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LETTER

Spatial heterogeneity of biomass turnover has contrasting effects on synchrony and stability in trophic metacommunities

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Abstract

Spatial heterogeneity is a fundamental feature of ecosystems, and ecologists have identified it as a factor promoting the stability of population dynamics. In particular, differences in interaction strengths and resource supply between patches generate an asymmetry of biomass turnover with a fast and a slow patch coupled by a mobile predator. Here, we demonstrate that asymmetry leads to opposite stability patterns in metacommunities receiving localized perturbations depending on the characteristics of the perturbed patch. Perturbing prey in the fast patch synchronizes the dynamics of prey biomass between the two patches and destabilizes predator dynamics by increasing the predator's temporal variability. Conversely, perturbing prey in the slow patch decreases the synchrony of the prey's dynamics and stabilizes predator dynamics. Our results have implications for conservation ecology and suggest reinforcing protection policies in fast patches to dampen the effects of perturbations and promote the stability of population dynamics at the regional scale.

KEYWORDS
asymmetry, conservation, dispersal, food chain, source-sink, stochastic perturbations

INTRODUCTION

Since May (1972) demonstrated that stability was not an inherent property of ecological interaction networks, ecologists have been relentlessly looking for the mechanisms ensuring ecosystem stability. Spatial heterogeneity has long been identified as one of the main factors promoting the maintenance of biodiversity and the stability of ecosystems. For instance, in competitive metacommunity models, spatial heterogeneity provides local favourable conditions to each species of the regional pool (Amarasekare & Nisbet, 2001; Chesson, 2000; Holt, 1984), which in turn ensures species persistence in less favourable patches by source-sink dynamics (Loreau et al., 2003; Mouquet & Loreau, 2002, 2003). The stability of the temporal dynamics of species biomass is generated by the asynchrony of the dynamics between patches, which leads to compensatory dynamics (Loreau et al., 2003; Loreau & de Mazancourt, 2008). In trophic metacommunities, spatial heterogeneity has also been identified as a stabilizing factor (Hastings, 1977, 1978; Steele, 1974), but the underlying mechanisms are more complex due to the interplay between trophic and spatial dynamics.

Inspired by the description of fast and slow energy channels by soil ecologists (i.e. in terms of biomass turnover), Rooney et al. (2006) highlighted the stabilizing effect of the asymmetry of energy flows in ecosystems with a food web model consisting of one mobile predator feeding on two energy channels. In their model, the asymmetry of energy flow is generated by different interaction strengths between predators and prey (i.e. increased attack rate in one energy channel compared with the other one, see Figure 1) and different consumption rates of a common resource by the two basal species, which in turn promotes the asynchrony of prey biomass dynamics in response to the perturbation of predators. This asynchrony explained the increase in stability, as measured by asymptotic resilience, that is the rate at which a system returns to equilibrium after a perturbation in the very long run. Asynchrony of local population dynamics leads to more stable dynamics (low coefficient of variation (CV) of biomass) at higher hierarchical levels due to compensatory dynamics (Gonzalez & Loreau, 2008; Loreau et al., 2003; Loreau & de Mazancourt, 2013; Wilcox et al., 2017). Although synchrony patterns are

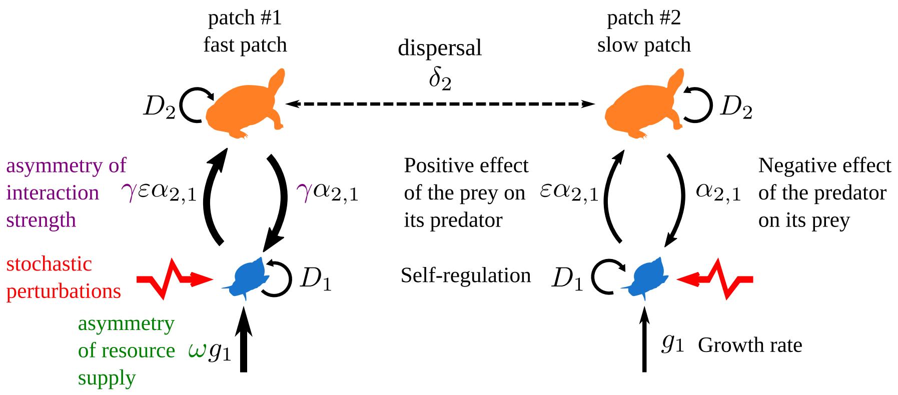

FIGURE 1 The metacommunity model consists of two patches, each sustaining a predator–prey couple linked by predators, which disperse at a very high scaled rate δ_2. Prey grow at a rate g_1 and species populations i are also limited by self-regulation D_i (negative intraspecific interactions or density-dependent mortality). Predators attack prey at a rate $\alpha_{2,1}$ (interaction strength) and assimilate a fraction ε of the ingested biomass. Spatial heterogeneity is embodied by the asymmetry of resource supply (green) and the interaction strength (purple), which are higher in patch #1 by factors ω and γ, respectively. Consistent with Rooney et al. (2006), patch #1 is called the fast patch, and patch #2 is called the slow patch. Prey receive stochastic perturbations either in patch #1 or in patch #2 (red arrows).

tightly linked to stability patterns, subsequent studies suggested that increased asymmetry does not necessarily lead to increased stability. For example, Ruokolainen et al. (2011) presented a model in which biomass fluctuations can become more variable with increasing asymmetry. Hence, the relationship between asymmetry and stability is not trivial and the mechanisms governing asynchrony through differences in energy flow between the fast and slow channels are not well understood. To fill this gap, we propose to consider the effects of asymmetry from a metacommunity perspective since recent theoretical studies were able to accurately explain synchrony and stability patterns in metacommunities (Quévreux, Barbier, & Loreau, 2021; Quévreux, Pigeault, & Loreau, 2021).

Metacommunities embody the spatial dimension of interaction networks: they consist of distant patches connected by the dispersal of the organisms living in each patch (Leibold et al., 2004; Leibold & Chase, 2017). The metacommunity framework is particularly suitable to represent the spatial heterogeneity observed in ecosystems because each community has its own characteristics such as biomass turnover. Heterogeneity of biomass turnover is common in nature, for instance in the form of a highly productive autotroph-based channel (aboveground or pelagic compartment) and a slow detritus-based channel (belowground or benthic compartment; Ward et al., 2015; Wolkovich et al., 2014). Following Rooney et al.'s (2006) model, many studies implemented spatial heterogeneity through the asymmetry of interaction strength and/or resource supply to manipulate differences in biomass turnover between the energy channels in each patch (Anderson & Fahimipour, 2021; Goldwyn & Hastings, 2009; Ruokolainen et al., 2011). In particular, interaction strength is key in community dynamics because it governs food web structure, stability (Neutel et al., 2002) and biomass distribution (Barbier & Loreau, 2019) by simultaneously determining predator growth and prey mortality. Therefore, its significant variations observed in nature, often reported as predation risk by prey in field studies (Table 1), should lead to dramatic variations in community functioning across space.

TABLE 1 Approximative relative increase in predation risk between low-risk and high-risk environments (equivalent to the asymmetry of interaction strength γ in Figure 1). See Gorini et al. (2012) for an extended review and more references.

Predator	Prey	γ	References
American marten	Vole species	1.6	Andruskiw et al. (2008)
Wolf	Moose	14–100	Gervasi et al. (2013)
Wolf	Roe deer	2.5–8	Gervasi et al. (2013)
Wolf	Elk	10	Kauffman et al. (2007)
Savannah predators	Savannah ungulates	1.5–4.5	Thaker et al. (2011)
Artificial gecko	Australian predators	2.8	Hansen et al. (2019)
Lynx	Roe deer	2	Gehr et al. (2020)
Puma	Vicuña	1.6	Donadio and Buskirk (2016)

In addition to the asymmetry of interaction strength, Rooney et al. (2006) highlighted the importance of mobile predators coupling two different energy channels, a keystone role in ecosystem functioning largely reported by empirical studies (Dolson et al., 2009; Olff et al., 2009; Schindler & Scheuerell, 2002; Schmitz, 2004; Schmitz et al., 2010; Vadeboncoeur et al., 2005). In Rooney et al.'s (2006) model, perturbation of the mobile predator leads to an asynchronous response of prey, which stabilizes the food web. However, Quévreux, Barbier, and Loreau (2021) showed that the perturbation and dispersal of particular trophic levels govern synchrony and stability in symmetric metacommunities. In asymmetric metacommunities, the perturbation of particular patches should lead to different synchrony and stability patterns at the metacommunity scale because of the different dynamics in each patch in response to perturbations. In parallel to the keystone role of mobile predators, keystone communities (sensu Mouquet et al. (2013), which are equivalent to keystone patches), should have a major influence on synchrony and stability patterns. Therefore, we expect that asymmetry is not a generic stabilizing factor, as claimed by Rooney et al. (2006), but strongly depends on characteristics of the perturbed patch. To explore this hypothesis, we consider a simple metacommunity model of two patches hosting a predator–prey couple and with asymmetric interaction strength and resource supply. The stability of the metacommunity is assessed by the response at different scales (e.g. CV of the biomass of a species at the local and regional scales) when prey receive stochastic perturbations in one of the two patches. We show contrasting effects of asymmetry: perturbing prey in the fast patch (equivalent to the fast channel defined by Rooney & McCann, 2012) promotes prey synchrony and decreases predator stability at the metapopulation scale while perturbing the slow patch has the opposite effects.

METHODS

Rooney et al. (2006) studied the effect of asymmetry in the context of a food web in which a mobile predator feeds upon two energy channels, each consisting of a consumer feeding on a primary producer, which itself takes up a common resource. They only considered the asynchrony of the dynamics of the consumer populations in response to the perturbation of the mobile predator, thus neglecting the dynamics of the other species and the effect of perturbations that selectively affect one channel. In addition, they used asymptotic resilience as a measure of stability, but recent theoretical advances have shown that this measure is not representative of the stability of the whole community (see below). Therefore, we revisit the consequences of asymmetry on stability by replacing Rooney et al.'s (2006) model in the context of a metacommunity, which allows us to study the system response to perturbations of specific local populations.

Metacommunity model

We use the model proposed by Quévreux, Barbier, and Loreau (2021) based on the food chain model developed by Barbier and Loreau (2019). The model consists of two patches that each sustain a food chain with Lotka-Volterra predator–prey interactions defined by Equations (1a–1d).

$$\text{Fast patch (1)}\begin{cases}\dfrac{dB_1^{(1)}}{dt}=B_1^{(1)}\left(\omega g_1-D_1B_1^{(1)}-\gamma\alpha_{2,1}B_2^{(1)}\right)+\delta_1\left(B_1^{(2)}-B_1^{(1)}\right)\\ \dfrac{dB_2^{(1)}}{dt}=B_2^{(1)}\left(-r_2-D_2B_2^{(1)}+\gamma\varepsilon\alpha_{2,1}B_1^{(1)}\right)+\delta_2\left(B_2^{(2)}-B_2^{(1)}\right)\end{cases} \tag{1a–1b}$$

$$\text{Slow patch (2)}\begin{cases}\dfrac{dB_1^{(2)}}{dt}=B_1^{(2)}\left(g_1-D_1B_1^{(2)}-\alpha_{2,1}B_2^{(2)}\right)+\delta_1\left(B_1^{(1)}-B_1^{(2)}\right)\\ \dfrac{dB_2^{(2)}}{dt}=\underbrace{B_2^{(2)}\left(-r_2-D_2B_2^{(2)}+\varepsilon\alpha_{2,1}B_1^{(2)}\right)}_{\text{Intra-patch dynamics}}+\underbrace{\delta_2\left(B_2^{(1)}-B_2^{(2)}\right)}_{\text{Dispersal}}\end{cases} \tag{1c–1d}$$

$B_1^{(1)}$ and $B_2^{(1)}$, and $B_1^{(2)}$ and $B_2^{(2)}$ are the biomasses of prey and predators, respectively, in patch #1 and #2, with superscripts indicating the patch and subscripts the trophic level of populations. g_i, r_i, D_i and δ_i are the growth, density-independent death, density-dependent mortality (intraspecific competition) and dispersal rates, respectively, of each species i (note that we will set g_i=0 for $i > 1$, see below). $\alpha_{i,j}$ is the interaction strength between consumer i and prey j and ε is the biomass conversion efficiency. According to Quévreux, Barbier, and Loreau (2021), the time scale of the system is rescaled by the metabolic rate of prey, and biological rates of each species i are rescaled by its intraspecific interaction rate D_i. Considering scaled parameters enables us to efficiently explore a wide range of ecological situations and to assess the robustness of our results. The details of the rescaling are given in Appendix S1 since description of the original model is enough to fully understand our results and the values of scaled parameters are summarized in Table S1 in the supporting information.

We retain the two main features of Rooney et al.'s (2006) model. First, predators disperse at a very high rate $\delta_2 \gg 0$ and strongly couple the two patches, while prey are immobile ($\delta_1 = 0$). Slightly mobile prey ($0 < \delta_1 \ll \delta_2$) should not change the results because Quévreux, Barbier, and Loreau (2021) showed that the species for which dispersal has the strongest influence drives the coupling between the two patches. Second, resource supply and interaction strength are asymmetric between patches since they are higher in patch #1 by factors γ and ω respectively (Figure 1). Patch #1 corresponds to the fast energy channel, in which biomass has a high turnover, while patch #2 corresponds to the slow channel. Therefore, we call patch #1 the fast patch and patch #2 the slow patch. We set $\gamma = \omega$ to ensure species persistence over the entire range of parameters (see Appendix S2-2-2 and Figure S2–8), and to reflect the correlation between these two parameters in nature. For instance, herbivores enhance primary production in their grazing lawns through nutrient cycling and carnivores target resource-rich patches (Hopcraft et al., 2010). In the following, we use the generic term 'asymmetry' to refer to joint variations of these two parameters in patch

#1, which leads to asymmetry of biomass turnover between the two patches. We explore the response of the metacommunity to independent variations of γ and ω in Appendix S2-2-5.

Response to stochastic perturbations

We use the same methods as Quévreux, Barbier, and Loreau (2021) to study the response of metacommunities to stochastic perturbations. Indeed, recent studies advocate for the use of the temporal variability of biomass (Arnoldi et al., 2018; Haegeman et al., 2016), which is measured by the coefficient of variation (CV), and can be easily measured experimentally. In addition, Wang and Loreau (2014, 2016), Wang et al. (2019), and Jarillo et al. (2022) showed that CVs scale up from local populations to community, regional and metacommunity levels, therefore providing a comparison of stability at different scales. Many other measures of stability are considered in ecology (Arnoldi et al., 2016), such as the asymptotic resilience used in Rooney et al. (2006), but Haegeman et al. (2016) have showed that the latter is only representative of the response of rare species to perturbations (also see Quévreux, Barbier, & Loreau, 2021). Here, we provide only a brief description of the main concepts, but a thorough description is available in Appendix S1.

Prey in the fast or slow channel receive stochastic perturbations that are represented by Equation (2).

$$\frac{dB_i}{dt} = \underbrace{f_i\left(B_1, \ldots, B_S\right)}_{\text{Deterministic}} + \underbrace{\sigma_i \sqrt{B_i^*}\frac{dW_i}{dt}}_{\text{Perturbation}} \tag{2}$$

$f_i\left(B_1, \ldots, B_S\right)$ represents the deterministic part of the dynamics of species i, as described by (1a–1d). Stochastic perturbations are defined by their standard deviation σ_i and dW_i / dt, a white noise term with a mean of 0 and variance of 1. Perturbations also scale with the square root of the biomass at equilibrium B_i^* of the perturbed population. Such scaling makes the perturbations similar to demographic stochasticity (from birth to death processes) that evenly affect each species regardless of abundance (Arnoldi et al., 2019). In other words, the ratio of mean species biomass variance to perturbation variance is roughly independent of biomass, which disentangles the effect of asymmetry on perturbation transmission from its effect on species abundance. Therefore, for different perturbations affecting different species with the same value of standard deviation σ_i, we generate a similar variance at the metacommunity scale regardless of the abundance of the perturbed species and excite the entire metacommunity with the same intensity (see Figures S2 and S3).

In the following, we assess the temporal variability of the biomass of each population induced by stochastic perturbations affecting the metacommunity. Therefore, we linearize the system in the vicinity of equilibrium to obtain Equation (3) where $X_i = B_i - B_i^*$ is the deviation from equilibrium.

$$\frac{d\vec{X}}{dt} = J\vec{X} + T\vec{E} \tag{3}$$

J is the Jacobian matrix, which represents the linearized direct effects between populations in the vicinity of equilibrium, and T defines how the perturbations $E_i = \sigma_i dW_i / dt$ apply to the system (i.e. which species they affect and how they scale with biomass, where T is a diagonal matrix whose terms are $T_{ii} = \sqrt{B_i^*}$).

The stationary variance–covariance matrix C^* of species biomasses (variance–covariance matrix of $\vec{X}$, see proof in Appendix S1) can be directly calculated from the variance–covariance matrix of perturbations V_E (variance–covariance matrix of $\vec{E}$) by solving the Lyapunov Equation (4) without simulating the response to an actual stochastic perturbation (Arnold, 1974; Arnoldi et al., 2016; Quévreux, Barbier, & Loreau, 2021; Wang et al., 2015).

$$JC^* + C^*J^\top + TV_ET^\top = 0 \tag{4}$$

The expressions for V_E and T and the method to solve the Lyapunov equation are detailed in Appendix S1-6. From the variance–covariance matrix C^*, we compute the coefficient of correlation of the biomass dynamics between the two populations of each species (see Equation (S1-18)) and we measure the stability with the coefficient of variation (CV) of the biomass.

In addition, biomass CVs can be measured at different scales: population scale (e.g. biomass CV of prey in patch #1), metapopulation scale (e.g. CV of the total biomass of prey) and metacommunity scale (e.g. CV of the total biomass of predator and prey put together) to assess the effects of asymmetry at local and regional scales (Figure 3a and see Appendix S1). Finally, we quantify the synchrony of the dynamics of the different populations with the coefficient of correlation, which is also computed from the variance–covariance matrix C^* (Appendix S1).

This framework based on small perturbations is common in ecological stability theory (e.g. asymptotic resilience) and gives a first idea of the consequences of large perturbations. However, it does not take into account nonlinearities and further work is needed to generalize to larger perturbations.

RESULTS

Effects on stability

We describe how the asymmetry of interaction strength γ and resource supply ω shape metacommunity stability at different scales. Since predators have a very high-scaled dispersal rate ($d_2 = 10^6$), their populations are perfectly correlated and display the same dynamics. Our main result is that prey become more correlated when they are perturbed in the fast patch, while they become more anticorrelated when they are perturbed in the slow patch (Figure 2). Increasing asymmetry amplifies the difference in correlation between these two scenarios, and this pattern qualitatively holds for various combinations of the physiological and ecological parameters (see Figures S2–S11). We still observe this correlation pattern in the presence of additional trophic levels (see Figures S2–S24 and S2–S32), which means the system described in Figure 1 acts as a 'metacommunity module' leading to a consistent correlation pattern regardless of the presence of lower or higher trophic levels.

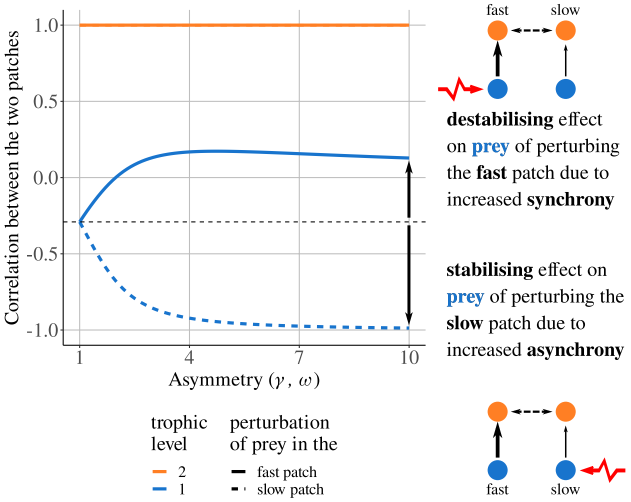

FIGURE 2 Spatial correlation between the populations of each species depending on asymmetry of interaction strength γ and resource supply ω when predators disperse, and prey are perturbed in the fast or slow patch. The horizontal dashed line emphasizes the value of the correlation of prey populations without asymmetry ($\gamma = \omega = 1$). Note that the curves for predators overlap because their high dispersal that perfectly correlates their dynamics regardless of the perturbed patch.

Increasing asymmetry has contrasting effects on biomass CV at different scales as well (Figure 3a). At the population scale, it increases the biomass CV of each population when prey are perturbed in the fast patch (Figure 3b). When prey are perturbed in the slow patch, increasing asymmetry slightly alters the biomass CV of prey in the fast patch, increases the biomass CV of prey in the slow patch and decreases the biomass CV of predators. This discrepancy can be attributed to the strong effect of the asymmetry of interaction strength γ on prey biomass in patch the slow patch (Figure 4): prey biomass strongly decreases with γ in the slow patch, which increases their biomass CV.

At the metapopulation scale, asymmetry increases the biomass CV of prey in both scenarios of perturbation (Figure 3c). However, this result is not true for all values of physiological and ecological parameters (Figures S2–S12A) because of the various responses of prey biomass to asymmetry among patches (Figures S2–S10A). The biomass CV of predators is higher when prey are perturbed in the fast patch compared with the case in which prey are perturbed in the slow patch (Figure 3c), which is consistent for all values of physiological and ecological parameters (see Figures S2–S12A).

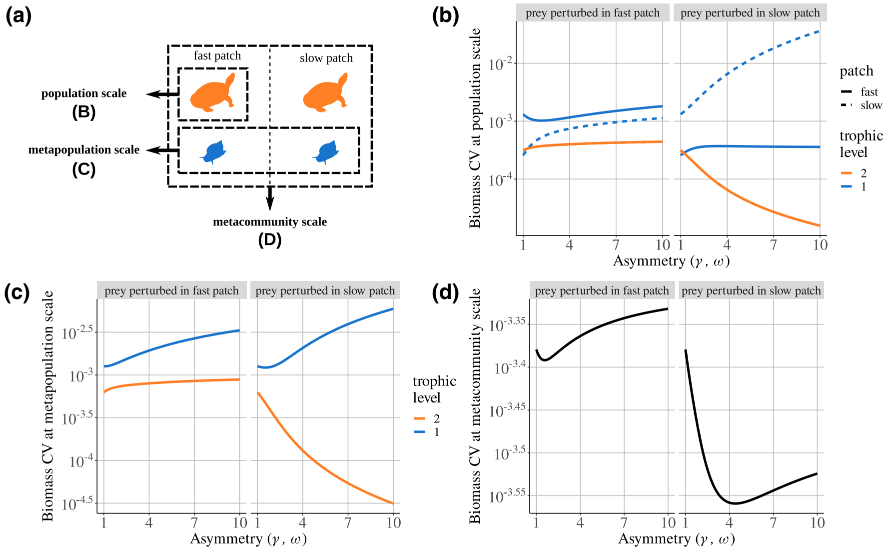

FIGURE 3 Stability at different scales depending on asymmetry of interaction strength γ and resource supply ω when predators disperse and prey are perturbed in the fast or slow patch. (a) The temporal variability in the metacommunity is assessed by the coefficient of variation (CV) of biomass at different scales: population scale (biomass CV of one species in one patch), metapopulation scale (CV of the total biomass of one species across patches) and metacommunity scale (CV of the total biomass of the entire metacommunity). (b) Biomass CV at the population scale. Note that the curves for predators overlap because their high dispersal perfectly balances their biomass distribution between the two patches. (c) Biomass CV at the metapopulation scale. (d) Biomass CV at the metacommunity scale.

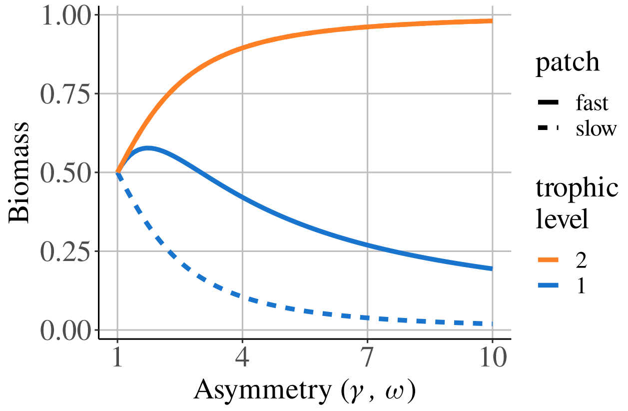

FIGURE 4 Distribution of the biomass of each species among patches depending on the asymmetry of interaction strength γ and resource supply ω. Note that the curves for predators overlap because their high dispersal that perfectly balances their biomass between the two patches.

Finally, stability at the metacommunity scale depends on the distribution of biomass and CV among species. In our particular case ($\varepsilon a = 1$ and $ma = 1$, see Appendix S1 for the description of scaled parameters), predators have the largest total biomass (Figure 4) and drive the biomass CV at the metacommunity scale for low asymmetry (Figure 3d). For high asymmetry, when prey are perturbed in the slow patch, the CV of total biomass increases with asymmetry because it is driven by prey in the slow patch, whose biomass CV is much higher than the biomass CV of predators, which compensates for their lower biomass. Other values of physiological and ecological parameters lead to other distributions of biomass and CV among species, which can make prey drive the stability at the metacommunity scale (see Figures S2–S10 and S2–S12).

Underlying mechanisms

To unveil the mechanisms governing the stability of heterogeneous metacommunities, we look deeper into the dynamics after a pulse perturbation (Figure 5a) and explain them with the direct effects between species quantified by the Jacobian matrix (see Equation (3)). When the perturbation of prey occurs in the fast patch, the strong direct effect of prey on predators (and vice versa) in the fast patch due to the asymmetry of interaction strength γ (Figure 5b) leads to a strong response of predators ①, which in turn drives the response of the two prey populations ②. In detail, predator biomass in the fast patch first increases because of the abundance of prey. Then, predators deplete prey biomass in both patches and correlate their dynamics, which explains why asymmetry of interaction strength γ increases prey correlation when prey are perturbed in the fast patch.

When the perturbation of prey occurs in the slow patch, the weak direct effect of prey on predators (Figure 5b) leads to a small response of predators ③. In turn, the very low direct effect of predators on prey in the slow patch does not allow perturbations to ripple back to the slow patch where prey slowly respond from the initial perturbation ④ (Figure 5b). This slow response also synergizes with the source-sink dynamics in the metacommunity (Figure 4; Figures S2–S7), which leads to a lower biomass of prey in the slow patch compared to a metacommunity without dispersal, therefore decreasing biomass flows in the slow patch and further decreasing its response speed. This difference in response speed between the fast and slow patches leads to the anti-correlation of prey populations because it increases the time interval in which they have opposite variations: an increase in the biomass of prey in the fast patch, which follows the initial decrease due to predation, and a slow decrease in prey biomass in the slow patch.

DISCUSSION

We have explored the response of a spatially heterogeneous two-patch metacommunity model to single-patch perturbations. Differences in interaction strength and resource supply between patches generated a patch with high biomass turnover, the 'fast' patch, and one with low biomass turnover, the 'slow' patch. We showed that this spatial heterogeneity has contrasting effects on stability depending on which patch is perturbed. Perturbing prey in the fast patch (in which interaction strength and resource supply are the highest) tends to synchronize the dynamics of prey biomass and increases the temporal variability of predator dynamics at the metapopulation scale, while perturbing prey in the slow patch decreases the synchrony of prey dynamics and the temporal variability of predator dynamics. These contrasting effects are due to asymmetric transmission of perturbations within each patch, itself caused by different biomass distributions and interaction strengths between the two patches. Perturbations are strongly transmitted from the fast to the slow patch, while the reverse transmission is weak. Consequently, the fast patch drives the dynamics of the metacommunity and synchronizes prey dynamics, while the slow patch does not, and the nearly independent responses to perturbation in the two patches decreases the synchrony of prey dynamics.

Stability in a heterogeneous world

Our results show that spatial heterogeneity, which is represented by the asymmetry of interaction strength and resource supply as in Rooney et al. (2006), generates mechanisms that alter local and regional dynamics, which deeply changes the synchrony of population dynamics and the stability of the metacommunity at different scales. Quévreux, Barbier, and Loreau (2021) showed that, in a homogenous metacommunity,

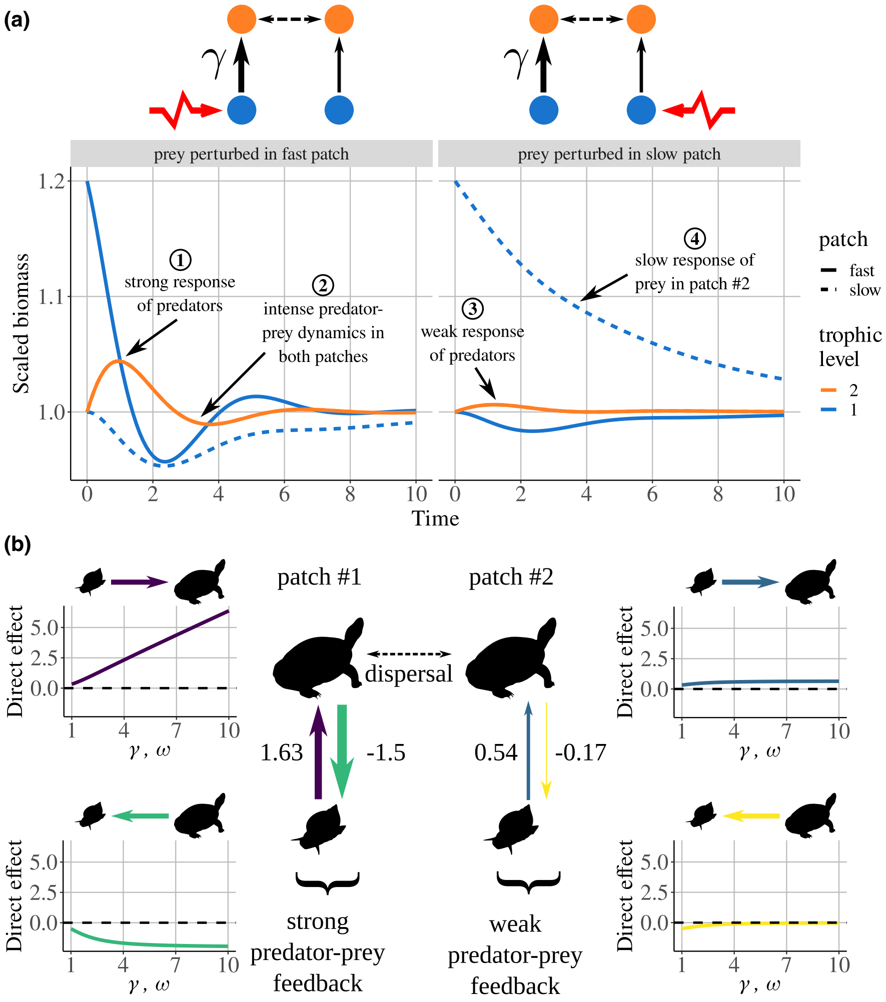

FIGURE 5 (a) Time series of biomasses rescaled by their value at equilibrium after an increase of 20% in prey biomass in the fast (left panel) or slow patch (right panel) for a value of asymmetry of interaction strength $\gamma = 3$ and resource supply $\omega = 3$. (b) Direct effect of prey on predator (and vice versa) depending on the asymmetry of interaction strength γ and resource supply ω. Direct effects correspond to the terms of the Jacobian matrix and the dashed line emphasizes the null direct effects. On the central schema, the numbers are the numeric values of the terms of the Jacobian matrix corresponding to each arrow for $\gamma = \omega = 3$.

spatial correlations between patches can be obtained from within-patch correlations, the dispersing species making the link between the two (see Figures S2–S38 for a summary of the results of Quévreux, Barbier, & Loreau, 2021). In other words, knowledge of the dynamics at the local scale is enough to understand the stability pattern at the metacommunity scale. In a heterogeneous metacommunity, a similar approach does not work because patches do not contribute equally to the dynamics. In particular, a patch with fast energy flow can have an overwhelming impact (see Figures S2–S9). Clearly, the dynamics at the metacommunity scale cannot be assessed from the dynamics at the local scale, as in Quévreux, Barbier, and Loreau (2021); it is an emergent property resulting from the tight interplay between the strengths of perturbation transmission in the two patches.

Rooney et al. (2006) explained that each patch has dynamics with different speeds: the fast channel (with higher interaction rates and resource supplies) enables a quick response after a perturbation while the slow channel dampens the dynamics in the long term and prevents the system from overshooting. However, two aspects of our approach allow us to generalize their results. First, Rooney et al. (2006) only considered a perturbation of the top mobile predator, which simultaneously transmits perturbations to the two channels and leads to the mechanism they detailed. In our model, we locally perturb non-mobile species, which makes the local transmission of perturbations through trophic interactions more important, generates the dominance of the fast patch on the slow patch (Figure 5), and thus reveals the local context dependency of the effect of perturbations. Second, they measured food web stability by asymptotic resilience (dominant eigenvalue of the Jacobian matrix of the system), which is often determined by rare species (Haegeman et al., 2016). Instead, we consider stability at different scales in response to perturbations, which allows us to derive more relevant results. On the one hand, the asynchrony of prey dynamics, when they are perturbed in the slow patch (Figure 2), stabilizes the dynamics of predators because their resource supplies are asynchronous. On the other hand, the dynamics of prey at the metapopulation scale are not stabilized by their asynchrony (Figure 3c) because of the low local stability in the slow patch (Figure 3b), which decreases the overall stability of prey. The potential stabilizing effect of asymmetry depends both on the perturbed patch and the considered trophic level. Therefore, the overall stability at the metacommunity scale is governed by the relative contributions of the various populations in response to local perturbations, and asymmetry *per se* does not have a stabilizing effect.

Our description of the mechanisms underlying the apparent stabilizing effects of spatial heterogeneity shed new light on the results of previous theoretical studies. Goldwyn and Hastings (2009) and Ruokolainen et al. (2011) found that the asymmetry of interaction rate leads to asynchrony by generating out-of-phase dynamics in a system with endogenous oscillations. In particular, Ruokolainen et al. (2011) found a U-shaped relationship: for moderate asymmetry, the spatial asynchrony of predator and prey populations is maximal, which leads to optimum stability at the metacommunity scale. Our results suggest that moderate asymmetry would alter the phase of the oscillations in each patch while keeping the amplitude of oscillations equivalent, therefore promoting asynchrony. Conversely, a strong asymmetry would increase the imbalance between oscillation amplitude and enable the fast patch to take over the slow patch, which would bring back synchrony. However, their results rely on phase-locking (Goldwyn & Hastings, 2008; Jansen, 1999; Lloyd & May, 1999; Vasseur & Fox, 2009), which is the coupling of the phase of oscillators embodied by predator–prey pairs in each patch. Although our results provide interesting insights into metacommunity dynamics, they cannot capture the fine mechanisms underlying non-linear phenomena such as phase-locking, and thus further studies are needed to identify these mechanisms.

Generality of the effects of asymmetry on stability

Our main result is that asymmetry is stabilizing for predators when the slow patch is perturbed, while it is destabilizing when the fast patch is perturbed. Prey stability decreases with increasing asymmetry regardless of which patch is perturbed. This result is robust to several deviations from the original model we have described. First, we show that the described mechanisms are valid for a wide range of ecological and physiological parameters leading to various distributions of biomass among predators and prey (see Figures S2–S10 and S2–S11) and to variations in the dispersal rate of predators (see Figures S2–S20). In addition, we observe the same results for longer food chains as long as prey populations are directly coupled by the dispersing top predator (see Figures S2–S24 and S2–S25). Currently, we do not identify clear patterns for species lower in the food chain over a wide range of ecological and physiological parameters. Further studies are needed to investigate the potential indirect effects propagating across the food chain. Based on our preliminary results, we hypothesize that the setup studied here can be considered as a 'metacommunity module' leading to correlation and stability patterns robust to the presence of other trophic levels (see Figures S2–S31 to S2–S33). Second, the mechanisms are not restricted to prey populations coupled by a mobile predator but also apply to predator populations coupled by a mobile prey (see Figures S2–S28). Therefore, we anticipate that mobile predators are not the only major drivers of synchrony and stability in ecosystems (Dolson et al., 2009; Olff et al., 2009; Rooney & McCann, 2012; Schindler & Scheuerell, 2002; Vadeboncoeur et al., 2005), and resource species may also have a similar impact. Taken together, these two points strongly suggest that the mechanisms underlying stability and synchrony in response to perturbations should be general to metacommunities regardless of the ecological parameters, biomass distribution and dispersal among species.

Spatial heterogeneity has often been presented as a generic condition generating mechanisms ensuring stability, but our results contradict this statement. Models focusing on asymmetric feeding by consumers on different energy channels or different patches showed that it promotes the existence of stable equilibria (McCann et al., 1998), greater asymptotic resilience (Rooney et al., 2006), asynchrony of prey in response to predator perturbation (Rooney et al., 2006) and out-of-phase limit cycles (Goldwyn & Hastings, 2009; Ruokolainen et al., 2011). All these studies considered measures of stability aiming to capture general stability properties of metacommunities and missed the targeted effects of perturbations, as we explained earlier. Although asymmetry does not necessarily promote stability, our results show that general mechanisms drive the response of metacommunities to localized perturbations, therefore providing a valuable framework to assess the response of ecosystems to localized perturbations due to human activity. Additionally, these mechanisms enable us to understand the effect of environmental perturbations affecting all patches. As demonstrated by Arnoldi et al. (2019), environmental perturbations affect abundant populations the most. Since in our model the prey population in the fast patch is the most abundant population (see Figures S2–S34), we anticipate that the fast patch governs the dynamics of metacommunities in which all populations are perturbed (see Figures S2–S36). Finally, our finding that the fast patch drives the dynamics of the slow patch suggests similar responses in a metacommunity with more than two patches. In a three patch metacommunity, the fastest patch drives the dynamics of all the slower patches and thus is central in the correlation and stability patterns at the metacommunity scale (see Figures S2–S37).

Implications for conservation

The metacommunity framework has long been used in conservation ecology (Johnson et al., 2013; Patrick et al., 2021; Schiesari et al., 2019). Conservation efforts are usually concentrated on particular locations and useful management must consider the ecological processes acting at the landscape scale (Chase et al., 2020; Van Teeffelen et al., 2012). For instance, spatial heterogeneity is key to ensuring species coexistence and diversity at the regional scale, which ultimately provides important ecosystem services in agricultural landscapes (Bennett et al., 2006). A large corpus of theoretical studies explored the local response of communities in a landscape receiving perturbations (Economo, 2011; Holyoak et al., 2020; Jacquet et al., 2022; Mouquet et al., 2011). However, these studies focused on extinction events recovered by dispersal events in a patch dynamics framework, and little is known about the effect of moderate or small perturbations. In this context, the present study provides valuable insight into fine-scale dynamics in response to perturbations.

Our results show that species interactions are a major driver of synchrony in heterogeneous metacommunities. Even if the species of interest does not disperse significantly, the synchrony of the dynamics of its different populations can strongly depend on the interactions with another species with a higher dispersal across the landscape. For instance, Howeth and Leibold (2013) showed that predatory fish promote the asynchrony of oscillating populations of zooplankton in a mesocosm experiment. Therefore, species endorsing this role are called 'mobile link organisms' (Lundberg & Moberg, 2003) and are particularly targeted by conservation policy because they have major impacts on community dynamics and ecosystem functioning (Brodie et al., 2018; Soulé et al., 2005). Such species can be considered keystone species (Mills & Doak, 1993) and must be clearly identified to properly manage the conservation of the other interaction species. However, our results show that mobile link organisms are not the only driver of metacommunity stability, and the patch being perturbed also has a major impact. The concept of a keystone community, defined by Mouquet et al. (2013) for communities whose destruction causes species extinction or a decrease in biomass production, can be applied to better assess the stability of metacommunities. Keystone communities are usually identified as those patches that are strongly connected to other patches in the spatial network (Resetarits et al., 2018), but our results suggest that the dynamical properties of each patch can be important as well. For instance, the fast patch can be identified as a keystone patch because of its ability to synchronize the dynamics of the other patches. Therefore, identifying the communities living in fast and slow patches should be key for conservation management aiming to mitigate the effects of perturbations.

According to our results, mitigating the effects of perturbations affecting the patch in which interaction strength is the highest is critical to avoid the synchrony of prey dynamics (Figure 2) and ensure predator stability (Figure 3c). Then, the patch in which the interaction strength between the species of interest and the mobile link organism is the highest must be identified. Conservation policies usually target preserved areas because they are characterized by high species richness but identifying them as fast or slow patches is not trivial. Urban ecology is a relevant example because many species dwell in cities and less anthropized ecosystems (e.g. agricultural and natural landscapes). Urban areas can be considered fast patches because of the abundance of resources (parameters ω in our model) for opportunistic species, but they can also be considered slow patches because of the reduced predation pressure (parameter γ in our model), cities acting as safe spaces (see Shochat et al. (2006) and Shochat et al. (2010) for review). Typically, some bird and rodent species can find plenty of food due to human wastes, public parks and feeding while experiencing less predation (Rebolo-Ifrán et al., 2017). Therefore, focusing conservation efforts on urban areas to mitigate the perturbations affecting their ecosystem may be as important as protecting wild areas to protect species at the metapopulation scale.

CONCLUSION

Asymmetry of interaction strength, and spatial heterogeneity in general, is not a stabilizing factor *per se* because perturbing prey in the fast patch leads to synchronous dynamics of prey populations and increases the temporal variability of the mobile predator linking the two patches. Therefore, the response of metacommunities to perturbations is strongly context-dependent, that is a good knowledge of the characteristics of each patch relative to each other is required to assess stability at the metacommunity scale. Based on our findings, we advocate for conservation efforts to target key patches not only according to species richness or biomass density but also according to the distribution of interaction strength across the metacommunity.

AUTHOR CONTRIBUTIONS

Conceptualization: PQ, BH and ML. Funding acquisition: ML. Model analysis: PQ, BH and ML. Coding simulation and original draft writing: PQ. Supervision: BH and ML. Review and editing: BH and ML.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The R code of the simulations and the figures is available on Zenodo (10.5281/zenodo.8169853).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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