

Research



Cite this article: Martignoni MM, Hart MM, Tyson RC, Garnier J. 2020 Diversity within mutualist guilds promotes coexistence and reduces the risk of invasion from an alien mutualist. *Proc. R. Soc. B* **287**: 20192312. <http://dx.doi.org/10.1098/rspb.2019.2312>

Received: 2 October 2019

Accepted: 28 February 2020

Subject Category:

Ecology

Subject Areas:

ecology, theoretical biology

Keywords:

mutualism, arbuscular mycorrhizal fungi, model, invasion, diversity, pollination

Author for correspondence:

Maria M. Martignoni

e-mail: maria.martignonimseya@ubc.ca

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4891026>.

Diversity within mutualist guilds promotes coexistence and reduces the risk of invasion from an alien mutualist

Maria M. Martignoni¹, Miranda M. Hart², Rebecca C. Tyson¹ and Jimmy Garnier³

¹Department of Mathematics, and ²Department of Biology, University of British Columbia, Kelowna, Canada

³Laboratoire de Mathématiques (LAMA), CNRS and Université de Savoie-Mont Blanc, Chambéry, France

MMM, 0000-0002-0192-8228; RCT, 0000-0002-7373-4473

Biodiversity is an important component of healthy ecosystems, and thus understanding the mechanisms behind species coexistence is critical in ecology and conservation biology. In particular, few studies have focused on the dynamics resulting from the co-occurrence of mutualistic and competitive interactions within a group of species. Here we build a mathematical model to study the dynamics of a guild of competitors who are also engaged in mutualistic interactions with a common partner. We show that coexistence as well as competitive exclusion can occur depending on the competition strength and on strength of the mutualistic interactions, and we formulate concrete criteria for predicting invasion success of an alien mutualist based on propagule pressure, alien traits (such as its resource exchange ability) and composition of the recipient community. We find that intra guild diversity promotes the coexistence of species that would otherwise competitively exclude each other, and makes a guild less vulnerable to invasion. Our results can serve as a useful framework to predict the consequences of species manipulation in mutualistic communities.

1. Introduction

Recent decades have seen a drastic increase in biological invasion by alien organisms, for instance owing to climate change or to anthropogenic disturbance [1]. These invasions have led to significant ecological and economic damage throughout the world [2], and it has thus become increasingly important to better understand the mechanisms behind the invasion process, in order to identify the causal factors promoting or hindering invasion success [3,4].

Invasion is a three stage process [5], involving (i) the introduction of an alien species, (ii) its local establishment (which may cause different scales of biodiversity loss within the recipient community), and eventually (iii) its regional spread. Factors making biological invasion more likely to occur have been identified in the recipient ecosystem [6,7], in the introduced species [8,9], and in the interaction between the two [3,10]. Studies agree that propagule pressure (i.e. the number of individuals introduced in a potential invasion site) plays a decisive role in determining the establishment of an alien species [11,12]. Resource availability is also a main factor contributing to successful establishment [13,14], as well as the capacity of the alien species to make an effective use of the resources acquired [15,16]. Resource availability is strongly influenced by abiotic factors [17,18], by the interactions of the organisms and the environment [19,20], or by the direct and indirect interactions between the alien species and the existing community [7,21]. Additionally, the establishment of the alien species can in turn have an impact on resource availability and affect the invasion dynamics [22,23]. Thus, biological invasion is a complex process, and although individual ecological factors determining invasibility have been identified, it remains challenging to understand how their interplay determines invasion success [24,25].

Ecological modelling can illuminate the investigation of mechanisms driving invasion, as models can disentangle the roles played by different factors in the invasion process. Numerous mathematical approaches and simulation models have been developed to analyse the processes involved in biological invasions [26]. Many results focus on the spreading speed of the invasion [26] (step (iii) of the invasion process), while establishment success has received little attention. In particular, the invasibility of mutualistic communities by an alien species has remained under-explored theoretically [27–30].

In nature, mutualistic interactions often involve multiple species of mutualists (the mutualist guild) sharing a resource supplied by one or more partner (or host) species [31]. A single plant, for example, can associate with dozens of species of beneficial mycorrhizal fungi that coexist in the plant roots and surrounding soil and compete between each other for access to the plant resource [32,33]. Similarly, different competing animal pollinators can coexist on the same floral resources [34,35]. Understanding of the mechanisms behind the persistence of diversity among mutualists and the factors that can threaten this stability has become crucial not only from an ecological point of view, but also for our socio-economical well-being [36]. Indeed pollination and below-ground mutualisms, two of the most widespread earth-mutualisms, are essential drivers of agricultural productivity. Two recent meta-analyses of experimental studies of plant–pollinator relationships [37,38], underline how challenging it is to untangle these relationships with experimental tools alone.

In this work, we will use an ordinary differential equation (ODE) model to study the second stage of the invasion process, i.e. alien species establishment, in a community of mutualists sharing the same host. Additionally, we will explore the ability of the guild to prevent establishment of the alien species. We are interested in the context wherein a native community is threatened with invasion by a foreign species. We thus use the terms ‘mutualist guild’, ‘native community’ and ‘established community’ to refer to the assemblage of species that was initially present (not necessarily at equilibrium). We use the terms ‘alien mutualist’, ‘introduced species’ and ‘introduced mutualist’ to indicate an organism that can associate with the same partner as the existing guild members. We assume that the alien species might differ in its mutualist quality and/or competitive ability

More specifically, we study the relative effect on the growth dynamics of (i) invator traits, such as competition strength and resource exchange ability, (ii) propagule pressure, expressed in terms of initial biomass of the introduced species, and (iii) composition of the recipient community, in terms of diversity and initial biomass. Finally, we will discuss the impact of the introduction of an alien species on the diversity of the native guild and on resource availability, i.e. the biomass of the partner species, often associated with productivity in mutualistic communities (for example in terms of crop yield) [39].

We show that the presence of multiple species in a guild promotes species coexistence and reduces the risk of invasion by an alien mutualist. As our model is general, our conclusions apply to a broad range of mutualisms. To simplify our presentation, however, our case study will be the mutualistic interactions between arbuscular mycorrhizal (AM) fungi and their host plant.

2. Model and methods

(a) Formulating a model for multi-species mutualisms

We formulate a model to study the dynamics of a guild of competing mutualists sharing a resource supplied by the same partner. Mutualists compete for access to a common resource, whose abundance in the model uniquely corresponds to the biomass of the partner species. Resource availability is in turn affected by the benefit that the partner species receives from its associated mutualists, and hence by the guild composition [40,41]. The guild and resource dynamics are therefore intrinsically coupled.

We focus on a system consisting of a plant and a guild of mutualist AM fungi. AM fungi facilitate the plant’s absorption of nutrients (phosphorus in particular) that are limiting to plant growth [42]. In exchange, the plant provides fixed carbon to the fungi [42]. We use an existing model allowing for the coexistence of multiple mutualists [43] to model plant–fungi interactions, and consider the effect of adding direct competition between fungi. This new model therefore includes both mutualistic (plant to fungi) and competitive (fungi to fungi) interactions. The model equations describe the evolution in time of the biomass of the plant (p) and the biomass of the fungal species (m_j) as a function of the exchange of these critical nutrients. We write:

$$\frac{dp}{dt} = \overbrace{r_p(p)}^{\text{plant fitness}} + \sum_j [\overbrace{\alpha_j f_{hp}(p, m_j)}^{\text{phosphorus received}} - \overbrace{\beta_j f_{cp}(p, m_j) C(m_j, m_j)}^{\text{carbon supplied}}], \quad (2.1a)$$

$$\frac{dm_j}{dt} = \underbrace{r_{m_j}(m_j)}_{\text{fungal maintenance}} + \underbrace{\beta_j f_{cm_j}(p, m_j) C(m_j, m_j)}_{\text{competition carbon received}} - \underbrace{\alpha_j f_{hm_j}(p, m_j)}_{\text{phosphorus supplied}}. \quad (2.1b)$$

The components of the model are explained below.

(b) Mutualistic interactions between the plant and the arbuscular mycorrhizal fungi

In the absence of AM fungi, plant fitness is given by the function $r_p(p)$, which takes into account the intrinsic growth of the plant as well as maintenance costs, such as respiration, or energy costs related to nutrient absorption. In the presence of fungi, the plant receives phosphorus from each fungal mutualist ($f_{hp}(p, m_j)$), and supplies carbon in return ($f_{cp}(p, m_j)$). Fungal biomass increases owing to the carbon received by the plant ($f_{cm_j}(p, m_j)$), and decreases owing to the phosphorus supplied to the plant ($f_{hm_j}(p, m_j)$), as well as owing to costs related to the maintenance of the existing fungal biomass ($r_{m_j}(m_j)$). AM fungi are obligate mutualists and can not survive in the absence of a host plant, therefore no intrinsic growth term is present in the equation describing fungal growth. Parameters α_j and β_j represent the ability of fungal species j to exchange phosphorus and carbon respectively.

The choice of the functional forms of the $f(\cdot, \cdot)$ functions, describing nutrients transfer, is tied to the biology and fully explained in [43]. Here we present a brief summary. Phosphorus transfer is proportional to fungal and plant biomass, when plant biomass is small, and to fungal biomass only, when plant biomass is large enough, while carbon transfer

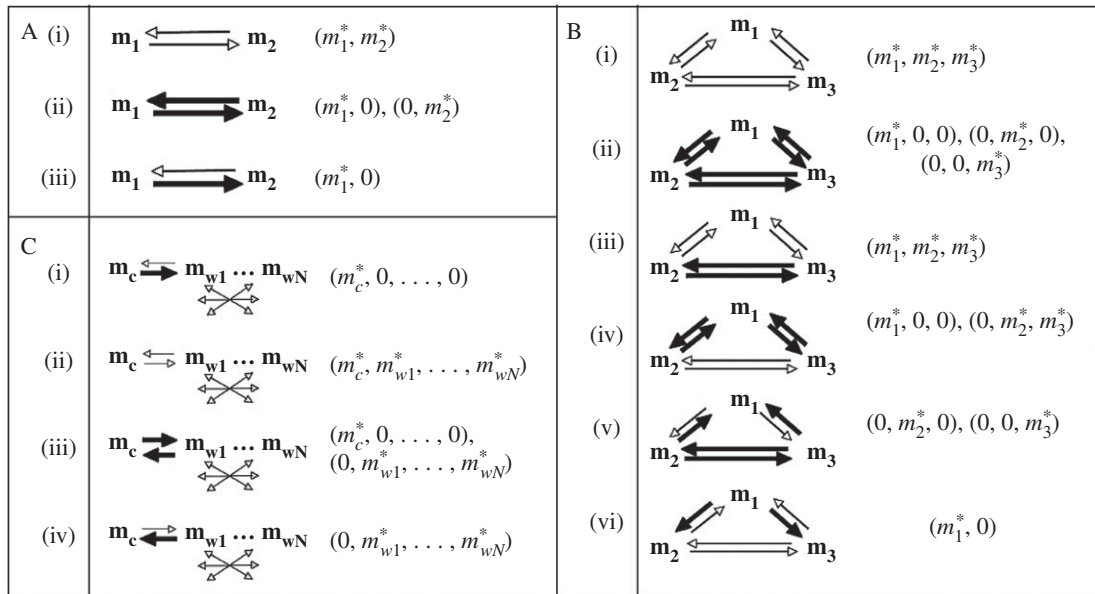


Figure 1. Representation of the direct interactions between fungal species (m_i) sharing a resource supplied by the same host plant (not included in the figure), and corresponding steady state stability (presented in the electronic supplementary material). Arrows indicate competition between mutualists where competition can be weak (thin arrows) or strong (thick arrows).

is proportional to both, plant and fungal biomass. We write

$$f_{hp}(p, m_j), f_{hm_j}(p, m_j) \propto m_j \frac{p}{d+p}, \quad \text{and} \quad f_{cm_j}(p, m_j), f_{cp}(p, m_j) \propto m_j p. \quad (2.2)$$

The complete forms of the $f(\cdot, \cdot)$ and $r(\cdot, \cdot)$ functions are given in the electronic supplementary material (equation (6)).

(c) Competitive interactions between arbuscular mycorrhizal fungi

Competition between fungal species reduces the amount of carbon received/supplied in a way that depends on the specific community composition, where

$$C(m_j, m_i) = 1 - \frac{\sum_{i \neq j} m_i}{a_j + \sum_{i \neq j} m_i}. \quad (2.3)$$

When only one fungal species is present, $C(m_j, m_i)$ is equal to 1 and equation (2.1) reduces to the original model of Martignoni *et al.* [43]. When two or more species are present, competition between fungi reduces the carbon uptake capacity of each of the fungal species. The value of a_j determines how the presence of other fungal mutualists in the community influences the carbon uptake capacity, and therefore the growth, of species j .

The literature shows that competition between fungi, for example for access to plant roots, can limit fungal growth in a way that depends on both the species present and their abundance [44–46]. To determine a_j , we assume that each of the fungal species present has a direct negative effect on the growth rate of other fungi that depends on its identity, determining the strength of the competitive interaction between those two species, and depending on the mass proportion occupied by the competitor. Hence, we define a_j as the mean competition strength experienced by species j , where the competitive strength of each paired interaction is weighted by the proportion, in terms of biomass, that each species occupies

within the competing community. We write

$$a_j = \sum_{i \neq j} a_{ij} \frac{m_i}{\sum_{i \neq j} m_i}. \quad (2.4)$$

The a_{ij} parameter determines how much the biomass of species i affects the carbon uptake capacity of species j . Competition between species i and j constitutes two reciprocal interactions quantified by a_{ij} and a_{ji} .

We will study the system of equation (2.1) through linear analysis and numerical simulations (performed with the ODE solver ode45 of the software Matlab R2017a). We will consider multiple scenarios (see figure 1 for a summary), but we will discuss only the most ecologically relevant cases. To understand the impact of alien species invasion on plant biomass we will simulate plant growth over time for different combinations of the initial biomass of the introduced species (propagule pressure) and of the existing community.

3. Results

The stability analysis of equation (2.1) is presented in detail in the electronic supplementary material, and summarized in figure 1. Below, we present the key ecological insights emerging from the mathematical results.

(a) Mutualism promotes coexistence among competitors

Coexistence of two mutualists (m_1 and m_2) is observed if competition between the two species is weak, while competitive exclusion occurs when competition is strong (case A of figure 1). This outcome is similar to the output of classical competition models [47], that predict coexistence of weak competitors and competitive exclusion of strong competitors.

The presence of a third species (m_3) that competes only weakly with the other two mutualists, can change the exclusion scenario to one of coexistence (case B(iii) of figure 1).

More specifically, indirect interactions are created that promote the coexistence of two strong competitors that would otherwise competitively exclude each other. The growth of the weak competitor (m_3) is not significantly reduced by the presence of the other mutualists in the guild, and m_3 improves the growth of the associated plant (p). An increase in plant biomass corresponds to an increase in resource availability for all mutualists present, with a consequent reduction in competition strength between m_1 and m_2 , allowing their coexistence (indeed a_1 and a_2 in equation (2.4) increase in the presence of m_3). This scenario is illustrated in the electronic supplementary material, figure S4.

(b) Alien species introduction and invasion success

The different possible outcomes, following the introduction of an alien mutualist in a guild, are summarized in figure 2. Four possible scenarios can be observed: (1) the alien species displaces the native community, (2) the alien species coexists with the native community, (3) either the alien or the native community is competitively excluded, depending on their initial biomasses, or (4) establishment of the alien species is prevented by the presence of a native community. Which scenario occurs depends on the competition strength between the alien mutualist and the native community, corresponding to the horizontal and vertical axes of figure 2 (parameters a_{wc} and a_{cw}). Small a parameters indicate strong competitive interactions, while large a parameters indicate weak competition. The values a_{wc}^* and a_{cw}^* determine the thresholds above and below which the different scenarios (1)–(4) occur.

If a weak competitor is added to a guild (figure 2, right column), two outcomes are possible: either the new species establishes and coexists with the community (scenario (2), top), or it is competitively excluded by the native community (scenario (4), bottom). Coexistence is achieved when competition between the alien mutualist and the community is weak (i.e. $a_{cw} > a_{cw}^*$ and $a_{wc} > a_{wc}^*$). Exclusion is the outcome when the community competes strongly with the introduced mutualist (i.e. $a_{cw} > a_{cw}^*$ and $a_{wc} < a_{wc}^*$). If competition between the introduced species and the community is strong in both directions (i.e. $a_{cw} < a_{cw}^*$ and $a_{wc} < a_{wc}^*$), the existing community is displaced by the strong competitor or the community persists and the new species is driven to extinction (scenario (3)). The outcome depends strongly on the initial biomass of the introduced species (propagule pressure) and of the biomass and diversity of the existing fungal community (electronic supplementary material, figure S5). Finally, if the introduced species is a strong competitor but the community competes only weakly against it (i.e. $a_{cw} < a_{cw}^*$ and $a_{wc} > a_{wc}^*$), the introduced mutualist will competitively exclude all of the other guild members (scenario (1) in figure 2), independent of its initial biomass.

The minimal competition strength needed in the community to overcome an invasion of the alien species, i.e. the value of a_{wc}^* determining whether scenario (1) or scenario (3) occurs, can be computed as

$$a_{wc}^* = \frac{\rho_w(\alpha_c/\beta_c)}{1 - \rho_w(\alpha_c/\beta_c)} \sum_{j=1}^N m_{wj}^* \quad (3.1)$$

where $\sum_j m_{wj}^*$ represents the total biomass of the native community, α_c/β_c is the ratio of phosphorus to carbon exchange capacity of the alien species and ρ_w is a constant that depends

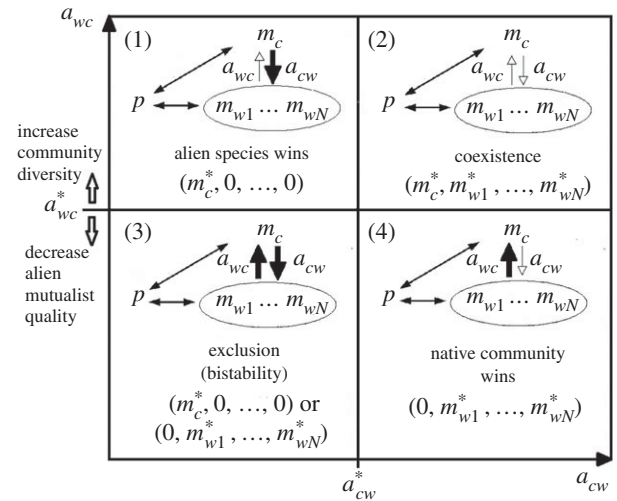


Figure 2. Representation of the possible outcomes following the introduction of an alien species into a guild of coexisting mutualists. The diagrams represent the direct interactions between the plant (p), its mutualist guild (m_{w1}, \dots, m_{wN}) and the introduced mutualist (m_c), where plant–fungi interactions are mutualistic, while interactions among fungal species are competitive. Arrow thickness represents the strength of the interactions. In the figure, competition between the introduced mutualist and the guild (parameters a_{wc} and a_{cw}) is varied along a gradient of strong competition (a 's parameters are small) to weak competition (a 's parameters are large). The critical values a_{wc}^* and a_{cw}^* define the boundary between the occurrence of the different scenarios, and depend on diversity in the native community and on the mutualist quality of the introduced species.

on the plant biomass and on the characteristics of the native community (explicitly stated in equation (33) of the electronic supplementary material). As long as $a_{wc} < a_{wc}^*$, extinction of the native community is unlikely to happen (cf. scenarios (3) and (4)). A large a_{wc}^* indicates, therefore, a more stable community. From equation (3.1) we can see that a_{wc}^* increases with increasing total biomass of the native community, and decreases for decreasing mutualist quality of the introduced species (i.e. for smaller α_c/β_c). Hence diversity increases the resilience of the guild against invasion (electronic supplementary material, figure S5), and cheaters are more likely to invade (electronic supplementary material, figure S6).

(c) The impact of invasion on resource availability (i.e. plant biomass)

To understand how plant biomass is affected by the introduction of an alien mutualist, we look at the evolution dynamics of an ecosystem composed of a plant, a native guild of two coexisting fungal species, and an introduced species, where competition between the introduced species and the native fungi is either strong (figure 2, scenario (2)) or weak (scenario (3)).

The introduction of a weak competitor in the guild results in the establishment of the introduced species and its coexistence with the rest of the community (figure 2, scenario (2)). In this case, the addition of a new species increases both plant growth rate and final plant biomass (electronic supplementary material, figure S2). If the introduced species is a strong competitor (scenario (3)), the consequences on plant growth (and therefore on resource availability) depend largely on the initial biomass of the introduced species and on the total biomass of the native community (figure 3). If

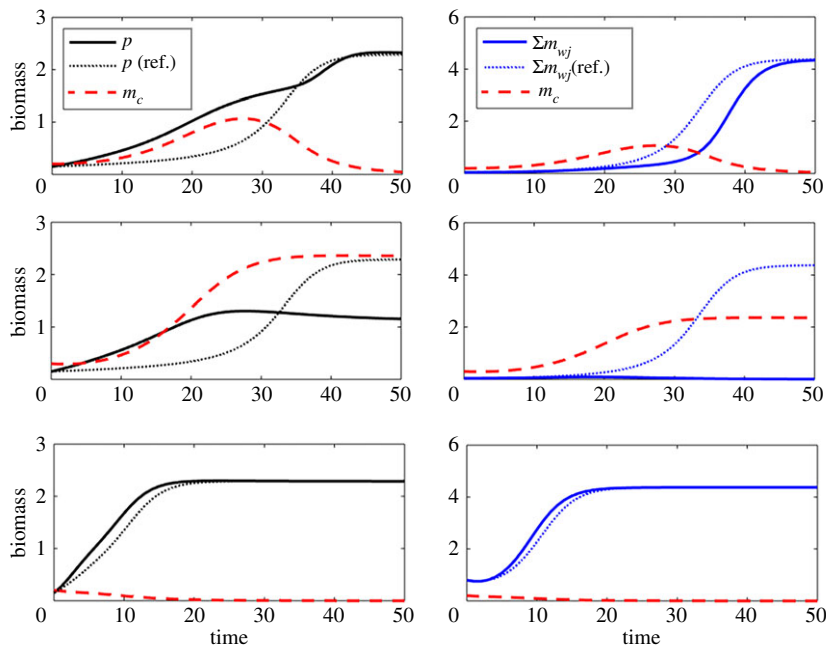


Figure 3. Plant biomass (left panels, solid black lines) and fungal biomass over time (right panels, solid blue lines) in response to the addition of an alien species that is a strong competing mutualist (dashed red lines) to the native community, for the situation corresponding to scenario (3) of figure 2. The dotted lines show plant growth (left panels) and fungal growth (right panels) in the absence of the introduced species. Simulations were run with a guild of two native species (i.e. $n = 2$). In the top panels, the biomass of the introduced species is too low to guarantee persistence ($m_c = 0.2$, $2 m_{wj} = 0.04$). In the middle panels, the alien species establishes and displaces the native community ($m_c(0) = 0.3$, $2 m_{wj}(0) = 0.04$). In the bottom panels, the initial biomass of native fungi is much larger than the alien propagule biomass, and species introduction has a very little effect on plant and fungal growth ($m_c(0) = 0.2$, $2 m_{wj}(0) = 0.8$). The plant initial biomass used for the simulations is $p(0) = 0.15$, competition parameters are $a_{ww} = 2.2$, $a_{cw} = a_{wc} = 0.3$. Other parameters correspond to those for the electronic supplementary material, figure S6. (Online version in colour.)

initially the biomass of the community is low, the addition of a new species initially speeds up plant growth, and at the same time reduces the growth rate of the community of mutualists (see figure 3, top two rows). When the initial biomass of the introduced species is not large enough to guarantee persistence, the community will displace the strong competitor, with no consequences on final plant and fungal biomass in the long term (figure 3, top row). When the introduced species can persist, the native community will be displaced with negative consequences on the plant final biomass (figure 3, middle row). If initially the total biomass of the community is large, the effect of the introduced species on the plant and fungal growth rates is minimal (figure 3, bottom row). In this case, the introduced species cannot establish, therefore not affecting the final biomass reached by the plant or by the fungal community.

4. Discussion

(a) Mutualism promotes coexistence among competitors

We suggest that the presence of a weak competing mutualist within a guild can indirectly facilitate the coexistence of species that would otherwise competitively exclude each other. If all guild members depend on the resource provided by a single plant, the presence of a weak competitor increases plant biomass and therefore resource availability. Increasing the amount of resource available leads to a consequent reduction in competition among other mutualists present.

It has been acknowledged that the presence of particular species in a community can enhance resource availability and

provide habitat to the establishment of other organisms that could not have otherwise survived [48,49]. More specifically, the role of mutualism in mediating competition and enhancing diversity has also been noted experimentally [50–52]. However, very few models have dealt with this issue [40]. We find that the removal of a key species, such as a weak competitor from a community of strongly competing mutualists (e.g. species m_3 in the electronic supplementary material, figure S4), may cause the extinction of other species in the guild (e.g. species m_1 or species m_2 in the electronic supplementary material, figure S4).

(b) Predicting the invasion success of an alien mutualist

In our results, we formulate testable predictions on biological invasion in mutualist guilds. We disentangle the effect of competition, propagule pressure and traits of the alien mutualist and the recipient community, in determining the establishment of an introduced species. We found that if competition between the introduced species and the existing community is weak, e.g. owing to functional complementarity among species, the alien species will establish and coexist with the rest of the community (scenario (2) in figure 2). In agreement with our findings, niche opportunities have already been identified as important drivers of invasion success [10,53].

We show that if competition between the alien species and the existing community is strong, coexistence is not possible (scenario (3) in figure 2). The introduced species will either competitively exclude the whole community, or fail to persist. Simulations show that when the native community has a large biomass, establishment of the alien species is unlikely. However, when the biomass of the native community is low, establishment of the alien species occurs when its initial

biomass is large enough. Hence, the biomass of the native community at the time of introduction of the alien species and the propagule pressure of the alien species are key factors determining invasion success. The literature shows that early arrivals can establish and colonize available resources, and prevent their exploitation by late arrivals. This phenomenon has been observed for competitors in general [54,55], as well as in the context of mutualistic communities [56–58]. Priority effects can therefore play a fundamental role in creating invasion opportunities for competitors. Our model supports this finding, as early arrivals have time to increase their biomass, and by doing so, gain a competitive advantage over an introduced species.

We found that the most worrisome scenario occurs when the competitive ability of the introduced species is largely superior than that of the existing community (scenario 1) in figure 2). In this case, the alien species invades and displaces the existing guild, independent of its propagule pressure. The literature has reported cases where the introduction of a strong competing alien pollinator, sharing nesting and floral resources with native species, causes the decline or extinction of native pollinators [59,60]. We show that invasion is more likely to occur when the alien species has low mutualist quality, and when diversity in the existing community is low. In the model, weak competitors, e.g. species occupying different niches, do not significantly hinder each others' growth. Hence, the biomass of a group of weak competitors increases much faster than the biomass of a single species, even when the species in question is a strong competitor. A larger biomass provides a competitive advantage to the coexisting community, by preventing access by the introduced species to the common resource. The larger the number of weak competitors (e.g. functionally different species), the faster the growth in terms of total biomass, and the easier it becomes to outcompete a strong competitor. A large community can therefore prevent the invasion of a strong competitor in cases where a smaller community would be competitively excluded.

Whether diversity promotes resilience of a community has been a frequent matter of debate in recent decades [61]. Generally, similarly to our predictions, functional complementary is reputed to lead to a better use of the resource available, what is directly related to fitness of a community, and therefore to higher resistance to disturbance [62,63]. However, empirical observations have been inconsistent [64–66]. In particular, the role of species identity in promoting or opposing invasion is still under investigation [67]. Our work adds further theoretical evidence in support of diversity promoting resilience, this time in the specific context of a community of mutualists. We say that a diverse community can efficiently monopolize the available resource, in a way that makes it more resilient to invasion by a strong competitor.

(c) The impact of invasion on productivity

Although the short-term effect of the introduction of an alien species on plant growth can be extremely positive, the situation changes when looking at its long-term consequences. The introduction of a mutualist that is a weak competitor (e.g. a species whose function is complementary to the native community) can result in an overall positive effect on both plant growth rate and final size. However, the introduction of a highly competitive species and its permanent establishment may result in

an initial increase in the plant growth rate, but also in the subsequent displacement of native species, with a consequent decrease in final plant size (figure 3).

Experimental studies show that it is not clearly understood whether the short term positive effects on productivity are related to diversity by itself, or are rather owing to a general increase in the abundance of mutualists [68,69]. Our predictions suggest that abundance, and not diversity, is positively related to plant growth rate on a short time scale. Long-term productivity and resilience are increased by diversity in the mutualist community. In order to assess the impact of alien species introduction on productivity, field studies should take into account the long-term abundance and diversity of the existing fungal community.

(d) Future work

The model presented in this article sheds light on the mechanisms behind the stability of mutualistic communities. Our results have direct implications for conservation biology, by providing insights into the possible consequences of species manipulation among a group of mutualists depending on the same resource, such as below-ground microbial communities or pollinators [70–72]. For example, our model could be used to investigate the consequences for fungal diversity and plant productivity following the introduction of commercially grown AM fungi, commonly used as organic fertilizers [73]. The scientific community has raised important concerns about the potential invasiveness of these commercial fungi, and their possible detrimental consequences on productivity [74–77]. However, the invasion risk has never been fully assessed. Because the model is based on a consumer-resource framework for mutualistic interactions [78], simulations predicting the output of competition within a guild are easily testable in an experiment.

Fungal species or pollinators can often associate simultaneously with multiple different plants. To better simulate this real world scenario, our model should be extended to multiple possible partners. Considering associations with multiple different plants could, for example, answer questions related to the impact of plant diversity on pollination services and productivity [79], or give insights into community assemblage and invasion dynamics in forests or agroecosystems [80,81].

Spatial factors may play an important role in invasion dynamics, or in creating heterogeneous patterns of guild and host persistence [82–85]. Future modelling efforts should therefore focus on the development of a spatially explicit version of the model.

Data accessibility. This article has no additional data.

Authors' contributions. M.M.M. was the lead investigator, responsible for the major areas of model development, analysis and interpretation, as well as manuscript composition. R.C.T. and J.G. were involved throughout the project providing constant supervision and mentoring of the theoretical aspect of the project. M.M.H. provided supervisory support to the ecological aspect of the project. M.M.H., R.C.T. and J.G. all significantly contributed to manuscript edits.

Competing interests. We declare we have no competing interest.

Funding. J.G. acknowledges NONLOCAL project (ANR-14-CE25-0013), GLOBNETS project (ANR-16-CE02-0009) and the European Research Council (ERC) under the European Unions Horizon 2020 research and innovation programme (grant agreement no. 639638, MesoProbio). M.M.H. acknowledges the NSERC Discovery grant. R.C.T. acknowledges NSERC Discovery grant no. RGPIN-2016-05277 and the 'Make our planet great again (MOPGA)' grant.

References

- Lockwood JL, Hoopes MF, Marchetti MP. 2013 *Invasion ecology*. New York, NY: John Wiley & Sons.
- Cardinale BJ *et al.* 2012 Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67. (doi:10.1038/nature11148)
- Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J. 2013 Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecol. Evol.* **3**, 182–196. (doi:10.1002/ece3.431)
- Vanbergen AJ, Espindola A, Aizen MA. 2018 Risks to pollinators and pollination from invasive alien species. *Nat. Ecol. Evol.* **2**, 16–25. (doi:10.1038/s41559-017-0412-3)
- Williamson M, Griffiths B. 1996 *Biological invasions*. London, UK: Chapman and Hall.
- Lonsdale WM. 1999 Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–1536. (doi:10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2)
- Olyarnik SV, Bracken ME, Byrnes JE, Hughes AR, Hultgren KM, Stachowicz JJ. 2009 Ecological factors affecting community invasibility. In *Biological invasions in marine ecosystems* (eds G Rilov, JA Crooks), pp. 215–238. Berlin, Germany: Springer.
- Fournier A, Penone C, Pennino MG, Courchamp F. 2019 Predicting future invaders and future invasions. *Proc. Natl Acad. Sci. USA* **116**, 7905–7910. (doi:10.1073/pnas.1803456116)
- Kolar CS, Lodge DM. 2001 Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**, 199–204. (doi:10.1016/S0169-5347(01)02101-2)
- Shea K, Chesson P. 2002 Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* **17**, 170–176. (doi:10.1016/S0169-5347(02)02495-3)
- Lockwood JL, Cassey P, Blackburn T. 2005 The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* **20**, 223–228. (doi:10.1016/j.tree.2005.02.004)
- Simberloff D. 2009 The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Syst.* **40**, 81–102. (doi:10.1146/annurev.ecolsys.110308.120304)
- Davis MA, Grime JP, Thompson K. 2000 Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* **88**, 528–534. (doi:10.1046/j.1365-2745.2000.00473.x)
- Sher AA, Hyatt LA. 1999 The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biol. Invasions* **1**, 107–114. (doi:10.1023/A:1010050420466)
- Funk JL, Vitousek PM. 2007 Resource-use efficiency and plant invasion in low-resource systems. *Nature* **446**, 1079–1081. (doi:10.1038/nature05719)
- Pyšek P, Richardson DM. 2008 Traits associated with invasiveness in alien plants: where do we stand? In *Biological invasions* (ed. W Nentwig), pp. 97–125. Berlin, Germany: Springer.
- Dethier MN, Hacker SD. 2005 Physical factors vs. biotic resistance in controlling the invasion of an estuarine marsh grass. *Ecol. Appl.* **15**, 1273–1283. (doi:10.1890/04-0505)
- Menke SB, Holway DA. 2006 Abiotic factors control invasion by Argentine ants at the community scale. *J. Anim. Ecol.* **75**, 368–376. (doi:10.1111/j.1365-2656.2006.01056.x)
- Byers JE. 2002 Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia* **130**, 146–156. (doi:10.1007/s004420100777)
- Williamson J, Harrison S. 2002 Biotic and abiotic limits to the spread of exotic revegetation species. *Ecol. Appl.* **12**, 40–51. (doi:10.1890/1051-0761(2002)012[0040:BAALTT]2.0.CO;2)
- White EM, Wilson JC, Clarke AR. 2006 Biotic indirect effects: a neglected concept in invasion biology. *Divers. Distrib.* **12**, 443–455. (doi:10.1111/j.1366-9516.2006.00265.x)
- Didham RK, Tylianakis JM, Gemmill NJ, Rand TA, Ewers RM. 2007 Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22**, 489–496. (doi:10.1016/j.tree.2007.07.001)
- Goldstein LJ, Suding KN. 2014 Applying competition theory to invasion: resource impacts indicate invasion mechanisms in California shrublands. *Biol. Invasions* **16**, 191–203. (doi:10.1007/s10530-013-0513-0)
- Byun C, de Blois S, Brisson J. 2015 Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion. *Oecologia* **178**, 285–296. (doi:10.1007/s00442-014-3188-z)
- Gurevitch J, Fox G, Wardle G, Taub D. 2011 Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecol. Lett.* **14**, 407–418. (doi:10.1111/j.1461-0248.2011.01594.x)
- Lewis MA, Petrovskii SV, Potts JR. 2016 *The mathematics behind biological invasions*, vol. 44. Berlin, Germany: Springer.
- Bray SR, Fan Y, Wang B. 2019 Phase transitions in mutualistic communities under invasion. *Phys. Biol.* **16**, 045001. (doi:10.1088/1478-3975/ab0946)
- Minoarivelo H, Hui C. 2016 Trait-mediated interaction leads to structural emergence in mutualistic networks. *Ecol. Evol.* **30**, 105–121. (doi:10.1007/s10682-015-9798-z)
- Minoarivelo HO, Hui C. 2016 Invading a mutualistic network: to be or not to be similar. *Ecol. Evol.* **6**, 4981–4996. (doi:10.1002/ece3.2263)
- Traveset A, Richardson DM. 2014 Mutualistic interactions and biological invasions. *Annu. Rev. Ecol. Syst.* **45**, 89–113. (doi:10.1146/annurev-ecolsys-120213-091857)
- Palmer TM, Stanton ML, Young TP. 2003 Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. *Am. Nat.* **162**, S63–S79. (doi:10.1086/378682)
- Douds Jr DD, Millner PD. 1999 Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. *Agric. Ecosyst. Environ.* **74**, 77–93. (doi:10.1016/S0167-8809(99)00031-6)
- Verbruggen E, Van Der HEIJDEN MG, Weedon JT, Kowalchuk GA, Røling WF. 2012 Community assembly, species richness and nestedness of arbuscular mycorrhizal fungi in agricultural soils. *Mol. Ecol.* **21**, 2341–2353. (doi:10.1111/j.1365-294X.2012.05534.x)
- Button L, Elle E. 2014 Wild bumble bees reduce pollination deficits in a crop mostly visited by managed honey bees. *Agric. Ecosyst. Environ.* **197**, 255–263. (doi:10.1016/j.agee.2014.08.004)
- Sardiñas HS, Kremen C. 2015 Pollination services from field-scale agricultural diversification may be context-dependent. *Agric. Ecosyst. Environ.* **207**, 17–25. (doi:10.1016/j.agee.2015.03.020)
- Bronstein JL. (ed.) 2015 *Mutualism*. New York, NY: Oxford University Press.
- Charlebois JA, Sargent RD. 2017 No consistent pollinator-mediated impacts of alien plants on natives. *Ecol. Lett.* **20**, 1479–1490. (doi:10.1111/ele.12831)
- Morales CL, Traveset A. 2009 A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* **12**, 716–728. (doi:10.1111/j.1461-0248.2009.01319.x)
- Xu W, Mage JA. 2001 A review of concepts and criteria for assessing agroecosystem health including a preliminary case study of southern Ontario. *Agric. Ecosyst. Environ.* **83**, 215–233. (doi:10.1016/S0167-8809(00)00159-6)
- Bever J. 1999 Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecol. Lett.* **2**, 52–61. (doi:10.1046/j.1461-0248.1999.21050.x)
- Bever JD. 2002 Host-specificity of AM fungal population growth rates can generate feedback on plant growth. *Plant Soil* **244**, 281–290. (doi:10.1023/A:1020221609080)
- Smith SE, Read DJ. 2010 *Mycorrhizal symbiosis*, 3rd edn. New York, NY: Academic Press.
- Martignoni MM, Tyson RC, Hart MM. Submitted. Parasitism within mutualist guilds explains the maintenance of diversity in multi-species mutualisms.
- Engelmoer DJ, Behm JE, Toby Kiers E. 2014 Intense competition between arbuscular mycorrhizal mutualists in an *in vitro* root microbiome negatively affects total fungal abundance. *Mol. Ecol.* **23**, 1584–1593. (doi:10.1111/mec.12451)
- Hepper CM, Azcon-Aguilar C, Rosendahl S, Sen R. 1988 Competition between three species of *Glomus* used as spatially separated introduced and indigenous mycorrhizal inocula for leek (*Allium porrum* L.). *New Phytol.* **110**, 207–215. (doi:10.1111/j.1469-8137.1988.tb00254.x)
- Mummy DL, Antunes PM, Rillig MC. 2009 Arbuscular mycorrhizal fungi pre-inoculant identity determines community composition in roots. *Soil*

- Biol. Biochem.* **41**, 1173–1179. (doi:10.1016/j.soilbio.2009.02.027)
47. Volterra V. 1928 Variations and fluctuations of the number of individuals in animal species living together. *ICES J. Mar. Sci.* **3**, 3–51. (doi:10.1093/icesjms/3.1.3)
48. Floerl O, Inglis GJ. 2005 Starting the invasion pathway: the interaction between source populations and human transport vectors. *Biol. Invasions* **7**, 589–606. (doi:10.1007/s10530-004-0952-8)
49. Schwindt E, Iribarne OO. 2000 Settlement sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. *Bull. Mar. Sci.* **67**, 73–82.
50. Aschehoug ET, Callaway RM. 2015 Diversity increases indirect interactions, attenuates the intensity of competition, and promotes coexistence. *Am. Nat.* **186**, 452–459. (doi:10.1086/682901)
51. Schmitt RJ, Holbrook SJ. 2003 Mutualism can mediate competition and promote coexistence. *Ecol. Lett.* **6**, 898–902. (doi:10.1046/j.1461-0248.2003.00514.x)
52. Siefert A, Zillig KW, Freisen ML, Strauss SY. 2019 Mutualists stabilize the coexistence of congeneric legumes. *Am. Nat.* **193**, 200–212. (doi:10.1086/701056)
53. Vall-Iloera M, Llimona F, de Cáceres M, Sales S, Sol D. 2016 Competition, niche opportunities and the successful invasion of natural habitats. *Biol. Invasions* **18**, 3535–3546. (doi:10.1007/s10530-016-1246-7)
54. Schantz MC, Sheley RL, James JJ. 2015 Role of propagule pressure and priority effects on seedlings during invasion and restoration of shrub-steppe. *Biol. Invasions* **17**, 73–85. (doi:10.1007/s10530-014-0705-2)
55. Wainwright CE, Wolkovich EM, Cleland EE. 2012 Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *J. Appl. Ecol.* **49**, 234–241. (doi:10.1111/j.1365-2664.2011.02088.x)
56. Kennedy PG, Bruns TD. 2005 Priority effects determine the outcome of ectomycorrhizal competition between two *Rhizopogon* species colonizing *Pinus muricata* seedlings. *New Phytol.* **166**, 631–638. (doi:10.1111/j.1469-8137.2005.01355.x)
57. Peay KG. 2018 Timing of mutualist arrival has a greater effect on *Pinus muricata* seedling growth than interspecific competition. *J. Ecol.* **106**, 514–523. (doi:10.1111/1365-2745.12915)
58. Werner GD, Kiers ET. 2015 Order of arrival structures arbuscular mycorrhizal colonization of plants. *New Phytol.* **205**, 1515–1524. (doi:10.1111/nph.13092)
59. Ings T, Ward N, Chittka L. 2006 Can commercially imported bumble bees out-compete their native conspecifics? *J. Appl. Ecol.* **43**, 940–948. (doi:10.1111/j.1365-2664.2006.01199.x)
60. Morales CL, Arbetman MP, Cameron SA, Aizen MA. 2013 Rapid ecological replacement of a native bumble bee by invasive species. *Front. Ecol. Environ.* **11**, 529–534. (doi:10.1890/120321)
61. McCann KS. 2000 The diversity–stability debate. *Nature* **405**, 228. (doi:10.1038/35012234)
62. Cardinale BJ. 2011 Biodiversity improves water quality through niche partitioning. *Nature* **472**, 86–89. (doi:10.1038/nature09904)
63. Tilman D. 2004 Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl Acad. Sci. USA* **101**, 10 854–10 861. (doi:10.1073/pnas.0403458101)
64. Fargione JE, Tilman D. 2005 Diversity decreases invasion via both sampling and complementarity effects. *Ecol. Lett.* **8**, 604–611. (doi:10.1111/j.1461-0248.2005.00753.x)
65. Levine JM. 2000 Species diversity and biological invasions: relating local process to community pattern. *Science* **288**, 852–854. (doi:10.1126/science.288.5467.852)
66. Wisser SK, Allen RB, Clinton PW, Platt KH. 1998 Community structure and forest invasion by an exotic herb over 23 years. *Ecology* **79**, 2071–2081. (doi:10.1890/0012-9658(1998)079[2071:CSAFIB]2.0.CO;2)
67. Zheng Y-L, Burns JH, Liao Z-Y, Li Y-p, Yang J, Chen Y-j, Zhang J-I, Zheng Y-g. 2018 Species composition, functional and phylogenetic distances correlate with success of invasive *Chromolaena odorata* in an experimental test. *Ecol. Lett.* **21**, 1211–1220. (doi:10.1111/ele.13090)
68. Freeman CJ, Thacker RW, Baker DM, Fogel ML. 2013 Quality or quantity: is nutrient transfer driven more by symbiont identity and productivity than by symbiont abundance? *ISME J.* **7**, 1116. (doi:10.1038/ismej.2013.7)
69. Pellegrino E, Bedini S, Avio L, Bonari E, Giovannetti M. 2011 Field inoculation effectiveness of native and exotic arbuscular mycorrhizal fungi in a Mediterranean agricultural soil. *Soil Biol. Biochem.* **43**, 367–376. (doi:10.1016/j.soilbio.2010.11.002)
70. Hanna C, Foote D, Kremen C. 2013 Invasive species management restores a plant–pollinator mutualism in Hawaii. *J. Appl. Ecol.* **50**, 147–155. (doi:10.1111/1365-2664.12027)
71. Ings TC, Ings NL, Chittka L, Rasmont P. 2010 A failed invasion? Commercially introduced pollinators in southern France *Apidologie* **41**, 1–13. (doi:10.1051/apido/2009044)
72. Menz MH, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW. 2011 Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends Plant Sci.* **16**, 4–12. (doi:10.1016/j.tplants.2010.09.006)
73. Gianinazzi S, Vosátka M. 2004 Inoculum of arbuscular mycorrhizal fungi for production systems: science meets business. *Can. J. Bot.* **82**, 1264–1271. (doi:10.1139/b04-072)
74. Hart MM, Antunes PM, Abbott LK. 2017 Unknown risks to soil biodiversity from commercial fungal inoculants. *Nat. Ecol. Evol.* **1**, 0115. (doi:10.1038/s41559-017-0115)
75. Ricciardi A *et al.* 2017 Invasion science: a horizon scan of emerging challenges and opportunities. *Trends Ecol. Evol.* **32**, 464–474. (doi:10.1016/j.tree.2017.03.007)
76. Schwartz MW, Hoeksema JD, Gehring CA, Johnson NC, Klironomos JN, Abbott LK, Pringle A. 2006 The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecol. Lett.* **9**, 501–515. (doi:10.1111/j.1461-0248.2006.00910.x)
77. Thomsen CN, Hart MM. 2018 Using invasion theory to predict the fate of arbuscular mycorrhizal fungal inoculants. *Biol. Invasions* **20**, 2695–2706. (doi:10.1007/s10530-018-1746-8)
78. Holland JN, DeAngelis DL. 2010 A consumer–resource approach to the density-dependent population dynamics of mutualism. *Ecology* **91**, 1286–1295. (doi:10.1890/09-1163.1)
79. Isbell F *et al.* 2017 Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.* **105**, 871–879. (doi:10.1111/1365-2745.12789)
80. Horn S, Hempel S, Verbruggen E, Rillig MC, Caruso T. 2017 Linking the community structure of arbuscular mycorrhizal fungi and plants: a story of interdependence? *ISME J.* **11**, 1400–1411. (doi:10.1038/ismej.2017.5)
81. Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P. 2003 Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* **84**, 2628–2642. (doi:10.1890/02-0136)
82. Kerr B, Riley MA, Feldman MW, Bohannan BJ. 2002 Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors. *Nature* **418**, 171–174. (doi:10.1038/nature00823)
83. Melbourne BA *et al.* 2007 Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol. Lett.* **10**, 77–94. (doi:10.1111/j.1461-0248.2006.00987.x)
84. Westphal C, Steffan-Dewenter I, Tschamtkke T. 2006 Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia* **149**, 289–300. (doi:10.1007/s00442-006-0448-6)
85. Yu DW, Wilson HB. 2001 The competition–colonization trade-off is dead; long live the competition–colonization trade-off. *Am. Nat.* **158**, 49–63. (doi:10.1086/320865)