Colonization, covariance and colour: Environmental and ecological drivers of diversity–stability relationships

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HIGHLIGHTS

► We model competitive communities to investigate diversity–stability relationships.
► Most previous theory points to positive diversity–stability relationships.
► Direction of these relationships depends on community assembly.
► Environmental colour and correlation interact to alter diversity–stability patterns.
► Our results contradict earlier work based on various simplifying assumptions.

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ABSTRACT

Understanding the mechanisms that underlie the relationship between community diversity and biomass stability is a fundamental topic in ecology. Theory has emphasized differences in species-specific responses to environmental fluctuations as an important stabiliser of total biomass fluctuations. However, previous analyses have often been based on simplifying assumptions, such as uniform species abundance distributions, uniform environmental variance across species, and uniform environmental responses across species pairs. We compare diversity–stability relationships in model communities, based on multi-species Ricker dynamics, that follow different colonization rules during community assembly (fixed or flexible resource use) forced by temporally uncorrelated (white) or correlated (red) environmental fluctuations. The colonization rules generate characteristic niche-dependent (hierarchical, HR) environmental covariance structures, which we compare with uncorrelated (independent, IR) species' environmental responses. Environmental reddening increases biomass stability and qualitatively alters diversity–stability patterns in HR communities, under both colonization rules. Diversity–stability patterns in IR communities are qualitatively altered by colonization rules but not by environmental colour. Our results demonstrate that diversity–stability patterns are contingent upon species' colonization strategies (resource use), emergent or independent responses to environmental fluctuations, and the colour of environmental fluctuations. We describe why our results arise through differences in species traits associated with niche position. These issues are often overlooked when considering the statistical components commonly used to describe diversity–stability patterns (e.g., Overyielding, Portfolio and Covariance effects). Mechanistic understanding of different diversity–stability relationships requires consideration of the biological processes that drive different population and community level behaviours.

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1. Introduction

The relationship between species richness and the relative size of population and community fluctuations (biomass stability) in ecosystems under stochastic environmental variation is a classic ecological question, which has provoked considerable theoretical and empirical research (reviewed by McCann, 2000; Ives and Carpenter, 2007; Gonzalez and Loreau, 2009; Hector et al., 2010; Campbell et al., 2011). Two conceptually related approaches have been used to investigate this theoretically: statistical and dynamical models (Hughes et al., 2002). Tilman et al. (1998) demonstrated that biomass stability increases with species richness

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when the variance of individual species fluctuations increases geometrically with mean density, assuming independent species responses to environmental fluctuations. Alternatively, stability decreases when population variances decrease asymptotically with increasing diversity. This approach was extended to account for asymmetric species interactions and correlations among species responses to environmental variation, features that were shown to affect the direction of the diversity–stability relationship (Lhomme and Winkel, 2002). Dynamical models have allowed a different range of relationships to be examined that can drive these statistical patterns and highlight the relative importance of species–species vs. species–environment interactions (Ives et al., 2000; Ives and Carpenter, 2007; but see Fowler et al., 2012).

Three statistical components are often used to describe why biomass stability varies with species diversity, relating changes in mean community level biomass and the covariance matrix of species fluctuations with changes in diversity (Lehman and Tilman, 2000): Overyielding, an increase in total community biomass with increasing diversity, tends to stabilise biomass fluctuations; the Portfolio effect, a reduction in summed species-level variances with increasing diversity, stabilises community level fluctuations through statistical averaging; and the Covariance effect, which results in increased stability if the relative contribution of negative between-species covariances increases with diversity. However, Ives and Carpenter (2007) recently questioned the general applicability of these components for understanding the complex manners in which species and the environment can interact to influence biomass stability, a view emphasized in experimental work (Petchey et al., 2002; Leary and Petchey, 2009). Species in natural communities are not expected to contribute equally to community biomass, nor to the elements of the species variance-covariance matrix (Leary and Petchey, 2009; Roscher et al., 2011).

Most previous theoretical analyses have assumed that environmental correlation is constant across species pairs – in other words, if species i and j respond to fluctuations in the environment with a positive correlation of 0.5, so do species i and k, as do species j and k – all off diagonal elements of the correlation matrix describing the similarity of species' responses to the environment take the same value. Relaxing this assumption can have important consequences on different population- and community-level stability measures (Lehman and Tilman, 2000; Hughes et al., 2002; Gonzalez and De Feo, 2007; Ruokolainen et al., 2009a). Environmental fluctuations that cause spatial or temporal variation in shared resources will generate characteristic covariance patterns among species, while fluctuations in unshared resources generate independent responses among species. Understanding how a broader range of different environmental covariance structures affects community dynamics is therefore important.

Another interesting aspect of community structure concerns how the pattern of resource use develops with increasing diversity. Does the addition of more species to a community affect the partitioning of a resource gradient among community members? In terms of community biomass stability, this is one feature that has received little attention so far (but see Hughes et al., 2002), with previous models dealing with explicit resource gradients relying on random community assembly methods (Lehman and Tilman, 2000), or approaches lacking species interactions that were simplified enough to allow analytical treatment (Hughes et al., 2002). Here, we investigate how different patterns of resource use along an environmental gradient change with increasing diversity, and what impact this has on biomass stability.

Finally, an important assumption of most previous research on this topic is that environmental variation is uncorrelated (white) over time (or space). However, natural environmental variation can be reddened (positively autocorrelated; Vasseur and Yodzis, 2004).

Environmental colour is considered important for population stability across various scales of biological organisation (reviewed by Ruokolainen et al., 2009b), and recent work hints that environmental reddening, while generally destabilizing community biomass, might have a qualitative impact on the relationship between species richness and stability under some conditions (Gonzalez and De Feo, 2007; Ruokolainen et al., 2009a).

We therefore investigate the interplay of species niche colonization rules, the emergent environmental covariance structures and the colour of environmental fluctuations, on community diversity–biomass stability relationships. We compare biomass stability results for different colonization rules for each community size, controlled to have identical patterns of competition for a given community size, but differing in the emerging environmental covariance structures and the distribution of species' long-term densities. Species were either introduced around the long-term environmental mean with a constant (fixed) distance between their niche optima; or flexibly, with distances between niche optima decreasing as community size increases. Communities were perturbed with two different stochastic environmental treatments: (1) independent environmental fluctuations (*IR* communities); or (2) an emergent (hierarchical) environmental covariance structure, based on species' relative niche position (*HR* communities). The above scenarios were tested under the influence of both white and red environmental variation. All the communities we analysed were long-term persistent (feasible, locally stable) in the absence of environmental variability.

The diversity–biomass stability relationships in these model communities are sensitive to each of the factors we vary, with complex interaction patterns. Environmental reddening stabilises biomass fluctuations in *HR* communities (species respond to environmental fluctuations according to relative niche positions), leading to qualitative changes in diversity–stability patterns. However, reddening has little effect when species respond independently to environmental fluctuations (*IR*), but different colonization rules show qualitatively different diversity–stability patterns. Our results demonstrate novel mechanisms that can qualitatively alter the direction of the diversity–biomass stability relationship, highlighting particular questions that can be considered in natural systems. For example, investigating how species resource use varies with community size, and how this influences community stability under fluctuating environmental conditions. We discuss these results in terms of the components commonly referred to for describing diversity–stability relationships (Overyielding, Portfolio and Covariance effects) and explore the strengths and limitations of these approaches.

2. Methods

2.1. The basic community model

We consider dynamics in a competitive community, where population dynamics follow the multi-species Ricker model:

$$N_{i,t+1} = N_{i,t} \exp\left[r \left(1 - \frac{\sum_j^S \alpha_{ij} N_{j,t}}{K_{i,t}} \right) \right], \tag{1}$$

where $N_{i,t}$ is the density of species i at time t, r is the intrinsic growth rate (common for all species, $r=1$), $K_{i,t}$ is the species-specific carrying capacity at time t, and α_{ij} is the *per capita* effect of species j on the growth rate of species i, in an S-species community. The α_{ij} values form an $S \times S$ interaction matrix **A**. Total community biomass at time t is $X_t = \sum_{i=1}^S N_{i,t}$.

We assume that species traits (K_i, α_{ij}) are determined by their positioning along an environmental gradient, such as temperature or nutrient concentration, where each species position (m_i)

indicates its optimum. Species carrying capacities are found as:

$$K_{i,t} = \exp\left[-\frac{(m_i - \tau_t)^2}{2\sigma^2}\right], \tag{2}$$

where σ is the width of species' environmental tolerances (here $\sigma = 0.5$ for all species). The environmental condition (e.g., temperature) at each time step is represented by τ_t. Thus, species performance declines with increasing niche distance from optimal conditions (where $K_i = 1$). Similarly, the strength of interspecific competition is assumed to decrease as a function of the distance between species' environmental optima (May, 1973):

$$\alpha_{ij} = \exp\left[-\frac{(m_i - m_j)^2}{4s^2}\right], \tag{3}$$

where s is the niche width. This parameter is set as $s = 1/S$, ensuring that all community sizes investigated here are feasible and locally stable with these parameter values—i.e., all species have positive densities at equilibrium, which return to equilibrium following a small perturbation.

2.2. Hierarchical covariance of environmental fluctuations

We assume that fluctuations in the environment affect population carrying capacity, K [Eq. (2)]. Variation in environmental conditions is modelled as a first-order autoregressive process

(Ripa and Lundberg, 1996):

$$\tau_t = \kappa\tau_{t-1} + \omega\varphi_{t-1}, \tag{4}$$

where κ is the autocorrelation coefficient (colour) and φ is a normal random variable with zero mean and unit variance. Parameter ω is used to scale the variance of the noise process τ_t (here $\omega = 0.15$). While this process is assumed to follow a normal distribution (but see Fowler and Ruokolainen, 2013), the filtering of environmental variation through the non-linear species environmental tolerances [Eq. (2)] means that the environment each species is tracking (via $K_{i,t}$) tends to have a non-normal frequency distribution (see also, e.g., Laakso et al., 2001).

Species stochastic carrying capacities ($K_{i,t}$) decline as a bell-shaped curve with increasing niche distance from the environmental optimum (Fig. 1a). While environmental fluctuations are normally distributed around this optimum, the distribution of species specific $K_{i,t}$ values is dependent on their niche position (m_i). This leads to the variability of $K_{i,t}$ being maximized at intermediate distances from the environmental optimum (Fig. 1b). Species' niche position also affects Skewness in K_i (Fig. 1c): species at the gradient margins ($|m_i|$ close to 1) have their $K_{i,t}$ skewed to the right, those near the gradient centre ($|m_i|$ close to 0) have their $K_{i,t}$ skewed to the left, and those at intermediate niche positions ($|m_i|$ close to 0.5) show more symmetrically distributed $K_{i,t}$ values.

Due to the relationship between the common environmental variation and the different environmental optima for each species, the correlation between species-specific environmental effects ($\rho[K_i, K_j]$, 'environmental correlation') depends on the spacing
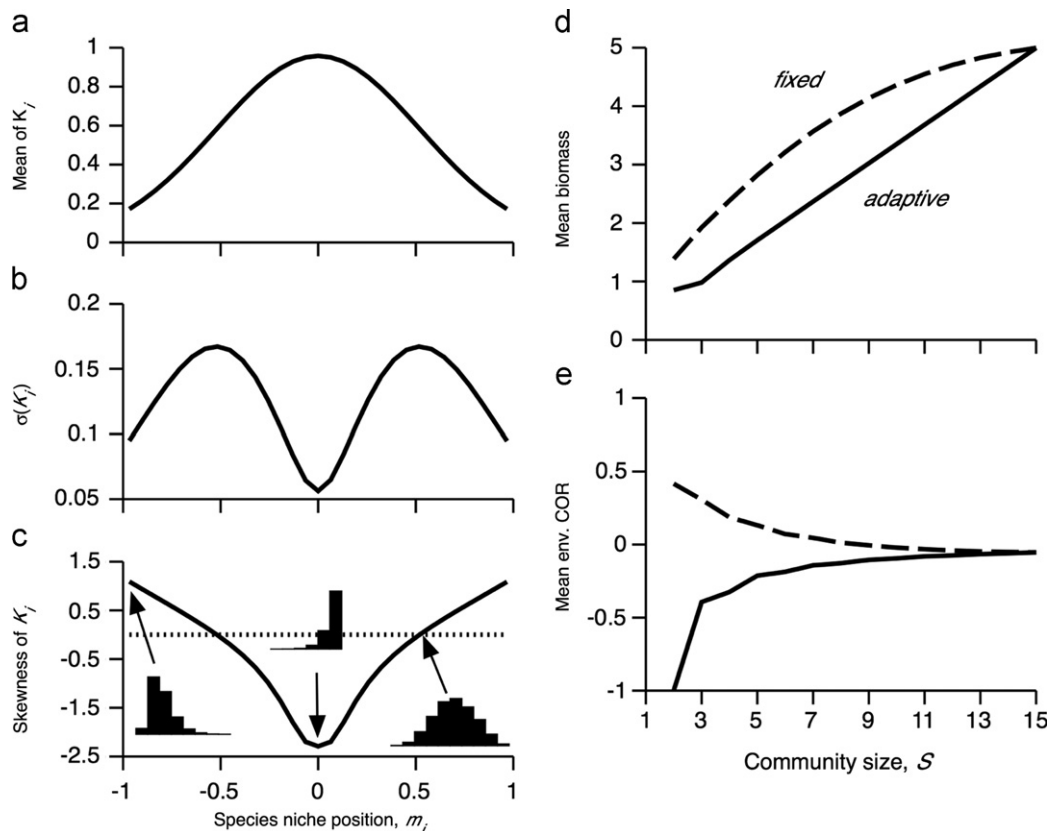
Fig. 1. Environmental and biomass characteristics of a stochastic, multi-species, resource competition model. Distributions of species carrying capacities over time ($K_{i,t}$) are dependent on species niche position (m_i): (a) Expected long-term K_i values decline with increasing distance between m_i and the environmental optimum τ_0 (at $m_i = 0$). (b) The standard deviation of species $K_{i,t}$ is maximised at an intermediate niche position ($m_i = {}^8/_{15}$), due to non-linear environmental filters [Eq. (2)], resulting in (c) asymmetrically distributed $K_{i,t}$ values. Species close to the environmental optimum ($m_i \to 0$) show left skewed $K_{i,t}$ (Skewness < 0), those close to the niche margins ($|m_i| \to 1$) have right skewed $K_{i,t}$ (Skewness > 0), while intermediate species have more symmetric $K_{i,t}$ values (Skewness ≈ 0). (d) Mean total biomass differs between fixed (dashed line) and flexible colonization (solid line). (e) Mean environmental correlation $\rho(K_{i,t}, K_{j,t})$ also differs between colonization methods (correlation between species-specific environmental effects). Parameters: $r = 1$, $\omega = 0.15$, $\sigma = 0.5$.

between their niche optima (e.g., Lehman and Tilman, 2000), as well as the size of environmental fluctuations (Ruokolainen et al., 2009a). Hughes et al. (2002) proposed an analytical formula for deriving $\rho[K_i, K_j]$, which allows an analytical analysis of the diversity–stability relationship. However, as this derivation was based on the assumptions that (i) the species environmental effects are normally distributed (a condition not met here, Fig. 1c), (ii) the correlation is independent of the amplitude of environmental variation (not met in stochastic simulations; Ruokolainen et al., 2009a), and (iii) there is no resource competition between species ($\alpha_{ij} = 0$, $i \neq j$), so environmental fluctuations cannot be filtered through species interactions; we use stochastic simulations to investigate the diversity–stability relationships in these communities.

We term the emergent environmental correlation structure 'hierarchical' [environmental correlation is a function of the distance between species environmental optima; $\rho = f(\Delta m)$] and refer to communities affected by such environmental fluctuations as 'hierarchical (*HR*) communities' (Ruokolainen et al., 2009a). To control for the influence of the *HR* environmental correlation on biomass stability, we remove this structure using a method called spectral mimicry (Cohen et al., 1999). This method can be used to randomise time series while maintaining their temporal properties (such as mean, variance, and colour). When this is done separately for each time series $K_{i,t}$, species environmental effects become independent (environmental correlation $\rho_{K(i),K(j)} \approx 0$, $i \neq j$). In this case communities are referred to as 'independent (*IR*) communities'. We therefore used the *HR* time-series of $K_{i,t}$ values in combination with normally distributed, random series and spectral mimicry, to generate *IR* environmental series, which were uncorrelated between species, yet composed of the same (re-ordered) values as used in the *HR* series.

2.3. Species colonization rules

In this model, species distribution along the resource gradient has consequences for interspecific competition, as well as the correlation between species-specific environmental effects. We present results from two particular cases of distributing species along the resource gradient, although note that other methods are possible (Lehman and Tilman, 2000; Tilman, 2004; Hughes et al., 2002): (i) species entering the system have a fixed difference between their environmental (niche) optima. Adding more species to the system this way expands the range of utilised resources linearly; and (ii) species environmental optima vary flexibly with community size, being evenly distributed between the limits $[\pm (S-1)/S]$. This models a colonisation process where species are simultaneously trying to adapt to match the long-term environmental mean (of τ_t) and minimise between-species competition.

We also examined a random colonization scenario, where each species in a given community size has its niche optima drawn at random from a uniform distribution with limits $[\pm (S_{max}-1)/S_{max}]$ (Lehman and Tilman, 2000). Controlling the species interaction matrix **A** under random colonization is not straightforward, as we outline below for the other two cases. Results from random colonization qualitatively mirrored those of Lehman and Tilman (2000), i.e., all scenarios lead to a positive diversity–biomass stability pattern, so we do not repeat them here. While diversity–stability patterns can be predicted statistically for random colonization methods (e.g., through the broken stick model; Lehman and Tilman, 2000), uncovering the mechanistic basis for these results is not easy. The behaviour of individual communities is also masked by other communities associated with different biomass stability relationships. In addition, many randomly assembled communities are unfeasible, clouding interpretation, as feasible and unfeasible communities cannot be compared easily over long time scales (Hughes et al., 2002).

The two colonization scenarios are used to ask how increasing community size affects the stability of community biomass. To simplify comparison, we set the distance between environmental optima in fixed colonization equal to $2/S_{max}$ leading cases (i) and (ii) to converge to the same community structure at S_{max}. In addition, the realised species' niche width was set as $s = 1/S_{max}$ for fixed colonization. This scaling ensures that the interaction matrix **A** is identical between fixed and flexible colonization for a given community size. However, as the two cases lead to different distributions of species optima along the environmental gradient, there are differences in mean community biomass, which is higher in fixed than flexible colonization when $S \leq S_{max}$ (Fig. 1d), as species have higher K_i values closer to the resource centre [Eq. (2)]. Species' stochastic equilibrium densities are found as $\mathbf{N}^* = \mathbf{A}^{-1}\boldsymbol{\mu}_K$ where $\mathbf{N}^*$ is a vector of long-term mean densities and $\boldsymbol{\mu}_K$ is a vector containing the mean from stochastic realisations of species-specific carrying capacities, $K_{i,t}$. The two colonization scenarios also differ in the distribution of environmental correlation values. Mean environmental correlation decreases to zero with increasing S for fixed colonization, but increases from -1 to 0 under flexible colonization (Fig. 1e).

2.4. Analysing community stability

We focus on the effect of increasing community size ($S = 2, 3, \ldots, 15$) on the variability of total community level biomass (measured as the inverse coefficient of variation),

$$CV_X^{-1} = \frac{T^{-1}\Sigma X_t}{\sigma(X_t)}, \tag{5}$$

for both *HR* and *IR* environmental variation, and fixed and flexible colonization rules. Here, T indicates the number of time points taken to the analysis, and $\sigma(\ldots)$ represents the sample standard deviation of the given time series. Sample time series of coloured environmental and community dynamics are presented in Fig. 2.

Lehman and Tilman (2000) proposed three community-level features that contribute to community biomass stability: *portfolio effect*, *covariance effect*, which relate to the components of biomass variance, and *overyielding*, which considers changes in mean total biomass. Biomass stability [Eq. (2)] consists of two parts; the mean and standard deviation of biomass. The variance of community biomass is found as:

$$\sigma^2(X_t) = \sum_{i=1}^{S} \sigma^2(N_{i,t}) + 2\sum_{i=1}^{S}\sum_{j=1}^{i-1} Cov(N_{i,t}, N_{j,t}) \tag{6}$$

That is, total biomass variance is given as the grand sum of the community variance-covariance matrix.

Population densities were initiated at the stochastic equilibrium $\mathbf{N}^*$ for each replicate. The system is simulated for 10000 time steps, with the first 2000 transient steps discarded prior to analysis (while populations are initiated at their equilibria, it takes some time before the community converges to its stationary distribution in stochastic environments). Each parameter combination is replicated 100 times. Environmental variation was modelled within the range of white ($\kappa = 0$) to reddened ($\kappa = 0.8$) noise [Eq. (3)].

3. Results

3.1. Community diversity–biomass stability patterns

When species respond independently to fluctuations in the environment (*IR*), environmental reddening has no qualitative effect on community diversity–biomass stability patterns. However, community colonization method does have a qualitative effect in this case; a negative diversity stability relationship under
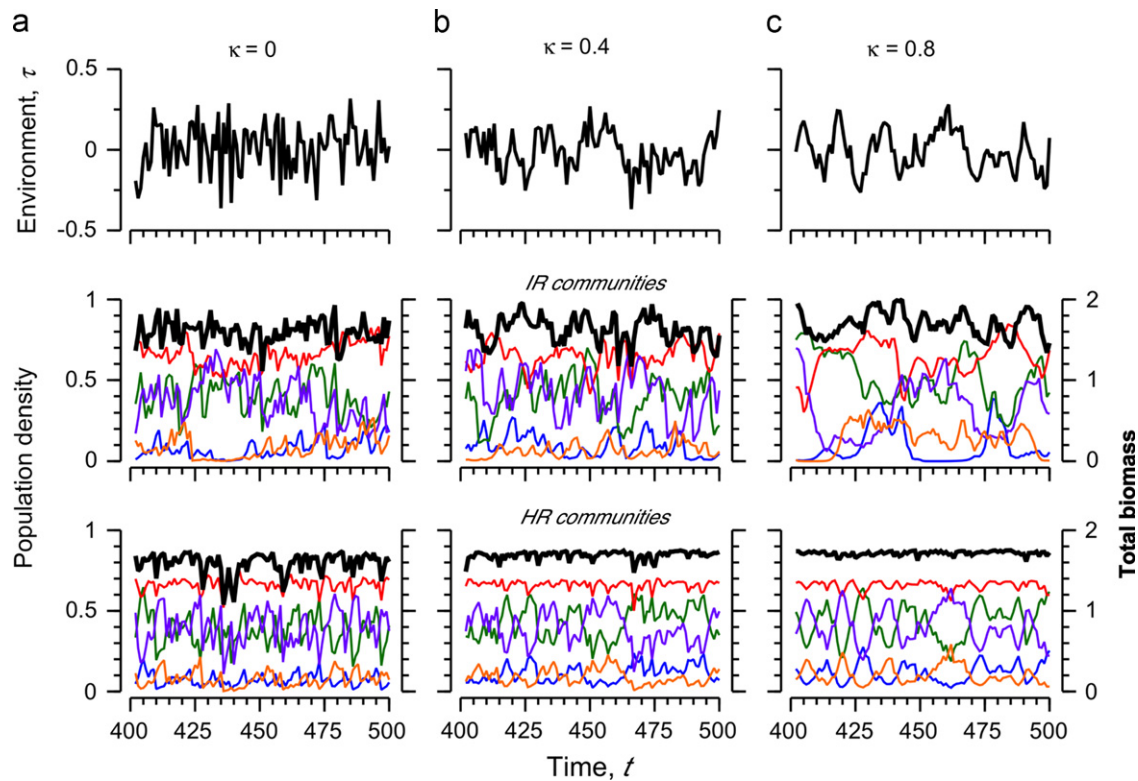
Fig. 2. The effect of environmental reddening (increasing κ) on fluctuations in environmental conditions (top row) and community dynamics in response to reddening in both *IR* (middle row) and *HR* communities (bottom row). Subplots for community dynamics show variation in population densities (coloured lines) on the left axis and total community biomass (X_t; black line) on the right axis in five-species flexible colonization communities. Parameter values: $r=1$, $\sigma=0.5$, $\omega=0.15$. Environmental variation is either (a) white ($\kappa=0$), (b) slightly reddened ($\kappa=0.4$), or strongly reddened ($\kappa=0.8$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fixed colonization becomes positive under flexible colonization (Fig. 3a and b). When species respond to environmental fluctuations as a function of their niche position (*HR*), environmental reddening stabilises biomass fluctuations (Fig. 3c and d). Reddened environments are associated with positive diversity–stability patterns while white environments show negative diversity–stability patterns, for both fixed and flexible colonization methods (Fig. 3c and d).

3.2. Specific patterns in biomass stability

In fixed colonization communities, total biomass stability decreases with increasing community size under both white and red environmental variation when species respond independently (*IR*) to environmental fluctuations (Fig. 3a). With *IR* and flexible colonization, biomass stability increases with diversity under both white and red noise (Fig. 3b). Three-species, flexible *IR* communities show higher stability than otherwise expected due to the dominance of community level dynamics by the central species ($m_i=0$). This species dominates total biomass fluctuations given its relatively high mean abundance (N_i^*) and low variability in carrying capacity (Fig. 1a and b), while the marginal species ($m_{j,k}=\pm 2/3$) contribute relatively little to total biomass due to the low, but highly variable mean abundances associated with their low, but highly variable K_i values (Fig. 1a and b). This somewhat unusual behaviour of three-species communities is due to the flexible colonization rule used here.

Two species, flexible *HR* communities show relatively unstable (large) biomass fluctuations under white environments, driven by the large distance between both species' niche optima ($m_{i,j}=\pm 1/2$) and the environmental mean ($\tau=0$). This couples relatively low mean biomass (low K_i, therefore low N_i^*) with high

population variability as the white environment alternates between favouring one species, then the other. The addition of further species means some community members will always be closer to the centre of the niche gradient compared to a two species system. Such central species experience favourable conditions more often, preventing the dominance of community level dynamics by edge species with large fluctuations.

Slow (red) environmental variation leads to a qualitative shift from negative to positive diversity–stability patterns for both fixed and flexible *HR* (Fig. 3c and d), but not *IR* communities (Fig. 3a and b). An environmental autocorrelation around $\kappa > 0.4$ is required for both fixed and flexible colonization for a strictly positive diversity–stability pattern to arise in *HR* communities (Fig. S1 in Supporting material).

3.3. Mechanisms behind diversity–stability patterns

Many studies explain patterns in biomass stability by describing patterns in its statistical components (Overyielding, Portfolio and Covariance effects). These are useful summary statistics, but do not give unambiguous insight into the biological features that drive diversity–stability patterns. By equalising competition under fixed and flexible colonization for a given community size, it is possible to isolate the influence of other model features on these statistical components. Overyielding (a stabilising effect) occurs for both colonization methods, as species do not show perfect Overlap in resource usage. Total density increases more quickly (i.e., Overyielding is a more stabilising effect) for fixed than flexible communities, as the niche positions in fixed communities are initially closer to the resource maximum. This gives higher K_i (and consequently N_i^*) values for the same community size (Fig. 1d). This stabilising feature is balanced by the destabilising influence of increasing summed
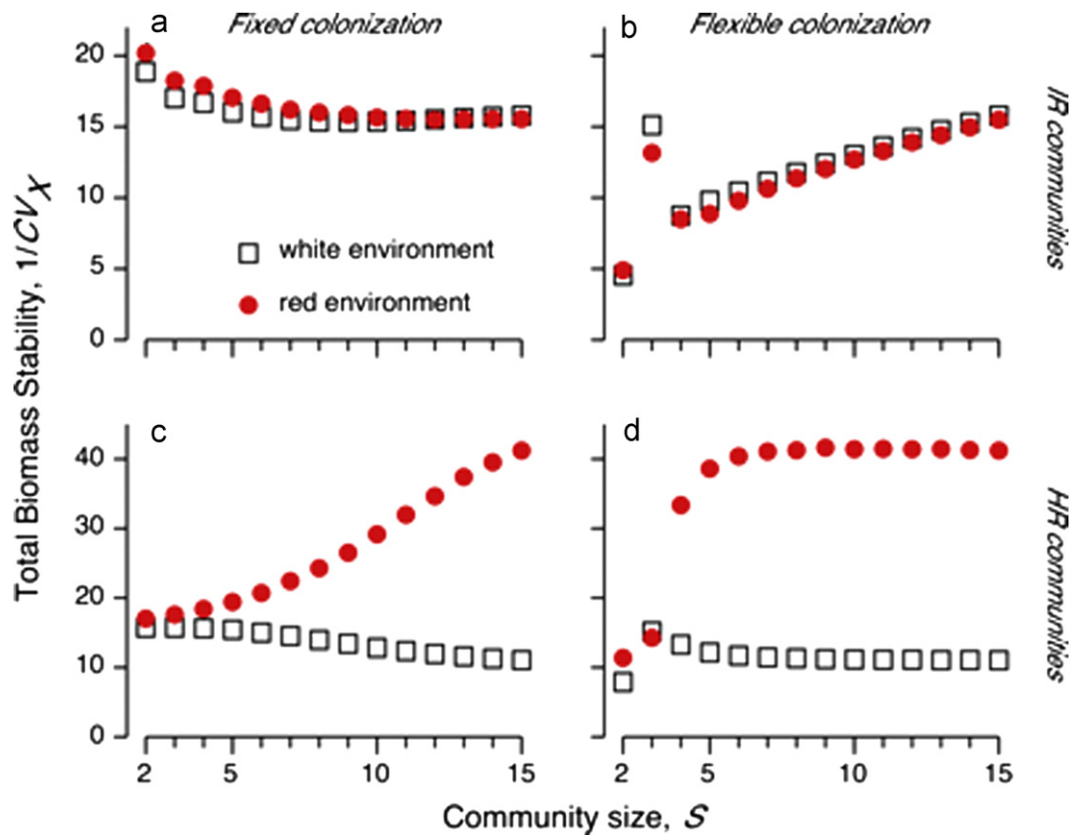
Fig. 3. Temporal stability of community biomass fluctuations ($1/CV_X$) varies with community size (S) under white (open squares; $\kappa=0$) or reddened environmental variation (filled circles; $\kappa=0.8$). Specific patterns depend on the community colonization method ((a) and (c)=fixed; (b) and (d)=flexible) and species environmental responses, being independent ((a) and (b); IR) or directly related to colonization method and niche position ((c) and (d); HR).

population level variances in all cases, and either stabilising negative summed covariances or destabilising positive summed covariances (Fig. 4), which in turn depends upon the colonization method, as we now describe.

3.3.1. Summed variances

Summed population variances generally increase with species diversity (Fig. 4a-d), mirroring the patterns of variance of K_i series for fixed and flexible colonization (Fig. 1b). Increasing S with fixed colonization initially introduces new species with higher variability than the existing community members. When $S \geq 9$, the variability in K_i (and N_i) values decreases, as the niche position of the new species exceeds the point where environmental variance is maximized ($m_i \approx 0.5$; Fig. 1b). K_i (and N_i) values closer to the niche centre and edge tend to show highly skewed frequency distributions (Fig. 1c), associated with lower variances. Edge species only have competitors on one side of the gradient therefore experience less (dampening) competition, resulting in slightly higher variability than expected from K_i fluctuations alone. Flexible colonization communities initially cover a wider range of the environmental gradient than fixed colonizers, leading to the different patterns in summed population variance between fixed and flexible colonization. Two species, flexible communities show high summed population variability given the high variability in K_i values associated with niche position (Fig. 1b).

Population variances are generally higher under red than white environments, due to an amplification effect between intrinsic dynamics and extrinsic forcing (Ripa and Heino, 1999; Greenman and Benton, 2005). Species (and community) level dynamics are undercompensating and these slow intrinsic dynamics are amplified by slow extrinsic (red environmental) fluctuations.

Differences between the summed variances of IR and HR communities can also be understood by considering the filtering of environmental fluctuations through competitive interactions. Strongly synchronous dynamics of neighbours in HR communities tend to dampen population fluctuations: neighbouring (strongly competing) species tend to experience good (or bad) conditions at the same time, therefore dampen each other's response to changes in K_i. Independent fluctuations in K_i values (IR) mean there is no constant damping effect between neighbours: species are released from strong competition sufficiently often to result in faster population growth, leading to larger population fluctuations.

3.3.2. Summed covariances

IR communities show declining (stabilising) summed covariances with increasing S (Fig. 4e and f), whereas HR communities show increasing, positive (destabilising) covariances under white and decreasing, negative (stabilising) covariances under red environmental fluctuations (Fig. 4g and h). The same exceptions arise as outlined above for total biomass stability (2 species HR and 3 species IR communities with flexible colonization).

IR communities show compensation between nearest neighbours under both white and red environmental fluctuations, as species interactions filter the uncorrelated environments to modify population fluctuations (Fig. S2). While most species pairs show little correlation (approximately zero covariance), nearest neighbours ($m_{i \pm 1}$) are negatively correlated while the second neighbours ($m_{i \pm 2}$) are positively correlated. The positive covariances have a lower absolute value than the negative covariances between nearest neighbours, $|Cov(N_i, N_{i \pm 1})| > |Cov(N_i, N_{i \pm 2})|$. As S increases, so does the number of negative (and weaker
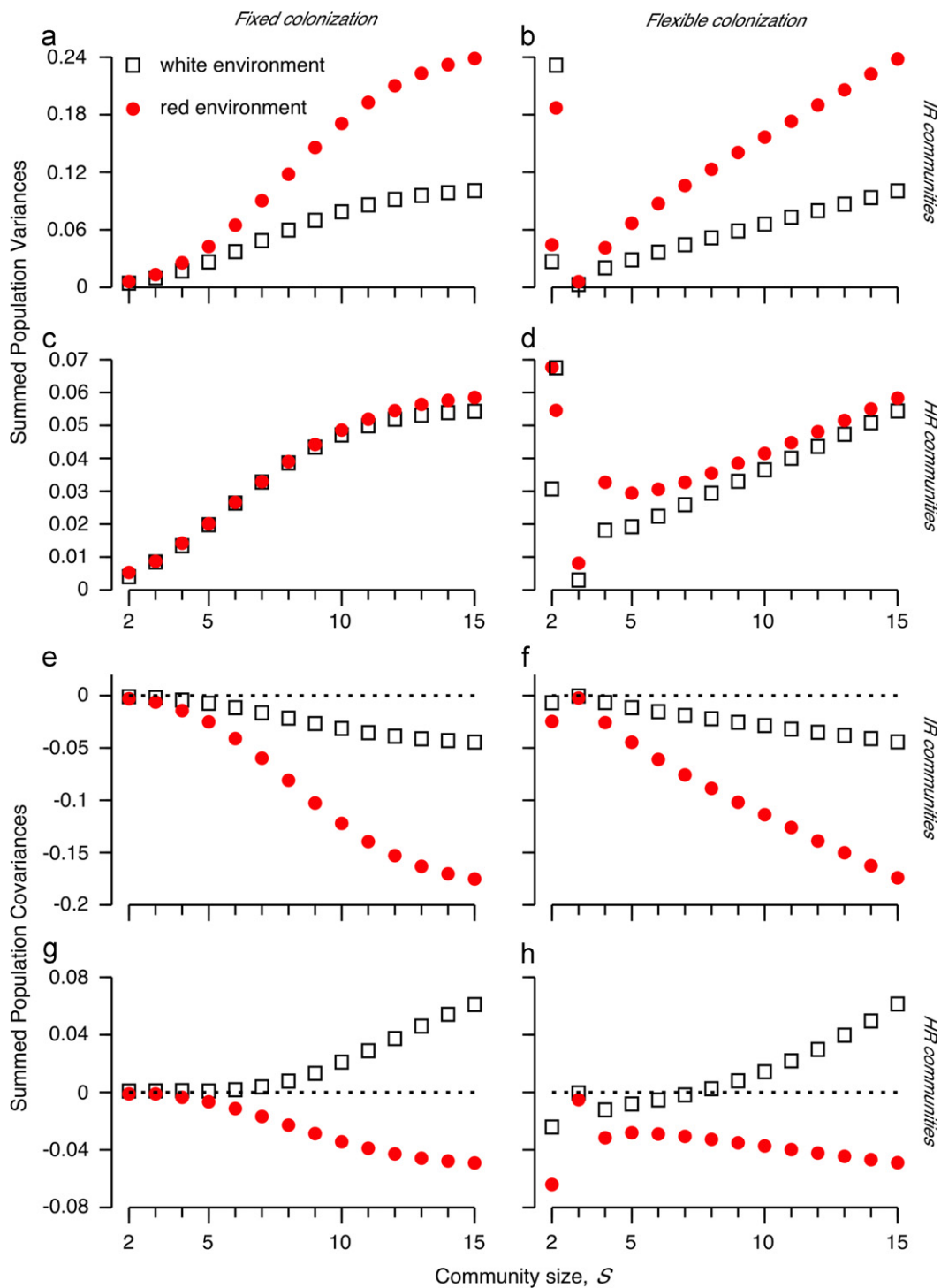
Fig. 4. Summed population variances ((a)–(d)) and covariances ((e)–(h)) vary with community size (*S*) under white (open squares; $\kappa = 0$) or reddened environmental variation (filled circles; $\kappa = 0.8$), depending on species' environmental response (*IR*: (a), (b), (e), and (f); *HR*: (c), (d), (g), and (h)) and the method of species niche colonization (fixed: left hand panels; flexible: right hand panels).

positive) elements, resulting in the increasingly negative summed covariances. In other words, competition filters the independent environmental fluctuations to create non-independent covariance patterns of stronger compensation between nearest neighbours than the weak synchrony between second neighbours. These patterns are magnified by red environmental variation (Fig. S2).

The summed covariance patterns in *HR* communities are driven by niche separation $(m_i - m_j)$ differently. Species close to each other along the resource gradient fluctuate very synchronously (strong, positive covariances/correlations), while more distant species tend

to fluctuate out of phase with each other (negative covariances; Fig. S3). *HR* population fluctuations in white environments are always more synchronous between neighbouring species than the compensating patterns between species spaced further apart on the resource gradient (Fig. S3). An inability to track the (relatively rapidly changing) white environment easily means more distant species tend not to fully compensate each other (negative covariances are weaker), resulting in positive summed covariances.

Improved environmental tracking under (slower) red environmental fluctuations results in declining summed covariances in both

fixed and flexible *HR* communities (Fig. S3). The slow environmental fluctuations allow species more time to respond to good (or poor) conditions, increasing (decreasing) their densities under the longer periods of good (poor) conditions. This decreases the synchrony between distant species on the resource gradient more than under (faster) white environmental variation (Fig. S3). The strongly synchronous fluctuations between nearest neighbours are now compensated by the more negative covariances between more distant species pairs (Fig. S3). These patterns are apparent in smaller flexible than fixed communities, as they initially colonize a wider range of the resource gradient, leading to the slight observed differences in their summed covariances.

4. Discussion

The influence of species diversity on biomass stability remains a fundamental topic in community and ecosystems ecology (Ives and Carpenter 2007; Fowler et al., 2012; Maestre et al., 2012). Little research has so far investigated the impact of coloured environmental variation on diversity–stability patterns. We demonstrated that environmental reddening stabilises biomass fluctuations, but this result is contingent upon species responses to the environment (Fig. 3): whether they respond to environmental fluctuations in shared resources (*HR*; red environments are stabilising) or independently (*IR*; no consistent effect of environmental reddening). Reddened environmental variation produces positive diversity–stability relationships in *HR* communities, which arise because the environment changes sufficiently slowly for species to recover from low densities and track the environmental changes more easily (Kaitala et al., 1997; Ruokolainen et al., 2007; Ruokolainen and Fowler, 2008). This leads to a reduction in population synchrony between species at opposite sides of the environmental gradient (Fig. S3). Reddening has no effect on the diversity–stability relationship in *IR* communities, as decreased synchrony between interacting populations due to competitive filtering (Ranta et al., 2008a; Ruokolainen and Fowler, 2008) is compensated by the amplification of undercompensating population dynamics by the slow external fluctuations (Ripa and Heino, 1999).

Gonzalez and De Feo (2007) studied communities similar to our *HR* communities with flexible colonization, reporting reduced biomass stability in association with environmental reddening and no qualitative switch in diversity–stability patterns with reddening, contrary to our findings. Preliminary simulations of their system indicate that the reduction in biomass stability they noted is due to environmental reddening increasing summed population variances more than it decreases summed covariances. This effect is related to explicit variation in resource availability: optimal environmental conditions for a given species can be associated with suboptimal resource availability from time to time; when high, temperature-dependent resource consumption occurs in combination with relatively low resource densities, the consumer does not benefit from favourable environmental conditions. Further detailed comparison between Gonzalez and De Feo (2007) and our model is difficult, as their results are based on non-equilibrium (unfeasible) communities, while we only considered feasible, locally stable communities.

We also investigated how species colonisation patterns affect diversity–stability relationships. Species colonized a resource gradient either with a fixed distance between neighbours, or responded flexibly by minimising competition between neighbours whilst trying to maximise proximity to the maximum resource concentration. *IR* communities switched from a negative (fixed colonization) to a positive (flexible colonization) diversity–stability pattern but were unaffected by environmental colour. *HR* communities changed from negative to positive diversity–stability patterns as the environment changes from white to red, but were qualitatively unaffected by colonization rules. These

results can be understood by considering how niche position couples with environmental responses to drive the observed variance and covariance patterns (Figs. S2 and S3).

Traditionally, different patterns in community biomass stability have been attributed to differences in the balance of the statistical components of biomass stability: between species covariances, total population variance and total biomass (e.g., Lehman and Tilman, 2000; Jiang and Pu, 2009). However, recent work has shown that simply describing patterns in these statistical components tells us little about the underlying processes driving community dynamics (Petchey et al., 2002; Ives and Carpenter, 2007; Loreau and de Mazancourt, 2008; Ranta et al., 2008a, 2008b; Leary and Petchey, 2009). We showed here that adding biologically relevant complexity to simple community models, by linking environmental variability to species biology via relative niche positions and carrying capacities, increases the range of diversity–stability patterns these models can generate. Fowler et al. (2012) also recently introduced biological detail into simple models by relaxing the common assumption that all community members have simple, stable equilibrium dynamics (all $r_i < 2$). They introduced qualitative variation in species level dynamics, by allowing r_i values to differ among species, generating a range of stable, cyclic and chaotic intrinsic species dynamics ($0.5 \leq r_i \leq 3.5$), while maintaining local stability at the community level (see also Fowler, 2009). Relaxing the assumption of stable species level dynamics generates negative diversity–stability when species environmental responses are positively correlated. However, Fowler et al. (2012) did not find any effect of environmental colour on their results, probably due to the simple correlation structure of species environmental responses they employed (all $\rho_{\varepsilon(i,j)} = \rho$).

Many previous analyses of diversity–stability relationships have assumed that all species contribute equally to the size of biomass fluctuations (e.g., Ives et al., 1999; Hughes and Roughgarden, 2000; Lehman and Tilman, 2000; Hughes et al., 2002; Ives and Hughes, 2002). However, if species do not have a uniform abundance distribution, selection effects become important as different species contribute unequally to the total biomass (Loreau and Hector, 2001; Petchey et al., 2002). This becomes a problem if biomass stability is only explained by summarizing the community variance-covariance matrix. When environmental conditions favour species differently – depending on species responses to niche position, e.g., temperature adaptation – uneven biomass distributions are expected in real systems (Gonzalez and Descamps-Julien, 2004). Recent empirical studies suggest that summing covariances masks important stabilizing species pairs, giving limited information about the biological mechanisms behind community dynamics (Petchey et al., 2002; Isbell et al., 2009; Leary and Petchey, 2009; Roscher et al., 2011; Sasaki and Lauenroth, 2011).

4.1. Relation to empirical observations

There is a general tendency for increasing species richness to promote community level stability in experimental systems (Tilman et al., 2006; Jiang and Pu, 2009; Hector et al., 2010; Campbell et al., 2011; Gustafsson and Boström, 2011), but this is not ubiquitous and patterns can be harder to identify in more realistic natural systems (Romanuk et al., 2009; Valdivia and Molis, 2009). Different species-specific adaptations to local environmental conditions can generate characteristic differences in population abundances, variances, and covariances, resulting in unequal contributions to biomass level stability (Petchey et al., 2002; Leary and Petchey, 2009). Our approach demonstrates interactions between competition, colonization and environmental responses—that constitute the biological basis of community level (biomass) patterns. Meaningful interpretation of species

variance-covariance patterns estimated from time-series data can be very difficult, if not impossible, even in very simple systems (Loreau and de Mazancourt, 2008; Ranta et al., 2008a, 2008b). Our results show that when there are fluctuations in unshared resources (*IR*), competition is an important feature in terms of generating compensating fluctuations between strongly interacting (neighbouring) species (Fig. S2). When the environment drives fluctuations in shared resources (*HR*), the environmental responses driven by relative niche positioning dominate competitive interactions in driving population and community fluctuations (Fig. S3).

The effect of environmental colour on community diversity–stability relationships has received little empirical attention so far. Gonzalez and Descamps-Julien (2004) showed no significant effect of species richness on community biomass *CV*, but did find a stabilising effect of reddened environments on community fluctuations, compared to a constant environment. Two other microcosm studies have suggested that slow (red) environmental variation tends to increase total biomass variability, compared to faster fluctuations (Petchey et al., 2002; Hiltunen et al., 2008). Petchey et al. (2002) results also indicate that environmental reddening could potentially change the direction of the diversity–stability relationship, from negative under fast environmental variation to weakly positive under slow variation, qualitatively resonating with our model results.

While the statistical components of population variances, covariances and mean biomass can be uncovered easily, this is only the first step in helping us to understand the biological mechanisms underlying diversity–stability relationships in natural systems. The results presented here, previous theoretical (e.g., Ives and Carpenter, 2007; Loreau and de Mazancourt, 2008; Ranta et al., 2008a), and empirical work (e.g., Petchey et al., 2002; Valone and Barber 2008; Leary and Petchey, 2009; Sasaki and Lauenroth, 2011) suggest that understanding the mechanisms behind the statistical behaviour of individual populations is crucial for a fuller understanding of community biomass fluctuations. To this end, experimental manipulations (Micheli et al., 1999; Leary and Petchey, 2009), as well as more sophisticated statistical tools (Gonzalez and Loreau, 2009) are likely to be needed for a deeper understanding of specific diversity–stability relationships in natural systems.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2013.01.016.

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