

**GENERAL ECOLOGY: COLONIZATION (REF. 472)**

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## **Synopsis**

Colonization is the arrival of individuals to areas of suitable habitat that are currently uninhabited. Populations are established by the successful colonizers that survive and reproduce. Colonization is a spatial process central to several fundamental concepts in ecology, including species coexistence, disturbance and recovery, succession, metapopulations, biodiversity, invasive species, and speciation. We consider the influence of colonization on each of these processes around the central theme of colonization-extinction balance. At the smallest scale, individual recruitment (colonization) and mortality (extinction) determine the density and persistence of a population. At a slightly larger scale, small disturbances of a competitive dominant can open space allowing good colonizers to coexist with dominant competitors via competition-colonization tradeoff. Large disturbances may result in a landscape with communities in different successional stages and, therefore, higher regional biodiversity. On continental scales, colonization-extinction balance sheds light on patterns of biodiversity through Island Biogeography Theory. Finally, we consider the influence of colonization on disease dynamics, range expansion, and spatial spread, with particular emphasis on anthropogenic effects that enhance colonization rates. Finally, over a longer timescale, colonization of new niche space may lead to niche expansion or speciation.

## Introduction

Colonization is the arrival of individuals to areas of suitable habitat that are currently uninhabited by individuals of the same species. Populations are established (or re-established) in uninhabited areas by the successful colonizers that survive and reproduce. Colonization, or recolonization, is a spatial process central to several fundamental concepts in ecology, including the spatial structure of populations (*cf* Spatial Distribution), species coexistence (*cf* Coexistence), succession (*cf* Succession), disturbance and recovery, invasive species (*cf* Invasive Species), and speciation.

Colonization is one possible consequence of dispersal. Dispersal is the permanent movement of an individual from one location to another (commonly, a seed, larva, or juvenile stage moving from its natal area to the area it will inhabit as an adult; *cf* Dispersal/Migration). If the individual disperses to an area uninhabited by conspecifics, then dispersal has resulted in colonization. If that colonizer survives to reproduce, then a new population has been established.

Colonization occurs at a range of spatial scales. For sessile organisms in which space is a primary resource (e.g. plants, sessile marine invertebrates), the death of an individual may open space for recolonization by another individual. At this smallest scale, the balance between extinction (individual mortality) and colonization (settlement of another individual in that location) determines the persistence of a population. Small disturbances, such as gopher mounds in grasslands or tear-outs in intertidal mussel beds, create small habitat patches that allow good colonizers to coexist with dominant competitors, enhancing local biodiversity through competition-colonization tradeoff. Larger scale disturbances, due to fire, logging, or sedimentation-erosion dynamics, may result in a successional mosaic: a landscape in which different areas were disturbed at different times in the past, resulting in a range of successional stages and, therefore, higher regional biodiversity. Colonization is also essential for range expansion and spatial spread. Anthropogenic effects have increased the rates of spread of many species by enhancing colonization. Finally, over a longer timescale, colonization of new niche space may lead to niche expansion or speciation.

We first consider characteristics which enhance species' colonization ability. Then, we use the central ecological concept of colonization-extinction balance to consider the implications of colonization from the smallest scale of an individual to the largest scale of species ranges. In doing so, we consider the implications of colonization for population growth, species coexistence, disturbance, succession, species invasions, and speciation.

## Factors Enhancing Colonization Ability

Organisms vary considerably in their ability to colonize new habitat. Figures 1a and 1b illustrate the variation between taxa of freshwater zooplankton in the time needed to colonize experimental mesocosms, and in the total number of mesocosms colonized over the course of two years (from Caceres and Soluk 2002; see Further Reading). In general, whether or not a particular organism colonizes a given new habitat depends on life-history characteristics, behavior, and environmental factors. Classically, the r-selected life-history strategy (*cf* K-strategist/r-strategist) is associated with strong colonization ability through the production of many, low-quality propagules, often adapted to long-distance dispersal via wind or water. This strategy increases the probability that propagules will arrive in a patch because of the vast

number of propagules released. However, strategies that increase the probability of establishment, rather than simply the probability of arrival, also enhance colonization success, including habitat selection and competitive ability. Many animals use habitat selection (*cf* Habitat selection) to detect appropriate habitat, thereby increasing the probability of arrival and subsequent establishment. This is particularly true for specialist organisms with highly specific habitat requirements or organisms that utilize short-lived resources (e.g., rotting fruit or hydrothermal vents). Good competitors, especially those with clonal growth, often make good colonizers: few propagules may arrive, but those that do are likely to be successful.

Among herbaceous plants, an annual life-history strategy, rapid growth, and the production of many, small seeds are characteristic of the “ruderal” strategy (*sensu* Grime; see Further Reading). Ruderals (see also Pioneer Species) rapidly colonize habitat opened by disturbance, allowing them to coexist with stronger competitors that colonize more slowly but ultimately exclude the ruderal species (*cf* Competition and Competition Models, Plant Competition). Ruderals are *r*-strategists that increase colonization ability by increasing the probability of arrival at a new patch. Other life-history characteristics may enhance the probability of establishment after arrival, such as phenotypic plasticity and the ability to reproduce asexually. Phenotypic plasticity allows an organism to use the morphology or behavior that is appropriate to its new environment. The ability to reproduce asexually, whether by clonal growth or selfing, is clearly advantageous to establishment because only a single individual is necessary to produce a viable population. In their experimental mesocosms, however, Caceres and Soluk (2002) found that the colonization ability of freshwater zooplankton was not necessarily predicted well by mode of reproduction (see Further Reading).

Among sessile marine invertebrates, there are two contrasting life-history strategies that may enhance colonization ability. Some taxa produce many, small larvae that feed during an extended larval period (weeks to months) in the plankton and are, therefore, transported over long distances. This long larval period results in long distance transport far from their natal areas, enhancing the probability of arrival in uninhabited areas. Other taxa produce fewer, larger, larvae with enough yolk to survive a shorter (hours to days), non-feeding planktonic period or, more extreme, larvae that crawl away and have no planktonic transport at all. While these taxa are less likely to be transported far from their natal areas, when they do arrive they are more likely to colonize successfully and establish a new population. This increased colonization success is due to the increased survival of colonizing individuals but also to more rapid local population growth since subsequent reproduction is retained locally. These examples make it clear that there are two strategies for colonization success: produce many propagules to ensure arrival at new habitat or produce well-supplied or highly competitive propagules that are likely to succeed if they arrive.

## **Competition-Colonization Tradeoff**

Ecologists contrast *r*- and *K*-strategy life-histories (*cf* *r*-strategist/ *K*-strategist) to identify the broad pattern of life-history tradeoffs between short-lived organisms with fast maturation, good dispersal ability, and many, small propagules and long-lived organisms with slow maturation, strong competitive ability, and few, well-supplied propagules, respectively. Because resources are finite, selection has forced a tradeoff between colonization ability and competitive ability. This tradeoff also produces a mechanism of species coexistence, called competition – colonization tradeoff.

In systems where disturbance creates colonization opportunities, competition–colonization trade-offs can lead to coexistence between multiple competitors that share a single, limiting resource. This tradeoff is most easily imagined when the limiting resource is space: the dominant species is a better competitor and will overgrow the fugitive species, which is a better colonizer. Disturbance results in mortality of both species and opens space on the landscape. If the fugitive species can colonize and exploit this new space fast enough, then the dominant and fugitive species can coexist.

We can see competition-colonization tradeoff as one case of colonization-extinction balance. Species coexistence is determined by the relative colonization rates of each species, the mortality rate of both species due to disturbance, and the mortality rate of the fugitive species by competitive exclusion. For coexistence to occur, the fugitive species and dominant species must each solve the problem of colonization-extinction balance: the dominant species must have a high enough colonization rate to avoid extinction by disturbance alone, while the fugitive species must have a higher colonization rate to withstand extinction from both disturbance and competitive exclusion. It acts at the scale of an individual or small group of individuals and determines whether one or both species will persist.

This pattern of coexistence has been best documented between organisms that compete for space. One classic example of competition-colonization tradeoff is the interaction between the annual sea palm, *Postelsia palmaeformis*, and the long-lived mussel, *Mytilus californianus*, in the rocky intertidal of the northeast Pacific. *M. californianus* is the competitive dominant, which will exclude *P. palmaeformis* over time. However, in areas of high wave energy, patches of *M. californianus* are ripped from the rocky substrate and *P. palmaeformis* colonizes these open patches more quickly than *M. californianus*. Transplant experiments demonstrate that *P. palmaeformis* can survive and reproduce in areas of low wave energy; however, in the absence of wave disturbance, it is overgrown by *M. californianus*. Therefore, when wave energy is high enough, *M. californianus* mortality due to disturbance and the faster colonization rate of *P. palmaeformis* allow these two species to coexist.

In Laikipia district of Kenya, fire-prone bushland savannah is dominated by a single species of swollen-thorn acacia tree, *Acacia drepanolobium*, which is host to four acacia-ant species that are obligate mutualists with *A. drepanolobium*. The ants nest within the swollen thorns and feed on nectaries of *A. drepanolobium*; the presence of ants deters herbivores from browsing on *A. drepanolobium*. Any one acacia tree hosts a single colony of ants. The four species of ants coexist on a single limiting resource of host trees; the species form a strict competitive hierarchy, in which more dominant species displace subordinate species from neighboring host trees. Unoccupied trees arise due to fire and elephant disturbance, which destroys colonies but not trees, and by small trees growing into a habitable size. A tree may be colonized by a colony from a neighboring tree or by a foundress queen. The two subordinate ant species both have higher colonization rates: the most subordinate species produces many more foundress queens to colonize newly available mature trees while the second most subordinate species has a higher than expected rate of colonizing empty neighboring trees by colony expansion. This tradeoff between competitive dominance and colonization ability is one mechanism of coexistence for these four species sharing a single limiting resource.

## **Competition-Colonization Tradeoff and the Successional Mosaic**

In systems where disturbances act on larger spatial and temporal scales, competition-colonization tradeoffs can maintain regional species diversity. Large scale disturbances, such as fire, logging, or sedimentation-erosion dynamics, open up tracts of unoccupied habitat. These newly opened areas are colonized by a predictable sequence of species in a process called ecological succession (*cf* Succession). Newly disturbed areas are first colonized by ruderal pioneer species (*cf* Pioneer Species). These species may be out-competed or overgrown by larger or longer-lived organisms. Over time, competitively superior species will dominate. When different areas in a landscape are disturbed at different times, the landscape becomes a patchwork of communities in different stages of succession, called a “successional mosaic”. When disturbance is moderate, this successional mosaic is thought to result in high diversity at the regional scale because communities in all successional stages are represented. This is called the “intermediate disturbance hypothesis” and is discussed in detail in another entry in this volume (*cf* Intermediate Disturbance Hypothesis).

The intermediate disturbance hypothesis has been proposed as an explanation for patterns of macroinvertebrate diversity in lotic streams in the Taieri River catchment in New Zealand. In this system, the intensity and frequency of disturbance are determined by the flow rate and frequency, respectively, of periodic high discharge events. Disturbance varies from reach to reach in the catchment due to stream slope, distance from headwaters, and local topography, among other factors. Macroinvertebrate diversity is a unimodal function of disturbance intensity. At high disturbance intensity, some stream macroinvertebrates cannot survive a disturbance or colonize fast enough after a disturbance to persist in high disturbance reaches. At low disturbance intensity, macroinvertebrates are distributed evenly, indicating competition among the species that remain long after a disturbance.

A critical piece of this “successional mosaic” is the availability of colonists from other populations on the landscape. In streams, these colonists can come from several sources: upstream habitat, flying adults from another reach, or refuge habitat that organisms use to escape the effects of disturbance. If disturbance is too frequent (or too rare) across the entire landscape, then there will be no areas in the later (or earlier) stages of succession to provide colonists to areas in other stages of succession. At this scale, colonization-extinction balance can influence the diversity of local communities (e.g., stream reaches) with different disturbance regimes and whole regions (e.g., river catchment) through the successional mosaic.

## **Metapopulation biology**

On larger spatial scales still, extinction of entire populations can provide the requisite unoccupied suitable habitat for colonization to occur. If recolonization from extant local populations occurs quickly enough to balance local extinction, persistence of a species on a regional scale can occur. Such a regional population, called a metapopulation, is an important concept for understanding population dynamics in patchy habitats.

A classic metapopulation is a regional population composed of many local populations, each of which may be extant or extinct at any one point in time. This situation occurs when patches of suitable habitat are separated by uninhabitable areas. If habitat patches are essentially equal, and the dynamics of individual populations are fast relative to inter-patch dynamics, then the important characteristic of a given patch is whether or not it is occupied. Thus, the primary

variable in classic metapopulation theory is the proportion of patches that is occupied (or the proportion of populations that is extant), and the determinants of this proportion are the rate of local population extinction and the colonization rate. Extinction occurs because of demographic stochasticity: no finite population can persist indefinitely. Colonization occurs via movement of individuals from extant populations to empty patches, and all patches are assumed to be equally accessible to all others. The theory, first set out in 1970 by Richard Levins, describes the dynamics of patch occupancy by the equation:

$$dp/dt = cp(1-p) - ep.$$

Here,  $p$  is the proportion of occupied patches,  $e$  is the extinction rate per occupied patch, and  $c$  is the rate of colonization per occupied patch per unoccupied patch. Alternatively, if  $p$  is the probability that a given patch is occupied,  $e$  is the probability that a given extant population goes extinct, and  $c$  is the probability that an individual from a given extant population colonizes a given empty patch. The equilibrium proportion of extant populations is  $P = 1 - e/c$ . Thus, the colonization rate must exceed the extinction rate to ensure persistence of the regional ensemble, and the magnitude of the excess determines the species' regional abundance. Factors such as the number of potential colonists leaving occupied patches, their dispersal ability, and their ability to establish new populations in unoccupied habitat patches are all included in the overall rate of colonization,  $c$ , in this model framework.

The classic metapopulation model involves several assumptions. While few natural populations may strictly meet these assumptions, the model provides a powerful conceptual framework for patchy populations, with important implications for conservation and evolution as well as population biology. It also serves as a starting point for introducing complications such as spatially restricted dispersal, spatial aggregation of and/or correlation between local populations, differential size or quality of habitat patches, and so on. Such modifications may allow the model to describe the dynamics of the many natural populations that meet a looser definition of a metapopulation as a regional population comprised of local populations that are interconnected by dispersal.

The metapopulation approach is perhaps most useful for modeling disease dynamics, since many of the classic model's assumptions are best met by populations of microorganisms. From the point of view of the disease, occupied patches are infected hosts and empty ones are susceptible hosts. The disease spreads if colonization via infection of susceptible hosts exceeds extinction via host immune response. The Kermack-McKendrick model, proposed to describe the dynamics of bubonic plague and cholera, is one of the simplest examples of this approach. The model consists of three differential equations describing the dynamics of susceptible hosts (suitable, unoccupied patches), infected hosts (suitable, occupied patches), and recovered hosts who have developed immunity from disease (unsuitable patches):

$$\begin{aligned}\frac{dS}{dt} &= -\beta SI, \\ \frac{dI}{dt} &= \beta SI - \gamma I, \\ \frac{dR}{dt} &= \gamma I,\end{aligned}$$

where  $\beta$  is the infection rate per infected host per susceptible host, and  $\gamma$  is the recovery rate per infected host. The infection rate in this epidemic model is thus analogous to the colonization rate in the classic metapopulation model. The major difference in this case is that with extinction of disease populations due to host immune response, habitat patches are also rendered unsuitable. Therefore, the question of most interest is not how many patches are infected at equilibrium, but whether or not the disease ever spreads. In this model, spread occurs if  $R_0 > 1$ , where

$$R_0 = \frac{\beta S}{\gamma}.$$

Thus, although models of disease dynamics and the questions they ask and answer may differ in important ways from basic metapopulation models, the role of colonization and its balance with extinction is clear in both cases. More sophisticated metapopulation models for disease allow host population dynamics and host mobility, as well as any of the refinements to the metapopulation model mentioned above.

## Island biogeography

We turn now to considering the balance between colonization and extinction on the spatial scale of continents, oceanic islands, and the distances between them. In so doing, we move from a single species occupying many patches to many species in a single large patch. The influential theory for this situation is Island Biogeography Theory, and another chapter in this volume (*cf* Island Biogeography) covers it in detail. In brief, the theory predicts that the number of species on an island depends on a dynamic balance between colonization of the island by species from the mainland and extinction of species already on the island. The mainland serves as a permanent pool of a fixed number of colonist species, and the island is permanently suitable for all of them, but each species colonizes the island only when not currently present there. As a result, as the number of species occupying the island increases, the rate of colonization per unit time decreases. If all species were equal in their colonization ability, then the colonization rate would decrease linearly with the number of species on the island. Since species usually differ in colonization ability, however, as we discussed above, the poorer colonizers take longer to arrive, and the better colonizers are likely already present when they do. Thus, we expect the decrease in the colonization rate to be more gradual at higher island species richness, and the rate should be a convex decreasing function of species richness on the island. The exact value of the colonization rate function at any richness depends on the specifics of a given situation, including the identities of the species in the colonist pool and the isolation of the island from the mainland. The intersection of the colonization function with the extinction function (an increasing function of island richness, *cf* Island Biodiversity) determines the richness at which colonization and extinction balance. This is the island's equilibrial or long-term species richness.

Empirical tests of the general theory have upheld its essential points. The classic model, however, does not detail interaction between colonizing species (such as facilitation of colonization by earlier colonists, for example, *cf* Community Assembly Rules) and also excludes any effects on species richness of evolution on either the mainland or the island. Despite these omissions, the model provides a valuable conceptual framework for understanding colonization's role in determining diversity and community composition over large spatial scales, and also provides a starting point for understanding spatial systems other than oceanic islands. For instance, the theory can apply to habitat islands such as mountaintops or lakes, as long as a permanent "mainland" habitat exists to provide colonists. Island Biogeography Theory, where

colonization occurs between pairs of very unequal habitat patches, and metapopulation theory, where colonization takes place between many equal patches, are two special cases of colonization-extinction interactions in patchy habitats. The two theories are thus useful tools for understanding the dynamics of the many patchy natural systems on regional to continental spatial scales.

### **Availability of new, suitable habitat on a large scale**

Biological invasion is a prominent example of colonization of new areas of suitable habitat. Invasive species often have life-history characteristics that make them good colonizers. In the cases where invasive spread occurs most quickly, many secondary colonization events follow the initial introduction, so that rapid spread occurs by the establishment, increase, and eventual coalescence of many small and widely dispersed populations descended from the initial colonizers of the new habitat. Species that exhibit such rapid, patchy spread include cheatgrass, *Bromus tectorum*, in western North America; smooth cordgrass, *Spartina alterniflora*, in Willapa Bay, Washington State; and the Argentine ant, *Linepithema humile*, which disperses poorly on its own but covers long distances when assisted by humans. Because many conspicuous invasive species disperse widely, invaders often fall into the 'ruderal' or 'fugitive' life-history categories; but many (such as yellow star thistle yellow starthistle, *Centaurea solstitialis*, and the Argentine ant, *L. humile*) are very strong competitors, while others (such as saltcedar, *Tamarix ramosissima*) tolerate extreme environments very well. Whether they are good colonizers because they disperse often, survive well during dispersal, and/or find many types of habitat acceptable for vigorous growth (sometimes despite the presence of a prior resident), invasive species increasingly take advantage of new dispersal pathways opened by the global human economy to reach previously unavailable areas of suitable habitat. These issues are of primary importance in attempts to slow, stop, or prevent biological invasions that are potentially devastating to native communities (*cf* Species Invasions).

Changes in habitat suitability can provide new opportunities for colonization on large spatial scales. One way to be a good colonizer is to enhance the suitability of a new habitat, and some species can facilitate their own spread into new areas by changing the properties of the surrounding ecosystem. For instance, colonization by alien grasses can increase the fuel available to fire and thereby increase fire frequency, area, and intensity. The grasses recover quickly from fire and colonize burned areas, generating a positive feedback loop that favors the grasses' spread. Alternatively, one colonist can open large areas of suitable habitat for another: when the European green crab, *Carcinus maenas*, arrived in San Francisco Bay, its predation upon two species of native clams reduced their densities dramatically and allowed the rapid spread of the eastern gem clam, *Gemma gemma*. Finally, climatic change can also drive changes in habitat suitability, with colonization of the newly suitable areas resulting in geographic shifts in species' ranges. Northward plant colonization of newly uncovered habitat after withdrawal of glaciers at the end of the last ice age is well documented in the pollen record. In recent decades, changes in intertidal community composition in the northeastern Pacific reveal northward shifts of several southern species into waters that previously were too cold for them. Climate change can also lead to colonization by facilitating dispersal. Low sea levels may have facilitated the spread of humans from Eurasia to the Americas by revealing the Bering land bridge. Understanding interactions between climate change and colonization is an urgent priority for conserving biodiversity and anticipating likely novel community assemblages, given rapid predicted natural and anthropogenic habitat changes in the future.

One of the most dramatic instances of colonization of new habitat occurs not in physical space but in niche space. Organisms can increase the area of suitable habitat by evolving to use new areas. The global influenza pandemic of 1918, recently shown to be derived from avian influenza, is a spectacular example of a virus' evolution to take advantage of an entirely new host, and other deadly human diseases throughout history (including recent times) may have their origin in niche shifts of animal disease (cf. Zoonosis). Colonization of a completely new habitat type frequently occurs after colonization in physical space, as evidenced most clearly by adaptive radiation on species-poor islands. The lag between the initial colonization of a new area by an invasive species and the onset of rapid spatial spread is sometimes also attributed to genetic adaptation to the new environment. Genetic founder effects may also play a role in this adaptation process. In any case, niche shifts precipitated by physical colonization can be an important process in allopatric speciation.

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## Figure Captions

Figure 1a. Time to colonization (weeks) into each mesocosm for each of 26 zooplankton taxa. Taxa are listed in order of average time to colonization. Diamonds: cladocera. Circles: copepods. Triangles: rotifers. Squares: all other taxa. Reprinted with permission from Caceres and Soluk 2002 (see Further Reading). Because colonization by individuals is difficult to observe, 'colonization' here also includes establishment of reproducing populations large enough to be detected in samples.

Figure 1b. Negative correlation between the week each taxon was first found in the array, and the number of mesocosms that were invaded over the 2 years. The Other category includes annelids, flatworms, water mites, and Ostracods. Reprinted with permission from Caceres and Soluk 2002.

Figure 1a.

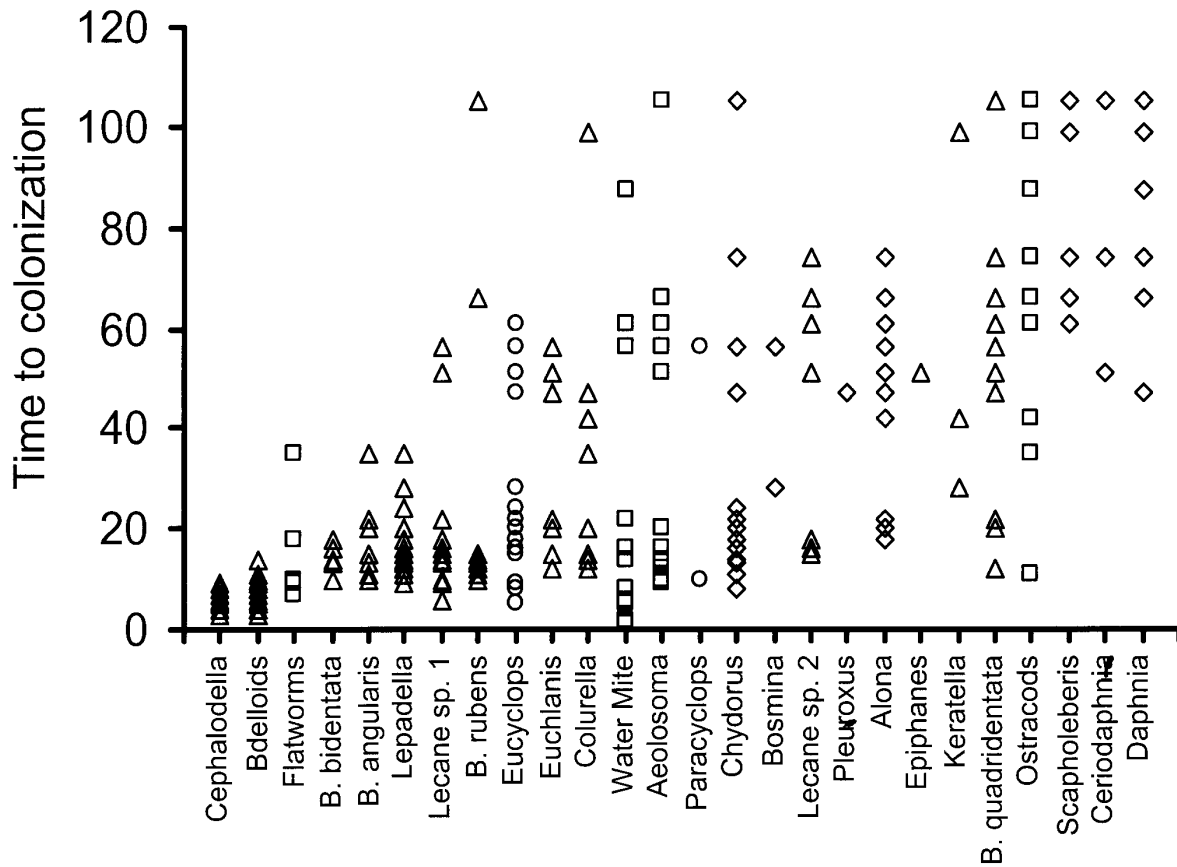


Figure 1b

