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CHAPTER 16: HABITAT SELECTION, SPECIES INTERACTIONS, AND PROCESSES OF COMMUNITY

ASSEMBLY IN COMPLEX LANDSCAPES: A METACOMMUNITY PERSPECTIVE

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Chapter 16: Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective.

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How are communities assembled? This simple question drives a great deal of theoretical and empirical research in community ecology (reviews: Cody and Diamond 1975; Diamond 1975; Strong et al. 1984; Belyea and Lancaster 1999; Weiher and Keddy 1999), but elucidation of mechanisms or “rules” of community assembly remain a challenge (e.g., Brown et al. 2000; Stone et al. 2000). The majority of community assembly studies focus on the role of internal dynamics (e.g., species interactions, abiotic tolerances) in determining composition of local communities. However, there is increasing awareness that processes operating at larger scales can have important consequences for local and regional dynamics (Danielson 1991; Wilson 1992; Holt 1993; Ricklefs and Schluter 1993; Leibold 1998; Belyea and Lancaster 1999; Mouquet and Loreau 2002; Amarasekare and Nisbet 2001). One such process is the movement of

individuals among communities (Tilman et al. 1994; Holt 1997; Holyoak 2000). If local communities are linked by dispersal, mechanisms structuring them must be examined in a larger spatial framework. When communities are linked across space and time new processes and emergent properties may arise from the resulting complex dynamics, hence the metacommunity perspective (Wilson 1992).

The metacommunity perspective represents a logical extension of the metapopulation concept: discrete local populations or communities linked by periodic dispersal. For clarity we identify a local community as the collection of organisms occurring within a discrete habitat patch. Although rates of individual movement among local populations are central to metapopulation and metacommunity models, studies have only recently considered the manner of dispersal among different populations (e.g., Hanski and Singer 2001; Holt and Barfield 2001).

Our work on habitat selection has focused on colonization, the necessary consequence of dispersal. Here we examine ways individuals can select among local communities and how processes of colonization can affect local and regional dynamics. Specifically, we focus on what we call “interactive habitat selection”. We have two purposes: to review concepts of habitat selection relevant to metacommunities and to use our ongoing studies of pond communities to illustrate these concepts.

Recent work suggests that habitat selection can dramatically affect both population and community dynamics (Rosenzweig 1991; Brown 1998; Bernstein et al. 1999; Abrams 2000; Remes 2000; Schmidt et al. 2000; Delibes et al. 2001a,b; Hanski and Singer 2001; Heithaus 2001; Holt and Barfield 2001; Grand 2002; Krivan and Sirot 2002; Spencer et al. 2002; Morris 2003). However, few empirical or theoretical studies have examined the effects of habitat selection on local communities composed of more than two species.

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<A> Aquatic mosaic landscapes as a model system for understanding linkages among communities

Linkages among communities may be especially critical for persistence of species in complex landscapes where habitats vary both spatially and temporally. Because freshwater habitats typically have more discrete boundaries than their terrestrial or marine counterparts, they are ideal for illustrating many of the processes relating to habitat selection, dispersal and metacommunities. While we focus here on aquatic habitats as individual communities and linked metacommunities, the concepts apply to a variety of systems.

Freshwater aquatic systems are often comprised of isolated patches linked to each other and the surrounding terrestrial matrix by species with complex life cycles. The fauna contains the larval stages of many organisms that are primarily (semi)terrestrial adults, or that must leave the water to complete their life cycle (Merritt and Cummins 1984; Duellman and Trueb 1986; Hutchinson 1993; Schneider and Frost 1996). Persistence of many such species is dependent on seasonal invasion and/or oviposition by dispersing adults. Colonization/oviposition behavior can play a major role in the assembly of individual aquatic communities and link communities across landscapes. The importance of such linkages varies with stability (persistence) of local communities and degree of dispersal. The extent and pattern of spatial variation among communities and temporal variation within and among communities has implications for habitat quality and the dynamics of colonization. If dispersal is minimal, landscape level dynamics are simply the sum of within-community processes across all local community types. If dispersal is substantial, both local and metacommunity dynamics depend on the interaction of dispersal with spatial and temporal variation in habitat quality.

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<A> Types of organisms and types of colonization

The causes of dispersal have generated much interest (e.g., Skellam 1952; Gadgil 1971; Maynard-Smith 1972; Hamilton and May 1977; Harper 1977; Parker 1984; Cohen and Levin 1987; Cohen and Mitro 1989; Clobert et al. 2001). Although the impetus for dispersal (e.g., drift, aggression, population density) has implications in a number of domains (Holt 1997), we focus here on the consequences of dispersal for (re)distribution of individuals among habitat patches. It is useful, however, to distinguish between *obligate* and *facultative dispersers*. Obligate dispersers have life cycles that force dispersal at some stage, while facultative dispersers depend on current conditions for cues to initiate dispersal (or not). From a probabilistic perspective obligate dispersers form more consistent links among communities, whereas facultative dispersers may generate more dynamic linkages. Impact of both depends on colonization strategies used by dispersing individuals. Current metacommunity models (e.g., Holyoak et al. Chapter 1; Mouquet et al. Chapter 10) often follow the lead of metapopulation models in assuming random colonization for simplicity (but see Danielson 1991) and as a starting point (Hanski and Gilpin 1997). Even simple colonization mechanisms can generate complex dynamics (Skellam 1951; Levin 1992); however, the type of colonization may play a central role in determining identity, extent, and strength of linkages among communities. We will use three general types—random colonization, philopatry, and interactive habitat selection—to illustrate how colonization strategies can affect the connectedness of communities.

Random colonization—Random colonizers have no control over their passive dispersal and settlement patterns, or they actively disperse with random settlement patterns. Random colonization is the mode primarily used in current metacommunity models and gives rise to the

notion of the “propagule rain” where all patches have an equal likelihood of receiving propagules from any other patch <Figure 16.1> (Figure 16.1a). Random colonization can also be modeled in other ways. For example, proximity and prevailing physical conditions may cause dispersers to have a greater probability of colonizing nearby patches by chance alone (Figure 16.1b).

Philopatry—philopatry is translated as “father loving” and taken to mean “to breed in one’s birthplace”. However, current usage includes scenarios with very different consequences. Both species breeding at their natal site because of simple encounter probabilities and those actually exhibiting natal homing are included. In the former case, philopatry represents an extreme form of random colonization where proximity effects or spatial structure dictate that colonization of other patches is unlikely. While this distinction has consequences, it is beyond the scope of our current discussion. We simply define philopatry as a high probability of breeding in one’s natal site (Figure 16.1c).

Interactive habitat selection—IHS—This is classic habitat selection. An organism assesses habitats during active search and chooses that deemed most appropriate (Baker 1978)(most likely to generate the highest fitness; Fretwell and Lucas 1970). Individuals may either avoid or be attracted to certain patches relative to others (Figure 16.1d; Rausher 1993). While avoidance and attraction could be viewed different descriptions of the same response (e.g., are treefrogs avoiding fish or attracted to fishless habitats?), each can produce different species distributions. “Interactive” indicates that patches are continually assessed, and the same habitat will be perceived differently should it undergo substantive change. This is the most labile of mechanisms and provides the greatest opportunity for matching phenotypes (both adult and propagule) to habitats (Resetarits 1996). This is the focus of much of the discussion below.

At a community level: 1) any local community will include both obligate and facultative

dispersers and species with various colonization strategies; 2) communities differ in the relative representation of dispersal/colonization types; and 3) different forms of dispersal/colonization operate at different life history stages within a single species. Our aquatic communities contain species exhibiting the entire range of dispersal/colonization types. However, our focal species are mostly obligate dispersers since complex life cycles require leaving the aquatic habitat at some point. Many of these species (e.g., certain frogs and beetles) exhibit interactive habitat selection (e.g., Resetarits and Wilbur 1989, Resetarits 2001, Binckley and Resetarits 2002, 2003), while others appear to be philopatric (e.g., damselflies; McPeck 1990). Still others may be essentially random colonizers (e.g., zooplankton, phytoplankton, aquatic plants, and others with passive dispersal; Bilton et al. 2001; Caceres and Soluk 2002).

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<A> Consequences of different forms of colonization for metacommunities

Clearly the frequency distribution of different types of colonization (as well as dispersal) affects linkages among communities in complex landscapes (Figure 16.1). The greatest extent may derive from random dispersal (propagule rain model), where all communities within a certain radius have non-zero probabilities of receiving colonists from a given community (Figure 16.1a). The spatial dynamics under random colonization depend on whether colonization is modeled as a propagule rain or whether internal spatial structure and proximity are included but linkages are specifically manifested through changes in population size (mass effects; Shmida and Ellner 1984).

Philopatry reduces connections among communities and fosters isolation and local adaptation. Philopats might be expected to contribute relatively little to dynamic linkages among communities in complex landscapes (Figure 16.1c). Only with major disturbance would

philopatric populations “reconnect” to others within the landscape, unless philopatry is under dynamic control (which is not indicated by any existing literature). Thus, the extent of philopatry within a community limits the potential for linkages.

The extent of linkages among communities under IHS is intermediate between complete linkage among all patches (propagule rain, Figure 16.1a) and no or few linkages (philopatry, Figure 16.1c). However, a number of emergent patterns deriving from the process of IHS have implications for metacommunity dynamics. Some of these include:

Compression—species can be compressed into a smaller number of patches via IHS. For example, all ponds in a given landscape are ideally suitable for species X before invasion of a subset of ponds by a predator, species Y. In the absence of IHS all ponds are still colonized resulting in loss of individuals to sinks <Figure 16.2> (Figure 16.2a). With IHS the number of ponds available to X is compressed because it avoids ponds with Y (Figure 16.2b). This decreases one set of interspecific interactions (e.g., predation) but can increase the intensity of other intra- and/or inter-specific interactions and affect (meta)population dynamics (Rosenzweig 1991; Blaustein 1999). This is simply habitat loss driven by colonization behavior. All patterns described below potentially involve habitat compression.

Contagion—the perceptions of a given habitat “bleed” over into adjacent habitats, affecting their perceived (but not actual) suitability; suitable patches take on the characteristics of the nearby unsuitable habitats in the “eye” of the colonists. This can accelerate habitat loss and generate compression or compromise (the next emergent pattern). In the case of avoidance, contagion causes loss of otherwise favorable habitats perceived as unsuitable due to proximity to truly unsuitable habitats (Figure 16.2c). In a changing landscape where processes render habitats unsuitable, contagion accelerates habitat loss by reducing available patches and increasing strain

(because of higher densities) on remaining habitats perceived as suitable. In contrast, contagion based on attraction results in colonization of unsuitable habitats perceived as suitable. Regional population size is reduced because these habitats function as persistent sinks (Delibes et al. 2001a,b). These “attractive sinks” can have a disproportionate effect on population persistence (Delibes et al. 2001a,b; see Hoopes et al. Chapter 2).

Compromise—when preferred habitats do not exist, or are co-opted by incompatible species, habitat selection forces species either to local extinction or habitat compromise (Figure 16.2d); in habitat compromise species select the best remaining habitat, though average fitness may be considerably below that seen in the preferred habitats (sensu the Ideal Despotic Distribution, Fretwell and Lucas 1970) and may even be below replacement rates, resulting in a sink population. This process may also place species into new ecological contexts and into new sets of species interactions.

Covariance—while attraction and avoidance can directly generate patterns of covariance among species <Figure 16.3> (Figure 16.3a), they can also generate patterns of secondary covariance via independent species responses to the same or correlated factors. For example, gray (*Hyla chrysoscelis*) and squirrel treefrogs (*H. squirella*) avoid fish, and thus if fishless habitats are limited (and treefrogs do not avoid one another) they will positively covary to a greater extent than if all habitats were fishless and provided other axes across which they could assort (Figure 16.3a,b). Alternatively, treefrog A avoids fish, B avoids shade; if open canopy ponds are less likely to harbor fish, then the two have greater covariance as a result of sharing open canopy, fishless ponds. This could result in competition for enemy-free space (Jeffries and Lawton 1984; Holt and Lawton 1994).

Avoidance (habitat loss) and attraction (habitat gain) cascades—are similar to cascading

effects in other contexts and arises from some combination of processes above. Imagine Z as a predator that excludes X and Y (competitors that have partitioned Z-free habitats along some other axis)(Figure 16.3a). Z invades a proportion of habitats suitable to X, forcing X into marginal habitats (for X) normally occupied by Y. If X is either avoided by Y or is a superior competitor, Y's options become very limited (Figure 16.3c). Increase in frequency of habitats containing Z results in cascading habitat loss. Cascades can occur as a result of attraction as well. If suitable habitat is defined (in part) by presence of Z, increase in frequency of Z results in cascading habitat gain. We can envision interactions between avoidance and attraction that generate more complex behavioral dynamics (via trait-mediated direct and indirect effects) and also complex dynamics arising from the operation of both density and trait mediated effects over time.

Maladaptive habitat selection—thus far we have assumed that species select habitats in which their performance is enhanced, or in which fitness of individuals selecting among habitats remains constant (Fretwell and Lucas 1970). However, organisms may also make maladaptive choices (Remes 2000; Delibes et al. 2001a, 2001b). Random colonization commonly leads to inappropriate habitat matching, and philopatry can fail if habitats change. If cues used to assess habitats under IHS fail, the consequences can be dramatic. One of the truly puzzling patterns we observed in frogs is oviposition in extremely ephemeral habitats, which often occurs in active agricultural fields adjacent to forested areas. Both forested and open areas contain potential breeding sites; forested sites are cooler, deeper and less ephemeral; open sites are warm, very shallow and very ephemeral, often not lasting long enough for hatching much less metamorphosis. What precipitates these seemingly disastrous choices by large numbers of ovipositing females? The strong predilection of females for open canopy sites has been

established (Binckley and Resetarits, unpublished data), suggesting that, historically, selection of the most open (warmest, most productive) sites was favored because such sites generated the fastest growth and development. However, rapid anthropogenic change has shifted the frequency of open canopy sites from rare to common, and the upper extreme of the distribution from ponds in forest light gaps to puddles in barren fields. Simple, historically “adaptive” decision algorithms such as, “choose the highest available temperature”, now lead to maladaptive selection of population sinks (Remes 2000; Delibes et al. 2001a, 2001b). This consequence is possible whenever the relationship between preference and performance breaks down (Rieger et al., in review).

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<A> Populations, communities and metacommunities

Incorporating habitat selection into population models affects population size (Holt 1985; Smith et al. 2000; Spencer et al. 2002), growth rate, and persistence (Pulliam and Danielson 1991; Sutherland 1996) because individuals actively avoid “sinks” while selecting “source” habitats. In dynamic landscapes, where distribution of sinks changes, IHS provides a mechanism for coping with the changing fitness landscape (Pulliam and Danielson 1991; Resetarits 2001). This is because individuals are not immediately lost from the population by mortality or reproductive failure but are initially redistributed spatially and concentrated into remaining “source” habitat, which can then undergo secondary changes due to increased density, and so on (Resetarits and Wilbur 1989; Abrams 1993; Watkinson and Sutherland 1995; Blaustein 1999; Resetarits 2001).

Similarly, the presence and specific form of habitat selection can also have important consequences at the community and metacommunity levels. We typically think of linkages

among communities being generated by shared species that connect habitats through dispersal. IHS can contribute to this type of linkage in a variety of ways and can even increase the number of species shared as a result of common avoidance or attraction behaviors or as a result of shared responses to habitat loss. IHS also generates another form of linkage. We typically assume species that do not co-occur do not interact, communities lacking shared species are not connected, and species with complimentary distributions do not contribute to metacommunity dynamics. However, our work demonstrates that communities can be linked both by shared species and by species segregation driven by habitat selection. Numerous amphibians and insects avoid fish when colonizing/ovipositing (see “Empirical perspectives”), and the mutually exclusive distributions seen for squirrel treefrogs and fish, for example (Binckley and Resetarits 2002), derive from behavioral avoidance not from typical “face to face” interactions (e.g., competition and predation). Thus, determination of the distribution of squirrel treefrogs occurs at the colonization stage, and changes in fish distribution affects both treefrog distribution at the landscape scale and their local abundance in available fish-free habitats, linking communities at the landscape level. These “phantom interactions” (direct but cryptic effects driven by past interactions, *sensu* Connell 1980) are a missing element in community ecology and are particularly germane to metacommunity dynamics.

The idea that behavior can generate patterns of negative and positive covariance among species on the landscape scale generates potentially strong linkages among communities that derive from such phantom interactions. Present distributions reflect the past history of species interactions. This idea was once dominant in ecology, spawning Connell’s (1980) classic denunciation of the “Ghost of Competition Past”; however the experimental evidence called for by Connell now exists (see “Empirical perspectives”).

Species can have different metapopulation structures and even those structures may be determined by phantom interactions. For example, fish in landscapes such as pine flatwoods in the Southeast US or other extensive wetlands (e.g., Great Dismal Swamp) typically exist as island-mainland metapopulations with some internal connections (rescue effect). In contrast, fish intolerant species are characterized by internal colonization metapopulations, because larger habitats likely contain fish, precluding an island-mainland structure and restricting spatial dynamics. Landscape level processes, including those driven by IHS, can determine both the structure of individual populations and communities as well as interactions among communities.

Behavioral production of diversity patterns suggests local community structure results from species interactions both within and among communities (at the metacommunity scale). While community ecology has historically emphasized local interactions, recent work (see “Empirical perspectives” below) suggests that distributions can be determined by species interactions even though species do not co-occur at the local scale. For these species, habitat selection defines the exact nature and extent of interactions occurring within local communities by reducing the frequency of specific deleterious interactions while simultaneously elevating the probability of an entirely different set of local interactions.

Both specific colonization strategies and exchange of individuals among communities can impact metacommunity dynamics (Rosenzweig 1985; McPeck 1989; Bilton et al. 2001; Binckley and Resetarits 2002). When species actively select sites for feeding and reproduction, regional processes (e.g., dispersal and colonization) interact with local processes (e.g., predation, competition) to determine species distributions and community structure. IHS species subdivide regional landscapes into different habitat types, each occurring in a specific spatial configuration, based on shared characteristics that can be quite specific (e.g., species composition). Under IHS

priority effects and phenology (e.g., Morin 1984; Alford and Wilbur 1985; Wilbur and Alford 1985; Alford 1989) assume greater significance in the assembly of local communities and regional metacommunities because current occupants can affect habitat choices of later colonists.

Theory emphasizes that habitats differ in their fitness consequences, which are detectable to individuals who match their choice of habitats to these consequences (e.g., Fretwell and Lucas 1970, Fretwell 1972, Holt and Barfield 2001). Habitat types are defined by specific factors that consistently and predictably affect fitness, and may be biotic, abiotic, or a combination of multiple variables (Fretwell and Lucas 1970; Werner and Gilliam 1984; Moody et al. 1997). Habitat quality declines with increased densities of competitors leading to colonization of initially inferior habitats (Fretwell and Lucas 1970). Thus, habitat selection is a context dependent process, where suitability of any patch is relative to all other potential patches. Diversity patterns, patterns of community linkages, and metacommunity dynamics for species exhibiting IHS depend not simply on the relative quality of patches, but on their frequency distribution and spatial configuration in complex landscapes.

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<A> Axes of habitat selection: empirical perspectives.

Thus far we have focused on how IHS affects communities and their linkages, but what evidence exists that habitat selection can determine species distributions? Many aquatic insects and amphibians can discriminate and selectively colonize different patches based on a variety of factors (Resetarits and Wilbur 1989; Walton et al. 1990; Crump 1991; Petranka and Fakhoury 1991; Kats and Sih 1992; Blaustein and Kotler 1993; Hoey and Petranka 1994; Sherratt and Church 1994; Holomuzki 1995; Laurila and Aho 1997; Spieler and Linsenmair 1997; Blaustein 1999; Stav et al. 1999; Summers 1999; Marsh and Borrell 2001; Resetarits 2001; Binckley and

Resetarits 2002, 2003). Selective colonization/oviposition indicates that individuals possess sensory mechanisms and behaviors that facilitate selection of favorable habitats (Rausher 1983, 1993; Singer 1984, 1986; Thompson and Pellmyr 1991; Renwick and Chew 1994; Resetarits 1996; Blaustein 1999). Variation in environmental conditions and resulting success in different local communities (habitats or patches) provides the backdrop for the evolution of interactive habitat selection (Resetarits 1996; Remes 2000). Below we describe studies on habitat selection in treefrogs and aquatic beetles to illustrate the consequences of habitat selection and the range of factors that may effect habitat suitability.

 Biotic factors

Our study of habitat selection traces back to an experiment (Resetarits and Wilbur 1989, 1991) examining the response of ovipositing gray treefrogs to variation in the faunal composition of experimental ponds <Figure 16.4> (Figure 16.4a). In this and all subsequent experiments we tested the responses of naturally colonizing populations to experimental conditions presented in as realistic a field setting as possible. We typically set up pools containing base communities that then vary in biotic and/or abiotic conditions(e.g., Morin 1983, Fauth and Resetarits 1991) and allow our focal species to colonize (Resetarits and Wilbur 1989). We assay the responses by removing eggs daily (frogs) or adults and egg cases periodically (beetles).

Our initial goal was to determine whether *H. chrysofelis* could detect and respond to (avoid) species important in its larval ecology. That experiment established habitat selection as a significant factor in the distribution of larval *H. chrysofelis* (Figure 16.4a). Ovipositing *H. chrysofelis* detected and avoided fish (*Enneacanthus chaetodon*), salamanders (*Ambystoma maculatum*), and high densities of conspecifics. Not all predators (nor competitors) were equal; other predators (*Notophthalmus viridescens* and *Tramea carolina*) and a potential competitor

(*Rana catesbeiana*) were not avoided, either because they could not be detected or did not have significant effects on potential fitness (Resetarits and Wilbur 1989; Resetarits 1996). The critical implication for communities was that behavior in response to the expected levels of predation and competition could determine the distribution of species, even in the absence of what we commonly think of as species interactions. These “phantom interactions” were the first experimental evidence that past species interactions did in fact determine the present distribution of species (sensu Connell 1980).

Since then we have examined the responses of numerous species to variation in both the density and identity of predatory fish. We have recently returned to the role of competitors in colonization, but predator experiments support the role of conspecific densities, because habitats typically avoided by frogs receive eggs only on nights with considerable oviposition activity (Binckley and Resetarits 2003; Rieger et al., in review). Since we remove eggs after each oviposition event, this within-night variation in density is the only density variation accessible to frogs. As activity (=density) increases, preference for preferred habitats weakens, as predicted by the ideal-free distribution (Fretwell and Lucas 1970). This suggests that responses to habitat characteristics may be hierarchical.

We have found that a variety of frogs and aquatic beetles show strong responses to predatory fish, even stronger than that observed in the initial experiment. Given the choice between fish and fishless habitats, *H. squirella* deposits 95% of eggs in fishless pools (Binckley and Resetarits 2002). Even higher avoidance rates (a staggering 99.3%!) occurred for *H. femoralis* in an experiment examining habitat selection on two spatial scales (see Figure 16.8) (Resetarits, in review). This appears to represent a generalized response to fish, being elicited by species representing six families (in five orders) of freshwater fish (with one interesting

exception still under investigation - see Figure 16.4b) (Binckley and Resetarits 2003; Binckley, unpublished data).

While the response to fish continues to impress us, more impressive is that the response can be elicited at densities of 0.53g of fish/100 L (a single, 2 g *Umbra pygmaea* in 375 L of water) (Figure 16.4c). This response also precisely mirrors the actual effects on performance (Rieger et al. in review). Interestingly, the four species (Figure 16.4b) that elicit avoidance have very different effects on larval anurans (Chalcraft and Resetarits 2003a, 2003b); the non-lethal, phantom effects on species distribution are equivalent among predators, while their lethal effects are very different, providing a complex twist on the concept of functional equivalence (Binckley and Resetarits 2003).

Our work on beetles has revealed similar responses for individual species, plus we have both adult colonization responses and oviposition responses for at least one species. <Figure 16.5> Figure 16.5a shows both responses for *Tropisternus lateralis*; adults colonize fishless habitats with greater frequency and their oviposition directly reflects this (Resetarits 2001). Adults may choose habitats for themselves (egg distribution is a byproduct), their offspring (adult distribution is a byproduct), or they may attempt to optimize both simultaneously. We cannot yet separate these alternatives.

The diversity of beetles has allowed us to examine the effects of fish on multispecies assemblages. <Figure 16.6> Figure 16.6 illustrates these effects of habitat selection alone (there is no mortality due to fish), which are almost identical to the results obtained in field surveys: reduction of common species, elimination of rare species, and significantly higher species richness and biomass in the absence of fish (Kenk 1949; Weir 1972; Healey 1984; Fairchild et al. 2000). Thus, the primary filter leading to characteristic communities in fish vs fishless habitats

(Wellborn, et al. 1996) may be behavior, rather than predation (Binckley and Resetarits 2003; Binckley et al. in review).

 Abiotic factors and biotic-abiotic interactions

We have recently begun to study effects of abiotic factors on habitat selection and examine interactions between biotic and abiotic factors. Attempts to examine interactions between other factors and predation have been limited by the strong fish response. A similar problem occurs with canopy types (open versus closed); the majority of both treefrogs and beetles prefer open canopy ponds (Figure 16.5b). Both preferences are so strong we are unable to test for (meaningful) biological interactions with other factors. For *T. lateralis* we see a significant effect of nutrients in open canopy ponds but no colonization of closed canopy ponds regardless of nutrient level, giving a statistically significant, but not biologically relevant, interaction (Figure 16.5b)! We see similar results with treefrogs. In the presence of fish or in closed canopy ponds, other factors cannot override the strong primary effects of fish or canopy. <Figure 16.7> (Figure 16.7).

 Spatial dimensions of habitat selection

How habitat selection functions in larger landscapes and at multiple spatial scales impacts the extent of linkages among communities. This is an experimental question, but we have gained some insights into this issue from several relevant experiments. Clearly different organisms will have different capacities to choose among habitats at larger spatial scales. Our treefrogs appear to make decisions at the scale of hundreds of meters, but beyond that we can say little (e.g., Resetarits and Wilbur 1989, Resetarits 1996, in review; Resetarits et al., in review). Aquatic beetles vary in flying abilities but certainly outstrip treefrogs and can be expected to cover kilometers or more, depending on species. For other taxa, such as dragonflies, individuals of

certain species can cover hundreds of kilometers (or even thousands for *Pantala*), whereas others move very little. This leads to the potential for linkages ranging from local to global (McPeck and Gomulkiewicz, Chapter 15). Ovipositing pinewoods treefrogs, *H. femoralis*, prefer sets of fishless ponds over those containing one or more pools with fish (regional—illustrating contagion), but also distinguish within sets of ponds between fish and fishless (local). The results are quite striking <Figure 16.8> (Figure 16.8) and indicate that our experimental arrays capture variation in the landscape on at least two meaningful levels with respect to oviposition site choice and (meta)community assembly.

While the study of habitat selection itself is interesting and productive, it is its role in the distribution and abundance of species that brings it fully into the realm of ecology. The types of behavioral decisions we have observed and their apparent prevalence indicate that choice of habitats by organisms is a dynamic and fundamental process in ecology that can serve as a primary filter in determining species distributions and abundances. These decisions provide a framework for linkages between communities that has fundamental implications for the emerging field of metacommunity ecology.

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<A> Conclusions—dynamics of habitat selection in complex landscapes

Metapopulation and metacommunity theory have primarily used random dispersal in modeling landscape level processes. The form of dispersal/colonization can have important consequences for the existence and extent of linkages among local communities (patches, habitats). Whether a landscape is comprised of numerous individual communities or linked into larger, metacommunities depends partly on the nature of dispersal and colonization. Interactive habitat selection has the greatest potential to form complex links among populations of multiple

species. As we expand the study of community assembly beyond the local scale (Danielson 1991; Wilson 1992; Holt 1993), and from stable to temporally dynamic communities, we must expand our vision beyond individual populations and species pairs, or risk generating a science of metacommunities as simply assembled metapopulations (Holyoak et al. Chapter 1). At present most models and empirical studies of habitat selection focus on one or two species. Competition in nature is not constrained to the pairwise construct of the Lotka-Volterra equations, and processes such as diffuse competition and community-wide character displacement have much broader implications for the assembly of natural communities than can be derived from two species models (Leibold 1998; Stevens and Willig 2000; Mouquet and Loreau 2002; Stanton 2003; Bernardo and Resetarits, in review; Resetarits and Bernardo, in review). Similarly, habitat selection has much broader implications at the community and landscape level that affect how we view sets of communities and processes of community assembly in complex landscapes.

We have shown various ways in which habitat selection can influence metacommunities and illustrated the types of decisions species are capable of making. We have also touched on how behavioral decisions can translate into species distributions and compositional patterns in natural communities. Much more work is required before we can begin to understand the role of habitat selection at the population/species and landscape/metacommunity scales. We are continuing our work on habitat selection in aquatic systems along several lines: focusing on issues including the spatial dynamics of habitat selection and tradeoffs between habitat quantity and quality; relationships between habitat preference and offspring performance, multiple risks and decision rules (e.g. minimize mortality rate divided by growth rate, minimize adult risk); and effects of habitat alteration and introduced species. It is our hope that this work will lead to a better understanding of habitat selection itself, but more importantly, the consequences of habitat

selection for the assembly of communities across complex landscapes.

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Figure Legends

Figure 16.1. Types of dispersal/colonization, illustrating consequences for linkages among local

communities: a) Random dispersal and recolonization in a large, panmictic population.

Emigrants enter regional pool and are randomly resorted among original habitats. b) Random

dispersal in a spatially structured (meta)population. Dispersal is random from each node but

colonization probabilities are determined by spatial proximity (and patch size) as in internal

colonization metapopulation models. c) Philopatry: individuals breed in their natal ponds with

probability = 1; all other ponds with probability = 0. d) IHS where linkages derive from shared

habitat traits independent of spatial locations (e.g., closed vs. open canopy, fish vs. fishless,

temporary vs. permanent).

Figure 16.2. Differing modes of dispersal/habitat selection and distribution of hypothetical

species X (obligate disperser) in a changing landscape. Initial set of habitats all suitable to X

except one. a) Distribution of colonists of X under passive dispersal/propagule rain model as

habitat suitability changes through invasion of incompatible species Y, (shaded ponds); no

change in colonization and propagules placed in unsuitable habitats are lost. b) Distribution of

colonists of X with IHS. X detects and avoids Y as an indicator of unsuitable habitat, propagules

redistributed among remaining suitable habitats, increasing densities of X. Increased densities

may have further population consequences (see text). c) Habitat contagion in the context of IHS;

suitable habitats in close proximity those invaded by Y are viewed as unsuitable by X, resulting

in loss of otherwise suitable habitats and further constriction of the population. Different

consequences obtain depending on whether attraction or avoidance is involved (see text). d)

Habitat compromise resulting from habitat loss. Smallest patch initially considered unsuitable by

X; after invasion by Y and subsequent loss of habitat, X forced into previously unused habitats as a result of increased densities in remaining high quality habitats (sensu Fretwell and Lucas 1970).

Figure 16.3. Interactive habitat selection and species covariances in dynamic landscapes. a) Two species with allotopic distributions, X (triangles) and Y (squares). b) Z invades (dark shading). Neither X nor Y can persist with Z, generating negative covariances between Z and X, and Z and Y; X and Y are now forced into syntopy in remaining “Z-free” habitats (half-circles); Z generates positive covariance between X and Y. c) Same as in “b” except X is competitively superior and coopts suitable patches previously occupied by Y, forcing it into the smallest (marginal) patch; Y may even move into even smaller, more marginal habitats (not illustrated). Habitat selection can generate negative covariances among species by avoidance, and positive covariances by attraction (not illustrated) or by shared avoidance and habitat compression.

Figure 16.4. a) Responses of ovipositing *H. chrysoscelis* to predators and competitors. ** indicates significant difference from controls (dashed line) at $P < 0.01$. Data represents distribution of >144,000 eggs into two categories, avoided species (*Enneacanthus chaetodon*, *Ambystoma maculatum* and conspecifics) and Control equivalents (*Rana catesbeiana*, *Notophthalmus viridescens* and *Trapezia carolina*). Modified from Resetarits and Wilbur 1989. b) Oviposition responses of a natural population of *H. chrysoscelis* to (non-lethal) presence of 5 species of predatory fish; only *Aphredoderus sayanus* was not significantly different from controls (modified from Binckley and Resetarits 2003), a result obtained with other taxa as well (unpublished data); monotypic family is only species/family of seven tested not eliciting strong avoidance. c) Oviposition responses of a natural population of *H. femoralis* to a gradient of (non-

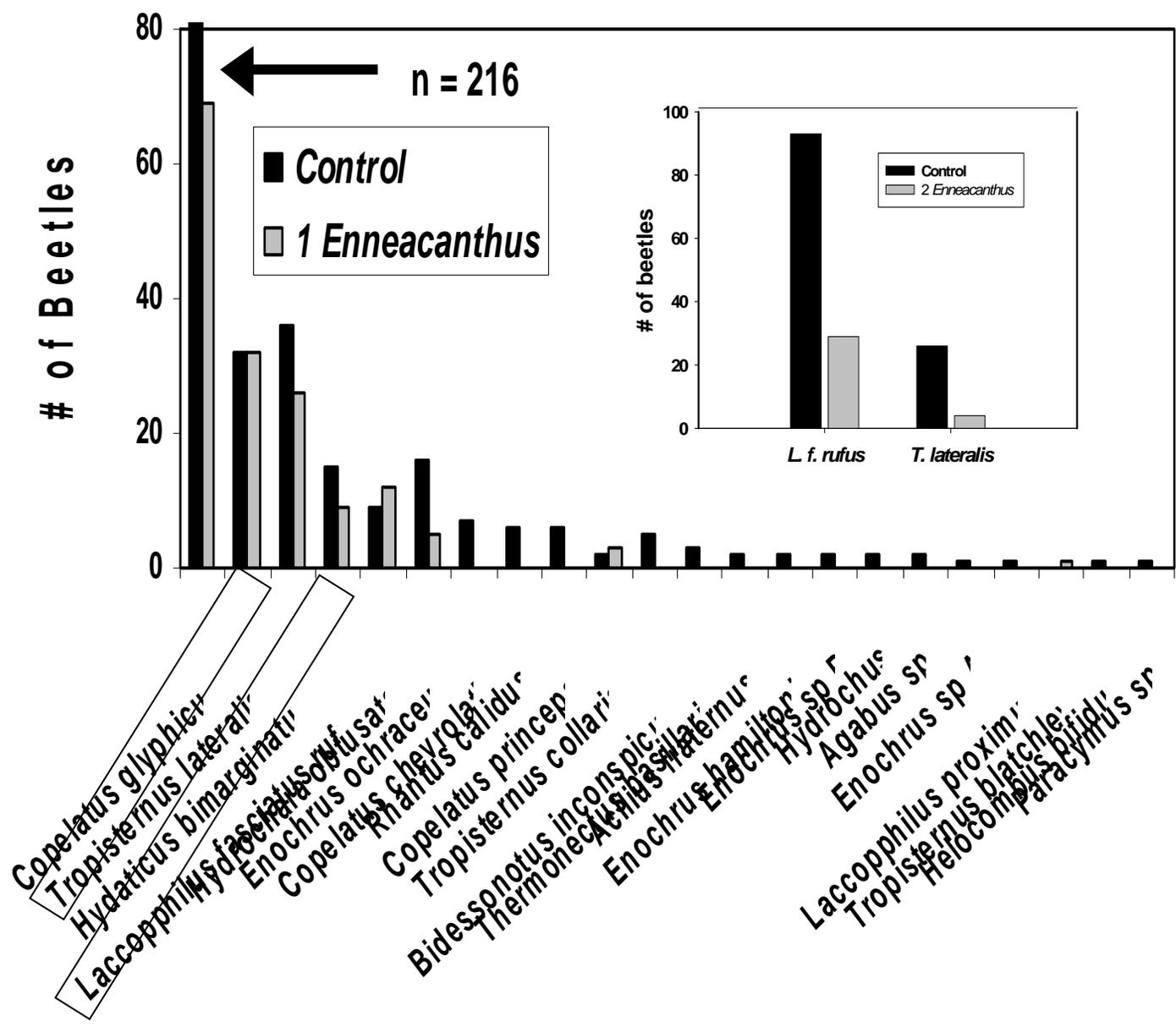
lethal) fish density (2 g *Umbra pygmaea*). All treatments significantly differ from controls but not one another. The threshold response density lies below the 1 fish level (<0.53 g/100 L) (Rieger et al. in review)

Figure 16.5. a) Responses of naturally colonizing aquatic beetles, *Tropisternus lateralis*, to (non-lethal) presence of pumpkinseed sunfish (*Lepomis gibbosus*). Number of adults explained 96% of variation in number of egg cases (modified from Resetarits 2001). b) Responses of *T. lateralis* to open vs closed canopy crossed with nutrient levels showing dramatic response to canopy cover and effects of nutrients only in open canopy ponds (unpublished data).

Figure 16.6. Effects of low density fish (non-lethal) presence (1 fish/375 L) on beetles colonizing experimental aquatic habitats. Results match field surveys; common species are reduced and rare species are absent. Eight species found with fish and 21 in fishless pools. Inset: response of two common beetles, *Laccophilus fasciatus rufus* and *Tropisternus lateralis* at density of 2 fish/375 L, suggesting main graph is conservative estimate of beetle response. This is the strongest evidence to date that IHS can determine species distribution and affect community assembly (Binckley et al. in review).

Figure 16.7. Potential effect of shared habitat preferences for open canopy, fishless ponds on covariance in distribution and abundance of *T. lateralis* (black arrows) and *H. squirella* (gray arrows), and effects of variation in preferences (nutrients) on potential covariance. Avoidance generates negative covariance between both species and fish.

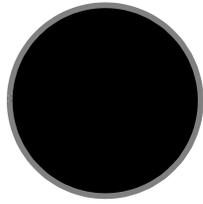
Figure 16.8. Responses of a natural population of ovipositing *H. femoralis* to (non-lethal) presence of predatory fish (*Enneacanthus obesus*) at regional (among sites) and local (among pools within sites) scales. Top panel illustrates 1 of four experimental blocks. At regional scale, females strongly preferred sets of fishless pools, demonstrating a non-linear response to increasing frequency of fish pools (indicating contagion - see Figure 16.2c). At local scale, avoidance of specific pools with fish was nearly complete [only 153 eggs out of 22605 (0.7%)] (Resetarits in review).



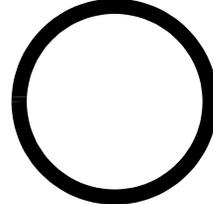
Ovipositing ♀ *T. lateralis*

Ovipositing ♀ *H. squirella*

CANOPY

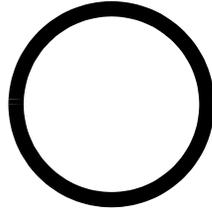


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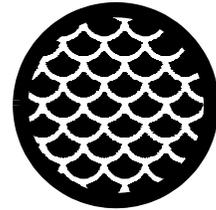


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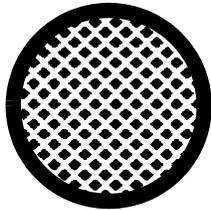


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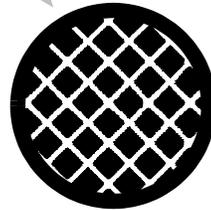


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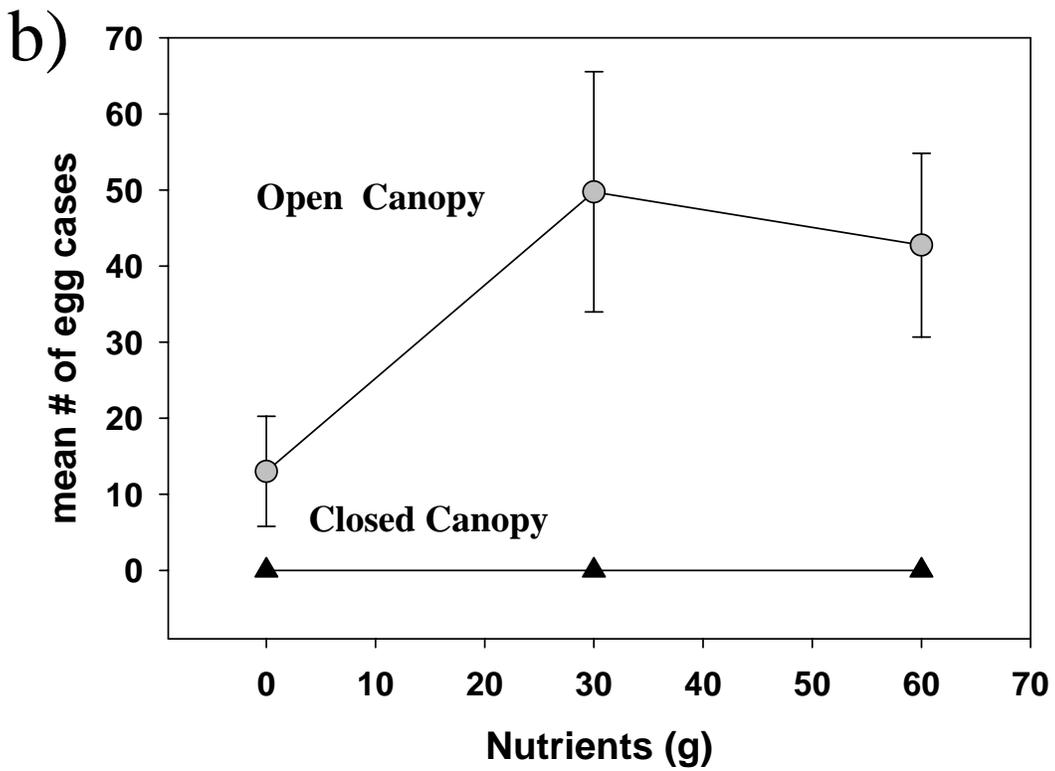
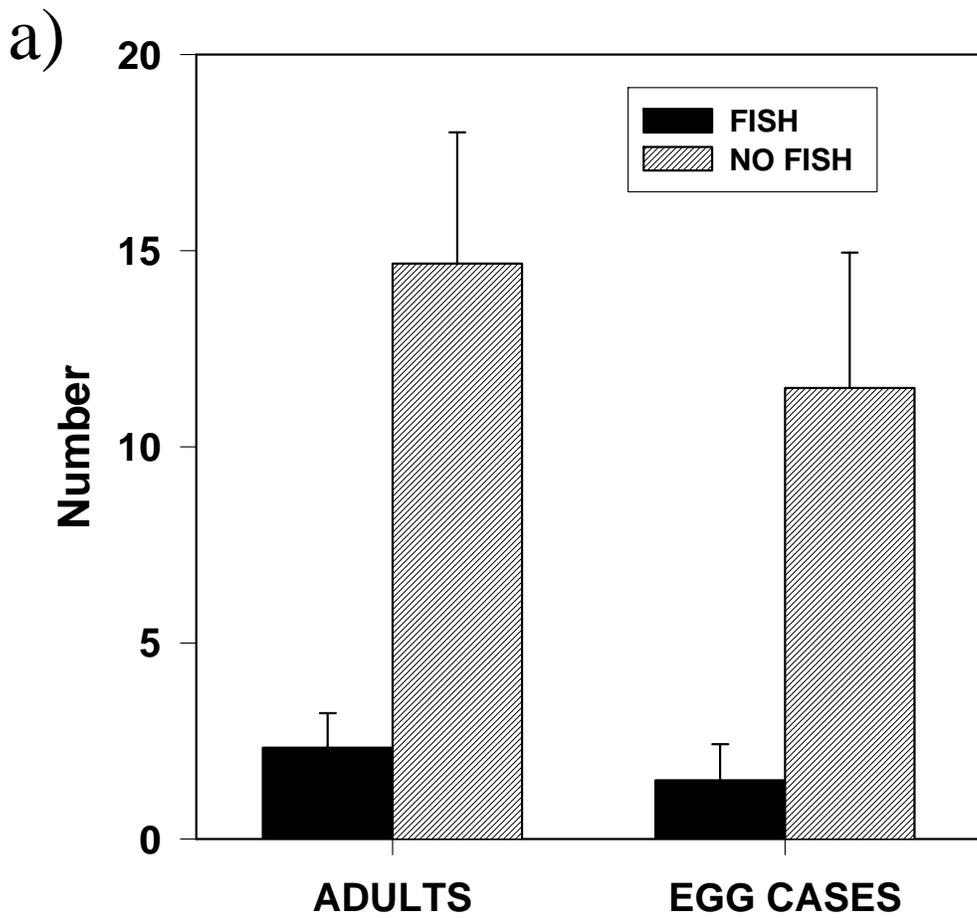


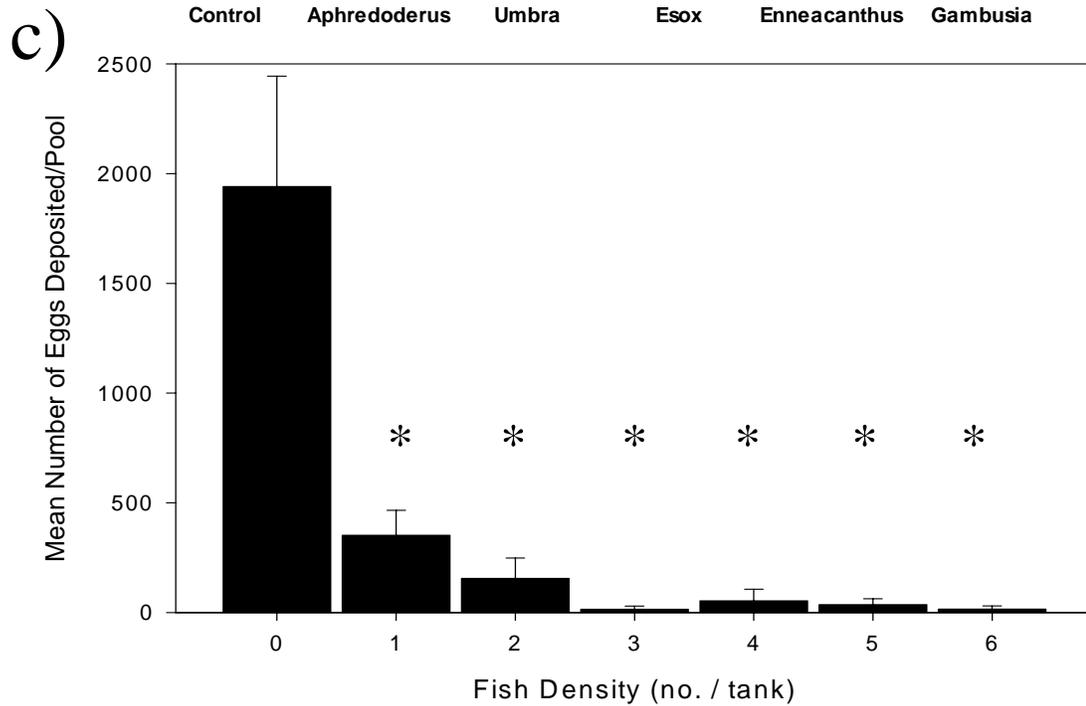
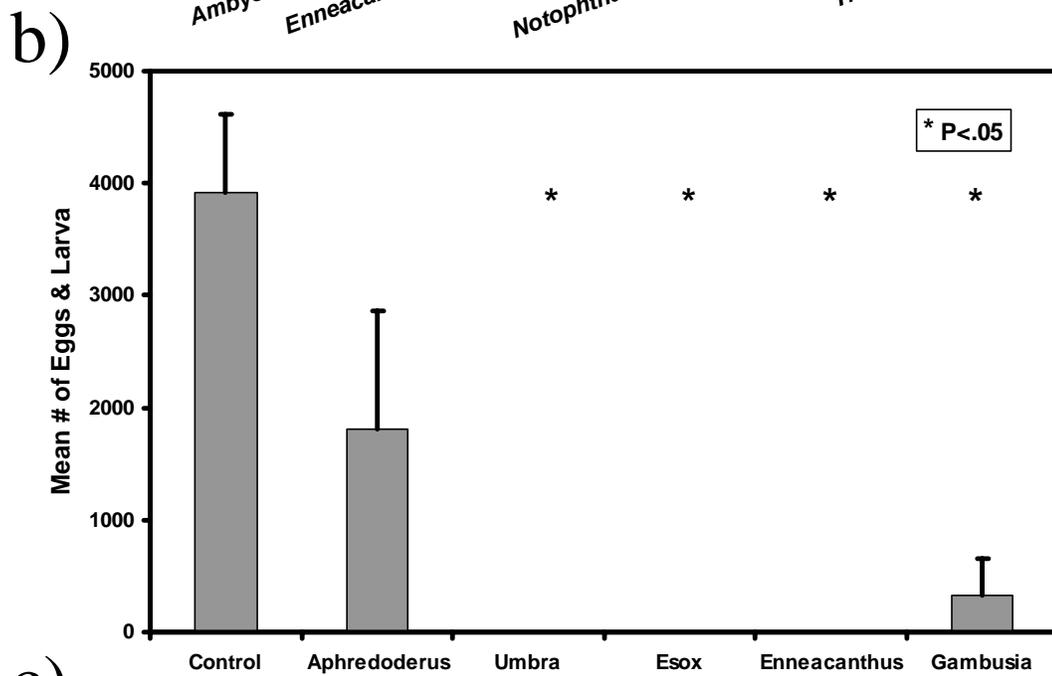
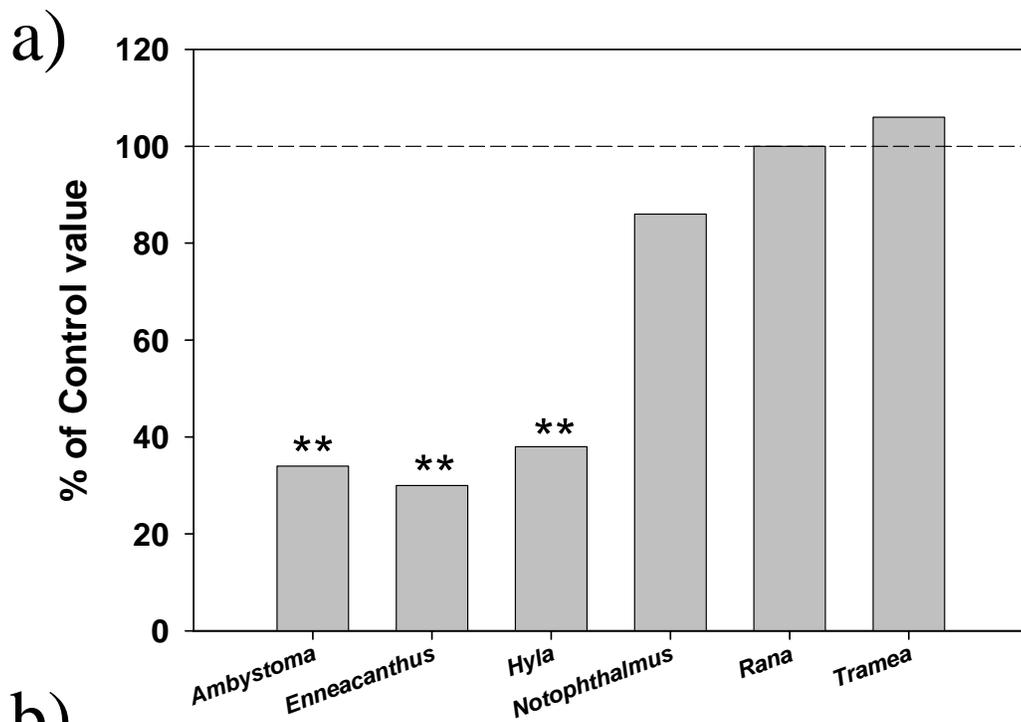
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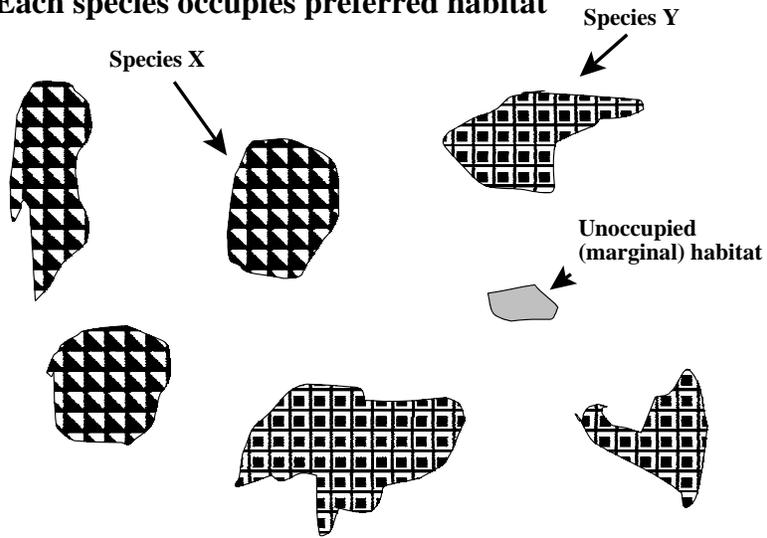
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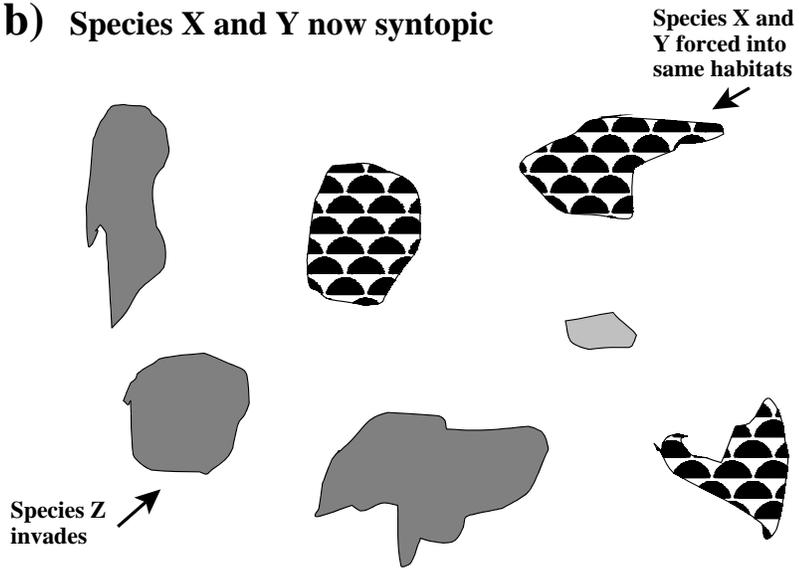




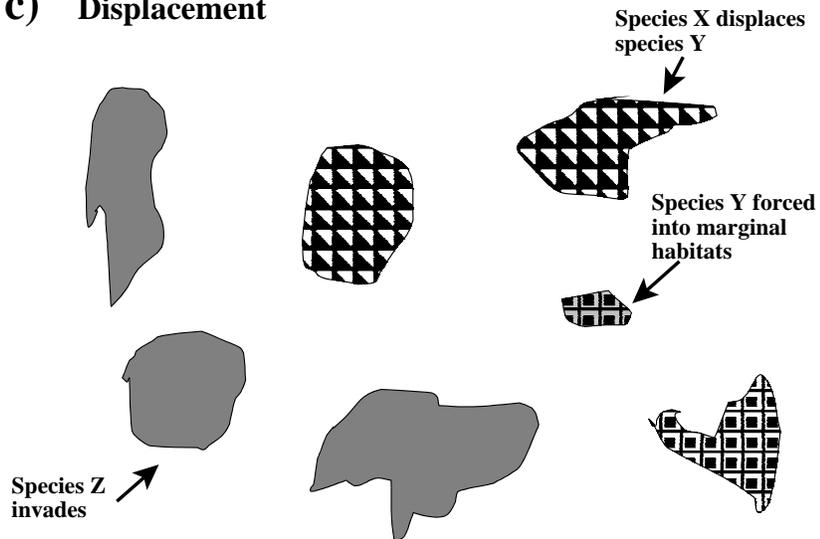
a) Each species occupies preferred habitat



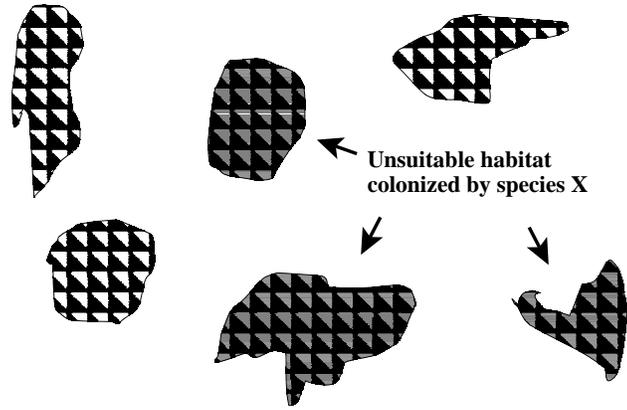
b) Species X and Y now syntopic



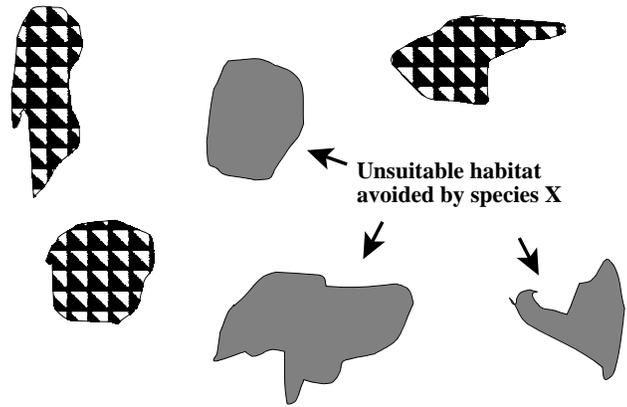
c) Displacement



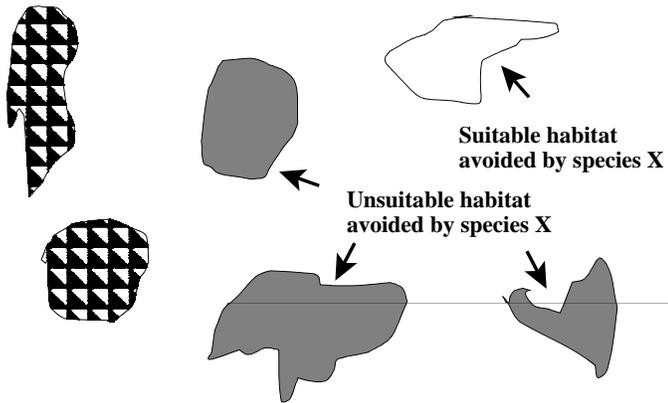
a) Propagule rain



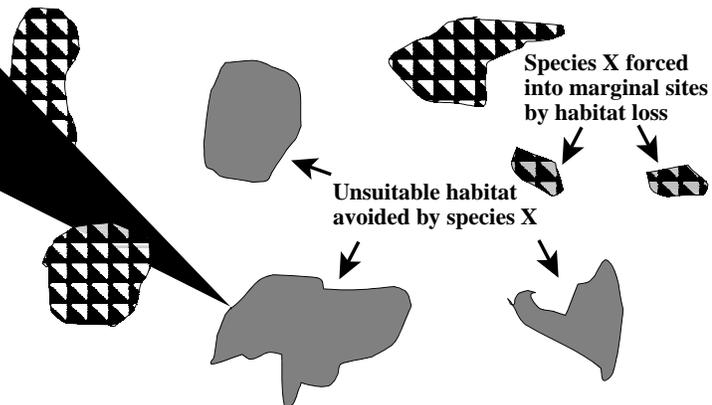
b) Interactive habitat selection

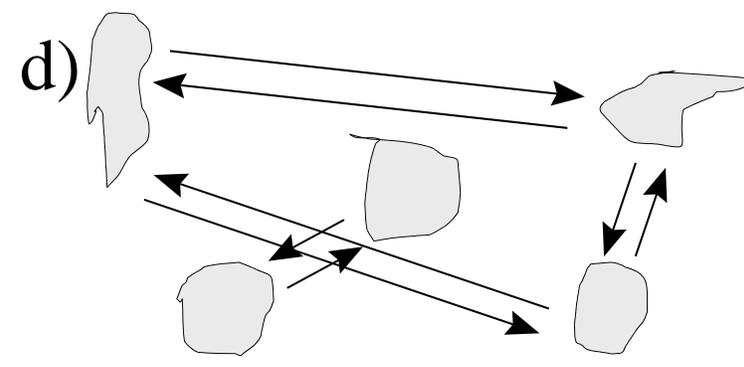
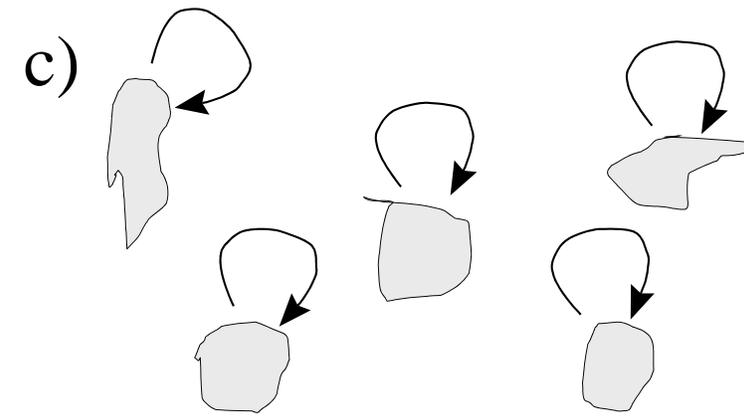
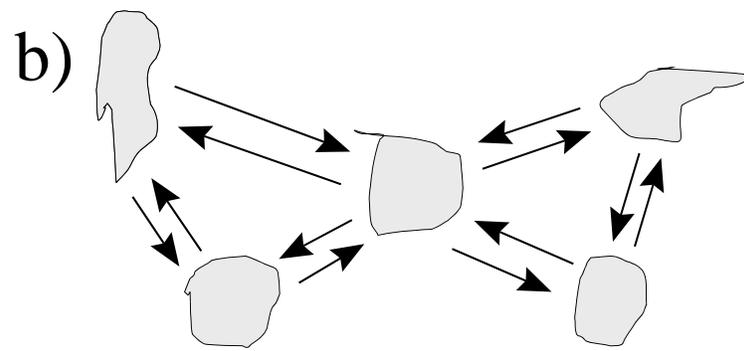
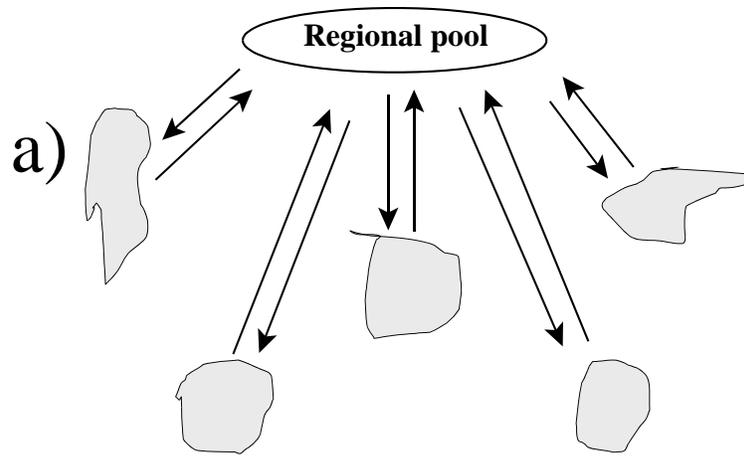


c) IHS plus "contagion"

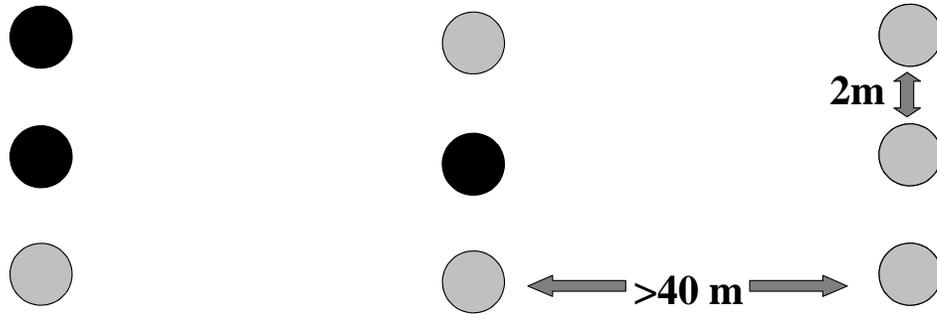


d) IHS and "compromise"

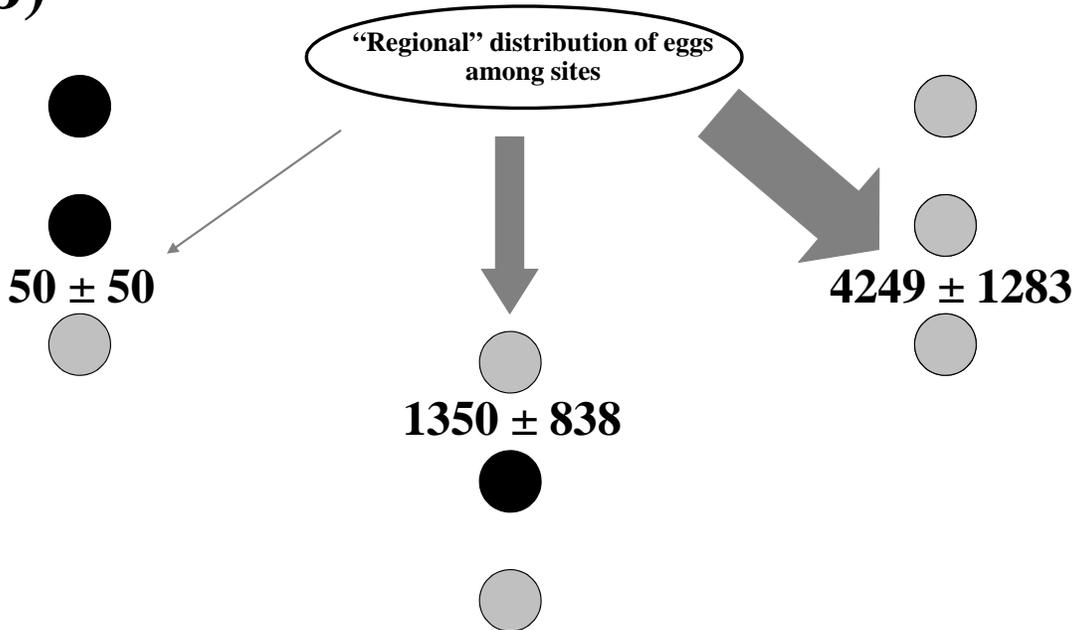




a)



b)



c)

