

Evolution of Local Facilitation in Arid Ecosystems

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Submitted July 26, 2007; Accepted January 30, 2008;

Electronically published May 28, 2008

ABSTRACT: In harsh environments, sessile organisms can make their habitat more hospitable by buffering environmental stress or increasing resource availability. Although the ecological significance of such local facilitation is widely established, the evolutionary aspects have been seldom investigated. Yet addressing the evolutionary aspects of local facilitation is important because theoretical studies show that systems with such positive interactions can exhibit alternative stable states and that such systems may suddenly become extinct when they evolve (evolutionary suicide). Arid ecosystems currently experience strong changes in climate and human pressures, but little is known about the effects of these changes on the selective pressures exerted on the vegetation. Here, we focus on the evolution of local facilitation in arid ecosystems, using a lattice-structured model explicitly considering local interactions among plants. We found that the evolution of local facilitation depends on the seed dispersal strategy. In systems characterized by short-distance seed dispersal, adaptation to a more stressful environment leads to high local facilitation, allowing the population to escape extinction. In contrast, systems characterized by long-distance seed dispersal become extinct under increased stress even when allowed to adapt. In this case, adaptation in response to climate change and human pres-

ures could give the final push to the desertification of arid ecosystems.

Keywords: habitat modification, evolutionary suicide, desertification, positive feedback, nurse plant, adaptive dynamics.

Many sessile organisms can make their habitat more hospitable for themselves and others by buffering environmental stress or increasing resource availability (Bertness and Callaway 1994; Holmgren et al. 1997; Stachowicz 2001). This ability of organisms to modify the conditions of their local environment plays an important role in many ecosystems, in particular harsh environments (Callaway and Walker 1997). For instance, in arid ecosystems, severe stress results from water and nutrient deficiency, extreme temperatures, wind desiccation, and soil erosion (Schlesinger et al. 1990; Callaway and Walker 1997). In these extreme conditions, physical protection, shade, and increased resource availability under the canopy of a “nurse plant” (Niering et al. 1963) significantly improve the conditions for establishment or growth of other individuals close to the nurse plant (Schlesinger et al. 1996; Aguiar and Sala 1999). In subalpine and alpine plant communities, plant interactions are facilitative at high elevations (Callaway et al. 2002) because surrounding vegetation maintains warmer temperatures, prevents frost, and provides protection from strong winds and desiccation (Choler et al. 2001). In salt marshes, species tolerant of extreme edaphic conditions prevent salt accumulation in the soil because their cover limits surface evaporation by shading (Bertness and Hacker 1994). Certain species also aerate anoxic soils by rhizosphere oxidation (Bertness and Leonard 1997). On rocky shores, shading by conspecifics buffers heat and desiccation stress and increases survivorship (Bertness and Leonard 1997). In intertidal areas, aquatic and marine vascular plants reduce physical disturbance of the flow and enhance deposition and stabilization of the substrate (Bruno 2000).

All these mechanisms of habitat amelioration are cases of niche construction (Odling-Smee et al. 2003) and ecosystem engineering (Jones et al. 1994, 1997), where sessile organisms buffer the stressful environment for themselves and others locally. We use the term “local facilitation” to

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describe this assortment of physical and biological mechanisms that affect the space below and close to a sessile individual because of its physical structure (Kéfi et al. 2007a). In this term, “local” stresses the spatial component of these mechanisms, and “facilitation” refers to the positive effect on other individuals (Stachowicz 2001; Bruno et al. 2003).

Local facilitation can have profound effects on the spatial distribution of organisms, on their abundance, and on ecosystem resilience (Bertness and Leonard 1997; Kéfi et al. 2007b). Theoretical studies show that systems involving such positive interactions between their component parts can exhibit alternative stable states, meaning that two stable states can be reached by the population, depending on the initial conditions and given the same parameter values (Harada and Iwasa 1994; Rietkerk and van de Koppel 1997; Scheffer et al. 2001; Kéfi et al. 2007a, 2007b). Moreover, ecosystems with local positive interactions often show striking spatial patterning, such as regular bands of blue mussel beds perpendicular to the flow of the water (van de Koppel et al. 2005) or regular stripes (“tiger bush”), labyrinths, spots (“leopard bush”), and gaps in the vegetation cover of arid ecosystems (Rietkerk et al. 2002). In some ecosystems, such pattern formation and alternative stable states are directly linked (Rietkerk et al. 2004).

Although the ecological importance of local facilitation is widely established, the evolutionary aspects have received less attention (Laland et al. 1996). Yet the consequences of the evolution of habitat amelioration are potentially far-reaching. By locally modifying the level of environmental stress, organisms performing local facilitation modify the sources of natural selection and can therefore affect their own evolution as well as that of any other organisms that happen to be neighbors (Laland et al. 1996, 1999; Odling-Smee et al. 2003). Laland et al. (1996, 1999) were the first to explore the evolutionary consequences of niche construction. Using a two-locus frequency-dependent selection model, their analysis suggested that the changes that organisms bring about in their own selective environment (or niche) can be an important source of modified natural-selection pressures. A limit of their approach for the ecosystems previously cited is that it does not take the spatial aspects into account. The observed spatial organization of individuals in harsh environments suggests that the spatial context could be very important for understanding the evolutionary aspects of local facilitation.

This article studies the evolutionary dynamics of local facilitation in harsh environments, explicitly addressing the spatial context and focusing on the case of arid ecosystems. Currently, arid ecosystems experience increasing external pressures by human activities and climate change (Reynolds and Stafford Smith 2002; Karl and Trenberth 2003;

Cook et al. 2004). Models of arid ecosystems including local positive feedbacks investigated how these ecosystems might respond to changes in external conditions, such as grazing pressure or precipitation, but ignore the possibility that plants could adapt to new external conditions (Lejeune et al. 1999; d’Herbès et al. 2001; von Hardenberg et al. 2001; Rietkerk et al. 2002; Kéfi et al. 2007a). Empirical evidence suggests that strong external changes can induce rapid adaptive evolution of life-history traits (Morris et al. 1995; Thompson 1998), meaning that consideration of evolutionary processes might be essential for understanding ecosystems’ responses to external changes. Consideration of evolutionary processes is particularly important because it has been shown that nothing prevents adaptive evolution from causing population declines or extinctions (Dieckmann and Ferrière 2003). Gyllenberg and Parvinen (2001) demonstrated, in the context of the evolution of dispersal, that for adaptation to cause extinction, the population should exhibit alternative stable states, one of them corresponding to extinction. Evolution to extinction (also known as evolutionary suicide) is a process during which a viable population adapts in such a way that it can no longer persist (Ferrière 2000; Gyllenberg et al. 2000). This phenomenon might happen when cheaters—which do not facilitate and are not viable alone—grow in a population of facilitators (thus benefiting from the facilitation performed by the facilitators) and by competition push the facilitator population away from its original stable state into the basin of attraction of the other stable state, the extinction state; eventually, the cheaters become extinct as well. Without leading to extinction, adaptation may also cause substantial reduction in population size (Matsuda and Abrams 1994; Dieckmann and Ferrière 2003), which renders populations more susceptible to extinction by stochastic causes.

Because of the links between local facilitation and alternative stable states on the one hand and between alternative stable states and evolution to extinction on the other hand, it is of particular interest to investigate the possibility that plants of arid ecosystems could adapt to changes in external conditions by modifying their investment in local facilitation and to analyze the consequences of such adaptation for the dynamics of arid ecosystems. Here we use a lattice-structured model of arid ecosystems, explicitly considering local interactions among plants (Kéfi et al. 2007a), and we study the evolutionary dynamics of local facilitation, using the framework of adaptive dynamics (Metz et al. 1992, 1996; Geritz et al. 1998). Evolution of local facilitation is expected to depend strongly on the strategy of the plants’ seed dispersal (see van Baalen and Rand 1998 and Le Galliard et al. 2003, 2005 for examples of studies highlighting the role of dispersal on the evolution of helping), which is, together with local facilitation,

the trait driving the spatial organization of the system. We therefore analyzed the effects of changes in external conditions—here aridity and grazing pressure—on the evolutionary dynamics of local facilitation for different seed dispersal strategies. We looked at the consequences of this adaptation for the spatial organization and the viability of the population. More specifically, if after changes in external conditions the system happens to be close to a transition to extinction, we investigated whether evolution would cause the system to move away from this boundary or toward it. In the latter case, adaptation would exacerbate the consequences of changes in external conditions.

Model and Analysis

Vegetation Dynamics in Arid Ecosystems

We base our analysis on the model developed by Kéfi et al. (2007a). This spatially explicit model was designed to study the ecological aspects of local facilitation. Here we extend the model to address its evolutionary aspects.

States of the System. Consider an arid ecosystem as a lattice-structured habitat consisting of an infinite number of sites, each roughly a square meter in size. Each site can be in one of three possible states: occupied by vegetation, unoccupied by vegetation but colonizable, and degraded soil that cannot be recolonized by vegetation. In addition to global competition for resources, we assume that a plant directly interacts with its nearest neighbors. All sites have the same number of nearest neighbors, z ($z = 4$). At each time instant, a site has a certain probability of realizing a transition from one state to another, depending on the state of its neighboring sites. To obtain more insight into the dynamics of the lattice model, we derived an analytic approximation, called “correlation dynamics” or “pair approximation” (Matsuda et al. 1992; Harada and Iwasa 1994; van Baalen and Rand 1998; Rand 1999; Iwasa 2000; van Baalen 2000). We now briefly review this correlation dynamics model.

Following Iwasa’s (2000) notation, the state of a site is denoted by σ , which can be a plus sign (occupied by vegetation), 0 (unoccupied but recolonizable), or a minus sign (degraded soil). Let ρ_σ be the probability that a randomly chosen site is a $\{\sigma\}$ site; this is a global density. Let the local density $q_{\sigma|\sigma'}$ be the conditional probability that a randomly chosen nearest neighbor of a $\{\sigma'\}$ site is in state σ . According to Bayes’s formula, this local density can be expressed in terms of the doublet density $\rho_{\sigma\sigma'}$, which is the probability that a randomly chosen pair of nearest neighbor sites is in state $\{\sigma\sigma'\}$:

$$\rho_{\sigma\sigma'} = \rho_{\sigma'\sigma} = \rho_\sigma q_{\sigma|\sigma'} = \rho_{\sigma'} q_{\sigma'|\sigma}$$

Dynamics of the System. It is well known that vegetation in arid ecosystems improves its microenvironment (Schlesinger et al. 1996; Callaway and Walker 1997; Aguiar and Sala 1999; Greene et al. 2001; Tongway and Ludwig 2001; Rietkerk et al. 2002). Therefore, we consider that there is a higher probability that a degraded site becomes recolonizable by vegetation when it is surrounded by vegetation (Kéfi et al. 2007a, 2007b). In the model, regeneration of a degraded site occurs at a rate $w_{\{-,0\}}$, with

$$w_{\{-,0\}} = r + f q_{\{+,-\}},$$

where r is a positive constant corresponding to the regeneration rate of a site without vegetation in its neighborhood; f is the maximum facilitative effect of vegetation on the regeneration of neighboring degraded sites, realized when all nearest-neighbor sites are $\{+\}$ (f is a positive constant). Hereafter, f is called “strength of local facilitation.”

Local facilitation is likely to be costly, in terms of either increased mortality or reduced fertility. For example, plants of arid ecosystems have to invest in a root system that not only is efficient for taking up water and nutrients but also can hold the soil (preventing erosion) and increase water infiltration. The actual cost will, of course, depend on the precise mechanism by which plants achieve facilitation. As detailed knowledge about the precise shape of the relationship is lacking, we assume a general positive relationship between a plant’s investment in facilitation and its mortality rate. We chose the same shape of the relationship as Le Galliard et al. (2003),

$$w_{\{+,0\}} = m_0 + \alpha f^\gamma,$$

where m_0 is the baseline mortality rate, a characteristic of the vegetation that may be influenced by grazing; α is the sensitivity of the cost; and γ determines the shape of the cost function. The relationship can be curved in such a way that mortality accelerates ($\gamma > 1$), decelerates ($\gamma < 1$), or varies linearly ($\gamma = 1$) with investment in facilitation. As long as this relationship is positive, our results do not change qualitatively, depending on the precise shape of the relationship. After the death of the vegetation occupying a given site, the site reverts to the recolonizable state.

A recolonizable site can be either recolonized by vegetation or eroded by rain and wind. To keep the model simple, we assume that degradation is a chance process not dependent on the neighboring sites: $w_{\{0,-\}} = d$.

Plants reproduce by spreading seeds across the lattice. The recruitment of a new individual has a probability of being successful only if the seeds reach a recolonizable site. We supposed that a fraction of the seeds produced by a vegetated site are locally dispersed, while the rest are glob-

ally dispersed (Harada and Iwasa 1994; van Rheede van Oudtshoorn and van Rooyen 1999). An assumption of our model is that the probability of seedling establishment depends negatively on the total number of $\{+\}$ sites in the lattice because of global competition for water and other limiting resources (negative density dependence). When these mechanisms are taken into account, colonization of a recolonizable site by vegetation occurs at rate $w_{\{0,+\}}$, with

$$w_{\{0,+\}} = \beta[\delta\rho_+ + (1 - \delta)q_{+\{0\}}]G(\rho_+),$$

where β is a positive constant that represents the intrinsic seed production rate per vegetated site multiplied by the survival and the germination probabilities; $1 - \delta$ is the fraction of seeds dispersed in the nearest neighborhood of a vegetated site, and δ is the fraction dispersed all over the lattice; G is a competition function describing the effect of the global density of $\{+\}$ sites on seedling establishment. Again, to keep the model simple, G is expressed as a linear function of ρ_+ ,

$$G(\rho_+) = \varepsilon - g\rho_+,$$

where ε is the establishment probability of seeds that have reached a recolonizable site in a system without vegetation (ε is a positive constant) and g is the competitive effect of the global density of $\{+\}$ sites on the establishment of new individuals (g is a positive constant). The particular

shape of this competition function does not affect our results qualitatively. For brevity, let b be $\beta\varepsilon$ and c be βg . Then we have

$$w_{\{0,+\}} = [\delta\rho_+ + (1 - \delta)q_{+\{0\}}](b - c\rho_+).$$

The full model and the derivation of its five ordinary differential equations are presented in appendix A. See table 1 for an overview of parameters and variables. Figure 1 displays a schematic representation of the model.

Spatial Invasion of Mutants

Consider a population of individuals characterized by a certain local facilitation strength f (we call this population the “resident population”). Suppose now that one of the external conditions changes (e.g., grazing pressure or aridity increases). How will this change affect the selective pressures on local facilitation, and what will be the consequences? We used the framework of adaptive dynamics to address this question (Metz et al. 1992, 1996; Geritz et al. 1998).

The theoretical approach commonly called adaptive dynamics seeks to describe the phenotypic evolution of a population through the successive substitutions of mutations. Mutations that differ from the monomorphic resident population occur randomly and recurrently. These can be thought of as attempting to “invade” the resident

Table 1: Notation

Class, symbol	Interpretation
Parameters:	
m_0	Baseline mortality rate of a vegetated site
α	Sensitivity of the cost of investing in local facilitation
f	Local facilitation strength: maximum effect of a neighboring vegetated site (resident or mutant) on the regeneration of a degraded site (the maximum effect is realized when all the nearest neighbors are vegetated sites)
m	$m_0 + \alpha f$
β	Intrinsic seed production rate per vegetated site \times survival probability \times germination probability
ε	Establishment probability of seeds on $\{0\}$ site in a system without competition
b	$\beta\varepsilon$; b measures the severity of the environmental conditions; a lower b value reflects a higher aridity level
δ	Fraction of seeds globally dispersed
g	Competitive effect of the global density of $\{+\}$ and $\{*\}$ sites on the establishment of new individuals
c	βg
r	Regeneration rate of a $\{-\}$ site without vegetated sites in its neighborhood
d	Degradation rate of $\{0\}$ sites
Variables:	
ρ_+	Density of vegetated sites (resident)
ρ_*	Density of vegetated sites (mutant)
ρ_-	Density of degraded sites
ρ_0	Density of recolonizable sites
$\rho_{\sigma\lambda}$	Density of pairs of neighboring sites $\{\sigma\lambda\}$ (σ and λ can be $+$, $*$, 0 , or $-$)
c_{++}	Clustering intensity of the vegetated sites

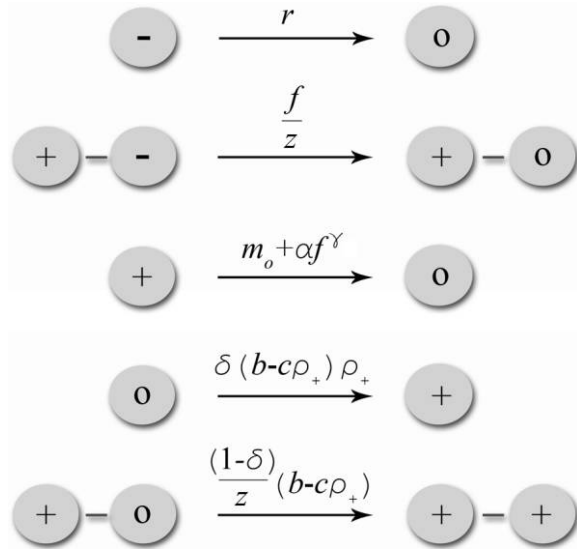


Figure 1: Transition rules among the different states of the model. Each cell of the cellular automaton is occupied by vegetation (*plus sign*), empty (*0*), or degraded (*minus sign*). See table 1 for a description of the parameters and variables.

population. Mutations are supposed to be small and rare (Metz et al. 1996). The basic principle of the approach is to follow the fate of rare mutants with a local facilitation strength slightly different from that of the resident population. When rare mutants appear, they experience the environment created by the common type in the resident population. Their evolutionary success is determined by the mutant's invasion fitness, the initial per capita growth rate of the mutant when rare in this environment (Metz et al. 1992; Geritz et al. 1998; Ferrière and Le Gaillard 2001). In spatially heterogeneous populations, the invasion fitness depends on the local spatial context around the mutants and is called “spatial invasion fitness” (van Baalen and Rand 1998; Ferrière and Le Gaillard 2001). If this spatial invasion fitness is positive, the mutant f^* will invade the resident population f and (in most cases) becomes the new resident. If it is negative, the mutant cannot invade and will eventually become extinct, so that the situation remains the same as before the mutation. Mutants with different trait values succeed each other until a situation is reached in which no new mutant can invade. The value of local facilitation strength at this point is the evolutionarily stable level of f .

Note that local facilitation is indiscriminate: it occurs not only among residents and among mutants but also between residents and mutants. Local facilitation indeed favors the creation of recolonizable sites, which has benefits for both mutants and residents.

When a mutant appears in the resident population at

equilibrium, a site can be in any of four states: $\{+\}$, $\{0\}$, or $\{-\}$, as before, or $\{*\}$ if it is occupied by a mutant. Incorporating all possible transitions leading to gains or losses of $\{*\}$ sites, the equation for the global density of the mutant is given by

$$\frac{d\rho_*}{dt} = [\delta\rho_* + (1 - \delta)q_{*|0}](b - c\rho_+ - c\rho_*)\rho_0 - (m_0 + \alpha f)\rho_*.$$

The entire system of equations corresponding to the dynamics of the mutant is presented in appendix B. Using $q_{*|0}\rho_0 = \rho_{0*} = q_{0|*}\rho_*$, we can express the spatial invasion fitness of a rare mutant with trait f^* in a resident population at equilibrium with trait f :

$$\frac{1}{\rho_*} \frac{d\rho_*}{dt} = \varphi_f(f^*) \approx [\delta\rho_0 + (1 - \delta)q_{0|*}](b - c\rho_+) - (m_0 + \alpha f^*).$$

The spatial invasion fitness of the mutant depends on the local density of recolonizable sites in the neighborhood of the mutants ($q_{0|*}$), which implies that the spatial structure that develops soon after the introduction of a mutant will play a crucial role in the invasion success of the mutant.

More information is provided by the “selection derivative” (Marrow et al. 1992; Ferrière and Le Gaillard 2001), also called the “fitness gradient” (Geritz et al. 1998), which determines the (local) direction of adaptive change, that is, whether adaptation will lead to an increase or a decrease of local facilitation strength in a resident population of trait f . In other words, the selection derivative determines what type of mutants can invade in a given resident population:

$$\left. \frac{\partial \varphi_f(f^*)}{\partial f^*} \right|_{f^*=f} = (1 - \delta)(b - c\rho_+) \left. \frac{\partial q_{0|*}}{\partial f^*} \right|_{f^*=f_{cs}} - \alpha.$$

When the selection derivative is positive, mutants with a trait f^* slightly higher than f will have an advantage, compared with the residents. Considering the components of the selection derivative helps in identifying the selective pressures driving the evolutionary dynamics of local facilitation. The first term on the right-hand side of the equation quantifies the pressure for increasing the quantity of $\{0\}$ sites created in the neighborhood of mutants when f^* increases. The second term measures the pressure to decrease the cost of local facilitation, α . One key element of the evolution of local facilitation therefore lies in the way local facilitation influences the creation of empty sites

(either by mortality of vegetation or by regeneration of degraded sites) for the spread of the mutants. Trait values f^* that satisfy $[\partial\varphi(f^*)/\partial f^*]|_{f^*=f_{es}} = 0$ are called “evolutionary singularities,” f_{es} , and correspond to values of the trait at which the two selective pressures exactly balance. These are the points we are interested in because they are possible end points for the evolutionary process. In principle, evolutionary singularities may be unstable in a variety of ways (Geritz et al. 1998), but in our model, they are always evolutionarily stable and convergence stable. In the rest of the article, we therefore simply use the term “evolutionary equilibria.”

Analysis

A full analysis of the equilibria of the resident population is not possible, since the dynamics of that population is governed by five nonlinear ordinary differential equations (app. A). However, analytical conditions could be derived under which an initially rare state ($\{+\}$, $\{0\}$, or $\{-\}$) can increase into a system dominated by another state (see Kéfi et al. 2007a for details). Bifurcation diagrams of the resident model were derived numerically with the software package CONTENT (Kuznetsov and Levitin 1997). Spatially explicit simulations of the model were run on lattices of 100×100 cells with periodic boundary conditions (probabilistic cellular automaton). The initial spatial distributions were random for given initial densities. Simulations were carried out using a stochastic asynchronous update algorithm.

The value of the spatial invasion fitness of a mutant in a resident population at equilibrium was numerically obtained (see app. B for details). Pairwise invasibility plots (PIPs) portray the sign structure of the spatial invasion fitness across all possible combinations of the mutant trait value, f^* , and the resident value, f . PIPs indicate the location of potential evolutionary equilibria, f_{es} , and can be used to infer the evolutionary dynamics of the trait (Geritz et al. 1998). We looked at the effect of changes in external conditions on the value of the evolutionary equilibrium, f_{es} , for different seed dispersal strategies (δ).

We studied the likely evolutionary consequences of changes in aridity and grazing pressure. Aridity is assumed to affect b , the probability of recruitment of a new vegetated site in a system without competition. A lower b value reflects a higher aridity level. Higher grazing pressure was modeled by higher plant mortality, m_0 .

The “viability area” is defined as a set of local facilitation strength values (f) for which there exists at least one non-zero-population stable equilibrium. The “extinction boundary” is the boundary of the viability area.

We also looked at an “area of extinction risk,” which we defined as a parameter space where the vegetation cover

is less than a threshold value. In this area (parameter space), extinction risk is high because of genetic and environmental stochasticity. Consequences of adaptation for the viability and the stability of the system were addressed by analyzing the characteristics of the populations at the evolutionary equilibria. Bifurcation diagrams displaying the vegetation density at equilibrium for all possible values of f were traced for different external conditions (i.e., different levels of aridity or grazing pressure). On these diagrams, the value of the evolutionary equilibrium was plotted for each external condition, which revealed the characteristics of the population at the evolutionary equilibrium. To quantify the clustering intensity of vegetation, we calculated the ratio $c_{++} = \rho_{++}/\rho_+^2$ (van Baalen 2000). If there is no spatial correlation in the system, $\rho_{++} = \rho_+^2$ and $c_{++} = 1$. If vegetated sites aggregate, the probability that two nearest neighbors are $\{+\}$ is higher than in a random lattice and $c_{++} > 1$. The curves of variation of c_{++} at equilibrium when f varies were traced for different external conditions. Plotting on the same graph the f_{es} corresponding to each external condition allowed us to address the consequence of adaptation on the spatial organization of the vegetation.

Results

The resident system has two kinds of stable equilibria: a desert equilibrium ($\rho_+ = 0$) and a vegetation equilibrium ($\rho_+ > 0$; fig. 1A), which co-occur for a certain range of parameter values (app. A; fig. 2A, 2B). In the latter case, the system has two alternative stable states, meaning that the system can reach one of these two alternative states, depending on the initial population density. If such an area of alternative stable states is crossed under changes in external conditions (i.e., changes in aridity level or grazing pressure), the system undergoes a sudden transition to extinction, mathematically called “discontinuous transition” (fig. 2A, 2B). In the absence of alternative stable states, the transition is continuous, and under changes in external conditions, the population density gradually decreases until extinction. Strong local facilitation (f) favors continuous transitions (fig. 2B). The extinction risk area, that is, the parameter space where the vegetation cover at equilibrium is less than 10%, is extremely small and limited to continuous transitions to extinction. This indicates that whenever extinction is imminent in our system, vegetation cover is usually high. The resident system, moreover, exhibits vegetation clustering as an outcome of internal dynamics only, which therefore can be considered as spatial self-organization (fig. 2C). Detailed analyses of the ecological dynamics of the system without cost (i.e., such that $\alpha = 0$) are presented by Kéfi et al. (2007a).

When aridity increases (lower b), the plant population

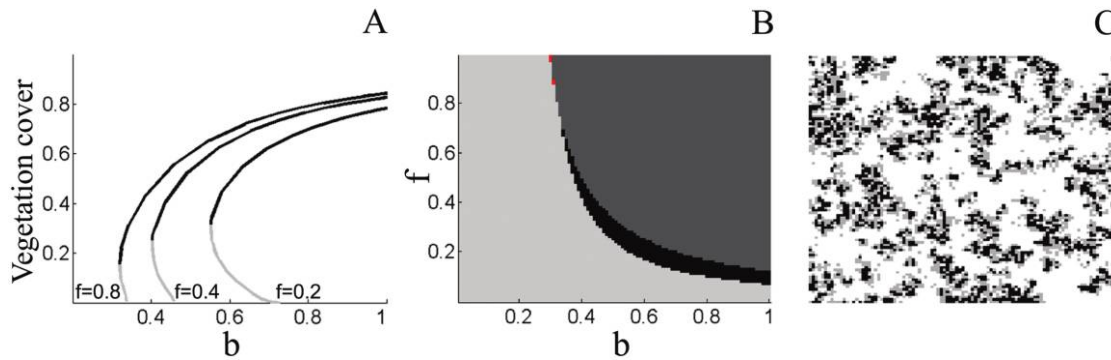


Figure 2: Effect of local facilitation strength on the resident population. *A*, Effect of local facilitation strength on the bifurcation diagram of the resident population. The global density of vegetated sites at equilibrium, $(\rho_+)_{\text{eq}}$, is displayed as a function of b , which decreases when aridity increases. The local facilitation strength, f , is the effect of neighboring vegetated sites on the regeneration of a degraded site. *Black lines*, stable equilibria; *gray lines*, unstable equilibria. *B*, Effect of local facilitation strength on the characteristics of the resident population. *Light gray*, extinction of the resident population (desert system at equilibrium); *black*, bistable resident population; *dark gray*, maintenance of the resident population independent of the initial conditions (vegetation system at equilibrium); *red*, the population density at equilibrium is less than 0.1 (risk of extinction). *C*, Spatial organization of the resident population. Outcome of a spatially explicit simulation (grid of 100×100 cells). *Black*, sites occupied by vegetation; *gray*, recolonizable sites; *white*, degraded sites. $b = 0.34$, $f = 0.8$. Other parameter values: $c = 0.2$, $d = 0.1$, $r = 0.001$, $m_0 = 0.1$, $\delta = 0.1$, $\alpha = 0.01$, and $\gamma = 1$.

will eventually die out and the system will become a desert (fig. 2A, 2B). The same will happen if grazing pressure increases (higher m_0). However, the plant population may adapt to the new external conditions, leading to new plant trait values and thus to different dynamics. We are interested in the consequences of such adaptation for the population. Here, we first briefly describe in an intuitive way the adaptive dynamics approach that we used to tackle this question. We look at a resident population whose local facilitation trait is at its evolutionary equilibrium, f_{es} . One of the external conditions changes (i.e., either grazing pressure or aridity increases), and we investigate how the evolutionary equilibrium subsequently changes.

Therefore, we study the outcome of multiple mutations occurring in the initial population, and we check at which value of the trait the population eventually stabilizes. We do that by investigating the fate of rare mutants characterized by the trait value f^* in the initial resident population characterized by the trait value f_{es} . An evolutionary equilibrium is reached when no mutants (with an f different from that of the resident population) can invade. To predict the outcome of invasions in a resident population, the necessary information can be summarized in a PIP (Geritz et al. 1998). Invasion of a rare mutant of trait f^* in a resident population of trait f at equilibrium is determined by the sign of the spatial invasion fitness, $\varphi_r(f^*)$. PIPs display the sign of the spatial invasion fitness for different values of f and f^* (fig. 3A). In PIPs, intersections between the first bisectrix (where $\varphi_r(f^*) = 0$) and the limiting contour lines of the dark gray area (where the

mutant invades, $\varphi_r(f^*) > 0$) and the white area (where the mutants disappears, $\varphi_r(f^*) < 0$) define the potential evolutionary equilibrium, f_{es} . On the PIP in figure 3A, at f values less than f_{es} , the dominant selective pressure is due to the presence of $\{0\}$ sites in the neighborhood of mutants. Mutants with a slightly higher f^* will invade (*dark gray area*) and replace the resident. Thus, increased local facilitation strength is favored until f reaches f_{es} . In the same vein, at f values greater than f_{es} , the selective pressure induced by the cost of local facilitation leads to a decrease in f , and the evolutionary dynamics of the trait converges to f_{es} . Thus, in the case of figure 3A, f_{es} is an attractive stable singularity. The value of f_{es} obtained with PIPs can then be followed when the external conditions vary.

For plants characterized by local seed dispersal, when external conditions deteriorate (b decreases or m_0 increases), f_{es} increases until it reaches 1, its maximal value (fig. 3B, 3C). Thus, under severe external conditions, the selective pressure for increasing the amount of $\{0\}$ sites in the neighborhood of mutants is more important than decreasing the mortality of the mutants. Indeed, establishment of new vegetated sites is difficult under stressful conditions, and because a high proportion of seeds are locally dispersed, it becomes important to have $\{0\}$ sites close by. As a consequence of adaptation, vegetation can maintain itself under harsher environmental conditions (because adaptation keeps f in the viability area; fig. 3B, 3C).

For plants characterized by global seed dispersal, when external conditions deteriorate, the evolutionary singularity progressively tends toward the extinction boundary (fig.

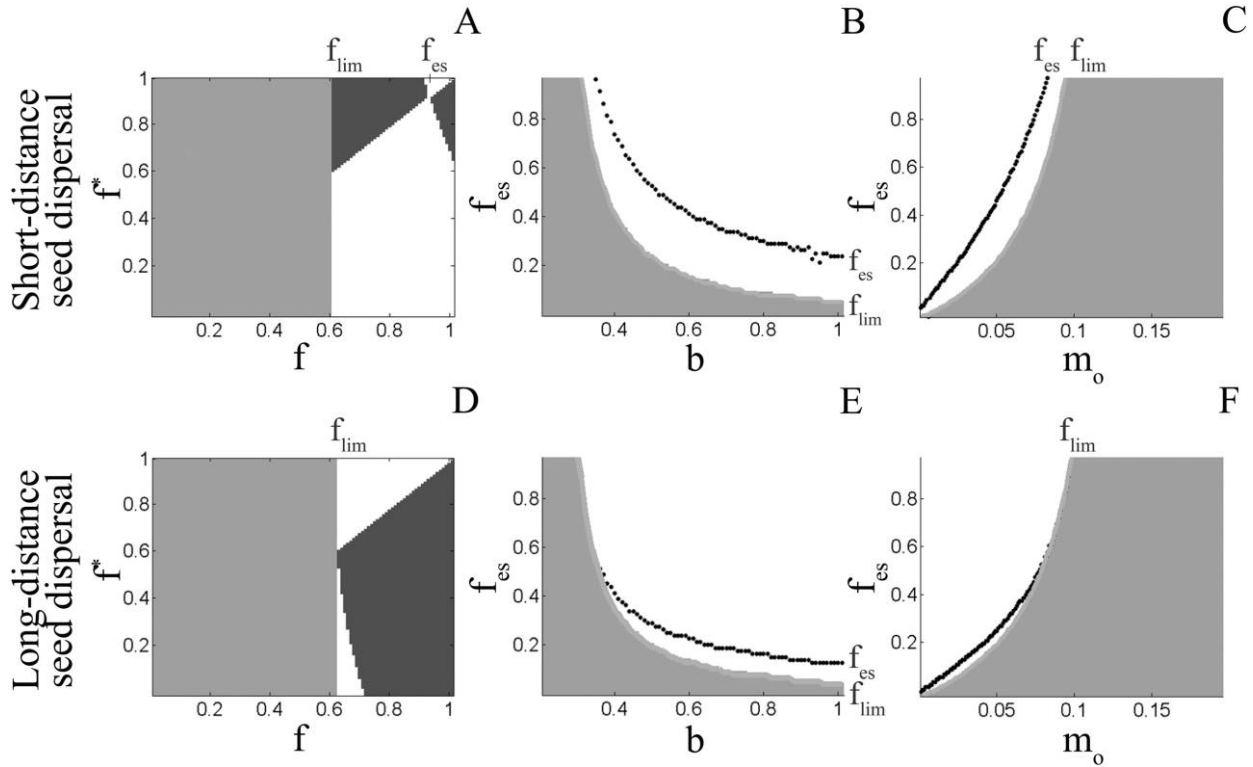


Figure 3: Effect of external conditions (b , m_0) on the evolution of local facilitation (f_{es}). *A, D*, Pairwise invasibility plots (PIPs). *Dark gray*, invasion of the mutant (positive fitness); *white*, extinction of the mutant (negative fitness). The light gray rectangles at the left of the panels correspond to value of the resident strategy, f , for which the population is not viable (i.e., where a desert system is the only stable equilibrium). PIPs allow the determination of f_{lim} (the minimum value of f for which the resident population is viable) and f_{es} (the value of the evolutionary equilibrium). *A*, Example of evolutionarily stable and attractive singularity; $b = 0.35$. *D*, Example of extinction as a result of adaptation; $b = 0.33$. *B, C, E, F*, Effect of external conditions on the evolutionarily stable strategy. A lower b value reflects a higher aridity level. A higher m_0 value reflects higher grazing pressure. *Light gray*, extinction area (whose upper limit is f_{lim}); *black*, f_{es} . δ is the proportion of seeds globally dispersed. *A–C*, $\delta = 0.1$; *D–F*, $\delta = 0.6$. *A, B, D, E*, $m_0 = 0.1$. *C, F*, $b = 0.3$. Other parameter values: $c = 0.2$, $d = 0.1$, $r = 0.001$, $\alpha = 0.01$, and $\gamma = 1$.

3E, 3F). Selection eventually moves the facilitation strategy across the extinction boundary into the interior of the extinction area, and the population becomes extinct even when it is allowed to adapt (fig. 3D). Investing in the creation of recolonizable sites in its neighborhood (by having a high f) indeed provides little advantage to a mutant with global seed dispersal.

As the external conditions deteriorate, the viability area shrinks to such an extent that the population would become extinct in the absence of evolution, but at the same time directional selective pressures are induced that allow the evolutionary equilibrium f_{es} to progress in the same direction as the extinction boundary, toward higher values of f (fig. 4A, 4C). The outcome of adaptation to changes in external condition is determined by the relative speed of changes of the evolutionary equilibrium and the extinction boundary. In the case of local seed dispersal, the evolutionary equilibrium advances faster than the extinc-

tion boundary. Adaptation keeps the system away from the extinction boundary and protects the population from extinction (fig. 4A). In the case of global seed dispersal, however, the evolutionary equilibrium is caught up by the extinction boundary, and the population becomes extinct (fig. 4C). In both cases, the populations that have reached their evolutionary equilibrium ($f = f_{es}$) are spatially more clustered under harsher external conditions (fig. 4B, 4D).

For a given grazing pressure (m_0), there is a critical fraction of seeds globally dispersed (δ), above which adaptation leads to population extinction (fig. 5). Consider the ecological characteristics of populations that reached their evolutionary equilibrium ($f = f_{es}$): the system always crosses an area of alternative stable states before going into the area of evolution to extinction (fig. 5). Thus, when extinction as a result of adaptation is imminent, the resident population has two attractors: both extinction and an equilibrium corresponding to strictly positive vegeta-

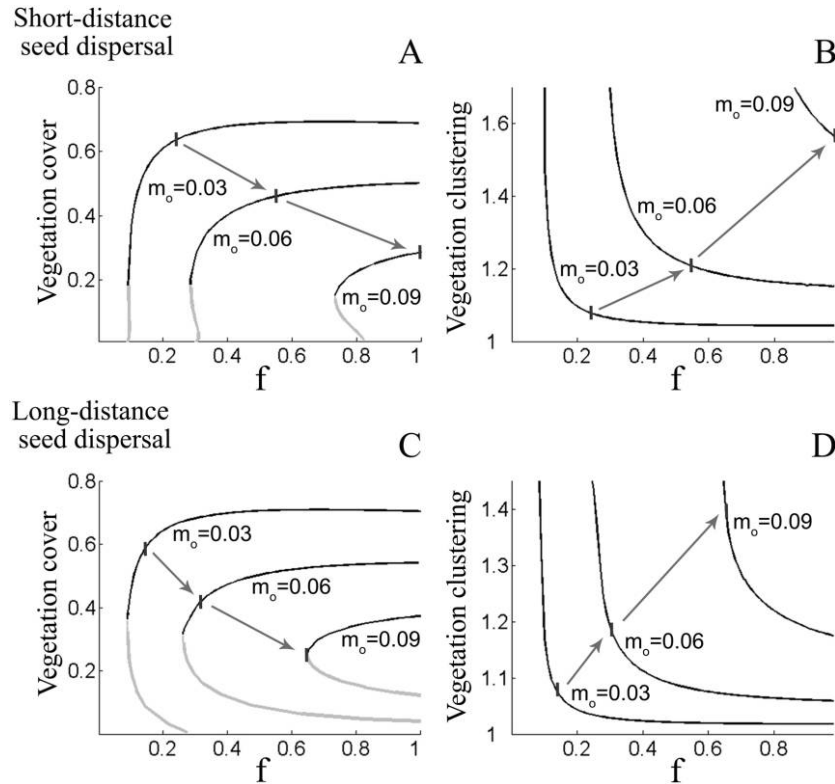


Figure 4: Consequences of the evolution of local facilitation on the functioning of arid ecosystems. *A, B*, Population survival as a result of adaptation. *C, D*, Extinction as a result of adaptation. *A, C*, Effect of local facilitation strength on the stability of the system. A higher m_0 value reflects higher grazing pressure. The global density of vegetated sites at equilibrium, $(\rho_+)_{\text{eq}}$, is displayed as a function of f , the local facilitation strength. *Black lines*, stable equilibria; *light gray lines*, unstable equilibria; *bars on lines*, values of the evolutionary equilibrium, f_{es} . Qualitatively similar results are obtained with decreasing b instead of increasing m_0 . *B, D*, Effect of local facilitation strength on the spatial organization of the vegetation. Y-axis shows c_{++} , the clustering intensity of vegetated sites. For each value of the external condition, the value of the f_{es} is indicated on the bifurcation curve. Arrows show how f_{es} varies with increasing m_0 . *B*, For $m_0 = 0.03$, $f_{\text{es}} = 0.24$ and $c_{++} = 1.09$; for $m_0 = 0.06$, $f_{\text{es}} = 0.55$ and $c_{++} = 1.21$; for $m_0 = 0.09$, $f_{\text{es}} = 1$ and $c_{++} = 1.55$. *D*, For $m_0 = 0.03$, $f_{\text{es}} = 0.14$ and $c_{++} = 1.08$; for $m_0 = 0.06$, $f_{\text{es}} = 0.31$ and $c_{++} = 1.17$; for $m_0 = 0.09$, evolution to extinction (just before extinction: $f_{\text{es}} = 0.65$ and $c_{++} = 1.36$). δ is the proportion of seeds globally dispersed. *A, B*, $\delta = 0.1$; *C, D*, $\delta = 0.6$. Other parameter values: $c = 0.2$, $d = 0.1$, $r = 0.001$, $b = 0.3$, $\alpha = 0.01$, and $\gamma = 1$.

tion density are stable. Increasing aridity (decreasing b) has a qualitative effect similar to that of increasing grazing pressure (m_0). The area of extinction risk (where the vegetation cover is less than 10% at equilibrium) does not occur, meaning that evolution of local facilitation does not lead to populations with low vegetation cover that would be susceptible to extinction by stochastic processes.

To understand how adaptation can lead to extinction, we consider a population characterized by global dispersal at the extinction boundary (such as in fig. 3D). A mutant with a lower local facilitation strength, f , has an advantage compared to the resident because it pays fewer costs than the resident, and its population initially grows. Because dispersal is global, the mutant population does not form clusters and benefits from the $\{0\}$ sites created by the resident for its expansion. Its spatial invasion fitness is there-

fore initially positive. This invasion, however, decreases the creation of $\{0\}$ sites, thus robbing the population of an essential resource (fig. 6B). When the mutant invades, it pushes the resident population into the basin of attraction of the extinction equilibrium (fig. 6B). However, once the resident has disappeared, there are not enough $\{0\}$ sites in the neighborhood of the mutant for its maintenance, and its fitness becomes negative. In the end, both the mutant and the resident populations become extinct (fig. 6B₁–6B₃). In contrast, in a situation where evolution allows the population to escape extinction, mutants with an f higher than that of the resident population can increase in size because of their positive fitness, and they finally replace the resident (fig. 6A, fig. 6A₁–6A₃). This happens because these populations are characterized by local dispersal. So the mutant population forms clusters, and only

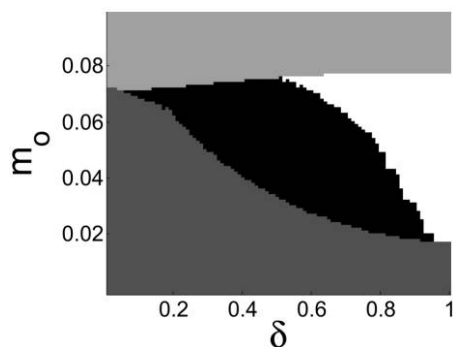


Figure 5: When does adaptive evolution lead to the extinction of the population? Evolutionary outcome as a function of grazing pressure (m_0) and fraction of seeds globally dispersed (δ). Light gray indicates extinction area for the resident population (desert system is the only stable equilibrium). For the combinations of values of m_0 and δ for which the resident population was viable, we derived the value of the evolutionary equilibrium, f_{es} (through the pairwise invasibility plots). If the result of adaptation was the survival of the population, we looked at the characteristics of the corresponding resident population: resident populations characterized by two alternative stable states are displayed in black, and populations characterized by one stable state (i.e., maintenance of the resident population independently of the initial conditions) are displayed in dark gray. The zone where adaptation rescues the population from extinction corresponds to the dark gray and black areas. We checked whether the vegetation density at equilibrium was below 0.1 (independent of whether there were one or two stable states), but this did not happen for any of the parameter combinations in this figure. White indicates adaptation-driven extinction. Qualitatively similar results are obtained with decreasing b instead of increasing m_0 . $c = 0.2$, $d = 0.1$, $r = 0.01$, $\alpha = 0.01$, $b = 0.4$, and $\gamma = 1$.

mutants viable on their own can invade the resident population.

Discussion

Local facilitation allows plants to ameliorate their local environment and thus to favor the installation of new individuals in their neighborhood. We carried out an analysis of the adaptive evolution of local facilitation, and we investigated the consequences of this adaptation under increasing external pressure in arid ecosystems.

As external conditions deteriorate (increasing aridity or increasing grazing pressure), the range of local facilitation strength values for which the plant population can survive (i.e., the viability area) shrinks. Whether the population survives under the new external conditions depends on whether adaptation can keep the new value of local facilitation strength in the viability area. Survival of the population is therefore a race between the extinction boundary and the evolutionary equilibrium of local facilitation strength.

Our results suggest that the outcome of the evolutionary

dynamics of local facilitation depends on the seed dispersal strategy. Two contrasting cases emerge. For systems characterized by local seed dispersal (low δ), adaptation to more stressful external conditions leads to an increase in local facilitation strength (higher f_{es}) and drives the population away from the extinction boundary. The evolution to strong local facilitation under increased external pressure has major consequences for the ecological functioning of the system. Vegetation can maintain itself under harsher conditions because of adaptation, and it becomes spatially more clustered because of increased stress. Moreover, strong local facilitation decreases the probability of discontinuous transitions so that the population is more resilient to short-term climatic fluctuations.

In contrast, systems characterized by global seed dispersal (high δ) tend to move toward and across the extinction boundary under increased external pressure, which ultimately results in the extinction of the entire vegetation population. In this case, natural selection drives a population that is viable at the ecological timescale to extinction. This phenomenon has become known as evolutionary suicide (Ferrière 2000). Evidence of evolution to extinction in natural systems is still scarce (but see Rankin and Lopez-Sepulcre 2005 for a discussion about three recent empirical studies that lend support to the evolution-to-extinction hypothesis).

Under the assumption that there is no coevolution of seed dispersal with local facilitation, the latter result has two main implications. First, species characterized by long-distance seed dispersal are not expected to be common in arid ecosystems because they may have been driven to extinction as a result of adaptation under the changes in external conditions that occurred in the past. This result is consistent with the field observations that plants of arid environments have often developed survival strategies to restrict dispersal (reduction of dispersal structures in seeds and development of anchorage mechanisms), also called “proxichory” (Friedman and Stein 1980; van Rheede van Oudtshoorn and van Rooyen 1999). Long-distance seed dispersal can indeed be a disadvantage in systems with severe environmental conditions, where many suitable sites are in the neighborhood of the mother sites and could be reached by local dispersal. Our results are consistent with observed dispersal strategies in the field. However, we acknowledge that this is no proof that the evolution of local facilitation is responsible for these observed dispersal strategies (see Ellner and Shmida 1981 for a discussion). Second, even for plants characterized by short-distance seed dispersal, our model shows that any factor that would artificially increase the number of seeds dispersed far away (e.g., water runoff after rain shower, strong winds, or even grazing in some cases; Van Auken 2000) could drive the system toward extinction as a result of

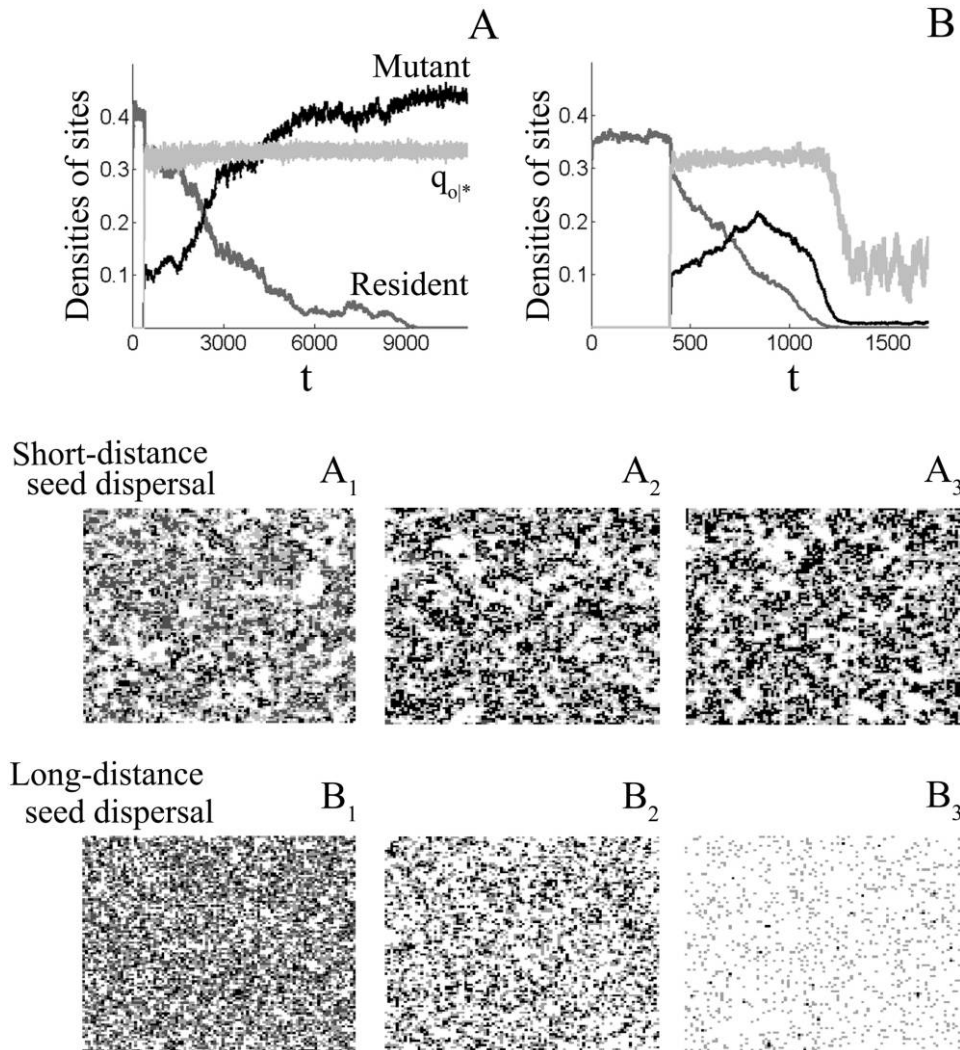


Figure 6: Spatially explicit simulations (cellular automaton) displaying the invasion of a mutant in case of short-distance seed dispersal (A) and long-distance seed dispersal (B). Introduction of a mutant ($f^* = 0.9$ [A]; $f^* = 0.25$ [B]) in a resident population at equilibrium ($f = 0.8$ [A]; $f = 0.3$ [B]). In both cases, the mutants were introduced at $t = 400$. A, Invasion and replacement of the resident. *Black*, density of mutants; *dark gray*, density of residents; *light gray*, local density of recolonizable sites in the neighborhood of a mutant (q_{01*}). A_1 – A_3 , Snapshots of mutant invasion in the resident population. *Dark gray*, vegetated (resident) sites; *black*, vegetated (mutant) sites; *light gray*, recolonizable sites; *white*, degraded sites. A few mutant sites were randomly introduced into the resident population at equilibrium. Time after introduction of the mutant: $t = 100$ (A_1), $t = 1,000$ (A_2), $t = 10,000$ (A_3). Parameter values: $f = 0.8$, $f^* = 0.9$, $c = 0.2$, $d = 0.1$, $r = 0.001$, $\alpha = 0.01$, $m_0 = 0.1$, $b = 0.35$, $\delta = 0.1$, and $\gamma = 1$. B, Evolution to extinction. *Black*, density of mutants; *dark gray*, density of residents; *light gray*, local density of recolonizable sites in the neighborhood of a mutant (q_{01*}). B_1 – B_3 , Snapshots of mutant invasion in the resident population. Time after introduction of the mutant: $t = 100$ (B_1), $t = 600$ (B_2), $t = 850$ (B_3). Parameter values: $f = 0.3$, $f^* = 0.25$, $c = 0.2$, $d = 0.1$, $r = 0.01$, $\alpha = 0.01$, $m_0 = 0.1$, $b = 0.4$, $\delta = 0.9$, and $\gamma = 1$.

adaptation. When such factors are operating, adaptation could be the final push to the desertification of arid ecosystems.

The mechanisms by which individual adaptation can lead to the extinction of the entire population in our model are related to the fact that the spatial invasion fitness is frequency dependent (i.e., the fitness depends on the fre-

quencies of individuals with different trait values; Matsuda and Abrams 1994; Metz et al. 1996; Kisdi 1998; Gyllenberg and Parvinen 2001). The fact that a mutant does well in the initial environment determined by the resident population does not guarantee the success of the mutant once its trait is widespread in the population. At the extinction boundary, mutants with a lower investment in local fa-

cilitation can increase in the resident population because they benefit from the {0} sites created by the resident population. Selection then favors strategies that are initially beneficial for the individuals (individuals with a lower f have a lower mortality) but harmful for the population as a whole (the mutant population is not viable alone because of a lack of {0} sites available for the installation of new individuals; Matsuda and Abrams 1994; Metz et al. 1996; Kisdi 1998; Gyllenberg and Parvinen 2001). Evolution to extinction has been observed in other evolutionary models in the context of the evolution of body size under asymmetric competition (Gyllenberg and Parvinen 2001), the evolution of mutualism (Ferrière and Le Galliard 2001), and the evolution of altruism (Le Galliard et al. 2003).

Interestingly, evolution of local facilitation does not lead to low population densities at which the population is seriously threatened by extinction due to stochastic processes. But populations can evolve toward trait values that are not viable. We found that these populations are always characterized by alternative stable states. This result is consistent with the findings of Gyllenberg et al. (2000), who demonstrated in a structured metapopulation model that the extinction boundary is evolutionarily repelling if the transition to extinction is continuous. A system undergoing a continuous transition has a very low population density close to the extinction boundary. In this context, only mutants that are viable in the absence of the resident (i.e., mutants characterized by strong local facilitation in our case) can invade. In this way, the strategy is kept in the interior of the viability area. Thus, when the transition to extinction is continuous, extinction due to adaptation cannot occur. A sudden transition to extinction (i.e., alternative stable states) is therefore a necessary (but not sufficient) condition for evolution to extinction to occur (Gyllenberg et al. 2000).

The evolution and persistence of positive interactions, in particular mutualism and altruism, have long been puzzling because of their apparent evolutionary instability (Hamilton 1963; Axelrod and Hamilton 1981). In a mutualistic interaction, each of the two partner species receives a net benefit. Cheaters who benefit from partner species without investing in costly commodities to exchange with the partner species should be favored by selection (Axelrod and Hamilton 1981). In altruistic interactions, a donor increases a recipient's fitness at the expense of its own. Nonaltruists, who do not pay the cost associated with altruism, should always outcompete the altruists.

In many cases, local facilitation can be seen as a specific case of altruism, where individuals that invest in local facilitation do not directly increase the fitness of the recipient but do indirectly increase the probability of its recruitment into the system by creating favorable sites. In

this sense, the example of local facilitation presented here resembles the case of group augmentation (Kokko et al. 2001), where individuals are assumed to survive and reproduce better in large groups and therefore receive a direct benefit from raising new members even if they are unrelated. However, local facilitation as it is modeled here implies, at most, a delayed benefit for the facilitator (i.e., there is no direct benefit). The facilitator favors the recruitment of individuals in the system. These individuals will eventually contribute to the creation of favorable sites in their neighborhood (the facilitative effect being local only) that could be used by the facilitator's offspring. The seeds of the facilitator will be able to reach these favorable sites if dispersal is local. This means that the facilitator has a chance of getting its investment back only if dispersal occurs at a spatial scale similar to that of facilitation. In our model, the evolution of local facilitation is therefore crucially dependent on the spatial component of the different ecological mechanisms.

As early as 1964, Hamilton proposed that cooperation should evolve more readily in populations with limited dispersal, which he referred to as "viscous" populations (Hamilton 1964). This led to many theoretical studies addressing the evolution of altruism in spatially heterogeneous populations (see Lion and van Baalen 2008 for a recent review). In populations with limited dispersal, offspring tend to remain close to their parents and individuals are likely to have relatives in their neighborhood. According to kin selection, altruism can evolve in such populations (see Lehmann and Keller 2006 for a review of the necessary conditions for the evolution of altruism and cooperation). However, population viscosity also increases the intensity of competition for space or resources among neighbors, which can impede the evolution of altruism (West et al. 2002). Le Galliard et al. (2005) showed that habitat saturation, which measures the strength of competition on altruists, is a crucial factor mediating the evolution of altruism but need not be detrimental to the evolution of altruism in viscous populations. In a review of recent theoretical advances on the evolution of altruism, Lion and van Baalen (2008) pointed out that the conditions for the evolution of altruism are in general more favorable in viscous populations where dispersal is local than in well-mixed populations that lack spatial structure. When population viscosity decreases (e.g., because dispersal increases), the investment in altruism decreases and eventually vanishes or even reverses (e.g., Le Galliard et al. 2003, 2005; Lehmann et al. 2006; Lion and van Baalen 2007).

In a recent study, Lehmann (2007) investigated what happens when an altruistic act has not only a spatial component but also a temporal one. This study addressed the case where individuals create physical alteration of the

habitat that can last over several generations (ecological inheritance; Odling-Smee et al. 2003). In this way, individuals can (positively or negatively) affect the fitness of individuals in the future, which can be referred to as a niche-constructing behavior (Odling-Smee et al. 2003). By posthumously helping relatives living in the future, an actor is helping individuals that are not in direct competition with itself, which decouples kin competition and kin selection benefits. Lehmann (2007) showed that in this case, the evolution of altruistic helping is favored under limited dispersal. This study is a very interesting step in understanding how the way individuals modify their environment might feed back on the selective pressures they experience.

Although recent theoretical advances have increased our understanding of the evolution of helping and altruism (e.g., Lehmann and Keller 2006; Lion and van Baalen 2007 for recent reviews), few models take the underlying mechanisms of altruism explicitly into account as we do here in the case of local facilitation. Our model results show how adaptation could modify the response of an ecosystem to changing external conditions, by comparison with what would be expected from the ecological dynamics only. Consider an ecosystem at the edge of a transition to extinction. If only the ecological dynamics are taken into account, further changes in external conditions are necessary to push the ecosystem beyond the extinction thresh-

old. However, adaptation could lead the system to either move away from the extinction threshold or move across it, resulting in extinction without further changes in external conditions. Local facilitation by sessile organisms is also ubiquitous in physically harsh habitats other than arid ecosystems, such as salt marshes, alpine areas, and intertidal zones (Bertness and Callaway 1994; Bertness and Leonard 1997; Stachowicz 2001; Callaway et al. 2002; van de Koppel et al. 2005), and our results may be further generalized to study the evolution of local facilitation in a wider range of ecosystems. To further link adaptive and ecological dynamics of ecosystems in a changing world is essential not only for increased understanding of degradation processes but also for the development of adequate conservation strategies.

Acknowledgments

The manuscript greatly benefited from the comments of R. Chaves, P. de Ruiter, J. van de Koppel, and A. van Noordwijk. We also thank S. Lion for insightful suggestions on earlier versions of the manuscript. We thank two anonymous reviewers for constructive comments and criticisms on the manuscript. The research of S.K. and M.R. is supported by a personal Vidi grant of the Netherlands Organization of Scientific Research/Earth and Life Sciences (NWO-ALW) to M.R.

APPENDIX A

The Resident Model

Let m be $m_0 + \alpha f$. Four conservation equations are available:

$$\rho_+ + \rho_0 + \rho_- = 1, \quad (\text{A1})$$

$$\rho_{++} + \rho_{+0} + \rho_{+-} = \rho_+, \quad (\text{A2})$$

$$\rho_{00} + \rho_{0+} + \rho_{0-} = \rho_0, \quad (\text{A3})$$

$$\rho_{--} + \rho_{-0} + \rho_{-+} = \rho_-. \quad (\text{A4})$$

In this system, there are three singleton variables (ρ_o) and six distinct doublet variables ($\rho_{\sigma\sigma'}$), because $\rho_{\sigma\sigma'} = \rho_{\sigma'\sigma}$. There are thus nine variables. As there are also four conservation equations, we need five equations to solve the system. We chose $d\rho_{++}/dt$, $d\rho_{+-}/dt$, $d\rho_{--}/dt$, $d\rho_+/dt$, and $d\rho_-/dt$. The five equations for the resident model are

$$\frac{d\rho_{++}}{dt} = 2\rho_{0+}w_{\{0,+\}} - 2\rho_{++}w_{\{+,0\}} \quad (\text{A5})$$

$$\frac{d\rho_{+-}}{dt} = \rho_{0-}w_{\{0,+\}} + \rho_{0+}w_{\{0,-\}} - \rho_{+-}(w_{\{+,0\}} + w_{\{-,0\}}) \quad (\text{A6})$$

$$\frac{d\rho_{--}}{dt} = 2\rho_{0-}w_{\{0,-\}} - 2\rho_{--}w_{\{-,0\}} \quad (\text{A7})$$

$$\frac{d\rho_+}{dt} = \rho_0 w_{\{0,+\}} - \rho_+ w_{\{+,0\}} \quad (\text{A8})$$

$$\frac{d\rho_-}{dt} = \rho_0 w_{\{0,-\}} - \rho_- w_{\{-,0\}} \quad (\text{A9})$$

Using the conservation equations (A1)–(A4) and substituting the transition probabilities by their expression in the above equations lead to the following closed system of equations:

$$\frac{d\rho_{++}}{dt} = 2(\rho_+ - \rho_{+-} - \rho_{++}) \left[\delta\rho_+ + \frac{1-\delta}{z} + (1-\delta) \frac{z-1}{z} \frac{(\rho_+ - \rho_{+-} - \rho_{++})}{1 - \rho_+ - \rho_-} \right] (b - c\rho_+) - 2\rho_{++}m,$$

$$\begin{aligned} \frac{d\rho_{+-}}{dt} = & d(\rho_+ - \rho_{+-} - \rho_{++}) + (\rho_- - \rho_{--} - \rho_{+-}) \left[\delta\rho_+ + \frac{z-1}{z} (1-\delta) \frac{\rho_+ - \rho_{+-} - \rho_{++}}{1 - \rho_+ - \rho_-} \right] (b - c\rho_+) \\ & - \rho_{+-} \left(r + \frac{f}{z} + \frac{z-1}{z} f \frac{\rho_{+-}}{\rho_-} + m \right), \end{aligned}$$

$$\frac{d\rho_{--}}{dt} = 2d(\rho_- - \rho_{--} - \rho_{+-}) - 2\rho_{--} \left(r + \frac{z-1}{z} f \frac{\rho_{+-}}{\rho_-} \right),$$

$$\frac{d\rho_+}{dt} = \left[\delta\rho_+ + (1-\delta) \frac{\rho_+ - \rho_{+-} - \rho_{++}}{1 - \rho_+ - \rho_-} \right] (b - c\rho_+) (1 - \rho_+ - \rho_-) - m\rho_+,$$

$$\frac{d\rho_-}{dt} = d(1 - \rho_+ - \rho_-) - \left(r + f \frac{\rho_{+-}}{\rho_-} \right) \rho_-.$$

APPENDIX B

The Mutant Model

The Model of the Mutant for the Evolution of f

Let m be $m_0 + \alpha f$, and let m^* be $m_0 + \alpha f^*$.

$$\frac{d\rho_*}{dt} = [\delta\rho_* + (1-\delta)q_{*|0}] (b - c\rho_+ - c\rho_*) \rho_0 - m^* \rho_*,$$

$$\frac{d\rho_{**}}{dt} = 2\rho_{0*} \left[\delta\rho_* + \frac{1-\delta}{z} + (1-\delta) \frac{z-1}{z} q_{*|0} \right] (b - c\rho_+ - c\rho_*) - 2\rho_{**} m^*,$$

$$\frac{d\rho_{*-}}{dt} = d\rho_{0*} + \rho_{0-} \left[\delta\rho_* + \frac{z-1}{z} (1-\delta) q_{*|0} \right] (b - c\rho_+ - c\rho_*) - \rho_{*-} \left(r + \frac{f^*}{z} + \frac{z-1}{z} f^* q_{*|-} + \frac{z-1}{z} f q_{+|-} + m^* \right),$$

$$\frac{d\rho_{*+}}{dt} = \rho_{*0} \left[\delta\rho_+ + \frac{z-1}{z} (1-\delta) q_{+|0} \right] (b - c\rho_+ - c\rho_*) - \rho_{*+} \left[\delta\rho_* + \frac{z-1}{z} (1-\delta) q_{*|0} \right] (b - c\rho_+ - c\rho_*) - \rho_{*+} (m + m^*).$$

Derivation of the Spatial Invasion Fitness

The spatial invasion fitness depends only on $q_{0|*}$ and the variables of the resident at equilibrium. Thus, simulations of the resident equations (app. A) until equilibrium is reached provide the value of the resident variables at equilibrium. The following method allows us to obtain the value of $q_{0|*}$.

The statistic $q_{0|*}$ converges very rapidly to equilibrium, compared to ρ_{σ^*} (relaxation property; Matsuda et al. 1992; van Baalen and Rand 1998; Le Galliard et al. 2003). Therefore, to obtain a measure of the spatial invasion fitness, we can write an auxiliary system of differential equations for the variables $q_{*|*}$, $q_{-|*}$ and $q_{+|*}$ ($q_{0|*}$ can be obtained with the conservation equations). Taking into account the facts that the resident population is at equilibrium and that the mutant is rare (ρ_* negligible in front of ρ_+), this system can be written as a closed system of three equations (using the equations of app. A and the fact that $\rho_{\sigma_1\sigma_2} = q_{\sigma_1|\sigma_2}\rho_{\sigma_2}$):

$$\begin{aligned}\frac{dq_{*|*}}{dt} &= 2q_{0|*}\left(\frac{1-\delta}{z}\right)(b - c\rho_+) - q_{*|*}m^* - q_{*|*}[\delta(1 - \rho_+ - \rho_-) + (1 - \delta)q_{0|*}](b - c\rho_+), \\ \frac{dq_{-|*}}{dt} &= q_{-|0}[\delta(1 - \rho_+ - \rho_-) + (1 - \delta)q_{0|*}](b - c\rho_+) + q_{0|*}d - q_{-|*}\left(r + \frac{f^*}{z} + f\frac{z-1}{z}q_{+|-}\right) \\ &\quad - q_{-|*}[\delta(1 - \rho_+ - \rho_-) + (1 - \delta)q_{0|*}](b - c\rho_+), \\ \frac{dq_{+|*}}{dt} &= q_{0|*}\left[\delta\rho_+ + (1 - \delta)\frac{z-1}{z}q_{+|0}\right](b - c\rho_+) + q_{+|0}[\delta(1 - \rho_+ - \rho_-) + (1 - \delta)q_{0|*}](b - c\rho_+) \\ &\quad - q_{+|*}[m + \delta(1 - \rho_+ - \rho_-) + (1 - \delta)q_{0|*}](b - c\rho_+).\end{aligned}$$

Let $q_{0|*}$ be w . At equilibrium, $dq_{*|*}/dt = 0$, $dq_{-|*}/dt = 0$, and $dq_{+|*}/dt = 0$.

$$\begin{aligned}\frac{dq_{*|*}}{dt} = 0 &\Rightarrow q_{*|*} = \frac{2w[(1 - \delta)/z](b - c\rho_+)}{m^* + [\delta(1 - \rho_+ - \rho_-) + (1 - \delta)w](b - c\rho_+)}, \\ \frac{dq_{-|*}}{dt} = 0 &\Rightarrow q_{-|*} = \frac{q_{-|0}\{\delta(1 - \rho_+ - \rho_-) + (1 - \delta)[(z - 1)/z]w\}(b - c\rho_+) + wd}{r + (f^*/z) + f[(z - 1)/z]q_{+|-} + [\delta(1 - \rho_+ - \rho_-) + (1 - \delta)w](b - c\rho_+)}, \\ \frac{dq_{+|*}}{dt} = 0 &\Rightarrow \\ q_{+|*} &= \frac{w\{\delta\rho_+ + (1 - \delta)[(z - 1)/z]q_{+|0}\}(b - c\rho_+) + q_{+|0}\{\delta(1 - \rho_+ - \rho_-) + (1 - \delta)[(z - 1)/z]w\}(b - c\rho_+)}{m + [\delta(1 - \rho_+ - \rho_-) + (1 - \delta)[(z - 1)/z]w](b - c\rho_+)}.\end{aligned}$$

Here, $q_{*|*}$, $q_{-|*}$, and $q_{+|*}$ are functions of $q_{0|*}$ only.

$$q_{0|*} = w = 1 - q_{*|*} - q_{-|*} - q_{+|*};$$

that is,

$$0 = w - 1 + q_{*|*} + q_{-|*} + q_{+|*}.$$

Let β be $\beta(w) = w - 1 + q_{*|*} + q_{-|*} + q_{+|*}$. Here, β is continuous and derivable between 0 and 1. Moreover, $\forall w \in [0, 1]$, $\beta'(w) > 0$, $\beta(0) < 1$, and $\beta(1) > 1$. There is thus a unique solution of the equation $\beta(w) = 0$ between 0 and 1 (intermediate-values theorem). The solution (i.e., $q_{0|*}$) can be numerically obtained (e.g., by the method of the tangent of Newton).

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