Competition among plant species that interact with their environment at different spatial scales

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Clonal plants that are physiologically integrated might perceive and interact with their environment at a coarser resolution than smaller, non-clonal competitors. We develop models to explore the implications of such scale asymmetries when species compete for multiple depletable resources that are heterogeneously distributed in space across two patches. Species are either ‘non-integrators’, whose growth in each patch depends on resource levels in that patch alone, or ‘integrators’, whose growth is equal between patches and depends on average resource levels across patches. Integration carried both benefits and costs. It tended to be advantageous in poorer patches, where the integrators drew resources down further than the non-integrators (more easily excluding competitors) and might persist by using resources from richer adjacent patches. Integration tended to be disadvantageous in richer patches, where integrators did not draw resources down as far (creating an opportunity for competitors) and could be excluded due to the cost of supporting growth in poorer adjacent patches. Complementarity between patches (each rich in a separate resource) favoured integrators. Integration created new opportunities for local coexistence, and for delayed susceptibility of patches to invasion, but eliminated some opportunities for regional coexistence. Implications for the interpretations of species’ zero net growth isoclines and R^* s are also discussed.

Keywords: resource competition; clonal integration; resource-ratio theory; heterogeneity; spatial scale; consumer–resource feedback

1. INTRODUCTION

Competing organisms that differ in size or mobility potentially experience (and affect) their environment at different spatial resolutions and so are likely to differ in their response to spatial heterogeneity. Consider for example competition between clonal and non-clonal plant species. Clonal plants with physiologically integrated ramets may be effectively larger than their non-clonal competitors, foraging over a larger spatial scale and ‘averaging over’ spatial heterogeneity in resource levels. The implications of resource heterogeneity and clonal integration have received a great deal of attention (e.g. reviewed by Hutchings & Wijesinghe 1997). Integration has been shown to be advantageous to plants in a number of cases (e.g. Hartnett & Bazzaz 1983; Salzman & Parker 1985; Alpert & Mooney 1986; Slade & Hutchings 1987a,c), and clonal species may play a key role in plant community responses to resource heterogeneity (Reynolds *et al.* 2007). However, the full costs and benefits of integration as a strategy remain unclear, particularly in the face of non-clonal competitors.

Multiple resources, and the explicit dynamics of those resources, are likely to be central in determining those costs and benefits. Clonal plants often benefit from ramets experiencing different resources as locally rich (e.g. Alpert & Mooney 1986; Friedman & Alpert 1991; Stuefer *et al.* 1996; van Kleunen & Stuefer 1999), and the transport of resources to and from a ramet should alter

that ramet’s capacity to draw down resources, and thus its impact on competitors. Most theoretical models exploring the implications of competition between clonal and non-clonal plants have not considered these effects, focusing instead on competition for a single, non-depletable resource and the implications of the spatial and temporal availability of sites (e.g. Oborny *et al.* 2000; Oborny & Kun 2002; Magori *et al.* 2003). Magyar *et al.* (2007) model competition between clonal and non-clonal plants for two resources, but do not include feedback of plants on resource dynamics. It remains unclear what the resource-mediated effects of clonal and non-clonal competitors on one another should be.

A framework that incorporates size asymmetries into models of competition for multiple resources has relevance beyond clonal plants. Several single-resource models have considered analogous situations where competitors (animals or plants) of different effective sizes are able to coexist as a result of differential abilities to preferentially experience higher quality patches (Abrams & Wilson 2004; Namba & Hashimoto 2004) or to perceive (Szabo & Mesznera 2006a) or use (Ritchie & Olff 1999) resources at different scales. From a multiple-resource perspective, models have explored how exploitative competition might be affected by community-wide changes in organism size (Tilman & Pacala 1993) or dispersal ability (Moquet *et al.* 2006), by differences between resources in the scale at which feedback occurs on them (Szabo & Mesznera 2006b), or differences between competitors in whether each resource is perceived to occur together versus apart (Chase & Leibold 2003, pp. 81–82). However, none have taken the familiar scenario of exploitative competition for multiple,

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co-occurring resources, and asked what the implications are of species that interact with their environment at different spatial scales.

Here, we extend models of competition for multiple limiting resources to explicitly consider asymmetries between the competitors in the scale at which they interact with their environment. We focus on competition between clonal and non-clonal (or large and small) plants. We model a two-patch environment using a resource-ratio model (MacArthur 1972, pp. 33–58; Leon & Tumpson 1975; Tilman 1980, 1982). Consumers in our model are either ‘non-integrators’ that experience the two patches separately, or ‘integrators’ that experience the average resource availability across both patches and allocate biomass/growth equally between the two patches. We explore how interactions between these two strategies change the outcome of competition, as well as the interpretations of quantities that predict those outcomes in standard resource-ratio models, and which environmental conditions favour one strategy over the other.

2. MODELS

We consider resource competition among two consumer species that occupy an environment with two patches (A and B). Patches differ in their quality with respect to two essential limiting resources (R_1 and R_2). If consumer j is a non-integrator, its growth in patch A is given by

$$\frac{dC_{jA}}{dt} = \min\{a_{j1}R_{1A}C_{jA}, a_{j2}R_{2A}C_{jA}\} - mC_{jA}, \quad (2.1)$$

where m is a loss rate (common to all consumers here); R_{1A} and R_{2A} are densities of resources 1 and 2, respectively, in patch A; and C_{jA} is the density of consumer j in patch A. Because we will consider integrators to be clonal plants growing across both patches, C_{jA} represents plant biomass per patch. We use type I (linear) functional responses, where a_{j1} is consumer j 's *per capita* rate of consumption of R_1 multiplied by the conversion efficiency of units of R_1 to units of consumer j . Changing patch subscripts in equation (2.1) from A to B gives j 's growth in patch B.

Resource dynamics are modelled as a chemostat as follows:

$$\frac{dR_{1A}}{dt} = D(S_{1A} - R_{1A}) - \min_{jA} Q_{j1}, \quad (2.2)$$

where Q_{j1} is the amount of R_1 needed to produce a unit of biomass of species j ; S_{1A} is patch A's supply point for resource 1; D is a dilution rate common to both resources in both patches; and $\min_{jA}$ is shorthand for the output of the minimum function in equation (2.1) (which equals consumer j 's growth in patch A). The last term gives consumer j 's uptake of resources, and an analogous term would be added for each additional consumer species. Switching the appropriate subscripts in equation (2.2) yields the dynamics for other resources and/or patches. Although part of a_{i1} (the conversion efficiency) is the inverse of Q_{i1} , we vary each a independently of each Q in numerical analyses to facilitate changing consumption vectors without changing zero net growth isoclines (ZNGIs).

Equations (2.1) and (2.2) correspond to standard resource-ratio theory (MacArthur 1972, pp. 33–58; Leon & Tumpson 1975; Tilman 1980, 1982). The growth

rate of a consumer in a patch is determined by the resource most limiting to its growth, generating L-shaped ZNGIs for each species. When the two species' ZNGIs do not cross, the species with the lower ZNGI excludes its competitor by drawing resources down to levels too low for the competitor to maintain positive growth. If the ZNGIs do cross, the range of (R_1, R_2) supply points that are above both species' ZNGIs can be divided into three regions, by lines emanating from the intersection point with slopes matching the ratio of $R_2 : R_1$ consumed by each species (termed consumption vectors and given by Q_{i2}/Q_{i1}). When a patch's supply point is in either outer region, the model predicts exclusion of the species with the higher ZNGI in the direction of the adjacent axis. When supply points are in the middle region, there are two possibilities: if each species consumes more of the resource that limits its growth at equilibrium, then either species when rare can invade an equilibrium population of the other (we will refer to this arrangement of consumption vectors as the coexistence scenario) and if each consumes more of the resource limiting its competitor's growth, neither can invade the other (henceforth the founder control scenario).

Our model adds the possibility that consumers integrate across both patches. For simplicity, we assume that integrators maintain equal biomass in each patch, i.e. $C_{iA} = C_{iB}$. The growth of an integrator (i) in either patch is given by

$$\frac{dC_{iA}}{dt} = \min\left\{a_{i1}\frac{R_{1A} + R_{1B}}{2}C_{iA}, a_{i2}\frac{R_{2A} + R_{2B}}{2}C_{iA}\right\} - mC_{iA}, \quad (2.3)$$

and resource dynamics with that integrator are given by

$$\frac{dR_{1A}}{dt} = D(S_{1A} - R_{1A}) - 2\min_{iA} Q_{i1}\frac{R_{1A}}{R_{1A} + R_{1B}}. \quad (2.4)$$

Equation (2.3) describes a consumer that experiences two patches as if they were a single large patch, within which resources are effectively homogeneous (as they are homogeneous within patch A or B alone to a non-integrator). This formulation is consistent with the way in which Tilman & Pacala (1993) model changes in consumer size in a heterogeneous resource environment. Integrators consume resources from each patch based on their biomass across both patches, and proportional to the relative resource availability in each patch (hence the $2\min_{iA}$ and $R_{1A}/(R_{1A} + R_{1B})$, respectively, in equation (2.4)). As with equations (2.1) and (2.2), the dynamics for different resources and patches can be obtained by switching the appropriate subscripts, and terms can be added for resource uptake by additional consumer species. The implications of the assumptions used here, as well as alternate models, are discussed in depth in the electronic supplementary material, appendix.

Here, we focus on competition between two species, whose ZNGIs cross (necessary for coexistence in standard resource-ratio models), and with resource supply points that allow each species to persist in each patch in the absence of competition. We assess the behaviour of the system via invasibility analyses, both analytically and numerically, and also carry out time-course simulations (to explore delayed invasibility; discussed below).

3. RESULTS

(a) R^* s and ZNGIs for multi-patch consumers

Resource-ratio models are commonly analysed graphically. In the standard graphical analysis, ZNGIs (combinations of R_1 and R_2 leading to zero net growth) and consumption vectors (ratio of R_1 to R_2 needed for each unit of consumer growth) of each species are used to divide (R_1, R_2) space into regions, and the outcome of competition in a patch is determined by the region in which the patch's supply point falls. This graphical approach can be extended to consider a system containing multiple patches, where species may obtain resources from more than one patch simultaneously (integrators). However, this extension to multiple patches has consequences for how we view species' ZNGIs, R^* s and consumption vectors (some of which have been previously discussed by [Abrams & Wilson \(2004\)](#) in relation to a one-resource metapopulation model). We explore the consequences for our model below. Equilibrium levels in patch A of the resources that are limiting (L) and non-limiting (NL), respectively, under a resident integrator i are

$$R_{LA}^* = \left(\frac{S_{LA}}{S_{LA} + S_{LB}} \right) \left(\frac{2m}{a_{iL}} \right) \quad (3.1)$$

and

$$R_{NLA}^* = S_{NLA} - \frac{Q_{iNL}}{Q_{iL}} \left[(S_{LA} + S_{LB}) - \frac{2m}{a_{iL}} \right] \left(\frac{S_{NLA}}{S_{NLA} + S_{NLB}} \right). \quad (3.2)$$

The equilibrium values of the limiting and non-limiting resources, respectively, under a resident non-integrator j are

$$R_{LA}^* = \frac{m}{a_{jL}} \quad (3.3)$$

and

$$R_{NLA}^* = S_{NLA} - \frac{Q_{jNL}}{Q_{jL}} \left(S_{LA} - \frac{m}{a_{jL}} \right). \quad (3.4)$$

Resource equilibria for patch B can be found by switching the subscripts A and B in equations (3.1)–(3.4).

Equation (3.3) gives both the level to which a non-integrator draws a limiting resource in a patch and the ZNGI for the species. In the absence of competitors, the non-integrator will persist in all patches with supply points greater than equation (3.3) for each resource. However, the supply point of a limiting resource in patch A that will lead to zero net growth for a resident integrator is not specified by equation (3.1), but rather by

$$S_{LA} = \left(\frac{2m}{a_{iL}} \right) - S_{LB} \quad (3.5)$$

The minimum S_{LA} that will allow an integrator to persist in the absence of competition depends on the supply point in patch B and does not correspond with the resource level that will be left behind at equilibrium (R_{LA}^*). Also note that while equations (3.3) and (3.4) show that a line drawn from patch A's supply point (S_{1A}, S_{2A}) to the (R_{1A}^*, R_{2A}^*) left behind by a resident non-integrator will have a slope matching that species' consumption vector (Q_{j2}/Q_{j1}), the same does not hold

true under a resident integrator, for whom that slope is

$$\frac{Q_{i2} \left(\frac{S_{2A}}{S_{2A} + S_{2B}} \right)}{Q_{i1} \left(\frac{S_{1A}}{S_{1A} + S_{1B}} \right)}. \quad (3.6)$$

An integrator ZNGI drawn instead in the space of the averages of R_1 and R_2 across patches has more properties in common with non-integrator ZNGIs. The vertical and horizontal lines, respectively, constituting that ZNGI would be given by

$$\frac{1}{2}(R_{1A}^* + R_{1B}^*) = \frac{2m}{a_{i1}} \quad \text{and} \quad \frac{1}{2}(R_{2A}^* + R_{2B}^*) = \frac{2m}{a_{i2}}. \quad (3.7)$$

This ZNGI depends only on m , a_{i1} and a_{i2} , and gives both the average supply point an integrator needs for growth and the average equilibrium level of a limiting resource it leaves behind. Further, the slope of a line drawn from the average supply point to the average equilibrium resource point will match the integrator's consumption vector (figure 4 in the electronic supplementary material), and is therefore useful for graphically determining which resource will limit a resident integrator. This analogue of the ZNGI based on averages across patches is consistent with the interpretation that the difference between the integrators and non-integrators lies in the scale at which a patch is defined. It also matches the conclusion of [Abrams & Wilson \(2004\)](#) that it is best not to redefine R^* in a metacommunity context. We therefore argue that this is the most appropriate analogue of the ZNGI for integrators in our model and use the term ZNGI to refer to it from this point on.

This interpretation also tells us the maximum number of species that can coexist in our two-patch system, four. An integrator limited by R_1 will draw $1/2(R_{1A} + R_{1B})$ to its ZNGI. A non-integrator limited by R_1 in patch A may coexist with this integrator and will draw R_{1A} to its ZNGI. For another non-integrator limited by R_1 in patch B to coexist with these two species, its ZNGI would have to be precisely the same distance from the integrator's ZNGI as the other non-integrator's, but in the opposite direction. This is infinitely unlikely. Following the same reasoning for R_2 shows that one integrator and one non-integrator limited by each resource (four species total) may coexist (see figure 5 in the electronic supplementary material). One integrator may also coexist with three non-integrators (one limited by the same resource as the integrator and two limited by the opposite resource, each of the latter in a different patch). In standard resource-ratio theory, four species may also coexist in a two-patch system. However, with integrators, all four species can coexist locally in the same patch. For the remainder of this paper, we focus on two-species competition.

(b) Invasibility analyses: key mechanisms

We use invasibility analysis to determine the outcome of competition between two species based on the ability of a rare invader to increase in the presence of (i.e. with the resource levels left behind by) a resident competitor at equilibrium. A species wins in competition if it can invade when its competitor is resident and also resist invasion by that competitor. Either species being able to invade implies coexistence, and neither being able to invade constitutes

Table 1. Integration's typical impacts on competitive (a) effect and (b) response.

(a) integration's typical effect on a species' ability to resist invasion in a more productive (richer) patch		in less productive (poorer) patch	
when patch resource supply ratios are similar	when patches are highly complementary	when patch resource supply ratios are similar	when patches are highly complementary
–	+	+	+
(b) integration's effect (if any) on a species' ability to invade patches relatively poorer in the resource for which the resident competitor has a lower R^*		patches relatively richer in the resource for which the resident competitor has a lower R^*	
+		–	

founder control (where the two species will not coexist but initial conditions determine the winner).

Integration has a few straightforward consequences for a species' interaction with resources that determine integration's effect on competition (summarized in table 1). A resident integrator's ability to resist invasion is determined by its effect on resources (i.e. its competitive effect *sensu* Goldberg & Werner 1983), and two closely related mechanisms are important here. When a non-integrator is limited by the same resource in both patches, it produces more biomass in the patch that is richer in that resource and less in the poorer patch. However, as an integrator, the same species produces an equal, intermediate biomass in each patch. This means that the integrator will draw the limiting resource down further in the poorer patch than an equivalent non-integrator would, but will not draw it down as far as the non-integrator in the richer patch. Thus, levels of the limiting resource will be below a resident integrator's ZNGI in the poor patch and above it in the rich patch (figure 1). For brevity, we refer to this enhanced and reduced resource drawdown, respectively, as 'over-depletion' and 'under-depletion'. Owing to these effects, integration often helps a species resist invasion in poor patches, but reduces the species' ability to resist invasion in rich patches. In fact, under-depletion can allow a non-integrator with a higher ZNGI for both the resources to coexist with an integrator (e.g. a non-integrator whose ZNGI lies just above i 's in figure 1b).

When a non-integrator would instead be limited by a different resource in each patch, an equivalent integrator can take advantage of the complementarity between patches (each being relatively richer in a different resource) to achieve a higher total biomass. If patches are sufficiently complementary, resources in both patches can be drawn below the integrator's ZNGI (figure 1). Looking at resources separately, each is drawn below the ZNGI in the patch where it is scarce and remains above the ZNGI where it is abundant. However, because each patch has a low supply of one resource, the overall levels are drawn below the ZNGI in both patches. We distinguish this as a separate mechanism and refer to it as 'co-depletion'. Note that co-depletion can allow an integrator to exclude a non-integrator that has lower ZNGIs for both resources (e.g. a non-integrator whose ZNGI lies just below i 's in figure 1d; see appendix and figure 6 in the electronic supplementary material for further discussion of integration's effects on resources).

When an integrator invades, its response to resources, rather than its effect on them (i.e. its competitive

response *sensu* Goldberg & Werner 1983), determines its success. In the scenarios we consider here, integration becomes important for an invader's success when resource levels (under a resident competitor) are above the invader's ZNGI in one patch but below it in the other. As a non-integrator, the invader would be successful in the former patch, but not the latter. However, integrators cannot successfully invade only one patch but rather must either succeed (or fail) across both patches simultaneously. If average resource levels are above its ZNGI, the invader does better as an integrator, successfully invading both patches. If average resource levels are below its ZNGI, the invader does worse as an integrator, unable to invade either patch. Resource levels left behind by a non-integrator resident can match either of these situations when that resident is limited by the resource for which it has a higher ZNGI in one (figure 2) or both patches. An integrator may also be able to invade two patches that are both non-invasible to an equivalent non-integrator, when those patches are sufficiently complementary (figure 2). However, a resident non-integrator cannot generate this situation in the cases we focus on here. The inability of an integrator to invade only one patch also precludes regional coexistence without local coexistence (each species persisting alone in separate patches), an outcome possible with two non-integrators.

Below, we give specific analytical invasibility criteria and highlight how the mechanisms discussed above influence them. All of the invasibility conditions follow from equations (3.1)–(3.4), requiring R_1^* and R_2^* under a resident at equilibrium to be above the minimum needed by an invader for positive growth. For simplicity, we consider only cases where ZNGIs cross and supply points would allow the growth of each species in both patches in the absence of competition.

(c) Invasibility with two non-integrators

Let k be a non-integrator that is limited by R_1 when it is resident. The successful invasion of patch A by another non-integrator j requires

$$\frac{m}{a_{j1}} < \frac{m}{a_{k1}} \quad \text{and} \quad \frac{\left(S_{2A} - \frac{m}{a_{j2}}\right)}{\left(S_{1A} - \frac{m}{a_{k1}}\right)} > \frac{Q_{k2}}{Q_{k1}}. \quad (3.8)$$

Switching the patch subscripts gives the conditions for invasion of patch B. The conditions for successful invasion by k depend on which resource limits j as the resident.

Figure 1. Integration's impact on competitive effect. Single-species equilibria for two arrangements of supply points under (a,c) a resident non-integrator (j) versus (b,d) an otherwise identical integrator (i ; thick lines indicate integrators throughout all figures). Grey circles indicate resource supply points, grey dotted lines give resource trajectories over time and grey crosses give equilibrium resource levels, in each patch (a different shade of grey is used for each patch). Black symbols correspond to grey symbols but show the averages across patches (only shown when the species is an integrator). Numbers above each patch are equilibrium consumer densities (biomasses) in the patch.

When a resident j is limited by R_1 , the condition is

$$\frac{m}{a_{k1}} < \frac{m}{a_{j1}} \quad \text{and} \quad \frac{\left(S_{2A} - \frac{m}{a_{j2}}\right)}{\left(S_{1A} - \frac{m}{a_{j1}}\right)} > \frac{Q_{j2}}{Q_{j1}}. \quad (3.9)$$

When a resident j is limited by R_2 , the condition for k 's successful invasion is

$$\frac{m}{a_{k2}} < \frac{m}{a_{j2}} \quad \text{and} \quad \frac{\left(S_{2A} - \frac{m}{a_{j2}}\right)}{\left(S_{1A} - \frac{m}{a_{k1}}\right)} < \frac{Q_{j2}}{Q_{j1}}. \quad (3.10)$$

These conditions draw the regions corresponding to each outcome in the graphical analysis of standard resource-ratio theory. The species with the lower ZNGI for R_1 wins when the slope of a line drawn from the intersection of the two species' ZNGIs to the supply point is steeper than either species' consumption vector and the species with the lower ZNGI for R_2 wins when that slope is shallower than either consumption vector. Slopes between the two consumption vectors generate either coexistence (mutual invasibility) or founder control (mutual non-invasibility),

depending on which consumption vector is steeper. Note that the leftmost inequalities of equations (3.8) and (3.9) cannot both be true (so long as $a_{k1} \neq a_{j1}$), meaning that coexistence is impossible when each species as resident is limited by the same resource.

(d) Invasibility with two integrators

When two integrators compete, the conditions for each to invade the two-patch system are given by expressions nearly identical to equations (3.8)–(3.10), except that S_{1A} and S_{2A} are replaced with $1/2(S_{1A} + S_{1B})$ and $1/2(S_{2A} + S_{2B})$, respectively, wherever they occur. This means that the outcome of competition between two integrators can be predicted graphically using the average supply point across patches in the same manner that the outcome of competition between two non-integrators can be predicted using separate supply points.

(e) Non-integrator invasion against an integrator

Against a resident integrator (i) limited by R_1 , the conditions for a non-integrator (j) to successfully invade

patch A are

$$\left. \begin{aligned} \frac{m}{a_{j1}} &< \frac{m}{a_{i1}} \left(\frac{2S_{1A}}{S_{1A} + S_{1B}} \right) \quad \text{and} \\ \left[\frac{S_{2A} - \frac{m}{a_{j2}}}{\frac{S_{1A} + S_{1B}}{2} - \frac{m}{a_{i1}}} \right] &> \frac{Q_{j2}}{Q_{i1}} \left(\frac{2S_{2A}}{S_{2A} + S_{2B}} \right). \end{aligned} \right\} \quad (3.11)$$

The conditions for patch B are identical but with the patch subscripts reversed.

When comparing j 's ability to invade a non-integrator versus an integrator, it must be remembered that a species limited by R_1 as an integrator could be limited either by R_1 in both patches as a non-integrator or by a different resource in each patch. If i would be limited by R_1 in both patches as a non-integrator, equations (3.11) and (3.8) must be compared. Here, patch A is easier to invade with an integrator resident than with a non-integrator resident when it is richer in the limiting resource ($S_{1A} > S_{1B}$) and poorer in the opposite resource ($S_{2A} < S_{2B}$). The former condition reflects both the cost of under-depletion (in the richer patch) and benefit of over-depletion (in the poorer patch) to an integrator.

If i would have been limited by a different resource in each patch (let us say R_1 in A and R_2 in B), the appropriate comparison is between the pair of equations (3.9) and (3.10) (with species subscripts reversed and patch subscripts changed to B in the latter) and equation (3.11). With highly complementary patches, this would mean that $S_{1A} < S_{1B}$ and $S_{2A} > S_{2B}$. In this case, the ratios of supply points that appear in equation (3.11) inhibit invasion in both patches, showing the benefit of co-depletion to the integrator. We can also observe that against a non-integrator, j can only invade if its ZNGI is lower for the resource locally limiting the resident, but no part of j 's ZNGI need be lower for successful invasion against an integrator (showing the cost of under-depletion for the integrator).

(f) Integrator invading a non-integrator limited by the same resource

There are three possibilities when the non-integrator (j) is the resident: it can be limited by the same resource (R_1) in both patches that the integrator would be when resident; by the opposite resource (R_2) in both; or by a different resource in each patch. In the first case, successful invasion by the integrator (in both patches) requires that

$$\frac{m}{a_{i1}} < \frac{m}{a_{j1}} \quad \text{and} \quad \left[\frac{S_{2A} + S_{2B} - \frac{m}{a_{j2}}}{\frac{S_{1A} + S_{1B}}{2} - \frac{m}{a_{j1}}} \right] > \frac{Q_{j2}}{Q_{j1}}. \quad (3.12)$$

It is possible for the leftmost inequalities of both equations (3.11) and (3.12) to be true provided S_{1A} is sufficiently lower than S_{1B} . This means that (unlike with two integrators or two non-integrators) mutual invasibility is possible when both the species are limited by the same resource. This is possible only if the integrator has a lower ZNGI for that resource and only in the patch with higher supply of that resource (where under-depletion occurs).

(g) Integrator invading a non-integrator limited by the opposite resource

When a non-integrator resident is instead limited by R_2 in both patches, the conditions for the integrator (i) to

Figure 2. Integration's impact on competitive response. Resource levels left behind (crosses) by a resident non-integrator (j), relative to an invading integrator's (i) ZNGI. Symbols and colours are the same as given in figure legend 1. The integrator may be either (a) able or (b) unable to invade both patches, when as a non-integrator it would have been able to invade one patch but not the other. If at least one supply point is to the right of the dashed line, the integrator will be able to invade. Integration can allow invasion when (c) both patches would be non-invasible as a non-integrator but only with arrangements of ZNGIs and supply points different than those we focus on here.

invade are

$$\left[\frac{S_{2A} + S_{2B} - \frac{m}{a_{j2}}}{\frac{S_{1A} + S_{1B}}{2} - \frac{m}{a_{i1}}} \right] < \frac{Q_{j2}}{Q_{j1}} \quad \text{and} \quad \frac{m}{a_{i2}} < \frac{m}{a_{j2}}. \quad (3.13)$$

Both equations (3.12) and (3.13) are the same conditions that invasion by an equivalent non-integrator would require, except that average supply points across both patches replace supply points in each separate patch. Thus, in these two cases, the success of invasion by the integrator can be predicted by the same graphical regions as standard resource-ratio theory, but using the average supply point. This reflects how integration might either allow a species to invade a patch whose supply point would otherwise prevent invasion or cost a species its ability to invade a patch whose supply point would otherwise allow invasion. In either case, the non-integrator must have a higher ZNGI for the resource by which it is limited as a resident.

(h) Integrator invading a non-integrator limited by a different resource in each patch

Finally, when the non-integrator is limited by a different resource in each patch (let us say patch A is where it is limited by R_1), the condition for integrator invasion is (rearrangement into this form requires assuming the left-hand denominator is positive)

$$\frac{\left(S_{2B} - \frac{m}{a_{j2}}\right)}{\left(S_{1B} - \frac{m}{a_{j1}}\right) + 2\left(\frac{m}{a_{j1}} - \frac{m}{a_{i1}}\right)} < \frac{Q_{j2}}{Q_{j1}} < \frac{\left(S_{2A} - \frac{m}{a_{j2}}\right) + 2\left(\frac{m}{a_{j2}} - \frac{m}{a_{i2}}\right)}{\left(S_{1A} - \frac{m}{a_{j1}}\right)}. \quad (3.14)$$

If the second terms in the left-hand denominator and right-hand numerators were removed, equation (3.14) would have to be satisfied because it would merely give the condition for the non-integrator to be limited in each patch by the resource that we have assumed it is limited by. Invasion by i is therefore guaranteed when its ZNGI is lower than j 's for each resource, and also possible when its ZNGI is higher for one or both resources. Higher levels of the resource not limiting to j in each patch facilitate integrator invasion. If the integrator's ZNGI for a resource is higher, then where that resource is not limiting to j , the amount j leaves behind must equal at least i 's ZNGI plus the difference between the two ZNGIs (figure 2). Otherwise, the average level of the resource will be below i 's ZNGI and it will be unable to invade.

(i) Overall patterns of invasibility

When an integrator and a non-integrator compete, invasion by the integrator can be predicted graphically by the average supply point if the non-integrator is limited in both patches by the resource for which it has the higher ZNGI. Otherwise, regions of supply points leading to different outcomes can only be drawn in two dimensions when the supply point for one patch (let us say patch A) is held constant. Boundaries between those regions are not drawn by ZNGIs and consumption vectors, when plotted against either the average supply point or patch B's supply point (figure 3). However, those boundaries reflect the criteria in equations (3.11)–(3.14), and the previously discussed mechanisms by which costs and benefits of integration tend to arise. Following equation (3.11), when patches A and B differ only in the supply of one resource (i.e. moving horizontally or vertically from the star in any panel), if the non-integrator is able to invade only one patch, it is the richer patch. This reflects the effects of over-depletion and under-depletion by integrators. The effect of co-depletion by

integrators can be seen in figure 3a,c; although the location of patch A's supply point favours the non-integrator, the integrator tends to win both patches ($I:I$) when patch B has a high supply of the resource that is rare in patch A (R_1) but a low supply of the resource that is common there (R_2). Vertical and horizontal lines separating regions where j can versus cannot invade a patch follow from the l.h.s. of equation (3.11). Regions where the integrator can versus cannot invade are separated by a line whose slope but not location matches the non-integrator's consumption vector, which follows from equations (3.12)–(3.14).

To gauge the effect of integration by one or both species on the frequencies of competitive outcomes, we determined invasibility numerically for all pairs of supply points where $R_1 = 3$ –8 by increments of 0.25 and $R_2 = 3.1$ –6.1 by increments of 1.5. We used parameter values of $m = 0.4$, $D = 0.2$, $a_{i1} = a_{j2} = 0.2$, $a_{i2} = a_{j1} = 0.16$, and $Q_{i1} = Q_{j2} = 0.6$ and $Q_{i2} = Q_{j1} = 0.4$ in the founder control scenario or $Q_{i1} = Q_{j2} = 0.4$ and $Q_{i2} = Q_{j1} = 0.6$ in the coexistence scenario (the same used for figure 3). We compared cases where i was an integrator and j a non-integrator to cases where both were non-integrators or both integrators. As the number of integrators increased from none, to one, to two, regional exclusion of either species occurred more often. Neither strategy was clearly superior in terms of how often it versus its competitor was excluded. While regional coexistence tended to decline, local coexistence within at least one patch was most common when an integrator and a non-integrator competed (see figure 7 in the electronic supplementary material). Similar results were obtained using other Q values (see figures 9–16 in the electronic supplementary material).

(j) Delayed invasibility

The coupling of patches by a resident integrator can also facilitate non-integrator invasion via a mechanism the single-species equilibrium conditions above do not capture. This is because an integrator's competitive effect in a patch depends on conditions in the adjacent patch (or, conversely, its response to a competitor extends beyond the patch where that competitor is present). Thus, a patch that is resistant to invasion when occupied by an integrator at its single-species equilibrium may be susceptible to invasion when occupied by an integrator that is coexisting with a non-integrator in the opposite patch. Consider cases where, initially, one patch is invulnerable but the other is not (outcomes $\mathcal{J}:F$, $F:\mathcal{J}$, $C:I$ and $I:C$ in figure 3). A successful invader in the former patch consumes resources from that patch, lowering the average resource levels. As a result, the resident integrator's biomass decreases across both patches. This causes resource levels in the latter patch to rise. Depending on how far they rise, the latter patch may or may not also become susceptible to invasion, with a time lag occurring between when the former patch is initially invaded and when the latter patch becomes susceptible (see figure 17 in the electronic supplementary material). In the $\mathcal{J}:F$ and $F:\mathcal{J}$ cases, successful invasion in the latter patch consistently led to exclusion of the integrator from both patches. Delayed invasibility was not uncommon; time-course simulations found it to occur in over 14, 70, 60 and 76% of the cases where it was possible in figure 3a–d, respectively. The conditions for invasion of this type are given in the electronic supplementary material, appendix.

Figure 3. Regions of outcomes when an integrator (*i*) and a non-integrator (*j*) compete, plotted against the location of patch B's supply point (sampled at increments of 0.025 for each resource). (a,c) versus (b,d) shows the results for different patch A supply points (stars), in (a,b) founder control versus (c,d) coexistence scenarios. In each region, the first letter gives the outcome in patch A and the second the outcome in B. Letters are either those of the winning species, *F* indicating founder control or *C* indicating coexistence. Shades of grey have no significance other than to highlight regions within a panel.

4. DISCUSSION

As modelled here, integration as a strategy carries both costs and benefits. Costs often arise in rich patches, while benefits arise in poorer patches. An integrator may fail to invade a rich patch that a non-integrator could invade when average resource levels are low, but may gain the ability to invade a poor patch when they are high. The integrators often deplete resources less in richer patches (under-depletion), and further in poorer patches (over-depletion), than an equivalent non-integrator would. This reduces competition in the richer patch, potentially allowing a non-integrator to invade there, but intensifies competition and reduced invasibility of poor patches. This mechanism also could be relevant for understanding competitive interactions among animal or other species that differ in migration rates or size of their home ranges. It is analogous to the mechanism allowing persistence of an inferior competitor in one-resource metapopulation models by Abrams & Wilson (2004) and Namba &

Hashimoto (2004). There, the superior competitor's emigration from a richer patch reduces its ability to draw down resources there, allowing an inferior competitor to persist. When patches are highly complementary (each having high supply of a different resource), integrators benefit by escaping limitation by the scarce resource in each patch. They also draw the locally rare resource in each patch below their ZNGI, more easily excluding competitors. Previous models consider complementarity that arises when essential resources occur in separate patches for one (Chase & Leibold 2003, pp. 81–82) or more (Vincent *et al.* 1996) competitors. In our models, both resources co-occur in each patch. However, when each patch is relatively rich in a different resource, integrators experience the two resources as co-occurring to a greater extent than non-integrators do. Clonal plants have been shown to take advantage of complementary patches (Alpert & Mooney 1986; Friedman & Alpert 1991; Stuefer *et al.* 1996; van Kleunen & Stuefer

1999), although this can be due in part to specialization by ramets for acquiring locally abundant resources (reviewed by Hutchings & Wijesinghe 1997), which was not possible in our models. The degree to which complimentary patch use by integrators might apply to animals is less clear, as resources used by animals are likely to be more substitutable than those modelled here.

McLaughlin & Roughgarden (1992) and de Roos *et al.* (1998) show how a consumer that operates at a wider spatial scale than its resource can maintain or exacerbate underlying heterogeneity in that resource. Here, something analogous occurs when patches have similar resource supply ratios. In those cases, an integrator maintains greater resource heterogeneity at equilibrium than a non-integrator. However, when patches are sufficiently complementary, integrators instead reduce resource heterogeneity relative to non-integrators. Thus, integration's impact on resource heterogeneity could be context dependent when multiple resources are involved.

Because integrators either persist in or are excluded from both patches simultaneously, it is impossible to have regional coexistence without that coexistence also being local (within-patch). This reduces the potential for regional coexistence, as well as the range of possible outcomes. However, competition between an integrator and a non-integrator allows local coexistence to occur when each consumes more of the resource limiting the other (i.e. the founder control scenario), and when both are limited by the same resource (because the level of that resource within a patch can be at the non-integrator's ZNGI while the average across patches is at the integrator's ZNGI). This means that species can also coexist when their ZNGIs do not cross (i.e. one species is a superior competitor for both resources). Coexistence is more common in richer patches, where integration often reduces a species' impact on competitors. This differs from competition between two non-integrators, where only the ratios, not the absolute amounts, of resources in each patch determine coexistence.

Integrators also couple patches such that a competitor's successful invasion in one patch can lead to the second patch, originally resistant to invasion, to eventually become susceptible as well. This introduces cases where both founder control and coexistence occur simultaneously (outcomes $\mathcal{J}:F$ and $F:\mathcal{J}$ in figure 3, if the F patch remains resistant to invasion). The initial conditions then determine whether the integrator is excluded globally or coexists with the non-integrator. Chase & Leibold (2003) found that the outcome of competition could similarly depend on the order in which species arrive if two resources are substitutable for one competitor but essential for the other (pp. 77–79), or if one competitor perceives resources as occurring in entirely separate patch types but the other competitor does not (pp. 81–82).

Defining integrator ZNGIs, R^* 's and consumption vectors in terms of average resource levels and supply points across patches allows graphical determination of the resource by which a resident integrator is limited for any combination of supply points. It also allows the outcome of competition between integrators, and sometimes the ability of an integrator to invade a non-integrator resident, to be predicted with the same graphical analysis commonly applied to resource-ratio models. Patterns of non-integrator invasion against an integrator resident

follow intuitively from the mechanisms discussed earlier. However, boundaries between regions of (R_1, R_2) space leading to different outcomes are not drawn by species' ZNGIs and consumption vectors when an integrator and a non-integrator compete.

We have kept these models simple to gain insight into basic consequences of species differences in the scales of integration. As such, many factors that are potentially important to coexistence (e.g. dispersal) are not taken into account. Perhaps most importantly, the integrators in our models are non-plastic in their response to heterogeneity, in that they allocate growth equally between patches even if this allocation pattern is not optimum. Our integrators thus suffer a cost for allocation to poorer patches, which plasticity in allocation or limited integration could potentially ameliorate. Empirical studies have suggested that such a cost can be either present (Salzman & Parker 1985; de Kroon *et al.* 1998) or insignificant, perhaps due to plant plasticity (Roiloa & Retuerto 2006) or partial integration (Slade & Hutchings 1987c). Plants also can avoid costs of supplementing ramets in poorer patches by avoiding growth there (Hartnett & Bazzaz 1983; Slade & Hutchings 1987a–c; Evans 1988; Sutherland & Stillman 1988; Evans & Cain 1995).

Models suggest that plants with more plastic allocation strategies (e.g. Magyar *et al.* 2007) or more moderate degrees of integration (e.g. Magori *et al.* 2003) can perform better than all-or-nothing integrators like those in our models. However, those models and others (e.g. Oborny *et al.* 2000, 2001) still include the potential for allocation to ramets in poorer patches to be one of the costs of integration. To the extent that ramets in richer patches do supplement ramets in poorer patches, and that doing so entails some cost, the mechanisms by which integration is detrimental in our model should still operate. Our results further suggest that supplementing ramets in a poorer patch can be detrimental for an integrator even when resource supply ratios in either patch separately would favour that species. This emphasizes the impact that feedbacks between focal plants, competitors and resources can have on competitive outcomes, and shows that these factors might interact to determine whether a site is suitable or unsuitable for a ramet.

The simple models developed here demonstrate that size differences can have dramatic effects on coexistence via resource competition. They highlight straightforward costs and benefits of integration, and yield general conclusions as to what types of resource distributions within and across patches will favour integrators versus non-integrators. The impact of integration on competitive interactions should be explored further in models allowing more sophisticated foraging and allocation strategies.

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