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Competition–colonization trade-off between perennial plants: exclusion of the rare species, hysteresis effects and the robustness of co-existence under replacement competition

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ABSTRACT

We consider a simple model of two species competing for the available living sites with Poisson-distributed number of arrivals, and assume that juveniles of one species are competitively superior to the juveniles of the other species but established adults cannot be displaced by colonizing propagules of either species (replacement competition). We find that, in addition to protected co-existence by the competition–colonization trade-off, the two species may also co-exist in an unprotected manner (i.e. such that a single-species equilibrium is also stable), and the rare species may be excluded and the common species preserved regardless of which of the two species is rare. In the case of unprotected co-existence, a small change in the environment (e.g. in site density) can cause the abrupt extinction of a species, with no advance warning from its density approaching zero. To restore biodiversity, a substantial change, or (if exclusion of the rare species also occurs) a more complicated non-monotonous change in the environment, is necessary. We investigate the robustness of the model with respect to introducing seed banks, changing the degree of competitive asymmetry and assuming partial displacement of adults by juveniles.

Keywords: asymmetric competition, colonization, displacement competition, fugitive co-existence, hysteresis, perennial plants, replacement competition, safe site model, seed bank.

INTRODUCTION

Co-existence by a trade-off between competition and colonization is one of the most studied mechanisms for maintaining biodiversity in spatially structured populations. Following Skellam (1951) and Levins and Culver (1971), many authors have explored ‘fugitive’ co-existence either in metapopulations or in populations of plants (or other sessile organisms) that compete within sites, each capable of supporting only one adult individual (e.g. Fagerström and Ågren, 1979; Hastings, 1980; Nee and May, 1992; Hanski and Zhang, 1993; Dytham, 1994; May and Nowak, 1994; Pacala and Tilman, 1994; Tilman, 1994;

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Tilman *et al.*, 1994; Moilanen and Hanski, 1995; Abrams, 1996; Fagerström and Westoby, 1997; Holmes and Wilson, 1998; Neuhauser, 1998; Pacala and Rees, 1998; Kinzig *et al.*, 1999; Adler and Mosquera, 2000; Yu and Wilson, 2001; Ohsawa *et al.*, 2002). Possible mechanistic underpinnings of the competition–colonization trade-off between plant species include the allocation between roots and reproduction: plants with more extended roots can deprive soil resources to lower levels, but produce fewer seeds for colonization (Gleeson and Tilman, 1990; Tilman and Wedin, 1991). Allocation between the size and the number of seeds can also lead to a competition–colonization trade-off: seedlings from large seeds tend to be more competitive than seedlings from small seeds, but small seeds can be produced in greater numbers and hence are better for colonizing empty sites (Black, 1958; Cipollini and Stiles, 1991; Houssard and Escarré, 1991).

Yu and Wilson (2001) drew attention to a potentially important distinction between displacement versus replacement competition among perennial plants. In displacement competition, a seedling of one species can outcompete an established adult individual of the other species in the same site. This may happen, for example, in competition for soil resources, if the seedlings of one species can grow at a lower level of resources than the level set by an established plant of the other species. By further suppressing the resource, such a seedling can eventually displace the established adult (Wedin and Tilman, 1993; Pacala and Rees, 1998). In replacement competition, a seedling cannot take over a site from an adult plant; seedlings compete only with each other for sites vacated by adult death. This may be the case in competition for light, where tall adults have a strong competitive advantage over seedlings of any species (Weiner, 1986; Wedin and Tilman, 1993). [A third possibility in addition to displacement and replacement is that sites are ephemeral in the sense that when the adult dies, the site is no longer suitable for colonization, but new vacant sites are continuously produced by small-scale disturbances in the vegetation (Geritz, 1995; Geritz *et al.*, 1999). This third possibility is not pursued in the present paper.]

Most models of the competition–colonization trade-off assume displacement competition. In a short note that is the predecessor of this article (Kisdi and Geritz, 2003), we extended Skellam's (1951) model (originally for annuals) to perennial plants with replacement competition (see Fagerström and Ågren, 1979, for a closely related model). We confirmed that perennials can co-exist also under replacement competition. Moreover, we found that replacement competition can also lead to qualitatively new phenomena, such as the exclusion of the rare species (regardless of which one is rare) and multiple equilibria with unprotected co-existence, provided that the adult survival probability of the species with competitively inferior seedlings is sufficiently higher than that of the species with competitively superior seedlings. In this paper, we perform a bifurcation analysis of the model of Kisdi and Geritz (2003) and explore the consequences of habitat loss. Next, we extend the model in three directions. First, we introduce delayed germination and seed banks, assuming that seeds do not germinate until the adult that occupies the site dies. Second, we relax the assumption of perfect competitive asymmetry. Third, we introduce partial displacement competition. For each extension, we investigate the robustness of protected co-existence, of unprotected co-existence and of the exclusion of the rare species.

THE NULL MODEL

Consider two species competing for the same living sites, and assume that there is a strict competitive hierarchy such that a single seedling of one species (henceforth called the 'superior' species) wins the site against any number of seedlings of the other species (henceforth called the 'inferior' species). Adult plants are, however, invulnerable to seedlings. Assume further that all seeds germinate at the beginning of the season, and that seeds are randomly dispersed with a Poisson-distributed number of seeds landing in individual sites. The dynamics of the two-species community is then given by the equations

$$x_{t+1} = ux_t + (1 - ux_t - vy_t)(1 - \mathrm{e}^{-\alpha x_t}) \tag{1a}$$

$$y_{t+1} = vy_t + (1 - ux_t - vy_t)\mathrm{e}^{-\alpha x_t}(1 - \mathrm{e}^{-\beta y_t}) \tag{1b}$$

where x and y are the fractions of sites occupied by the superior and the inferior species respectively (the remaining fraction $1 - x - y$ is empty), u and v are the superior species' and the inferior species' adult survival probabilities respectively, and α and β are the per capita number of seeds that survive and germinate in the next season (Kisdi and Geritz, 2003).

Figure 1 shows typical outcomes of the model [see Kisdi and Geritz (2003) and Appendix 1 for methods]. The two species co-exist in a protected manner if both increase when rare, or, in other words, if they can invade each other's equilibrium population. Protected co-existence occurs if both species are annual [Fig. 1a; this case corresponds to Skellam's (1951) model] and if both are perennial with identical adult survival probabilities (Fig. 1b) in a comparable range of parameter values. Not surprisingly, co-existence requires high fecundities of the inferior species if the superior species is perennial and the inferior species is annual or has a low adult survival probability compared with the superior species (Fig. 1c; see also Holmes and Wilson, 1998).

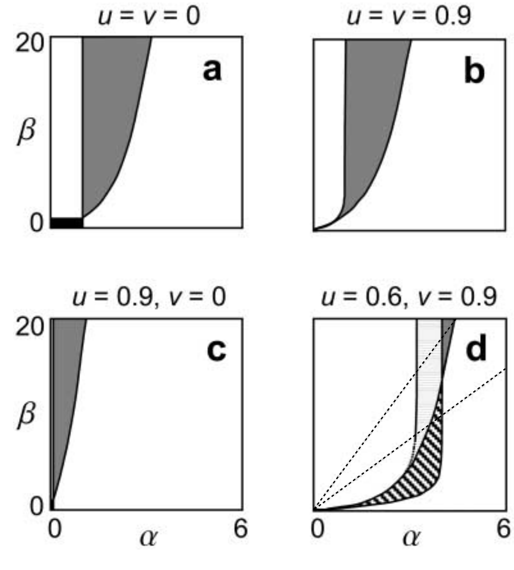

Fig. 1. Replacement competition. Dark grey shading: protected co-existence; light grey shading: unprotected co-existence; hatched: disadvantage of the rare species; black: both species are inviable. Left of the grey/hatched area, the inferior species wins; right of the grey/hatched area, the superior species wins. (a) $(u,v) = (0,0)$, (b) $(u,v) = (0.9,0.9)$, (c) $(u,v) = (0.9,0)$, (d) $(u,v) = (0.6,0.9)$. With $(u,v) = (0,0.9)$, protected co-existence is possible only with extremely high fecundities (not shown). The dotted lines in (d) show the effect of habitat loss with $\beta/\alpha = 4.5$ and $\beta/\alpha = 2.5$, respectively.

Qualitatively new results emerge if the inferior species is perennial and the superior species is annual, or both are perennial but the superior species has a much lower adult survival probability (Fig. 1d). At low fecundities for both species, whichever species is rare is at a disadvantage and goes extinct; thus either species, when common, resists invasion by the other. At high fecundities, however, there is always a range of parameter values where protected co-existence occurs. In an adjacent parameter range, the two species can co-exist in an unprotected way, such that the superior species cannot invade the inferior species, but if the superior species is sufficiently common at the onset, the two species reach a stable equilibrium (Kisdi and Geritz, 2003).

For a heuristic understanding of the phenomena of unprotected co-existence and of disadvantage of the rare species, note that under replacement competition, plants can claim living sites in two ways: by competitive superiority of seedlings they gain access to vacant sites, and by high adult survival they retain sites already occupied. In an established population of the inferior species with high adult survival, many sites are occupied by surviving adult plants and, consequently, many seeds die because of competition with adults. This prevents invasion by the superior species if it is not very fecund. If the superior species is common, then fewer sites can be colonized by the inferior species; but on the other hand, fewer seeds are lost in sites containing adults. The two species can form an unprotected co-existence provided that the inferior species is fecund enough to persist in the face of losing seeds in competition with superior seedlings. If, however, the inferior species is less fecund, it goes extinct when the superior species is sufficiently common, resulting in the exclusion of the rare species.

Below we investigate the precise conditions under which combinations of α and β exist such that the rare species is excluded. We refer to the line in Fig. 1 that gives the minimum fecundity required for species A to invade the equilibrium population of species B as the invasion boundary of species A. The rare species is excluded for at least some combinations of α and β, for given u and v, if, in Fig. 1, the invasion boundary of the superior species lies below the invasion boundary of the inferior species. The invasion boundaries are given by $(\alpha/(1-u))\ (1-v\hat{y})=1$ for the superior species and $(\beta/(1-v))\ (1-u\hat{x})e^{-\alpha\hat{x}}=1$ for the inferior species, respectively (where hats denote the equilibrium densities of single-species populations; see Appendix 1). Both invasion boundaries connect to the point $(\alpha, \beta)=(1-u,\ 1-v)$, the minimum fecundities for viability. At this point, the invasion boundary of the inferior species is steeper, and hence the invasion boundary of the superior species lies below that of the inferior species, if $(1/(1-v))-(1/(1-u))>\frac{1}{2}$ (Fig. 2; see Appendix 1 for derivation). The rare species can be at a disadvantage only if the inferior species has a sufficiently higher adult survival probability than the superior species; the minimum difference becomes zero only when both survival probabilities tend to 1 (this is not only biologically unrealistic, meaning immortal adults, but also mathematically a degenerate limit, since the adults that are initially present could retain their sites indefinitely). Exclusion of the rare species may occur in only a narrow range of α and β, but it also may cover a wide range of α and β such that protected co-existence appears only at extremely high fecundities. According to numerical investigations, unprotected co-existence is possible for the same combinations of adult survival probabilities for which disadvantage of the rare species is also possible (Fig. 2) but for different values of α and β (cf. Fig. 1d).

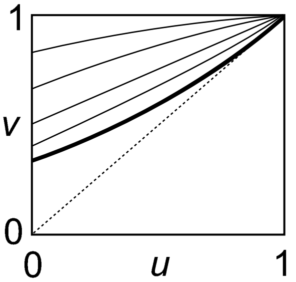

Fig. 2. Disadvantage of the rare species and unprotected co-existence. Above the line, the rare species is excluded for some combinations of α and *β* in the null model (bold line) and with partial displacement competition (fine lines, $w = 0.75$, 0.5, 0.25, 0.1 starting with the lowest fine line). According to numerical investigations, there is unprotected co-existence for the same adult survival probabilities (but for different values of α and *β*). The dotted line $u = v$ is shown for comparison.

Habitat destruction: hysteresis effects

In the case of unprotected co-existence and of the disadvantage of the rare species, the dynamics of the two-species community (equation 1) has two alternative stable equilibria, which can give rise to hysteresis effects when model parameters vary due to some change in the environment. Perhaps one of the most important environmental factors is the density of sites (see, for example, Nee and May, 1992). Since seeds landing outside a site die, varying site density amounts to varying the effective seed numbers α and *β* proportionally (in Fig. 1, this amounts to moving along a straight line through the origin).

First assume that α and *β* change such that the community crosses the regions of protected and unprotected co-existence (Fig. 1d, upper dotted line; Fig. 3a). As site density decreases (Fig. 3a, upper panel), co-existence first becomes unprotected and then is lost through a saddle-node bifurcation, such that the superior species' density falls abruptly to zero. To regain co-existence, it is not sufficient to increase site density just over the point where extinction happened: the superior species is able to invade only at a higher site density, where the region of protected co-existence is reached (Fig. 3a, lower panel). Note that, under displacement competition, decreasing site density also results in the extinction of the superior species, but there is no hysteresis effect: the superior species is able to invade as soon as site density exceeds the level at extinction (Nee and May, 1992).

Restoration of co-existence following habitat loss is even more cumbersome if α and *β* cross the regions of unprotected co-existence and of rare disadvantage (Fig. 1d, lower dotted line; Fig. 3b). Here the two species can co-exist only in an unprotected way. As site density decreases, the superior species goes extinct as before (Fig. 3b, upper panel). After extinction, increasing site density has no effect at all, while the system crosses the regions of unprotected co-existence and of rare disadvantage. The superior species can invade back only after leaving the region of rare disadvantage. Once the superior species is able to invade again, it will now also exclude the inferior species (Fig. 3b, lower panel). Now site density must be decreased again, crossing the region of rare disadvantage in the opposite direction, eventually reaching the region of unprotected co-existence. Since the inferior species is able to invade the superior species in this region (but not the other way), co-existence is eventually restored.

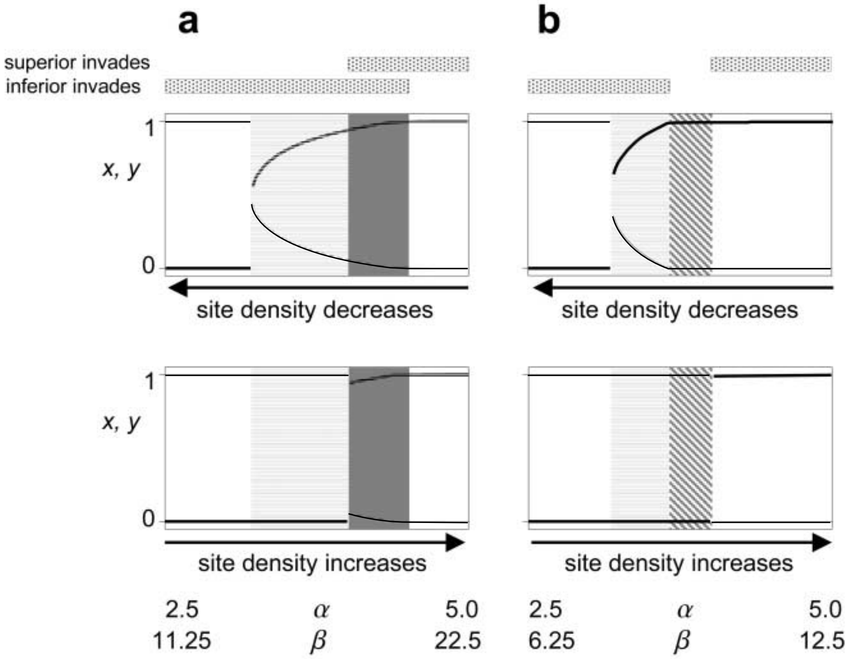

Fig. 3. Hysteresis effect. Bold and fine lines show the equilibrium densities of the superior species and of the inferior species, respectively, in response to changing α and *β* proportionally (e.g. due to changing density of safe sites). In the upper panels safe site density decreases, whereas in the lower panels safe site density increases. Dark grey, light grey and hatched backgrounds correspond to protected co-existence, unprotected co-existence and disadvantage of the rare species, respectively; bars on top indicate the intervals of α and *β* where the superior and inferior species are able to invade. Note that only stable equilibria are shown (the converging bold and fine lines correspond to two species and not to the stable–unstable equilibria colliding at the saddle-node bifurcation). Adult survival probabilities are as in Fig. 1d ($u = 0.6$, $v = 0.9$).

SEED BANKS

In the null model above, we assumed that all seeds germinate at the beginning of the season and all seedlings that emerge in sites already occupied by adult plants die. Seeds are, however, often capable of sensing the presence of an established plant, for example via the spectral properties of light filtered through shading leaves (e.g. Fenner, 1985; Rees, 1997) or by allelopathy (Hutchings, 1986). We therefore now assume that seeds falling in an occupied site do not germinate, but enter dormancy until the adult plant dies and the site becomes free.

Since seeds may accumulate over several years until the adult plant dies, on average a larger number of seedlings compete for each vacant site; consequently, it is less likely that there is no superior seedling competing for a given site. Dormancy, therefore, favours the superior species, and since inferior seedlings can get established only if there is no superior seedling in the site, it may be expected that the accumulation of seeds in the seed bank significantly impedes co-existence.

The population dynamical equations of the model with seed bank [i.e. the analogue of equations (1) of the null model] are much more complicated, because they must keep track of the frequency of occupied sites containing a specific number of viable dormant seeds (separately for the two species). For the present analysis, however, the equilibrium equations suffice. Assuming, for simplicity, that dormant seeds survive in the soil with the same probability s in the two species, the equilibrium equations are

$$x = ux + (1 - x - y)(1 - e^{-\alpha x}) +$$

$$(1 - u)x\sum_{\tau=1}^{\infty} f_{\tau-1}\left(1 - e^{-\alpha x\frac{1-s^{\tau}}{1-s}}\right) + (1 - v)y\sum_{\tau=1}^{\infty} g_{\tau-1}\left(1 - e^{-\alpha x\frac{1-s^{\tau}}{1-s}}\right) \tag{2a}$$

$$y = vy + (1 - x - y)e^{-\alpha x}(1 - e^{-\beta y}) +$$

$$(1 - u)x\sum_{\tau=1}^{\infty} f_{\tau-1}e^{-\alpha x\frac{1-s^{\tau}}{1-s}}\left(1 - e^{-\beta y\frac{1-s^{\tau}}{1-s}}\right) + (1 - v)y\sum_{\tau=1}^{\infty} g_{\tau-1}e^{-\alpha x\frac{1-s^{\tau}}{1-s}}\left(1 - e^{-\beta y\frac{1-s^{\tau}}{1-s}}\right) \tag{2b}$$

where

$$f_{\tau-1} = \frac{u^{\tau-1}}{\sum_{T=1}^{\infty} u^{T-1}} \quad \text{and} \quad g_{\tau-1} = \frac{v^{\tau-1}}{\sum_{T=1}^{\infty} v^{T-1}}$$

denote the frequency of $\tau - 1$ year-old adults of the superior and of the inferior species, respectively, in the stable age distribution. Population census is immediately after the establishment of seedlings; as in the null model, α and β contain the pre-competitive seed survival between seed set and the next census. The first term on the right-hand side represents the surviving adults, whereas the second term corresponds to the colonization of previously empty sites. In the third term of equation (2a), the density of superior adults that died during the previous year is multiplied by the probability that at the previous census they reached age $\tau - 1$ and that the site has accumulated at least one surviving superior seed during the last τ years ($e^{-\alpha x}e^{-\alpha xs} \ldots e^{-\alpha xs^{\tau-1}} = e^{-\alpha x\frac{1-s^{\tau}}{1-s}}$ gives the probability that no superior seed arrived that survives to the present year); the last term is the same for sites occupied by the inferior species. The last two terms of equation (2b) are analogous, but they also contain the probability that there is no surviving superior seed present. The calculation of the invasion boundaries and of the line of saddle-node bifurcation that gives the border of the area of unprotected co-existence, shown in Fig. 4, is detailed in Appendix 2.

There are two easily interpretable limiting cases of this model. First, if the common species is annual, then dormancy has no effect on the rare species' invasion boundary, since all seeds germinate in the first season just like in the null model. Second, if the survival probability of dormant seeds (s) is very high, then the superior species does not lose seeds due to competition with adults of the inferior species; those seeds that fall into a site occupied by the inferior species survive in the soil and merely germinate at some later time (delay has no effect in equilibrium populations). In this case, the superior species only needs to be viable [its lifetime seed production, $\alpha/(1 - u)$, must exceed 1] in order to persist (see Fig. 4b,d,g).

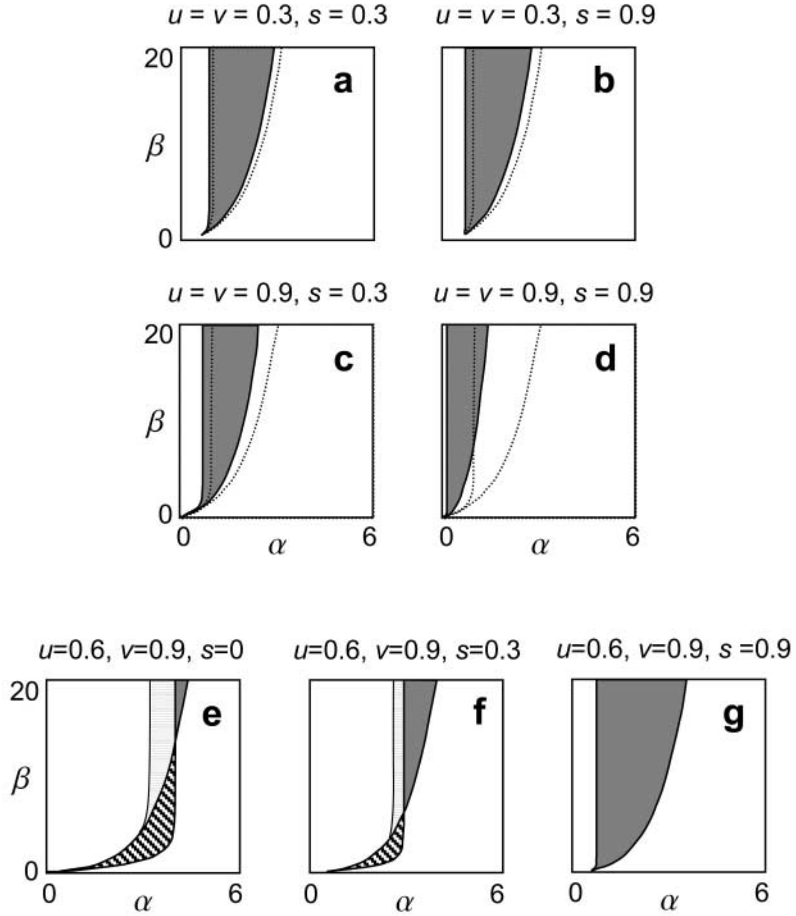

Fig. 4. The effect of seed banks. Shading as in Fig. 1: dark grey, protected co-existence; light grey, unprotected co-existence; hatched, disadvantage of the rare species. Adult survival probabilities (u,v) and survival in the seed bank (s) are shown in the panel titles. In panels (a–d), the dotted lines show the invasion boundaries with no seed bank ($s = 0$) for comparison.

To see how robust protected co-existence is with respect to dormancy, first consider two species with similar adult survival probabilities (Fig. 4a–d). Since dormancy favours the superior species, the region of co-existence shifts towards smaller values of α. However, the numerical effect is strong only if both the probability of adult survival (u,v) and of seed survival (s) are high: if adults do not live long, there is no time to accumulate seeds, whereas if seeds do not live long, mostly dead seeds accumulate. Co-existence remains robust also if the superior species has higher adult survival probability than the inferior species (not shown).

Next assume that the adult survival probability of the superior species is lower such that, without seed banks, regions exist with unprotected co-existence and with disadvantage of the rare species (Fig. 4e). At low levels of seed survival, the qualitative outcome of the model does not change (Fig. 4f), but as seed survival increases, the area where the rare species is excluded shrinks, and instead there is a broad range of fecundities where the two species co-exist in a protected manner. Again, this is because dormancy helps the superior species to cope with the inferior species' long-lived adults that hold onto sites; the region of protected co-existence appears primarily due to a large shift to the left of the superior species' invasion boundary.

LESS-THAN-PERFECT COMPETITIVE ASYMMETRY

In this section, we relax the assumption of perfect competitive asymmetry and instead assume a weighted lottery between the competing seedlings. If M seedlings of the superior species compete with N seedlings of the inferior species, then with probability $cM/(cM+N)$ the site is won by the superior species, whereas with the remaining probability $N/(cM+N)$ the site is won by the inferior species. $c \geq 1$ measures the degree of competitive asymmetry: with $c = 1$ there is no difference in competitiveness at all, whereas $c = \infty$ corresponds to perfect competitive asymmetry. Assuming Poisson-distributed seed numbers and no seed bank as in the null model, the densities of the two species change according to the equations

$$x_{t+1} = ux_t + (1 - ux_t - vy_t)\sum_{M=1}^{\infty}\sum_{N=0}^{\infty}\frac{(\alpha x_t)^M}{M!}\mathrm{e}^{-\alpha x_t}\frac{(\beta y_t)^N}{N!}\mathrm{e}^{-\beta y_t}\frac{cM}{cM+N} \tag{3a}$$

$$y_{t+1} = vy_t + (1 - ux_t - vy_t)\sum_{M=0}^{\infty}\sum_{N=1}^{\infty}\frac{(\alpha x_t)^M}{M!}\mathrm{e}^{-\alpha x_t}\frac{(\beta y_t)^N}{N!}\mathrm{e}^{-\beta y_t}\frac{N}{cM+N} \tag{3b}$$

This model is analysed in Appendix 3. For finite fecundities, the results agree qualitatively with the null model if c is sufficiently large – that is, the null model is mathematically robust with respect to relaxing perfect competitive asymmetry. With more realistic values of c, however, there are significant differences (Fig. 5). Even with fairly strong competitive asymmetry ($c = 10$), the region of protected co-existence changes considerably compared with the case of perfect competitive asymmetry when the two species have similar adult survival probabilities (Fig. 5a,b) and changes in a similar direction (though to a lesser extent) when the superior species has much higher survival (Fig. 5c). Weakening the competitive strength of the superior species obviously favours the inferior species and, therefore, the region of protected co-existence shifts towards higher values of α. As c decreases to 1, the region of protected co-existence shrinks to the line of neutral co-existence of equally competitive species with equal lifetime seed production $[\alpha/(1-u) = \beta/(1-v)]$. When the inferior species has high adult survival compared with the superior species, protected co-existence can disappear altogether even at very large values of c. The region where the rare species is excluded shrinks eventually to the neutral line as c decreases to 1 (Fig. 5d–f).

It is informative to investigate this model at very high fecundities. With equal adult survival probabilities ($u = v$), the invasion boundaries converge to the same straight line as α and β increase, such that protected co-existence eventually disappears. Note that this is in stark contrast with the null model of perfect competitive asymmetry, where the area of protected co-existence keeps broadening towards high fecundities. At infinite fecundities, protected co-existence is thus not robust with respect to relaxing perfect competitive asymmetry, and the limits when the fecundities go to infinity ($\alpha, \beta \to \infty$) and when competitive asymmetry goes to infinity ($c \to \infty$) are not interchangeable. If the two species have

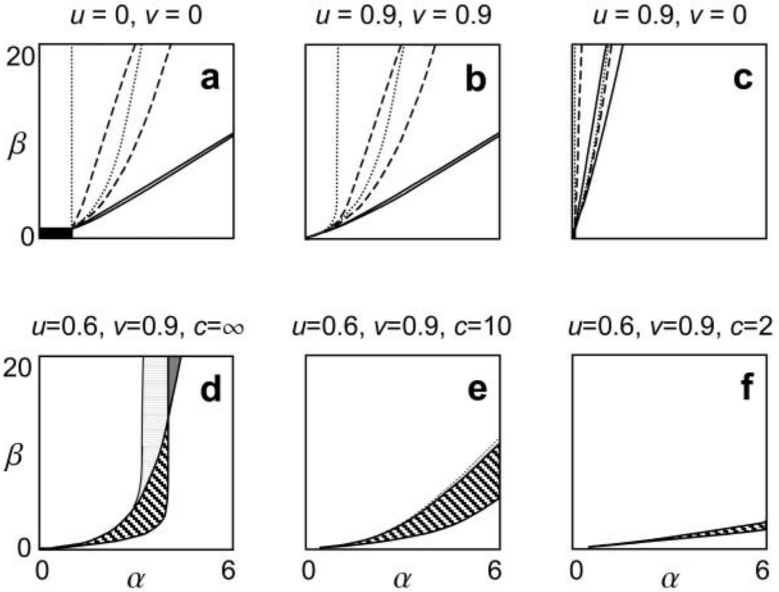

Fig. 5. Less-than-perfect competitive asymmetry. Top row of panels: the effect on protected co-existence with (a) $u = v = 0$, (b) $u = v = 0.9$ and (c) $u = 0.9$, $v = 0$. Dashed lines, $c = 10$; continuous lines, $c = 2$; dotted lines, perfect asymmetry shown for comparison. There is protected co-existence in between the lines (shading omitted for clarity). Bottom row of panels: $u = 0.6$, $v = 0.9$, with (d) perfect asymmetry, (e) $c = 10$ and (f) $c = 2$. Shading as in Fig. 1: dark grey, protected co-existence; light grey, unprotected co-existence; hatched, disadvantage of the rare species.

different adult survival probabilities, the invasion boundaries converge to parallel straight lines as α and β increase. With $u > v$, a band of protected co-existence remains even at very high fecundities ($\beta = 10{,}000$). With $u < v$ and very strong asymmetry, the rare species is excluded at low fecundities and there is protected co-existence at medium fecundities similar to the null model (see Fig. 5d); at high fecundities, however, the invasion boundaries cross for a second time, and a band with rare disadvantage appears (for $u = 0.6$, $v = 0.9$ and $c = 200$, the first crossing point is at $\alpha = 4.4$ and $\beta = 17$, whereas the second one is at $\alpha = 7.3$ and $\beta = 164$). If competitive asymmetry decreases, the two crossing points collide, the region of protected co-existence disappears and the invasion boundaries straddle an area with rare disadvantage (this happens at about $c = 100$ with $u = 0.6$, $v = 0.9$).

The band of protected co-existence or that of rare disadvantage at very high fecundities is of constant finite width: expressed as a percentage of fecundity, the size of the interval goes to zero as the fecundities go to infinity. In this sense, we recover the result of Chesson and Warner (1981) that, with infinite fecundities, the superior (inferior) species wins whenever $(c\alpha/(1 - u))/(\beta/(1 - v))$ is greater (smaller) than 1.

PARTIAL DISPLACEMENT COMPETITION

So far, we have assumed that an adult plant is not affected by seedlings that emerge in its site (replacement competition). Whether this assumption holds may depend on environmental factors (see, for example, Wedin and Tilman, 1993), and in a spatially heterogeneous environment it is conceivable that in some of the sites competition is permanently more like the replacement type, whereas in others competition is more like the displacement type. In this case, the two species will partially segregate between the site types and, therefore, a structured population model is necessary for both species. Here we investigate a simpler possibility, where in each site displacement occurs with some probability whenever an adult of the inferior species is challenged by one or more seedlings of the superior species. This could be envisaged if some kind of local, random damage (by herbivory, trampling, etc.) renders adult plants temporarily vulnerable to competitively superior seedlings. We assume that the probability of displacement is independent of the number of seedlings present in the site, and that superior adults are never displaced by inferior seedlings. In all other aspects, we retain the assumptions of the null model. Denoting the probability of displacement by $1 - w$, the population dynamical equations are

$$x_{t+1} = ux_t + (1 - ux_t - wvy_t)(1 - e^{-\alpha x_t}) \tag{5a}$$

$$y_{t+1} = wvy_t + (1 - w)vy_t e^{-\alpha x_t} + (1 - ux_t - vy_t)e^{-\alpha x_t}(1 - e^{-\beta y_t}) \tag{5b}$$

On the right-hand side of equation (5b), the first term gives the density of surviving inferior adults that cannot be displaced (e.g. no damage), whereas the second term is the density of those adults that could be displaced but escape because no superior seedling is present. Compared with equations (1a,b), the superior species wins and the inferior species loses an extra fraction $(1 - w)vy_t(1 - e^{-\alpha x_t})$ of the sites due to displacement. With $w = 1$, we recover the null model with replacement competition only. Details of the analysis of this model are given in Appendix 4.

If the inferior species is annual ($v = 0$), superior seedlings never encounter inferior adults and, therefore, there is no difference between replacement and displacement competition. Otherwise, if the two species have similar adult survival probabilities or if the superior species has higher survival, the region of protected co-existence shifts to smaller values of α as $1 - w$ increases, because displacement favours the superior species (Fig. 6a,b). If the inferior species has high adult survival probability compared with the superior species, the regions with unprotected co-existence and where the rare species is excluded shrink as displacement competition becomes more frequent (Fig. 6c,d). Under full displacement ($w = 0$), the superior species does not notice the presence of the inferior species at all: the superior species is able to invade whenever it is viable ($\alpha > 1 - u$), and its equilibrium density is not affected by the inferior species. This implies that there is no unprotected co-existence and no disadvantage of the rare species; instead, the two species can co-exist only in a protected way (Fig. 6e).

The greater the probability of displacement ($1 - w$), the greater difference is necessary between the adult survival probabilities of the inferior species and of the superior species for the rare species to be excluded at least for some combinations of α and β (Fig. 2). As in the null model, numerical investigations show that unprotected co-existence is possible whenever rare disadvantage is possible [although the region of unprotected co-existence on the (α,β) plane may be so narrow that it is hard to find numerically].

DISCUSSION

Co-existence by the competition–colonization trade-off under replacement competition requires (i) that seedlings compete with one another (this is most easily formulated in

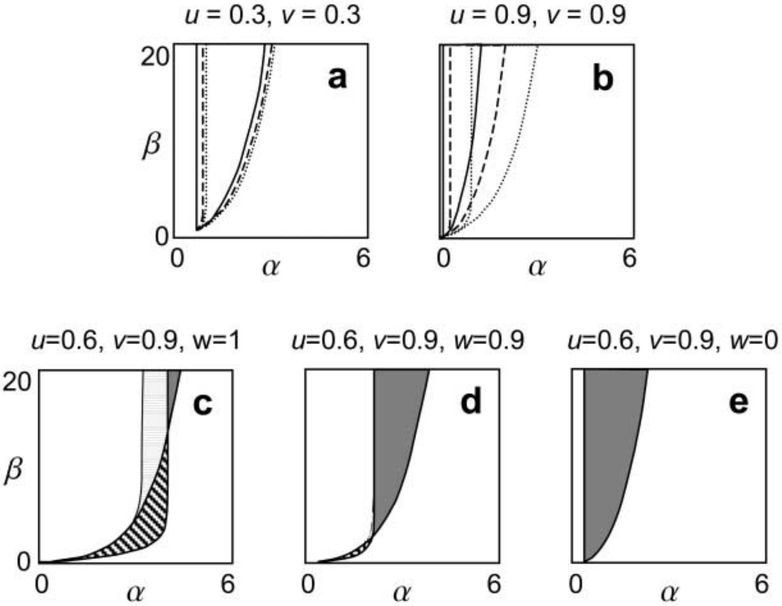

Fig. 6. Partial displacement competition. Top row of panels: the effect on protected co-existence with (a) $u = v = 0.3$ and (b) $u = v = 0.9$. Continuous lines, $w = 0$ (full displacement); dashed lines, $w = 0.75$; dotted lines, $w = 1$ (full replacement shown for comparison). There is protected co-existence in between the lines (shading omitted for clarity). Bottom row of panels: $u = 0.6$, $v = 0.9$, with (c) $w = 1$ (full replacement), (d) $w = 0.9$ and (e) $w = 0$ (full displacement). Shading as in Fig. 1: dark grey, protected co-existence; light grey, unprotected co-existence; hatched, disadvantage of the rare species.

discrete-time models where all seeds germinate at the beginning of the season), and (ii) that seed numbers are limited and dispersal is random such that, by chance, some vacant sites do not receive any superior seed. The inferior species, due to its higher fecundity, is able to persist by colonizing sites free of superior seeds. This is the mechanism underlying co-existence in Skellam's (1951) model for annual plants and it readily extends to perennials.

As we argued previously (Kisdi and Geritz, 2003), simple differential equation models have difficulties in capturing competition among seedlings [they easily violate condition (i) above]. In these models, only one seed arrives at a vacant site at a time and it instantly turns into an established adult. If seedlings never compete with one another, the superior species cannot realize its competitive advantage under replacement competition and is excluded by the more fecund 'inferior' species (if adult survival probabilities also differ, then the species with greater lifetime seed production wins). Co-existence is thus impossible by the competition–colonization trade-off alone, although it may occur due to partial displacement competition (Armstrong, 1976; Nowak and May, 1994) or competition among adults (Yu and Wilson, 2001).

In discrete-time models that assume very high fecundities [the opposite of condition (ii) above], co-existence by the competition–colonization trade-off alone is again impossible under replacement competition. Here each site receives a representative sample of the seeds dispersed by the entire population and, consequently, the superior species wins each colonizable site. Chesson and Warner (1981) showed that if competition is not perfectly asymmetric, then the species that maximizes the product of competitiveness and lifetime seed production will outcompete every other species. Co-existence may occur if competitive rank varies spatially either in a persistent way (Pacala and Tilman, 1994; see also Abrams, 1996) or by changing both temporally and spatially ('uniformly variable' environment; Comins and Noble, 1985), or co-existence may be facilitated by mechanisms unrelated to the competition–colonization trade-off (such as temporally stochastic environments; Chesson and Warner, 1981).

With discrete generations and limited fecundity, we found that co-existence by the competition–colonization trade-off is not only possible, but also robust with respect to introducing seed banks (Fig. 4) and, of course, also with respect to partial displacement competition (Fig. 6). Co-existence is, however, sensitive to changes in competitive asymmetry (Fig. 5). If the inferior species has higher adult survival probability than the superior one, then protected co-existence is possible under the simple assumption of perfect competitive asymmetry, but may not be possible even under biologically very strong asymmetry. Protected co-existence of a short-lived superior species with a long-lived inferior species by the replacement competition–colonization trade-off thus appears to be rather unlikely in nature.

Perennials under replacement competition can exhibit the exclusion of the rare species (whichever of the two is rare) and unprotected co-existence (both co-existence and a single-species equilibrium are locally stable, but co-existence is not persistent under large perturbations). These are qualitatively new phenomena compared with models of the competition–colonization trade-off assuming annuals (Skellam, 1951) or models of displacement competition (e.g. Levins and Culver, 1971; Nee and May, 1992; Tilman, 1994). Unprotected co-existence leads to a hysteresis effect highly significant for the conservation of diversity. A continuous decrease in the density of sites can lead to abrupt extinction of the superior species: the population crashes without rarity warning of impending extinction. Worse, increasing site density to the level preceding extinction is not sufficient to restore co-existence (unless the superior species is reintroduced in very large numbers), because the inferior species is still resistant to the invasion of the superior species when the latter is rare. Co-existence can be restored by increasing site density substantially if this ensures protected co-existence (Fig. 3a), or otherwise only via a complicated route of first increasing and then decreasing site density (Fig. 3b). Our model is a new addition to the lengthening list of hysteresis effects found in many diverse ecological systems (e.g. May, 1977; Cushing, 1992; Hanski and Gyllenberg, 1993); hysteresis is also known in an evolutionary context (e.g. Kisdi and Geritz, 1999; Ronce and Kirkpatrick, 2001; Dercole *et al.*, 2002). Populations abruptly crashing, or at least declining very sharply to extinction, have also been found in various ecological and evolutionary systems (e.g. Matsuda and Abrams, 1994; Gyllenberg and Parvinen, 2001; Abrams, 2002; Gyllenberg *et al.*, 2002).

Unprotected co-existence and the exclusion of the rare species occur only if the adult survival probability of the inferior species is sufficiently higher than that of the superior species (Fig. 2). These phenomena disappear if competition is partly of the displacement type (Figs 2 and 6), and are also sensitive to seed dormancy (Fig. 4). The exclusion of the rare species is, however, robust with respect to relaxing the assumption of perfect competitive asymmetry, and it disappears only when competitive asymmetry vanishes (Fig. 5).

In this paper, we have investigated the co-existence of only two species with fixed life-history parameters and no evolution. Will this co-existence be maintained on an evolutionarily time-scale? That is, are the co-existing species likely to evolve fecundities and associated adult survival probabilities that remain within the region of co-existence? In the simplest case, the answer is trivial and negative. It is easy to prove that both species evolve to maximize their lifetime production of seeds (this is a direct consequence of density regulation though seedling death; see Mylius and Diekmann, 1995; Pásztor *et al.*, 1996). Assume that the two species are closely related such that their life-history trade-offs are similar, and in particular competitive superiority does not entail a significant cost. This may be the case if competitive superiority is, for example, due to a metabolically 'cheap' allelopathic agent. Then the two species will evolve approximately the same fecundities and associated adult survival probabilities, which excludes co-existence: with everything else being equal, the competitively superior species excludes the inferior species.

Among species with otherwise similar life histories, the competition–colonization trade-off exists when competitive superiority is costly. For example, seedlings from larger seeds may be superior to seedlings from smaller seeds (Black, 1958; Cipollini and Stiles, 1991; Houssard and Escarré, 1991), but given a certain amount of nutrients for seed production, increasing seed size inevitably means decreasing seed number. The size–number trade-off then implies the competition–colonization trade-off (with large-seeded species being good competitors and small-seeded species being good colonizers) and leads to evolutionarily stable co-existence (Geritz, 1995). The number of co-existing species increases with the degree of competitive asymmetry (Geritz *et al.*, 1999). The ideal case of perfect asymmetry implies infinitely many species in the evolutionarily stable coalition (barring any Allee effects), but even a slight deviation from perfect asymmetry makes only a finite number of co-existing species possible (Geritz *et al.*, 1999; Adler and Mosquera, 2000; see also M. Gyllenberg and G. Meszéna, submitted).

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APPENDIX 1: ANALYSIS OF THE NULL MODEL

Assume that the inferior species is in equilibrium [$y = \hat{y}$, where $\hat{y}$ is the solution of the single-species equilibrium equation $\hat{y} = v\hat{y} + (1 - v\hat{y})(1 - e^{-\beta\hat{y}})$; cf. equation (1)]. The superior species is able to invade when rare if its invasion growth rate, $\lim_{x_t \to 0} (x_{t+1}/x_t)$, is greater than one. Substituting x_{t+1} from equation (1a), we get

$$\lim_{x_t \to 0} \frac{x_{t+1}}{x_t} = u + (1 - v\hat{y}) \lim_{x_t \to 0} \frac{1 - e^{-\alpha x_t}}{x_t} = u + (1 - v\hat{y})\alpha > 1$$

or $(\alpha/(1 - u))(1 - v\hat{y}) > 1$. Analogously, the inferior species is able to invade the superior species' equilibrium population if $(\beta/(1 - v))(1 - u\hat{x})e^{-\alpha\hat{x}} > 1$. In both conditions, the rare species' lifetime reproductive success (lifetime seed number times the probability of surviving competition and thus becoming an established adult) needs to exceed 1.

To obtain the invasion boundaries by setting the lifetime reproductive success equal to 1 and solving for β as a function of α (with fixed values of u and v), the equilibrium densities $\hat{x}$ and $\hat{y}$ must be calculated. The single-species equilibrium equations [$\hat{x} = u\hat{x} + (1 - u\hat{x})(1 - e^{-\alpha\hat{x}})$ for the superior species] have at most one non-trivial solution ($0 < \hat{x} < 1$), which can be obtained, for example, by bisection. It is much easier, however, to assume a particular value of $\hat{x}$ and solve the equilibrium equation analytically for the corresponding $\alpha = [\ln((1 - u\hat{x})/(1 - \hat{x}))]/\hat{x}$ (holding u fixed). Once corresponding values of α and $\hat{x}$ are known, the critical value of β, above which value the inferior species can invade, follows immediately; by varying $\hat{x}$, one obtains the inferior species' invasion boundary. The superior species' invasion boundary is obtained similarly. The invasion boundaries delineate the regions of protected co-existence and of rare disadvantage in Fig. 1.

For rare disadvantage (i.e. exclusion of the rare species regardless of which species is rare) to occur at low fecundities, the inferior species' invasion boundary must be steeper at the lowest viable point $(\alpha, \beta) = (1 - u, 1 - v)$ than the superior species' invasion boundary. Using implicit differentiation to calculate the slope of the superior species' invasion boundary, we get $\frac{\mathrm{d}\beta}{\mathrm{d}\alpha} = \frac{1 - v\hat{y}}{\alpha v(\partial\hat{y}/\partial\beta)}$, which simplifies to $\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|_{\substack{\alpha = 1 - u \\ \beta = 1 - v}} = \frac{1}{(1 - u)v(\partial\hat{y}/\partial\beta)}$ at the point $(\alpha, \beta) = (1 - u, 1 - v)$ because $\hat{y}$ is zero at the border of viability. At this point, $(\partial\hat{y}/\partial\beta)$ can be calculated by implicit differentiation of the inferior species' equilibrium equation $\hat{y} = v\hat{y} + (1 - v\hat{y})(1 - \mathrm{e}^{-\beta\hat{y}})$, by first approximating $\mathrm{e}^{-\beta\hat{y}}$ with $1 - \beta\hat{y} + \frac{1}{2}(\beta\hat{y})^2$ for low equilibrium densities, to obtain $\left.\frac{\partial\hat{y}}{\partial\beta}\right|_{\beta = 1 - v,\ \hat{y} = 0} = \frac{2}{1 - v^2}$. Substituting this result, we finally obtain the slope of the superior species' invasion boundary, $\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|^{(\mathrm{sup})}_{\substack{\alpha = 1 - u \\ \beta = 1 - v}} = \frac{1 - v^2}{2(1 - u)v}$. An analogous calculation for the slope of the inferior species' invasion boundary yields $\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|^{(\mathrm{inf})}_{\substack{\alpha = 1 - u \\ \beta = 1 - v}} = \frac{2(1 - v)}{1 - u^2}$. The inferior species' invasion boundary is steeper if $\frac{2(1 - v)}{1 - u^2} > \frac{1 - v^2}{2(1 - u)v}$ or, equivalently, if $\frac{1}{1 - v} - \frac{1}{1 - u} > \frac{1}{2}$; this condition is shown in Fig. 2.

The line of the saddle-node bifurcation that delineates the region of unprotected co-existence in Fig. 1d was found by the following numerical procedure. A saddle-node bifurcation occurs when, on the (x,y) plane, the zero-growth isoclines of the two species are tangent to each other – that is, they have a single common point where their slope is equal. Three equations are thus satisfied at the point of the saddle-node bifurcation: the superior species has zero growth, i.e. $x = ux + (1 - ux - vy)(1 - \mathrm{e}^{-\alpha x})$ from equation (1a) or, equivalently,

$$y = \frac{1}{v}\left[1 - x\frac{\mathrm{e}^{\alpha x} - u}{\mathrm{e}^{\alpha x} - 1}\right]; \tag{A1}$$

the inferior species has zero growth, i.e. $y = vy + (1 - ux - vy)\mathrm{e}^{-\alpha x}(1 - \mathrm{e}^{-\beta y})$ from equation (1b) or, equivalently,

$$x = 1 - y\frac{\mathrm{e}^{\beta y} - v}{\mathrm{e}^{\beta y} - 1} \tag{A2}$$

[where we used $\mathrm{e}^{-\alpha x}(1 - ux - vy) = 1 - x - vy$ from the superior species' zero growth condition]; and the two curves determined by (A1) and (A2) are tangent to each other. To derive the latter condition, we take the derivative of (A1) and simplify it using the zero growth conditions yielding

$$\frac{\mathrm{d}y^{(\mathrm{sup})}}{\mathrm{d}x} = \alpha\frac{(1 - ux - vy)(1 - x - vy)}{(1 - u)vx} - \frac{1 - vy}{vx} \tag{A3}$$

The derivative of (A2) is simplified to

$$\frac{\mathrm{d}x^{(\mathrm{inf})}}{\mathrm{d}y} = \beta \frac{(1-x-vy)(1-x-y)}{(1-v)y} - \frac{1-x}{y} \tag{A4}$$

The two zero-growth isoclines have equal slopes if

$$\frac{\mathrm{d}y^{(\mathrm{sup})}}{\mathrm{d}x} \cdot \frac{\mathrm{d}x^{(\mathrm{inf})}}{\mathrm{d}y} = 1 \tag{A5}$$

To find numerically the (α, β) pairs where the three conditions of the saddle-node bifurcation, (A1), (A2) and (A5), are satisfied for given values of u and v, first we choose α and x arbitrarily, find y using (A1) and calculate β by solving (A2). Then we have a pair (α, β) with the corresponding values of x and y that satisfy the first two conditions. Condition (A5) is checked numerically, and the procedure is repeated for a large set of initial α and x values to find the line of saddle-node bifurcation in Fig. 1. Next, we repeated the same procedure for various adult survival probabilities (u, v). We found saddle-node bifurcations (and hence unprotected co-existence) for the same combinations of u and v where rare disadvantage also exists (Fig. 2).

APPENDIX 2: ANALYSIS OF THE MODEL WITH SEED BANKS

To calculate the invasion boundary of the inferior species, we set $y = 0$ in equation (2a) and solve it for the equilibrium density of the superior species alone, $\hat{x}$, by bisection. The inferior species is able to invade if its lifetime reproductive success when rare,

$$\frac{\beta}{1-v}\left[(1-\hat{x})\mathrm{e}^{-\alpha\hat{x}} + (1-u)^2\hat{x}\sum_{\eta=1}^{\infty}\sum_{a=0}^{\infty}u^{a+\eta-1}s^{\eta-1}\exp\left(-\alpha\hat{x}\frac{1-s^{a+\eta}}{1-s}\right)\right] \tag{A6}$$

is greater than one. Setting (A6) equal to one, it can be solved directly for the critical value of β above which invasion is possible.

The lifetime reproductive success of the superior species, when rare in the equilibrium population of the inferior species, is much simpler,

$$\frac{\alpha}{1-u}\left[1-\hat{y}+\hat{y}\frac{1-v}{1-sv}\right] \tag{A7}$$

because the superior seed will win the site if only it stays alive in the seed bank until the adult dies. This occurs with probability $(1-v)/(1-sv)$ and applies to the fraction $\hat{y}$ of all sites, which were occupied when the superior seed arrived; otherwise, the superior seed surely wins the site. Setting (A7) equal to one, we obtain the critical value of α above which the superior species is able to invade.

The line of the saddle-node bifurcation at the left edge of the region of unprotected co-existence in Fig. 4e–g was found by the same conditions as in the null model (see Appendix 1). However, since the analogue of (A2) for the present case with seed banks cannot be solved for β explicitly, we used a continuation technique implemented in Mathematica™ to find simultaneous solutions to the analogues of (A1), (A2) and (A5) by the Newton-Raphson method, starting with the known solutions for $s = 0$ and increasing s incrementally. Unprotected co-existence was not checked elsewhere.

APPENDIX 3: ANALYSIS OF THE MODEL WITH LESS-THAN-PERFECT COMPETITIVE ASYMMETRY

The inferior species is able to invade the equilibrium population of the superior species if its lifetime reproductive success when rare is greater than one; that is, if

$$\frac{\beta}{1-v}(1-u\hat{x})\sum_{M=0}^{\infty}\frac{(\alpha\hat{x})^{M}}{M!}\,\mathrm{e}^{-\alpha\hat{x}}\,\frac{1}{cM+1}>1 \tag{A8}$$

where the equilibrium density of the superior species alone, $\hat{x}$, is the same as in the null model. For the numerical evaluation of (A8), note that the result of the infinite summation is in between the truncated summation

$$\sum_{M=0}^{L}\frac{(\alpha\hat{x})^{M}}{M!}\,\mathrm{e}^{-\alpha\hat{x}}\,\frac{1}{cM+1}$$

and

$$\sum_{M=0}^{L}\frac{(\alpha\hat{x})^{M}}{M!}\,\mathrm{e}^{-\alpha\hat{x}}\,\frac{1}{cM+1}+\left[1-\sum_{M=0}^{L}\frac{(\alpha\hat{x})^{M}}{M!}\,\mathrm{e}^{-\alpha\hat{x}}\right]$$

For any set of parameters, L can be chosen such that both the lower and the upper estimates of (A8) are on the same side of 1. We evaluated (A8) on a 50 × 50 grid covering the planes shown in Fig. 5, and determined the inferior species' invasion boundary by interpolation. The invasion boundary of the superior species is obtained analogously, using that its lifetime reproductive success when rare is

$$\frac{\alpha}{1-u}(1-v\hat{y})\sum_{N=0}^{\infty}\frac{(\beta\hat{y})^{N}}{N!}\,\mathrm{e}^{-\beta\hat{y}}\,\frac{c}{c+N} \tag{A9}$$

To find unprotected co-existence, we simulated the joint population dynamics given by equations (3a,b) and determined whether the invading species outcompetes the other species or whether they reach a joint equilibrium outside the region of protected co-existence.

APPENDIX 4: ANALYSIS OF THE MODEL WITH PARTIAL DISPLACEMENT

The methods used for the analysis of the null model (Appendix 1) generalize to this model straightforwardly. The superior species can invade the inferior species if $(\alpha/(1-u))\,(1-wv\hat{y})>1$, whereas the inferior species can invade the superior species if $[\beta(1-u\hat{x})+(1-w)v]\mathrm{e}^{-\alpha\hat{x}}/(1-wv)>1$. The invasion boundary of the superior species is steeper at $\alpha=1-u$, $\beta=1-v$, and hence there is a region of rare disadvantage if $u<(2wv-1+v)/(2wv+1-v)$ (Fig. 2). The conditions for the saddle-node bifurcation line in Fig. 6 are:

$$y=\frac{1}{wv}\left[1-x\,\frac{\mathrm{e}^{\alpha x}-u}{\mathrm{e}^{\alpha x}-1}\right] \tag{A10}$$

(from population dynamical equilibrium in equation 5a),

$$\beta = -\frac{1}{y}\ln\left[1 - y\,\frac{1 - v(w + (1 - w)\mathrm{e}^{-\alpha x})}{(1 - ux - vy)\mathrm{e}^{-\alpha x}}\right] \tag{A11}$$

(from population dynamical equilibrium in equation 5b), and

$$\frac{1}{wv}\left[\frac{(1 - u)\alpha x\mathrm{e}^{\alpha x}}{(\mathrm{e}^{\alpha x} - 1)^2} - \frac{\mathrm{e}^{\alpha x} - u}{\mathrm{e}^{\alpha x} - 1}\right] = \frac{\alpha(1 - w)vy + (u + \alpha(1 - ux - vy))(1 - \mathrm{e}^{-\beta y})}{(vw - 1)\mathrm{e}^{\alpha x} + v(\mathrm{e}^{-\beta y} - w) + \beta(1 - ux - vy)\mathrm{e}^{-\beta y}} \tag{A12}$$

which is the analogue of (A5).