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Contrasting effects of habitat reduction, conversion and alteration on neutral and non neutral biological communities

Anne Teyssèdre and Alexandre Robert

A. Teyssèdre (anne.teyssedre@free.fr) and A. Robert, UMR 7204, Centre d'Ecologie et des Sciences de la Conservation, Muséum National d'Histoire Naturelle, 55 rue Buffon, FR-75005 Paris, France.

While habitat transformation driven by human activities is the main driver of current biodiversity changes, there is still no framework to explore and forecast the effects of different types of habitat changes on the richness and composition of biological communities. To tackle this issue, we modeled the dynamics of a regional meta-community, composed either of ecologically equivalent species (neutral model) or of generalist and specialist species (specialization model), and explored the impact of the overall reduction, patch conversion or alteration of an original habitat into one or several other habitats of different total carrying capacity on the community metrics at equilibrium. Our simulations reveal strong interactions between the community model considered (neutral or specialization model) and the type of habitat change. Under neutrality, the impact of habitat changes on richness can be approached by a power law species–individual relationship (SIR), which may at constant density be simplified into the widely used power law species–area relationship (SAR), independent of the type of change. However, in the presence of generalist and specialist species, we found that 1) while habitat reduction in area also leads to approximately power law SIRs and SARs, 2) patch conversion and alteration have more complex effects on regional species richness, and 3) habitat alteration elicits the functional homogenization of communities, involving a decrease of their average level of specialization.

Habitat transformation, either due to land use changes, physicochemical pollution or climate change, is the main driver of the current biodiversity crisis (Vitousek et al. 1997, Rosenzweig 2001a, Bradshaw et al. 2009). While biodiversity declines at a high rate (Butchart et al. 2010), understanding the impact of these habitat changes on the organization and functioning of biological communities should provide a basis to evaluate the present rates of biodiversity loss, anticipate changes in species and community distributions expected under various scenarios of human induced habitat changes (MEA 2005, Pereira et al. 2010), and hence to propose actions at different scales aiming to reduce or redirect these changes (Balmford et al. 2005, Dawson et al. 2011).

In order to simulate the impact of habitat transformations driven by agriculture expansion or climate change on species richness, many authors have used models involving the empiric Arrhenius law (Rosenzweig 1995)

$$S = c\,A^z \qquad (1)$$

which relates the species richness at equilibrium (S) of a regional community of similar (i.e. same trophic level) organisms to the area (A) of the habitat it occupies. In this equation, the values of c and z depend on the taxon, on the immigration rate from the mainland (Rosenzweig 1995, 2001a, Triantis et al. 2012), and on the speciation rate per individual (for z) (Hubbell 2001). The Arrhenius law can be combined or not with other models such as niche envelop models (Thomas et al. 2004).

However, the application of this power law species–area relationship (SAR), also formulated as a log–log linear SAR, to estimate the impact of habitat changes on living communities, is limited by several practical and conceptual difficulties.

A first conceptual issue, related to the practical difficulty of assessing the value of z, is the diversity and shape of the SARs. Rosenzweig (1995, 2001a) proposed three main types of SARs (regional, island and continental types), each characterized by a different but constant z exponent, depending on the immigration rate from an external reservoir of species. Other authors proposed a unique but triphasic (Hubbell 2001, O'Dweyer and Green 2010), or biphasic (Storch et al. 2012) SAR of varying z exponent, depending on the spatial scale.

Another important conceptual issue is that using a SAR to assess the impact of land use changes or other habitat transformations equalizes these changes with simple reductions in area. In other terms, all these SARs assume that the carrying capacity of the converted or degraded habitat – or that of the 'matrix' in the case of habitat fragmentation in a surrounding less favorable habitat – is nil, which clearly is not the case (Ricketts 2001, Daily et al. 2003, Teyssèdre and Couvet 2007, Koh et al. 2010). Openfields used for agriculture in initially forested lands, for instance, still harbour large communities of mammals, birds, arthropods and plants long after deforestation (Ricketts et al. 2001, Daily et al 2003, Gaston et al. 2003).

In order to take into account the diversity of suitable habitats colonized by a living community at regional or higher scale, several authors recently developed alternative equations linking species richness to a power law function combining area (either total area or the areas of different habitats) and other variables such as the number of habitats (Triantis et al. 2003), the affinity of subgroups of species for the different habitats (Pereira and Daily 2006), and the community density (in number of individuals per unit area) in the different habitats (Teyssèdre and Couvet 2007). Besides the difficulty to assess the exponent (and the number of habitats, for Triantis et al.'s proposal), these three proposed relationships have some limits. Noteworthy, the first two relationships are based on (for Pereira and Daily's 2006 countryside SAR) or inspired by (for Triantis et al.'s 2003 Choros model) an empirical relationship – the power law SAR – which underlying mechanisms are still poorly understood (but see Triantis et al. 2012), while the third proposed relationship is based on a theoretical species–individual relationship (SIR) predicted by a much debated analytical model (Hubbell's 2001 neutral theory of biodiversity and biogeography or NTB). Moreover, these three proposed models focus on species richness, without regard to other potentially important community characteristics or metrics.

With an analytical approach, other researchers explored the mechanisms underlying species coexistence or diversity patterns and dynamics in communities of similar species (i.e. same trophic level) through building community or meta-community models and studying their response to the variation of external or internal variables, at different spatial scales. Among these models, Hubbell's (2001) NTB is much puzzling because, although based on a seemingly improbable approximation – the hypothesis that species competition and selection processes can be neglected and neutralized by stochastic demographic events at the community level, which equalizes the selective values of all species and causes an "ecological drift" in the meta-community – it succeeds in predicting many of the basic patterns of biodiversity observed at landscape or higher scale (Hubbell 2001, Chave 2004, Bell 2005, Etienne and Olff 2005, Walker 2007), among which the well-known Arrhenius law.

More precisely, the NTB predicts a power law species-individual relationship (or SIR) relating the total size (N) of the meta-community, in number of individuals, to the number of species (S) it harbors at equilibrium

$$S = c' N^z \tag{2}$$

which at constant density, simplifies into Eq. 1 (Hubbell 2001).

Despite of its recognized heuristic power, the NTB seems unable to explain some general trends in biodiversity change currently observed, such as the sustained decline of specialist species, the expansion of many generalist or human commensalist species, and the associated functional homogenization of communities (McKinney and Lockwood 1999, Olden 2006, Clavel et al. 2010). To our knowledge, no formal model has yet been proposed to explore such general dynamics.

Theoretically, the mean reproductive success of a species in a specific habitat depends on the fit between the resources of that habitat and the species' biological needs (Hutchinson 1958, Kassen 2002). By definition, a habitat specialist species has a higher growth rate than a generalist species in its few preferred habitats, but a lower growth rate in numerous other habitats (Straub et al. 2011). Hence habitat conversion, fragmentation or alteration into new anthropogenic habitats should favour either generalist or human commensal species against specialists of natural or semi-natural habitats.

In order to explore the impact of habitat changes on a regional meta-community composed of specialist and generalist species, we developed a simple dynamic model combining competition processes and species sorting (between ecological categories of species) with neutral processes (among species belonging to the same ecological category), inspired by Devictor and Robert (2009)'s meta-community model. More precisely, simulating the growing modification of an initially rich homogenous regional landscape into other (homogenous or heterogeneous) habitat configurations, of lower regional carrying capacity for the considered community, we explored the impact of directional habitat changes on species richness and other biodiversity metrics. We paid particular attention to compare: 1) the type of habitat change; 1.1) habitat reduction in area; 1.2) habitat conversion, i.e. replacement of patches of an original habitat by patches of another one, of lower carrying capacity (like conversion of forest patches into openfield patches); 1.3) habitat alteration, i.e. transformation of an original homogenous regional landscape into a poorer homogenous secondary regional habitat of lower carrying capacity (like regional habitat alteration through increasing aridity or chemical pollution) (Fig. 1), and 2) the community model type: 2.1) neutral (i.e. all species have the same replacement rate in all habitats); 2.2) model with both generalist and specialist species (hereafter, specialization model).

Material and methods

Model structure and meta-community properties

We used a stochastic and spatially implicit population-based island type model, including two nested levels: local communities and a regional meta-community. We assumed that this later was fueled by an inflow of species from a mainland pool (which was not explicitly modeled).

Each local patch j was occupied by local populations of different species issued of a mainland pool of $Q = 500$ species, forming a local community of total size Nj(t) at time t. We assumed a continent–island type model with one-way migration from the mainland to the regional

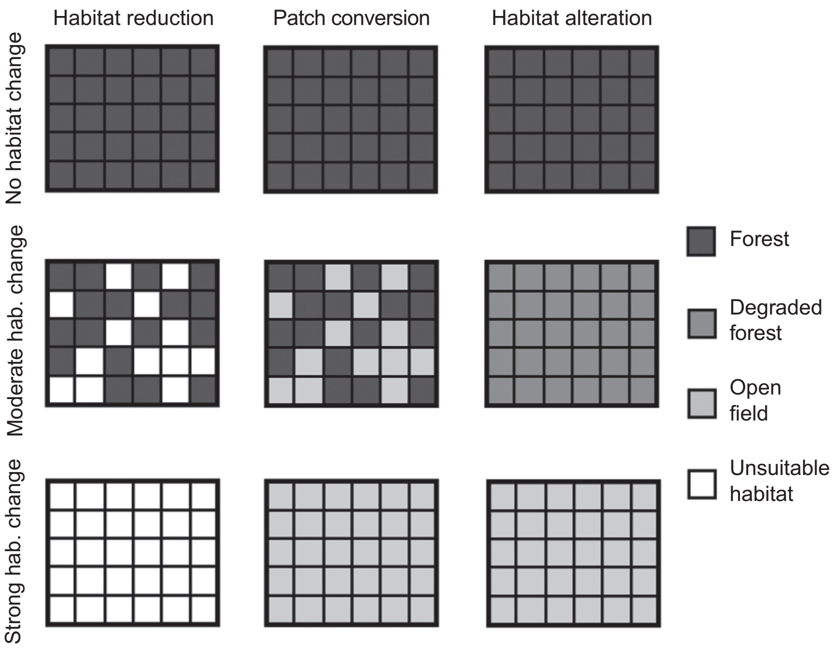

Figure 1. Schematic representation of the three scenarios of habitats changes. Squares represent patches of habitat in the regional meta-community.

meta-community, composed of $N(t) = \sum Nj(t)$ individuals at time t. The region was formed of P patches of habitats. For the purpose of comparison, we assumed that all patches had the same area.

Habitats were characterized by their ecological type and their level of degradation, which together determined their carrying capacity K_j per unit area for the considered community (i.e. the maximum number of individuals of any species that a unit area of habitat j could sustain) and the replacement rates of the different types of species (generalists or specialists) composing that community.

Three ecological types of habitat were considered, differing noteworthy by their maximum carrying capacity, reached when intact (i.e. non degraded), for the considered community. Although our model can be applied to various types of habitats and meta-communities (terrestrial or aquatic), we illustrate our results throughout the paper in the context of human induced habitat changes and agriculture development in a (temperate or tropical) terrestrial region, using the following habitat types: 1) forests, with a maximum carrying capacity (when intact) K_{fmax} per unit area; 2) openfields, with a maximum carrying capacity K_{omax} per unit area lower than K_{fmax} ($K_{omax} = K_{fmax}/3$); and 3) unsuitable habitats, with a carrying capacity assumed nil for the considered community ($K_u = 0$).

Community dynamics were investigated considering three types of species: forest specialist (s_f), openfield specialist (s_o) and generalist (g) species, characterized by distinct replacement rates in the different habitat types. The replacement rates of these three categories of species were respectively noted $r_{sf(f)}$, $r_{so(f)}$ and $r_{g(f)}$ in forests and $r_{sf(o)}$, $r_{so(o)}$ and $r_{g(o)}$ in openfields. The values of the parameters used in the simulations presented in the main results are listed in Table 1.

Community dynamics

The dynamics of each species i in each local community j occurred according to three phases (forming together a time step), repeated until equilibrium for each landscape configuration, and described below:

- colonization of each patch by locally absent species
- growth of each species i in each patch j, according to a replacement rate r_{ij};
- density dependent regulation in each local community.

Colonization

At each time step, in each patch, species that were locally absent could colonize the community. Colonization events occurred in each patch according to the composition of the whole regional meta-community (discussed in Devictor and Robert 2009). The colonization rate of a given species i to a given patch j had two components: 1) colonization by individuals coming from the mainland, according to a rate $c_{mi}(t)$ which was assumed constant through time (in a given simulation) and identical for all species ($c_{mi}(t) = c_m$); 2) colonization by individuals coming from the regional meta-community, at a rate $c_{ai}(t)$ assumed proportional to the abundance $N_i(t)$ of the species in the whole regional meta-community, i.e. $c_{ai}(t) = c_a N_i(t)$, with c_a a constant rate of immigration per individual.

The occurrence or not of colonization events was stochastic; for each species i, colonization of patch j at time t depended on a Bernoulli drawing of expectation $c_{ij}(t) = c_{mi}(t) + c_{ai}(t)$. In case of colonization, a number imm of individuals of the considered species were added to the local community. Hence for each species i and patch j, the number of immigrants $imm_{ij}(t)$ at time t was either imm or 0.

Table 1. Values of input parameters used in simulations.

Parameter	Value
Number of species in the mainland pool (Q)	500
Number of generalist species	250
Number of forest specialist species	125
Number of openfield specialist species	125
Number of patches in the region (P)	30
Local carrying capacity in forest patches (K_{fmax})	200
Local carrying capacity in openfield patches (K_{omax})	67
Local carrying capacity in unsuitable habitat patches (K_u)	0
Replacement rate of forest specialists in forests ($r_{sf(f)}$)	1.1
Replacement rate of forest specialists in openfields ($r_{sf(o)}$)	1.01
Replacement rate of open field specialists in forests ($r_{so(f)}$)	1.01
Replacement rate of open field specialists in openfields ($r_{so(o)}$)	1.1
Replacement rate of generalist species ($r_{g(f)}$ and $r_{g(o)}$)	1.09
Rate of colonization from the mainland, per species (c_m)	10^{-4}
Rate of colonization from the region, per individual (c_a)	10^{-5}
Number of immigrants per colonization event (imm)	10
Number of independent trajectories per scenario	250

Replacement rate

In each patch j, the intrinsic replacement rate r_{ij} of species i depended on the type of species i (forest specialist s_f, openfield specialist s_o or generalist g) and on the type of habitat of patch j (forest or openfield). Before regulation, the abundance of species i in patch j at time t was given by a Poisson drawing of expectation $N_{ij}(t) = r_{ij}[N_{ij}(t-1) + imm_{ij}(t)]$ where $imm_{ij}(t) = imm$ or 0.

Density dependent regulation

Finally, in each patch j, the overall number of individuals N_j of the local community was limited by the carrying capacity K_j of that patch. If the total size of community j, following the immigration and intrinsic growth phases, was higher than K_j, individuals where removed proportionally to their abundance before regulation, until abundance was equal to K_j. The final expected abundance of species i in patch j at time t was thus:

$$N'_{ij}(t) = \frac{K_j N_{ij}(t)}{\sum_{k=1}^{Q} N_{kj}(t)} \qquad (3)$$

All values of $N'_{ij}(t)$ were then rounded to the nearest integer and the total abundance of the local community was computed as $N_{j(t)} = \sum N'_{ij(t)}$

The global meta-community dynamics were described by a matrix $M_{ij(t)}$ giving the abundance of each species i in each patch j at time t. Transition from t to t + 1 was determined by the following processes, in order of occurrence: colonization, local growth of species in each community, local community regulation.

We verified that the simulated community saturated locally and hence regionally its habitats (i.e. at equilibrium, $(K_j - N_j)/K_j < 2\%$ for all j), as assumed by community theoreticians (Hubbell 2001). In other terms, the mean number of individuals per unit area of any habitat j, d_j, is a measure of its carrying capacity (K_j) for the considered community.

Scenarios of habitat changes

Several scenarios were investigated in order to mimic the effects of changes in land use on the properties of biological communities. In all cases, an all forest region composed of P = 30 patches of intact forest (i.e. $K_f = K_{fmax}$) was changed into various human-modified habitats of lesser mean carrying capacity according to three scenarios of habitat change. We did not consider any temporal dynamics in habitats: all results correspond to equilibrium results obtained for various scenarios of habitat change, as compared with the reference (all forest region) situation. In these scenarios, schematized in Fig. 1 and detailed below, the carrying capacity of the regional landscape was lowered, either by uniformly reducing the carrying capacity of all patches (habitat alteration), or by replacing a growing fraction of the initial forest patches by openfield patches (patch conversion) or unsuitable patches (habitat reduction).

Habitat reduction

The first scenario involved the reduction in area of an all forest region by replacing intact forest patches, capable of sustaining K_{fmax} individuals per unit patch, by patches of unsuitable habitat ($K_u = 0$).

Patch conversion

Starting from the same all forest region, patches of intact forest (each having a carrying capacity K_{fmax}) were replaced by patches of openfield habitat, each of carrying capacity K_{omax} ($0 < K_{omax} < K_{fmax}$).

Habitat alteration

Starting from the same all-forest region, all patches were cleared of the same fraction of their trees. The magnitude of habitat transformation was noted x (x = 0 for intact forests and x = 1 for forests completely transformed into openfields) and both the carrying capacity per patch and the replacement rates of the different categories of species in the patches were computed as linear functions of x (Supplementary material Appendix A1).

Outputs, initial conditions and simulation protocol

For each simulated regional habitat configuration, we computed equilibrium values of community size (or abundance) in number of individuals (main symbol N), and of species richness in number of species (main symbol S), in each habitat patch j (Nj and Sj, respectively) and for the whole regional meta-community (N = ΣNj and S, respectively).

We also computed the number of individuals and species per ecological category in each habitat patch and in the whole regional meta-community, as well as a simple index reflecting the functional composition of the community (CSI), based on each species specialization index (here equal to 1 for specialist species and 0 for generalist species). To do so, we simply averaged specialization indices of all individuals within each community.

For each type of habitat change, from the initial common all-forest configuration, we computed meta-community indices at equilibrium for growing intensity of regional habitat change (i.e. with decreasing values of the regional carrying capacity K). For generality, most results were graphically expressed in terms of log-transformed S–K and CSI–K relationships. Because, as mentioned above, communities were saturated at equilibrium, all K-S relationships presented hereafter are equivalent to N–S relationships at equilibrium.

Meta-community indices were investigated by using Monte Carlo simulations in which 250 meta-community trajectories were drawn. At the beginning of each scenario, we imposed the initial landscape composition and let colonization by species occur progressively via immigration from the mainland until equilibrium was reached (details of the protocol are provided in the Supplementary material Appendix A1).

The model was implemented in Pascal language and compiled under Delphi 7.0. The source code is available upon request.

Results

Neutral model

When considering all species in the community as ecologically equivalent, the log–log species individual relationship (SIR) was monotonical, positive and approximately linear (as predicted by the NTB) whatever the type of habitat transformation: habitat reduction, patch conversion or habitat alteration (cf. the upper curves in Fig. 2a, c and e).

Further analysis indicated that the SIR mostly varied with the immigration rate from the mainland and was only marginally affected by the type of habitat transformation (Fig. 3). Noteworthy, we found that increasing the inflow of species from the mainland mainly increases the height of the approximately linear log–log SIR (i.e. the c coefficient of the approximated power law SIR), with a lesser effect on it slope (corresponding to the z exponent).

Specialization model

All species–abundance relationships simulated with the specialization model laid below the corresponding neutral curves (Fig. 2), due to the selectivity of the model. Starting from a lower richness value in the all forest region, the SIR was similar to that of the neutral model for habitat reduction (Fig. 2a), but exhibited more complex patterns in the other scenarios of land use change.

Impact of habitat reduction

The SIR driven by habitat reduction was monotonic, positive, approximately linear in log–log scale (and parallel to the neutral log–log curve), and associated with a high and constant community specialization index (CSI) due to the high dominance of forest specialist species (Fig. 2a–b).

Impact of patch conversion

Simulating the conversion of an all-forest region into a mixed forest–openfield region led to a highly convex or hill shaped SIR (Fig. 2c). The CSI was again high and approximately constant in forest patches, but lower in openfield patches due to the lower carrying capacity of these patches, which increases the relative local frequency of recent generalist immigrants. The maximal richness obtained for an intermediate value of abundance corresponded to a situation where g, s_f and s_o species were evenly distributed at the regional meta-community level.

Impact of habitat alteration

With habitat alteration, the SIR was more complex, with two locally maximal values of richness for two distinct values of abundance (Fig. 2e) and a non monotonical variation of the average level of specialization with abundance, where the CSI was minimum for an intermediate value of abundance (Fig. 2f). This complex pattern is related to variations in relative fitness of the three categories of species (generalists (g), forest specialists (s_f) and openfield specialists (s_o)) along the gradient of intensity of habitat transformation, at the local and meta-community levels (see an illustration in Supplementary material Appendix 1 Fig. A1). The highest local maximum value of regional species richness corresponds to the (low) level of forest transformation where the fitness of forest specialists equals that of generalist species, while the lowest local maximum value corresponds to the (high) level of habitat transformation where the fitness of openfield specialists equals that of generalist species. These two points correspond to the maximum values of 'fitness evenness' among categories of species, resulting in high regional species richness as in the neutral model. At the opposite, the minimum values of regional species richness and CSI are obtained for intermediate levels of habitat transformation, where generalists have a higher fitness than the specialists of the two habitats.

Further analyses indicate that all observed qualitative patterns presented here are independent of model parameters (Supplementary material Appendix 1 Fig. A2–A4) as long as both generalists and specialists occur in the considered pool of species. Our qualitative results are also robust to variation in colonization rate or number of immigrants among species. Results however indicate that such variation in colonization rate consistently leads to reduced regional species richness for all scenarios of habitat change (see Supplementary material Appendix A2 for additional scenarios and more detailed results on the effect of habitat changes on diversity).

Discussion

Our general approach stems in the observations that 1) anthropogenic changes (e.g. land use or climate changes) do not lead to the simple reduction or disappearance of habitats, but rather to the transformation of original habitats into new habitats with different and often lower carrying capacity for defined communities (Gaston et al. 2003); 2) even when species play similar functional roles (e.g. same trophic level), they are not necessarily equivalent in terms of both their preferential habitat and their tolerance to habitat changes. Although recent works in the fields of ecology and biogeography have shown that these changes can lead to a biotic homogenization of communities linked, at least for bird communities, to a decline of the mean specialization level of communities (Davey et al. 2011, Le Viol et al. 2012), there is still no theoretical framework

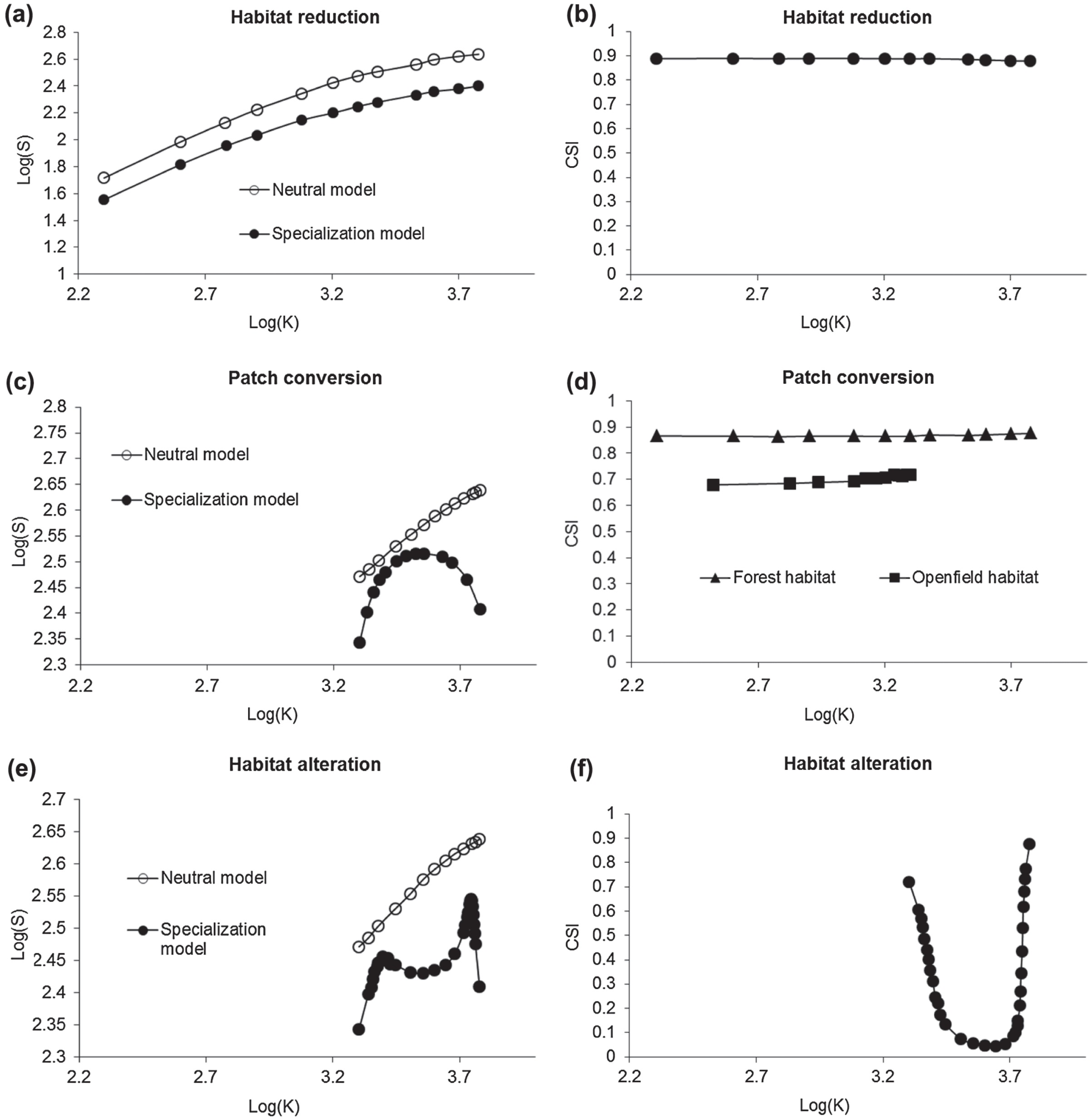

Figure 2. Relationships between regional meta-community carrying capacity (K, x-axes), richness (S, left panel) and specialization index (CSI, right panel) at equilibrium. Both K and S are base 10 log-transformed. [Since habitat patches were saturated at equilibrium, the log–log K–S relationships are equivalent to log–log SIRs at equilibrium.] Within each panel, K varies according to either a reduction of patch number (habitat reduction, a, b), a random conversion of forest patches into open field patches (patch conversion, c, d) or a simultaneous alteration of all forest patches into habitat patches of lesser carrying capacity (habitat alteration, e, f). Species of the regional meta-community are issued from a mainland pool of 500 generalist species (neutral model) or 250 generalist, 125 forest specialist and 125 open field specialist species (specialization model).

allowing to understand and project the effects of realistic changes in habitats on community properties and metrics.

Our simulations reveal strong interactions between the community model considered (neutral versus specialization model) and the type of habitat change. In particular, whereas habitat reduction, conversion and alteration have similar effect on species richness under neutrality, using a specialization model we show that the type of habitat change has strong, qualitative effects on the structure and composition of communities at equilibrium.

Impact of habitat changes on regional species richness under neutrality

Hubbell's (2001) neutral theory of biodiversity and biogeography (NTB) predicts that, from landscape to global scale, regional species richness at equilibrium may be approached by a power law (or log–log linear) species–individual relationship (SIR), which at constant density of individuals simplifies into the well-known power law species–area relationship (SAR) (Hubbell 2001), and applied to homogenous

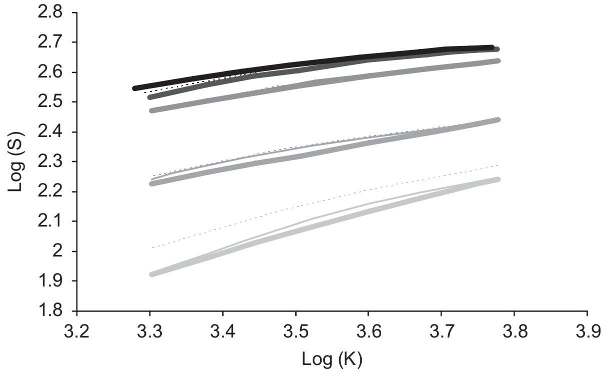

Figure 3. Relationship between regional meta-community carrying capacity K and richness S at equilibrium (neutral model). Both K and S are base 10 log-transformed. [Since habitat patches were saturated at equilibrium, these log–log K–S relationships are equivalent to log–log SIRs at equilibrium.] K varies according to either a reduction of patch number (habitat reduction, from 1 to 30 patches, thin dotted lines), a random conversion of forest patches into open field patches (patch conversion, 30 patches with a proportion of forest patches varying from 0 to 100%, thin continuous lines) or a simultaneous alteration of all forest patches into degraded patches (habitat alteration, 30 patches, with alteration intensity varying from 0 to 1, thick continuous lines). Colors indicate immigration rates from the mainland (C_m) (darker greys indicate high immigration rates). Species of the regional meta-community are issued from a mainland pool of 500 generalist species.

habitats of same area may be simplified into a power species–density relationship (Teyssèdre and Couvet 2007). Our simulations with the neutral model confirm these predictions.

Comparing the SARs under neutral and specialization models

Our simulations involving only changes in area of a unique habitat – i.e. habitat reduction – robustly leads to an approximately linear log–log SAR whatever the model used (neutral or not). In other words, the linear log–log SARs (or power law SARs) observed in nature for more than a century cannot be used to infer the ecological neutrality of living communities. The height of the log–log SAR (which gives the c coefficient of the power law SAR) was lower under the specialization model, confirming the selectivity of this model.

Impact of the colonization rate on the power law SIRs and SARs

Our simulations under the neutral model show that increasing the inflow of species from the mainland mainly increases the height of the approximately linear log–log SIR and SAR, and has a negative effect on their slope. This suggests that the c parameter and z parameter of (island or regional) empiric SARs respectively increases and decreases with the rate of colonization of the involved meta-communities from the mainland, as predicted by the theory of island biogeography (Triantis et al. 2012).

Specialization model, species richness and diversity at regional scale

Unlike the NTB, our specialization model predicts that, although reducing the total abundance of the regional community in number of individuals, reducing the carrying capacity of an initially ‘rich’ regional homogenous habitat into a ‘poorer’ homogenous secondary habitat (patch conversion and habitat alteration scenarios) paradoxically raises regional species richness and diversity at the regional scale until a certain threshold. This occurs because such habitat changes benefit to a large number of generalist species or/and to specialists of the secondary habitat, whose massive colonization (in number of species) from the mainland pool exceeds the rarefaction of ‘native’ regional specialist species.

More precisely, our simulations show that regional species richness is maximal in cases where two categories of species have similar fitness in a homogeneous intermediary habitat, or when habitat heterogeneity is high at the regional scale. The coexistence of ecologically non-equivalent species in spatially/temporally heterogeneous environments is at the core of the intermediate disturbance hypothesis (Norberg et al. 2001) and in agreement with dynamic models (Münkemüller et al. 2009, Dos Santos et al. 2011) as well as empirical results (Buckling et al. 2000).

In the context of global changes, several authors have stressed the contrasted impact of environmental changes on species richness at different spatial scales through genetic, taxonomic or functional biotic homogenization, based on theoretical, paleontological and empirical arguments (Vermeij 1991, Rosenzweig 2001b, Sax and Gaines 2003, Smart et al. 2006). While at global scale, massive habitat transformation and biological invasions drive a loss of species, linked to biotic homogenization, these ecological changes may locally or regionally increase species richness, where the number of new colonizing species at least temporarily exceeds that of extirpated species. Our results with the specialization model support these observations.

Functional biotic homogenization and beta diversity

Several authors observed that functional and taxonomic similarities among communities do not necessarily coincide (Olden and Rooney 2006, Smart et al. 2006). Smart et al. (2006) indeed found that the functional biotic homogenization of (native and exotic) plant communities in British human-modified ecosystems was associated to higher taxonomic biodiversity. Our simulations with the specialization model support these findings. We found that the functional homogenization among local communities driven by increasing habitat alteration was associated with growing beta diversity. This pattern results from the demographical equivalence of species assumed within each ecological category by this model.

CSI as an indicator of habitat quality

The use of a community specialization index (CSI) allows the monitoring or simulation of directional (structural and functional) trends in living communities, at local and larger scales. Devictor et al. (2008) found that the CSI of common bird communities, used to measure their functional homogenization, varies with habitat perturbation, and hence proposed to use this metric as an indicator of habitat quality. Our results confirm these findings and point out habitat alteration at the regional scale (linked to growing pressures like increasing temperature, nitrate level or CO_2 concentration) as a major cause of functional homogenization, in contrast to habitat conversion (land use change) or reduction (Fig. 2).

Moreover, we found a negative correlation between regional species richness and the CSI at equilibrium (until a threshold) in degraded regional habitats, similar to that observed in diverse European bird communities (Davey et al. 2011), which confirms that local and even regional species richnesses are poor indicators of habitat quality and ecosystem functioning, in contrast to community composition (Filippi-Codaccioni et al. 2009).

Diversifying processes generated under the specialization model

Leibold et al. (2004) identified four main mechanisms underlying species coexistence in meta-community models: patch dynamics, mass effects (source–sink effects), species sorting and neutral stochastic processes. Our simulations show that modelling several species categories differing by their selective value in different habitats (here, one generalist and two habitat specialist species categories) elicits three of these diversifying mechanisms: species sorting (among species belonging to different categories), source–sink processes (among populations occupying different habitats), and neutral processes (among species belonging to the same ecological category).

Conclusion

Several authors stressed the importance of improving the realism of biological community models to simulate the impact of current environmental changes on communities (Matias et al. 2013), and possibly reject the neutral hypothesis (Münkemüller et al. 2009, Dos Santos et al. 2011). Here we showed that integrating non neutral processes between ecological categories of species and neutral processes inside each category allows to simulate many empirical biodiversity patterns and trends not predicted by the NTB (nor by other existing meta-community models, as far as we know), among which the functional homogenization of communities currently observed at local and regional scales. We hence propose to use this kind of model, simulating competition and selection processes between ecological categories of interchangeable species, to explore the dynamics of living communities in response to environmental changes.

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Supplementary material (available online as Appendix oik-00928 at <www.oikosjournal.org/readers/appendix>). Methodological details (Appendix 1) and additional results (Fig. A1–A4 and Appendix 2).