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Multi-scale regulated plant community dynamics: mechanisms and implications

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Plant competition is not a direct interaction, but operates via environmental feedback loops, which interconnect population densities and environmental regulating variables. It is suggested that due to scale dependent elements of these feedback loops, competition may occur eventually on very different scales, necessitating a cross-scale extension of plant competition theory. After introducing the concept of cross-scale competition, we incorporate its elements into a metacommunity model and study its implications on community organization. It is found that both the equilibrium community composition, regarding coexisting functional types, and its stability depend on scale dependent attributes of environmental feedback loops and disturbance regimes. We argue that plant communities are likely to exhibit properties, which are in line with the hierarchical ecosystem concept. Environmental feedback loops on different scales act as distinct organizational levels, what can be affected by disturbances of corresponding spatial extent.

Ecosystems, including plant communities, are often regarded as complex, adaptive systems (Von Bertalanffy 1968, Hartvigsen et al. 1998, Levin 1998, Anand 2000, Gassmann et al. 2005). From the viewpoint of spatial organization this means that the plant community of a given spatial area exhibits properties which go beyond the features of an ensemble of independent small-scale subunits. In the simplest case, emergent phenomena may be a result of simple, local interactions between the subunits, in some cases accompanied with the phenomena of scale-invariance (Pagnutti et al. 2005). Nevertheless, both empirical and theoretical studies indicate that they often originate from diverse processes, acting on different spatial and temporal scales (O'Neill et al. 1986, Levin 1992, Perry 1995, Peterson et al. 1998), Therefore, the state of each site is influenced by both its immediate as well as its broader neighbourhood. In spite of the suggested variety of scale dependent processes in verbal models of ecosystems, in formal plant ecological models cross-scale dynamics is almost exclusively exemplified with the interaction of local scale competition and regional scale dispersal (Czárán 1998, Hanski 1999, Leibold et al. 2004). Although these models proved to be immensely useful in understanding the interaction of these two mechanisms, they ignore scale dependent aspects of competitive interaction (but see Molofsky et al. 2002).

Competition and population regulation

The notion of regulating factors and environmental feedback loops provides a useful conceptual framework to demonstrate scale dependent elements of plant competition and to study its implications on community organization. Plant individuals compete with each other mostly via modifying environmental variables, like resource abundances. Krebs (2001) calls these density dependent competitive processes 'regulating factors'. Hereby, following Meszéna et al. (2006), who introduced a formal framework for analyzing population regulatory processes, we use the term 'regulating factor' for variables. According to their definition, any kind of environmental variable, which is part of the environmental feedback loop, is a regulating factor. While they have a positive effect on

population growth rates, they are also subject to the negative effect of population density. The loop is closed via a positive effect of the population growth rate on the population density (Fig. 1).

Resources are the primary examples for regulating factors. Increased resource abundance grants higher growth rate and thus leads to higher population density. In turn, large population density results in a decline of the abundance of the available resources. Apart from resource densities, there are several other environmental variables which may also act as regulating factors, like the level of herbivory or parasitism (Leibold 1995). The analogy is transparent if we consider the lack of herbivory or lack of parasitic burden as resources that plants compete for, leading to a wide variety of physiological adaptations. In this sense, the concept of regulating factors might be regarded as a generalization of the concept of resources.

The environmental feedback loop ensures that population densities remain within a certain positive interval. Such kind of density dependence is an indispensable component of any explanatory theories of long term, stable survival or coexistence of species (Chesson 1991, Wolda and Dennis 1993, Hanski 1999, Turchin 1999, Krebs 2001).

Each plant community is under the control of several regulating factors. Individuals compete for

various mineral nutrients, try to avoid being eaten by herbivores, etc. The resource-ratio theory of Tilman (1980, 1982) states that individual growth rates are functions of resource availability, while resource availability is a function of species consumption. This concept can serve as a basis for a functional characterisation of plants in line with the notion of regulating factors. According to this theory, species differ in their sensitivity towards the regulating factors; some species are more adapted to low levels of some resources, but not of others. Due to tradeoffs, each species is expected to be competitively superior under certain conditions which can be characterized by ratios of the regulating variables.

Scale dependent elements of the environmental feedback loop

All three elements of the environmental feedback loop, namely, the population growth rate, the population density and the regulating variables can be evaluated on different spatial scales (Fig. 1). The growth rate of a population depends on its local environment, thus when expressing growth rate as a function of environmental variables, they must be considered on the very same scale. A similar relationship holds between growth



Fig. 1. The environmental feedback loop. (a) Interactions between the three components. Population density p, population growth rate r and regulating variable v are connected with arrows, indicating direct effects. Plus and minus signs denote beneficial or detrimental effects, respectively. In subfigures (b) and (c), embedded circles represent nested spatial units. Values of p, r and v at different places are denoted by indexes a-c. The dynamically relevant and irrelevant scales are denoted by solid or dashed ellipses, respectively. The relevant scale of population densities and growth rates is defined by our scale of interest; it is the smallest spatial scale the population density is defined on. For the regulating variable, the relevant scale may be either the same or a larger one, depending on whether the population dynamics is a function of its small-scale values or only their larger scale average. (b) Small-scale regulation densities on the same scale. (c) Large-scale feedback. In case of fast dynamics of the regulating variable, its small-scale values become irrelevant. Effects of population density changes propagate quickly in space and small-scale values of population growth rates are determined by the large-scale average population density.

rate and population density. On the contrary, it is not necessary that the value of any regulating variable within a given area is a function of population density on the very same scale. The interdependence of spatial scales is a consequence of the possible time scale difference between plant population growth and the inherent spatial dynamics of the particular regulating factors. If the latter one is relatively fast, then the consequences of increased population size propagate quickly in space. This way, on the descriptive level of relatively slow plant population dynamics these processes appear as spatial scale dependent elements, because their effect can propagate over smaller or larger spatial scales within a short time interval over which population densities might be regarded constant. This means that the value of the given regulating factor on a small site can be expressed as a function of population densities within its larger spatial neighbourhood.

As an example let us consider two mineral resources in the soil with low and high diffusion rates, respectively. Small-scale abundance of the resource with slow diffusion is determined primarily by local uptake mechanisms of the consumer plant population within the same area. On the contrary, the abundance of a resource with a very high diffusion rate is a function of population densities on a much larger scale, because resource abundance equilibrates within a large area almost instantaneously and all uptake processes within this large area influence its abundance on any smaller scales. Another good example for this phenomenon is herbivory. Grazing pressure within any small-scale area might be a function of average plant density on a much larger scale, depending on perceptive scales of the herbivores.

Underlying process rates, which determined scale dependence in these two examples, were diffusion rate and perceptive area, i.e. the area roamed about during a given time interval. It is their relatively fast dynamics that makes both competition for nutrients with fast diffusion and competition for the lack of megaherbivores large-scale processes, just like dispersal is regarded as a regional scale process, because it may transfer propagules over large distances within very short time intervals. Depending on the particular regulating factors, underlying mechanisms might change from case to case and the spatial scale of the feedback between population density and regulating variables may eventually vary over orders of magnitude.

Community level consequences of cross-scale competition are investigated by incorporating cross-scale elements of the environmental feedback loop into a metacommunity competition model. The model has a low number of implicit spatial scales, enabling a comprehensive study of community organizing potential of scale dependent processes within its framework. The simplest case of two regulating factors is considered and, based on feedback scales of these two regulating factors, a few model communities are distinguished. These model communities are in turn subject to recurrent environmental disturbances of various spatial scales which generate heterogeneities in population densities. Investigating equilibrium composition of plant functional types, characterized by their sensitivity towards the two regulating factors, it turns out that scale dependence of both regulating factors and disturbance regimes are important determinants of community composition. Based on the results it is claimed that in real plant communities, similarly to this model system, embedded feedback loops form a hierarchy of regulating processes (see Kolasa 2005, 2006 about hierarchies in ecological systems in general).

Model definition

Let us denote the density of a population within a spatial area with p^{β} , where β denotes our scale of interest. Thus, p^{β} expresses population density averaged over smaller or larger scales, depending on the value of β . A simple mathematical representation of the density dependent environmental feedback is the logistic population growth model. Using our notation it reads as follows:

$$\frac{\mathrm{d}p^{\beta}}{\mathrm{d}t} = r_0 p^{\beta} \left(1 - \frac{p^{\omega}}{K} \right) \tag{1}$$

where r_0 stands for intrinsic growth rate and K denotes attainable equilibrium population density. p^{β} denotes population density averaged over the spatial unit under consideration (β), while p^{ω} stands for average population density on the scale of the environmental feedback (ω). As it is usual in the logistic type formulation, the regulating variable itself is not represented explicitly. According to our arguments in the previous section, scales β and ω are in general not equal, but $\beta \leq \omega$. When two regulating factors, which are essential in the sense that population growth is always limited by the one with the lower concentration, are considered, Eq. 1 becomes

$$\frac{\mathrm{d}p^{\beta}}{\mathrm{d}t} = r_0 p^{\beta} \min\left(1 - \frac{p^{\omega_A}}{K^A}; 1 - \frac{p^{\omega_B}}{K^B}\right) \tag{2}$$

where K^{A} , K^{B} , ω_{A} , ω_{B} are the attainable equilibrium population densities and feedback scales, corresponding to regulating factors A and B, respectively.

Metacommunity context

In a metacommunity context we can distinguish three implicit scales (Leibold et al. 2004). At the smallest

scale, microsites (scale α) hold single individuals, which are in turn nested within localities (scale β) that hold local communities. Local communities are linked via dispersal and form the metacommunity of a region (scale γ). In line with the previous section, β also denotes our scale of interest; it is the smallest scale we define population density on.

In our case the metacommunity consists of L=1000 number of local communities. Each locality might be inhabited by N number of species, each corresponding to a given functional type. Let p_{in}^β denote local population population density of species $n \in \{1, 2, \ldots, N\}$ on locality $i \in \{1, 2, \ldots, L\}$. We introduce $p_{in}^\gamma = \sum_{j=1}^L p_{jn}^\beta / L$ to denote density of species n on the metacommunity scale. Notice that the value of p_{in}^γ is independent of i, but we use this index for notational convenience. Populations of all species within a given locality are under the control of two regulating factors and (by analogy with Eq. 2) obey the equation

$$\frac{dp_{in}^{\beta}}{dt} = r_{0}^{n} p_{in}^{\beta} \min\left(1 - \frac{\sum_{n=1}^{N} p_{in}^{\omega_{A}}}{K_{n}^{A}}; 1 - \frac{\sum_{n=1}^{N} p_{in}^{\omega_{B}}}{K_{n}^{B}}\right) + cp_{in}^{\gamma},$$
(3)

where r_0^n , K_n^A , K_n^B are species specific traits, characterizing the different functional types, and c is a colonization constant. Since in the present context we are not interested in colonization ability related coexistence, c is equal for all species.

By virtue of the scales $\omega_A, \omega_B \in \{\beta, \gamma\}$ we can distinguish three model communities.

- Model community I. Both regulating factors are subject to local scale density feedback ($\omega_A = \beta$, $\omega_B = \beta$).
- Model community II. Both regulating factors are subject to regional scale density feedback (ω_A = γ, ω_B = γ).
- Model community III. Regulating factors A and B are subject to local and regional scale density feedback, respectively $(\omega_A = \beta, \omega_B = \gamma)$.

Plant functional types

We define each species with its sensitivity towards different regulating factors, expressed by three species specific parameters. For the species n, K_n^A and K_n^B denote sensitivity towards regulating factors A and B, while r_0^n is intrinsic growth rate, which is realized only if density dependent competition, imposed by the two regulating factors, is negligible due to low densities. We assume the constraint $K_n^A + K_n^B + r_0^n = 1$ to incorporate the tradeoff relationship between these quantities. Due to practical reasons we discretize the

continuum of possible functional types and restrict our attention to those N = 171 species, for which the values of K_A, K_B, r₀ are positive multiplies of 0.05 and satisfy the above trade-off constraint.

Disturbance regimes

The metacommunity is subject to recurrent environmental disturbances, occurring with rate d. We fix the rate d and distinguish disturbance regimes on the base of the extent of the affected spatial area.

 α disturbance regime: affects individual plants by destructing microsites. This kind of disturbance can be incorporated into Eq. 2 by adding a disturbance term, yielding

$$\frac{dp_{in}^{\beta}}{dt} = r_0^n p_{in}^{\beta} min\left(1 - \frac{\sum_{n=1}^{N} p_{in}^{\omega_A}}{K_n^A}; 1 - \frac{\sum_{n=1}^{N} p_{in}^{\omega_B}}{K_n^B}\right) + cp_{in}^{\gamma} - dp_{in}^{\beta}$$
(4)

- β disturbance regime: affects local population denities by destructing localities. Localities perish with rate d and can be recolonized only from other localities.
- γ disturbance regime: affects metacommunities by destructing whole regions. Whole metacommunities perish with rate d. Since this hinders recolonization of localities from within other localities within the same metacommunity, in order to determine the amount of various colonizers we will use the assumption that each metacommunity is in turn part of an even larger ecosystem, consisting of several parts with similar characteristics.

The model is defined by Eq. 3 and the disturbance rules. In order to study competitive dynamics in the nine cases, provided by the three model communities and disturbance regimes, we solved the equations by numeric integration. At t =0 we had $p_{in} = \frac{g_i}{N}$ for all i and n, where g_i were random numbers between 0 and 1. We ran simulations until approaching an equilibrium density distribution at t =200 000, and recorded metacommunity level average densities, $p_n^* = \sum_{j=1}^L p_{jn}^\beta / L = p_{in}^\gamma$, averaged over the last 10 000 temporal units. Results for γ disturbance regimes were derived heuristically, based on the fact that these cases are rescaled versions of the previous ones.

Results

The equilibrium community composition, i.e. coexisting species of different functional types, depends both on the scales of regulating feedback loops and the scale of environmental disturbances. We present simulation results for the three model communities in turn (Fig. 2). Results for the three model communities under β scale disturbance regime represent the three qualitatively different outcomes. Dynamics of these cases are shown in more detail in Fig. 3, displaying average trait value changes within localities.

Given the first model community, where both feedback loops operate on the scale of localities, we can distinguish two types of equilibrium communities, depending on disturbance scales. Asynchronous α scale disturbances affect single individuals on microsites, but this effect is incorporated on a higher level; local population densities remain high and plants experience intensive competition through both regulating variables. Competitive superiority requires tolerance against low levels of both regulating variables, hence the species with equally high K^A and K^B values outcompetes the others. If disturbances affect localities, i.e. microsite disturbances are synchronised within localities, after each local disturbance p^B_{in} local population densities



Fig. 2. Equilibrium species densities p_n^* in the three model communities under various disturbance regimes. Equilibrium communities are represented by circles within the strategy triangle, corresponding to coexisting species with different r_0 , K_A and K_B values. The center of the triangle represents a species with equal r_0 , K_A and K_B values, whereas points closer to any of the three corners represent species with a higher value of the given trait at the expense of the other two trait values, due to their tradeoff relationship. The darkness of the inner color of the circles is proportional to p_n^* densities, normalized with respect to the highest density value.

drop to zero, ceasing regulatory effects of both feedback loops (Fig. 3a). Temporarily, sensitivity towards regulating factors becomes irrelevant and the optimal functional type will have high r_0 and low K^A , K^B values. As local density increases, negative density dependence starts to operate again in both feedback loops and species are replaced by more competitive ones with higher K^A and K^B values. Due to the asynchrony between local disturbances, the metacommunity is a mosaic of recently disturbed and more or less recovered localities with different population densities, with a corresponding heterogeneity in regulating variables. This heterogeneity provides habitat for species with various r_0 , K^A and K^B values where K^A is equal to K^B, because regulating factors A and B change synchronously. The same argument applies to any situation when the scale of disturbances exceeds that of the feedback loops. Consequently, exploiting our assumption, that colonizers may also come from other metacommunities with similar properties, the equilibrium community under γ disturbances will be the same as under β disturbances. Within each locality, p_{in}^β densities follow the same trajectories as in the case of local disturbances, without any competitive impact on the neighbouring ones.

Let us consider model community II next. In this case, the scale of disturbances needs to be larger to reach the scale of feedbacks. Until feedback loops remain intact, in the sense that population densities on the corresponding scale do not vary, each species remains permanently under the constraints of regulating factors A and B. This condition holds for α and β disturbances (Fig. 3b). The community consists of only one species, with low r_0 and equally high K^A and K^B values. Introducing heterogeneities in regulating variables requires metacommunity scale disturbances. The result for γ disturbance regime can be derived again heuristically. Notice, that a model community of type II with γ scale disturbances is a rescaled equivalent of model community I with β scale disturbances. Accordingly, the equilibrium community will be the same, consisting of species with various r_0 and $K^A = K^B$ values.

Model community III exhibits features of both I and II, because regulating factor A is locally regulated, while regulating factor B belongs to a metacommunity level feedback loop. Microsite level disturbances do not affect any of these feedback loops, because they do not alter population densities on larger scales, thus the constraints before and after disturbances are the same. The equilibrium community will consist of the same single species, as in model communities I and II with α disturbances. Metacommunity level disturbances also have the same result as before, for similar reasons. Due to synchronous disturbances of localities and parallel dynamics of the two regulating variables, p_{in}^{β} is always equal to p_{in}^{γ} . Although regulating factor A is linked to



Fig. 3. Average functional trait value and density changes within localities for the three model communities under β disturbance regime. Average values of r_0 , K^A and K^B functional trait values are plotted as a function of the elapsed time since the last disturbance event. If $K^A = K^B$, then only K^A is displayed. p^β stands for the summed population density of all species within the locality, while p^{γ} stands for the γ scale average population density, shown for comparison. The average occurrence of a disturbance event is indicated with an arrow. Dynamics of localities are shown for (a) model community I, (b) model community II and (c) model community III, corresponding to the three different equilibrium community types. Plotted values were averaged over all localities of the same age, evaluated at equilibrium (over the last 10 000 temporal units).

 p_{in}^{β} , while B is linked to p_{in}^{γ} , due to their equality, the results will be the same as if both would be linked to the latter one, similar to model community II. The effect of β scale disturbances is more intricate (Fig. 3c). After each disturbance local density drops, that affects feedback loop A, but not that of B. This way, immediately after a disturbance, species experience strong competition via regulating loop A, but not via B, resulting in the spread of species with high KA and low KB. Later, as local population density increases, competition via feedback loop B becomes important too, and species with high K_A and K_B values spread. Occasionally, if other disturbances do not happen, a long time after disturbance the local density of all species $\Sigma_{n=1}^N p_{in}^\beta$ might become larger than metacomminity scale density $\sum_{n=1}^{N} p_{in}^{\gamma}$, thus density dependence of feedback loop B might become stronger than that of A, leading to the appearance of species with $K_B > K_A$ values.

Discussion

Describing competition in the form of environmental feedback loops reveals that plant competition incorporates a scale dependent element: the effect of population density on the regulating variables. Scale dependence in this context means that the value of the environmental variables at a given spatial area might be a function of population densities on the same or a larger scale. Depending on characteristic scale values, the interdependence between the processes of competitition and disturbance manifests itself in diverse coexistence patterns. By incorporating these aspects into a formal model of plant competition, a sophisticated picture of community organization emerges, revealing a hierarchical structure of regulatory feedback loops. This spatial hierarchy consists of a nested set of feedback loops over several orders of magnitude. Large-scale feedback processes, constituting the top of the hierarchy, impose homogeneous ecological constraints over a large spatial area, while going down the hierarchy towards smaller scale feedback loops, the regulatory effect gradually becomes more and more localized. Large-scale disturbances affect all regulatory processes down from the top of the hierarchy, while the effect of smaller scale disturbances is restricted to its lower levels.

Competition and disturbance are often considered as opposing forces (Huston 1979, 1994). As disturbance decreases population density, it weakens competition. Diminished competition, in turn, is supposed to eliminate competitive exclusion and increases diversity. The difficulty with this antagonistic picture is that any population should be regulated somehow. Neither temporal fluctuation nor metapopulation structure alleviate that requirement (Chesson 1991, Hanski 1999). If the growth of different populations are constrained in the same way, there should be a "struggle for existence", i.e. competition, between them. Here we suggest a more intimate relationship between competition and disturbance by considering their relative scales.

Competition is mediated via regulating factors, like resources. Within the competition picture, plant community composition, concerning the set of coexisting functional types, is determined by experienced values of regulating variables (Tilman 1982), which depend negatively on population densities. Disturbance reduces competition because decreasing population density lessens the burden on resources. Asynchronous disturbances create a spatial heterogeneity in values of regulating variables. The resulting spatial variability of adaptive forces contributes to the coexistence of different functional types (Tilman 1990, 1994).

Scale dependence of environmental disturbances enters at this point. A small-scale disturbance is unable to influence a larger scale feedback loop. However, when the scale of disturbance becomes commensurable to the scale of the feedback, competition is temporarily eliminated on that scale. If all feedback loops were acting on the same scale the behaviour of the system would be relatively simple. Once the scale of disturbances reaches that of the feedbacks, the given regulatory loops collapse locally from time to time and the increased spatial variance of regulating variables is reflected in a changed community composition. This situation has been extensively studied within the context of competitive dynamics in spatial models (Tilman 1994, Hanski and Gyllenberg 1997, Hanski 1999, Gyllenberg and Metz 2001, Mathias et al. 2001, Metz and Gyllenberg, 2001) which rely on the assumption that the spatial unit under consideration is chosen to be equal to the relevant scale of competition. This spatial unit is often also assumed to be equal to the spatial extent of environmental disturbances (but see, for example, Guichard et al. 2003). The fragmentation of the competition neighbourhood was investigated by Guichard (2004), who introduced the concept of competitive clusters, that could be affected by environmental heterogeneity.

However, it is reasonable to assume that the uniformity of feedback loops is not the typical case in real ecosystems. Instead, an ecosystem is under the control of feedback loops belonging to various regulating factors with specific feedback scales. In such a system, which consists of a hierarchy of spatially nested feedback loops, any disturbance of a given scale is able to generate heterogeneity by perturbing feedback loops of the same or smaller scale, while leaving the larger ones intact. This way, the range of viable functional types, in line with the nature of the emergent spatial heterogeneity, will depend on the actually perturbed feedback loops. This property has substantial corollaries if we take into account that natural communities are subject to environmental disturbances of various spatial scales and frequencies. In contrast to single scale disturbances, which affect always the same feedback loops, composite disturbance regimes may create a diversity of local conditions following disturbance events, as disturbances of different sizes affect different feedback loops. It may lead again to an increased diversity of functional forms.

This way, a hierarchical structure of environmental feedback loops implies a corresponding nested set of competitive constraints in accordance with the hierarchical ecosystem concept of O'Neill et al. (1986). Once the system is disturbed, some constrains disappear and what next happens will depend on the new set of constraints. During regeneration, a new hierarchical structure is established according to the new constraints. In conformity with this view, ecosystems are recently regarded rather as ensembles of distinct organizational levels with a broad range of functional scales than as entities with strict spatial boundaries. Accordingly, the concept of stability also deserves a scale dependent treatment (Levin 1992, O'Neill 2001). In spite of the traditional view that considers dispersal as the only mechanism that plays a key role in large-scale stability of plant communities, it is suggested that this kind of role of large-scale environmental feedback loops may be equally important.

In other words, disturbance acts via restructuring, instead of eliminating competition. In the case of single-scale disturbance the species with the highest K value is eliminated by, or it is coexisting with, a lower-K variant because competition for the newly emptied habitats (i.e. the large-scale competition) becomes relatively more important as compared to small-scale competition within a single habitat (Hastings 1980, Crawley and May 1987, Nee and May 1992). It may happen that local competitive ability matters in one respect and the global one in the other. Considering different feedback loops with the inevitable scale differences between them, the possibilities are numerous. Disturbance may increase diversity by making the pattern of feedbacks more complex rather than by eliminating it.

Disturbances are an integral part of community dynamics (Miles 1979, White 1979, Sousa 1984, Pickett and White 1985, Wiegand et al. 1998) that has both temporal and spatial dimensions. Temporal aspects of disturbance regimes, including its potential implications on coexistence, diversity or stability are widely studied, and the scope of research also includes the exploration of relevant temporal scales in population dynamics (Padisák 1994). Taking into account that scale dependence of disturbance patterns also has a spatial dimension, finding relevant spatial scales in population dynamical processes seems to be inevitable to uncover the role of scale dependent dynamics in community ecology (Pickett et al. 1989). Multi-scale extension of competition mechanisms in formal models might be a useful tool in this undertaking.

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