**Temporal changes in multiple site community differentiation derived from shift in individual species occurrences**

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**Abstract:**

1. Non-random species losses and gains in local communities change the compositional differentiation between communities over time, which is traditionally quantified with distance-based approaches. Yet, distance metrics summarize the multivariate species data into a univariate index and obscure the species-level patterns of change, which are central to understand the causes and consequences of the community changes.

2. We propose using generalized linear models to quantify species-level effects of time period, sum them up across species to test the consistency of the shifts in individual species occurrences, and provide a general conclusion for the sites about community convergence or divergence. Species fall into four response types, showing how they influence the changes in community differentiation.

3. Simulated data were used to show that, unlike distance metrics, the approach does not confound dispersion and location effects and is not a priori related to changes in local species richness. The exclusion or
Inclusion of joint absences is another key difference between distance metrics and the new GLM-based approach, respectively.

4. Our approach was applied to a data set of 23 forest understorey resurvey studies across Europe and results showed that the outcomes of species gains and losses were decreases as well as increases in community differentiation. Though species occurrences and communities have not changed in a consistent way along continental-scale environmental gradients such as climatic conditions, several species shifted in a similar way across most of the studies in which they occurred.

5. Visualizing species-level changes and testing their significance in a unified framework provides a very intuitive tool for community resurvey studies. The approach explicitly considers the relative roles of species gains and losses, allows identifying the nature of the species involved and illustrates the relationship between changes in local species richness and community differentiation.
Temporal changes in multiple site community differentiation derived from shift in individual species occurrences

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3. Simulated data were used to show that, unlike distance metrics, the approach does not confound dispersion and location effects and is not a priori related to changes in local species richness. The exclusion or inclusion of joint absences is another key difference between distance metrics and the new GLM-based approach, respectively.

4. Our approach was applied to a data set of 23 forest understorey resurvey studies across Europe and results showed that the outcomes of species gains and losses were decreases as well as increases in community differentiation. Though species occurrences and communities have not changed in a consistent way along continental-scale environmental gradients such as climatic conditions, several species shifted in a similar way across most of the studies in which they occurred.

5. Visualizing species-level changes and testing their significance in a unified framework provides a very intuitive tool for community resurvey studies. The approach explicitly considers the relative roles of species gains and losses, allows identifying the nature of the
species involved and illustrates the relationship between changes in local species richness and community differentiation.

**Key words** biodiversity – community composition – biotic homogenization – binomial deviance – dissimilarity – multivariate analysis – meta-analysis – resurvey – forest understorey
Introduction

Global biodiversity has been declining at rates exceeding expectation by far (e.g., Pereira, Navarro, & Martins 2012), which necessarily means local communities have been losing species. It is much less appreciated, however, that the communities that lose species often simultaneously gain others – native and alien species expanding in response to environmental change, though possibly with a time lag (McKinney & Lockwood 1999). As result, although global biodiversity is decreasing, species richness at local scales may either decrease or increase (Sax & Gaines 2003). Predicting the impact of simultaneous species gains and losses on terrestrial ecosystems has currently become a topic of great interest in ecology that requires that we first identify the nature of the species involved (Wardle et al. 2011; Cardinale et al. 2012). Global evidence across taxonomic groups shows that the species gained and lost are often a non-random set from the regional pool (Baiser et al. 2012) and, independent from the impact on the local diversity, the directional interchanges of species may reduce (community convergence) or increase (community divergence) the compositional differentiation between communities over time.

Despite the establishment of an extensive ‘biotic homogenization’ conceptual framework, focussing on the potentially large ecological and evolutionary consequences of changes in community differentiation (Olden et al. 2004; Clavel, Julliard, & Devictor 2010), there has been surprisingly little effort in developing methods to actually quantify those changes. Studies have principally relied on multivariate distance measures, looking at shifts in the average pairwise community dissimilarities between time periods (Olden & Rooney 2006). However, a major disadvantage of distance measures is that they summarize the multivariate species data into univariate dissimilarities. For instance, if the species that show significant changes over time share particular functional response and effect traits, those species-level patterns that are fundamental to understand the potential causes and consequences of the community changes remain concealed.
Most metrics are also confounded by differences in the local species richness between sites (Koleff, Gaston, & Lennon 2003), so disentangling temporal changes in the community differentiation from changes in local richness requires the use of alternative techniques such as null-models (Vellend et al. 2007; Chase et al. 2011). Furthermore, although multivariate species data have typical mean-variance relationships associated with them – as the mean abundance increases the variance also tends to increase – the distance metrics used to analyse those data often assume different mean-variance relationships (Warton, Wright, & Wang 2012). This makes it often difficult to isolate the change in the multivariate dispersion between time periods, which is generally used as a measure of community differentiation (Anderson, Ellingsen, & McArdle 2006; Anderson et al. 2011), from the compositional shifts caused by the changes in species abundances (see Warton, Wright, & Wang 2012 for a schematic overview).

Here we developed a new method that accounts for the deficiencies of the traditional approaches. It builds on simple generalized linear models and their multivariate extensions, following the recommendations of Warton (2011) and Warton et al. (2012). Using community composition data from multiple sites recorded at two points in time, we quantify species-level effects of time period, sum them up across species to test the consistency of the shifts in species occurrences, and provide a general conclusion for the sites about community convergence or divergence. In the next sections we (i) describe the method, with emphasis on particular species response types, (ii) illustrate how it compares to traditional dissimilarity approaches using simulated data, and (iii) provide a case study with a large data set of 23 independent understory vegetation resurveys across semi-natural deciduous forests in Europe (Verheyen et al. 2012). In this case study, we show that the method also allows to test the consistency of species shifts across several data sets, i.e., do forest plants show consistent trends across the European forest landscapes in which they occur.
GLMs to quantify changes in community differentiation

Changes in individual species occurrences: The binomial deviance metric

The rationale of the method is that the community differentiation is quantified in terms of the species data that were originally observed for a group of sites and not based on distance metrics calculated from those data. Working with species presence-absence data, we are interested in whether the predicted probability of presence of each species moved towards zero or one over time, i.e., indicating whether they were lost from many sites or tended to be gained, respectively.

The changes in the compositional differentiation among sites over time can be derived from those species-level patterns, in terms of a multiple site heterogeneity and not for each pair of sites separately (see also next section). For instance, if relatively many species in the species pool became either rare or widespread, the communities assembled from this pool will have a high probability of becoming compositionally very similar.

The building blocks of our analyses are GLMs of the binomial family that are fit to the species data to estimate the probability of presence of each species in a study and survey period. We used the deviance of those models, which is exactly zero when the probability of presence of a species is zero or one (the species is completely absent or omnipresent, respectively) and rises to a maximum when this probability is 0.5 (species presence and absence are equally likely). The binomial deviance is

\[
D_j = -2 \sum_{i=1}^n [y_{ij} \ln(\hat{p}_{ij}) + (1 - y_{ij}) \log(1 - \hat{p}_{ij})]
\]  
(Eq. 1)

with \(n\) the number of sites, \(y_{ij}\) the presence or absence (1 or 0) of a species \(j\) in site \(i\), and \(\hat{p}_{ij}\) the predicted probability of presence of the species in that site. In the case where no explanatory
(environmental) variables are included in the model, the deviance may be rewritten in relation to the overall predicted probability of presence of a species in the data set $\hat{p}_j$:

$$D_j = -2 \left[ \hat{p}_j \log(\hat{p}_j) + (1 - \hat{p}_j) \log(1 - \hat{p}_j) \right] \quad \text{(Eq. 2)}$$

The deviance thus measures the heterogeneity in the species occurrence for each sampling period, i.e., it is low if the species is principally absent or rather occurs in most communities. One could equivalently think of it as Shannon entropy expressing the uncertainty associated with predicting a species’ presence (and absence). For a related approach using the binomial deviance, though as a dissimilarity measure among pairs of sites, see Anderson and Millar (2004). The symmetry in $D$ is very useful because both rare and omnipresent species will have similar (low) $D$ values, in accordance with their similar influence on community similarities. Our approach thus includes joint-absence information (Anderson et al. 2011): a species with a low predicted probability of presence is likely to be jointly absent in a random pair of sites, which we consider to increase community similarity.

For each species $j$, the difference in deviance $\Delta D_j$ between time 2 and time 1, generally an older and more recent community survey, is a measure of its change in heterogeneity of occurrence. Based on the change in deviance, we can identify four species response types (see Fig. 1 for a schematic overview). First, species whose frequencies changed in such a way that $\Delta D_j < 0$ decreased their heterogeneity of occurrence and are referred to as “community-convergence species”. They come in two distinct forms – relatively rare species (found in less than half of the sites) that became more rare between two surveys and prevalent species (found in more than half of the sites) that became more prevalent. For any pair of sites, the species show a higher probability of being jointly absent (for the rare species) or jointly present (prevalent species) in a recent compared to the older survey. “community-divergence species”, are those whose frequencies changed so that $\Delta D_j > 0$. They also
came in two forms – rare species that became less rare, and prevalent species that became less prevalent. Their predicted probability of presence shifted towards 0.5, increasing the chance of finding the species in only one plot in any pair of plots (i.e., increasing community differentiation).

The significance of the change in deviance can be tested with a permutation test, where sampling period labels are permuted within sites before calculating a $\Delta D_{\text{random}}$. Under the null hypothesis of no change in deviance, the species presence data are equally heterogeneous in each time period, and, hence, we can choose the time ordering of the two surveys of each site at random. The significance ($P$-value) of $\Delta D_j$ was calculated as the proportion of the permutations with an absolute change in deviance equal or larger than the observed absolute change (absolute values to test two-sided), hence comparing $|\Delta D_{\text{random}}| \geq |\Delta D_j|$. This test results in a list of significant community-convergence and convergence species. All analyses in this paper were done in R 2.15.2 and graphs were made using ggplot2 (Wickham 2009; R Core Team 2012). The function bDEV.test is provided in the Supplementary Material (Appendix S4).

**SUMMARIZE SPECIES-LEVEL EFFECTS TO ASSESS COMMUNITY DIFFERENTIATION**

To go from species-level changes in occurrence to the change in multiple site compositional heterogeneity, we need to test whether there is a consistent trend of change in prevalence across all the species. The species-level test statistics $\Delta D_j$ are either positive or negative, so their sum indicates a consistent change if it strongly deviates from zero ($\Sigma \Delta D_j = \Delta D_{\text{sum}}$) – a similar permutation test can be used to test its significance (cf. the “sum-of-likelihood-ratio” test approach; Warton, 2011; Warton et al., 2012). Hence, the test statistic is a multiple site measure of community convergence ($\Delta D_{\text{sum}} < 0$) or divergence ($\Delta D_{\text{sum}} > 0$) in a typical resurvey study – much like a classic approach uses the mean dissimilarity of a site against all other sites in a time period 1 and 2,
calculates the mean difference of this dissimilarity between time 2 and 1 across sites and tests its significance with a paired test.

In essence, the summed change in deviance quantifies the balance between the number (and the strength of their change) of community-convergence versus community-divergence species that are present across the sites. The idea of developing different scenarios by which the balance between species gains and losses can lead to various trajectories of change in community similarities somewhat resembles the distance-based approach proposed by Olden and Poff (2003). For example, when $\Delta D_{\text{sum}}$ is significantly below zero, the majority of the species are community-convergence species showing a consistent pattern of change in frequency: rare becoming more rare and prevalent becoming more prevalent. So, we look for species-level effects and sum them across species to arrive at a single global conclusion across all species about trends for community convergence or divergence. Referring back to Fig. 1, if the species show a consistent departure from the x=y line, with most species falling in the red areas, the heterogeneity of occurrence generally decreases – for instance, rare species that decrease or become locally extinct between two surveys and frequent species that become omnipresent. The compositional similarity between any two arbitrary communities in the pool of sites then increases as well because of the higher probability that they share the very frequent species while both lacking the increasingly rare ones. The multiple site community differentiation thus decreases.

**Comparison with a traditional dissimilarity approach**

While a multiple site dissimilarity is most appropriate to quantify the compositional heterogeneity among a group of sites in a distance-based framework (Baselga 2013), the traditional approach in biotic homogenization literature is based on the average of simple inter-site dissimilarities using one out of several distance measures (‘variation beta diversity’; Anderson et al. 2011). Here we
used the Jaccard dissimilarity, which has been widely used in this context (Table 1 in Olden and Rooney 2006). For a particular site, the mean of the pairwise dissimilarities against all other sites measures that site’s compositional differentiation. The change in mean Jaccard dissimilarity between the time periods (Δjaccard; new survey – old survey) is a measure of the degree of taxonomic homogenization (Olden and Rooney 2006). To compare such traditional approach with our method, we simulated different scenarios of temporal change, each time generating communities for 50 sites with a total species pool of 110 species, i.e., roughly the mean number of plots and mean number of species observed across the 23 studies of the next section’s case study.

Data were generated under the hypothesis of temporal nestedness – there was no change in the community composition over time, the only difference is in overall prevalence (a full description is in Appendix S1).

In a first scenario, relatively rare species became more rare between two surveys, i.e., there were more community-convergence species than divergence species, so the ΔD_{sum} decreased and we conclude community differentiation decreased (Fig. 2a). The mean Jaccard dissimilarity, however, increased and suggests that community divergence prevails. The problem with the Jaccard index is that the metric is biased in two important ways. First, since the total richness of a pair of sites forms the denominator of Jaccard, sites will appear more differentiated if richness decreases. Lots of species were lost from the sites in which they previously occurred under this scenario and the increased Jaccard dissimilarity largely expresses a decrease in local richness (Appendix S1). The influence of species richness is increasingly considered an important disadvantage for biotic homogenization studies (Vellend et al. 2007; Van Calster et al. 2008; Baeten et al. 2012). Second, if the multivariate dispersion is used as a measure of the compositional heterogeneity between sites, it is critical to use a dissimilarity measure that assumes the correct intrinsic mean-variance relationship of the data (Anderson et al. 2006; Warton et al. 2012). Otherwise, the metric confounds
location and dispersion effects, illustrated by the incorrect compositional shift over time in the
NMDS plots (Fig. 2a and c).

The second scenario assumes that many initially low frequency species could expand and occurred
in considerably more sites in the second survey (Fig. 2b). Since their heterogeneity of occurrence
increased – i.e., the probability a species will be only present in one out of two random sites
increased – the summed change in deviance was strongly positive. The decrease in Jaccard would
suggest, on the other hand, community convergence because it quantifies at least partly the
increase in local richness. Only in the third scenario, we arrive at a similar conclusion with the
Jaccard and the deviance approach. Community differentiation increased because a lot of
prevalent species became less prevalent. A prevalent species has a high homogeneity of occurrence
(it is relatively easy to predict its presence) and, if it disappears from many sites, joint presences of
the species become less likely and cause community divergence.

To conclude, the Jaccard index is always biased by the changes in local richness in the same way. If
there are more species that disappear from many sites than species that expand, mean local
richness goes down and sites will appear more differentiated. There is, however, no *a priori*
relation between the deviance metric and the change in local richness: positive, negative as well as
no relationships are possible and depend on the overall prevalence of the species involved.
Communities may for instance become more similar because either joint absences or joint
presences become more common: the differentiation would decrease in both scenarios, but the
species richness would decrease in the former and increase in the latter.
Changes in forest understorey community differentiation across Europe

SELECTED DATASETS

To illustrate the approach, we used the data of 23 independent forest understorey resurvey studies collected in semi-natural deciduous temperate forests across Europe: from Switzerland to mid Sweden (South-North) and from the United Kingdom to the Czech Republic (West-East) (Table S2). All vascular plant species in the understorey layer (<1 m plant height, incl. woody saplings) were recorded using permanent and semi-permanent plots at two time periods. The intercensus intervals were at least ca. two decades (median 31 years, range 17-67 years). The first surveys were carried out between 1935 and 1989 and the recent surveys between 1987 and 2009. The mean number of plots per study was 52 (range 17-139; total 1197 plots) and plot sizes ranged between 1 m² – 1000 m². A total of 640 different herb layer species were recorded (mean number of species per study = 110 ± 11 SE) and species occurred on average in 4.0 different studies (SE ± 0.17). All plots were in ancient forest sites (*sensu* Peterken 1996), i.e., sites that had been continuously forested at least since the oldest available land-use maps (usually minimum 200 years). No forest stand replacement had taken place between the surveys (e.g., no clear cutting and replanting). Generally, forest management had become less intensive over the past decades: all sites were either unmanaged or experienced only low intensity thinning at low frequency in the most recent survey period. More detailed information on the study selection, study sites descriptions and decadal changes in local species richness and species composition can be found in Verheyen et al. (2012).

META-ANALYSIS OF CHANGES IN DIFFERENTIATION

We calculated and tested the significance of ΔD_total for each individual study, summarizing the species-level effects for that study. A correction for multiple comparisons was required since the
same hypothesis of no change is tested repeatedly: the classical one-stage method to calculate False  
Discovery Rate (FDR) adjusted $P$-values was used based on a threshold value $q = 0.05$, i.e., the error  
rate in the set of comparisons that are called significant (Pike 2011). The summed deviance  
decreased significantly for eight studies (FDR-adjusted $P < 0.05$; Fig. 3), indicating community  
convergence, i.e., the number of community-convergence species strongly exceeded the number of  
divergence species. The community-convergence species were mainly the rare species that became  
more rare (or went locally extinct), not prevalent species that became more prevalent (Appendix  
2). In five studies, community differentiation increased because many initially rare species  
increased between surveys. For the remaining ten studies, the number of community-convergence  
and -divergence species was similar and many species did not change their frequency much. This  
result challenges the general notion in the literature that deceases in community differentiation  
would be the default outcome of contemporary species gains and losses (Olden 2006; Baiser  
2012). Some of the forest understorey resurvey studies have explicitly determined within-study  
variation of the changes in differentiation, and, also at that scale, variable outcomes are being  
reported depending on the nature of the local environmental changes such as different alterations  
of the forest management (Van Calster et al. 2008; Rogers et al. 2008).

The changes in community differentiation were clearly paralleled by changes in local species  
richness (Fig. 3b): studies for which local species richness decreased were also the studies  
experiencing a reduction in community differentiation. As shown in the simulations, such relation  
reflects the nature of the species gains and losses in the studied vegetation: the predominant loss of  
many relatively rare species caused local species richness to decrease and forest understorey  
communities to become more similar. If these losses would have been counterbalanced by several  
prevalent species that expanded further, the differentiation would still decrease but local species  
richness would not change much. No obvious spatial patterns of community convergence or
divergence emerged, illustrating that the species occurrences and communities have not changed in a consistent way along gradients in climatic conditions (temperature, precipitation) and nitrogen deposition rates over the past decades (non-significant correlations with those environmental variables; Appendix S2). Local factors such as changes in management, susceptibility of the soil to acidification or desiccation, altered grazing pressure or pest outbreaks are predicted to be much more important (Lameire, Hermy, & Honnay 2000; Rooney et al. 2004; von Oheimb & Brunet 2007; Van Calster et al. 2008; Rogers et al. 2008; Dierschke 2009; Baeten et al. 2012), or at least they obscure the large-scale patterns of change (Verheyen et al. 2012). This would explain why studies that are only hundred kilometres away showed contrasting patterns of change.

A TEST OF SPECIES-LEVEL SHIFTS ACROSS STUDIES

Just like we looked for species-level effects and summed them across species to come to a study-level conclusion, we also looked at study-level effects and summed them up to test the consistency of the species-level shifts across the studies. A binomial model was fitted again, but now using the species occurrence data pooled across the studies (in which the species occurred at least in one plot, so excluding all studies in which it never occurred) and with a study indicator as a predictor variable (so the deviance calculated as in Eq. 1). In R terms: \( y_{ijk} \sim \text{study}_k, \text{family}="\text{binomial}" \), with \( y_{ijk} \) the presence/absence of species \( j \) in plot \( i \) of study \( k \). By including a predictor variable in our approach, this analysis illustrates the generality of our approach, which can be extended to other environmental predictors. Again, the difference in deviance was the test statistic (\( \Delta D_{\text{species}} \)), the significance was assessed by permuting sampling period labels within sites (2000 permutations) and the P-values were FDR adjusted because multiple species were tested. Only species occurring in at least three studies were modelled. The interpretation is analogous to the study-level analysis with negative and positive changes in deviance for community-convergence and -divergence.
For example, a species that occurred in several studies with a low frequency, but became consistently more rare over time in most of those studies is an overall community-convergence species. The results for four species that were selected to illustrate contrasting patterns of change are provided in Fig. 4; a full list of significant species in Appendix S3. For example, the estimated change in deviance for *Ajuga reptans* across the 19 studies in which the species occurred was very negative, hence it is an overall community-convergence species in the meta-dataset. The species decreased its frequency in 14 studies, while it increased in only two, so *A. reptans* is a typical rare species that became more rare between surveys (consistent departure from the x=y line; Fig. 4).

**Discussion**

A solid theoretical framework describing the causes and consequences of temporal changes in community differentiation has rapidly emerged during the past two decades (McKinney & Lockwood 1999; Olden et al. 2004; Clavel et al. 2010), but methods to actually quantify the nature and strength of the underlying non-random species interchanges are scarce (cf. Olden & Rooney 2006). Although the biotic homogenization framework emphasises the potentially large ecological and evolutionary consequences of ‘few winners replacing many losers’ (McKinney and Lockwood 1999), the relative importance of local species gains versus losses often remains poorly explored (Olden 2006, Wardle et al. 2011). Indirect estimations are common in the literature, with several resurvey studies quantifying the species (groups) that increased or decreased over time and relating the changes in differentiation to those patterns (e.g., Rooney et al. 2004; Rogers et al. 2008; Naaf & Wulf 2010). Therefore, we developed a method that quantifies the changes in community differentiation directly from the changes in individual species occurrences, balancing four species response types: community-convergence and community-divergence species that are rare or prevalent.
While community-convergence and -divergence species do not necessarily fall within the traditional winners and losers categories, respectively, the groups may largely overlap. Species usually have a low relatively frequency of occurrence among a group of sites in nature, only few are omnipresent, and the losses and gains of such locally rare species correspond to convergence and divergence. If losses predominate, the potential ecological consequences strongly depend on whether the species that are lost represent unique trait states for particular traits compared to the complete collection of traits in the community (Olden et al. 2004; Clavel et al. 2010). Likewise, increases in differentiation and local richness would only have ecosystem effects if the expanding species also add complementary traits to the extant community. Such predictions can be easily explored within our framework, e.g., by relating trait values to our species-level test statistic (ΔDj), with or without accounting for phylogenetic relatedness, and forms an important direction for future research.

The compositional heterogeneity between sites is derived from species replacement (turnover) and species loss or gain (creating patterns of nestedness) from one site to another. Additive partitioning methods have been developed relatively recently (Baselga 2010; Carvalho et al. 2013) and applied in few biotic homogenization studies to show whether changes in community differentiation were mainly caused by either changes in species turnover or richness differences between plot pairs (Baeten et al. 2012; Baiser et al. 2012). In our approach, the underlying shifts in community structure can be inferred otherwise, by comparing trends (increases, decreases) in community differentiation and local species richness simultaneously. Communities may become more similar because either joint absences or joint presences become more common, both of which have different ecological consequences. Our deviance measure would decreased in both scenarios, but the local species richness would decrease in the former and increase in the latter. Many pairwise distance indices such as Jaccard just exclude joint-absence information: joint presences
decrease the differentiation among communities, joint absences not. Ignoring double-zeros is indeed relevant for pairwise metrics because the similarity of two sites should not increase because of the joint absence of some arbitrary species – e.g., the joint absence of a tropical tree seedling in our European forest understorey resurvey plots. However, in our multiple site approach, we only analyse the species that occurred at least in one site or, in case of the species-level shifts across studies, only include the studies in which the species occurred at least once. So, if a species was absent from all sites at both sampling times this would have no effect on the differentiation (the species is simply not modelled or the study is not included), and we believe this ignoring of such ‘complete absences’ is a more relevant criterion than completely ignoring joint absences. In sum, we consider joint-absence information to be relevant in our context because we are specifically interested in the losses of species (Anderson et al. 2011).

To conclude, we applied a novel approach to analyse changes in the compositional differentiation of communities over time that addresses several challenges and research needs in biotic homogenization literature reviewed by Olden (2006): it provides a unified framework to quantify changes in community differentiation across studies, it determines the relative roles of species gains and losses and it improves our understanding of the relationship between changes in species richness and community differentiation over time by looking at species-level patterns of change. One of the future directions is to integrate this approach into the analysis of the ecological consequences of the observed temporal community dynamics. In their recent review on biodiversity-ecosystem functioning research, Cardinale et al. (2012) stated that predicting the ecosystem consequences of simultaneous species gains and losses requires that we understand which traits predispose species to a higher chance of local extinction or establishment (response traits) and how those traits covary with traits that influence ecosystem functioning (effect traits) (Suding et al. 2008; Wardle et al. 2011). Such analyses rely, however, on the development of
techniques that first analyse the species-level data and identify the winners and loser species involved (Gosselin 2012). Our approach offers such technique and may provide a crucial step preceding further trait-based analyses.

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References


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Fig. 1 (a) Schematic overview of the relation between the ‘deviance’ test statistic and the relative frequency of a species in a survey. The arrows show the changes in deviance for different scenario’s in which a species \( j \) with initial frequency \( P_j = 0.2 \) increases or decreases between two surveys. (b) Changes in the relative frequency of occurrence of a species over time. Each point represents a species for which the change in frequency corresponds to one of the scenario’s in (a), indicated with numbers. A species falling in an orange area is a community-convergence species – its relative frequency shifted to 0 or 1 so that its heterogeneity of occurrence decreased; such species follow a trajectory of decreasing deviance. The species in a green area are community-divergence species. Their relative frequency shifts towards 0.5 and their deviance increases.
Fig. 2 Simulated temporal changes in the occurrence of 110 species in 50 sites. Data were generated under the hypothesis of temporal nestedness – there was no change in composition over time. Top row: the relative frequency of occurrence of each species in a first and second survey. Bottom row: NMDS plots (Jaccard dissimilarities). (a) Scenario with most species occurring in < 50% of the sites and many species becoming more rare. Note that the NMDS suggests a location effect, while there is actually only a dispersion effect. (b) Many species increased their frequency across sites. Jaccard suggests decreased differentiation, illustrated by the lower dispersion of the sites in survey 2 in the NMDS plot. (c) Many species with a frequency > 50%, but frequencies generally decreased over time. Note that the Jaccard and deviance approach lead to a similar conclusion about the change in community differentiation here.
**Fig. 3** Changes in community differentiation among 23 independent forest understorey resurvey studies in Europe. (a) Spatial distribution of the 23 studies, with symbols indicating community divergence (black circles), convergence (white circles) or not change (grey circles). (b) Relationship between the study-level mean change in species richness – expressed as a log ratio $\ln(SR_{\text{new}}/SR_{\text{old}}) \pm 2SE$ – and the mean change in deviance of the study ($\Delta D_{\text{sum}}$/number of species in study). Toponyms and country codes in (a): 1: Gaume (BE); 2: Binnen-Vlaanderen (BE); 3: Zoerselbos (BE); 4: Herenbossen (BE); 5: Vorte Bossen (BE); 6: Meerdaalwoud (BE); 7: Florenne (BE); 8: Tournibus (BE); 9: Dalby (SE); 10: Tullgarn (SE); 11: Elbe-Weser (DE); 12: Děvín (CZ); 13: Milovice Wood (CZ); 14: Rychlebské hory Mts. (CZ); 15: Wytham Woods (GB); 16: Göttingen (DE); 17: Miličovský les (CZ); 18: Switzerland (CH); 19: Hirson/Saint-Michel (FR); 20: Andigny (FR); 21: Speulderbos (NL); 22: Lady Park (GB); 23: München (DE)
Fig. 4 Relative frequency changes of four understorey species between the old and recent vegetation surveys of the studies in which they occurred. The species were selected to illustrate contrasting patterns of change. 

*Ajuga reptans:* a typical community-convergence species that generally decreased in frequency ($\Delta D_{\text{species}} = -300$, FDR-adjusted $P < 0.01$, $N$ studies = 19). *Dryopteris carthusiana:* community-divergence species that generally increased where it was initially not very frequent ($\Delta D_{\text{species}} = 150$, adj. $P < 0.01$, $N$ studies = 17). *Mercurialis perennis:* community-divergence species through a decrease in some studies where it was initially quite frequent ($\Delta D_{\text{species}} = 116$, adj. $P < 0.01$, $N$ studies = 14). *Pteridium aquilinum:* species frequency did not change much, it is scattered around the diagonal indicating no change ($\Delta D_{\text{species}} = -1$, adj. $P = 1$, $N$ studies = 14).
Supporting information

Appendix S1 Methodology for simulations

Appendix S2 Forest understorey data sets and study-level patterns of change

Appendix S3 Species-level changes across studies

Appendix S4 R function ‘bDEV.test.R’