

A SPECTER OF COEXISTENCE: IS CENTRIFUGAL COMMUNITY ORGANIZATION HAUNTED BY THE GHOST OF COMPETITION?

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ABSTRACT

In a centrifugally organized community species prefer the same habitat (called “core”) but differ in their secondary habitat preferences. The first model of centrifugal community organization (CCO) predicted that optimally foraging, symmetrically competing species would share use of the core habitat at all density combinations. But one might also assume that the competition in the core habitat is asymmetrical, that is, that one of the species (the dominant) has a behavioral advantage therein. In this study, we asked how should habitat use evolve in a centrifugally organized community if its species compete asymmetrically in the core habitat? To address this question we developed an “isoleg model”. The model predicts that in a centrifugally organized community, asymmetric competition promotes the use of the core habitat exclusively by the dominant species at most points in the state space. The separation of the core habitat use by the species (“the ghost of competition past”) may be either complete or partial (“partial ghost”), and behavior at the stable competitive equilibrium between the species could determine whether coexistence should occur at the “complete-” or the “partial ghost” regions. This version of CCO should be a common feature of competitive systems.

Keywords: centrifugal community organization, isoleg, asymmetric competition, density dependent habitat selection, ghost of competition past

INTRODUCTION

The study of community organization allows classification of community types based on key properties such as niche and competitive relationships (Rosenzweig, 1981; Pimm et al., 1985; Rosenzweig and Abramsky, 1986; Morris, 1988; Rosenzweig, 1991; Brown, 1996; Wisheu, 1998). The classification was developed originally in the context of

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habitat selection (Rosenzweig, 1981), but may also refer to other niche dimensions such as resource type (Pimm et al., 1985) or even time (Ziv et al., 1993). Since the original development of this concept, at least twenty community organization forms have been identified (see reviews in: Morris, 1988; Rosenzweig, 1991; Brown, 1996; Wisheu, 1998). We suggest that these can be grouped into three basic niche relationship types: exclusive, nested, and centrifugal (Rosenzweig, 1991; Wisheu, 1998).

Exclusive niches refer to the classical MacArthurian concept of niche differentiation (MacArthur and Levins, 1967; MacArthur, 1972): the fitness peaks of the fundamental niches of competing species occur in different regions along a resource or habitat gradient(s) (Fig. 1). Interspecific competition is symmetrical and each species specializes on a different peak. In contrast, the peaks of “nested niches” are stacked one on top of the other in the same region of a niche variable (Fig. 1). Coexistence is based on a specialist–generalist trade-off: the specialist has a higher but narrower fundamental niche. Its specialization allows it to outcompete the generalist in the part of the niche space represented by the peak. But the broader niche of the generalist allows it to exploit resources unavailable to the specialist. Such competition is asymmetric. Centrifugal niches represent a combination of the exclusive and nested niche principles. They resemble nested niches in that each species reaches its peak fitness at approximately the same value of niche (termed, the core). But, the niches of a centrifugal set of species do differ in their secondary habitats, i.e., the niche positions of those values that are almost

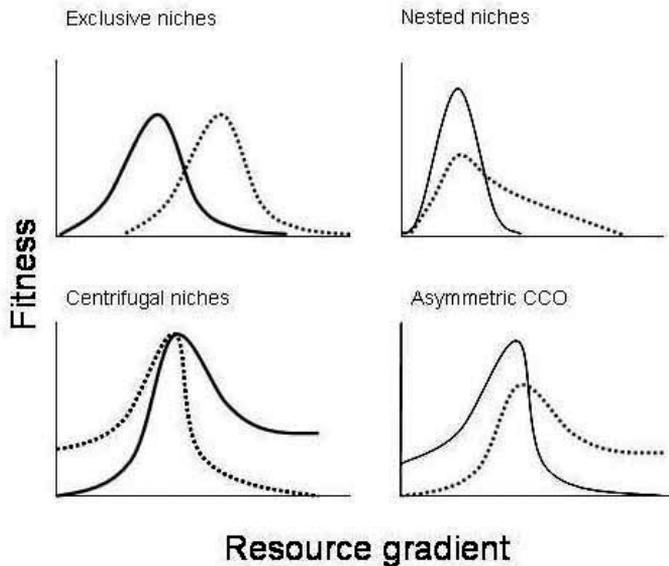


Fig. 1. The three basic forms of niche relations: exclusive, nested, and centrifugal. Also showing the expected form of a special case of centrifugal niche relations where interspecific competition is asymmetric, the asymmetric centrifugal community organization.

as useful as the core. This difference in specialization resembles that of exclusive niches (Rosenzweig and Abramsky, 1986) (Fig. 1) and often leads to the separate use of the secondary habitats by the competitors.

Rosenzweig and Abramsky's (1986) model predicts that at low population densities both species should use only the core habitat. As its density increases, each species should spread out beyond the core into its own distinct secondary habitat. At very high densities, the two competing species should use all three habitats.

In this study, we modify a single assumption about centrifugal organization. We make competitors of the centrifugal mode asymmetric in the core habitat. That is, we assume that one of the species has a behavioral advantage (the dominant). The dominant species capitalizes on its strength to reduce the value of the core habitat for the subordinate species. The subordinate species may, thus, be forced to its secondary habitat in apparent preference to the core (Fig. 1).

Both exclusive and nested niche relationships have received much empirical support (Rosenzweig, 1989; Rosenzweig, 1991; Wisheu, 1998). Centrifugal organization, on the other hand, has received very little. However, our new centrifugal model produces a wealth of novel predictions, suggesting that centrifugally organized communities may be much more common than previously recognized.

THE MODEL

Isolog theory (Rosenzweig, 1981) assumes that individuals are optimal foragers that select habitats to maximize their fitness in the face of varying population sizes (Fretwell and Lucas, 1969; Fretwell, 1972). What is an isolog? It is a line drawn in the state space of species densities such that the optimal strategy of habitat utilization for the individuals of one species is equal at each point on the line. The most important isologs divide regions of qualitatively distinct optimal behaviors, especially state-space points at which there is a total rejection of a habitat type from those at which there is at least some acceptance (Rosenzweig, 1991).

Following the previous model (Rosenzweig and Abramsky, 1986), we focus on a system with a pair of competing species in a 3-habitat landscape (the general theory, however, can apply to any competitive system with n -species and $n+1$ habitats). All species share a preference for a single habitat but differ in their secondary habitat preferences. We make the model asymmetric, by assuming that one of the species has a behavioral advantage (the dominant). By definition, a dominant individual reduces the value of the core habitat for the subordinate species much more than a member of the subordinate species reduces its value for the dominant. The subordinate species may thus be forced to use its secondary habitat in apparent preference to the core.

In an appendix, we deduce all parts of the isolog model. In this section however, we shall describe the fitness–density graph of one of the species when alone. Then we shall present an example of the process of deducing its isologs when the other species is also present. Finally, we shall describe the entire optimal-habitat-use isolog map with both species isologs overlaid on it.

FITNESS–DENSITY LINES OF THE SPECIES WHEN ALONE

Following Fretwell and Lucas (1970), we plot population density against fitness in a particular habitat. The ranking of the line's intercept with the fitness axis indicates the species innate habitat preference. In this system, we assume that both species prefer habitat *a* (the core habitat) but differ in their preference for habitats *b* and *c* (the marginal habitats) (Fig. 2A). It follows that at low densities, both species should use only the core habitat. As density increases fitness in the core habitat decreases due to intraspecific competition. At certain density (N_{1a}) of the dominant species, its fitness in the core habitat decreases to the level where it equals that in the unoccupied secondary habitat. For simplicity, we assume that this decrease is monotonic and linear. From this density and the above, the ideal-free-distribution theory predicts that dominant animals will distribute themselves such that the per capita fitness is equal in both habitats (Fretwell and Lucas, 1970). At an even higher density, the per capita fitness in the core and the secondary habitat might equal that in the tertiary habitat. From this density and above, the species should use all three habitats (Fig. 2A). Precisely the same predictions hold for the subordinate species, except at different threshold densities.

FITNESS–DENSITY LINES OF ASYMMETRICALLY COMPETING SPECIES

What happens in the presence of a competing species? Since in the CCO system the second species prefers the same primary habitat it would occupy the core habitat first, thereby reducing the fitness reward for the first species. This reduction would be

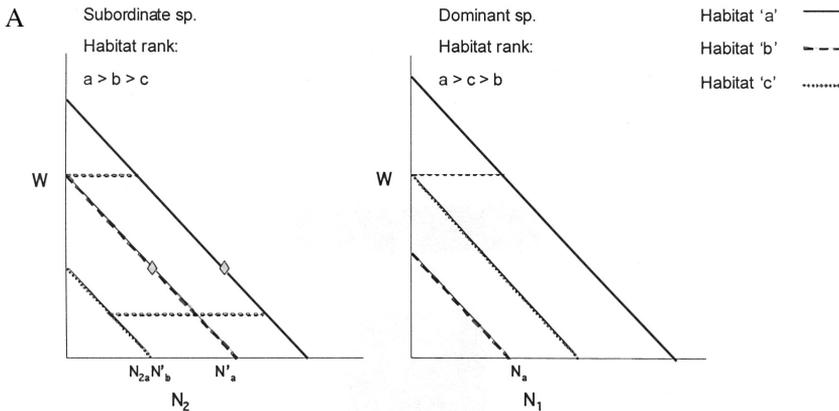


Fig. 2A. Illustration of the hypothetical relationship between fitness (W) and density (N) (fitness–density line) of the subordinate (S) and dominant (D) species when by themselves. The two species share a preference for the same core habitat (habitat *a*) but have distinct preferences for their secondary habitats (*b* and *c*, respectively). As density increases, the fitness in that habitat decreases. At density N_{1a} and N_{2a} the fitness in the occupied core habitat is equal to that in the unoccupied secondary habitat. Similarly, at density N' , which is the sum of the species densities at the core and the secondary habitats ($N'_a + N'_b$, respectively), fitness is equal in all three habitats. At higher densities the species are distributed among the two or three habitats such that the per capita fitness is equal among the habitats.

reflected as a monotonic, although not necessarily linear, decrease in the intercept of the fitness–density line of this habitat (Fig. 2B). For simplicity, we assume that adding the second species would affect only the intercept and not the slope of this line. In symmetric competitive systems the relative reduction in the quality of the core habitat by an incremental increase of the other species densities is approximately similar for the two species. In asymmetric systems, on the other hand, the dominant species would reduce the core habitat’s quality for the subordinate far more than the subordinate would for the dominant. As in the shared-preference model (Pimm et al., 1985; Abramsky et al., 1990), this would, eventually, result in reversal of the habitat preferences of the subordinate species such that at and beyond a certain density of the dominant, it would apparently prefer its secondary habitat over the core habitat. The ranking of habitat preferences of the dominant species would, on the other hand, remain intact (Fig. 2C).

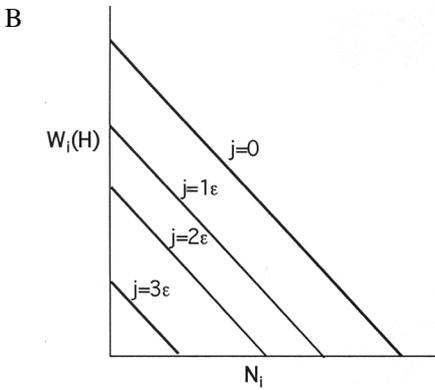


Fig. 2B. The effect of increasing density (ϵ) of one competing species (j) in a given habitat (H) on the fitness–density line ($W_i(H)$), N_i , respectively) of the other species (i) in that habitat. As the density of one competing species increases ($1\epsilon, 2\epsilon, \dots, n\epsilon$), the intercept of the fitness–density line of the other species gradually decreases.

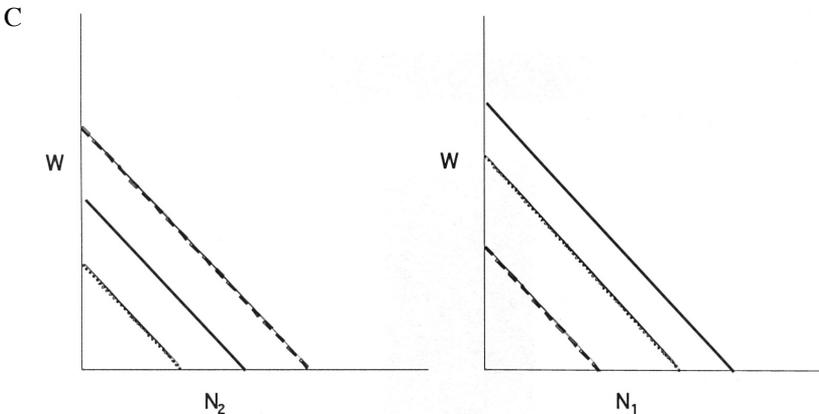


Fig. 2C. The fitness–density lines of the two species in the presence of one another. The dominant species retains its original ranking of its habitat preferences. For the subordinate, the presence of the dominant species in the core habitat suppresses its expected fitness there to the extent that it now perceives its secondary habitat as superior to the core.

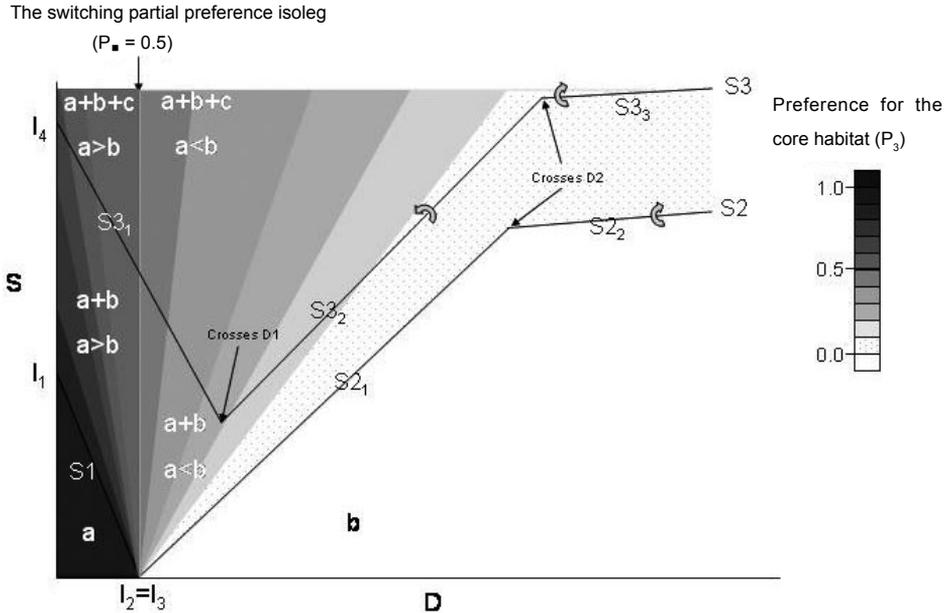


Fig. 3A. An illustration of the subordinate species (S) isoleg diagram. The subordinate species has three isolegs. The first (S1), indicates choice between one or two habitats (a or a and b , respectively). At its intercept with the dominant species (D) axis (I_2) its fitness–density line in the core habitat overlaps exactly with that of its secondary habitat. This is also the location of the intercept of the switching-preference partial-preference isoleg. To its left the subordinate prefers habitat a and to its right it prefers habitat b . The second isoleg (S2) represents choice between using only habitat b to using a and b combined (but with preference for b). Its intercept with the dominant species density axis (I_3) is assumed to overlap with (I_2). S2 is composed of two sections whose slopes are dictated by their intersection with the dominant's isolegs. Between S1 and S2 there is a range of partial preference isolegs where at least habitat a and b are being used but the relative preference for a decreases with the dominant's density (see legend). The third isoleg (S3) depicts the transition between use of two to use of three habitats. It is composed of three sections with different slopes dictated by its intersection with the dominant species' isolegs. Lowercase letters indicate the habitats being used. Comparison operators indicate habitat preferences. Straight arrows indicate the location of intersects with the dominant's isolegs, crescent-shaped arrows indicate the direction of the rotation of an isoleg section following an intersection with the isolegs of the other species, and subscript numbers indicate the isoleg section.

THE SUBORDINATE SPECIES ISOLEGS

The subordinate species (S) has three isolegs: the first (S1) describes the shift from using only the core habitat to using also the secondary habitat, the second (S2) describes the shift from using only the secondary to using also the core habitat, and the third (S3) describes the shift from using two habitats to using all three habitats.

The intercept of S1 with the subordinate density axis (I_1) (Fig. 3A) describes the density where, in the absence of the dominant species, the fitness in the core and the fitness in the secondary habitat are equal ($N_{2,a}$ in Fig. 2A). Introducing the dominant gradually reduces the quality of the core habitat (Fig. 2B), thereby reducing the threshold den-

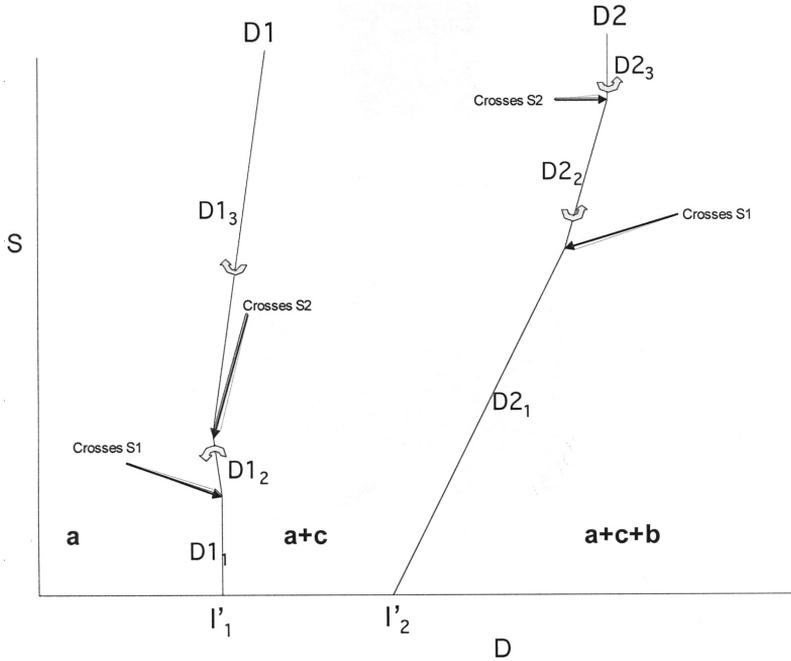


Fig. 3B. An illustration of the dominant species (D) isoleg diagram. In low densities the dominant species uses only the core habitat (habitat *a*). At higher densities it starts using two habitats, its primary (habitat *a*) and secondary (habitat *c*). D1 is the isoleg separating these two behavioral regions. At even higher densities it starts using all three habitats. This transition is depicted by the isoleg D2. I'_1 and I'_2 are the intercepts of these isolegs with their own density axis, respectively. Slope of the isolegs may change as they intersect the subordinate's isolegs. Lowercase letters indicate the habitats being used, comparison operators indicate habitat preferences, straight arrows indicate the location of intersects with the dominant's isolegs, crescent-shaped arrows indicate the direction of the rotation of an isoleg section following an intersection, and subscript numbers indicate the isoleg section.

sity for using the two habitats. This is reflected in a negatively sloped isoleg (Fig. 3A) (Rosenzweig and Abramsky, 1986). The intercept of this isoleg with the dominant's species density axis (I_2) (Fig. 3A) occurs when the dominant's densities are high enough to make the fitness–density lines of habitat *a* and *b* coincide.

The second isoleg of the subordinate (S2) has two sections: one with a positive slope ($S2_1$) and the other ($S2_2$) tilted clockwise (Fig. 3A). As densities of the dominant continue to increase, the fitness–density line of habitat *a* falls below that of habitat *b* (Fig. 2C). Now, in low intraspecific densities individuals of the subordinate species should first occupy habitat *b*. The subordinate should resume use of both habitats *a* and *b* only if N2 densities increase. The higher the density of the dominant, the lower should be the intercept of the fitness–density line for habitat *a* (Fig. 2B), and the higher should be the subordinate's intraspecific threshold densities. This is reflected as a positively sloped

isoleg section ($S2_1$) (Fig. 3A). The intercept of $S2_1$ with the dominant's density axis depends on our assumption regarding the cost of habitat selection (Rosenzweig, 1981). If habitat selection is cost-free, this intercept is equal to $S1$'s intercept (I_2) (Rosenzweig, 1986). However, if habitat selection is costly, then this intercept will occur further to the right (Appendix, Version A) (Pimm et al., 1985). Here, for simplicity, we assume no cost (Fig. 3A). In between $S1$ and $S2_1$ lies a region of partial preference isolegs (Brown and Rosenzweig, 1986) where the two habitats are being used but the proportional use of the core habitat gradually decreases, from left to right, in a fan-like fashion from 1 to 0 (Abramsky et al., 1990) (Fig. 3A). When the fitness-density lines of habitat a and b coincide exactly, the partial preference for habitat a equals 0.5 (Fig. 3A). We term this partial preference isoleg "the switching preference isoleg" since to its left the subordinate species prefers habitat a , whereas to its right it prefers habitat b . In Fig. 3A we draw it, arbitrarily, as perpendicular but it can attain any slope (Abramsky et al., 1990). At some point, $S2$ crosses the dominant's first isoleg ($D1$), which is where the dominant starts using its secondary habitat (habitat c). This should not affect $S2$ because the dominant still does not affect the quality of habitat b . However, when crossing the dominant's second isoleg ($D2$), where the dominant starts using habitat b , $S2$ should rotate clockwise ($S2_2$) (Fig. 3A) because from here on, the dominant suppresses the subordinate's fitness in habitat b , which is currently the subordinate's best habitat. The exact slope will depend on the relative habitat-specific competitive effect. If the dominant's competitive effects in habitat a and b are similar, then $S2_2$ should be horizontal (slope = 0). If the competitive effect is stronger in habitat a , the slope should remain positive but shallower, and if it is the reverse then the slope should become negative (we believe that the former is more likely) (Fig. 3A).

The subordinate's third isoleg ($S3$) has three sections. The first section ($S3_1$) has a negative slope parallel to that of $S1$ (Fig. 3A) because the effect of reducing the quality of the core habitat by the dominant species has a similar effect on reducing the threshold density for using two or three habitats. It is important to note that $S3$ can never cross $S2$ since, by definition, the density necessary for using three habitats must always be greater than that for using two habitats. At most, $S3$ can converge into $S2$, which means that for the subordinate habitat, c would no longer be a viable choice (the intercept of its fitness density line ≤ 0) (Appendix, Version C). When $S3$ intersects with the dominant's first isoleg ($D1$) it should rotate counterclockwise ($S3_2$) (Fig. 3A). Its exact slope depends, as discussed above, on the relative habitat-specific competitive effect (we believe that a positive slope is more likely since the competitive effect of the dominant in its secondary habitat (habitat c) should be greater than in its primary habitat (habitat a) because the former is the habitat to which the subordinate is least adapted). As discussed above regarding the second section of $S2$ ($S2_2$), $S3$ should tilt clockwise ($S3_3$) when crossing the dominant's second isoleg (Fig. 3A).

THE DOMINANT SPECIES ISOLEGS

The dominant species (Fig. 3B) has two isolegs: The first ($D1$) depicts the threshold density combinations in which the dominant species shifts from using only the core

(habitat *a*) to using also its secondary habitat (habitat *c*). The second (D2) describes the threshold density combinations for using also the tertiary habitat (habitat *b*). Both isolegs have three sections resulting from their intersections with the subordinate's isolegs (Fig. 3A).

We assume that due to its strong interspecific competitive effect the intercept of the dominant's first isoleg (D1) with its own density axis (I'_1) (Fig. 3B) should occur to the right of I_2 . There the subordinate species uses only its secondary habitat (habitat *b*) (Fig. 3A). Thus, since the habitat use behavior of the subordinate species does not affect that of the dominant, the first section of this isoleg ($D1_1$) should be perpendicular to its own density axis (i.e., slope = 0). Otherwise, if I'_1 occurred to the left of I_2 then $D1_1$ should attain a negative slope (Rosenzweig and Abramsky, 1986) (Appendix, Version B). In any case, when crossing the subordinate's first isoleg (S1), $D1_2$ should rotate counterclockwise because the subordinate now uses the core habitat. Upon crossing the subordinate's second isoleg, $D1_3$ should bend clockwise because now the subordinate starts suppressing also the fitness of the dominant in its secondary habitat (habitat *c*) (Fig. 3B). Note that $D1_3$ is bounded to the right by $S3_2$ (Fig. 3A) because below the latter the subordinate no longer uses habitat *c*.

The intercept of the second isoleg (D2) with the dominant's density axis (I'_2) occurs in the area where the subordinate uses only habitat *b*, which results in a positive slope of the first section of this isoleg ($D2_1$). Moving into the region where the subordinate uses also habitat *a* decreases the dominant's threshold for using all three habitats, which tilts $D2_2$ counterclockwise. Entering into the region where the subordinate uses all three habitats further reduces this threshold, causing an additional counterclockwise rotation in the slope of $D2_3$ (Fig. 3B).

PREDICTIONS OF THE ISOLEG MODEL—THE HABITAT USE MAP

Superimposing the isoleg diagrams of the two species (Figs. 3A and 3B) dissects the state-space into twelve distinct habitat-use regions (Fig. 4). In the region below S1 (region 1) the subordinate species uses only the core habitat. In the regions below S2 (regions 4, 5, 8) the subordinate uses only its secondary habitat. Above S1 and S2 and below S3 (regions 2, 2', 6, 9), the subordinate uses two habitats (habitats *a* and *b*), and above S3 (regions 3, 3', 7, 10), it uses all three habitats. Note, however, that to the left of the switching preference isoleg, the subordinate's primary habitat preference is for the core habitat (regions 1, 2, 3) while to its right (regions 2', 3', 4, and 5–10), it is for its secondary habitat (habitat *b*). For the dominant, left of its D1 isoleg (regions 1, 2, 2', 3, 3', 4), it uses only the core habitat; between its two isolegs (regions 5, 6, 7), it uses two habitats *a* and *c*; and to the right of D2 (regions 8, 9, 10) it uses all three habitats. Throughout the whole state-space the dominant always prefers the core habitat. Complete habitat-use segregation (complete ghost) occurs in regions 4 and 5, where the subordinate uses only habitat *b* while the dominant uses habitat *a* or *a+c*. Partial habitat-use segregation (partial ghost) occurs in regions 2', 3', and 6, where the two species overlap in the core habitat, but the subordinate mostly uses its secondary habitat (*b*), and the dominant mostly uses the core habitat (*a*) (Fig. 4). This isoleg model demonstrates that, in contrast with the symmetric CCO model, where habitat overlap always exists in

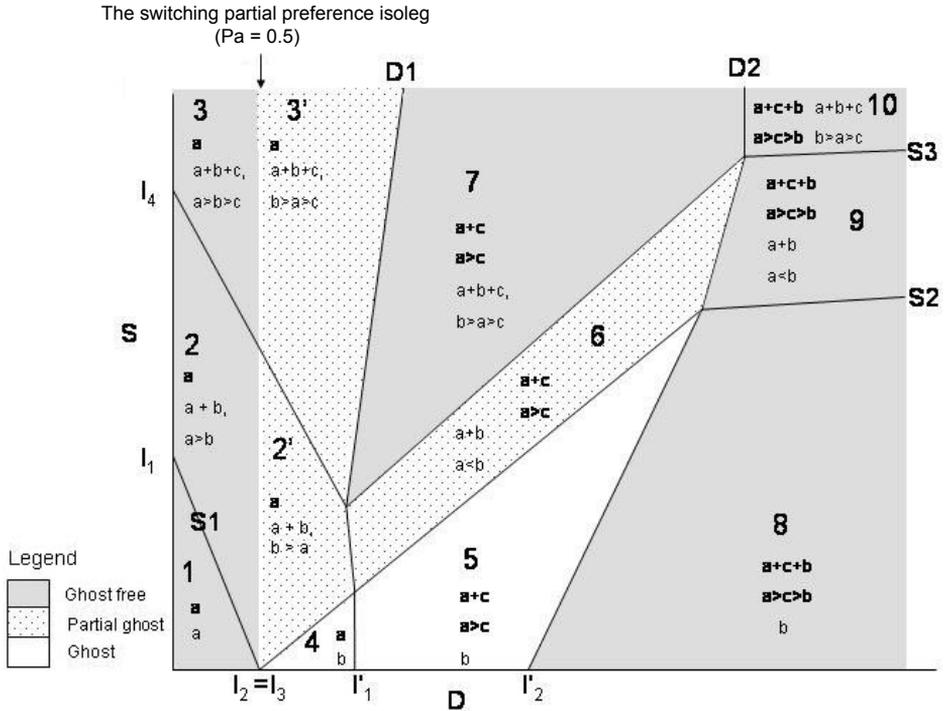


Fig. 4. The isoleg map: an illustration of the effect of intra- and interspecific densities on the habitat use (lowercase letters) and habitat preferences (comparison operators) of the dominant (D) (bold letters) and subordinate (S) (plain text letters) species. Numbers indicate regions of habitat-use behaviors. Regions of habitat overlap are gray. Regions of habitat partitioning (ghost of competition past) are white. Regions of partial habitat partitioning (partial ghost), where D uses mainly habitat *a* and S uses mainly habitat *b*, are stippled.

the core habitat, in the asymmetric CCO model a fairly large part of the state-space is susceptible to some degree of the ghost of competition past.

The isoleg model of the asymmetric CCO presented here is just one of several possible versions (see Appendix), although it is probably one of the more common ones. The specific shape of the isoleg model is sensitive to our assumptions regarding the cost of habitat selection, locations of the intercepts, the habitat-specific competitive effects, and the locations of the isoleg intersections (see text and Appendix). However, one prediction is common to all versions: If interspecific competition is asymmetric there should always be regions in the state-space of species densities where complete and/or partial habitat-use segregation should occur. In other words, asymmetric competition

renders a centrifugally organized community susceptible to being haunted by the ghost of competition past. This occurs because the dominant species causes the subordinate to switch its primary and secondary habitat preferences: The subordinate species has an apparent preference for its secondary habitat, while the dominant maintains its preferences for the core habitat (Fig. 2C). Such susceptibility to the ghost of competition past was shown theoretically (Rosenzweig, 1981; Rosenzweig, 1991) and empirically (Abramsky et al., 1994) to promote stable coexistence in competitive systems.

DISCUSSION

THE GENERALITY OF SYMMETRIC VERSUS ASYMMETRIC CCO

The theory of centrifugal community organization integrates two central concepts in community ecology: description of gradients and study of process. Centrifugal community organization (CCO) is based on the premise that habitats represent a specific combination of resources or microhabitats, with all competing species sharing preference for the same subset (the core habitat), but differing in their preference for the less preferable subsets (the marginal habitats) (Rosenzweig and Abramsky, 1986). Coexistence is achieved by habitat partitioning of secondary habitats, which constitute a competitor-free refuge. Yet, very little evidence for the existence such community organization exists (Rosenzweig and Abramsky, 1986; Rosenzweig, 1989; Rosenzweig, 1991; Wisheu, 1998).

Rosenzweig and Abramsky (1986) interpreted their gerbil community as supporting symmetric CCO. This was based on their observation that both gerbil species exhibited negatively sloped isolegs. They suggested that *Gerbillus andersoni allenbyi* and *G. pyramidum* both prefer the semi-stabilized sand habitat, but differ in their secondary habitats, preferring the stabilized and shifting sand habitat, respectively. Yet, revisiting Rosenzweig and Abramsky's (1986) results suggests the asymmetric CCO might be a better descriptor of this system. This is mainly because the isolegs of the two species are dissimilar: *G. pyramidum* has a shallow negatively sloped isoleg, whereas *G. andersoni allenbyi* has a sharp negatively sloped isoleg. In a separate study, we field tested this hypothesis experimentally (Wasserberg et al., 2007). We found that the community organization of gerbils in the coastal sand dunes of Israel fitted closely the predictions of the asymmetric CCO model: both species prefer the semi-stabilized sand habitat and differ in their secondary preferences for the shifting and stabilized sand habitats, but competition in the core habitat is highly asymmetric with *G. pyramidum* being the dominant species. As predicted by our model, this gerbil community is haunted by the ghost of competition past: *G. pyramidum* mostly uses the semi-stabilized core habitat whereas *G. allenbyi* mainly uses its secondary, stabilized sand habitat. Yet, habitat segregation in the core habitat is not complete (i.e., partial ghost) due to the higher foraging efficiency of the subordinate *G. andersoni allenbyi*, which allows it to utilize poor food patches that are not profitable for the dominant, albeit wasteful, *G. pyramidum* (Wasserberg et al., 2006).

Sunfish in freshwater lakes also represent a thoroughly studied system that appears to fit three-species asymmetric CCO (Werner and Hall, 1976). All three sunfish species (green, bluegill, and pumpkinseed sunfish), when alone, prefer to forage in the vegetated zone where most valuable food items occur. When together, however, the green sunfish uses its high foraging efficiency to force the other two species into different habitats. The bluegill shifts to feed on smaller prey types in the risky open water column, and the pumpkinseed shifts to a sediment-sifting foraging mode in the benthic habitat. This case is particularly interesting since it demonstrates that asymmetric CCO can also occur as a result of exploitation competition and is not restricted to interference competition.

Asymmetrical CCO also appears to explain the distribution patterns of multiple species and vegetation types along gradients caused by different combinations of environmental factors (Keddy and Maclellan, 1990; Wisheu and Keddy, 1992). The underlying mechanism assumes a competitive hierarchy with light as the main limiting resource. Weaker competitors are restricted to the most stressful end of the gradients. The benign ends of these gradients comprise the core habitat and are dominated by competitively superior species (Wisheu and Keddy, 1992). In wetlands, for example, the core habitat has low disturbance and high fertility, and is dominated by large, leafy species capable of forming dense canopies. The peripheral habitats result from different combinations of infertility and disturbance and support distinctive floras with unique adaptations (Keddy and MacLellan, 1990).

THE SCALE OF COEXISTENCE DETERMINES THE LOCATION OF COMPETITIVE EQUILIBRIUM

The scale of coexistence between the competing species should determine whether competitive equilibrium will occur in the ghost or the partial ghost regions. Mechanisms that allow local coexistence, such as those based on trade-offs in foraging efficiency in low vs. high resource abundance, microhabitat partitioning, or food partitioning, will allow some degree of habitat-use overlap in the core habitat. In such cases, the competitive equilibrium should occur in the partial ghost region, allowing the subordinate species to covertly enjoy the benefits of the core habitat. For the gerbil system, such shared use of the core habitat is attained via temporal partitioning and a “cream-skimmer” vs. “crumb-picker” trade-off (Ziv et al., 1993; Wasserberg et al., 2006): The bigger and dominant *G. pyramidum* is active early in the night when resources are abundant (Ben-Natan et al., 2004). The smaller and subordinate *G. a. allenbyi* is active later in the night, enjoying the “leftovers” by virtue of its high foraging efficiency and low energetic cost of maintenance (Linder, 1988). Landscape-level mechanisms, such as large-scale macro-habitat partitioning, would force the equilibrium point to occur at the ghost area. The dominant species uses mainly the core habitat and the subordinate uses only its secondary habitat. In many systems, coexistence will be determined by multiple mechanisms operating at different scales. So, to some extent, the interpretation of mechanisms, and ghostly coexistence, will depend as much on the investigator’s scale as it does on the organisms being studied.

IS ASYMMETRIC CCO AN ESSENTIALLY NEW FORM OF COMMUNITY ORGANIZATION?

In the introduction we suggested that the variety of community organization modes

reported during the last twenty years can be grouped into three basic niche relationships: exclusive, nested, and centrifugal (Fig. 1). Where does the asymmetric CCO model fit? The unique property of CCO is that coexistence is achieved not by what the competing species do best, but in what they do as a backup. In other words, for CCO, differential stress resistance along a variety of environmental gradients is the basis for coexistence (Rosenzweig and Abramsky, 1986; Rosenzweig, 1989). Is that the case for asymmetric CCO?

The answer depends on the mode of competition. For a two-species in three-habitat system, such as that described in our isolog model, coexistence is attained via a dominance–tolerance trade-off: the dominant species monopolizes the core habitat, while the subordinate species is restricted to its secondary habitat. The third habitat, representing the secondary and tertiary habitat preference for the dominant and subordinate species, respectively, is somewhat redundant. In such a scenario, asymmetric CCO can simply be seen as the reflection of shared preference in a three-habitat landscape. But the third habitat is nevertheless essential to differentiate CCO from shared-preference community organization.

For a multi-species system, however, asymmetric CCO appears to be a novel combination of both the shared-preference and the centrifugal community organization. The dominant and each of its subordinates are organized in a shared-preference manner based on a dominance–tolerance trade-off. Among the subordinates, however, coexistence is based on differential stress resistance along a variety of environmental gradients, as classically described by Keddy and Maclellan (1990) and Wisheu and Keddy (1992). In Werner and Hall's (1976) system, the green sunfish is the superior competitor. The bluegill and the pumpkinseed sunfish are able to differentially tolerate exposure to predators and high foraging cost associated with filter feeding, respectively.

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APPENDIX: FOUR ISOLEG-MODEL VERSIONS OF ASYMMETRIC CENTRIFUGAL COMMUNITY ORGANIZATION

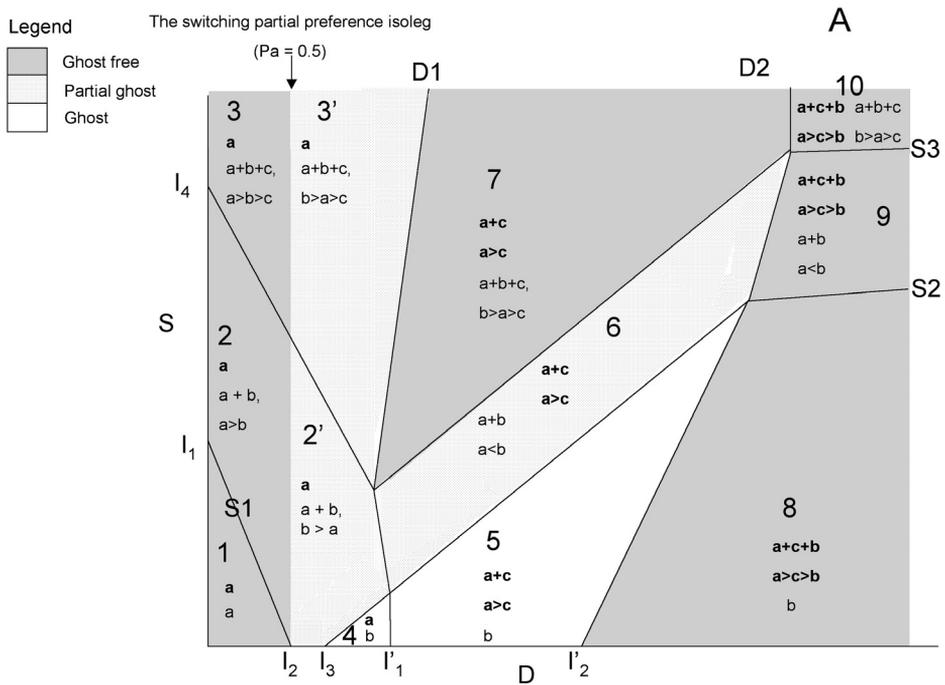
In this section we are analyzing the sensitivity of the main prediction of the asymmetric CCO model: susceptibility to the “ghost of competition past”, to our assumptions regarding the cost of habitat selection, and to the relative habitat-specific competitive effect.

VERSION A. WHEN THERE IS A COST TO HABITAT SELECTION

In this case, the intercepts of the first and second isolegs of the subordinate with the dominant’s density axis (I_2 and I_3 , respectively) do not overlap. Due to this cost of habitat selection there is a range of the dominant species density values where the fitness rewards from either habitat a or b are equal. Nevertheless, zones of complete and partial “ghost” are still prevalent (Fig. A).

VERSION B. WHEN I'_1 OCCURS TO THE LEFT OF I_2

When I'_1 occurs to the left of I_2 , the slope of the first section of the dominant’s first isoleg (D1) becomes negative until it intersects with the subordinate’s third isoleg, when



it turns clockwise. As a result, the subordinate's third isoleg (S3) intersects D1 at a much lower dominant species density. Its counterclockwise tilt at this stage increases substantially the "partial ghost" area where the two species use their primary and secondary habitats but where the subordinate has a preference for its secondary habitat (Fig. B).

VERSION C. WHEN THE SLOPE OF $S3_2$ IS SMALLER THAN THAT OF $S2_1$

This would happen when the dominant is suppressing the fitness of the subordinate in habitat *a* faster than it does in habitat *c*. At the intersection of S2 and S3 the fitness–density lines of the subordinate species for habitats *a* and *c* overlap. At this point, for the subordinate, the reward for selecting two habitats (*b* and any of the other two habitats) is equal to the reward for selecting all three habitats. At this point we find an additional switching-preference partial-preference isoleg (Fig. C). From this density rightward the subordinate perceives habitat *c* as superior to the core habitat (*a*). This creates a new behavioral region (region 8) where the subordinate uses its secondary and tertiary habitats but not the core. Also, in region 7' the subordinate uses all three habitats but with habitat *a* being the least preferred. Hence, the new isoleg S4 divides regions where the subordinate uses only habitat *b* to where it uses *b* and *c*. The first section of S4 should be horizontal since the dominant continues to suppress the fitness of habitat *c*. But, when it intersects the dominant second isolegs (D2), S4 should rotate clockwise. On the other hand, the new section of S3 isoleg ($S3_4$) should tilt counterclockwise since fitness in habitat *a* decreases at a faster rate. In any case, as can be observed, the regions of ghost and partial ghost are still prevalent (Fig. C).

VERSION D. WHEN THE COMPETITIVE EFFECT OF EACH SPECIES IS STRONGEST IN ITS SECONDARY HABITAT

In this case, we assume that each species exerts maximal competitive effect in its secondary habitat. This would have a major effect on the isoleg where each species shifts from using two to using three habitats. As shown in all previous model versions above, when each species starts using its secondary habitat the threshold density for using all three habitats by its competitor should increase. However, if interspecific competition suppresses the quality (expressed as the intercept of that fitness–density line) of the tertiary habitat at the highest rate then the threshold densities for using all three habitats should increase at an accelerating rate. As the quality of the tertiary habitat approaches zero, the intraspecific threshold density for using all three habitats should approach infinity (Fig. D). This results in an inability of S2 and S3 to cross D2, which results in loss of two behavioral regions: 9 and 10 from Fig. A. The outcome of this scenario is a substantial increase in the area of the partial- and especially the complete ghost regions.

The above four versions of the isoleg model of asymmetric CCO are by no means an exhaustive survey of all possible versions of this model. Nevertheless, they explore the qualitatively most important cases. The major conclusion of this analysis is that as long as interspecific competition in the core habitat is asymmetric "ghost of competition past" regions will occur. This result is insensitive to our specific assumptions regarding the cost of habitat selection, the location, and the slope of the different isolegs.

