Litter feedbacks, evolutionary change and exotic plant invasion

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Summary

1. Understanding the mechanisms driving exotic plant invasions is important for designing successful invader control strategies. Previous studies have highlighted different invasion mechanisms, including alteration of nutrient cycles through plant–soil feedback and evolutionary change toward more competitive genotypes.

2. We explored the possibility of these two mechanisms interactively affecting exotic plant invasion. Using data from recent experiments on the invasion of *Phalaris arundinacea (Phalaris)* in North American wetlands, we parameterized a classical resource competition model for nutrients and light, and expanded this model by including litter dynamics. We also examined the potential effects of evolutionary changes as observed in another set of recent experiments.

3. Both litter feedbacks and observed evolutionary changes may increase *Phalaris*' performance in invasive habitats. These mechanisms may amplify each other and this synergy may accelerate *Phalaris* invasion in areas where it is already present, leading to a high-litter state with *Phalaris* outcompeting other species. In areas with low nutrient supply where *Phalaris* is not yet present, a combination of litter feedbacks and evolutionary change may induce a critical transition from a low-litter, native-species-dominated state toward a high-litter, *Phalaris*-dominated state.

4. Our model results suggest that the importance of litter feedbacks and evolutionary change could be verified in future empirical studies through non-additive and nonlinear effects in litter addition experiments, and by increased litter : above-ground biomass ratios in biogeographical comparisons between plant communities with *Phalaris* in invasive and native habitats. The latter result may be caused by the accumulation of more recalcitrant litter from invasive genotypes.

5. *Synthesis.* Our study illustrates how exotic plant invasions may be exacerbated by the interaction between litter feedbacks and evolutionary change. This interaction may induce a positive feedback in the invasion process, suggesting that even short-term events, such as a nutrient pulse, may lead to relatively large and rapid ecosystem shifts that could be long-lasting and difficult to reverse.

Key-words: C:N ratio, *Carex hystericina*, critical transitions, decomposition, invasion ecology, litter:biomass ratio, modelling, *Phalaris arundinacea*, plant competition, threshold effects

Introduction

Exotic plant invasions are an important cause for changing ecosystem attributes, such as native species diversity (Keane & Crawley 2002), food web dynamics (Levin, Neira & Grosholz 2006) and services to humanity (Zavaleta 2000). These changes are mostly undesired, implying an urgent need to control the expansion of exotic plants (Pimentel 2002). The design of successful control strategies, in turn, requires a detailed understanding of the underlying mechanisms that drive exotic plant invasions (Levine *et al.* 2003). For example, plant invasions that are driven by a positive feedback mechanism may not only lead to species replacement in a successional way, but could also encompass a critical transition toward a new stable

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ecosystem state. In such cases, restoration attempts are unlikely to succeed if only successional-based restoration measures are used (Suding, Gross & Houseman 2004).

It has been argued that concepts from community ecology can also be used to study the establishment of exotic plants into new communities (Huston 1994; Eppstein & Molofsky 2007). The initial phase of invader establishment may be influenced by stochastic processes and propagule pressure (Tilman 2004; Eppstein & Molofsky 2007). Resource-based niche theory predicts that subsequent growth depends on the amount of limiting resources, such as nutrients and light, that are left unconsumed by the native species (Tilman 1999, 2004; Hierro, Maron & Callaway 2005), also referred to as the 'vacant niche' (e.g. Kawata 2002). Thus, this theory highlights the importance of resource supply and uptake for ecosystem invasibility (Tilman 1982). On the longer term, however, established invaders may actively modify resource supply and uptake dynamics through the alteration of soil nutrient cycling processes (Ehrenfeld 2003; Wardle *et al*. 2004). In turn, altered resource supply may induce changes in plant community composition and invader performance, creating the possibility of a plant–soil feedback influencing invader success.

Litter feedbacks have probably received most attention in empirical studies on plant–soil feedback (Ehrenfeld, Ravit & Elgersma 2005). The accumulation of a litter layer over time may influence both nutrient and light availability (e.g. Farrer & Goldberg 2009). Hence, the predictions of resource competition models may change when litter dynamics are included (Daufresne & Hedin 2005). Although previous resource competition models have been expanded to address competition for light (Reynolds & Pacala 1993; Perry, Neuhauser & Galatowitsch 2003; Diaz-Sierra, Zavala & Rietkerk 2010) or the role of litter dynamics on soil nutrient cycling (Daufresne & Hedin 2005), resource competition models that capture the influence of litter on both nutrient and light competition have not yet been developed.

Phalaris arundinacea (reed canarygrass, *Poaceae*, *Phalaris* from here) is a Eurasian macrophyte that has become one of the most noxious invaders of North American wetland ecosystems (Lavergne & Molofsky 2004). Previous empirical studies suggest that both nutrient (particularly nitrogen) and light availability are important factors determining the outcome of competition between *Phalaris* and native American wetland species (Wetzel & Van der Valk 1998; Maurer & Zedler 2002; Perry & Galatowitsch 2004; Perry, Galatowitsch & Rosen 2004). More specifically, Perry, Galatowitsch & Rosen (2004) showed that at low soil nitrogen availability, *Phalaris* was suppressed by the native species *Carex hystericina* (porcupine sedge, *Cyperaceae*, *Carex* from here), suggesting that *Carex* is a stronger competitor for nitrogen. In contrast, Perry & Galatowitsch (2004) showed that *Carex* was more inhibited by reduced light availability than *Phalaris*, suggesting that *Phalaris* is a stronger competitor for light.

The short-term experiments mentioned above (∼ one growing season) did not examine how litter feedbacks could affect plant competition on the longer term (multiple growing seasons). Litter manipulation experiments with other invasive macrophytes suggest that litter feedbacks may enhance invader success (Farrer & Goldberg 2009; Vaccaro, Bedford & Johnston 2009). Because litter feedbacks tend to reduce light availability (for which *Phalaris* is a strong competitor) and increase nutrient availability (for which *Phalaris* is a weak competitor), these feedbacks may also be involved in the invasion of *Phalaris* in North American wetlands. Field observations indeed suggest that *Phalaris*-invaded communities are characterized by the presence of a continuous and relatively thick litter layer as compared to native plant communities (Lesica 1997).

Evolutionary development of new genotypes may also contribute to the successful invasion of *Phalaris* (Lavergne & Molofsky 2007). Repeated introductions of *Phalaris* have lead to novel, strongly competitive genotypes of smaller genome size, forming invasive populations with high genetic variability and phenotypic plasticity (Lavergne & Molofsky 2007; Brodersen, Lavergne & Molofsky 2008; Lavergne, Muenke & Molofsky 2010). More specifically, novel genotypes have a higher growth rate and a higher leaf tissue C:N ratio than native genotypes when grown under the same nutrient and light conditions (Lavergne & Molofsky 2007; Lavergne, Muenke & Molofsky 2010; J. Molofsky *et al*. unpubl. data).

Exotic plant invasions may be driven by the interaction between several factors that amplify each other (Blumenthal 2006; Theoharides & Dukes 2007). In this study, our aim was to explore the possible effects of and interaction between litter feedback and evolutionary change on the competitive ability of *Phalaris* in invasive habitats. We identified how litter feedbacks and evolutionary change may synergistically increase invasion potential, and how the occurrence of this synergy could be detected in future empirical studies.

Materials and methods

MODEL DESCRIPTION

Our starting point was a classical resource competition model (Tilman 1982) in which *Phalaris* (Ph) biomass (indicated with B_{Ph} in Table 1 and 2) and *Carex* (C) biomass (B_C) compete for two resources: soil nitrogen (N) and light (L). The model also includes accumulation of litter from both plant species (D_{Ph} and D_C). The model equations are shown in Table 1, the interpretation and sources for parameter values are shown in Table 2. For further details about model parameterization see Appendix S1 in Supporting Information. *Carex* is a common species in native American sedge meadows, and may thus serve to mimic competition between *Phalaris* and native American wetland species more generally (Perry, Galatowitsch & Rosen 2004). For the sake of brevity, however, we will refer to the native competitor species as *Carex* from here.

In the model, plant biomass dynamics comprise growth (see model term I in Table 1) and mortality (II). Growth is determined by the availability of only one of the two resources. Which resource is limiting depends on the maximum growth rates of the plant species ($g_{N,i}$ and $g_{L,i}$, with i referring to either *Ph* or *C*) and on the saturation constants in the resource uptake function ($k_{N,i}$ and $k_{L,i}$). However, which resource is limiting also depends on the relative availability of each resource (dynamically varying over time). Hence, which resource is limiting may vary over time. The *per capita*

Table 1. Model equations

Variable	Equation

Biomass (B)

$$\frac{dB_i}{dt} = \underbrace{Min\left\{g_{L,i}\frac{L}{k_{L,i}+L}, g_{N,i}\frac{N}{k_{N,i}+N}\right\}B_i}_{\substack{(I)\\ \text{Growth}}} - \underbrace{m_i B_i}_{\substack{(II)\\ \text{Mortality}}}$$

Nutrients (N)

$$\frac{dN}{dt} = \underbrace{a(S-N)}_{\substack{(III)\\ \text{Supply}}} - \underbrace{\sum_{i=1}^{2}\frac{q_{N,i}}{\rho\, l_{Root}}Min\left\{g_{L,i}\frac{L}{k_{L,i}+L}, g_{N,i}\frac{N}{k_{N,i}+N}\right\}B_i}_{\substack{(IV)\\ \text{Plant uptake}}} - \underbrace{\sum_{i=1}^{2}\frac{q_{N,i}^2}{Q_{N,i}\,\rho\, l_{Root}}\alpha_{N,i}d_i D_i}_{\substack{(V)\\ \text{Nutrient release}}}$$

Litter mass (D)

$$\frac{dD_i}{dt} = \underbrace{m_i B_i}_{\substack{(VI)\\ \text{Litter input}}} - \underbrace{\frac{q_{N,i}}{Q_{N,i}}d_i D_i}_{\substack{(VII)\\ \text{Decomposition}}}$$

Light (L)

$$\frac{1}{c_{Rate}}\frac{dL}{dt} = \underbrace{L_0}_{\substack{(VIII)\\ \text{Supply}}} - \underbrace{\sum_{i=1}^{2}\gamma_{L,i}B_i L}_{\substack{(IX)\\ \text{Plant interception}}} - \underbrace{\sum_{i=1}^{2}\alpha_{L,i}D_i L}_{\substack{(X)\\ \text{Litter interception}}} - \underbrace{L}_{\substack{(XI)\\ \text{Loss}}}$$

Light in quasi-steady state (dL/dt=0)

$$\hat{L} = \frac{L_0}{1 + \sum_{i=1}^{2}\gamma_{L,i}B_i L + \sum_{i=1}^{2}\alpha_{L,i}D_i L}$$

mortality rate (m_i) is assumed to be constant. Note that mortality not necessarily involves the death of an individual plant, but also incorporates turnover of leaves, for example. We only consider above-ground biomass in the model, assuming that above-ground biomass determines a species' competitiveness (i.e. its *R** values, *sensu* Tilman (1982)) for both light and nitrogen. This implies a constant root:shoot ratio and a similar allocation strategy, which seems a reasonable assumption when focusing on wetland plants with similar life-history traits.

The nitrogen dynamics follow Tilman (1982) and Daufresne & Hedin (2005). Nitrogen dynamics comprise supply (III), uptake by both plant species (IV) and release from decomposition of litter of both plant species (V). Nitrogen supply can be viewed as the sum of a constant input (*S*) and a loss term, which increases linearly with nitrogen availability in the system. The turnover rate of nitrogen in the system is determined by the parameter *a*. The amount of nitrogen that is taken up is determined by the amount of plant growth multiplied by the nitrogen content of plant tissue ($q_{N,I}$, in mg g^{-1}). Because plant density is expressed in g m^{-2}, the nitrogen uptake by plants is also expressed on a per-area basis, namely mg m^{-2}. Soil nitrogen availability, however, is expressed in mg kg^{-1} soil. Therefore, to convert the nitrogen uptake by plants (in mg m^{-2}) into a decrease in soil nitrogen availability (in mg kg^{-1}), the nitrogen uptake needs to be divided by the amount of soil per area (kg m^{-2}). The amount of soil per area is the product of the soil bulk density (ρ, in kg m^{-3}) and the rooting depth of the plant species (l_{Root}, in m). Here we assumed a constant rooting depth for the plant species, and that nitrogen within this rooting zone is well mixed. Also, we made the assumption that the nitrogen content of plant tissue is constant (following e.g. Eppinga *et al.* 2009). Finally, release occurs through decomposition and mineralization of litter, of which a constant fraction (determined by the parameters $\alpha_{N,C}$ *and* $\alpha_{N,Ph}$) becomes available again for plants

(Daufresne & Hedin 2005). The decomposition rate of litter is assumed to increase linearly with litter quality (e.g. Enrìquez, Duarte & Sand-Jensen 1993), which is quantified in the model by the quotients $q_{N,C}/Q_{N,C}$ and $q_{N,Ph}/Q_{N,Ph}$. Again we made the simplifying assumption that the nitrogen content of litter remains constant (following e.g. Eppinga *et al.* 2009).

The other limiting resource is light. Light dynamics comprise light input (VIII), interception by both plant species (IX) and both litter types (X) and a light loss term (XI). Light input (L_0) is assumed to be constant. To model the rate of change in light availability (Table 1), all processes affecting light dynamics are governed by the rate parameter c_{Rate}. We note, however, that this rate parameter has no influence on the equilibrium light level of the system (Table 1). Light interception of both vegetation and litter is based on Lambert–Beer's law for light absorption. In the case of vegetation and litter, absorption efficiency depends on two properties: the height:mass ratio of the vegetation or litter layer and its shoot density (see Appendix S2). To enable analytical treatment, the Lambert–Beer equation can be approximated by a hyperbolic function of biomass, summarizing the two properties into a single parameter (e.g. Reynolds & Pacala 1993). Because Lambert–Beer's law is generally applicable to any light-absorbing material (e.g. Grace & Woolhouse 1973), we used the same approach to model light interception by plant litter. Since *Phalaris*, *Carex* and their litter have different properties in terms of their height:mass ratios and their shoot densities, values for $\gamma_{L,i}$ for biomass and $\alpha_{L,I}$ for litter were set accordingly (see Appendix S1, S2). It should be noted, however, that our approach does not consider vegetation height explicitly. This is a simplification, because the order of colonization may determine which species occupies the highest position in the canopy at a certain point in time, and thus intercepts most light at that point (Perry, Neuhauser & Galatowitsch 2003).

Table 2. Model parameters and state variables

Symbol	Interpretation	Value*	Units	References**
$g_{L,C}$	Maximum growth rate of *Carex* under light limitation	0.25	day^{-1}	1
$g_{L,Ph}$	Maximum growth rate of *Phalaris* under light limitation	0.25	day^{-1}	1
$k_{L,C}$	Light availability at which *Carex* reaches half its maximal growth rate (if light limited)	50	mol m^{-2}	2
$k_{L,Ph}$	Light availability at which *Phalaris* reaches half its maximal growth rate (if light limited)	21	mol m^{-2}	2
$g_{N,C}$	Maximum growth rate *Carex* under nitrogen limitation	0.25	day^{-1}	1
$g_{N,Ph}$	Maximum growth rate *Phalaris* under nitrogen limitation	0.25	day^{-1}	1
$k_{N,C}$	Nitrogen availability at which *Carex* reaches half its maximal growth rate (if *N* limited)	30	mg kg^{-1}	3
$k_{N,Ph}$	Nitrogen availability at which *Phalaris* reaches half its maximal growth rate (if *N* limited)	35	mg kg^{-1}	3
m_C	Mortality rate *Carex*	0.005	day^{-1}	4,5
m_{Ph}	Mortality rate *Phalaris*	0.01	day^{-1}	5
a	Turnover rate of nutrient supply	0.005	day^{-1}	2,3
S	Nitrogen availability in absence of plants	8–100	mg kg^{-1}	2,3
$q_{N,C}$	Nitrogen content of tissue of *Carex*	15	mg g^{-1}	1,6,7
$q_{N,Ph}$	Nitrogen content of tissue of *Phalaris*	15	mg g^{-1}	1,6,7
ρ	Soil bulk density	530	g.m^{-3}	8
l_{Root}	Rooting depth of plant species	1	m	9
$\alpha_{N,C}$	Nutrient–litter feedback coefficient *Carex*	0.7	-	10
$\alpha_{N,Ph}$	Nutrient–litter feedback coefficient *Phalaris*	0.7	-	10
d_C	*Carex* litter decomposition rate	0.003	day^{-1}	10,11,12,13
d_{Ph}	*Phalaris* litter decomposition rate	0.003	day^{-1}	10,11,12,13
L_0	Light supply rate	0.86–50	mol m^{-2} day^{-1}	2
$\gamma_{L,C}$	Light interception coefficient *Carex*	0.03	m^2 g^{-1}	14,15
$\gamma_{L,Ph}$	Light interception coefficient *Phalaris*	0.04	m^2 g^{-1}	14,15
$\alpha_{L,C}$	Light–litter feedback coefficient *Carex*	0.01	m^2 g^{-1}	14,15,16
$\alpha_{L,Ph}$	Light–litter feedback coefficient *Phalaris*	0.013	m^2 g^{-1}	14,15,16
$Q_{N,C}$	Nitrogen content of *Carex* litter at which it decomposes at rate d_C	15	mg g^{-1}	- (scaling parameter)
$Q_{N,Ph}$	Nitrogen content of *Phalaris* litter at which it decomposes at rate d_P	15	mg g^{-1}	- (scaling parameter)
c_{Rate}	Parameter determining the characteristic timescale of light dynamics	$\gg 1$	day^{-1}	- (scaling parameter)
B_C	Aboveground living biomass of *Carex*	–	g m^{-2}	–
B_{Ph}	Aboveground living biomass of *Phalaris*	–	g m^{-2}	–
N	Nitrogen availability in soil	–	mg kg^{-1}	–
D_C	Aboveground litter mass of *Carex*	–	g m^{-2}	–
D_{Ph}	Aboveground litter mass of *Phalaris*	–	g m^{-2}	–
L	Light availability	–	mol m^{-2} day^{-1}	–
t	Time	–	day	–

* For motivation of parameter values see Appendix S1.
** References: (1) Taub (2002) (2) Perry & Galatowitsch (2004) (3) Perry, Galatowitsch & Rosen (2004) (4) Aerts & De Caluwe (1995) (5) Ryser & Urbas (2000) (6) McJannet, Keddy & Pick (1995) (7) Kätterer, Andrén & Pettersson (1998) (8) Hansel *et al.* (2002) (9) Kätterer & Andrén (1999) (10) Hefting *et al.* (2005) (11) Boyd (1970) (12) Mason & Bryant (1975) (13) Brinson (1981) (14) Herr-Turoff & Zedler (2007) (15) Danais (1986) (16) Violle, Richarte & Navas (2006).

We refer to Appendix S2 for a comparison between the approach adopted here and the approach taken in a previous model study (Perry, Neuhauser & Galatowitsch 2003). This previous model study included hierarchical competition explicitly for light (but not competition for nitrogen), for the same species considered here (Perry, Neuhauser & Galatowitsch 2003). Finally, a light loss term is included, because light cannot be stored. Light dynamics can be assumed to be relatively fast as compared to other processes in the system (i.e. c_{Rate} is relatively large). Hence, a quasi-steady-state approach can be used, meaning that light availability is assumed to equilibrate instantaneously (e.g. Reynolds & Pacala 1993; Table 1,2)

The model also includes a litter pool for each plant species, the dynamics following Daufresne & Hedin (2005). For each litter pool, the dynamics comprise input of dead biomass (VI) and litter losses through decomposition (VII), which have already been described above. Note that the litter pools are treated as separate state variables to enable different litter characteristics of the two species, such as litter quality and decomposition rate. This is a simplification, because empirical studies have shown that mass loss from litter mixtures occurs at a different rate than would be expected from the sum of the species-specific mass losses (e.g. Nilsson, Wardle & Dahlberg 1999).

MODEL PARAMETERIZATION

As noted above, we parameterized the model to simulate competition between *Phalaris* and *Carex* for soil nitrogen and light. Parameter

values were derived from various sources (Table 2; see Appendix S1). Parameters describing soil nitrogen uptake and light interception were calibrated to mimic the results of previous competition experiments between *Phalaris* and *Carex* (Perry & Galatowitsch 2004; Perry, Galatowitsch & Rosen 2004). In general, these previous experiments suggest that *Phalaris* is a stronger competitor for light (Perry & Galatowitsch 2004), whereas *Carex* is a stronger competitor for soil nitrogen (Perry, Galatowitsch & Rosen 2004). Here, we consider a plant species to be a stronger competitor for a resource if it has the lowest *R** value for this resource. We calibrated the *R** values of *Phalaris* and *Carex* for soil nitrogen and light by tuning the saturation constants in the resource uptake functions. If a saturation constant is small, it means that a species can attain a relatively high growth rate at relatively low resource availability. Hence, a small saturation constant reflects a strong competitor.

The saturation constants were set in a way that at low light availability (L_0 = 0.86 mol m^{-2} day^{-1}, all light availabilities follow the treatment levels in Perry & Galatowitsch 2004), both species went extinct. This agreed with the observation of Perry & Galatowitsch (2004) that biomass of both species at this light intensity was reduced by 99%. Under high light availability (L_0 = 50 mol m^{-2} day^{-1}) and intermediate nitrogen availability (forced in the model by setting the supply rate at S = 60 mg kg^{-1}, all nitrogen supply rates are based on treatment levels in Perry, Galatowitsch & Rosen 2004), there was coexistence, which agreed with the observation that both species reached similar biomass at these levels of light and nitrogen (Perry & Galatowitsch 2004). At intermediate light availability (L_0 = 17 mol m^{-2} day^{-1}), *Carex* biomass was reduced more than that of *Phalaris*, as shown experimentally by Perry & Galatowitsch (2004). The exclusion of *Carex* that occurs in the model, however, was not observed within the time span of the experiment (Perry & Galatowitsch 2004). Saturation constants were set in a way that both species coexisted under intermediate nitrogen availability, which corresponded to the observation that both species reached similar biomass at intermediate soil nitrogen levels (Perry, Galatowitsch & Rosen 2004). At high nitrogen availability (S = 90 mg kg^{-1}) *Carex* was excluded, which agreed with the observation that *Carex* biomass was low when grown with *Phalaris* at high nitrogen availability (Perry, Galatowitsch & Rosen 2004). At low nitrogen availability (S = 30 mg kg^{-1}), however, *Phalaris* is excluded, which is in line with the observation that *Phalaris* biomass is low when grown with *Carex* at low nitrogen availability (Perry, Galatowitsch & Rosen 2004).

MODEL ANALYSES OF LITTER FEEDBACKS AND EVOLUTIONARY CHANGE

Including litter pool dynamics in the model creates the possibility of studying plant–litter feedbacks: changes in the litter pool may alter the availability of resources (nitrogen and light), which affects plant growth. In turn, these changes in plant growth feed back to changes in the litter pools. Because the model encompasses two resources, two types of feedbacks can be distinguished. First, decomposition of litter releases nutrients (in this case soil nitrogen), which become available again for plant uptake. This can change plant community composition in favour of weak competitors for nutrients and hence feed back to changes in litter pools. From here we refer to this feedback as *nutrient–litter feedback*. The strength of the nutrient–litter feedback is determined by the parameters $\alpha_{N,Ph}$ and $\alpha_{N,C}$. Second, the presence of litter decreases availability for light, which may change the plant community composition in favour of strong competitors for light. Again, such a change in community composition may feed back to changes

in litter pools. Henceforth we refer to this feedback as *light–litter feedback*. The strength of the light–litter feedback is determined by the parameters $\alpha_{L,Ph}$ and $\alpha_{L,C}$. In the model litter feedbacks could be switched off by setting the feedback coefficients ($\alpha_{L,Ph}$, $\alpha_{L,C}$, $\alpha_{N,Ph}$ and $\alpha_{N,C}$) to zero.

Our analyses focused on three *Phalaris* invasion scenarios. The first scenario considered how *Phalaris* invasion could be influenced by the nutrient–litter and light–litter feedbacks, through on-and-off switching of these feedbacks in a full-factorial design. We analysed graphically how these feedbacks affected the competitive outcome between *Phalaris* and *Carex* over a range of nitrogen and light supply parameter values. For the studied parameterization, we also calculated the extent to which litter feedbacks reduced the parameter space for coexistence.

In the second scenario, we considered the effect of two evolutionary changes that have been observed in invasive *Phalaris* genotypes: a higher growth rate and a higher C:N ratio as compared to native European genotypes. The evolutionary changes were documented in common-garden experiments in the greenhouse. For the growth rate experiment, 41 native European genotypes (from France and the Czech Republic) and 49 invasive genotypes (from Vermont and North Carolina, USA) were grown under the same nutrient and light conditions, for a period of 73 days. More details on this experiment can be found in Lavergne & Molofsky (2007). For the C:N ratio experiment, 46 native and 56 invasive genotypes were grown under the same nutrient and light conditions, for a period of 3 months (J. Molofsky *et al.* unpubl. data). During both experiments, dead biomass was removed from the pots, meaning that the results were not affected by above-ground litter. As noted above, *Phalaris*' growth rate is determined in the model by the parameters $g_{N,Ph}$ and $g_{L,Ph}$. The C:N ratio of *Phalaris* tissue is reflected by $1/q_{N,Ph}$, meaning that *Phalaris*' C:N ratio increases with a decreasing value of the parameter $q_{N,Ph}$. We analysed graphically the effect of higher values of $g_{N,Ph}$ and $g_{L,Ph}$ and a lower value of $q_{N,Ph}$ on the competitive outcome between *Phalaris* and *Carex* over a range of nitrogen and light supply parameter values. Taking the coexistence situation without feedbacks and evolutionary changes as a starting point, we also derived analytically the magnitude of evolutionary change that would be required to qualitatively alter the competitive outcome between *Phalaris* and *Carex* (all analytical analyses are presented in Appendix S3). We then compared these calculated critical points for the model parameterization with the observed changes in the experiments. The analytical results yield a general expression of critical points in terms of model parameters (see Appendix S3), but inserting the parameter values of a specific parameterization in this general expression yields a critical point for that parameterization. Apart from increasing invader competitiveness, evolutionary change may also enhance invader success by broadening the climatic niche of evolved genotypes (Gallagher *et al.* 2010). Thus, evolutionary change stimulating geographic expansion during the so-called spread phase of invasions (e.g. Theoharides & Dukes 2007) may also contribute to the success of *Phalaris* in North America (Lavergne & Molofsky 2007). To investigate this possibility, we also considered competition between *Phalaris* and native species in habitats that are outside the original climatic niche of *Phalaris* (i.e. warmer or colder). In order to focus the analysis on effects of evolutionary change in different climates, we assumed that the native species had the same characteristics as *Carex* considered in the other model scenarios. We thus considered competition between *Phalaris* and an ecological congener of *Carex* in a different climatic habitat. Habitat suitability was assumed to affect the maximum growth rate of *Phalaris* ($g_{N,Ph}$ and $g_{L,Ph}$) following Tilman (2004), who assumed the maximum growth rate of plant species being dependent on

temperature. We assumed a 20% reduction of *Phalaris'* maximum growth rates in different climatic habitats. Under cultivated and relatively dry conditions within one site, a reduction in *Phalaris'* photosynthesis rate of 20% was observed when the temperature was 5–6 °C away from the optimum temperature (Shurpali *et al.* 2009).

In the third scenario, we analysed effects of both litter feedbacks and evolutionary change (focusing on the effect of a higher C:N ratio in invasive genotypes) to explore whether these factors could interactively affect plant competition and invasion. In this scenario, we analysed how the stability of community and single-species equilibria changed with increasing C:N ratio for invasive *Phalaris* genotypes. We considered a system with higher nitrogen supply ($S = 10.25$ mg kg^{-1}) and a system with lower nitrogen supply ($S = 8$ mg kg^{-1}). Nitrogen supply rates were set in a way that in the absence of evolutionary change (but in the presence of litter feedbacks), *Phalaris* was excluded by *Carex* in the second system, but could coexist with *Carex* in the first system. Using analytical results (see Appendix S3), we also calculated for both systems the critical *Phalaris* C:N ratio at which the competitive outcome of the system changed. We examined how this critical *Phalaris* C:N ratio was affected by the absence or presence of litter feedbacks.

Finally, we performed two types of sensitivity analyses (see Appendix S4), to assess the model sensitivity to parameter values (using an elasticity analysis, e.g. Eppinga *et al.* 2009) and to assess the robustness of model results (by quantifying the sensitivity ranges of the model parameters, c.f. Eppinga *et al.* 2006).

Results

SCENARIO 1: LITTER FEEDBACKS INFLUENCING *PHALARIS* INVASION

The inclusion of litter feedbacks drastically reduced the parameter space for coexistence in the model and increased the parameter space in which *Phalaris* excludes *Carex* (Fig. 1). This result occurred because litter was a source of nitrogen (for which *Phalaris* is the weaker competitor), but it decreased light availability (for which *Phalaris* was the stronger competitor). Thus, the effects of litter on both nutrient and light availability favoured *Phalaris'* competitive ability, but in a slightly different manner (Fig. 1, see Appendix S3 for analytical justification of the results). Litter lowering light availability had a small effect on the equilibrium density of *Phalaris* (Fig. 1c), but made growing conditions much worse for *Carex*. Hence, there was an indirect positive effect on *Phalaris*. Litter increasing nitrogen availability had a direct positive effect by increasing the equilibrium density of *Phalaris* (Fig. 1b). There was synergy between the two litter feedback effects, in that their combined effect reduced the parameter space for coexistence further (96% reduction, Fig. 1d) than would be expected by the sum of their separate effects (91% reduction).
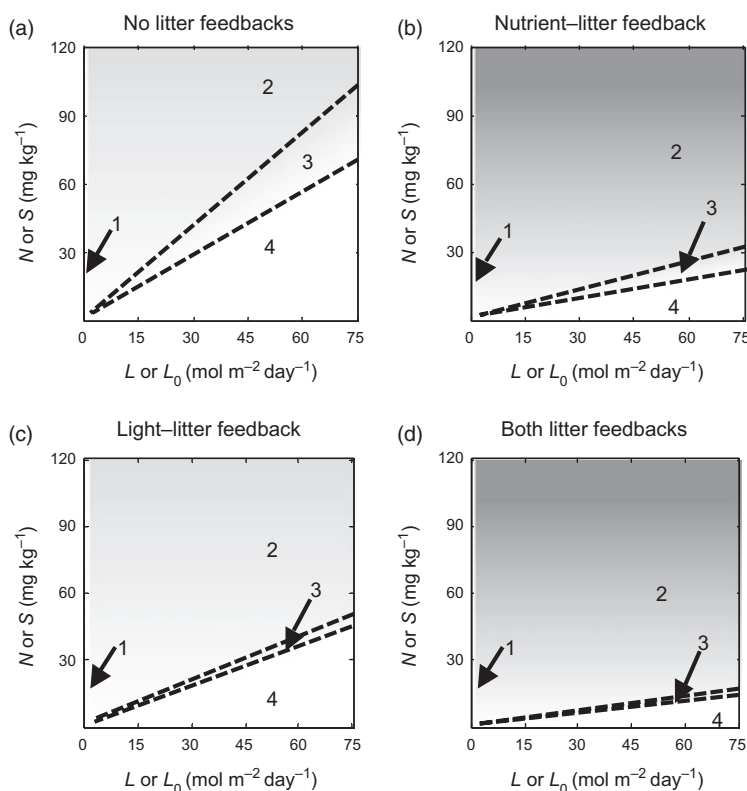

Fig. 1. The effect of litter feedbacks on the outcome of competition between *Phalaris* and *Carex*. Darker shades indicate higher *Phalaris* biomass in equilibrium. Numbers indicate regions of parameter space with different outcomes of competition: (1) Neither species can survive (2) Exclusion of *Carex* (3) Coexistence (4) Exclusion of *Phalaris*. (a) Without litter feedbacks. (b) The additional nutrient release through litter increases *Phalaris* equilibrium biomass and reduces the parameter region for coexistence. (c) Light absorbance of litter has little effect on *Phalaris* biomass, but the parameter region of *Carex* exclusion increases. (d) The combined effects of litter further reduce the parameter region for coexistence and increase the parameter region of *Carex* exclusion. Parameters as in Table 2.

SCENARIO 2: EVOLUTIONARY CHANGES INFLUENCING *PHALARIS* INVASION

Empirical research shows that invasive *Phalaris* genotypes have higher growth rates as compared to native European genotypes when grown under the same nutrient and light conditions (Fig. 2a, data from Lavergne & Molofsky 2007). In the model, a higher growth rate of *Phalaris* meant that the species induced lower R^* values for both soil nitrogen and light (Fig. 2b, see Appendix S3). For regions that are within *Phalaris*' climatic niche, there was a range of native European genotype characteristics that could lead to coexistence with *Carex*, but an evolutionary development of these genotypes toward a higher growth rate may result in *Phalaris* excluding *Carex* (Fig. 2c). For this situation to occur within our model parameterization, however, the required increase in growth rate was much higher (*c.* 240% increase) than observed in the experiment (Lavergne & Molofsky 2007; Fig. 2a). For regions that are outside *Phalaris*' climatic niche there could be a range of native European genotype characteristics that would not allow for *Phalaris* establishment, but an evolutionary development

of these genotypes toward a higher growth rate could result in *Phalaris* establishing and coexisting with native American species that have similar growth characteristics as *Carex* (Fig. 2d). For the considered parameterization, such a change required only a relatively small increase in growth rate (6%).

Invasive genotypes also have a higher C:N ratio as compared to native European genotypes when grown under the same nutrient and light conditions (Fig. 3a, data from J. Molofsky *et al.*, unpubl. data). In contrast to a change in growth rate, a change in *Phalaris*' C:N ratio did not affect the R^* values of *Phalaris* (Fig. 3b; see Appendix S3). This meant that a higher C:N ratio of *Phalaris* tissue did not affect the position of the plant species coexistence equilibrium (see Appendix S3). Instead, a change in C:N ratio modified the nitrogen:light consumption ratio, or consumption vector, of *Phalaris* (Fig. 3b). Hence, in regions within *Phalaris*' climatic niche there could be a range of ecosystem characteristics that could lead to coexistence between native *Phalaris* genotypes and *Carex*, but an evolutionary development of these genotypes toward a higher C:N ratio could result in *Phalaris* excluding *Carex* (Fig. 3c). There could also be a range of ecosystem characteristics under
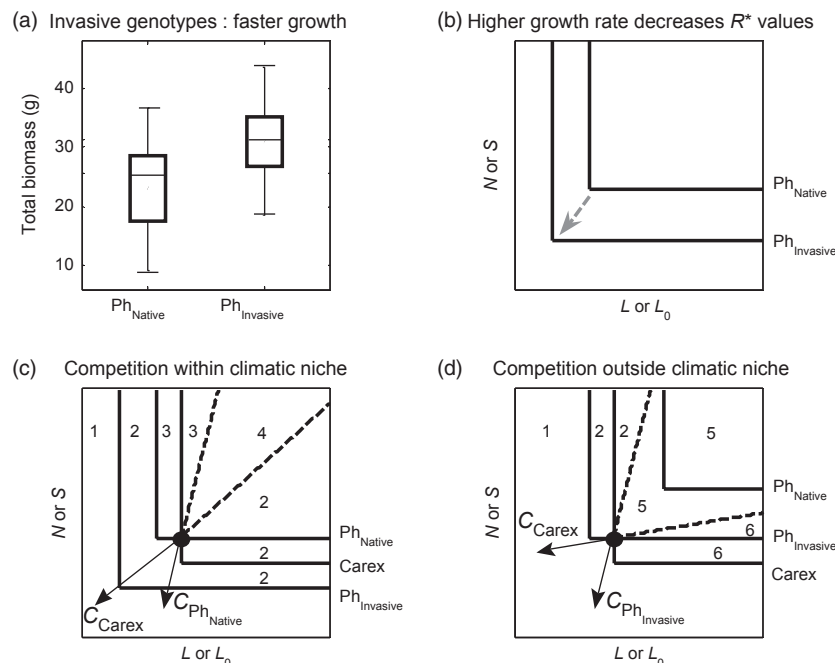

Fig. 2. Evolutionary change toward a higher growth rate of *Phalaris*, and its effects on competition with *Carex*, or ecological congeners in habitats outside *Phalaris*' climatic niche. (a) Boxplot showing total biomass for native European *Phalaris* genotypes (Ph$_{Native}$) and invasive *Phalaris* genotypes (Ph$_{Invasive}$) as observed in a common-garden experiment in the greenhouse, showing that invasive genotypes have a higher growth rate than native genotypes ($P < 0.05$, data from Lavergne & Molofsky 2007). The bottom and top limits of each box are the lower and upper quartiles, the horizontal band in each box is the median and error bars equal one standard deviation. (b–d) State space portraits showing the zero net growth isoclines (thick lines) of native European *Phalaris* genotypes, invasive *Phalaris* genotypes and *Carex* or congener species. Dashed lines indicate the boundaries of coexistence regions, which are determined by the consumption vectors (black arrows) of the different species. Numbers indicate regions of resource space with different outcomes of competition: (1) Neither species can survive (2) Native *Phalaris* genotypes get excluded by *Carex*, but invasive genotypes exclude *Carex* (3) Both native and invasive *Phalaris* genotypes exclude *Carex* (4) Coexistence (5) Native *Phalaris* genotypes get excluded by *Carex*, but invasive genotypes coexist with *Carex* (6) *Carex* excludes both native and invasive *Phalaris* genotypes. (b) A higher growth rate means that *Phalaris* decreases its R^* values. (c) In climate regions similar to *Phalaris*' original habitat, evolutionary development toward a higher growth rate may narrow the set of possible competitive outcomes from four (Neither species survives, *Carex* wins, *Phalaris* wins, Coexistence) to two (Neither species survives or *Phalaris* wins). (d) In climate regions less suitable for *Phalaris* growth, evolutionary development toward a higher growth rate may extend the set of possible competitive outcomes from two (Neither species survives, *Carex* wins) to four (Neither species survives, *Carex* wins, *Phalaris* wins, Coexistence).
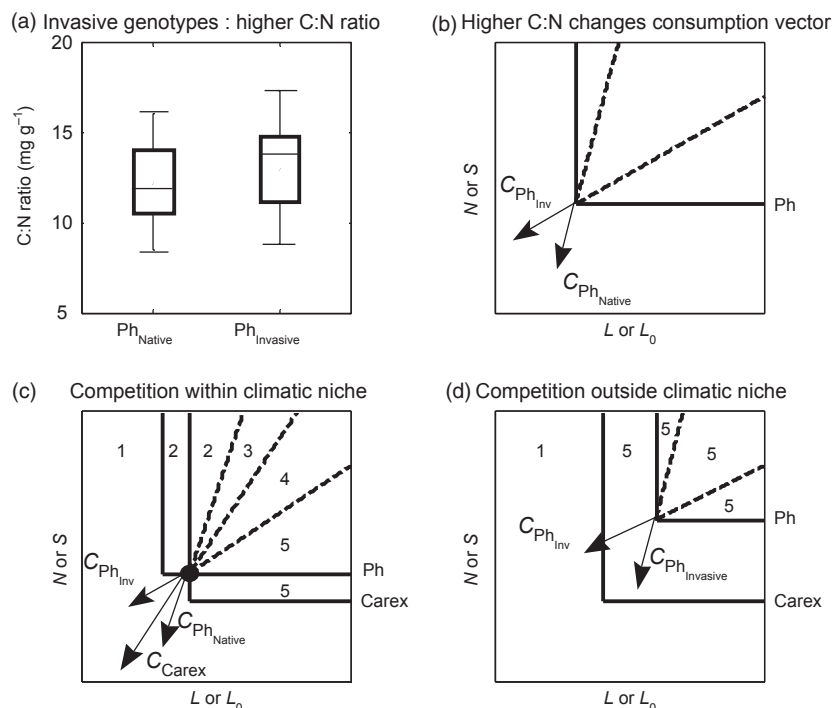
Fig. 3. Evolutionary change toward a higher C : N ratio in *Phalaris* tissue, and its effects on competition with *Carex*, or ecological congeners in habitats outside *Phalaris'* climatic niche. (a) Boxplots showing C:N ratios for native European *Phalaris* genotypes (Ph_{Native}) and invasive *Phalaris* genotypes ($Ph_{Invasive}$) as observed in a common-garden experiment in the greenhouse, showing that invasive genotypes have a higher C:N ratio than native genotypes ($P < 0.05$, data from J. Molofsky *et al.*, unpubl. data). The bottom and top limits of each box are the lower and upper quartiles, the horizontal band in each box is the median and error bars equal one standard deviation. (b–d) State space portraits showing the zero net growth isoclines (thick lines) of native European *Phalaris* genotypes, invasive *Phalaris* genotypes and *Carex* or congener species. Dashed lines indicate the boundaries of coexistence regions, which are determined by the consumption vectors (black arrows) of the different species. Numbers indicate regions of resource space with different outcomes of competition: (1) Neither species can survive (2) Both native and invasive *Phalaris* genotypes exclude *Carex* (3) Native *Phalaris* genotypes coexist with *Carex*, but invasive *Phalaris* genotypes exclude *Carex* (4) *Carex* excludes native *Phalaris* genotypes, but either invasive *Phalaris* genotypes or *Carex* could exclude the other species (founder control) (5) *Carex* excludes both native and invasive *Phalaris* genotypes. (b) A higher C : N ratio means that *Phalaris* can produce more biomass per unit resource, meaning that the nitrogen:light consumption ratio of *Phalaris* decreases. (c) In climate regions similar to *Phalaris'* original habitat, evolutionary development toward a higher C : N ratio may eliminate coexistence as a competitive outcome and introduce the possibility of founder control as a competitive outcome. (d) In climate regions less suitable for *Phalaris* growth, an evolutionary change toward a higher C : N ratio cannot trigger a change in the possible competitive outcomes between *Phalaris* and *Carex*.

which *Carex* excludes native *Phalaris* genotypes, but an evolutionary development of these genotypes toward a higher C:N ratio could result in a situation of founder control, where either *Phalaris* or *Carex* could be excluded (Fig. 3c). For these two situations to occur within our model parameterization, however, the required increase in *Phalaris'* C:N ratio (*c.* 35%) was at the upper end of the range observed in the experiment (Fig. 3a). In climate regions less suitable for *Phalaris* growth, an evolutionary change toward a higher C:N ratio could not trigger establishment of *Phalaris* (Fig. 3d).

SCENARIO 3: INTERACTIONS BETWEEN LITTER FEEDBACKS AND EVOLUTIONARY CHANGES

In the previous scenarios, we have treated litter feedbacks and evolutionary change separately, showing that both could increase the competitive advantage of *Phalaris* over native American wetland species such as *Carex*. As noted above, an evolutionary change toward a higher C:N ratio

in *Phalaris* tissue changed its consumption vector (Fig. 3b). This change was especially important when the *Phalaris* and *Carex* consumption vectors were relatively similar, because then even a small change in consumption vectors could alter the outcome of competition. Litter feedbacks could drastically reduce the parameter region of coexistence, meaning that the consumption vectors of both species became relatively similar (Fig. 1). Thus, even if the nutrient and light requirements of *Phalaris* and *Carex* would allow for a relatively large parameter region for coexistence, the synergy between litter feedbacks and evolutionary change could alter the outcome of competition. More specifically, two changes in competitive outcome were possible.

First, litter feedbacks and evolutionary change could shift a system in which *Carex* and *Phalaris* coexist into a state where *Carex* was excluded (Fig. 4a). In the absence of litter feedbacks, a relatively large change in C:N ratio would be required to establish this shift (*c.* 87%). In the presence of litter
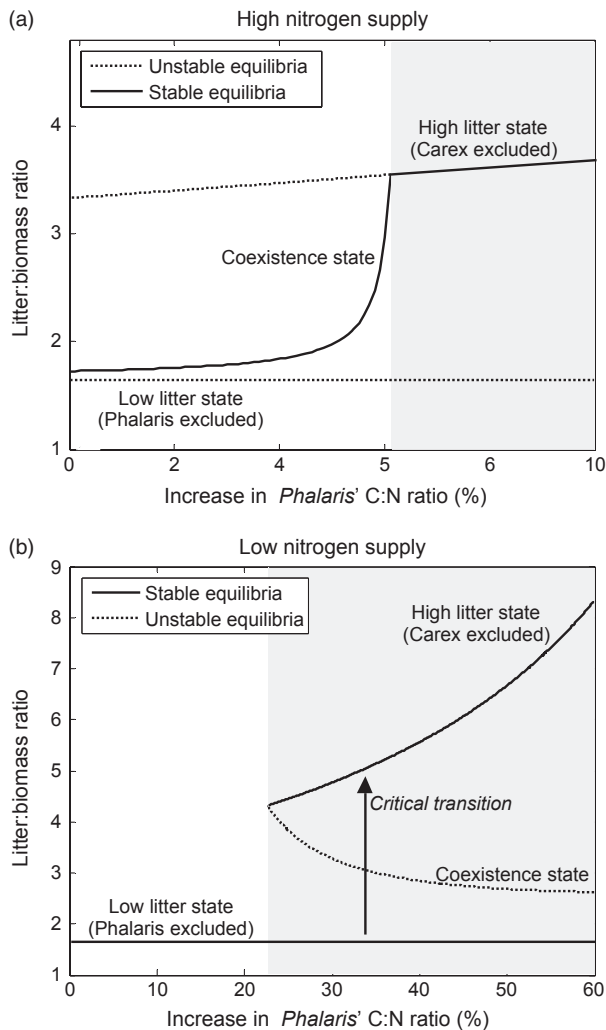
Fig. 4. Litter feedbacks and evolutionary change synergistically changing the outcome of competition between *Phalaris* and native American wetland species such as *Carex*. The graphs show the stability of coexistence and single-species equilibria over a range of evolutionary change (in C:N ratio) of *Phalaris* genotypes. (a) In habitats where *Phalaris* is present, litter feedbacks and evolutionary change may accelerate replacement of *Carex* by *Phalaris* (*S* = 10.25 mg kg^{-1}, other parameters as in Table 2). (b) In habitats where *Phalaris* is not yet present, due to lower nutrient supply for example, the invasion process may encompass a critical transition from a low-litter state to a higher-litter state (*S* = 8 mg kg^{-1}, other parameters as in Table 2).

feedbacks, however, a relatively small change in C:N ratio could establish this shift (c. 5%, Fig. 4a). Thus, litter feedbacks accelerated *Carex* exclusion in a scenario with evolutionary change leading to higher C:N ratios of *Phalaris* genotypes (Fig. 4a).

Second, even though *Phalaris* was a stronger competitor for light, the system could be in a state where *Phalaris* was excluded, due to low nitrogen supply for example. However, due to litter feedbacks and an increase in *Phalaris*' C:N ratio, the system could shift into a condition of alternative stable states, meaning that exclusion of either species would be a stable equilibrium ecosystem state (Fig. 4b). Under these con-

ditions, invasion of *Phalaris* entailed a critical transition from a low-litter to a high-litter ecosystem state. Such a critical transition could occur through a nutrient pulse into the system, for example. With *Phalaris* undergoing evolutionary change, the impact of a nutrient pulse would become more severe. With continuing increase of *Phalaris*' C:N ratio, a nutrient pulse could force the ecosystem over a threshold, shifting the system irreversibly into a state with *Phalaris* only (Fig. 4b).

SENSITIVITY AND ROBUSTNESS OF MODEL RESULTS

Biomass and litter density were most sensitive to changes in the litter feedback parameters, which supported the notion of the potential importance of litter feedbacks influencing plant competition (see Appendix S4). Biomass and litter density were also sensitive to nitrogen and light supply (see Appendix S4). Note that the influence of these parameters was studied in detail (Figs 1, 2, 3, 4). Equilibrium levels of light and nitrogen availability were only determined by a small number of parameters (for light: $k_{L,i}$, m_i and $g_{L,i}$, for nitrogen: $k_{N,i}$, m_i and $g_{N,i}$, see equations 5 and 6 in Appendix S3), as shown for the classical resource competition model by Tilman (1982). Most parameters could be varied over an order of magnitude without qualitatively altering the model results (see Appendix S4). The only exceptions were the plant mortality parameters (see Appendix S4). In general, plant mortality and turnover in wetland plants is low, unless there is a disturbance. Further, the mortality parameters could be varied only over a relatively narrow range when plant growth rates were kept constant; there was a broad range of plant growth–mortality characteristics that yielded similar results as presented here. Hence, our sensitivity analyses suggest that our findings were not very dependent on the specific parameter settings adopted in this study (see Appendix S4).

Discussion

The results presented here show how exotic plant invasions may be exacerbated by a combination of plant–litter feedbacks and evolutionary change. Evolutionary change toward higher C:N ratios in plant tissue may slow decomposition (Enríquez, Duarte & Sand-Jensen 1993; Cornwell *et al.* 2008) and thus stimulate accumulation of litter. Litter decreases light availability, but it is a source of nutrients. Both effects may change the outcome of competition between native and invasive species (Fig. 1). In cases where both effects favour the invader, as observed for *Phalaris* in North American wetlands (Perry & Galatowitsch 2004; Perry, Galatowitsch & Rosen 2004; Fig. 1), the synergy between evolutionary change and litter feedbacks may induce a positive feedback in the invasion process. This positive feedback may drive invasion into new habitats, encompassing a critical transition from a low-litter to a high-litter ecosystem state (Fig. 4). Our results also suggest that the importance of litter feedback and evolutionary change may be underestimated when studied in isolation. These mechanisms may amplify each other, which highlights the potential

importance of studying both evolutionary and ecological processes as drivers of exotic plant invasions.

Studies on invasive macrophytes other than *Phalaris* have stressed the potential of litter feedbacks driving ecosystem changes and facilitating invasion (Farrer & Goldberg 2009; Vaccaro, Bedford & Johnston 2009). More generally, litter feedbacks may affect the invasion of other exotic plants that stimulate litter accumulation by having higher C:N ratios than native vegetation. This trait has been observed for other invasive plants (Funk & Vitousek 2007; Ren & Zhang 2009; Ehrenfeld 2010). Previous experiments on *Phalaris*, however, have not taken into account the effects of litter and possible litter feedbacks on competition between *Phalaris* and native American wetland species. Our study generates a number of predictions on the role of litter feedbacks that could be tested in future empirical research. First, our model results suggest that positive feedbacks occur because litter effects on nutrient and light availability are non-additive; their combined effect may be larger than the sums of the separate effects. These effects could be disentangled in the field by addition of powdered litter (only acting as a nutrient source, e.g. Xiong, Nilsson & Johansson 2001), artificial litter (only acting as a light absorber, e.g. Sydes & Grime 1981) and untreated litter. Second, our model results suggest that in systems where *Phalaris* is subordinately present, the community response to litter addition may be nonlinear: litter addition is predicted to have little effect, until a threshold is passed, above which *Phalaris* excludes native species (Fig. 4b). Such threshold effects could be tested in experiments that use incremental levels of litter addition. Third, our results suggest that evolutionary change and litter feedbacks alter ecosystem functioning, leading to a high-litter state. An important component of identifying underlying mechanisms of invasion is a biogeographical comparison of species performance and ecosystem attributes in native and invasive ranges (Hierro, Maron & Callaway 2005). Our results suggest that litter : above-ground biomass ratios are higher in the invasive ranges where *Phalaris* is dominant (Fig. 4). The litter : above-ground biomass ratio would be relatively easy to measure in the field, and could provide valuable insight in the possible role of litter feedbacks in *Phalaris* invasion into non-native habitats.

Although further experimental testing of our model predictions is needed, it is interesting to note that some of our model results corroborate previous field observations of *Phalaris* invasion in North America. On a local and regional scale, *Phalaris* expansion is most pronounced in areas that receive agricultural run-off, which is rich in nitrogen compounds (Lavoie, Dufresne & Delisle 2005; Jakubowski, Casler & Jackson 2010). Our results also suggested that evolutionary change, which may be stimulated through multiple introductions (Lavergne & Molofsky 2007), could broaden the climatic niche of *Phalaris* (Fig. 2), and thus stimulate its geographic expansion at the range margins. Although the genetic variability within *Phalaris* populations has only been documented for a few sites, previous studies made two interesting observations in this context. First, successful populations in Vermont and North Carolina have high genetic diversity, suggesting multiple introductions and a high potential for recombination into new genotypes (Gifford, Ferdy & Molofsky 2002; Lavergne & Molofsky 2007). Second, *Phalaris* was not so frequently introduced in Québec, and here the geographic expansion has been very limited over the last century (Lavoie, Dufresne & Delisle 2005). On the other hand, our model results suggested that evolutionary changes alone, in the absence of litter feedbacks, need to be relatively large to improve *Phalaris*' invader success. This means that differences in competitiveness between native and invasive genotypes may be underestimated in short-term experiments that do not include litter accumulation and the possibility of the build-up of litter feedbacks.

In this study, we focused on how plant–litter interactions and evolutionary change may affect the competitive ability of *Phalaris* and native American wetland plant species such as *Carex*. Simulations in this study assumed a gradual increase in *Phalaris* C:N ratio over time, as inferred from experimental data (Fig. 4a). Investigating whether this is indeed a superior trait would require an evolutionary modelling approach that studies whether mutants with a higher C:N ratio take over the resident genotype. Such an approach was beyond the scope of this study. Also, we focused on vegetation and litter dynamics, but in wetlands both vegetation growth and litter decomposition are intimately linked with ecosystem hydrology (Belyea & Clymo 2001). Subsequent approaches could link the vegetation and litter dynamics to a hydrological submodel, as previously done for boreal and tropical peatlands (Hilbert, Roulet & Moore 2000; Larsen, Harvey & Crimaldi 2007; Eppinga *et al.* 2009). An important application of such a coupled model could be to investigate the possible consequences of *Phalaris* invasion on ecosystem functioning, such as carbon sequestration capacity.

Critical transitions in ecosystem states typically occur unexpectedly, and are relatively difficult to reverse (Scheffer *et al.* 2001). This study illustrates how invasion of exotic species that induce litter feedbacks in their new habitats may cause a critical transition toward a new, high-litter ecosystem state. These transitions may partly be driven by evolutionary changes toward a higher C:N ratio of plant tissue. Although more empirical research is required to establish the importance of synergy between litter feedbacks and evolutionary change, their occurrence would have important consequences for ecosystem management. For example, even if nutrient levels are generally kept low, a short pulse of nutrients may be enough to trigger the invasion process, which may be difficult to reverse. The study presented here suggests several approaches to test empirically whether positive feedback mechanisms are indeed involved in exotic plant invasions.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Model parameterization.

Appendix S2. Modelling light interception.

Appendix S3. Analytical justification of the results.

Appendix S4. Model sensitivity and robustness.

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