IDEA AND PERSPECTIVE

Extending the concept of keystone species to communities and ecosystems

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Abstract

Keystone species are defined as having disproportionate importance in their community. This concept has proved useful and is now often used in conservation ecology. Here, we introduce the concept of keystone communities (and ecosystems) within metacommunities (and metaecosystems). We define keystone and burden communities as communities with impacts disproportionately large (positive or negative respectively) relative to their weight in the metacommunity. We show how a simple metric, based on the effects of single-community removals, can characterise communities along a 'keystoneness' axis. We illustrate the usefulness of this approach with examples from two different theoretical models. We further distinguish environmental heterogeneity from species trait heterogeneity as determinants of keystoneness. We suggest that the concept of keystone communities/ecosystems will be highly beneficial, not only as a fundamental step towards understanding species interactions in a spatial context, but also as a tool for the management of disturbed landscapes.

Keywords

Burden, dispersal, habitat destruction, keystone, metacommunity, metaecosystem, patch dynamics., source–sink.

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INTRODUCTION

The concept of keystone species radically changed the field of ecology, exemplifying how ecological communities are more than just collections of species. A keystone species is defined as a species with key roles in community structure and/or ecosystem functioning (Mills *et al.* 1993; Power *et al.* 1996). This idea arose from marine ecology with the famous case study published by Paine in the late sixties on rocky intertidal communities (Paine 1966, 1969). A consumer species was deemed keystone because it promoted species coexistence at lower trophic levels. More general definitions of keystone species have subsequently been proposed to encompass not only predation, but also competition, mutualism, facilitation and any indirect effect driven at the local and regional scales, from individual to ecosystems (Mills *et al.* 1993; Bond 1994; Jones *et al.* 1994; Menge *et al.* 1994; Leibold 1996). Good examples have been found in both marine (e.g. sea otters as keystone predators Estes *et al.* 1978) and terrestrial (e.g. termites as keystone modifiers Debruyn & Conacher 1990) ecosystems (see Mills *et al.* 1993; Bond 1994; Power *et al.* 1996; for reviews). Power *et al.* (1996) further proposed distinguishing *keystone species* from *dominant species*, restricting keystone status to species whose 'impact on their community or ecosystem is disproportionately large relative to their abundance' (Power *et al.* 1996; Christianou & Ebenman 2005).

Along the same line, ecologists have foreseen that landscapes are more than a juxtaposition of communities in space. Species are embedded within complex interaction networks at both local and regional scales, forming metapopulations, metacommunities and metaecosystems (Hanski 1999; Loreau *et al.* 2003b; Leibold *et al.* 2004; Massol *et al.* 2011). Considering dispersal among ecological systems has helped explain patterns such as coexistence of weak and strong competitors through trade-off between competition and colonisation (Hastings 1980; Tilman 1994; Calcagno *et al.* 2006) or regional niche differentiation (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). Spatial flows are similarly expected to affect the dynamics of ecosystems (Polis *et al.* 1997; Loreau *et al.* 2003b; Gravel *et al.* 2010a). These approaches have opened the way for a more mechanistic landscape ecology (Massol *et al.* 2011), with implications for conservation biology (Polis *et al.* 1997; Loreau *et al.* 2003b; Gonzalez *et al.* 2009; Economo 2011; Mouquet *et al.* 2011).

The recognition that landscapes are more than simple collections of communities naturally paves the way for an extension of the keystone concept to metacommunities. At the species level, Amarasekare (2008) recently showed that spatial dynamics may switch keystone status from the top predator to the predator-resistant inferior competitor, depending on the level of dispersal between distant patches. The keystone concept can also be applied to biological levels above species. For instance, some habitat patches might be critically important for the long-term persistence of metapopulations (Hanski 1994; Hanski *et al.* 1996). Keystone ecological structures have been defined as 'distinct spatial structures providing resources,

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shelter or 'goods and services' crucial for other species' (Tews *et al.* 2004), and at an even larger scale, keystone habitats as sources maintaining biodiversity (Davidar *et al.* 2001).

More recently, theoretical ecologists have started to evaluate the consequences of habitat patches removal in metacommunities (Economo 2011; Mouquet *et al.* 2011) opening the way to formally extend the keystone concept to communities embedded within metacommunities. Metacommunity theory (reviewed in Leibold *et al.* 2004) has, however, focused more on how global metacommunity attributes impact the emerging dynamics and properties of meta-communities, paying little attention to the specific contributions of local communities (Fig. 1). However, in nature, it is likely that communities contribute unevenly to regional dynamics. Such unequal contributions open the possibility that some communities might be *keystone*, as their loss would disproportionately harm the metacommunity. We propose here a simple method to quantify how disproportionate an impact is, and illustrate its application using two spatially implicit models representative of different perspectives on metacommunity dynamics: a community coexistence model based on patch dynamics; and an ecosystem productivity model based on source–sink dynamics. We argue that the concept of keystone communities/ecosystems is needed to refine our understanding of species interactions in space. It may also yield a better understanding of the consequences of habitat loss, which is urgent as landscapes are increasingly disturbed by human activities leading to the lost of large spatial areas (Fahrig 2003; Melbourne *et al.* 2004; Dobson *et al.* 2006).

DEFINING KEYSTONE COMMUNITIES

As for keystone species, the problem of identifying a keystone community is twofold: (1) measuring the impact of a single community on a given metacommunity property and (2) comparing it to a reference value to ascertain whether it is disproportionate. We do so by selecting a metacommunity property such as diversity or productivity, and measure it before and after the removal of a community *j*. The difference Δ_j between the two is a measure of the 'general
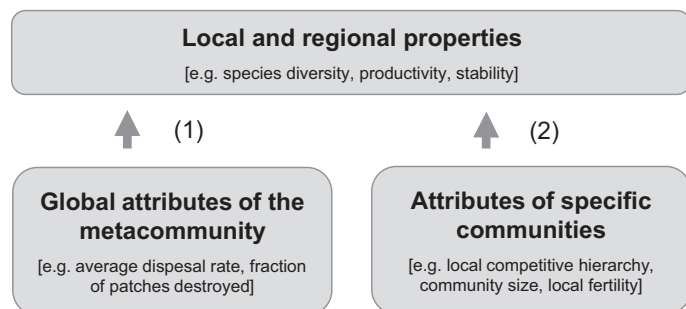
Figure 1 (1) Existing metacommunity theory has traditionally focused on how attributes of the entire metacommunity will impact some properties of interest; e.g. how average dispersal or the fraction of patches destroyed will impact some properties of interest, such as local and regional diversity (e.g. Nee & May 1997; Mouquet & Loreau 2003; Economo & Keitt 2008) or ecosystem functioning (e.g. Loreau *et al.* 2003a; Gravel *et al.* 2010b). (2) The keystone community concept is putting emphasis on the contribution of specific communities to the metacommunity properties. For instance, how competitive hierarchy or local fertility in particular communities will impact species richness and ecosystem functioning in the metacommunity.
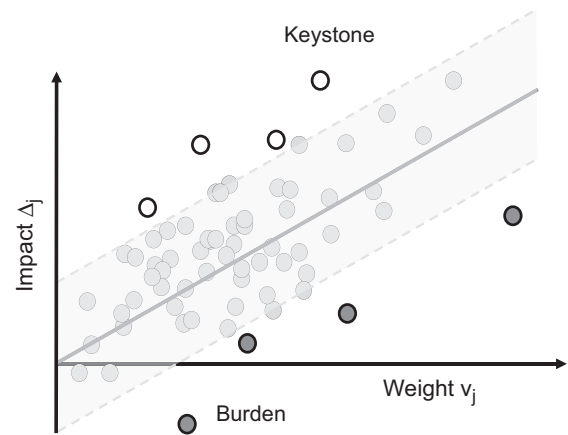
Figure 2 Conceptual steps in identifying keystone communities. Metacommunity state variables are used to compute a metacommunity property X (e.g. diversity). The impact of removing a focal community j from the metacommunity Δ_j, is calculated by subtracting from X the value of the metacommunity property computed after removing the focal community j. To identify atypical communities, impacts are related to the relative community weight v_j (e.g. patch area). The 'keystoneness' of a community is measured as its deviation from the expected impact (i.e. the residual). We define *keystone* (white circle) and *burden* (dark grey circle) communities as communities falling outside the threshold of a statistical envelope.

importance' (hereafter called 'community impact') of a community (Mills *et al.* 1993; Hurlbert 1997).

The second step requires deciding what an atypical community is. This step is much more arduous and has remained controversial in the keystone species literature (Mills *et al.* 1993; Hurlbert 1997). At least implicitly, one has to propose a reference model, which assigns to each entity an expected impact, given some knowledge of its characteristics. In the context of keystones, the focus has been on size, biomass or similar metrics of weight ('dominance effects'; Power *et al.* 1996). The proposed model was assuming simply that the impact of each entity should be proportional to their relative weight (dominance status). This comes with the limitation that it is not a statistical model and does not account for any deviations from the mean (Hurlbert 1997); and that such a simple linear scaling does not hold in general (Libralato *et al.* 2006).

Except for some trivial reference models, we cannot expect to analytically derive the expected distribution of impacts as a function of community weight. In general, it will have to be estimated from empirical data, with a suitable statistical model. Basically, one has to regress the impacts of community removal (Δ_j) over a relevant metric of community weight (e.g. carrying capacity or area), to (1) extract the trend between community weight and impact and (2) identify atypical communities as those deviating from this trend (Fig. 2). The 'keystoneness' of a community is thus its deviation from the expected impact of a community of similar weight (i.e. a standardised residual after regressing impact on weight). Communities with atypically strong positive deviation from the trend are called *keystones* (Fig. 2 white circles). Some communities may also have an atypically strong negative deviation from the trend, to the point that their impact is negative. Such communities actually increase the property of interest when removed, and we consequently refer to them as *burden* communities (Fig. 2 dark grey circles).

Note that different statistical models may be appropriate to capture the trend of community impact with community weight Depending on the data, one could use simple linear models, or more flexible Generalised Additive Models (GAMs), if necessary. Also, several alternative metrics of community weight might be included in the model to remove dominance effects (e.g. lake area and lake perimeter). A precise characterisation of the expected trend can require a significant amount of data, possibly rising operational issues in the field (see Discussion). Hence, it is recommended to adjust the complexity of the model to the amount of data available, using model selection techniques (Burnham & Anderson 2002).

To illustrate the concept, we took a simple Monte Carlo approach: we simulated many observations from a selection of metacommunity models, and regressed the impacts on a metric of community weight, as in Fig. 2. We compared several statistical models using Akaike Information Criterion (AIC) and retained the best one to identify keystone and burden communities (see Appendix 1 for a description of the statistical models we used). The basic model always regressed the impact of removing a community on the weight variable. We compared this model to a model with a 'metacommunity' effect to ascertain whether comparing all community impacts from all metacommunities makes sense (i.e. there is no metacommunity effect). We also incorporated heteroscedasticity to correct for potential biases in the location of keystones and burdens along the weight axis: if statistical dispersions and means were positively linked, keystones/burdens would more often

appear at high weights, just because of a larger dispersion of impacts around the mean. Finally, the keystoneness of a community was connected to possible explanatory variables, to determine which intrinsic properties of communities rendered them burdens or keystones.

ILLUSTRATING KEYSTONE COMMUNITIES

Patch dynamics

We first consider a simple patch-occupancy model (Calcagno *et al.* 2006) to illustrate the concept of keystone communities in systems where coexistence is maintained by a competition–colonisation (CC) trade-off. This model accounts for a metacommunity of many local patches, connected by random dispersal and subject to disturbance at a constant rate (Levins 1969). Regional coexistence occurs if species with lower colonisation rates are stronger competitors (Hastings 1980; Tilman 1994). The model and methods are fully described in Box 1 and Appendix S1.

We used a trade-off function f to link the colonisation rates of two species to the probability that one or the other wins when competing for a patch (Calcagno *et al.* 2006). Their shape is governed by two parameters: α (the competitive asymmetry) and γ (the pre-emption index). The greater α, the steeper the CC trade-off, and the smaller γ, the more difficult it is to overtake a patch already occupied by another species. Unlike most existing models of CC

Box 1 Simple description of the two models used. Complete description on these models and simulations methods are given in Appendix S1

Patch dynamics Metacommunity (CC)

$$\frac{dp_{ij}}{dt} = c_i \sum_x p_{ix}\left(t_j - \sum_k p_{kj}\right) + c_i \left(\sum_x p_{ix}\right)\left(\sum_{k \neq i} p_{kj}\, f_j(c_i, c_k)\right) - \mu p_{ij} - p_{ij} \sum_{k \neq i} \left(c_k \left(\sum_x p_{kx}\right) f_j(c_k, c_i)\right)$$

$$\text{with } f_j(c_i, c_k) = \frac{\gamma_j}{1 + \exp(\alpha_j(c_i - c_k))}$$

(2)

This model is adapted from Calcagno *et al.* (2006), where p_{ij} is the fractions of patches occupied by species i and belonging to community j. Colonisation rate for species i is c_i and μ the extinction rate for all patches, and f_j the trade-off function in patches of community j. The trade-off function f_j in patches of community j has a logistic shape governed by two parameters, α_j the competitive asymmetry and γ_j the pre-emption index. Communities have size determined by their number of patches (community j containing a fraction t_j of all patches).

Metaecosystem

$$\frac{dN_x}{dt} = I_x - e_N N_x - \sum_{i=1}^{S} \alpha_{ix} N_x P_{ix} + r D_x + \Delta_{Nx}$$

$$\frac{dP_{ix}}{dt} = \alpha_{ix} N_x P_{ix} - m_{ix} P_{ix} - e_P P_{ix} + \Delta_{Pix}$$

$$\frac{dD_x}{dt} = \sum_{i=1}^{S} m_{ix} P_{ix} - r D_x - e_D D_x + \Delta_{Dx}$$

(3)

This model is adapted from Gravel *et al.* (2010a), where we consider stocks and flows of a single inorganic nutrient N, multiple primary producer species P_i and detritus D. The inorganic nutrient of patch x is open to external input with flow I_x and to output at rate e_N. Nutrient consumption by primary producer i at patch x is given by the linear functional response $\alpha_{ix} N_x P_{ix}$, where α_{ix} is the per capita consumption rate of the inorganic nutrient at patch x by species i. Primary producers die at the density-independent rate m_i. Primary producers are exported out of the system at rate e_P. Dead biomass is incorporated into the detritus compartment, a fraction of which is leached at rate e_D and mineralised at rate r. The connection between patches for each compartment C is modelled using passive dispersal of the type $\Delta_{Cx} = d_C(\bar{C} - C_x)$, where overlined quantities represent regional averages (global dispersal d_C is assumed for simplicity).

trade-off in which the environment is spatially homogeneous, we introduced spatial heterogeneity by letting the trade-off function f vary in space. We considered that there were n distinct communities, community j being characterised by trade-off function f_j (with α_j and γ_j). The variability in the trade-off function could reflect spatial variation of abiotic (e.g. soil fertility, microhabitat structure) or biotic (e.g. presence/absence of predators) factors on competitive abilities. Communities have size determined by their number of patches (community j containing a fraction t_j of all patches).

In each randomly generated metacommunity, we performed every single-community removal to obtain the distribution of impacts (Appendix S1). We used species richness as the ecological variable
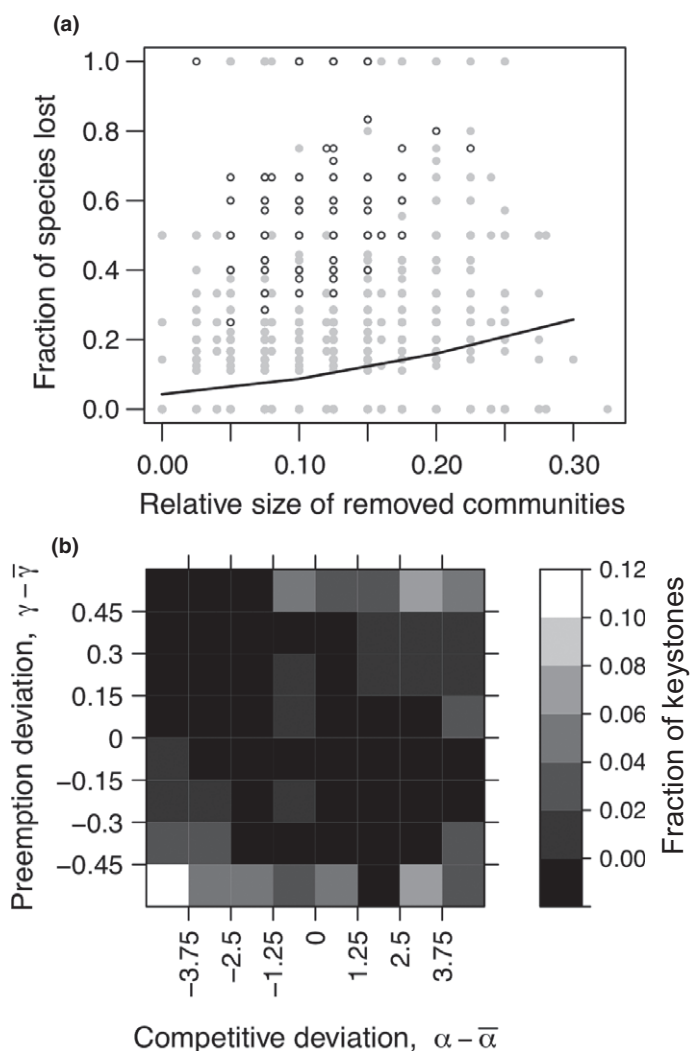
(a)

(b)

Figure 3 Keystoneness in patch dynamics metacommunities. (a) Community impacts Δ_j (fraction of species going extinct following community removal) as a function of the relative size of the removed community. Keystone communities, according to the best-fitting model with 80% coverage predictions (Table 1 in Appendix S1), are shown as white-filled circles. The average trend, according to the best-fitting model is represented by a black line. (b) The probability that a community was keystone as a function of its deviation from the average characteristics (competitive asymmetry α -x-axis- and pre-emption index γ - y-axis) of its metacommunity. Light grey areas correspond to higher probability of being keystone, darker areas, to lower probability.

of interest when calculating the impacts Δ_j, and relative community size t_j as community weight to control for dominance effects. We followed the model selection procedure described in Appendix S1 and tested eight different models incorporating initial species richness and/or metacommunity as additional explanatory variables. The best model was found to be the one including a metacommunity effect on the intercept (Table 1 in Appendix S1).

We found that a significant proportion of single-community removal experiments drove one or several species to extinction (up to 70% of species lost; Fig. 3a). The probability of causing at least one species extinction (i.e. having positive Δ_j) and the average number of species going extinct both increased with relative community size, reflecting dominance effects (Fig. 3a). There was a clear distinction between communities that did not cause any species extinction, and keystone communities, triggering one or more species extinction. Note that as we assumed no recolonisation from outside the metacommunity, species richness could not increase following habitat destruction, i.e. there could not be any burden in this particular example.

Keystone communities were characterised by having atypical species trait values: communities with higher than average, or lower than average, values of both competitive asymmetry α_j and preemption γ_j were the most likely to be keystones (Fig. 3b). In addition, the effects of α_j and γ_j were not independent: keystone communities were characterised by a positive association of α_j and γ_j values (Fig. 3b). Communities with low α_j and γ_j tended to be refuges for poorly competitive species: these species suffered less from stronger competitors in these communities owing to the weaker CC trade-off and the high level of pre-emption. Conversely, communities with high α_j and γ_j acted as refuges for highly competitive species as their ability to displace competitors was fully expressed in such communities. The presence of these two kinds of communities therefore contributed to species coexistence at the metacommunity level, and their loss had a strong negative impact on overall species richness.

Source–sink metaecosystem

We now consider a model of metaecosystem, defined as a set of local ecosystems connected together by exchanges of materials, organisms and nutrients (Loreau *et al.* 2003b). Deterministic coexistence in metaecosystems occurs because of species sorting, mass effect and patch dynamics, just as it does in typical metacommunities (Gravel *et al.* 2010a,b). However, spatial flows of materials, and their recycling, can considerably change the outcome of species interactions at the regional level. In a metaecosystem with passive spatial flows for instance, the biomass moves from the most productive localities to the least productive ones whereas the nutrients flow from the least productive localities to the most productive ones (Gravel *et al.* 2010a). The balance between these contrasting flows determines the net regional interaction between species located in different local ecosystems. Within metaecosystems, the impact of losing a local ecosystem derives clearly from both atypical species traits (e.g. competitive ability) and habitat characteristics (e.g. soil fertility).

We use here a simple source–sink metaecosystem model describing the dynamics of nutrient cycling and primary production in a heterogeneous landscape (Gravel *et al.* 2010a). We considered a single inorganic nutrient N, multiple primary producer species P_i and

detritus D. Local ecosystems (patches) were coupled by passive spatial flows among these compartments. The model described the stocks and flows for each compartment (full description in Box 1 and Appendix S1). Species were characterised by their local competitive abilities for the limiting nutrient N_i^* (the best competitor having the lowest N_i^* as in Tilman 1982). Competitive hierarchies were established by the spatial variation in species N_i^*. Parameters were chosen such that all species were expected to be, on average, regionally similar (Mouquet & Loreau 2002). We randomly assigned fertility to each patch. Consequently, only a few species could successfully establish in each patch in the absence of spatial nutrient flows (Gravel *et al.* 2010a). We simulated a metaecosystem of 10 primary-producer species competing in 10 different patches (Appendix S1 for details).
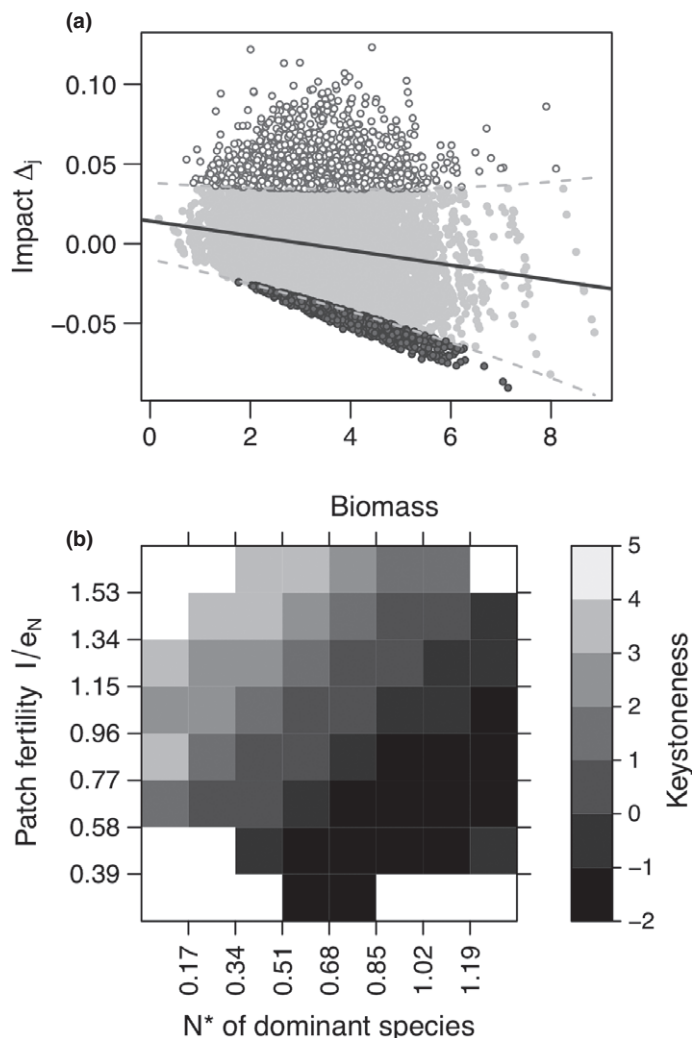

Figure 4 Keystoneness in metaecosystem. (a) Ecosystem impacts Δ_j (the change in primary productivity) as a function of total biomass within the focal ecosystem j (ecosystem weights). Keystone ecosystem (respectively burden), according to the best-fitting model (Table 2 in Appendix S1) with 80% coverage predictions (associated prediction interval is shown as a shaded area) are shown as white-filled circles (respectively dark grey circles). (b) Keystoneness (i.e. standardised residuals of the linear model at panel a) as a function of the competitive ability of the dominant species and patch fertility. White areas display no data point at all; light grey areas correspond to more likely keystones, darker areas, to more likely burdens.

To measure keystoneness, we considered metaecosystem primary productivity, a good proxy for the nutrient flows at the regional scale (Loreau *et al.* 2003b), measured as $\Phi = \sum_x \sum_i \alpha_{ix} N_x P_{ix}$ (where α_{ix} is the per capita consumption rate of the inorganic nutrient at patch x by species i). We took total biomass in the focal patch (prior to removal) to control for dominance effects. We tested eight different statistical models, six of which included metacommunity effects on the intercept and/or the slope of the productivity–biomass regression (Appendix S1). The best model included no metaecosystem effect at all, but had heteroscedasticity (Table 2 in Appendix S1).

We found a wide range of ecosystem impacts weakly correlated with total biomass (Fig. 4a), with the occurrence of keystone and burden ecosystems (points outside the envelope in Fig. 4a). Keystoneness in this setting was the result of a complex interplay between the distribution of species traits N^* and the patch fertility at both the local and the regional scales. Primary productivity in a patch was inversely related to the N^* of its dominant species (all other species had higher N^* and were thus less efficient at exploiting the nutrient than the dominant species). The removal of a patch dominated by a very efficient species with nutrient uptake (having a low N^*) had thus a much more important impact than the removal of a patch dominated by an inefficient species (Fig. 4b). This situation occurred because species with low N^* were good at producing biomass and exporting detritus to other patches, thus benefiting more to regional primary productivity. We also found that the fertility of the patch that was removed from the metaecosystem (Fig. 4b) was important to productivity with the most fertile patches having the highest impact on metaecosystem functioning than less fertile patches.

DISCUSSION

The keystone concept has a long history in community ecology, back to the seminal work by Paine on rocky intertidal communities (Paine 1966, 1969). Here, we suggest scaling up the concept to communities interconnected by dispersal and material flows (Loreau *et al.* 2003b; Leibold *et al.* 2004; Massol *et al.* 2011). We have investigated the impact of removing a focal community, using simple metrics of community weight to control for dominance effects. We defined keystone and burden communities as communities with disproportionately large impact (positive or negative) relative to their weight in the metacommunity. The metapopulation and landscape ecology literature has recognised that some habitat patches might be more important than others to regional dynamics. Hanski (1994) mentioned that some habitat patches could be more important to the long-term persistence of the entire metapopulation, e.g. when considering heterogeneity in patches area sizes (see also Hanski *et al.* 1996). While acknowledging variability in patch contribution to metapopulation dynamics (see also Brachet *et al.* 1999), no distinction was made between net and relative importance in these early studies. At the community level, good examples of key habitats for species recruitment and species diversity have been found both in marine and terrestrial ecology (e.g. Allison *et al.* 1998; Davidar *et al.* 2001; Tews *et al.* 2004). Our work provides a formalisation of this idea with clear connections to the historical definition of keystone effects and has broader applications for communities and ecosystems within complex landscapes of interconnected systems.

There are two reasons why a community or ecosystem might be keystone/burden in the two models we analysed. The first reason is environmental: if a patch possesses attributes (dis)favouring the focal property at the regional scale (e.g. high fertility in the meta-ecosystem model) regardless of the community it harbours, it may be a keystone (or a burden). This 'local quality' effect should be distinguished from dominance effects. For instance, in a metaecosystem, a patch may harbour a very high fertility, but at the same time display a very low standing biomass (e.g. if environmental constraints decreases the nutrient uptake efficiency of the dominant species). In such cases, the patch would fertilise other patches through inorganic nutrient flows, despite its low weight, and thus qualify as a keystone. The second reason is linked to species traits: if a patch harbours a community of species that play a critical role (e.g. communities with high or low values of competitive asymmetry and pre-emption in the CC model or communities with a very efficient producer specialised on certain patch types in the metaecosystem model), its removal is bound to critically impact the focal property. This 'local community composition' effect depends on the distribution of species traits within metacommunities/metaecosystems (as defined in Massol *et al.* 2011). Conversely, the local quality effect is dependent on the environmental characteristics of local communities/ecosystems.

The metaecosystem model also illustrates how local quality and local community composition effects can interact. Here, both effects are important in determining primary productivity at the regional scale. First, by considering a heterogeneous distribution of species' competitive abilities among communities, we generated 'source' patches dominated by very efficient species that stimulate global nutrient cycling and 'sink' patches dominated by very inefficient species promoting nutrient loss out of the metaecosystem (Gravel *et al.* 2010a). Second, by considering heterogeneity in fertilities, we also have obtained very productive patches with high impact on metaecosystem functioning and very unproductive patches that act as sinks for nutrients. In this context, a keystone ecosystem is a net exporter of nutrients, benefiting other patches by nutrient enrichment. On the contrary, a burden ecosystem is a net sink of nutrients, so that its removal ameliorates the regional distribution of nutrients. Overall, keystoneness will depend on a complex interplay between the distribution of traits (the competitive abilities N^*) and patch fertilities in the metaecosystem.

Keystoneness also depends on the importance of regional vs. local dynamics within the metacommunity, and thus on dispersal and landscape configuration (e.g. connectivity). For source–sink metacommunities and metaecosystems, strong community impacts (and thus potential for burden and keystone communities) should be expected mainly at intermediate dispersal, i.e. where the source–sink dynamics are the most important (Amarasekare & Nisbet 2001; Mouquet & Loreau 2003). The same pattern should hold for CC dynamics, especially regarding the dispersal between patches from different communities. It is likely that no keystone and burden communities will be found at very low or high level of dispersal because either the communities are too isolated or the metacommunity is homogenised. The landscape configuration may also be crucial in defining particular keystone communities. For instance, in metaecosystems, it has been shown that the source/sink status of each patch depends on the net balance between direct and indirect nutrient flows (e.g. inorganic nutrient vs. biomass fluxes as in Gravel *et al.* 2010a). This in turn does not depend only on the intrinsic local primary productivity, but also on neighbouring ecosystems. Thus, why a particular community/ecosystem may be keystone will also depend on the composition of the other communities within the metacommunity/metaecosystem.

Our two models are by nature spatially implicit with very simple landscape structures to maintain tractability. In a spatially explicit concept, a patch might have disproportionate effects on diversity or productivity not only because of its quality or its community composition, but also because it occupies a central or peripheral place in the spatial network of patches. In the same vein, certain patch networks might lead to a stronger or weaker dependence of the focal property on rare patch types (e.g. Economo & Keitt 2008), and thus alter the likelihood of finding keystone or burden communities. This spatial complexity could be incorporated by using metrics imported from network theory (e.g. Urban & Keitt 2001; Bodin & Norberg 2007; Urban *et al.* 2009) such as centrality or connectivity of nodes. For instance, Economo (2011) studied the impact of node removal in neutral metacommunities on the residual gamma diversity and found that the most connected communities are very important to maintain gamma diversity. Their centrality sustains larger populations and thus is essential to maintaining diversity across the other patches.

One challenge in applying the keystone community concept is choosing the right weight metric. We have been using simple metrics such as total abundances and biomass for the sake of simplicity, but a better strategy might be to explore what variable is most strongly correlated with impact, and use it as the weighting. In our flexible framework, there is no limit a priori on the number of weight variables one decides to control for. Model selection techniques (such as AIC) could be used to determine which, among a candidate set of community 'weight' variables, are most useful to predict community impact, and thus should be included in the reference model. Another difficulty will be deciding between different community properties, as it is likely that different properties (e.g. productivity and diversity in metacommunities Mouquet & Loreau 2003; Gravel *et al.* 2010b) will not yield similar keystoneness rankings of patches. A patch could potentially be a keystone for one property but a burden for another, and different patches may be keystones for different properties. How community properties such as diversity, stability and productivity are correlated has been intensively debated in the ecological literature both at the local and regional scales (Loreau *et al.* 2001; Bond & Chase 2002; Mouquet *et al.* 2002; Cardinale *et al.* 2004; Venail *et al.* 2010), but it not clear how they may covary after habitat removal within complex landscapes. A prospective direction for future research is to study these different community properties within a single modelling framework to identify synthetic community attributes and characterise general keystone communities. Insight will be gained by performing multivariate analyses (e.g. principal component analysis) including different properties of interest and calculating keystoneness on synthetic variables. Synthesising different properties, regressing them on a set of potential weight variables and accounting for spatial relations among communities may even be achieved in one step through redundancy analysis (e.g. Peres-Neto *et al.* 2006). As it is likely that different properties will contribute to the keystoneness of a community, such a multivariate approach might even become more useful in complex ecological systems.

The array of definitions for keystoneness that have been proposed all agree on one thing: keystone objects should be atypical in

terms of their impact when removed (Power *et al.* 1996; Hurlbert 1997; Libralato *et al.* 2006). They differ in what is intended by 'atypical': (1) atypical relative to other objects in the system (e.g. Mills *et al.* 1993), or (2) relative to what would be expected based on relative abundance/weight (e.g. Power *et al.* 1996). In this work, we have proposed a general framework that encompasses both aspects of the keystone concept. However, we recognise that this will be challenging to apply for natural systems, owing to experimental constraints or sample size limitations. Controlled experiments with microcosms might help explore community keystoneness with the advantage of high replication and a clear idea of the mechanisms underlying metacommunity dynamics during the experiment (Logue *et al.* 2011). In principle, removal experiments (as performed in our study) could also be done *in silico*, for natural systems that are documented enough and for which we can propose a realistic model of their dynamics.

The use of models, even general ones as we did here, can prove particularly useful to determine measurable characteristics of communities that are accurate proxies of keystoneness. Then, these characteristics could be measured in natural system to identify putative keystone communities without resorting to habitat removal experiments. For instance, the CC metacommunity model has highlighted two kinds of keystone patches: patches with either strong local CC trade-off (high α_j) and weak pre-emption (high γ_j), or weak CC trade-off (low α_j) and strong pre-emption (low γ_j). These two kinds of patches could in theory be identified without measuring actual parameters because they differ in the temporal turnover of species. Patches with low α_j and γ_j values are characterised by a low turnover of species, and little consistency in the turnover. In contrast, those with high α_j and γ_j values would present high turnover rates, and a strong successional pattern: species would most of the time be replaced with stronger competitors. The same approach could be applied to further models of community dynamics.

As a counterpart of the keystone concept, we introduced burden communities as communities whose removal increases the metacommunity property of interest. In source–sink metacommunities, burden communities hold species that are detrimental to the regional balance between competitive abilities. Within metaecosystems, they are sinks patches that contribute negatively to the regional nutrient balance. Note, that while this idea is an interesting extension of the keystone concept, it must be manipulated with caution as it might be seen as a plea for ecosystem engineering. Yet, as we have discussed above, community can be burden for some particular properties while being keystone for others. Thus, before applying these ideas to conservation biology and landscape management, more work needs to be done to find general community properties, e.g. by extending the idea of multifunctionality (Hector & Bagchi 2007; Isbell *et al.* 2011) to whole communities and ecosystems within complex landscape.

CONCLUSION

We have illustrated how the concept of keystone can be applied to communities and ecosystems. The fact that ecological systems are linked with each other in a network of interconnected patches naturally leads to the idea that some communities/ecosystems might be more important to regional properties than others. As we have shown, this importance can be related to community weight (dominance effects) or to more subtle effects related to the distribution of species traits among communities and environmental heterogeneity. Even if detecting keystone communities and ecosystems may prove as challenging as detecting keystone species in the field (Power *et al.* 1996), their importance, particularly in a context of unpreceded habitat destruction (Harrison & Bruna 1999; Fahrig 2003; Dobson *et al.* 2006) is central to landscape ecology and conservation. One of the next steps for metacommunity ecology should be to explore further the different mechanisms that lead to heterogeneity in the distribution of regional effects and develop appropriate tools to measure them in the field.

AUTHORSHIP

NM conceived the project. All authors contributed substantially to the modelling and analyses. All authors wrote the paper.

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