterns of homogenization determined using dissimilarity measures actually encompass both real species turnover and nestedness (review: Olden 2006; Olden and Rooney 2006). We observed no decrease in the mean Sørensen dissimilarity among plots over three decades of forest understorey vegetation development and so we could have concluded that no taxonomic homogenization has taken place. Yet, the among-community structure did change markedly over time. The vegetation of Lady Park Wood exhibited significant and directional changes over the past three decades, a decrease of the plot-level species richness and a strong reduction of the total species pool. Many species that used to occur in a limited number of plots, i.e., those that contributed much to the compositional differentiation among plots, were lost and were virtually not replaced by other species. In effect, the variation in the species composition from plot to plot shifted towards a structure with reduced true species turnover and larger differences in species richness derived from nested patterns (Fig. 2b, c). We argue that such temporal patterns clearly reflect homogenization, despite the fact that an analysis with a classic dissimilarity index would indicate otherwise.

Olden and Rooney (2006) defined taxonomic homogenization as 'the increase in the taxonomic similarity of two or more biotas over a specified time interval'. In the narrow sense, this refers to the reduction of the true turnover, without the influence of differences in species richness (i.e., α diversity). Here we used Simpson dissimilarity to show that the similarity of understorey vegetation significantly increased over time (cf. Naaf and Wulf 2010). Another possibility to discern whether the community dissimilarity results more from turnover or is rather due to differences in α diversity is to use null models (e.g., Van Calster et al. 2007; Baeten et al. 2010; Chase et al. 2011). Since biotic homogenization often goes together with changes in α diversity, similar measures of community dissimilarity that are not confounded by species richness are particularly suitable for homogenization studies. The βnes index in turn quantifies the relative difference in species richness among sites conditional upon the sites being nested (equation 4), i.e., it does not actually quantify species replacements. The question is therefore whether such metric is appropriate to partly assess homogenization. We argue it does because homogenization principally refers to the processes of local species loss and/or spread of already common species, which potentially create species richness differences and nestedness, and not to the patterns created by these processes and the metrics to quantify them (Olden and Poff 2003; Olden and Rooney 2006).

In addition to the changes in among-plot taxonomic similarities over time, we also determined within-plot shifts using the same indices to further unravel the patterns of vegetation change. The strong directionality of forest herb layer vegetation shifts is consistent with other resurvey studies (Fig. 3a; e.g., Lameire et al. 2000; Taverna et al. 2005; Baeten et al. 2009) and appeared to be mainly driven by species losses resulting in nested patterns rather than real species turnover within a plot. The considerable βnes dissimilarities between plot-pairs showed that the 2009 community was generally nothing more than an impoverished subset of the 1979 vegetation (Fig. 3c). Many of the locally rare species (not frequent in old records) were lost over time while their replacement by other

species was limited. Such findings are relevant for conservation, but, to date, not any other understorey resurvey study has distinguished between these temporal patterns of change.

The potential environmental drivers of understorey vegetation changes in temperate forests are various, and different drivers often occur simultaneously (review Verheyen et al., in press). Previous studies have for instance found clear evidence for the importance of changes in forest management or canopy succession (e.g., Kirby and Thomas 2000; Van Calster et al. 2008; Rogers et al. 2008; Baeten et al. 2009; Keith et al. 2009), changed deer abundances (e.g., Kirby and Thomas 2000; Rooney et al. 2004; Taverna et al. 2005), increased atmospheric deposition of acidifying and eutrophying pollutants (e.g., Lameire et al. 2000; Van Calster et al. 2007; Baeten et al. 2009; Keith et al. 2009) or past habitat loss and fragmentation (e.g., Rogers et al. 2009). For Lady Park Wood, canopy succession and deer (over)abundance are probably the main drivers. Since the last cutting intervention at least six decades ago, the canopy structure and composition shifted significantly (Peterken and Jones 1987, 1989). Tree and shrub inventory data in our vegetation plots showed significant increases in the average basal area (from about 24 $m^2$.ha-1 to 29 $m^2$.ha-1) and an increase in the dominance of later successional, highly shade casting species such as Fagus sylvatica and Tilia cordata. In this way, several light-demanding forest herbs were lost (e.g., Hypericum spp., Epilobium angustifolium) and other shade-tolerant or shade-avoiding species could persist and expand (e.g., Mercurialis perennis, Allium ursinum, Dryopteris filix-mas) (cf. Van Calster et al. 2008; Baeten et al. 2009).

The overabundance of deer and the impact on the vegetation are common in British woodlands (Kirby and Thomas 2000; Kirby 2001) and deer are also an important driver in Lady Park Wood. A population of fallow deer (Dama dama) has profoundly influenced forest regeneration at least since 1945 (Peterken and Jones 1989) and current densities are high enough to prevent any regeneration. Deer exclosures within the reserve, for instance, exhibit a more diverse vegetation that illustrate the impact of deer (Unpublished data). Certain shade-tolerant herbs such as Lamiastrum galeobdolon and Lysimachia nemorum did not persist in our plots, but were found in the exclosures. These species are expected to persist under canopy succession but were nevertheless lost due to grazing. Together, the vegetation changes in this strictly unmanaged forest reserve illustrate that the lack of forest management, in combination with other landscape-level changes such as increased deer populations, may cause the local flora to decline fairly rapidly. Lady Park Wood, itself, is a research reserve, so there is no question of resuming felling there, but in the rest of the Wye Valley woods there is a need to reduce deer populations and maintain regular forest management to favour the herb layer diversity. Of course, other species groups such as epiphytes and saproxylic species may respond differently to the lack of management and their conservation should also be taken into account.

In summary, the environmental changes in Lady Park Wood have reduced the local species richness and the pool of species occurring in the vegetation plots and profoundly restructured the plot to plot variation in species composition. The environmental changes filtered out many of the species that differentiated among plots (e.g., light demanding herbs), leading to lower turnover and increased nestedness where plots which have fewer species became merely a subset of the more species rich plots. Furthermore, in this paper, we illustrated that we should move beyond the simple quantification of homogenization using classical indices and approaches. We therefore strongly advocate that the conceptual development of the homogenization framework should be paralleled

with appropriate ways to quantify the patterns resulting from homogenization. This may be achieved easily, by carefully integrating the various recent progresses made in the β diversity research field.

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**Cited references**

Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117: 1227-1239

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26: 32-46

Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. Ecol Lett 9: 683-693

Anderson MJ, Crist TO, Chase JM, Vellend M et al (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecol Lett 14: 19-28

Baeten L, Bauwens B, De Schrijver A, De Keersmaeker L, Van Calster H, Vandekerkhove K, Roelandt B, Beeckman H, Verheyen K (2009) Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. Appl Veg Sci 12: 187-197

Baeten L, Hermy M, Van Daele S, Verheyen K (2010) Unexpected understorey community development after 30 years in ancient and post-agricultural forests. J Ecol 98: 1447-1453

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecol Biogeogr 19: 134-143

Baselga A, Jimenez-Valverde A, Niccolini G (2007) A multiple-site similarity measure independent of richness. Biol Lett 3: 642-645

Chase J, Kraft N, Smith K, Vellend M, Inouye B (2011) Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2: art24

Clavel J, Julliard R, Devictor V (2011) Worldwide decline of specialist species: towards a global functional homogenization? Front Ecol Environ 9: 222–228

Keith S, Newton A, Morecroft MD, Bealey CE, Bullock JM (2009) Taxonomic homogenization of woodland plant communities over 70 years. Proc R Soc B 276: 3539-3544

Kirby KJ (2001) The impact of deer on the ground flora of British broadleaved woodland. Forestry 74: 219-229

Kirby KJ, Thomas RC (2000) Changes in the ground flora in Wytham Woods, southern England from 1974 to 1991 - implications for nature conservation. J Veg Sci 11: 871-880

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J Anim Ecol 72: 367-382

Lameire S, Hermy M, Honnay O (2000) Two Decades of Change in the Ground Vegetation of a Mixed Deciduous Forest in an Agricultural Landscape. J Veg Sci 11: 695-704

Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. J Anim Ecol 70: 966–979

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14: 450-453

Naaf T, Wulf M (2010) Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. Biol Conser 143: 848-855

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2010) vegan: Community Ecology Package. R package version 1.17-4

Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. J Biogeogr 33: 2027-2039

Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. Am Nat 162: 442-460

Olden JD, Rooney TP (2006) On defining and quantifying biotic homogenization. Global Ecol Biogeogr 15: 113-120

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch K D (2004) Ecological and evolutionary consequences of biotic homogenization. Trends Ecol Evol 19: 18-24

Peterken GF, Jones EW (1987) 40 Years of Change in Lady-Park-Wood - the Old-Growth Stands. J Ecol 75: 477-512

Peterken GF, Jones EW (1989) 40 Years of Change in Lady-Park-Wood - the Young-Growth Stands. J Ecol 77: 401-429

Peterken GF, Mountford EP (1998) Long-term change in an unmanaged population of wych elm subjected to Dutch elm disease. J Ecol 86: 205-218

R Core Development Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Rogers DA, Rooney TP, Olson D, Waller DM (2008) Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89: 2482-2492

Rogers DA, Rooney TP, Hawbaker TJ, Radeloff VC, Waller DM (2009) Paying the Extinction Debt in Southern Wisconsin Forest Understories. Conser Biol 23: 1497-1506

Rooney T P, Wiegmann SM, Rogers DA, Waller DM (2004) Biotic impoverishment and homogenization in unfragmented forest understory communities. Conser Biol 18:787-798

Simpson GG (1943) Mammals and the nature of continents. Am J Sci 241: 1–31

Taverna K, Peet RK, Phillips LC (2005) Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. J Ecol 93: 202-213

Van Calster H, Baeten L, De Schrijver A, De Keersmaeker L, Rogister JE, Verheyen K, Hermy M (2007) Management driven changes (1967-2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. Forest Ecol Manag 241: 258-271

Van Calster H, Baeten L, Verheyen K, De Keersmaeker L, Dekeyser S, Rogister JE, Hermy M (2008) Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. Forest Ecol Manag 256: 519-528

Vellend M (2001) Do commonly used indices of beta-diversity measure species turnover? J Veg Sci 12: 545-552

Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85: 183-206

Vellend M, Verheyen K, Flinn KM, Jacquemyn H et al (2007) Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. J Ecol 95: 565-573

Verheyen K, Baeten L, De Frenne P, Bernhardt-Römermann M et al. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. J Ecol, in press. doi 10.1111/j.1365-2745.2011.01928.x