The effects of direct and indirect constraints on biological communities

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ABSTRACT

Human activities are expected to result in a diversity of directional or stochastic constraints that affect species either directly or by indirectly impacting their resources. However, there is no theoretical framework to predict the complex and various effects of these constraints on ecological communities. We developed a dynamic model that mimics the use of different resource types by a community of competing species. We investigated the effects of different environmental constraints (affecting either directly the growth rate of species or having indirect effects on their resources) on several biodiversity indicators. Our results indicate that (i) in realistic community models (assuming uneven resource requirements among species) the effects of perturbations are strongly buffered compared to neutral models; (ii) the species richness of communities can be maximized for intermediate levels of direct constraints (unimodal response), even in the absence of trade-off between competitive ability and tolerance to constraints; (iii) no such unimodal response occurs with indirect constraints; (iv) an increase in the environmental (e.g., climatic) variance may have different effects on community biomass and species richness.

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1. Introduction

All biological systems face constraints that may vary in space and time depending on the intrinsic properties of systems and their environment. Whereas the effects of temporal variations in environmental quality are well understood at the (single-species) population level (Grenfell et al., 1998; Johst and Dreckles, 2003; Lande, 1993), the effects on communities of species are more difficult to understand (but see Patten (1978) who introduced the conceptual basis for modelling the interactions between living organisms and their environment; see also the models developed in Kadmon and Benjami (2006), Varughese (2011), Xu and Li (2002)). This lack of knowledge about the effect of constraints on communities makes it difficult to diagnose and project the effects of current and future human-caused habitat changes on ecological communities.

1.1. Effects of constraints on biological communities

Biological communities are defined as assemblages of species that interact with each other and with their environment (Verhoef and Morin, 2010). These interactions can include competition, predation, commensalism, or parasitism. Many of these interactions can be directly or indirectly related to limited access to resources. At the population level, resources are defined as any substance or factor that is consumed or used by organisms and has an effect on their growth rate (Tilman, 1982). Resources include food, specific reproduction habitats, such as nesting places, available place on the ground, or the amount of light available for plants. Here we consider resources as essential resources such as defined by Tilman (1982), i.e., a resource is not substitutable by another.

All species constantly face constraints (i.e., all species have intrinsic biological limits to their growth even in an infinite and optimal environment, and all environments are finite), thus the term “constraints” is used in the relative sense. Hereafter, we will use the term constraint to refer to any environmental change having a negative effect on the intrinsic dynamics of one or several species (e.g., on species growth rate, carrying capacity, at the scale of the community, some species benefit from this constraint through competitive advantage). This variation can be permanent (a decrease in environmental quality) or fluctuating (i.e., an increase of the variability of the parameter considered).

Thus, constraints may be grouped into two main categories: (1) stress, which refers to a permanent (or in all places, or both) reduction in the average environmental quality for a given species, and (2) disturbance, which refers to a constraint, variable in space and time. As discussed in Dornelas (2010), some categories of environmental changes may lead to both stress and an increase of disturbances. Thus, importantly, a permanent increase in the environmental variance (in which, for example, occasional constraints, such as storms, become more frequent and/or stringent) could be considered a stress (i.e., each constraint is discrete, but the change...
in the disturbance regime is chronic). For example, climate change may lead to both chronic stress (elevated average temperature) and disturbances (e.g., higher storm frequencies and/or intensities).

Many studies have shown that human activities generally affect biodiversity through these constraints (see below). The constraints are usually classified into categories, such as climate change, habitat fragmentation and reduction, invasive species, and overexploitation (Diamond, 1989; Hamre, 1994; Hooper et al., 2005; IUCN, 2010; Jackson and Sax, 2010; Tilman et al., 1994, 1997). The distributions of these constraints may vary strongly in time (chronic/punctual, rare/frequent, random/cyclical) and in space (global/local, autocorrelated/aggregated/random) and may directly affect survival or fecundity (Yee and Barron, 2010) or have indirect effects that are mediated through the amount of resources available (Vargas et al., 2007).

Beyond preliminary theoretical work (Tilman, 1982), the conceptual links between the assemblages of interacting species and different types of constraints have not been formalised (Cardinale et al., 2009; Díaz et al., 2007). Large increases in constraints, such as drastic habitat destruction, frequent climatic perturbations or unsustainable levels of exploitation, are damaging all aggregate levels of biodiversity, from genes to meta-communities, although opportunistic species often stand to benefit. However, theory predicts that intermediate (i.e., non-zero) constraint levels may be optimal for biodiversity at the community level (intermediate disturbance hypothesis, Connell and Slater, 1977). Environmental variability is inseparable from the dynamics of ecological systems and allows for the maintenance of diversity within and among species (Norberg et al., 2001). When the effect of the constraint is strong, long-lived, slow-growing species cannot persist in the community. Contrarily, in the absence of constraints, short-lived, fast-growing pioneer species are driven to extinction by competitive exclusion. In an intermediate constraint system, both types of species can coexist (Buckling et al., 2000; Foden and Sommer, 1999; see Mackey and Currie, 2000; Shea et al., 2004). In communities, the complexity of inter-species interactions generates very different and potentially antagonistic responses to constraints for each species, depending on how the species are connected within the ecological network and between neighbouring networks. The global effects of constraints are therefore difficult to assess and may depend on the spatial and temporal scales of studies or on the type of constraints themselves (Chalcraft et al., 2009). Therefore, to simplify the systems analysed, many studies have ignored the impact of inter-species interactions and have analysed the effects of constraints as a “species average effect” (i.e., merely juxtaposing the effect of constraints on each species’ growth rate or focusing the analysis on a single population; Fleishman et al., 2001; Niemi and McDonald, 2004). However, the development of mechanistic models linking constraint levels to the impact of competition is very important to predict the future of biodiversity (Pereira et al., 2010).

In a recent work, Dornelas (2010) used a neutral community model (Hubbell, 2001) to explore the effect of the various “disturbances” on various community metrics. These disturbances were modelled by varying three parameters: the mortality rate of species, the reproductive rate of species and the carrying capacity of the community. The carrying capacity of the community (linked to resources) was identified as the main driver of species richness.

1.2. Modelling approach

Based on the observation that constraints are heterogeneous, not only in terms of origin (e.g., climate change, overexploitation of species ...), but also in terms of mode of action (e.g., stress versus disturbance, direct effects on species growth versus indirect effects mediated through the amount of resources available), we examine the effects of various kinds of constraints on a simple biological system. We use a mechanistic community model that describes several species competing for local resources to analyse the impact of constraints on community dynamics and various biodiversity indicators. We assume that species differ from each other in terms of (i) the quality of their requirements (i.e., resources needed to ensure a species’ growth); and (ii) the diversity of their requirements (i.e., the number of resource types needed for certain growth; see discussion). We assess the effects of constraints on community processes and properties using three classical biodiversity metrics: the species diversity, the overall biomass and the Simpson’s Diversity Index (Niemi and McDonald, 2004), which represents the probability that two randomly selected individuals in the community will not belong to the same species. Along with these classical community metrics, we use a new metric corresponding to the average diversity of individuals’ requirements at the community level.

2. Materials and methods

We developed a time-discrete, stochastic community dynamics model. The model mimicked the use of different types of resources by a community of S species, whose dynamics were affected by intraspecific and interspecific competitive interactions. We used a continent–island model with one-way migration from the continent.

2.1. Resources and populations

Following the approaches of Tilman (1982) and Chase and Leibold (2003), we considered a resource to be any substance limited in quantity that is consumed by an organism and positively influences its growth. We modelled different types of finite physical (e.g., space), chemical (e.g., nitrogen, potassium), or biological (e.g., prey) resources. Each resource type was different and identified by the index j, which was defined as a required resource or non-required resource for each of the S_{pool} species modelled. The quantity K_{j} of resource type j was an integer value corresponding to the number of “equivalent individuals” of any species that the resource can sustain. Here, one equivalent individual was defined as an individual of a species that would only require this particular resource (for example, in the case where a species i would require two types of resource in equal quantity, each individual of the species i would represent 0.5 equivalent individual for each of these resource types). Hence, whereas all species require the same overall quantity of resources, the number of types of resource needed may vary among species. The quantity K_{j}(i) of resource type j at time t was drawn from a normal distribution N(K_{j}, K_{ij}), where K_{ij} represented the magnitude of environmental variability (depending on the scenarios investigated, the drawing of K_{ij} was assumed to be independent or not among resources).

A community was constituted by a set of populations of different species that interact at a particular place. Here, each species i was described using three attributes per individual: its average growth rate (r_{i}, including both mortality and fecundity), its annual rate of immigration events (μ_{i}) (number of individuals of species i arriving from the continent) and its requirements (P_{ij}). P_{ij} represented the relative proportion of resource type j needed by each single individual of the species i (for each species i, the sum of P_{ij} was assumed to be equal to one). From the point of view of resources, P_{ij} represents the relative impact of each individual of species i on the resource. We assumed that species require several types of resources in a quantity sufficient to allow growth (“species requirements”). At the beginning of each simulation, for each species i, a number T_{i} of resource types was drawn (the requirement of each species was assumed constant through time).
We considered two models of resource requirements. The first model assumed that all species were equivalent (each had \(m\) requirements randomly drawn from among the \(R\) available resources, hereafter the “NULL” model). The second model assumed that the different species had variable numbers of requirements drawn from a uniform distribution (between one and \(R\), hereafter the “NES” or “Not-Equivalent Species” model).

2.2. Population dynamics

The dynamics of each population were modelled according to three stages: (i) immigration, (ii) species growth, and (iii) regulation. For each population \(i\), the growth stage was independent of the resources and the other populations, whereas the regulation stage depended on the quality and quantity of resources available and the abundance distribution of the other populations.

At time \(t\), for each species \(i\), the immigration was modelled by adding \(Imm_{i(t)}\) individuals to each species, where \(Imm_{i(t)}\) was either equal to zero or \(n_{imm}\) individuals (stochastic Bernoulli drawing of parameter \(\mu\) assumed equal for all species). The migrants had the same characteristics as the other individuals in the species. In real biological systems, immigration rates are highly variable and depend on complex interactions between species and landscape properties (Fahrig, 2007; Courtney et al., 2001). As we focused here on the effect of constraints on community’s local dynamics, we restricted our analysis to low immigration rates (\(\mu = 0.05\) in all results presented).

The intrinsic growth rate \(r_i(t)\) of species \(i\) at time \(t\) was drawn from a normal distribution \(N(r_i, \sigma_{env})\), where \(\sigma_{env}\) represented the magnitude of environmental variability (depending on the scenarios investigated, the drawing of \(r_i(t)\) in each time step was assumed to be independent or not among species). The abundance of species \(i\) at \(t+1\) before regulation was given by:

\[
N_{i(t+1)} = \exp[r_i(t)N_{i(t)} + Imm_{i(t)}]
\]

We assumed that all species had the same expected long-term growth rate \(r\) for all species).

2.3. Competition

The simple process described above represents the growth of the species in an environment where resources are infinite (i.e., the maximum growth of the species). The process of regulation due to limiting resources occurred according to the following steps:

1) The first step focused on the resources

\[R_j(t) = \sum_i N_{i(t)}P_{ij}\]

where \(N_{i(t)}\) is the abundance of population \(i\) at time \(t\) after immigration and growth.

2) For each type of resource \(j\), \(K_j\) represented the maximum number of consumers of this type of resource throughout the entire community. Each \(K_j\) was compared to \(R_j(t)\). When \(R_j(t) > K_j\), the resource type was considered to be limiting.

2.4. Outputs

We computed various biodiversity indicators to examine the effect of environmental quality on equilibrium community properties.

- The number of individuals \(N_{tot}\):

\[N_{tot} = \sum_i N_i\]

- The species richness \(S\):

- A community requirement index (hereafter CRI) that quantified the average number of resource types needed by community individuals:

\[CRI = \frac{\sum_i N_i \times T_i}{N_{tot}}\]

where \(T_i\) is the number of resource types required by species \(i\).

- The Simpson’s Diversity Index \(D\) (Simpson, 1949): index of balanced distribution of abundances across species in the community (this index corresponds to the probability that a randomly selected pair of individuals are from different species):

\[D = 1 - \sum_i \frac{N_i(N_i - 1)}{N_{tot}(N_{tot} - 1)}\]

Community dynamics were assessed for different environmental scenarios by averaging 100 community trajectories. In all cases, we ran the model until a quasi-equilibrium in species distribution was reached before computing biodiversity indicators (i.e., equilibrium indicators were independent of the distribution of species abundances at time zero, as long as \(r > 1\)). The statistical procedure used to check for equilibrium is described in Appendix 1. At this time, the values of the biodiversity indicators were computed by averaging indicator values over 100 time steps (after equilibrium was reached) and over the 100 iterations.

2.5. Initial conditions and constraint scenarios

We considered \(t = 0\) to be an empty site. All species would immigrate from the continent with an equal probability. Locally, \(T\) types of resources \(j\) were available, and we assumed that all resources had the same \(K_j = K_{mean}\).

We examined two putative effects of global changes by comparing biodiversity metrics for different scenarios:
(1) The effect of average environmental quality, by varying (i) the average intrinsic growth rate of species ($r_{mean}$); (ii) the average of the carrying capacity of each resource type ($K_{mean}$); and (iii) the number of resources ($T$).

(2) The effect of environmental variability, by varying (i) the temporal variation of $r$ ($r_{var}$) and (ii) the temporal variation of $K$ ($K_{var}$).

The model was written in Pascal language (Source code is provided in Appendix 2).

3. Results

3.1. Effects of a decrease in environmental qualities

Average environmental quality was assessed by varying the average growth rates ($r$) of the species, the average number of resource type ($K$) or the number of resource types present ($T$). The main results are summarised in Fig. 1.

3.1.1. Direct or resource-mediated constraints

Overall, the number of individuals ($N_{tot}$) in the community at equilibrium was driven by the quantity of each resource available (Fig. 1b, linear relationship), provided that: (i) the average population growth rate was positive (Fig. 1a), and (ii) the number of resource types was sufficient to sustain at least one species (Fig. 1c).

Contrary to the two other types of constraint, the reduction in the number of resource types strongly affected the distribution of abundance of species present in the community (i.e., Simpson index, see Fig. 11). Besides, reductions in the quantity of each resource type and in the number of resource types both led to strong decrease in the number of species at equilibrium $S$ (for both NULL and NES models). However, $S$ was less sensitive to a change in resource availability in the NES model than in the NULL model (Fig. 1e and f). In particular, even strong reductions in the quantity of resources had no substantial effect on $S$ (Fig. 1e). Surprisingly, the CRI at equilibrium was much more sensitive to the average growth rate than to the quantity of each resource type or number of resource types available (Fig. 1g–i).

The comparison of scenarios with different average growth rates (Fig. 1a, d, g, and j) allowed us to observe two contrasting situations: (i) in communities with low $r$, both the number of individuals and the species richness increased with $r$ (model NULL and NES); (ii) in communities with high $r$, the average biomass at equilibrium no longer depended on $r$. The NULL and NES models produced contrasting results for specific richness. For the NULL model, $S$ continuously increased with $r$ and reached a plateau close to the maximum number of species (100). In contrast, for the NES model, $S$ reached a maximum value for $r$ around one and then suddenly decreased (Fig. 1d).

Whereas systems with low and high $r$ may have similar $S$ for the NES model, the species assemblages are different for this model. For systems with low average growth rates, the average CRI value at equilibrium is close to its expected value in the pool of immigrants (five; i.e., the pool of migrants is the neighbourhood community composed of an infinite number of individuals of all 100 species), whereas the value is close to its minimum (one) in systems with high average growth rates (Fig. 1g).

3.1.2. Specific constraints

In the simulations presented in Fig. 1, temporal variations were considered to be correlated or non-correlated among species or resources. Overall, no substantial effect from this level of correlation was observed.

3.2. Effect of an increase in environmental variability

Here, various scenarios were compared concerning the magnitude of stochastic temporal variations in environmental quality. The impact of environmental variation was assessed by comparing different levels of temporal variation in either the average growth rates of species or the quantity of resources. The main results are summarised in Fig. 2.

3.2.1. Direct or resource-mediated constraints

In the simulations presented in Fig. 2, each constraint had a direct or indirect action mode. Overall, we observed a similar pattern of responses to each of the constraint action modes.
3.2.2. Specific or non-specific constraints

The average biomass of the community decreases with an increasing level of environmental variability. However, this decrease is stronger if the variation of the stochastic growth rate is correlated across species (Fig. 2a). In contrast, the impact of variability on resource availability is stronger if stochastic temporal variations in resource quantity are independent across species (Fig. 2b).

The sensitivity of the relationship between the biodiversity indicators (for the specific diversity and the CRI) and the constraint values depends on whether variability is correlated or not among species or resources. In the NES model, the relationship is stronger when the variability is correlated across both species or resources. The opposite pattern occurs for the NULL model (Fig. 2c, d, e, f).

4. Discussion

4.1. The effects of constraints on biodiversity metrics

Natural and human-induced constraints have negative effects on biodiversity at different levels and may reduce genetic diversity and fitness at the population level, causing local populations and species to go extinct (Brooks et al., 2002; Frankham et al., 2002; Thomas et al., 2004) and leading to biotic homogenisation at the community level (McKinney, 2006; Stachowicz et al., 2002). When some heterogeneity in functional systems is taken into account (between genotypes or between species), theory indicates that constraints can lead to increased diversity levels by diversifying the selection process within species (Kassen et al., 2004) through the sharing of different functional roles in meta-communities (e.g., specialist versus generalists, Devictor and Robert, 2009), the distribution of resources (Siemann, 1998) or through recurrent processes of colonisation and recolonisation (Pollock et al., 1998; Roberts and Gilliam, 1995, Vandermeer and Carvajal, 2001) because losers are replaced by a comparable number of winners.

The present model is the first to distinguish between direct and indirect (i.e., resource-mediated) constraints on interacting species with heterogeneous requirements. This discrimination is important because examining constraints that only affect growth rates would not allow us to consider all types of constraints. The consideration of heterogeneous requirements across species was motivated by the observation that, within some communities, species belonging to the same functional group may use different numbers of physical (e.g., sunny areas for plants, cavity nests for animals), chemical (e.g., elements necessary for plant growth) or biotic (e.g., prey, host or symbiotic species) resources.

Using simulations of neutral communities, Dornelas (2010) concluded that reduction in carrying capacity has stronger effects on species richness than reductions in survival or fecundity. Here we indeed observe that carrying capacity is an important driver of species richness with the NULL model (see red line on Fig. 1e). However, the reduction of the number of resource types has an even stronger negative effect on richness, since it leads to the local extinction of the species using these resources (in both NULL and NES models). Further analysis of the NES model leads to two major results regarding the effects of constraints on communities as described below.

First, the maximum specific diversity is obtained for an intermediate level of community productivity, which was defined in our model by the growth rate of the community (Figs. 1d and 2c). In particular, the comparison of scenarios with different average productivity levels allowed us to uncover two contrasting situations: (i) communities with low average productivity in which both the biomass and the species richness increase with productivity; and (ii) communities with high productivity in which the

Whereas an increase in the intensity of environmental variability leads to a reduction of S at equilibrium for the NULL model (Fig. 2c and d), the inverse pattern was observed for the NES model. However, the correlation between the intensity of environmental variability and the specific diversity is not linear. We observed a maximum diversity of species for an intermediate value of environmental variability (Fig. 2c).

![Figure 2](image-url)
average biomass at equilibrium no longer depends on productivity. In the first situation, community dynamics are primarily driven by intrinsic growth and immigration, whereas in the second, the dynamics are driven by regulation and competition, which is the process that reduces species richness most dramatically. Intermediate productivity levels allow high total biomasses with moderate levels of competition, yielding a maximal number of species. Our results are consistent with most existing theories that attribute the peak of species richness at intermediate productivity levels to differences in competitive ability among species (i.e., the competitive exclusion of inferior competitors from the community at high levels of average productivity, see e.g., Rosenzweig and Abramsky, 1993).

Second, increased temporal variation in productivity and in resource availability has non-linear effects on species richness (Fig. 2c and d) and under certain conditions on the equity-distribution of species (Fig. 2g and h). We observe a unimodal response of species richness to temporal variation with the NES model. This pattern is classically attributed to the trade-off between competitive ability and tolerance to disturbance (Petraitis et al., 1989; see also Mackey and Currie, 2001; Shea et al., 2004). Interestingly, our results demonstrate that a non-linear, unimodal response can be observed in the absence of such trade-off (in our simulations, we assumed that all species had the same average growth rate). We observe a greater homogeneity in species fitness when variability increases. Temporal variations in the productivity tend to reduce competition, which in turn reduces the advantage of species with low needs (Fig. 2e), leading to a greater number of species at equilibrium (Fig. 2c).

In contrast, for the NULL model, increasing constraints (i.e., decrease in average environment quality or increase in temporal variance) lead to an overall decrease in the overall number of individuals. At the community level, this phenomenon results in stronger demographic drift and reduced species richness at equilibrium. This result is in agreement with classical, theoretical expectations of the neutral theory of biodiversity (Hubbell, 2001), but contradicts recent results from Kadmon and Benjamiini (2006), who obtained unimodal responses of species richness to both average productivity and disturbance under the neutrality assumption. According to these authors, the decrease in species richness with increasing productivity at high levels of productivity (or high disturbance level) results from the lower proportion of immigrants in the pool of individuals of the local community when productivity increases. This result thus critically depends on the direct effect of immigration on the composition of the local community, which was assumed small in our simulations (i.e., we assumed that the number of immigrants was always much smaller than the number of individuals arising from local intrinsic dynamics).

4.2. Study limitations

Some limitations of our model need to be taken into account. First, we based our conclusions on a few sets of parameters. However, the effects of most important parameters driving community dynamics (i.e., average growth rate, quantity of resources, correlation of constraint effects across species, ...) are directly presented in figures. Additional analyses showed that other parameters (in particular, the immigration rate and overall number of species in the continental pool) had no qualitative effect on the conclusion. Second, we neglected predation and parasitism interactions between species. Considering such interactions would have implied that a given species can use both abiotic (resource as defined in the current model) and biotic (e.g., prey or host) resources. While trophic web models allow to model biotic resource use at several trophic levels (e.g., Kondoh, 2003), there is still no framework that allows the use of biotic and abiotic resources by species at different trophic levels.

We also ignored potential non-linear interactions between species or between species and resources (Abrams, 1980; Drossel et al., 2001) and we limited our study to a continent–island model (Hanski, 1999), where the continental species pool was not affected by constraints occurring in the community of interest. Similarly, we assumed that the growth rate is the same for all species in order to focus on the effects of the heterogeneity in resource requirement. This allowed us to demonstrate that non-linear, unimodal responses of species richness to both disturbance and stress can be observed in communities with similar levels of productivity among species.

Finally, since our study aims at comparing the effects of constraints with various modes of action, we did not investigate the interaction between stress and disturbance. Further work on this interaction is required since (1) global changes (and in particular those related to climate) are expected to affect both the mean and variance of local environments (Solomon et al., 2007); (2) previous theoretical work has reported strong interactions between average productivity and the disturbance level on species richness (Kadmon and Benjamini, 2006; Kondoh, 2001; Worm et al., 2002).

4.3. Classification and categories of constraints

Overall, results obtained from the NES model indicate that the effects of constraints on various biodiversity metrics may qualitatively vary according to the distribution of species and/or resources affected by these constraints. The complexity of these effects emphasizes the need for mechanistic approaches to constraint modelling (Seidl et al., 2011) and introduces the issue of how to best define and classify or categorise constraints. In the field of conservation biology, constraints, mainly of human origin, are categorised based on their “causes” (i.e., the original mechanism that generates the stress) and not on their “effects.” In 1984, Diamond proposed (Diamond, 1989) his “evil quartet” to categorise the constraints in four classes that are causes of ecological stress: habitat destruction, overexploitation, introduced species, and secondary extinctions. Similarly, the eleven IUCN threat categories (IUCN, 2010) consider the degradation of habitats, overexploitation, introduced species, pollution and climate changes as the main causes of extinction.

Based on the results of the present study, we propose an alternative classification system based on the effects, and not the causes, of constraints (see also Dornelas (2010), who proposed considering the demographic effects of disturbances on populations: mortality rates of species, birth rates of species or the carrying capacity of a community). Our classification would allow a description of constraints according to three axes: (i) direct (i.e., not mediated by resources) or indirect constraints (i.e., mediated by resources), (ii) selective (i.e., affecting some population in a community) or global perturbations (i.e., affecting all populations of a community), and (iii) deterministic (i.e., environmental forcing, increasing stress) or variable constraints (i.e., increasing variance in the space or time of an environmental parameter).

These categories are different from categories based on causes (Table 1). For instance, over-exploitation can affect all species of a community (e.g., drift-net fishing: Jennings and Kaiser, 1998) or a category targeted without any direct effects on other species (i.e., extinction of the Great Auk, Pinguinus Impens, Bengtson, 1984; overexploitation of sharks, Clarke et al., 2006). Pollution can have direct (i.e., mortality, Daszak et al., 2003; Dockery et al., 1993) or indirect (i.e., depletion of abiotic and biotic resources, Peterson et al., 2003) effects. Climate change leads to deterministic (i.e., an increase in average temperature, Solomon et al., 2007) and stochastic changes (increased variance of temperature and precipitation: Solomon et al., 2007).
Our model indicates that indirect and direct deterministic constraints have qualitatively different effects. Whereas indirect constraints have unconditionally deleterious effects, stochastic constraints generally increase species richness but decrease biomass. This increase in species richness is most pronounced when constraints similarly affect all species (global constraint).

Overall, these results suggest that the use of a classification of constraints based on their effects should improve the interpretation, comparison, and projection of the impacts of the constraints on communities. Such a system of classification could be complementary to traditional classification schemes based on the causes underlying constraints to biodiversity.

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Appendix A. Supplementary data


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