LETTER

Recruitment facilitation can promote coexistence and buffer population growth in metacommunities

Tarik C. Gouhier,* Bruce A. Menge
and Sally D. Hacker

*Department of Zoology, 3029
Cordley Hall, Oregon State
University, Corvallis, OR 97331, USA*

*Correspondence: E-mail:
tarik.gouhier@gmail.com*

Abstract

Although positive species interactions are ubiquitous in nature, theory has generally focused on the role of negative interactions to explain patterns of species diversity. Here, we incorporate recruitment facilitation, a positive interaction prevalent in marine and terrestrial systems, into a metacommunity framework to assess how the interplay between colonisation, competition and facilitation mediates coexistence. We show that when subordinate species facilitate the recruitment of dominant species, multi-species metacommunities can persist stably even if the colonisation rate of the dominant species is greater than that of the subordinate species. In addition, recruitment facilitation can buffer population growth from changes in colonisation rates, and thus explain the paradoxical mismatch between patterns of abundance and recruitment in marine systems. Overall, our results demonstrate that recruitment facilitation can have profound effects on the assembly, dissolution and regulation of metacommunities by mediating the relative influence of local and regional processes on population abundance and species diversity.

Keywords

Buffered population growth, coexistence, competition, metacommunity, recruitment facilitation.

INTRODUCTION

A fundamental goal of ecology is to understand how species can coexist despite competing for the same set of limiting resources (Gause 1934; Hutchinson 1961; Siepielski & McPeek 2010). To resolve this apparent paradox, studies have increasingly focused on how competition and dispersal interact to maintain patterns of diversity in spatially subdivided habitats (i.e. metacommunities; Levins & Culver 1971; Hastings 1980; Tilman 1994; Chesson 2000; Leibold *et al.* 2004). Metacommunity theory has shown that competitors can coexist on a single resource as long as competitively superior (i.e. dominant) species have lower colonisation rates than competitively inferior (i.e. subordinate) species (i.e. a competition–colonisation trade-off is required; Levins & Culver 1971; Hastings 1980; Tilman 1994). This intuitive life-history trade-off promotes coexistence because subordinate species are able to escape in space from the dominant but less dispersive species. Metacommunity frameworks are thus ideal for understanding the joint effects of local species interactions and regional dispersal on patterns of diversity across spatial scales (Leibold *et al.* 2004; Holyoak *et al.* 2005).

Recent studies have extended metacommunity theory by assessing how various forms of dispersal (Holyoak *et al.* 2005; Salomon *et al.* 2010), competitive interactions (Holyoak *et al.* 2005; Calcagno *et al.* 2006) and trophic structures (Briggs & Hoopes 2004; Gouhier *et al.* 2010a; Pillai *et al.* 2010) can mediate species coexistence. However, despite their prevalence in natural ecosystems, the effect of positive interactions (i.e. facilitation) on species coexistence and diversity remains underexplored (Bertness & Callaway 1994; Hacker & Gaines 1997; Callaway *et al.* 2002; Bruno *et al.* 2003; but see Klausmeier 2001). To rectify this discrepancy, recent reviews have called for the inclusion of positive interactions into ecological theory (Bertness & Callaway 1994; Hacker & Gaines 1997; Bruno *et al.* 2003; Brooker *et al.* 2008). Here, we extend metacommunity theory to determine how regional dispersal processes interact with local facilitation and competition to mediate patterns of species diversity and population abundance.

The role of positive interactions has been particularly well documented in plant communities, where nurse plants can facilitate the establishment of heterospecific competitors by reducing the negative effects of environmental stress (Bertness & Callaway 1994; Brooker *et al.* 2008; Gross 2008). Recent theory based on this empirically observed mechanism has shown that when dominant species facilitate subordinate species by reducing their mortality rates, species-rich communities can persist on a single limiting resource (Gross 2008). Here, facilitation promotes coexistence by generating a negative feedback between competitors. When a subordinate species becomes abundant (rare), it reduces (increases) the common resource, and thus the abundance of the dominant. The reduction (increase) in the abundance of the dominant then leads to an increase (reduction) in the mortality of the subordinate, and thus allows the dominant (subordinate) to rebound (Gross 2008). Such negative feedback can also promote coexistence between competitors within a spatial arena. For instance, subordinate shrubs can promote the recruitment of dominant trees by ameliorating local environmental conditions (Gómez-Aparicio *et al.* 2004; Chaneton *et al.* 2010). Such interspecific recruitment facilitation between competitors is prevalent in both terrestrial and marine ecosystems (Halpern *et al.* 2007) and can generate a negative feedback loop that can promote coexistence by counteracting interspecific differences in competitive ability. Indeed, by displacing the subordinate locally, the dominant reduces its own subsequent recruitment and abundance at the regional scale, thus potentially allowing the abundance of the subordinate to rebound. This type of facilitation-mediated negative feedback between local and regional processes could thus promote coexistence by buffering population growth in metacommunities.

The buffering effect of facilitation-mediated negative feedbacks could also play an important role in resolving a paradoxical mismatch:

abundance of sessile organisms in rocky intertidal metacommunities along the coasts of North America and Chile often does not reflect rates of recruitment (Lagos *et al.* 2007, 2008; Broitman *et al.* 2008; Menge *et al.* 2009, 2011; Caro *et al.* 2010). Current theory addressing this mismatch predicts that high recruitment rates will generate strong negative interactions (i.e. competition and predation) that will erode the relationship between recruitment and abundance, whereas low recruitment rates will lead to weak negative interactions, and thus a stronger match between recruitment and abundance (Connolly & Roughgarden 1998, 1999; Connolly *et al.* 2001). However, field tests have shown that patterns of recruitment do not drive the strength of negative species interactions (Menge *et al.* 2004, 2011). Instead, a positive species interaction in the form of recruitment facilitation of dominant mussels by subordinate barnacles was hypothesised to buffer the abundance of mussels from variability in their own recruitment rates in an intertidal metacommunity on the West coast of the US (Menge *et al.* 2009, 2011).

Motivated by the discrepancy between classical theoretical predictions based on negative interactions and current empirical explanations based on positive interactions, we incorporated recruitment facilitation into a metacommunity model to understand how the interplay between local and regional processes mediates species coexistence. We show that recruitment facilitation has important implications for both species diversity and population abundance. First, recruitment facilitation can promote diversity by allowing stable coexistence in multi-species metacommunities even when dominant species have higher colonisation rates than subordinates. In addition, by shifting control over patterns of abundance from regional dispersal to local competitive processes, recruitment facilitation can regulate metacommunities by buffering population growth from changes in colonisation rate. Using a field-parameterised model, we validate these predictions by showing that strong levels of recruitment facilitation are required to explain the coexistence and abundance of dominant mussels and subordinate barnacles in the field. The buffering effect of recruitment facilitation could thus explain the long-standing and paradoxical mismatch between patterns of abundance and recruitment observed in natural intertidal ecosystems.

MATERIALS AND METHODS

The two-species model

To assess the effects of recruitment facilitation on species coexistence in metacommunities, we extend a patch-dynamic model that describes competition for a single resource between a dominant and a subordinate species within a spatially subdivided habitat (Levins & Culver 1971; Hastings 1980; Tilman 1994). The model assumes that competition is strictly hierarchical in that the dominant can colonise both empty patches and those occupied by the subordinate, whereas the subordinate can only colonise empty patches. This type of hierarchical structure is well suited for describing competition between sessile species with mobile dispersal stages in both terrestrial (e.g. nursery-plants and trees in steppe-woodland systems; Gómez-Aparicio *et al.* 2004; Chaneton *et al.* 2010) and marine ecosystems (e.g. mussels and barnacles in intertidal systems; Connell 1961; Paine 1966). Dispersal is assumed to be global and competitive displacement within local patches is assumed to be instantaneous. However, our model results hold when competitive displacement is gradual as well (see Appendix S1). Patches can represent either single individuals or entire

populations (Levins & Culver 1971; Tilman 1994; Calcagno *et al.* 2006).

We implement recruitment facilitation by introducing parameter f that describes the dependency of the dominant on the subordinate ($0 \leq f \leq 1$; Fig. 1; Guichard 2005). When $f = 0$, there is no recruitment facilitation, and the model becomes equivalent to classical metacommunity frameworks that describe purely hierarchical competition between a dominant and a subordinate species (Fig. 1; Levins & Culver 1971; Hastings 1980; Tilman 1994). However, recruitment facilitation ($f > 0$) increases the dependence of the dominant on the subordinate (Fig. 1a), with obligate facilitation ($f = 1$; Fig. 1c) leading to a purely facilitative model whereby the dominant can only colonise patches occupied by the subordinate. This type of positive interaction is common in wave-swept intertidal systems, where subordinate species often facilitate the recruitment of dominant species by providing them with a rugose surface to settle onto and avoid disturbance (Connell & Slatyer 1977; Berlow 1997; Halpern *et al.* 2007; Menge *et al.* 2011). More generally, this formulation of facilitation corresponds to Connell & Slatyer's (1977) classical facilitative model of succession, whereby 'early succession species' (i.e. subordinates) modify the substrate and promote the subsequent colonisation of 'late succession species' (i.e. dominants). These processes are modelled with the following set of ordinary differential equations that describe the dynamics of the dominant (species 1; N_1) and the subordinate (species 2; N_2):

$$\frac{dN_1}{dt} = c_1 N_1 (N_2 + (1-f)(1 - N_1 - N_2)) - d_1 N_1$$
$$\frac{dN_2}{dt} = c_2 N_2 (1 - N_1 - N_2) - c_1 N_1 N_2 - d_2 N_2 \tag{1}$$

Where N_i, c_i, d_i, respectively, represent the proportion of patches occupied (hereafter referred to as abundance), the colonisation rate and the mortality rate of species i, and f represents the strength of
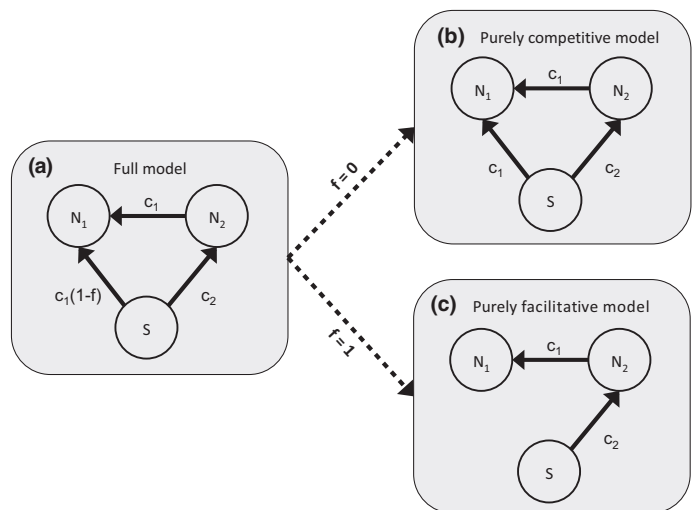

Figure 1 (a) Diagram of the recruitment facilitation model that describes competition between a dominant (N_1) and a subordinate (N_2) species for access to a limiting resource (space S) via colonisation (c_i). (b) When recruitment facilitation is nil ($f = 0$), the model becomes equivalent to the classical, purely competitive patch-dynamic frameworks that emphasise the importance of competition–colonisation trade-offs for the coexistence of competing species. (c) When recruitment facilitation is obligate ($f = 1$), the model becomes equivalent to a purely facilitative framework whereby the dominant species can only colonise patches occupied by the subordinate.

recruitment facilitation ($0 \leq f \leq 1$). The dominant can colonise all patches occupied by the subordinate (N_2) with colonisation rate c_1. The dominant can also colonise empty patches with colonisation rate c_1 depending on the strength of recruitment facilitation (i.e.,$(1-f)(1-N_1-N_2)$): reducing (increasing) f increases (reduces) the dominant's ability to colonise empty patches. Finally, the abundance of the dominant decreases because of mortality ($-d_1 N_1$). The subordinate can colonise empty patches ($1-N_1-N_2$) according to its colonisation rate c_2. The abundance of the subordinate decreases because of competitive displacement by the dominant species($-c_1 N_1 N_2$) and mortality ($-d_2 N_2$).

The multi-species model

The two-species model can be extended to understand the effects of recruitment facilitation on coexistence in metacommunities composed of S species:

$$
\frac{dN_i}{dt} = c_i N_i \left(\sum_{j=i+1}^{S} N_j + (1-f)\left(1 - \sum_{i=1}^{S} N_i\right) \right) - d_i N_i
$$

$$
- \sum_{j=1}^{i-1} c_j N_j N_i \text{ for } i = \{1, ..., S-1\} \tag{2}
$$

$$
\frac{dN_S}{dt} = c_S N_S \left(1 - \sum_{i=1}^{S} N_i \right) - d_S N_S - \sum_{j=1}^{S-1} c_j N_j N_S
$$

Where species are ranked from best (species 1) to worst (species S) based on their competitive ability, and subordinate species facilitate the recruitment of more dominant species. The abundance of species i decreases because of mortality ($-d_i N_i$) and displacement by competitively superior species ($-\sum_{j=1}^{i-1} c_j N_j N_i$), and increases via colonisation (c_i) of (1) patches occupied by subordinate species ($\sum_{j=i+1}^{S} N_j$) and (2) empty patches depending on the strength of recruitment facilitation (i.e.,$(1-f)(1 - \sum_{i=1}^{S} N_i)$). The abundance of the worst competitor (species S) decreases because of mortality ($-d_S N_S$) and displacement by competitively superior species ($-\sum_{j=1}^{S-1} c_j N_j N_S$), and increases via colonisation (c_S) of empty patches ($1 - \sum_{i=1}^{S} N_i$).

Model analysis

We used a two-pronged approach to determine the effect of recruitment facilitation on the assembly, dissolution and regulation of metacommunities. For the two-species model, we first found the equilibrium solutions of the model and determined their local stability using classical analyses. Briefly, this was done by linearising the model around each equilibrium solution, and finding the eigenvalues of the Jacobian matrix. If the real parts of all eigenvalues are negative, then the equilibrium solution is locally stable (see Appendix S2). We then determined the effects of recruitment facilitation on (1) the conditions required for coexistence and (2) population growth in response to changes in colonisation rates.

As the analytical solutions of the multi-species model are more unwieldy, we used Monte Carlo methods similar to those described by Calcagno *et al.* (2006) to determine the effect of recruitment facilitation on the probability that species randomly assembled from

the regional species pool would persist stably in a metacommunity. Specifically, to determine the probability of coexistence p_S for a metacommunity whose S species have a mortality rate of $d = 0.1$, a maximum colonisation rate of c_{max} and facilitation f, we (1) randomly drew the colonisation rate of each of the S species from a uniform distribution over the interval $(d, c_{max}]$, (2) determined the existence of a biologically relevant equilibrium solution where all species persist (i.e. all $\hat{N}_i > 0$ and $\sum_i^S \hat{N}_i < 1$) and (3) assessed the stability of this equilibrium by determining whether the real part of each eigenvalue of the Jacobian was negative. We repeated this procedure $k = 10^6$ times to determine how the number of stable and biologically relevant equilibrium solutions n_S for metacommunities composed of $S = \{2, 3, 4, 5\}$ species varied with facilitation f and maximum colonisation rate $c_{max} = \{1, 2, 5, 10\}$. We then computed the probability of coexistence as $p_S(f, c_{max}) = \frac{n_S}{k}$.

Model parameterisation and validation

To validate our predictions, we parameterised the two-species model using mortality and colonisation rates of dominant mussels (*M. trossulus* and *M. californianus*) and subordinate barnacles (*C. dalli* and *B. glandula*) observed at a field site located in central Oregon, and fit the parameterised model to a separate experimental time series (see Appendix S3 for details). Briefly, the experimental time series used to validate our model was obtained by averaging and smoothing the time series from five replicate patches that were cleared of all organisms at the onset, and tracked for a period of 2 years. We then fixed facilitation in the model at a specific level (from $f = 0$ to 1 in 0.01 increments) and applied a nonlinear optimisation method based on a simplex search algorithm (Lagarias *et al.* 1998) to find the model parameter estimates for colonisation and mortality within the range of values derived from the field (i.e. the minimum and maximum in Table C1) that minimise the difference between the model and experimental time series. We then determined the locally stable equilibrium solution for each level of facilitation using the colonisation and mortality rates selected by the optimisation method. This procedure allowed us to determine whether recruitment facilitation was required to explain (1) the patterns of abundance and (2) the coexistence of the subordinate and the dominant species given the colonisation and mortality rates measured in the field.

RESULTS

Analysis of the two-species model

The effect of recruitment facilitation on coexistence
The model presented in eq. 1 has four biologically relevant (i.e. non-negative and real) equilibrium solutions: (1) 'extinction' (both species abundances are zero), (2) 'dominant' (dominant only persists), (3) 'subordinate' (subordinate only persists) and (4) 'coexistence' (both subordinate and dominant persist). The local stability analysis of each equilibrium solution is presented in Appendix S2. Here, we focus on the interior equilibrium (i.e. the 'coexistence' solution) to assess the effect of recruitment facilitation on coexistence and population growth. At the interior equilibrium, the abundances of the dominant (species 1; $\hat{N}_1$) and the subordinate (species 2; $\hat{N}_2$) are:

$$
\hat{N}_1 = \frac{1}{1 + \frac{c_1}{c_2}f}\left(1 - \frac{d_1}{c_1} - \frac{d_2}{c_2}f\right) \tag{3a}
$$

$$\hat{N}_2 = \frac{1}{1 + \frac{c_1}{c_2}f}\left(\frac{d_1}{c_1} - \frac{1}{c_2}((c_1 + d_2)(1-f) - d_1)\right) \tag{3b}$$

Coexistence requires that $\hat{N}_1 > 0$ and $\hat{N}_2 > 0$, which occurs when:

$$c_1 > \frac{d_1}{1 - \frac{d_2}{c_2}f} \tag{4a}$$

$$c_2 > \frac{c_1((c_1 + d_2)(1-f) - d_1)}{d_1} \tag{4b}$$

In the absence of recruitment facilitation ($f = 0$), the model reduces to a purely competitive metacommunity (Fig. 1b) and the coexistence conditions in eq. 4 become (Tilman 1994; Grover 1997):

$$c_1 > d_1 \tag{5a}$$

$$c_2 > \frac{c_1(c_1 + d_2 - d_1)}{d_1} \tag{5b}$$

The condition outlined in eq. 5a states that the dominant species persists as long as its colonisation rate is greater than its mortality rate. Hence, the persistence of the dominant is solely dependent upon its own functional traits (i.e. colonisation and mortality rates). However, for the subordinate to persist, its colonisation rate must be sufficiently larger than that of the dominant to allow the subordinate to find refuge in patches that are inaccessible to the less mobile dominant (i.e. a competition–colonisation trade-off is required, as $c_2 > c_1$ is a necessary but not sufficient condition for coexistence assuming $d_1 = d_2$ in eq. 5b; Fig. 2). Therefore, the dominant species generates a 'limit to similarity' by preventing the invasion of subordinate species whose colonisation rates are not sufficiently larger than those of the dominant species (Tilman 1994; Kinzig *et al.* 1999).

By limiting the dominant species' ability to colonise empty patches, and increasing its dependence on the subordinate (Fig. 1a), recruitment facilitation ($f > 0$) increases the minimum colonisation rate required for the dominant to persist (eq. 4a; Fig. S2-1a). Thus, with recruitment facilitation, the persistence of the dominant species no longer depends solely on its own functional traits, but also on those of the subordinate species (eq. 4a). Conversely, recruitment facilitation reduces the minimum colonisation rate required for the subordinate to persist (i.e. $c_2 > c_1(1 - f)$ is a necessary but not sufficient condition for the subordinate to persist assuming $d_1 = d_2$ and $c_i \gg d_i$ in eq. 4b; Fig. 2a). Recruitment facilitation thus reduces the strength of the competition–colonisation trade-off required for the subordinate to persist by reducing the limit to similarity (eq. 4b; Fig. 2a and Fig. S2-1a). Indeed, recruitment facilitation can allow coexistence in the absence of any competition–colonisation trade-off (i.e. for $c_1 = c_2 = c$ and $d_1 = d_2 = d$) as long as:

$$1 + f < \frac{c}{d} < \frac{1 + f}{1 - f}. \tag{6}$$

Without recruitment facilitation ($f = 0$), inequality eq. 6 collapses and coexistence becomes impossible without a competition–colonisation trade-off (Fig. S2-2). Recruitment facilitation can even lead to coexistence when the colonisation rate of the dominant species is greater than that of the subordinate (i.e. $c_1/c_2 > 1$; eq. 4; Fig. 2a). Thus, with recruitment facilitation, coexistence can occur via (1) a competition–colonisation trade-off (i.e. by increasing c_2 relative to $c_1(1 - f)$), (2) via recruitment facilitation (i.e. by increasing f and thus
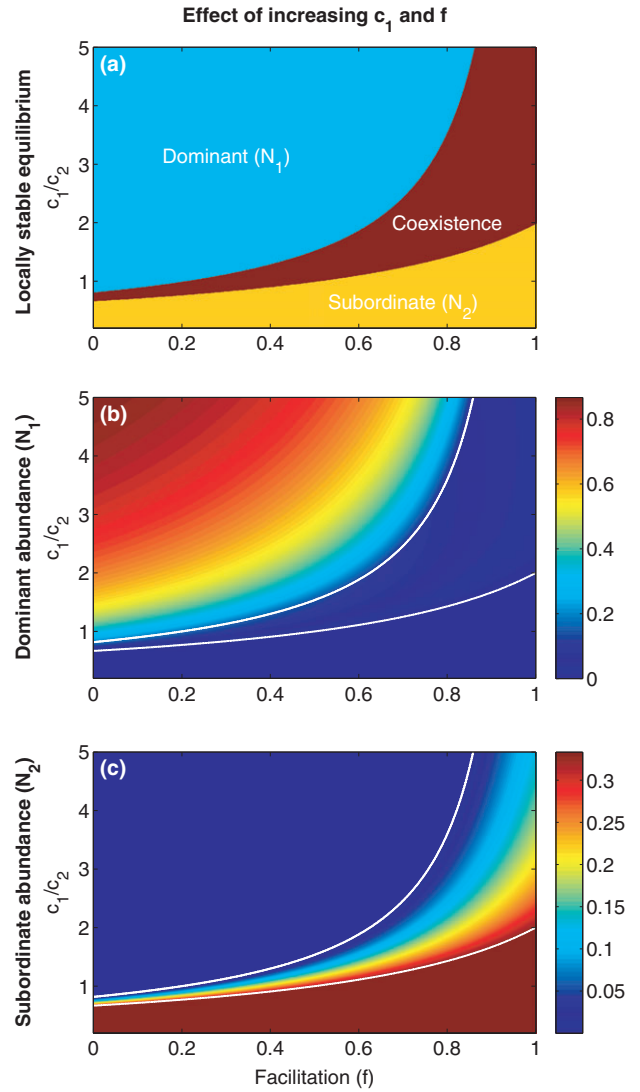
Effect of increasing c₁ and f

Figure 2 The effect of varying recruitment facilitation (f) and the colonisation rate of the dominant (c_1) on the locally stable equilibrium solution (a) and the equilibrium abundance of both the dominant (b) and the subordinate species (c). The white curves in (b) and (c) delineate regions with different locally stable equilibrium solutions. The parameter values are $c_2 = 0.3$, $d_1 = d_2 = 0.2$.

reducing $c_1(1 - f)$ relative to c_2) or (3) both (Fig. 2 and Fig. S2-1, S2-2). Overall, because recruitment facilitation reduces the minimum colonisation rate of the subordinate species faster than it increases that of the dominant species, its net effect will be to promote coexistence (Fig. 2 and Fig. S2-1). Hence, by increasing the dominant's reliance on the subordinate, recruitment facilitation shifts the burden of coexistence from the subordinate to the dominant species.

The effect of recruitment facilitation on population growth
The effects of recruitment facilitation on the equilibrium abundance of the dominant ($\hat{N}_1$) and the subordinate ($\hat{N}_2$) are straightforward and can be determined by taking their derivatives with respect to f:

$$\frac{\partial \hat{N}_1}{\partial f} = -\frac{c_2(c_1 - d_1 + d_2)}{(c_2 + c_1 f)^2} \tag{7}$$

$$\frac{\partial \hat{N}_2}{\partial f} = \frac{(c_1 + c_2)(c_1 - d_1 + d_2)}{(c_2 + c_1 f)^2} \tag{8}$$

As $c_1 > d_1 - d_2$ when both species coexist, $\frac{\partial \hat{N}_1}{\partial f} < 0$ and $\frac{\partial \hat{N}_2}{\partial f} > 0$, which means that recruitment facilitation both (i) reduces the equilibrium abundance of the dominant and (ii) increases the equilibrium abundance of the subordinate by reducing the dominant's ability to colonise empty patches (Fig. 2 and Fig. S2-1).

Recruitment facilitation has a less intuitive effect on the response of the dominant's equilibrium abundance to changes in its colonisation rate (c_1):

$$\frac{\partial \hat{N}_1}{\partial c_1} = \frac{d_1}{c_1^2} - \frac{f(c_2 + f(d_1 - d_2))}{(c_2 + c_1 f)^2} \tag{9}$$

In the absence of recruitment facilitation ($f = 0$), the dominant's equilibrium abundance will exhibit a saturating monotonic increase in response to increased colonisation (i.e. $\frac{\partial \hat{N}_1}{\partial c_1} = \frac{d_1}{c_1^2} > 0$; Fig. 3a). Indeed, as its colonisation increases, the dominant will gain access to more patches and consequently see its abundance rise. However, recruitment

facilitation ($f > 0$) will always reduce $\frac{\partial \hat{N}_1}{\partial c_1}$ because $\frac{f(c_2 + f(d_1 - d_2))}{(c_2 + c_1 f)^2} > 0$ and $c_2 > d_2$ at the interior equilibrium (eq. 9). Hence, facilitation reduces or buffers the growth in the dominant's equilibrium abundance $\hat{N}_1$ in response to increased colonisation c_1 by limiting the dominant's ability to occupy empty patches (Figs 2b and 3a vs. 3c and e). Recruitment facilitation ($f > 0$) can even lead to a seemingly paradoxical reduction in $\hat{N}_1$ in response to increased colonisation (i.e. $\frac{\partial \hat{N}_1}{\partial c_1} < 0$) when $d_1 < \frac{c_1^2 f(c_2 - d_2 f)}{c_2(c_2 + 2c_1 f)}$ (Fig. 3c and e). This occurs because recruitment facilitation forces the dominant to colonise patches occupied by the subordinate. As the dominant's colonisation rate increases relative to its mortality rate, the dominant becomes increasingly able to colonise and displace the subordinate, thus reducing the subordinate's equilibrium abundance and, ultimately, its own (Fig. 3c and e). Note that once the subordinate is competitively excluded by the dominant, this buffering effect is lost, and the equilibrium abundance of the dominant increases monotonically with its colonisation rate (Fig. 3c).

Overall, the shift from a positive to a negative relationship between the abundance and the colonisation rate of the dominant is due to the effect of recruitment facilitation on the configuration of species interactions. At low rates of recruitment facilitation, the configuration
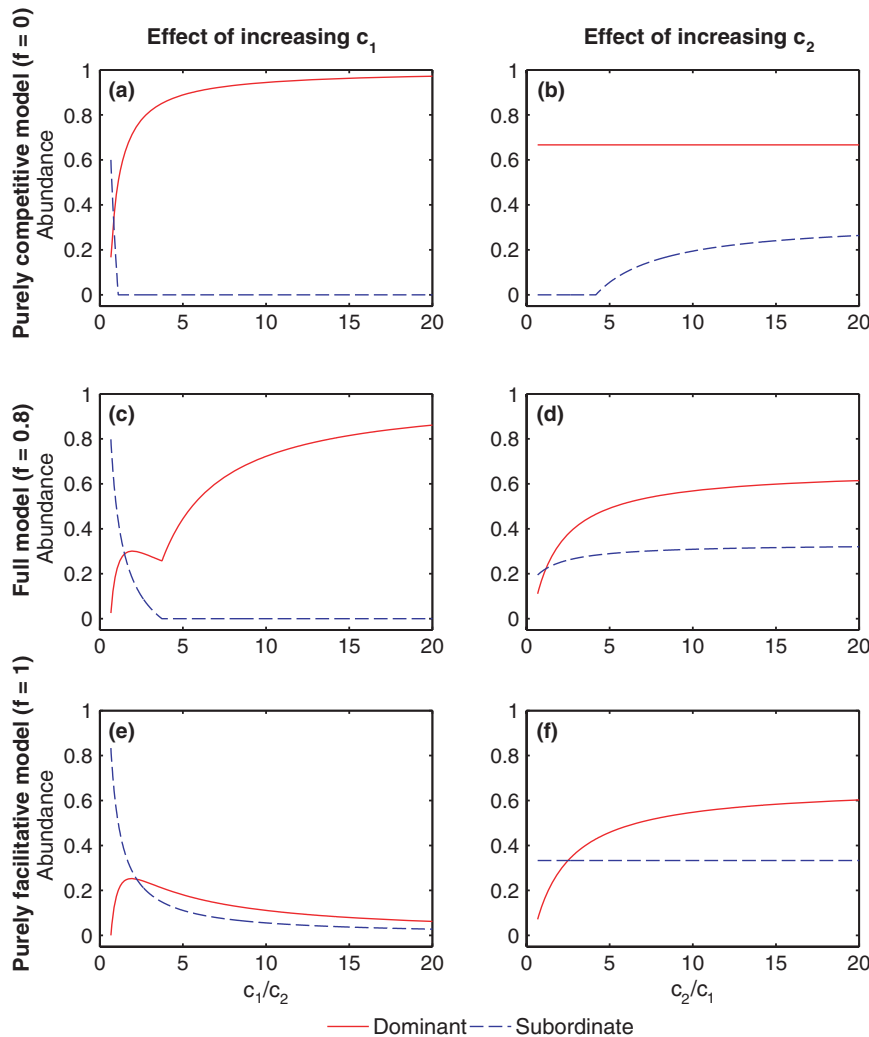

Figure 3 The effect of increasing the colonisation rate of the dominant (a, c, e) or the subordinate (b, d, f) on the equilibrium abundance of both the dominant (red full curves) and the subordinate (blue dashed curves) in the purely competitive model ($f = 0$; a, b), the full model ($f = 0.8$; c, d) and the purely facilitative model ($f = 1$; e, f). The parameter values are $c_2 = 0.6$, $d_1 = 0.2$, $d_2 = 0.1$ for panels a, c, e and $c_1 = 0.6$, $d_1 = 0.2$, $d_2 = 0.1$ for panels b, d, f.
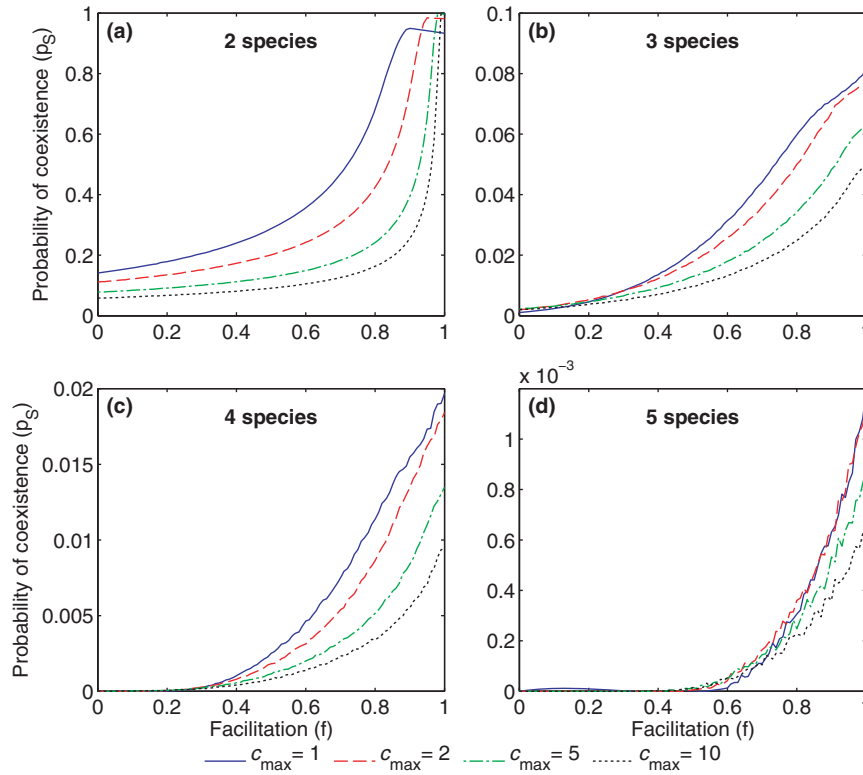
Figure 4 The effect of varying recruitment facilitation (f) and the maximum colonisation rate (c_{max}) on the probability of coexistence (p_S) for metacommunities of $S = 2$ (a), $S = 3$ (b), $S = 4$ (c) and $S = 5$ (d) species. The probability of coexistence was calculated by determining the proportion of randomly assembled metacommunities in which all species could coexist stably. These metacommunities were generated by randomly drawing the species' colonisation rates from a uniform distribution over the interval $(d, c_{max}]$. The parameter values are $d = 0.1$ and $c_{max} = 1$ (blue full curves), $c_{max} = 2$ (red dashed curves), $c_{max} = 5$ (green dash-dot curves) and $c_{max} = 10$ (black dot curves).

of species interactions is purely competitive (Fig. 1b), and so an increase in the dominant's colonisation rate will lead to a rise in its equilibrium abundance. However, at higher rates of recruitment facilitation, the configuration of species interactions more closely resembles a facilitative model where the dominant is dependent on the subordinate (Fig. 1a and c). Here, increasing the colonisation rate can reduce the dominant's abundance by reducing the abundance of the subordinate. This is akin to what happens in a predator–prey system when the predator's attack rate is raised beyond a critical threshold.

Recruitment facilitation also strongly affects the relationship between the subordinate's equilibrium abundance ($\hat{N}_2$) and its colonisation rate (c_2):

$$\frac{\partial \hat{N}_2}{\partial c_2} = \frac{(1-f)(c_1 - d_1 + d_2)}{(c_2 + c_1 f)^2} \qquad (10)$$

As $c_1 > d_1 - d_2$ at the interior equilibrium, recruitment facilitation ($f > 0$) limits the growth of the equilibrium abundance of the subordinate $\hat{N}_2$ in response to increased c_2 by reducing $\frac{\partial \hat{N}_2}{\partial c_2}$ (eq. 10; Figs 2c and 4b vs. 4d vs. 4f). This buffering effect is also due to the influence of recruitment facilitation on species interactions. By altering the configuration of species interactions from a competitive to a purely facilitative structure (Fig. 1), recruitment facilitation shifts control over the subordinate's abundance from regional supply side (i.e. colonisation c_2) to local competitive processes (i.e. displacement by the dominant) (Fig. S2-2c and Fig. 3b vs. 3d). Indeed, when recruitment facilitation is obligate ($f = 1$), $\frac{\partial \hat{N}_2}{\partial c_2} = 0$, which means that

changes in the subordinate's colonisation rate have no effect on its equilibrium abundance (eq. 10; Fig. 3f). However, under recruitment facilitation ($f > 0$), increasing the subordinate's colonisation rate always benefits the dominant species by increasing the number of patches that the latter can access (i.e. $\frac{\partial \hat{N}_1}{\partial c_2} = \frac{f(c_1 - d_1 + d_2)}{(c_2 + c_1 f)^2} > 0$ for $f > 0$ and $c_1 > d_1 - d_2$; Fig. S2-1b and Fig. 3b vs. 3d and f). Hence, recruitment facilitation can have a strong buffering effect on the abundance of the dominant and the subordinate by altering the relative importance of regional supply side and local competitive processes.

The effect of recruitment facilitation on coexistence in the multi-species model

The overall probability of coexistence decreases quasi-geometrically with species richness because of the increased dimensionality of the system (Fig. 4). However, recruitment facilitation consistently increases the probability of coexistence for metacommunities composed of two to five species (Fig. 4). The positive effect of recruitment facilitation on coexistence is stronger when the maximum colonisation rate c_{max} is low (i.e. $c_{max} = \{1, 2\}$; Fig. 4). This is because low c_{max} decreases the extent of interspecific differences in colonisation rates and thus requires lower levels of recruitment facilitation to prevent competitive exclusion due to limiting similarity (e.g. Fig. 2a). For two-species metacommunities and low c_{max}, the relationship between coexistence and recruitment facilitation is modal instead of monotonic, with coexistence reaching a plateau at high rates of
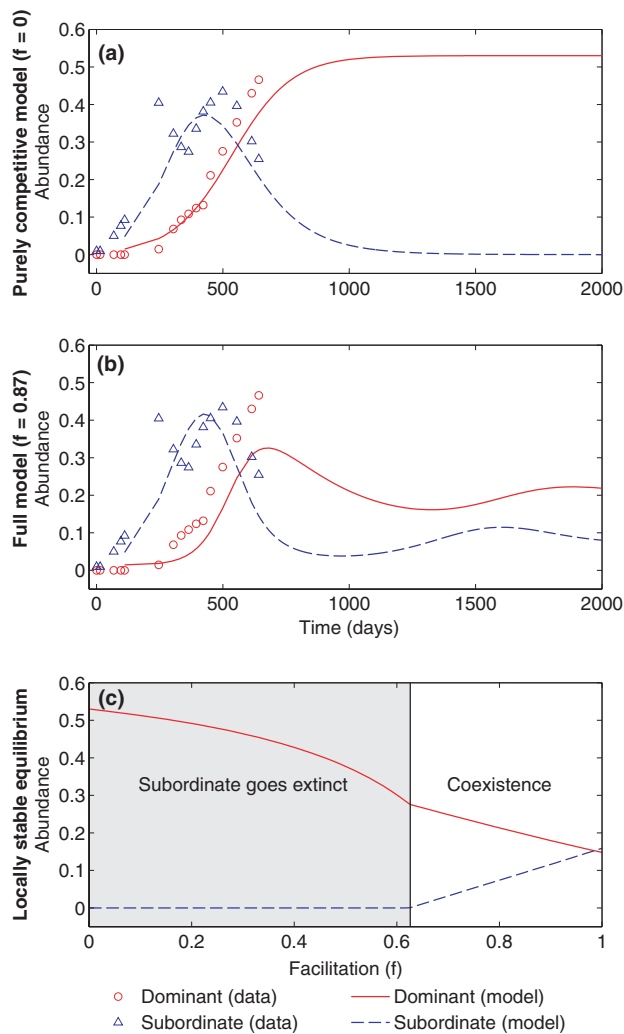
Figure 5 The effect of varying recruitment facilitation (*f*) on the dynamics (a, b) and the locally stable equilibrium (c) of the two-species model parameterised with colonisation and mortality rates observed in the field. For each level of facilitation, a nonlinear optimisation method was used to select the best colonisation and mortality rates within the range of values observed in the field to fit the model time series (curves) to the smoothed mean time series obtained from five replicate experimental patches (open circles for the dominant and open triangles for the subordinate). Coexistence occurs when recruitment facilitation is greater than ∼ 0.63 (white region in panel c), whereas the subordinate goes extinct when recruitment facilitation is lower than ∼ 0.63 (grey region in panel c). The fitted parameter values are $c_1 = 0.0159$, $c_2 = 0.0207$, $d_1 = 0.0075$, $d_2 = 0.0074$, $f = 0$ for panel A and $c_1 = 0.0382$, $c_2 = 0.0207$, $d_1 = 0.0075$, $d_2 = 0.0074$, $f = 0.8687$ for panel b. See Appendix S3 for details.

facilitation (∼ 0.8–0.9) before decreasing slightly (Fig. 4a). The slight decrease in coexistence at low c_{max} occurs because recruitment facilitation increases the minimum colonisation rate required for dominant species to persist. Hence, when c_{max} is low and recruitment facilitation is very strong, some dominant species are unable to persist and thus reduce the probability of coexistence of the metacommunity. Importantly, this reduction in coexistence is very slight and only occurs at high levels of recruitment facilitation in two-species metacommunities with low c_{max} (Fig. 4). Overall, the Monte Carlo simulations of the multi-species model echo the analytical results of the two-species model: recruitment facilitation generally promotes coexistence in metacommunities.

Validating predictions using a field-parameterised model and an experiment

To determine whether recruitment facilitation promotes coexistence and can explain the mismatch between patterns of abundance and recruitment in natural intertidal systems, we parameterised the two-species model using field-derived colonisation and mortality rates for subordinate barnacles and dominant mussels, and used a nonlinear optimisation method to find the best parameter values to fit the model to a 2-year experimental time series of barnacle and mussel abundance (see Appendix S3 for details). Our parameterised and fitted model shows that given the range of colonisation and mortality rates observed in the field, recruitment facilitation is required to explain both the patterns of abundance observed in the experimental time series and the coexistence of mussels and barnacles (Fig. 5a vs. 5b). Indeed, when recruitment facilitation is lower than a threshold value (∼ 0.63), barnacles are excluded by mussels (Fig. 5c) because the competition–colonisation trade-off is not strong enough to allow coexistence (Fig. 5a). These results, along with experiments showing that mussels almost never colonise patches from which barnacles have been removed (Menge *et al.* 2011), suggest that recruitment facilitation of mussels by barnacles occurs and promotes coexistence in nature. In addition, this empirical evidence for strong levels of recruitment facilitation in the field indicates that by buffering population growth from changes in colonisation, recruitment facilitation could explain the mismatch sometimes found between patterns of abundance and recruitment in natural intertidal systems.

DISCUSSION

We have shown that incorporating recruitment facilitation into what has traditionally been thought of as a competitive interaction can have profound effects on species coexistence and the relationship between population abundance and recruitment. Indeed, recruitment facilitation generates an interspecific dependence between dominant and subordinate species that affects the assembly and dissolution of metacommunities, and thus the maintenance of species diversity across spatial scales. Recruitment facilitation also mediates the relative influence of local species interactions and regional dispersal on the structure of metacommunities, and thus potentially resolves the paradoxical mismatch between patterns of abundance and recruitment observed in marine ecosystems.

The assembly and dissolution of metacommunities

A suite of coexistence mechanisms has been developed to explain the assembly of species-rich communities despite the prevalence of negative species interactions such as competition and predation (reviewed in Chesson (2000)). Among these mechanisms, trade-offs between functional traits have emerged as potentially important promoters of coexistence among competing species (Hastings 1980; Tilman 1994; Calcagno *et al.* 2006). In metacommunities, a trade-off between competitive ability and colonisation can promote coexistence by allowing inferior but more mobile competitors to escape from more dominant but less mobile species (Levins & Culver 1971; Hastings 1980; Tilman 1994). However, coexistence via the competition–colonisation trade-off has been criticised in the past because initial models assumed that (1) dominant species always displace subordinates regardless of the interspecific difference in competitive

ability (i.e. fully asymmetrical competition), (2) dominant species colonise patches occupied by subordinates as easily as they colonise empty patches (i.e. no pre-emption; Yu & Wilson 2001) and (3) competitive displacement occurs instantaneously (Pacala & Rees 1998). Calcagno *et al.* (2006) showed that although fully asymmetrical competition and the lack of pre-emption tend to promote coexistence, they are not absolutely necessary. Indeed, coexistence can occur via the competition–colonisation trade-off as long as competitive asymmetry is not too weak (Calcagno *et al.* 2006). Similarly, introducing pre-emption by decreasing the ability of dominant species to colonise patches occupied by subordinates generates a minimum colonisation requirement for dominant species to persist, while reducing the minimum colonisation requirement for subordinate species. Hence, increasing pre-emption shifts the burden of coexistence from the subordinate to the dominant, and its effects on coexistence will depend on the degree to which species are limited by their colonisation rates (Calcagno *et al.* 2006).

We have shown that when subordinate species facilitate the recruitment of dominants, stable coexistence can occur even when dominant species have higher colonisation rates than subordinates, regardless of the pace of competitive displacement (see Appendix S1). This occurs because, like pre-emption, recruitment facilitation shifts the burden of coexistence from subordinate to dominant species by reducing (increasing) the minimum colonisation rate of subordinate (dominant) species. Although pre-emption and recruitment facilitation have similar effects on the minimum colonisation rates, they operate differently. Pre-emption decreases (increases) the minimum colonisation rate of the subordinate (dominant) species by reducing the dominant's ability to displace the subordinate, whereas recruitment facilitation decreases (increases) the minimum colonisation rate of the subordinate (dominant) species by reducing the dominant's ability to colonise empty patches, and thus increasing the number of patches available for the subordinate. Hence, recruitment facilitation can promote coexistence (1) when dominant species always outcompete subordinate species locally and (2) in the absence of a competition–colonisation trade-off or even when species' competitive and colonisation abilities are correlated (i.e. inferior (superior) competitors are also inferior (superior) colonisers). Overall, detecting the effects of recruitment facilitation on community assembly will thus require experiments that focus on how regional recruitment depends on the local abundance of heterospecifics instead of identifying interspecific trade-offs between functional traits.

Determining the processes responsible for the assembly of metacommunities is crucial for understanding their potential dissolution in response to environmental change. Indeed, when competition is strong and coexistence requires a competition–colonisation trade-off, habitat loss can lead to the delayed extinction of more dominant but less mobile species in purely competitive metacommunities (Nee & May 1992; Tilman *et al.* 1994). However, when competition is weak and no competition–colonisation trade-off is required for coexistence, rare subordinate species will be the first to go extinct in response to habitat loss (Klausmeier 2001). Importantly, the loss of one species will not have cascading ramifications, because species do not depend on one another in purely competitive metacommunities. However, because species are interdependent in communities assembled via facilitation, the loss of a single species can lead to abrupt and cascading extinctions (Hacker & Gaines 1997; Klausmeier 2001; Gross 2008). Hence, the nature and the strength of the assembly mechanism can have important implications for the tempo and the mode of dissolution in metacommunities.

Local regulation and regional forcing in metacommunities

The nature and the strength of assembly mechanisms can also have a strong impact on the relative influence of local and regional processes on patterns of abundance in metacommunities. In marine systems, theory predicts that a latitudinal gradient in coastal upwelling currents controls larval supply and thus the strength of negative species interactions in invertebrate communities along the West coast of the United States (Connolly & Roughgarden 1998, 1999; Connolly *et al.* 2001) and Chile (Navarrete *et al.* 2005). However, surveys and experiments have revealed no clear latitudinal gradient in either the strength of species interactions or the relationship between recruitment and abundance (Menge *et al.* 2004; Gouhier *et al.* 2010b). Hence, patterns of abundance do not simply reflect the environmentally mediated latitudinal gradient in recruitment (Broitman *et al.* 2008; Caro *et al.* 2010; Gouhier *et al.* 2010b). Instead, Menge *et al.* (2011) proposed that local positive species interactions could modulate the relationship between recruitment and abundance. This hypothesis was motivated by the fact that the recruitment to collectors of the dominant mussel in this system has increased significantly in response to the recent shift in the phase of a climate index, the North Pacific Gyre Oscillation (NPGO; Di Lorenzo *et al.* 2008; Menge *et al.* 2009). Despite this strong climate-related increase in mussel recruitment and a lack of change in predation pressure, the abundance of the competitively dominant mussel changed minimally (Menge *et al.* 2009, 2011). As these observations seemingly defy metacommunity predictions based on negative interactions, the mismatch between mussel recruitment and abundance was ascribed to the potential buffering effect of a subordinate barnacle that facilitates mussel recruitment, but whose own recruitment and abundance remained unaffected by the recent shift in the phase of the NPGO (Menge *et al.* 2009, 2011).

Our model expands on this hypothesis and shows that recruitment facilitation of dominant species by subordinates can maintain coexistence and buffer metacommunities from strong increases in recruitment (> 20-fold) that would otherwise lead to the competitive exclusion of subordinate species. Importantly, this buffering effect is due to a facilitation-mediated change in the configuration of species interactions (Fig. 1). By effecting this structural change, recruitment facilitation can shift control of community structure and population abundance from regional, supply side processes driven by environmental conditions (e.g. larval supply, recruitment, colonisation) to local, competition-related processes (e.g. competitive displacement, succession). Hence, recruitment facilitation is a particularly powerful local process that can regulate patterns of abundance in metacommunities by modulating the effects of regional environmental forcing on recruitment.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Robustness of the recruitment facilitation model results to changes in the rate of competitive displacement.
Appendix S2 Local stability analysis of the recruitment facilitation model.
Appendix S3 Parameterising and validating the recruitment facilitation model using data from an intertidal ecosystem in central Oregon.

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