Interaction strength and extinction risk in a metacommunity

Frédéric Guichard*

Department of Biology, McGill University, 1205 Penfield, Montreal, Quebec, Canada H3A 1B1

Species interactions and connectivity are both central to explaining the stability of ecological communities and the problem of species extinction. Yet, the role of species interactions for the stability of spatially subdivided communities still eludes ecologists. Ecological models currently address the problem of stability by exploring the role of interaction strength in well mixed habitats, or of connectivity in subdivided communities. Here I propose a unification of interaction strength and connectivity as mechanisms explaining regional community stability. I introduce a metacommunity model based on succession dynamics in coastal ecosystems, incorporating limited dispersal and facilitative interactions. I report a sharp transition in regional stability and extinction probability at intermediate interaction strength, shown to correspond to a phase transition that generates scale-invariant distribution and high regional stability. In contrast with previous studies, stability results from intermediate interaction strength only in subdivided communities, and is associated with large-scale (scale-invariant) synchrony. These results can be generalized to other systems exhibiting phase transitions to show how local interaction strength can be used to resolve the link between regional community stability and pattern formation.

Keywords: synchrony; spatially explicit model; coastal ecosystems; species extinction risk; larval dispersal; scaling

1. INTRODUCTION

The management and conservation of ecological communities depends on our capacity to predict patterns of distribution at large spatial scales. In coastal marine habitats, for example, the regional distribution of sedentary species has been studied in relation to variability in physical factors at corresponding scales (Menge *et al.* 2003). In contrast, metapopulation theory shows how the intrinsic population growth rate can interact with limited dispersal in order to maintain patterns in homogeneous environments (Levin 1974; Hastings & Higgins 1994; Earn *et al.* 2000). Metacommunity theory similarly identifies dispersal as an important process explaining the diversity and stability of spatially subdivided communities (Loreau *et al.* 2003; Blasius & Stone 1999). However, the role of species interaction strength is still poorly understood in spatially subdivided communities, even if its influence on stability has been demonstrated in well mixed food webs (McCann *et al.* 1998; Thébault & Loreau 2003). Here I demonstrate how large-scale patterns can be associated with catastrophic shifts in stability and be explained as self-organized properties driven by the strength of species interactions in a spatially structured metacommunity.

Catastrophic and sudden shifts in natural ecosystems in response to environmental changes have recently received increasing attention from ecologists and conservation biologists (Gunderson & Holling 2002; Scheffer & Carpenter 2003), and are emerging as a challenge for reserve design theories (Levin 1999; Holling *et al.* 2002; Guichard *et al.* 2004). One important approach to reserve design relies on a direct and static link between patterns

and processes (ReVelle *et al.* 2002). But in coastal ecosystems where many benthic invertebrates and fish species have a pelagic larval phase, theories have suggested that the scale of larval dispersal, rather than static patterns, should dictate the distribution of reserves within a network (Hastings & Botsford 2003). However, localized processes such as dispersal have been shown to drive the formation of dynamic patterns at scales much larger than underlying processes (Hassell *et al.* 1991). These theories also suggest that such self-organized patterns could provide information about sudden shifts in abundance (Rietkerk *et al.* 2004). Among self-organized patterns, scale-invariant distribution of abundance has been observed in a number of terrestrial (Solé & Manrubia 1995; Kubo *et al.* 1996) and aquatic (Wootton 2001; Guichard *et al.* 2003) ecosystems. It has also been associated with abrupt biological transitions along smooth environmental gradients (Pascual & Guichard 2005). However, mechanistic models of scale invariance have focused on very simple ecological interactions, and we largely ignore the importance of community-level processes in their formation and maintenance. Understanding and testing self-organized pattern formation in relation to key community-level processes such as interaction strength is thus important to predict the large-scale response of ecosystems to slow environmental changes. It also provides the opportunity to integrate dispersal and community-based approaches towards an improved interpretation of large-scale patterns within reserve design theories.

In marine systems, species interactions, including competition, predation and facilitation, are recognized as important drivers of community dynamics (Paine 1980). Variability in the strength of predator–prey and competitive interactions has been predicted and observed between

* (frederic.guichard@mcgill.ca).

years and between locations (Connolly & Roughgarden 1999; Menge *et al.* 2004). Although most studies of interaction strength, including those applied to coastal communities, have focused on predation and competition, facilitation has been well documented in ecological successions (Bruno *et al.* 2003). The presence of subdominant species has, for example, been shown to facilitate and canalize the colonization by dominant species in rocky intertidal communities (Berlow 1997). The potential for interaction strength to drive shifts in large-scale patterns and stability of coastal ecosystems is of great consequence, given the increased role of community-level processes within marine conservation theories (Lubchenco *et al.* 2003). I first present a metacommunity model with local dispersal based on the dynamics of rocky intertidal communities. I show how local interaction strength in ecological succession dynamics can lead to an abrupt transition characterized by scale invariant distribution. I then demonstrate the association between self-organized patterns, regional stability and extinction risk in the metacommunity.

2. THE MODEL

(a) Rocky intertidal community dynamics

The metacommunity model is motivated by temperate marine intertidal systems where many species have sessile adult stages and pelagic larvae that are transported by currents. In these systems, local onshore dynamics have been studied as competition for space between subdominant and wave-disturbed dominant species (Paine 1984). This disturbance–succession dynamic is driven by wave disturbances, the major force explaining the maintenance of diversity, which locally causes the mortality of dominant species such as mussels, thus creating opportunities for subdominant invertebrates (e.g. barnacles) and algae (Paine & Levin 1981). These sequences have been shown to be deterministic, ending with the colonization by a single dominant species (Paine 1984). The presence of facilitative interactions has also been documented as a key interaction in these systems (Berlow 1997). The model presented here defines facilitative interaction strength based on the maximum *per capita* colonization rate of the dominant on the empty substratum relative to the colonization rate of areas already colonized by the subdominant (see below).

At the larger scale (among-site dynamics), an increasing number of studies suggest that dispersal of benthic species with a pelagic larval stage is spatially limited, and that recruitment is coupled to local larval production (Jones *et al.* 1999; Swearer *et al.* 1999), thus violating the assumption made by open system models. The metacommunity dynamics, i.e. among-site interactions, are here implemented as an integro-difference model (Neubert *et al.* 1995), where local production is exported according to a probability density function (i.e. dispersal kernel), and local recruitment depends on all neighbouring sites exporting larvae.

(b) Onshore disturbance dynamics

The model is more precisely based on a spatially explicit lattice model of the wave disturbance–recovery dynamics of mussels (Guichard *et al.* 2003), which is expanded here to define onshore succession dynamics. Within a site (local

community), I describe space occupancy as the cover ρ_i of each possible state i . I define the case of one dominant and one subdominant species. The possible states of space occupancy are then: *empty* ($i=0$), *subdominant* ($i=1$), *dominant* ($i=2$) and *disturbed* ($i=-$). Within-site dynamics are implemented as a successional sequence where the *subdominant* is not susceptible to disturbance and can facilitate colonization by the wave-disturbed *dominant* species according to a facilitation rate γ (i.e. interaction strength). As the dominant species is disturbed, free space becomes available for both species. If the colonization rate by the dominant is independent of the presence of the subdominant, the facilitation parameter $\gamma=0$ and the system is a competitive hierarchy. If the dominant strictly depends on the subdominant to colonize space, the facilitation is maximum and $\gamma=1$. The interaction strength (γ) is here defined from the maximum *per capita* colonization rate $(1-\gamma)$ of the dominant (ρ_2) on ρ_0 cover, relative to the colonization of ρ_2 on ρ_1 . It is similar to other interaction strength metrics used to characterize trophic interactions (Berlow *et al.* 2004), but because γ is not associated with a trade-off in the colonization of the alternative substratum, it defines the strength of a dependence rather than the strength of a preference often adopted (McCann *et al.* 1998). Within each site, colonization success of species i depends on their own density ρ_i , associated with positive density dependence during recruitment, and on a density-independent rate δ_i . Also, wave disturbance of the dominant is implemented as the mean-field formulation of the spatially explicit spreading process where disturbance depends on the presence of an existing disturbance in the eight neighbouring cells of a two-dimensional lattice (Guichard *et al.* 2003).

(c) Larval transport metacommunity dynamics

Metacommunity dynamics are implemented by first assuming that each local community (within-site dynamics) has an explicit location x along a coastline. Local larval production for each species is proportional to cover ρ_i and fecundity f_i , and recruitment rate C is a Poisson process with $C=1-e^{-\beta}$ (Caswell & Etter 1999), with β the larval concentration at x . β is the sum of larvae that were produced at other locations y and that dispersed to x . The following integro-difference system can then describe the dynamics of cover ρ_i of each state i at each location x

$$\left. \begin{aligned} \rho_{-}^{t+1} &= \rho_{-}^t (\delta_{-} + (1 - (1 - \rho_{-}^t)^8)), \\ \rho_0^{t+1} &= \rho_0^t + \rho_{-}^t - C_1^t \rho_0^t (\rho_1^t + \delta_1) - C_2^t (1 - \gamma) \rho_0^t (\rho_2^t + \delta_2), \\ \rho_1^{t+1} &= \rho_1^t + C_1^t \rho_0^t (\rho_1^t + \delta_1) - C_2^t \rho_1^t (\rho_2^t + \delta_2), \\ \rho_2^{t+1} &= 1 - \rho_1^{t+1} - \rho_0^{t+1} - \rho_{-}^{t+1}, \end{aligned} \right\} \quad (2.1)$$

with

$$\left. \begin{aligned} C_i(x) &= 1 - e^{-\beta_i(x)}, \\ \beta_i(x) &= \int \rho_i(y) f_i D_i(|x-y|) dy, \\ D_i(|x-y|) &= \frac{3|x-y|^2}{2} e^{-|x-y|^3}, \end{aligned} \right\} \quad (2.2)$$

where D_i is the dispersal kernel of species i resulting from larval transport at a constant speed and with a

time-dependent settlement rate (double Weibull distribution; Neubert *et al.* 1995). I assume symmetric dispersal and periodic boundary conditions, and identical dispersal properties for both species. In all simulations, space was discretized with average dispersal distance set at 5% of domain size. Fecundity of both species was set to be non-saturating with $f=7.5$ and external disturbance and colonization rates δ_i were all set to 10^{-3} . These parameter values lead to limit-cycles and the exclusion of the subdominant species for the well mixed (global dispersal) model with no facilitation (figure 1). I now use the model to define (i) the effect of local species interactions and dispersal on the large-scale distribution of the dominant species and (ii) the association of resulting large-scale patterns with regional stability of the metacommunity.

2. RESULTS

It can first be noted that with well mixed dispersal (figure 1), increased interaction strength (γ) necessarily leads to a monotonic decrease in the mean cover of the dominant species. This is explained by the increasing dependence of the dominant upon the subdominant as γ increases. Metacommunity dynamics with local dispersal results in a less intuitive role of interaction strength on regional dynamics. With local larval dispersal, mean cover (figure 2a; red line) is now maximum at intermediate facilitation $\gamma=\gamma_c\approx 0.7$. Mean cover is also strongly linked to spatial and temporal variability in relation to facilitation. More precisely, the competitive hierarchy ($\gamma=0$) leads to a quasi-equilibrium as shown by almost undetectable spatial and temporal variability (figure 2). Introducing facilitation ($\gamma>0$) into this competitive hierarchy leads to the emergence of spatio-temporal variability, as shown by the increase in temporal (figure 2a) and spatial (figure 2b) variability as γ is increased up to γ_c . Spatial variability peaks at γ_c , and $\gamma>\gamma_c$ results in homogenized distribution through regional synchrony, as revealed by the high temporal and low spatial variability (figure 2a versus b).

Interestingly, this result can be explained as a transition from a weakly oscillating regime at $\gamma=0$, to a strongly oscillating regime at $\gamma=1$, both extremes characterized by weak spatial variability. Below γ_c , facilitation allows for coexistence between dynamical regimes, with strong oscillations forming synchronized clusters along the transect (figure 2b; $\gamma=0.5$). The size of these clusters increases with facilitation strength until a sharp transition to a single infinite cluster leading to regional synchrony for $\gamma>\gamma_c$. This competition between weak oscillations (global attractor at $\gamma=0$) and strong oscillations (global attractor at $\gamma=1$) at intermediate interaction strength explains the spatial variability, and leads to a scale-invariant distribution at the critical value γ_c (figure 3). More precisely, when facilitation is close to its critical value γ_c , the decay of variability in dominant cover as a function of spatial scale follows a power law (log-log linear) distribution (figure 3). This log-log linear decay of variability is not observed for synchronous fluctuations ($\gamma>\gamma_c$), and is observed over a very narrow range of scales for $\gamma<\gamma_c$, indicating a limited scale of patchiness (figure 3). The response of metacommunity dynamics to interaction strength is thus similar to criticality observed in other biological systems going through phase transitions (Sornette 2000; Pascual &

Guichard 2005). This comparison suggests that scale-invariance can be used in metacommunities as a signature of local community-level processes. The sensitivity of the critical value reported here to parameters of the model and to important ecological processes should be the subject of future studies.

The metacommunity dynamics and facilitation also influence both regional and local extinction risks. Based on mean cover and on the amplitude of regional oscillations, risk of regional extinction of the dominant reaches a minimum for intermediate facilitation. For positive facilitation values below γ_c , increasing facilitation has a weak influence on the amplitude of regional oscillations (figure 2a). Mean cover, on the other hand, reaches its maximum value for intermediate facilitation ($\gamma_c\approx 0.7$). As mentioned above, high facilitation, above 0.7, rapidly leads to coherence, low mean cover and to high amplitude oscillations, which periodically drive mean cover close to zero with a high probability of regional extinction (figure 4a). Regional stability should thus be maximized for intermediate facilitation, before the onset of coherent oscillations. This prediction is supported by the coefficient of variation around the critical facilitation, which reaches a local minimum before the transition to regional synchrony (figure 4b). In contrast, spatial variability (figure 2b) explains why local extinction risk increases faster than regional extinction as a function of facilitation and is already at its maximum value at γ_c (figure 4a). Metacommunity dynamics thus show intermediate interaction strength to be associated with maximum local and minimum regional extinction risks (figure 4a), at the edge of regional synchrony.

3. DISCUSSION

Understanding the contribution of local ecological and environmental processes in predicting the collective stability and persistence of subdivided communities has major consequences for the ecological and conservation sciences (Levin 1999). Towards this goal, the results presented here provide a new interpretation of how the scaling properties of large-scale patterns can provide information about underlying ecological processes, and about the stability and persistence of regional coastal communities. They also suggest the high sensitivity of large-scale metacommunities to fluctuations in the intensity of community-level processes, therefore contributing to the current shift from single species to community-based approaches to reserve network design.

The results presented here are compatible with well mixed food-web models showing intermediate interaction strength to be associated with maximum stability (McCann *et al.* 1998). More importantly, they reveal how sharp transitions in extinction risk are associated with self-organized and large-scale cover distribution. In metacommunity models with homogeneous dispersal, intermediate dispersal rate (Mouquet & Loreau 2002) and population growth rates (Wilson 1992) have been shown to maximize diversity. In spatially explicit models, stability and coexistence have been associated with local asynchrony driven by the dispersal rate in metapopulation (Earn *et al.* 2000), host-parasitoid (Hassell *et al.* 1994) and food-web (Blasius & Stone 1999) models. The present study reports that sharp transitions in stability can be

Figure 1. Average (solid red line) and minimum and maximum cover (black dots) of the dominant species as a function of facilitation γ under global (well mixed) dispersal. The vertical dotted line is the minimum facilitation value allowing for coexistence, and transition diagrams illustrate community structure on each side of this threshold facilitation value for persistence of the subdominant species.

driven by interaction strength through their effect on spatial patterns. Moreover, dispersal-driven patterns often require unequal dispersal rates between species (Hassell *et al.* 1994; Neubert *et al.* 1995), fragmented landscapes (Hastings & Higgins 1994) or environmental heterogeneity (Blasius & Stone 1999), none of which were required in the model presented here. Even more surprising is the association between maximum regional stability and large-scale correlation in the distribution. Asynchrony and spatial chaos have usually been used to associate patterns with stability in metapopulation models. However, these models suggest that small-scale patterns should result in higher stability than large-scale (e.g. scale-invariant) patterns. This is because correlation length is small under chaotic dynamics and is more precisely proportional to the inverse of the largest Lyapounov exponent computed from spatio-temporal series (Bascompte & Solé 1995). What is new in the results presented here is the idea that regional stability is compatible with, and even enhanced by, very large correlation length resulting from scale-invariance at criticality. This result suggests a new interpretation of the relationship between patterns and stability in spatially explicit systems.

The relationship between spatio-temporal variability and scales has captured the attention of ecologists as a powerful tool to link patterns and processes (Levin 1992; Rietkerk *et al.* 2004). Among these relationships, scale-invariance (Rohani *et al.* 1997; Pascual & Guichard 2005) has proven particularly appealing because of its potential association with the self-organization of long-range correlation between individuals involved in localized interactions. Examples of self-organized scale invariance can be found in terrestrial (Solé & Manrubia 1995) and marine (Wootton 2001; Guichard *et al.* 2003) systems characterized by physical disturbance, and in the dynamics of diseases (Rhodes *et al.* 1997). However, gathering the data required to characterize variability over broad ranges of scales is a compelling task, and we have limited evidence of scale-invariance and of its explicit link with local processes (Allen *et al.* 2001).

Figure 2. (a) Temporal and (b) spatial bifurcation diagrams for the dominant species as a function of facilitation γ . For each facilitation value (horizontal axis), the temporal bifurcation diagram (a) highlights regional temporal variability by showing the average (red line) and all local minima and maxima from fluctuations in the regional cover (black dots) over 500 time-steps after removing the first 2500 time-steps. The spatial bifurcation diagram (b) similarly highlights spatial variability by showing the minimum and the maximum values found along the transect, averaged over 100 time-steps. (c) Spatio-temporal patterns (space along the horizontal axis and time along the vertical axis) with no facilitation (left), critical facilitation (centre) and strict facilitation (right). Patterns for intermediate facilitation $\gamma=0.5$ are shown in (b).

The long-term scaling properties shown here to emerge from metacommunity dynamics are testable predictions empirically, but will require large-scale survey data, and will potentially contribute to resolving the relative contribution of environmental fluctuations and of local species interactions for the regional dynamics of ecological systems. In coastal ecosystems, large-scale biological patterns have mostly been studied in relation to environmental variability over short temporal scales (Connolly *et al.* 2001). The results presented here suggest that species interactions such as competition

Figure 3. Scaling properties of large-scale patterns for interaction strength values illustrated in figure 2. Power spectrum of dominant cover distribution in the metacommunity with critical facilitation leading to maximum average cover ($\gamma = 0.7$), contrasted to power spectra for $\gamma = 0.5$ and 1.

and facilitation can scale up through larval dispersal and lead to large-scale spatio-temporal patterns with specific scaling properties (e.g. scale-invariance), shown here to provide a long-term signature of local community processes despite the apparent complexity of spatio-temporal series.

Predicting the local and regional extinction probabilities of species in response to large-scale environmental changes is of prime importance for conservation science. For the study of subdivided populations and communities, synchrony in the fluctuations of populations is an important process influencing extinction risk. Spatial synchrony can be attributed to autocorrelation in environmental conditions (Post & Forchhammer 2002), and to increased connectivity between populations (Earn *et al.* 2000). However, we know little about the role of community-level processes in driving synchronized fluctuations. Interaction strength is one such process and it has been shown to respond to environmental variability. Predation strength has, for example, been shown to vary along latitudinal gradients (Sanford 1999; Sanford *et al.* 2003). Variability in competition strength has also been predicted in marine systems with oceanographic fluctuations (Connolly & Roughgarden 1999; Menge *et al.* 2004). The results presented here reveal how large-scale environmental changes such as climate and oceanographic regimes could trigger dramatic changes in spatial synchrony and extinction risk through their effect on local species interaction strength. Of great relevance is the fact that these dramatic changes occur at intermediate interaction strength (γ_c), also associated with maximum cover and stability, and with minimum regional extinction probability. The prediction is thus that maximum regional stability in systems with no or weak environmental heterogeneity is associated with maximum sensitivity of the metacommunity to increasing environmental fluctuations. It follows that trends towards increasing environmental variability should affect our ability to extrapolate current data on the stability of subdivided communities. The prediction of sudden shifts in ecological systems has recently become a central research topic (Scheffer & Carpenter 2003). The idea that fluctuations in species

Figure 4. Extinction probabilities (local and regional) and stability (CV) of the dominant species in relation to interaction strength (facilitation). (a) Extinction probability measured as the probability of reaching zero cover across the transect (regional) or per site (local) following a regional perturbation drawn from a normal distribution with average 0 and standard deviation of 0.5. (b) Temporal coefficient of variation (CV) as a function of facilitation (γ) around the critical value. CV is shown for the dominant species and is computed on mean cover over 500 time-steps after removing the first 2500 time-steps. The line shows the linear fit on CV values before the transition.

interactions could explain such shifts between dynamical regimes, with direct consequences for the regional distribution and stability of communities, creates new research opportunities and will need to be integrated into the science of reserve design.

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