
Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions

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Recent studies have concluded that release from native soil pathogens may explain invasion of exotic plant species. However, release from soil enemies does not explain all plant invasions. The invasion of *Ammophila arenaria* (marram grass or European beach grass) in California provides an illustrative example for which the enemy release hypothesis has been refuted. To explore the possible role of plant–soil community interactions in this invasion, we developed a mathematical model. First, we analyzed the role of plant–soil community interactions in the succession of *A. arenaria* in its native range (north-western Europe). Then, we used our model to explore for California how alternative plant–soil community interactions may generate the same effect as if *A. arenaria* were released from soil enemies. This analysis was carried out by construction of a ‘recovery plane’ that discriminates between plant competition and plant–soil community interactions. Our model shows that in California, the accumulation of local pathogens by *A. arenaria* could result in exclusion of native plant species. Moreover, this mechanism could trigger the rate and spatial pattern of invasive spread generally observed in nature. We propose that our ‘accumulation of local pathogens’ hypothesis could serve as an alternative explanation for the enemy release hypothesis to be considered in further experimental studies on invasive plant species.

Dynamics of plants and soil communities are closely linked. Dead plant material provides organic carbon to the decomposing soil organisms that subsequently supply nutrients to the plants (Wardle et al. 2004). The living plant biomass also amplifies a characteristic subset of the soil community, consisting of root-associated herbivores, pathogens, and symbiotic mutualists (Kowalchuk et al. 2002). The specific effect of a plant species on the soil community, together with the return effect on plant growth, results in a net plant–soil

feedback effect (Bever et al. 1997). Positive plant–soil feedback stimulates growth of the host plant species, while negative plant–soil feedback limits this growth. Plant–soil feedbacks may drive important plant community processes, such as primary succession (Van der Putten et al. 1993), secondary succession (De Deyn et al. 2003), shifts in plant abundance (Klironomos 2002) and maintenance of plant diversity (Bever 1994, De Deyn et al. 2003).

A recent issue is to what extent altered patterns of plant–soil feedback influence exotic plant invasions. Several studies have suggested that the release from soil pathogens, while still encountering suitable root symbiotic mutualists provides an advantage for invasive plant species in their new habitat (Klironomos 2002, Reinhart et al. 2003, Callaway et al. 2004a). This observation is in compliance with the commonly acknowledged enemy release hypothesis (Maron and Vila 2001, Keane and Crawley 2002). However, not all exotic plant invasions can be explained by enemy release (Colautti et al. 2004). Other explanations focus on a negative impact of exotic plant species by producing toxic compounds (Bais et al. 2003, Vivanco et al. 2004).

However, the soil communities that are amplified in the root zone of one plant species may also affect the performance of other plant species, which influences the outcome of plant competition (Van der Putten and Peters 1997). Consequently, exotic plant species could indirectly influence the performance of plant species that are native in the invaded habitat. In order to examine

Accepted 27 February 2006
Subject Editor: Heikki Setälä

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ISSN 0030-1299

this possibility, we developed a mathematical model and analyzed the invasion of *Ammophila arenaria* (marram grass or European beach grass) in California.

In the 19th century, *A. arenaria* has been introduced in California for its sand stabilizing capacity (Pickart 1997). Following its introduction, *A. arenaria* started to exclude the native 'dune-mat' plant community (Buell et al. 1995, Wiedemann and Pickart 1996). In its native habitat (coastal foredunes in north-western Europe), *A. arenaria* is succeeded by other species such as *Festuca rubra* ssp. *arenaria* (sand fescue) (Van Dieren 1934). Here, negative plant-soil feedback accelerates succession (Van der Putten et al. 1993). The enemy release hypothesis cannot explain the invasion of *A. arenaria* in California, because it undergoes equal negative plant-soil feedback as in the native habitat, leaving the driving mechanism to be revealed (Beckstead and Parker 2003).

The aim of our model study was to analyze whether plant-soil community interactions other than enemy release provide an explanation for the invasiveness of *A. arenaria* in California. The model builds on the Lotka-Volterra based model of Bever (2003). Although our extension of this model increased complexity, model analysis was still possible because we developed a new analytical framework, the so-called recovery plane method. We used a comparative approach, meaning that we first modeled the effect of plant-soil community interactions on competition between *A. arenaria* and *F. rubra* in the native habitat. The results were checked with field observations from the native habitat in order to confirm the model. Then we applied the recovery plane method to derive alternative plant-soil community interactions that would give *A. arenaria* the same competitive advantage as soil enemy release. We parameterized the model with these alternative plant-soil community interactions and compared model results with field observations from California. Because these field observations (Buell et al. 1995) comprise both pattern and rate of invasive spread of *A. arenaria*, we used a spatially explicit model version for this comparison. With the model results we developed the 'accumulation of local pathogens' hypothesis.

Model and analytical framework

Model formulation

The starting point of our model is bare soil that will be colonized by the plant species *A. arenaria* and *F. rubra*. Each plant species amplifies a characteristic subset of the soil community. From here, this characteristic subset is referred to as the plant species' specific soil community. Subsequently, the densities of plants and specific soil communities build up in time. We quantify each specific soil community in density and assume logistic growth, which depends on host plant density (Cook and Baker

1983). The model equations describing the dynamics of the specific soil communities of *A. arenaria* and *F. rubra* then become:

$$\frac{dS_A}{dt} = r_A S_A \left(1 - \frac{S_A}{k_A} \right) \quad (1a)$$

$$\text{With: } k_A = \frac{N_A}{N_{\max,A}} S_{\max,A} \quad (1b)$$

$$\frac{dS_F}{dt} = r_F S_F \left(1 - \frac{S_F}{k_F} \right) \quad (2a)$$

$$\text{With: } k_F = \frac{N_F}{N_{\max,F}} S_{\max,F} \quad (2b)$$

In which S_A and S_F are the densities of the specific soil communities of *A. arenaria* and *F. rubra* (g m^{-2}), r_A and r_F are their relative growth rates (d^{-1}), k_A and k_F are their carrying capacities (g m^{-2}) that are linearly dependent on host plant density N (g m^{-2}). $N_{\max,A}$ and $N_{\max,F}$ represent the carrying capacities of *A. arenaria* and *F. rubra* (g m^{-2}). If plant density N is at carrying capacity, so $N = N_{\max}$, its specific soil community is able to reach its maximal carrying capacity S_{\max} (g m^{-2}).

We incorporate non-linear relationships between specific soil community density and effect on plant growth (Olf et al. 2000). More specifically, a Holling type III-response (Holling 1959) is assumed (Van der Stoel et al. 2002):

$$\sigma_{ij} = \frac{\sigma_{\max,ij} S_j^2}{\alpha_{ij}^2 + S_j^2} \quad (3)$$

(For $i, j = A, F$)

In which σ is the specific soil community effect (d^{-1}), $\sigma_{\max,ij}$ is the maximum effect that can be exerted (d^{-1}) and α is a half saturation constant, meaning the specific soil community density at which half of the maximum specific soil community effect is exerted (g m^{-2}). All coefficients are named according to Lotka-Volterra terminology; for example, σ_{AF} indicates the effect that *A. arenaria* undergoes, exerted by the specific soil community of *F. rubra*.

The model structure further follows Bever (2003). All interactions between plants and the specific soil communities and the model parameters quantifying these interactions are depicted in Fig. 1. The equations for plant growth then become:

$$\frac{dN_A}{dt} = g_A N_A \left(1 - \frac{N_A + c_{AF} N_F}{N_{\max,A}} + \frac{\sigma_{AA} + \sigma_{AF}}{g_A} \right) \quad (4)$$

$$\frac{dN_F}{dt} = g_F N_F \left(1 - \frac{N_F + c_{FA} N_A}{N_{\max,F}} + \frac{\sigma_{FF} + \sigma_{FA}}{g_F} \right) \quad (5)$$

Where g_A and g_F are the relative growth rates of *A. arenaria* and *F. rubra* (d^{-1}), c_{AF} and c_{FA} are above-ground competition coefficients (g g^{-1}).

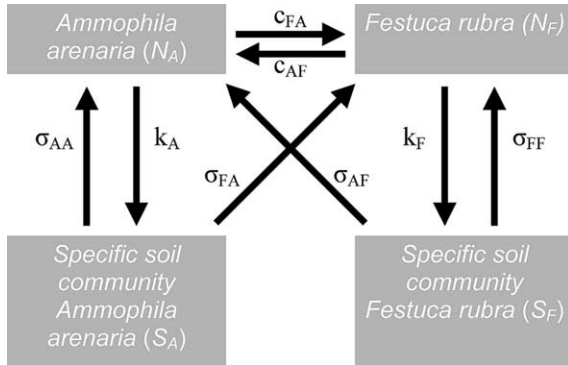


Fig. 1. Model concept; the interactions between *A. arenaria*, *F. rubra* and their specific soil communities (as proposed by Bever 2003), and the parameters quantifying these interactions in the model presented here.

The model equations for the spatially explicit model incorporate a dispersion term for the plant species. Dispersion of the specific soil communities is neglected, assuming that dispersal rates of soil organisms are slow compared to plants (Van der Putten 2003). A Laplacian operator models dispersion of the two plant species:

$$\frac{\partial N_A}{\partial t} = g_A N_A \left(1 - \frac{N_A + c_{AF} N_F}{N_{max,A}} + \frac{\sigma_{AA} + \sigma_{AF}}{g_A} \right) + D_A \left(\frac{\partial^2 N_A}{\partial x^2} + \frac{\partial^2 N_A}{\partial y^2} \right) \quad (6)$$

$$\frac{\partial N_F}{\partial t} = g_F N_F \left(1 - \frac{N_F + c_{FA} N_A}{N_{max,F}} + \frac{\sigma_{FF} + \sigma_{FA}}{g_F} \right) + D_F \left(\frac{\partial^2 N_F}{\partial x^2} + \frac{\partial^2 N_F}{\partial y^2} \right) \quad (7)$$

In which D_A and D_F are the dispersion coefficients for *A. arenaria* and *F. rubra* ($m^2 d^{-1}$). Parameter values were derived from literature (Table 1, see Appendix A for details).

Assemblage of the analytical framework

The mean field model (Eq. 1–5) could not be solved analytically, so that we will turn to graphical analysis of the model phase space. The classical Lotka–Volterra competition model has two state variables, namely the densities of the two competing plant species. As a result, a two-dimensional phase plane represents the phase

Table 1. Units and values of the model parameters used in the simulations.

Parameter	Meaning	Value	Unit	References [#]	Sensitivity range [§]
$\sigma_{max,AA}$	Maximum effect that specific soil community of <i>A. arenaria</i> exerts on <i>A. arenaria</i>	-1.0	day ⁻¹	1, 2, 3*	-1.15–-0.6
$\sigma_{max,AF}$	Maximum effect that specific soil community of <i>F. rubra</i> exerts on <i>A. arenaria</i>	-1.0	day ⁻¹	1, 2*	-1.15–-0.6
$\sigma_{max,FF}$	Maximum effect that specific soil community of <i>F. rubra</i> exerts on <i>F. rubra</i>	-0.15	day ⁻¹	4*†	-0.18–0
$\sigma_{max,FA}$	Maximum effect that specific soil community of <i>A. arenaria</i> exerts on <i>F. rubra</i>	-0.2–0	day ⁻¹	5, 6*	< -0.2 (= invasion threshold) 48–73
α_{AA}, α_{AF}	Half saturation constants of specific soil community effects on <i>A. arenaria</i>	50	g m ⁻²	4, 6*†	3–11
α_{FF}, α_{FA}	Half saturation constants of specific soil community effects on <i>F. rubra</i>	10	g m ⁻²	4, 6*†	3–11
$N_{max,A}, N_{max,F}$	Carrying capacities of <i>A. arenaria</i> and <i>F. rubra</i>	500	g m ⁻²	4, 7†‡	<50–>5000
g_A, g_F	Relative growth rates <i>A. arenaria</i> and <i>F. rubra</i>	0.2	day ⁻¹	8‡	0.14–>2
c_{AF}	Aboveground competition coefficient for <i>A. arenaria</i>	1.1	g g ⁻¹	6*	0–3.2
c_{FA}	Aboveground competition coefficient for <i>F. rubra</i>	1	g g ⁻¹	6*	0.9–3.6
Γ_A, Γ_F	Relative growth rates specific soil communities	0.03	day ⁻¹	9‡	<0.003–>0.3
$S_{max,A}, S_{max,F}$	Carrying capacities of specific soil communities	100	g m ⁻²	10‡	45–135
$N_A(t=0)$	Density <i>A. arenaria</i> at model initialization	10	g m ⁻²	6, 11*	2–>100
$N_F(t=0)$	Density <i>F. rubra</i> at model initialization	1	g m ⁻²	6, 11*	Relative to N_A , See above
$S_A(t=0), S_F(t=0)$	Densities specific soil communities at model initialization	1	g m ⁻²	(Model initialization)	<0.1–>10
D_A, D_F	Dispersion coefficients for <i>A. arenaria</i> and <i>F. rubra</i>	0.003	m ² day ⁻¹	12†‡	<0.0003–0.01

[#]References; 1: De Rooij-Van der Goes (1995) 2: Van der Putten and Van der Stoel (1998) 3: Beckstead and Parker (2003) 4: Olf et al. (2000) 5: Oremus and Otten (1981) 6: Van der Putten and Peters (1997) 7: Blomqvist et al. (2000) 8: Hunt and Cornelissen (1997) 9: Ferris et al. (1996) 10: Neher (1999) 11: Huiskes (1979) 12: D’Hertefeldt and Van der Putten (1998).

[§]When a parameter value is within the sensitivity range (and other parameters at the default values), the mean field model outcomes as shown in Fig. 3b and Fig. 3c remain qualitatively the same. Within the sensitivity range of the dispersion coefficients, the spatially explicit model outcomes as shown in Fig. 5a and Fig. 5b remain qualitatively the same.

*Reference used for qualitative differences between species (order-of-magnitude-realistic values were assigned).

†Based on information of comparable species (*Carex arenaria* and *Festuca rubra* ssp. *rubra*).

‡Reference used to determine realistic order-of-magnitude.

space of this model. The final equilibrium state of the classical Lotka–Volterra model can be predicted by analyzing this phase plane. Because we incorporated the specific soil community densities of these plants as dynamic state variables, the phase space becomes four-dimensional, which makes graphical analysis difficult. However, we developed a new method specifically to analyze this model. Using this method, the way in which plant–soil community interactions influence plant competition is conveniently visualized, which will be explained here first.

Because of linear density dependence of the plant species (Eq. 4, 5), the outcome of competition between the two plant species is determined by the values of the intercepts of their isoclines with the x- and y- axes of the two-dimensional phase plane. If the difference of the intercept values on the x-axis and y-axis are plotted against each other, a recovery plane occurs, in which every quadrant corresponds to one of the four possible outcomes; coexistence, exclusion of one of the two plants and founder control (Fig. 2a). Founder control refers to a competitive state in which the initial conditions of the plant densities determine which plant species will be excluded (Bolker et al. 2003). In the classical Lotka–Volterra model, parameter values determine the competitive state, and thereby the position of the system in the recovery plane. Because these parameters are constant in time, the position in the recovery plane does not change; it remains a point in this plane during a simulation run. So the two-dimensional phase plane that is spanned by the two state variables of the classical Lotka–Volterra model is now reduced to a single point in the recovery plane.

In the model presented here, the specific soil communities become involved and are able to increase in density during a simulation run. Subsequently, the specific soil communities affect plant growth as well. As a result, the competitive state of the system can change, and such change results in a trajectory through the recovery plane during a simulation run. The trajectory through this plane is determined by the magnitude of the specific soil community effects, relative to the plant reproduction rates, because these parameters are the only terms in Eq. 4 and 5 that can change after initialization. Simple algebra (Appendix B) yields that movement through the recovery plane away from the initialization point in positive x- and y-direction requires:

$$\text{Positive x-direction: } \frac{\sigma_{AF}}{g_A} > \frac{\sigma_{FF}}{g_F} \quad (9)$$

$$\text{Positive y-direction: } \frac{\sigma_{FA}}{g_F} > \frac{\sigma_{AA}}{g_A} \quad (10)$$

Equations 9 and 10 show that the effects exerted by the specific soil community of *A. arenaria* (In the Results section referred to as S_A) result in movement in

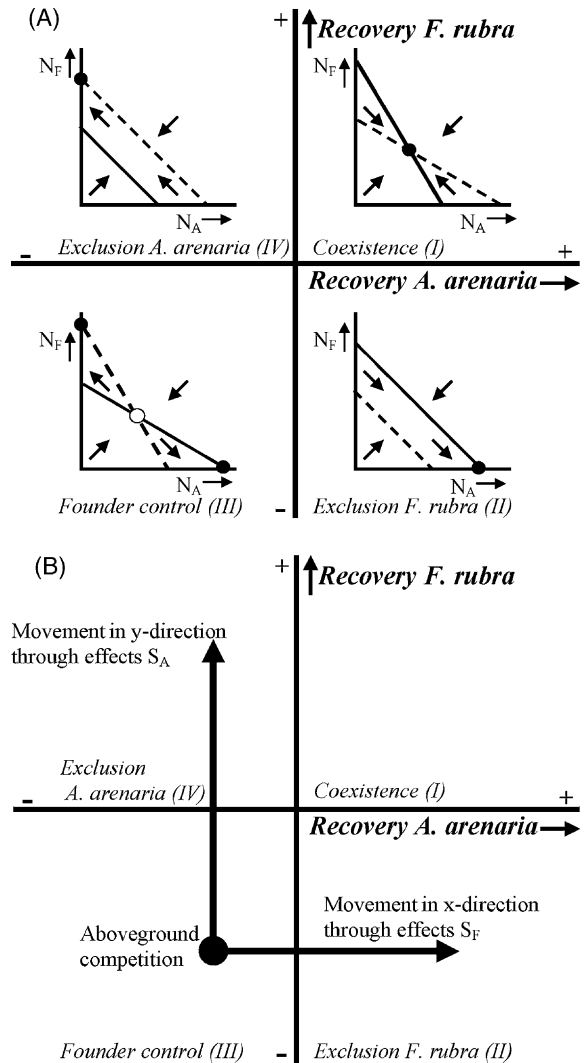


Fig. 2. (a) In the recovery plane shown here, the two dimensional phase plane spanned by *A. arenaria* and *F. rubra* is converted to a single point. As a result, the effects of *A. arenaria*'s specific soil community (S_A) (movement in x-direction) and *F. rubra*'s specific soil community (S_F) (movement in y-direction) can be conveniently analyzed graphically. The axes are obtained as follows: recovery of a plant requires that on the axis in the phase portrait where the plant species is zero, its isocline has the highest intercept value, in other words: intercept value (rare plant)–intercept value (dominant plant) > 0 (recovery is for both species analytically defined in Appendix B). When these differences between these intercept values are plotted on the x-axis (recovery *A. arenaria*) and y-axis (recovery *F. rubra*), every quadrant of the recovery plane shows one of the four standard Lotka–Volterra states. Solid isoclines are the isoclines of *A. arenaria*, the dashed isoclines of *F. rubra*. Equilibria are indicated with dots. Closed dots represent stable equilibria, open dots unstable ones. (b) Movement through the recovery plane after initialization is only governed by specific soil community effects. Movement is in positive x-direction if $\frac{\sigma_{FA}}{g_F} > \frac{\sigma_{AA}}{g_A}$, and in positive y-direction if $\frac{\sigma_{FA}}{g_F} > \frac{\sigma_{AA}}{g_A}$. These simple parameter requirements causing movement in x- and y-direction through the recovery plane are derived in Appendix B.

y-direction in the recovery plane, effects of the specific soil community of *F. rubra* (S_F) result in movement in x-direction (Fig. 2b).

Note that specific soil community effects can move the system into different quadrants of the recovery plane. When the system enters another quadrant, the ability to recover when rare changes for at least one plant species. Crossing a quadrant border in the recovery plane therefore coincides with a marked shift in plant competition, solely caused by specific soil community effects. Using Eq. 9 and 10, changes in specific soil community effects can be linked to shifts in plant competition.

Results

Without specific soil community effects, the Lotka–Volterra parameters determine that the initially dominating *A. arenaria* is finally succeeded by *F. rubra* (Fig. 3a). This is in agreement with the observation that this succession process is primarily driven by abiotic factors such as sand stabilization, nutrient accumulation and decalcification (Olf et al. 1993). However, incorporation of specific soil community effects mimicking native habitat conditions enhances the rate of succession (Fig. 3b). Sensitivity analysis shows that this model outcome is not very sensitive to changes in parameter values (Table 1).

If *A. arenaria* were released from soil pathogens in California, it could undergo neutral to positive effects from S_A , as observed for *Prunus serotina* (black cherry) in its non-native range in Europe for example (Reinhart et al. 2003). If we consider competition between *A. arenaria* and an ecological congener of *F. rubra* in California (meaning that besides σ_{AA} and σ_{FA} all parameters remain unchanged), Eq. 10 shows that a positive specific soil community effect on *A. arenaria* because of enemy release would result in a different movement in y-direction in the recovery plane (Fig. 4). However, in order to obtain an explanation that is in compliance with a negative specific soil community effect on *A. arenaria* in California, as established by Beckstead and Parker (2003), Eq. 10 reveals another possibility. The movement in negative y-direction can also be caused by σ_{FA} becoming more negative than σ_{AA} . In the native habitat, S_A contains pathogens that reduce growth of *A. arenaria*, while *F. rubra* is relatively insensitive (Van der Putten and Peters 1997), so $\sigma_{\max,FA}$ (native habitat) = 0 d⁻¹. However, if growth of the Californian species would be reduced by S_A more than *A. arenaria* itself, Eq. 10 shows that *A. arenaria* would experience the same competitive advantage as enemy release. When these alternative plant-soil community interactions are applied in the model, the result indeed shows invasive behavior of *A. arenaria* (Fig. 3c). The

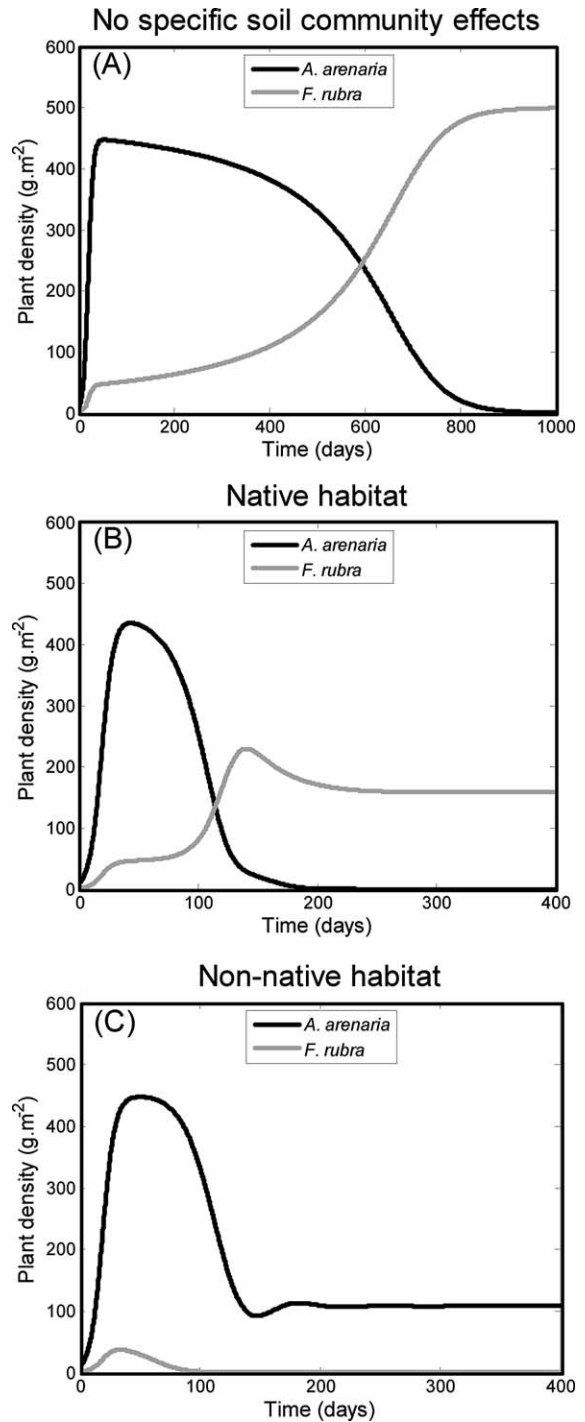


Fig. 3. Model simulations of the interactions between *A. arenaria*, *F. rubra* and their specific soil communities (parameter values are given in Table 1). (a) Competition without soil community effects. (b) The accelerated succession of *A. arenaria* in its native habitat. ($\sigma_{\max,FA} = 0$ d⁻¹). (c) Invasion of *A. arenaria*, driven by the effect of *A. arenaria*'s specific soil community, S_A on the ecological congener of *F. rubra* ($\sigma_{\max,FA} = -0.2$ d⁻¹).

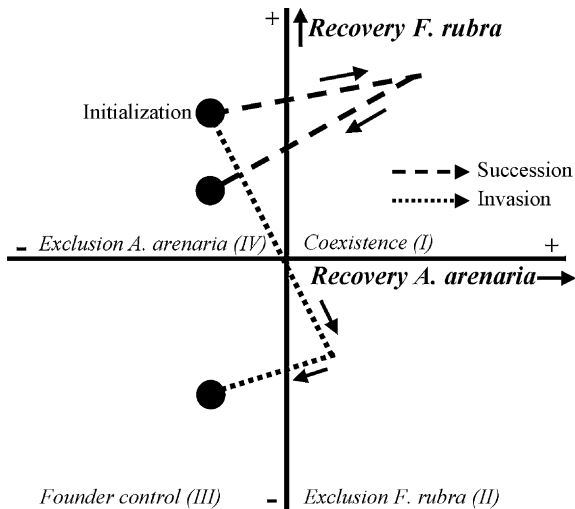


Fig. 4. The processes of succession of *A. arenaria* in native habitat and its invasion in California presented as trajectories through the recovery plane. The essential difference between the two processes is the movement in y-direction. This movement is caused by the negative effect that the specific soil community of *A. arenaria* (S_A) exerts on the ecological congener of *F. rubra* in the invasion simulation (σ_{FA}).

sensitivity analysis reveals the invasion threshold for the studied parameterization; $\sigma_{\max,FA} = -0.2$ (Table 1).

Now, the same parameterization is applied in the spatially explicit model version (that is the model described by Eq. 1, 2, 3, 6 and 7), to identify the resulting pattern of spread of *A. arenaria* due to these alternative plant–soil community interactions. This model simulation shows that *A. arenaria* increases in cover, forming densely vegetated patches around sites where it has been introduced (Fig. 5a). At this stage, the rest of the area is dominated by the ecological congener of *F. rubra* (data not shown). Subsequently, the patches of *A. arenaria* expand in typical traveling wave-like patterns (Holmes et al. 1994, Fig. 5b) as observed in the Californian foredunes (Buell et al. 1995). During this phase of expansion, the square root of the area occupied by *A. arenaria* linearly increases with time, which agrees observations in California (Buell et al. 1995) and general invasion theory (Hengeveld 1989). In the model, lack of space eventually decreases the rate of spread (Fig. 5c). The invasive spread of *A. arenaria* continues until it has fully covered the area.

Discussion

Our model results suggest that accumulation of local pathogens by *A. arenaria* could explain its invasiveness in California. Furthermore this mechanism could explain the wave-like patterns and rate of spread of *A. arenaria* that have been documented (Buell et al. 1995).

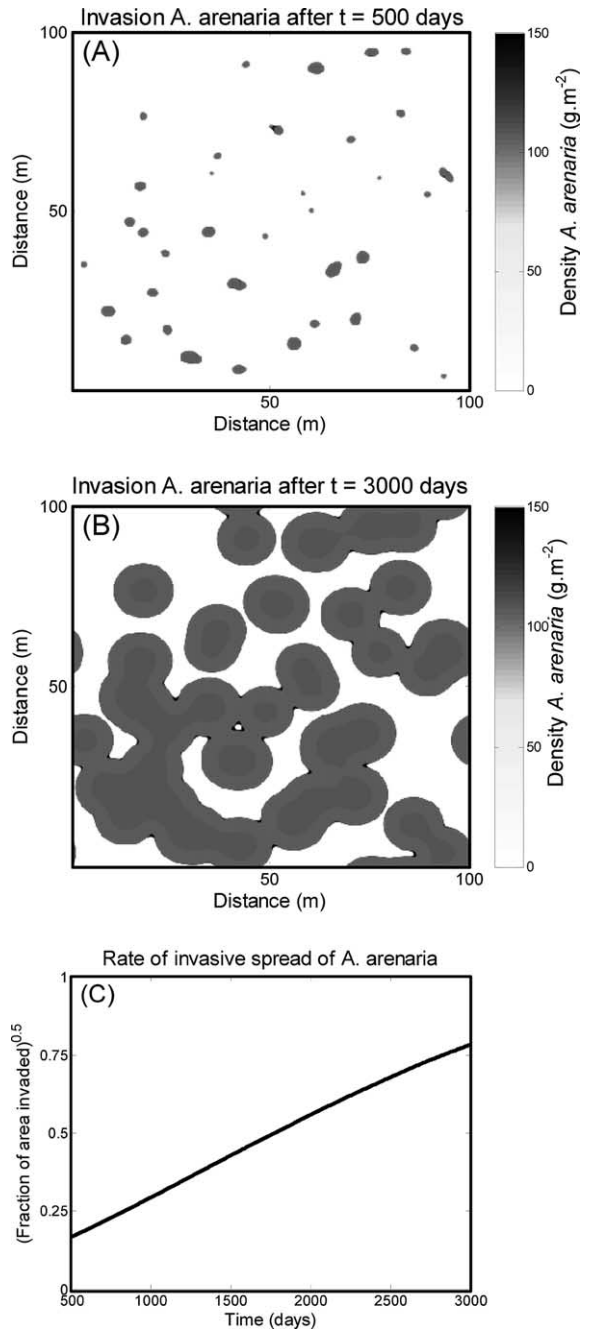


Fig. 5. Model results of the spatially explicit model version. Model output represented as the pattern of spread of *A. arenaria*. At initialization 2.5% of the gridcells is occupied by *A. arenaria*, 70% by the ecological congener of *F. rubra* (initial densities as in Table 1). (a) Snapshot of the distribution of *A. arenaria*, in an environment that is dominated by the ecological congener of *F. rubra* (density not shown). (b) Snapshot of invading *A. arenaria* at $t = 3000$ days. (c) The square root of the area occupied by *A. arenaria* in the period between the two snapshots. Conform invasion theory the increase is linear, until lack of space slowly decreases the rate of spread at the end of the simulation run.

This implies that besides of control of invasive species by speeding up the accumulation of their parasites (Clay 2003), such parasites may also enhance the severity of the invasion. The accumulation of local pathogens may limit the invaders abundance, but it might feed back more negatively to the native plant community.

Our model results suggest that the essential difference between the native and the invaded habitat is the effect of the specific soil community of *A. arenaria* on competing plant species. In the native habitat, the specific soil community of *A. arenaria* exerts little effects on succeeding plant species (Van der Putten et al. 1993). In the non-native range, however, accumulation of local soil pathogens could enhance dominance and rate of spread of *A. arenaria* as a result of negative specific soil community effects on native plant species. Empirical studies on *A. arenaria* provide an ecological explanation how this mechanism might operate. In introduced habitats, *A. arenaria* facilitates a specific soil community that has a different composition than in the native habitat (Van der Putten et al. 2005). In South Africa, where *A. arenaria* has been introduced as well, the species undergoes negative plant–soil feedback because it accumulates local generalist pathogens (Knevel et al. 2004). In California, *A. arenaria* has been released from most of its native soil pathogens (Van der Putten et al. 2005), but it still undergoes equal negative plant–soil feedback as in the native habitat (Beckstead and Parker 2003). Therefore, *A. arenaria* may accumulate local generalist pathogens in California as well. If introduced *A. arenaria* indeed accumulates local generalist pathogens, it is likely that native plant species are negatively affected as well. So, we conclude that *A. arenaria* could accumulate local generalist pathogens in California that have a more negative effect on native plant species than on *A. arenaria* itself. As a result, *A. arenaria* might gain competitive advantage that triggers its invasive behavior. We suggest that this may be a more general mechanism for exotic plant invasion that deserves further investigation.

The analytical framework derived here can be more generally applied to provide insight in the possible effects of soil organisms on plant competition. Using the recovery plane method, it becomes relatively easy to investigate how plant–soil community interactions alter plant competition, because only these interactions cause movement through the recovery plane. The method can thus be used to identify possible mechanisms driving plant community processes such as invasions. For example, Callaway et al. (2004b) found evidence that the invasion of *Centaurea maculosa* (spotted knapweed) in North America might be driven by a positive effect on *C. maculosa* by arbuscular mycorrhizal soil fungi that are associated with native plant species. Although a similar mechanism might drive the invasion of *A. arenaria*, application of our recovery plane method reveals that this mechanism could only result in move-

ment in x-direction in the recovery plane, meaning that this mechanism alone does not provide an explanation for the invasion of *A. arenaria* investigated here.

Our model provides the opportunity to relate plant–soil community interactions to plant competition. The recovery plane method conveniently shows how plant–soil community interactions could enforce marked shifts in plant competition, leading to a new hypothesis on plant–soil community interactions in areas invaded by exotic plant species. This ‘accumulation of local pathogens’ hypothesis needs to be tested in subsequent empirical studies.

Acknowledgements – The authors thank Sonia Kéfi and Remko Holtkamp for comments that improved the manuscript. The research of MBE and MR is supported by a VIDI grant to MR, the research of WHVdP is supported by a VICI grant, both from the Research Council Earth and Life Sciences of the Netherlands Organization of Scientific Research.

References

- Bais, H. P., Vepachedu, R., Gilroy, S. et al. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. – *Science* 301: 1377–1380.
- Beckstead, J. and Parker, I. M. 2003. Invasiveness of *Ammophila arenaria*: release from soil-borne pathogens? – *Ecology* 84: 2824–2831.
- Bever, J. D. 1994. Feedback between plants and their soil communities in an old field community. – *Ecology* 73: 165–177.
- Bever, J. D. 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. – *New Phytol.* 157: 465–473.
- Bever, J. D., Westover, K. M. and Antonovics, J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. – *J. Ecol.* 85: 561–573.
- Blomqvist, M. M., Olf, H., Blaauw, M. B. et al. 2000. Interactions between above- and belowground biota: importance for small-scale vegetation mosaics in a grassland ecosystem. – *Oikos* 90: 582–598.
- Bolker, B. M., Pacala, S. W. and Neuhauser, C. 2003. Spatial dynamics in model plant communities: what do we really know? – *Am. Nat.* 162: 135–148.
- Buell, A. C., Pickart, A. J. and Stewart, J. D. 1995. Introduction history and invasion patterns of *Ammophila arenaria* on the North Coast of California. – *Conserv. Biol.* 9: 1587–1593.
- Callaway, R. M., Thelen, G. C., Rodriguez, A. et al. 2004a. Soil biota and exotic plant invasion. – *Nature* 427: 731–733.
- Callaway, R. M., Thelen, G. C., Barth, S. et al. 2004b. Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. – *Ecology* 85: 1062–1071.
- Clay, K. 2003. Parasites lost. – *Nature* 421: 585–586.
- Colautti, R. I., Ricciardi, A., Grigorovich, I. A. et al. 2004. Is invasion success explained by the enemy release hypothesis? – *Ecol. Lett.* 7: 721–733.
- Cook, J. R., and Baker, K. F. 1983. The nature and practice of biological control of plant pathogens. – *Am. Phytopathol. Soc.*
- De Deyn, G. B., Raaijmakers, C. E., Zoomer, H. R. et al. 2003. Soil invertebrate fauna enhances grassland succession and diversity. – *Nature* 422: 711–713.
- De Rooij-Van der Goes, P. C. E. M. 1995. The role of plant-parasitic nematodes and soil-borne fungi in the decline of *Ammophila arenaria* (L.) Link. – *New Phytol.* 129: 661–669.

- D'Hertefeldt, T. and Van der Putten, W. H. 1998. Physiological integration of the clonal plant *Carex arenaria* and its response to soil-borne pathogens. – *Oikos* 81: 229–237.
- Ferris, H., Venette, R. C. and Lau, S. S. 1996. Dynamics of nematode communities in tomatoes grown in conventional and organic farming systems, and their impact on soil fertility. – *Appl. Soil Ecol.* 3: 161–175.
- Hengeveld, R. 1989. Dynamics of biological invasions – Chapman and Hall.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. – *Can. Entomol.* 91: 385–398.
- Holmes, E. E., Lewis, M. A., Banks, J. E. et al. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. – *Ecology* 75: 17–29.
- Huiskes, A. H. L. 1979. Biological flora on the British isles: *Ammophila arenaria* (L.) Link (*Psamma arenaria* (L.) Roem. et Schult.: *Calamagrostis arenaria* (L.) Roth). – *J. Ecol.* 67: 363–382.
- Hunt, R. and Cornelissen, J. H. C. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. – *New Phytol.* 135: 395–417.
- Keane, R. M. and Crawley, M. J. 2002. Exotic plant invasions and the enemy release hypothesis. – *Trends Ecol. Evol.* 17: 164–170.
- Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. – *Nature* 417: 67–70.
- Knevel, I. C., Lans, T., Menting, F. B. J. et al. 2004. Release from native root herbivores and biotic resistance by soil pathogens in a new habitat both affect the alien *Ammophila arenaria* in South Africa. – *Oecologia* 141: 502–510.
- Kowalchuk, G. A., Buma, D. S., De Boer, W. et al. 2002. Effects of above-ground plant species composition and diversity on the diversity of soil-borne microorganisms. – *Antonie van Leeuwenhoek* 81: 509–520.
- Maron, J. L. and Vilà, M. 2001. Do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. – *Oikos* 95: 363–373.
- Neher, D. A. 1999. Soil community composition and ecosystem processes. – *Agrofor. Syst.* 45: 159–185.
- Olf, H., Huisman, J. and Van Tooren, B. F. 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. – *J. Ecol.* 81: 693–706.
- Olf, H., Hoorens, B., De Goede, R. G. M. et al. 2000. Small-scale shifting mosaics of two dominant grassland species: the possible role of soil-borne pathogens. – *Oecologia* 125: 45–54.
- Oremus, P. A. I. and Otten, H. 1981. Factors affecting growth and nodulation of *Hippophaë rhamnoides* L. ssp. *rhamnoides* in soils from two successional stages of dune formation. – *Plant Soil* 63: 317–331.
- Pickart, A. J. 1997. Control of European beachgrass (*Ammophila arenaria*) on the west coast of the United States. – California Exotic Pest Plant Council, 1997 Symp. Proc.
- Reinhart, K. O., Packer, A., Van der Putten, W. H. et al. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. – *Ecol. Lett.* 6: 1046–1050.
- Van der Putten, W. H. 2003. Plant defense below ground and spatio-temporal processes in natural vegetation. – *Ecology* 84: 2269–2280.
- Van der Putten, W. H. and Peters, B. A. M. 1997. How soil-borne pathogens may affect plant competition. – *Ecology* 78: 1785–1795.
- Van der Putten, W. H. and Van der Stoel, C. D. 1998. Plant parasitic nematodes and spatio-temporal variation in natural vegetation. – *Appl. Soil Ecol.* 10: 253–262.
- Van der Putten, W. H., Van Dijk, C. and Peters, B. A. M. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. – *Nature* 362: 53–56.
- Van der Putten, W. H., Yeates, G. W., Duyts, H. et al. 2005. Invasive plants and their escape from root herbivory: a worldwide comparison of the root-feeding nematode communities of the dune grass *Ammophila arenaria* in natural and introduced ranges. – *Biol. Invasions* 7: 733–746.
- Van der Stoel, C. D., Van der Putten, W. H. and Duyts, H. 2002. Development of a negative plant-soil feedback in the expansion zone of the clonal grass *Ammophila arenaria* following root formation and nematode colonization. – *J. Ecol.* 90: 978–988.
- Van Dieren, J. W. 1934. Organogene Dünenbildung, eine geomorphologische Analyse der westfriesischen Insel Terschelling mit pflanzensoziologischen Methoden. – PhD thesis, Univ. of Amsterdam.
- Vivanco, J. M., Bais, H. P., Stermitz, F. R. et al. 2004. Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. – *Ecol. Lett.* 7: 285–292.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N. et al. 2004. Ecological linkages between aboveground and belowground biota. – *Science* 304: 1629–1633.
- Wiedemann, A. M. and Pickart, A. J. 1996. The *Ammophila* problem on the northwest coast of North America. – *Landscape Urban Plan.* 34: 287–299.

Appendix A. Model calibration

The model parameters were set to mimic competition between *A. arenaria* and *F. rubra* ssp. *arenaria* and the interaction with their specific soil communities (Table 1). Information about these plant–soil community interactions was derived from pot experiments using soil from the native habitat (the Netherlands). Also, information from pot experiments with *Carex arenaria* (sand sedge) and *F. rubra* ssp. *rubra* (red fescue) was used, because data on *A. arenaria* and *F. rubra* ssp. *arenaria* was insufficient, and the ecology of these species is similar (Olf et al. 2000). However, the sensitivity analysis reveals that the model is not very sensitive for the exact values of parameters (Table 1).

Festuca rubra is a slightly stronger competitor in sterile soil (Van der Putten and Peters 1997), therefore

interspecific aboveground competition that *A. arenaria* undergoes is set higher; $c_{AF} = 1.1$ (g g^{-1}) and $c_{FA} = 1.0$ (g g^{-1}). The relative growth rates and carrying capacities were set equal for both plant species and both specific soil communities. Values for these parameters were derived from various sources (Table 1). Only competition coefficients and specific soil community effects on *A. arenaria* and *F. rubra* were set different, therefore we theoretically examined how different specific soil community effects mediate competition between *A. arenaria* and *F. rubra* or an ecological congener. Because *A. arenaria* is better in colonizing bare dunes (Huiskes 1979, Van der Putten and Peters 1997), the initial density of this plant was set higher in all model simulations: $N_A(t=0) = 10 \text{ g m}^{-2}$, $N_F(t=0) = 1 \text{ g m}^{-2}$. It was assumed that *F. rubra* undergoes a stronger effect from its specific

soil community than *A. arenaria* does at low specific soil community densities, which was simulated by lower values of α for effects on *F. rubra*. It was assumed that the value of α is the same for the two specific soil community effects that the plant species undergo; $\alpha_{AA} = 50 \text{ g m}^{-2}$, $\alpha_{AF} = 50 \text{ g m}^{-2}$, $\alpha_{FF} = 10 \text{ g m}^{-2}$, $\alpha_{FA} = 10 \text{ g m}^{-2}$. With increasing density, the effect on *F. rubra* remains relatively constant (Van der Putten and Peters 1997, Olf et al. 2000), but the effect on *A. arenaria* becomes stronger than on *F. rubra*. The maximal reduction of *F. rubra* is $\sim 65\%$ (Olf et al. 2000), that of *A. arenaria* $\sim 80\%$ (De Rooij-Van der Goes 1995). To obtain similar reductions in the model when the plants are grown in monocultures (for the given values of other parameters, see Table 1) the maximal effects of the specific soil communities were set as follows: $\sigma_{\max,AA} = -1.0 \text{ d}^{-1}$, $\sigma_{\max,FF} = -0.15 \text{ d}^{-1}$. The effect of the specific soil community of *F. rubra* on *A. arenaria* was assumed to be as strong as the effect from *A. arenaria*'s own specific soil community (Van der Putten and Van der Stoel 1998), so $\sigma_{\max,AF} = -1.0 \text{ d}^{-1}$. Because the specific soil community of *A. arenaria* is relatively harmless to *F. rubra* (Van der Putten and Peters 1997), we set $\sigma_{\max,FA}(\text{native habitat}) = 0 \text{ d}^{-1}$.

Appendix B. Parameter requisites for movement through recovery plane

The values of the intercepts of the N_A and N_F isoclines on the y-axis (meaning $N_A = 0$) are mathematically as follows:

$$\begin{aligned} \frac{dN_A}{dt} = 0, \rightarrow \hat{N}_F(N_A = 0) \\ = \frac{N_{\max,A} \left(1 + \frac{\sigma_{AA} + \sigma_{AF}}{g_A} \right)}{c_{AF}} \end{aligned} \quad (\text{A1})$$

$$\begin{aligned} \frac{dN_F}{dt} = 0, \rightarrow \hat{N}_F(N_A = 0) \\ = N_{\max,F} \left(\frac{1 + \sigma_{FF} + \sigma_{FA}}{g_F} \right) \end{aligned} \quad (\text{A2})$$

In which \hat{N}_F denotes the equilibrium density of *F. rubra*. Coexistence of plants can be interpreted as the possibility for plants to recover when rare (Bever 2003). Now, recovery of *A. arenaria* requires that the intercept on the y-axis of the N_A -isocline is larger than the intercept of the N_F -isocline on the same axis. So the prerequisite of recovery of *A. arenaria* becomes:

$$\begin{aligned} \frac{N_{\max,A} \left(1 + \frac{\sigma_{AA} + \sigma_{AF}}{g_A} \right)}{c_{AF}} \\ > N_{\max,F} \left(1 + \frac{\sigma_{FF} + \sigma_{FA}}{g_F} \right) \end{aligned} \quad (\text{A3})$$

Because *A. arenaria* is very rare near the y-axis, its specific soil community will be very rare as well, so at this point, effects of S_A are negligible. Therefore, the parameter requirement for recovery of *A. arenaria* and (following the same procedure) also for *F. rubra* can be derived:

Recovery *A.arenaria*:

$$\frac{N_{\max,A} \left(1 + \frac{\sigma_{AF}}{g_A} \right)}{c_{AF}} - N_{\max,F} \left(1 + \frac{\sigma_{FF}}{g_{FF}} \right) > 0 \quad (\text{A4})$$

Recovery *F. rubra*:

$$\frac{N_{\max,F} \left(1 + \frac{\sigma_{FA}}{g_F} \right)}{c_{FA}} - N_{\max,A} \left(1 + \frac{\sigma_{AA}}{g_A} \right) > 0 \quad (\text{A5})$$

Movement in positive x- and y- direction in the recovery plane means that the left hand sides of inequalities A4 and A5 become larger. After initialization, the values of these terms can change if the values of the specific soil community effects change. So this movement requires:

$$\text{x-direction: } \left(1 + \frac{\sigma_{AF}}{g_A} \right) > \left(1 + \frac{\sigma_{FF}}{g_F} \right) \quad (\text{A6})$$

$$\text{y-direction: } \left(1 + \frac{\sigma_{FA}}{g_F} \right) > \left(1 + \frac{\sigma_{AA}}{g_A} \right) \quad (\text{A7})$$

Hence, addition of 1 cancels out.