



Measuring community responses to large-scale disturbance in conservation biogeography

Vincent Devictor*† and Alexandre Robert

UMR 5173 MNHN-CNRS-P6 'Conservation des espèces, restauration et suivi des populations', Muséum National d'Histoire Naturelle, 55 rue Buffon, CP 51, 75005 Paris, France

ABSTRACT

Aim Which community metrics should be used to reflect community response to large-scale habitat alterations is unclear. Here, we assess what and how community changes should be measured to accurately track community responses to large-scale disturbance in space and/or time.

Location France.

Method We first developed a simulation model to examine temporal changes in the species composition of large-scale metacommunities. Using this model, we assessed how species richness, Shannon index, trends of particular subset of species or community indices of habitat specialization were influenced by different disturbance scenarios, and whether these indices were biased by imperfect detectability. We further used more than 1000 empirical bird communities from the French Breeding Bird Survey recently exposed to disturbances of various intensities as a case study.

Results Our simulation and empirical results both demonstrate that species richness and diversity measures can show confusing trends and even provide misleading messages of communities' fate. In contrast, reflecting the composition of the community in terms of habitat specialist and generalist species was more robust and powerful to reflect disturbance effects.

Main conclusions We highlight the weakness of using community metrics that fail to incorporate ecological difference among species when summarizing community-level trends in disturbed landscapes.

Keywords

Breeding Bird Survey, biotic homogenization, detectability, disturbance, diversity indices, specialist–generalist.

*Correspondence: Vincent Devictor, UMR 5173 MNHN-CNRS-P6 'Conservation des espèces, restauration et suivi des populations', Muséum National d'Histoire Naturelle, 55 rue Buffon, CP 51, 75005 Paris, France.

E-mail: devictor@mnhn.fr

†Present address: Université Montpellier II, ISEM UMR 5554, Place E. Bataillon, 34095 Montpellier, Cedex 05, France

INTRODUCTION

Measuring whether and how communities differ in species composition and diversity is crucial for predicting the consequences of habitat loss and environmental degradation in conservation biogeography (Whittaker *et al.*, 2005). In this respect, numerous recent studies have stressed the need to focus on other aspects than changes in species richness or diversity indices (McGill *et al.*, 2006). Indeed, an index that solely aggregates information about richness, relative abundance and/or taxonomic distinctiveness is generally silent on the ability of each particular species to thrive in degraded landscapes (Weikard *et al.*, 2006).

Moreover, while numerous studies have focused on data availability and indicators' computation, theoretical aspects of

what ecological processes are reflected by widely used community metrics in conservation biogeography have yet to be explored. For instance, predictions about how species richness is expected to increase or decrease following fragmentation and disturbance often differ according to the time-scale and the habitat considered (Helm *et al.*, 2006; Kimbro & Grosholz, 2006). Other measures of diversity such as Shannon's diversity index are widely used but were early shown to be misleading in many cases, to the point of being considered a non-concept (Hurlbert, 1971). In fact, most indices based on information theory, although the most commonly used diversity indices, were also often considered to be unsatisfactory due to their lack of biological relevance (Washington, 2003).

In this context, accounting for more ecological difference among species should be straightforward to track community

response to land-use change. In particular, ordering species along a generalist/specialist gradient could be useful (Julliard *et al.*, 2006). Indeed, niche-breadth differences among species are the result of an evolutionary trade-off between the ability of species to exploit a range of resources and their capacity to use each one. Moreover, these strategies are expected to be unequal in variable environments: specialist species are expected to be more at risk when environment is disturbed in space and/or time (Levins, 1968; Kassen, 2002; Marvier *et al.*, 2004).

Using niche breadth (i.e. a measure of species specialization) was also shown to be a valuable predictor of species responses to habitat alteration (Warren *et al.*, 2001; Swihart *et al.*, 2003; Swihart *et al.*, 2006; Devictor *et al.*, 2008a). Finally, the decline of specialist species is occurring worldwide (Olden *et al.*, 2004) and likely results in functionally homogenized communities that are increasingly composed of generalist species (McKinney & Lockwood, 1999; Smart *et al.*, 2006). However, evidences linking anthropogenic disturbance and change in community composition in terms of specialist versus generalist species are still missing at large scale.

Beyond the considerations of what and how species should be considered when measuring community changes, the examination of major field constraints has also been overlooked in theoretical development of community indices. In practice, an important methodological concern has been emphasized when using field data of animal or plant surveys, the so-called heterogeneity of species detection. Indeed, surveys generally do not allow detecting all individuals of a given species, which can induce biases in parameter estimations either at population (Royle *et al.*, 2005), or at community level (Boulinier *et al.*, 1998).

In this paper, we use a metacommunity model to assess the link between several aspects of community (species richness, Shannon index, multispecies trends and ecological composition) and habitat disturbance. We addressed two main objectives: (1) assessing the ability of community metrics to detect an effect of habitat disturbance and (2) testing the robustness of community metrics to heterogeneity in species detection. To assess the usefulness of a given index to serve as an indicator of external forces, we also paid particular attention to the simplicity with which an observed change in the given index can be explained by the external disturbance. We illustrate our general findings with an empirical case study of bird community changes in disturbed landscapes, using the French Breeding Bird Survey.

METHODS

Model structure

We developed a stochastic species-based model including three levels: population, community and metacommunity. The biological system modelled (large-scale metacommunity) and the model outputs (see below) were designed to allow comparison between model projections and results obtained from biodiversity surveys such as a regional or national survey of a particular group. Such surveys are widely used in many countries for different taxonomic groups and were also shown to be a

major source of good quality data in conservation biogeography (Brotans *et al.*, 2007).

Each community was considered as a discrete patch occupied by individuals of different species from a limited regional pool made of 100 potential species. We assumed that habitat characteristics varied among patches (each patch was characterized by a given value along a habitat gradient) and that each patch faced a given disturbance level (i.e. temporal change in habitat). Communities were assumed to be distributed over a large area (i.e. size of a country), and each patch represented only a small proportion of the overall habitat of the region. Patches were assumed to be surrounded by an external matrix of habitat, which was not explicitly modelled. The probability of colonization events for each species was assumed proportional to its representation in the whole community. In other words, patches were not directly connected to each other (mainland-island type model).

In a given patch, all species were assumed to be in competition with each other. The relative competitive ability of each species in a given habitat depended on its growth rate in this habitat. The model was developed to make a distinction between habitat generalist species (having a high rate of increase over a wide range of habitat), and habitat specialist species.

More precisely, the ecological system considered was modelled using a 100×200 matrix ($M_{(t)}$) representing the population size of each species i in each patch j at time t (100 distinct species distributed in 200 discrete patches). The transition $M_{(t)} \rightarrow M_{(t+1)}$ depended on the interactions between patch and species characteristics in each time step. Each species i was characterized by four variables (which were constant in time): first, its intrinsic basic replacement rate r_{i0} (corresponding to the replacement rate of the species in its optimal habitat, in the absence of regulation or competitive interaction). This rate was defined by $N_{i(t+1)} = r_{i0} N_{i(t)}$, $N_{i(t)}$ being the species abundance at time t . Second, each species had a preferential habitat, $Hopt_i$ (continuous number) in which the local population growth of the species was optimal. Third, a specific trait I_i was attributed to each species to reflect its level of habitat specialization (this measure can also be considered as a measure of niche width). Finally, we considered that species were not equally detectable. Instead, each species had an intrinsic individual probability of detection p_i . This parameter corresponded to the probability of detecting an individual of the species i in a particular site, given that this individual was present at that site. All of the four parameters (r , H , I and p) were assumed independent from each other.

Each patch j was characterized by three variables: its carrying capacity K_j (constant through time), a parameter describing the habitat of the patch at time t , $H_{j(t)}$ (continuous number) and a parameter reflecting environmental disturbance D_j of the patch (i.e. the magnitude of change in H_j between t and $t + 1$).

Initialization of patch and species characteristics

Initially, all 100 species were present and equally distributed in each community (i.e. the population size of each species i in community j was equal to $N_{ij(0)} = K_j/100$). The intrinsic basic replacement rate r_{i0} was initialized for each species by drawing r_{i0}

from a normal distribution of mean r_0 and standard deviation sd_{r_0} . Similarly, the specialization level I_i for species i was initialized by drawing I_i from a beta distribution with mean I and standard deviation sd_I . The optimal habitat of each species $Hopt_i$ was drawn from a uniform distribution $[0, 1]$. The individual probability of detection p_i of species i was drawn from a beta distribution with expectation p and standard deviation sd_p .

The initial habitat type of each patch j (i.e. at time zero), $H_{j(0)}$ was drawn from a uniform distribution $[0, 1]$. Finally, the carrying capacity K_j of each patch j was initially drawn from a Poisson distribution of expectation K . The temporal pattern of disturbance distributed in each community across the whole metacommunity was modelled with D taken as the average level of disturbance (magnitude of habitat change between t and $t + 1$), and with sd_D which quantified the heterogeneity of disturbance among communities. At time zero, for each community, D_j was drawn from a normal distribution $N(D, sd_D)$.

Dynamics of patch habitats and intrapatch species dynamics

The global metacommunity dynamics (i.e. transition between $M_{(t)}$ and $M_{(t+1)}$) was determined by the following processes (in order of occurrence): disturbance in each patch (re)colonization of communities through dispersal, local growth of species in each community and local community regulation.

Habitat disturbance in each patch j was modelled by the variation in habitat characteristics (H_j) between t and $t + 1$. The magnitude of this variation could vary among patches (the parameter D_j was specific to each patch). In each time step, the new habitat parameter of patch j ($H_{j(t)}$) was drawn from a beta distribution with expectation $H_{j(t-1)}$ and standard deviation D_j .

The probability of local colonization of a given species was assumed to be proportional to its representation in the whole metacommunity and was thus given by $C_{ij(t)} = C(v_{i(t)}/v_{(t)})$; where C was a fixed average annual colonization probability, $v_{i(t)}$ the rate of local presence of species i in the metacommunity at time t (i.e. the proportion of communities where species i was present) and $v_{(t)}$ the average rate of local presence of all species in the metacommunity at time t . For each species, a colonization event occurred or not, according to this probability $C_{ij(t)}$ (Bernoulli trial). If colonization occurred, the number of immigrant individuals of each locally arriving species to each patch $IMM_{ij(t)}$ was determined by a Poisson drawing of expectation N_{col} (fixed to 10 in all presented results).

We considered that the local growth rate of each species was maximal in its optimal habitat $Hopt_i$, and that the reduction of the local growth rate of a species in suboptimal habitat was proportional to the absolute difference between $Hopt_i$ and the local habitat type H_j . This reduction was assumed to be inversely proportional to the specialization index of the species I . Therefore, the effective annual replacement rate of each species i within a patch j at time t was defined by the simple linear relationship: $r_{ij}(t) = r_{i0}[1 - I_i |Hopt_i - H_{j(t)}|]$. The expectation of the local abundance of a given species (before regulation) was thus computed as: $N_{ij(t+1)} = r_{ij(t)}(N_{ij(t)} + IMM_{ij(t)})$.

Note that we considered no active habitat selection during the migration process: the probability that species i would disperse to patch j did not depend on the suitability of the patch for species i . However, ability of a given species to grow and persist in a given habitat depended on habitat suitability for the species ($|Hopt_i - H_{j(t)}|$). Thus, the probability of successful colonization given migration of species i in habitat j depended on habitat suitability. This approach was chosen for its simplicity and its generality (the general model used can be applied to species with active movement that are not able to use cues indicative of suitable habitat, or even to species with passive movement). Moreover, accounting for habitat suitability for species during the migration process (i.e. making C_{ij} a function of habitat suitability for species i , $C_{ij(t)} = C(v_{i(t)}/v_{(t)})/(|Hopt_i - H_{j(t)}|)$) did not change the results.

Finally, in each community j , the overall number of individuals was limited by the local carrying capacity of the patch. We assumed that each patch j had a carrying capacity K_j and that the different species were in competition for resources. At time t , the expectation of local abundance of each species i in patch j after regulation was therefore computed as:

$$N'_{ij(t)} = \text{Min} \left(N_{ij(t)}, cK_j, \frac{K_j N_{ij(t)}}{\text{Max} \left(K_j, \sum_{k=1}^Q N_{kj(t)} \right)} \right)$$

with Q being the number of species in community j , and c a coefficient that quantified the amount of competition among species (assumed identical for all species). When $c = 1$, competition was maximal (i.e. competition between species equals competition within species). In contrast, when $c < 1/Q$, no interspecific competition occurred. The realized local abundance was then given by a Poisson drawing of parameter $N'_{ij(t)}$.

Model outputs

We first considered species richness (Q) (i.e. the number of species in a given community), and the Shannon–Wiener index (W), measuring how well abundance was distributed among species within a community. This index (W) was computed at the community level as:

$$W_j = - \sum_{i=1}^{Q_j} \alpha_i \ln(\alpha_i)$$

where α_i was the proportional abundance of species i and Q_j the species richness of the community j .

Second, we used an index based on multispecies population temporal trend widely used in national and supranational biodiversity assessment programs (e.g. farmland birds indicator, Gregory *et al.*, 2005). The values of such trends are calculated assuming a reference value of 100 at time $t = 0$. We computed such index based on each species' abundance in each community each year:

$$T_{ij}(t) = \frac{N_{ij}(t)}{N_{ij}(0)} * 100$$

We further focused either on the average trend of all species (T), the average trend of the 25 most specialist (T_s) or of the 25 most generalist species (T_g).

Third, we built a simple index reflecting the community composition in terms of the specialist–generalist species. To do so, we simply averaged, for each community, specialization indices I_i of all individuals present in the community. The community specialization index (*CSI*) was thus given by:

$$CSI_j = \frac{\sum_i^{Q_j} N_i I_i}{\sum_i^{Q_j} N_i}$$

Such index was shown to be easily available with monitoring data sets and sensitive to landscape degradation (Devictor *et al.*, 2008b).

Simulation protocol

We assessed whether and how each community indices was affected by imperfect detectability. The most important factor affecting the local detectability of a given species is its abundance, N , which induces heterogeneity in site-specific detection probabilities (Royle *et al.*, 2005). For a given species i in a community j , we thus considered that the detected abundance n_{ij} was dependent on the actual abundance N_{ij} , and on the individual detection probability of the species p_i . The value of $n_{ij(t)}$ was given by a binomial drawing of parameters $N_{ij(t)}$ and p_i . To test whether each community index was affected by species detectability, model outputs were computed using real local species abundances (N_{ij}) as well as detected abundances (n_{ij}).

Note that several aspects of the model structure are somehow similar to previous analytical metapopulation models (Hanski & Gyllenberg, 1997). Some properties of the metacommunity (e.g. species richness at equilibrium) may thus have been derived from analytical calculation. Yet, the comparison of each parameter at each time step was more easily achieved using simulation. Changes in metacommunity dynamics and community indices were thus investigated by using Monte Carlo simulations in which 5000 metacommunity trajectories were drawn. As we were interested in assessing the changes in community measures following disturbance, we first ran models with a low basal level of habitat change (D_b) until equilibrium was reached (1000–2000 years of simulation). We assumed that equilibrium was reached when no variation in any indices occurred with time over the last 50 years of simulation (whether equilibrium was reached or not was assessed by testing the time effect in a linear regression model for each index, $\alpha = 0.05$). Then, starting from this equilibrium, we increased the level of disturbance. After the beginning of disturbance, simulations were run over a fixed time horizon (100 years). To illustrate most model outputs, we used the indices averaged over all trajectories.

Case study: bird community changes following landscape disturbance

Our purpose was not to assess all model assumptions using a case study but rather to check whether community indices behave similarly in more or less disturbed landscapes using classical large-scale monitoring data. We used data from the French Breeding Bird Survey (FBBS), which is a standardized survey

program monitored by volunteer skilled ornithologists (Julliard & Jiguet, 2002). Each observer provides a locality, and a 2×2 km plot to be prospected is randomly selected within a 10-km radius around the locality (i.e. among 80 possible plots). In each plot, the observer samples 10 evenly distributed point counts. In each point count, every bird species heard or seen is recorded during exactly 5 min. Each plot ($n = 1028$) was monitored twice in the spring, once before and once after the 8 of May, with 4–6 weeks between sampling events. The same observer monitored the same plot each year.

Habitat disturbance affecting landscapes was provided by TERUTI, an independent landscape statistical survey, specifically developed for the estimation of variation in land use throughout space and time (Agreste, 2003). This landscape survey covers France with a systematic grid made of 15,500 2×2 km squares, which allowed measuring changes in habitat proportion between 1992 and 2002 in each plot of the FBBS. This habitat turnover was retained as a measure of landscape disturbance.

As data from the FBBS were only available for a short-term trend (2001–2004), we focused on the empirical relationships between community indices and landscape disturbance in space. Therefore, for each Breeding Bird Survey (BBS) plot, counts of the two annual sampling events were summed and averaged over 4 years (2001–2004). We then tested whether empirical species richness, Shannon-diversity indices and the *CSI* of each plot were related to landscape disturbance measured by TERUTI. To compute empirical *CSI*, we used the species specialization index (*SSI*) of bird recently proposed by Julliard *et al.* (2006). *SSI* is the coefficient of variation of species densities across habitat classes and available for each bird species monitored by the FBBS in Devictor *et al.* (2008a). We then assessed whether and how species richness, Shannon's index and *CSI* were correlated to the disturbance level (using Pearson correlation coefficient). This analysis was conducted using the 1028 BBS plots and the R statistical software version 1.9.1 (R Development Core Team, 2004).

RESULTS

First, the model was initialized at time zero assuming a low basal level of disturbance in each community until equilibrium was reached. Starting from equilibrium, we simulated an equal temporal increase of disturbance level in each community. In this simple context, community indices showed contrasting responses: species richness and Shannon's index increased following disturbance (Fig. 1a,b), while both trend of specialist species and *CSI* decreased (Fig. 1c,d).

As expected, assuming a less than 100% detectability of species led to an underestimation of species richness and Shannon index. Interestingly, the effect of detectability was negligible for other indices. Indeed, as T_s is computed assuming a reference value of 100 for the first year, the trend is not affected by underestimation of species abundance, simply because the bias is constant in time. Similarly, as *CSI* is computed using the specialization index of species, weighted by their local abundance, heterogeneous species detectability can induce higher estimation errors, but is not expected to induce any bias. When increasing the magnitude of disturbance, both species richness and

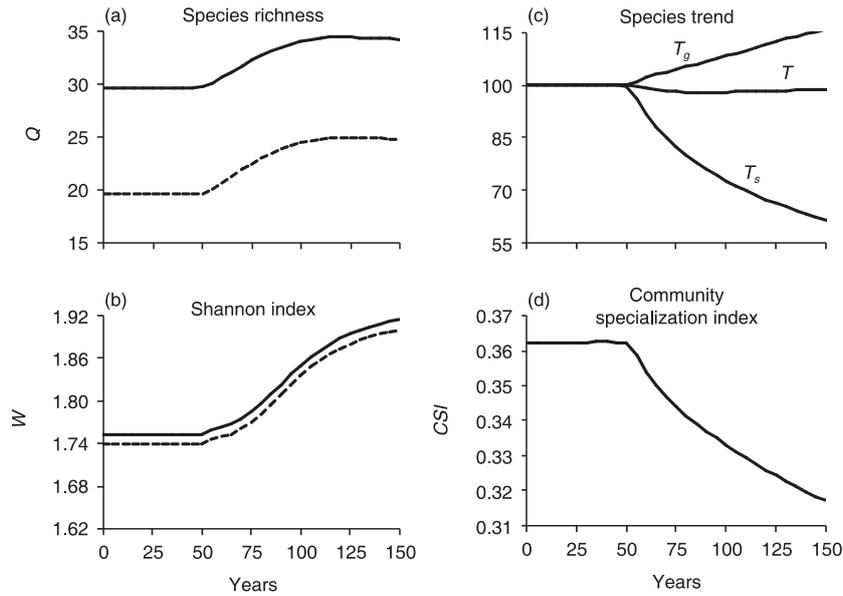


Figure 1 Sensitivity of diversity and specialization indices following disturbance. The model was initialized assuming a uniform distribution of all species in all communities ($N = 50$), and a low basal level of disturbance in each community ($D_b = 0.0025$). The model was run until equilibrium was reached (2000 time steps). Starting from this equilibrium, the level of disturbance was equally increased in each community ($D = 0.05$ starting from year 50). Each indicator was calculated assuming a 100% detection of all species (solid lines) or a heterogeneous species detectability (dashed lines; $p = 0.25$; $sd_p = 0.022$) with following parameters: $I = 0.5$; $sd_I = 0.25$; $r_0 = 1.05$; $sd_{r_0} = 0.015$; $c = 0.2$; $C = 0.025$; $N_{col} = 10$; $K = 5000$. Indices were subdivided into two diversity indices (a) species richness, Q , or (b) Shannon's index, W ; and two specialization indices: (c) Trend of the 25 most generalist (T_g) or specialist species (T_s), or of all species (T) (note that in this case detected and real values are confounded), or (d) the community specialization index, CSI .

Shannon index showed non-monotonic variation. Maximum values of these indices were obtained for intermediate disturbance levels. In contrast, the speed of decrease in specialization indices directly depended on the strength of disturbance (Fig. 2).

Sensitivity analyses indicated that patterns observed in Fig. 2 were not altered by changes in the disturbance level. For instance, strong disturbance can eventually lead to a decrease in species richness (due to local extinction of sensitive species to habitat change). However, this decrease was preceded by a transitory increase of richness (due to the colonization of species favoured by local habitat change), whereas the specialization indices always showed monotonous decreases with time (see Appendix S1 in Supporting Information). Further simulations indicated that these patterns were also maintained even if we changed the colonization probability of species C_{ij} or the competition coefficient c (respectively Appendix S2 and S3).

In a second set of simulations, we still assessed the ability of community metrics to detect an effect of habitat disturbance but assumed heterogeneous disturbance among communities (i.e. by drawing different values of D_i among patches instead of using a fixed mean D -value for all patches). In this case, an increase in the variation of disturbance between communities rapidly engendered a metacommunity made of communities with extreme levels of disturbance (either very strong or low disturbance). Some species were strongly negatively affected by disturbance which caused rapid local extinction/rarefaction of these species, resulting in a rapid decrease in both specific richness and Shannon index in time (not shown).

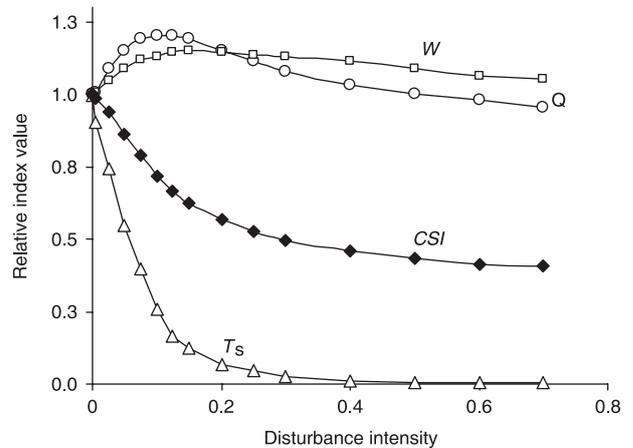


Figure 2 Difference in indicator responses with increasing level of habitat disturbance. The model was initialized assuming a uniform distribution of all species in all communities ($N = 50$), and a low basal level of disturbance in each community ($D_b = 0.0025$). The model was run until equilibrium was reached (2000 time steps). Starting from this equilibrium, the level of disturbance (D ; with same expectation in all communities) was increased. Results are presented after 100 years following disturbance increase. Each indicator was divided by its equilibrium value (i.e. before disturbance) to allow easier comparison. Each indicator was calculated assuming a 100% detection of all species and following parameters: $I = 0.5$; $sd_I = 0.25$; $r_0 = 1.05$; $sd_{r_0} = 0.015$; $c = 0.2$; $C = 0.025$; $N_{col} = 10$; $K = 5000$. Indices were subdivided into two diversity indices: species richness (circles, Q) and Shannon's index (squares, W); and two specialization indices: Trend of the 25 most specialist species (triangles, T_s), and community specialization index (diamonds, CSI).

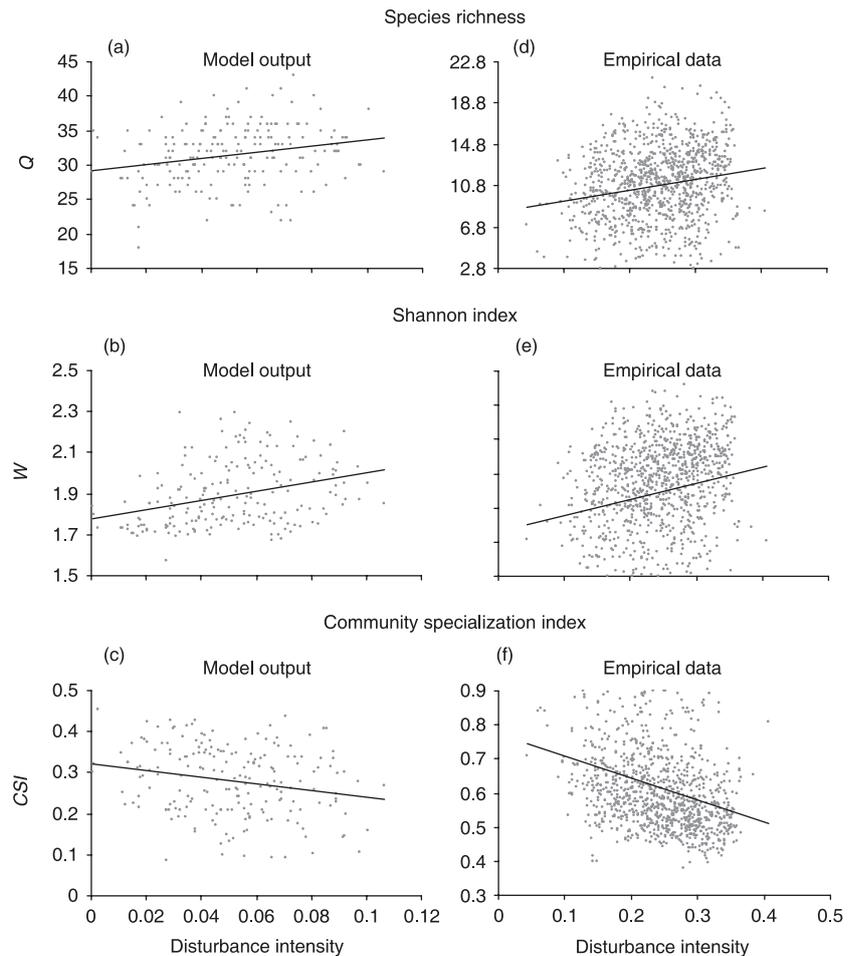


Figure 3 Simulated and empirical relationships between bird communities and landscape disturbance for species richness (Q), Shannon index (W) and the community specialization index (CSI). The model was initialized assuming a uniform distribution of all species in all communities ($N = 50$), and a low basal level of disturbance in each community ($D_b = 0.0025$). The model was run until equilibrium was reached (2000 time steps). Starting from this equilibrium, the level of disturbance (heterogeneous in space) was increased ($D = 0.05$, $sd_D = 0.025$). Model outputs (a), (b) and (c) are presented after 100 years following disturbance increase, with following parameters: $u = 1.0$; $I = 0.5$; $sd_I = 0.25$; $r_0 = 1.05$; $sd_{r_0} = 0.015$; $c = 0.2$; $C = 0.025$; $N_{col} = 10$; $K = 5000$. Empirical results (d), (e) and (f) are based on 1028 communities monitored by the French Breeding Bird Survey during 2001–2004.

We assessed the effect of spatial heterogeneity of disturbance by comparing the values of the different biodiversity indices for different local communities in the same metacommunity with heterogeneous disturbance levels (Fig. 3a,b,c). Again, diversity and specialization indices showed opposing trends. The CSI decreased with an increasing local disturbance intensity (Fig. 3c), reflecting the fact that specialists were less represented in most disturbed areas. In contrast, species richness (Fig. 3a) and Shannon index (Fig. 3b) were on average higher in most disturbed areas, as colonization of less sensitive (generalist) species tended to overcompensate for the extinction of most sensitive (specialist) species in these areas.

Interestingly, empirical data from FBBS showed the same qualitative trends (Fig. 3d,e,f): both species richness and Shannon indices increased with spatial landscape disturbance (respectively, Fig. 3d; Pearson product–moment correlation coefficient $r = 0.19$, $P < 0.0001$, $n = 1028$ and, Fig. 3e; $r = 0.18$, $P < 0.0001$, $n = 1028$). In contrast, we obtained a negative relationships between CSI and landscape disturbance (Fig. 3f; $r = -0.30$, $P < 0.0001$, $n = 1028$).

DISCUSSION

Our results indicated that simple community metrics may show contrasting responses even under similar disturbance regimes.

While both species richness and Shannon index are expected to decrease under a disturbance regime, our model generally showed that these indices actually increased (1) through time following an increase of disturbance; (2) after a given time with an increasing intensity of disturbance (3) with the level of local disturbance when disturbance is heterogeneous in space.

These results obviously depended on the time scale considered (i.e. the time lag after the beginning of disturbance). For instance, species richness was eventually reduced following strong disturbance but only after a long delay necessary to provoke local extinction of sensitive species. These non-monotonic results for species richness and Shannon's index are consistent with what one might expect according to the Intermediate Disturbance Hypothesis (IDH, Connell, 1978). According to the IDH, diversity maintenance under disturbance is higher for intermediate levels of disturbance. Here, we show that specialist species did not benefit from these intermediate levels of disturbance (as CSI was declining). Therefore, an understanding of the species attributes and of species responses to disturbance is thus necessary to identify coexistence mechanisms underlying an IDH pattern (Shea *et al.*, 2004). In addition, if community composition is not considered, a conclusion of greater community 'health' at intermediate disturbance levels would be erroneous.

We also showed that even indices based on abundances may fail in detecting disturbances when averaged without respect to species characteristics. Indeed, the relative abundance variation of all species (T) was not sensitive to disturbances, because the abundances of declining (specialist) species and increasing (generalist) species compensated each other.

In contrast, when using specialization indices, responses (1) showed monotonous variations through time; (2) showed an increasing sensitivity with an increasing magnitude of disturbance; and (3) were easier to interpret and more consistent with theoretical expectations.

Our model suggests that using the specialist–generalist approach is thus helpful to prevent confusion between losers and winners following landscape disturbance.

We then used empirical data from the French Breeding Bird Survey to compare theoretical and observed results. We showed that both species richness and Shannon indices were positively related to habitat disturbance in space, while CSI was negatively affected. Such empirical pattern was also consistent with our simulation analysis.

We believe that these empirical findings are partly driven by higher habitat diversity and turnover within disturbed landscapes allowing more species to coexist in those landscapes. This pattern can also be induced if generalist species are colonizing disturbed habitat more quickly than specialists are locally wiped out. Indeed, the empirical decrease in CSI with increasing disturbance suggests that generalist species are more likely to thrive in more disturbed landscapes. This latter pattern is consistent with the expected higher vulnerability of specialist species with increasing habitats turnover (Devictor *et al.*, 2008a). This probably induces competition relaxation between specialist and generalist species and allows more numerous generalist species to colonize disturbed landscapes.

Thus, these simple empirical findings emphasize that change in species richness is uninformative about the species that influence local species richness. Community indices that are independent of species attributes (e.g. species richness and Shannon index) can increase locally at the expense of specific attributes of the community composition (e.g. specialization). These results are not an outcome of the particular assumptions of the original metacommunity model but reflect differences in index sensitivities.

Managers should carefully consider the transient and long-run properties of indices when choosing what to monitor. At the community level, numerous ecological studies implicitly assume all species to be similar and ignore the functional contribution of each species (Petchey *et al.*, 2004). To build relevant and powerful predictors of community responses to disturbance, we believe that any indices ignoring species ecological sensitivity (even elaborated indices combining richness and abundance) would be less informative than community metrics embodying species-specific responses. Moreover, indicators are generally more valuable when they shed light on ecological processes driving the observed changes.

The CSI seems promising to reflect community change following disturbance in all kinds of habitats and for any organisms without relying on a selected subset of species. To compute CSI ,

the key idea is to rank all species according to a specific ecological trait (e.g. SSI) which can be considered as a measure of niche breadth. SSI can be computed for many groups and is a good proxy for ecological specialization in many situations (Devictor *et al.*, 2008a). The ecological specialization index recently proposed by Fridley *et al.* (2007) which only requires presence–absence data of species across sites can be used as well. Our simulations also showed that CSI was also not impaired by problems caused by imperfect detectability among species (Boulinier *et al.*, 1998). However, we did not incorporate the possibility that p and SSI could be linked or correlated. CSI was thus not biased in the simulation because specialization (SSI) and detection probability (p) were considered to be independent. Hidden links between species attribute and species detectability may bias trends of any indices. Accounting for imperfect detectability is likely still valuable in many cases and should require attention depending on the studied system and the question being asked.

Our aim was to tackle major properties and weakness of a few realistic community indices that are more or less linked with a specific species trait (specialization), rather than testing all available indices (for such systematic comparison see e.g. Washington, 2003). A first obvious limitation of our approach is that some of the results presented here may be quantitatively imprecise or exacerbated by modelling constraints and assumptions. Yet, our sensitivity analyses showed that all our qualitative conclusions are robust. Our results are also in accordance with previous studies on community responses following disturbance (Helm *et al.*, 2006).

Our model is based on a strong assumption linking a unique (integrative) species characteristic (habitat specialization) and species vulnerability to habitat disturbance. This assumption is expected by the niche evolution theory (Futuyma & Moreno, 1988; Marvier *et al.*, 2004), and has recently received much empirical support (McKinney & Lockwood, 1999; Olden *et al.*, 2004; Smart *et al.*, 2006; Devictor *et al.*, 2008b). More explicit modelling of how specialists distributed themselves across communities should enable us to refine our findings. For instance, for the purpose of simplification, we did not consider any difference in the strategies of patch selection among more or less specialized species, although it is likely that specialist and generalist species do not select their habitat in the same manner (Dall & Cuthill, 1997).

Conservation biologists, managers and politicians have highlighted the critical need to develop simple and realistic measures that summarize how biodiversity is affected by human-induced landscape disturbance at large scales. Understanding the strength and the limitations of community indices is thus a matter of considerable concern for conservation biogeography. In this respect, the need to account for more functional and ecological aspects of diversity was specifically highlighted. We showed that integrating specialization of species more explicitly in the quantification of community response to disturbance seems straightforward.

ACKNOWLEDGEMENTS

We greatly thank the hundreds of volunteers who took part in the national breeding bird survey (STOC EPS program). We thank

Denis Couvet and Joanne Clavel for helpful suggestions as well as Brendan Wintle, Atte Moilanen and two anonymous referees for their constructive comments.

REFERENCES

- Agreste (2003) Indicateurs paysagers élaborés à partir de l'enquête sur l'utilisation du territoire (TERUTI). Technical report N-151. SCEES, Paris, France.
- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, **79**, 1018–1028.
- Brotans, L., Herrando, S. & Pla, M. (2007) Updating bird species distribution at large spatial scales: applications of habitat modelling to data from long-term monitoring programs. *Diversity and Distributions*, **13**, 276–288.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Dall, S.R.X. & Cuthill, I.C. (1997) The information costs of generalism. *Oikos*, **80**, 197–202.
- Devictor, V., Julliard, R. & Jiguet, F. (2008a) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**, 507–514.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008b) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, **17**, 252–261.
- Fridley, J.D., Vandermaast, D.B., Kuppinger, D.M., Manthey, M. & Peet, R.K. (2007) Co-occurrence based assessment of habitat generalists and specialists: a new measurement of niche width. *Journal of Ecology*, **95**, 707–722.
- Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, **19**, 207–233.
- Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 269–288.
- Hanski, I. & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, **275**, 397–400.
- Helm, A., Hanski, I.K. & Pärtel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, **9**, 72–77.
- Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.
- Julliard, R. & Jiguet, F. (2002) Un suivi intégré des populations d'oiseaux communs en France. *Alauda*, **70**, 137–147.
- Kassen, R. (2002) The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology*, **15**, 173–190.
- Kimbro, D.L. & Grosholz, E.D. (2006) Disturbance influences oyster community richness and evenness, but not diversity. *Ecology*, **87**, 2378–2388.
- Levins, R. (1968) *Evolution in changing environments*. Princeton University Press, Princeton, NJ.
- Marvier, M., Kareiva, P. & Neubert, M.G. (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, **24**, 869–878.
- McGill, B.J., Enquist, B., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**, 450–453.
- Olden, J.D., Poff, N.L., Douglas, M.B., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, **19**, 18–24.
- Petchey, O.L., Hector, A. & Gaston, K.J. (2004) How do different measures of functional diversity perform? *Ecology*, **85**, 847–857.
- R. Development Core Team (2004) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org> (Accessed September 2006).
- Royle, J.A., Nichols, J.D. & Kéry, M. (2005) Modelling occurrence and abundance of species when detection is imperfect. *Oikos*, **110**, 353–359.
- Shea, K., Roxburgh, S.H. & Rauschert, E.S.J. (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters*, **7**, 491–508.
- Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. & Firbank, L.G. (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **273**, 2659–2665.
- Swihart, R.K., Gehring, T.M., Kolozsvary, M.B. & Nupp, T.E. (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and Distributions*, **9**, 1–18.
- Swihart, R.K., Lusk, J.J., Duchamp, J.E., Rizkalla, C.E. & Moore, J.E. (2006) The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. *Diversity and Distributions*, **12**, 277–287.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Washington, H.G. (2003) Diversity, biotic and similarity indices. A review with special relevance to aquatic ecosystems. *Water Research*, **18**, 653–694.
- Weikard, H.-P., Punt, M. & Wesseler, J. (2006) Diversity measurement combining relative abundances and taxonomic distinctiveness of species. *Diversity and Distributions*, **12**, 215–217.
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.

Editor: Brendan White

SUPPORTING INFORMATION

The following Supporting Information is available for this article:

Appendix S1 Sensitivity of diversity (Q and W) and specialisation indices (T_s and community specialization index (CSI)) to different disturbance magnitudes, D (green: 0, blue: 0.03, pink: 0.05, red: 0.10, orange: 0.5) either for real values (solid lines) or observed values assuming imperfect detectability (dashed lines). Note that in case of T_s and CSI , observed and real values are confounded.

Appendix S2 Sensitivity of diversity (Q and W) and specialization indices (T_s and community specialization index (CSI)) to

habitat disturbance under different scenarios of local colonization rates of species, C (green: 0, blue: 0.05, pink: 0.01, red: 0.02, orange: 0.05).

Appendix S3 Sensitivity of diversity (Q and W) and specialization indices (T_s and community specialization index (CSI)) to habitat disturbance under different levels of competition among species, c (green: 0.01, blue: 0.05, pink: 0.1, red: 0.5, orange: 1).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.