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Source: *The American Naturalist*, Vol. 147, No. 4, (Apr., 1996), pp. 558-575

Published by: The University of Chicago Press for The American Society of Naturalists

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CAN CONSUMER-RESOURCE DYNAMICS EXPLAIN PATTERNS OF GUILD ASSEMBLY?

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Submitted March 31, 1994; Revised June 29, 1995; Accepted August 7, 1995

Abstract.—Nonrandom assemblies of small mammals conform, on average, to a simple pattern discovered by Barry Fox: "Species entering a community will tend to be drawn from a different group until each group is represented, and then the rule repeats." We demonstrate that the Fox assembly pattern is a probabilistic consequence of adding guild structure to models of consumer-resource competition. Assemblies agreeing with the Fox pattern will occur more frequently than those that do not agree with it. High-probability states of coexistence occurring in heterogeneous habitats will frequently include lower-probability states in habitat subsamples. In communities composed of many guilds, low-probability "non-Fox" states representing *i* guilds should occupy a broader range of habitat variation than should subsets of high-probability Fox states representing fewer guilds. Differences in resource gradients among habitats should produce a correlated habitat bias in guild representation. Patterns of community assembly from diverse boreal rodent communities containing four different guilds were consistent with the theory's predictions. First, states agreeing with the Fox pattern occurred more frequently than expected to occur by chance. Second, low-probability states were nested in high-probability ones. Third, low-probability states from three guilds occupied a greater range of habitat variation than did subsets of high-probability states in fewer guilds. Finally, different rodent guilds were biased toward forest and cutover habitats.

Ecological communities are not simply random assemblies of species but represent structured subsets of regional species diversity that suggest repeated patterns of community assembly (Diamond 1975). Certain combinations of species, so-called favored states, occur more frequently than expected; other combinations representing "unfavored states" are less common than expected to occur by chance alone (M'Closkey 1978; Fox 1987, 1989; Fox and Kirkland 1992; Fox and Brown 1993; Kelt et al. 1995). These, and other assembly patterns, have been vigorously debated among ecologists attempting to reconcile polarized views on the deterministic versus stochastic nature of ecological communities (Salt 1983; Strong et al. 1984; Fox and Brown 1993, p. 358).

Recent studies by Fox demonstrate, nevertheless, that communities composed of different guilds appear to have an assembly pattern in which species entering a community tend to represent a different guild until each guild is represented,

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with the pattern then repeating (Fox and Brown 1993). We call an assemblage of species agreeing with this pattern a Fox assembly. We demonstrate that Fox assemblies, and at least one earlier assembly pattern described by M'Closkey, are logical outcomes of the interplay between resources and their competitive harvest by consuming species.

A CONSUMER-RESOURCE EXPLANATION

Fox assemblies can be explained by graphical models of consumer-resource dynamics (MacArthur 1972; Tilman 1982). According to these models, each species requires some minimal amount of resource to sustain its equilibrium population size. The combination of resource densities in which this is possible defines the species' zero net growth isocline (ZNGI; Tilman 1982; see fig. 1). Each species also will have a characteristic consumption rate for each resource in its diet. The joint consumption of two resources can be defined by a vector documenting the simultaneous reduction of both resources. Species that consume more of resource A than resource B will have a resultant consumption vector biased toward resource A. The equilibrium abundance of resources available to a species depends on resource supply points, consumption rates, and ZNGIs.

Consumption rates and ZNGIs define which, if any, species can exist, or coexist, in a habitat with a given supply of resources. Figure 1A illustrates an example of a resource supply point that leads to an unstable equilibrium (*filled circle*) for species 2 because species 3 can harvest the resources to a new equilibrium (*open circle*) below that required to sustain species 2. A supply point located between the consumption vectors for the two species would enable both to coexist at equilibrium (see fig. 2).

The MacArthur-Tilman theory assumes a direct correspondence between the location of the ZNGI and resource harvest (the consumption vector). The angle between adjacent species' consumption vectors must thereby be proportional to the "niche distance" between their respective ZNGIs. In communities composed of many species, stable points of two-species coexistence occur for only those species with adjacent but crossing ZNGIs (fig. 1B), that is, only for nearest neighbors in niche space. This prediction is confirmed by M'Closkey's observation that, in local habitats, coexisting species of desert rodents represent those combinations of species with minimal resource separation (M'Closkey 1978).

The MacArthur-Tilman model can be easily expanded to include two or more guilds (or other functional groups) of species. Members of each guild will, by definition, be more similar in resource use than will members of different guilds (their ZNGIs will cluster together; fig. 1B). This means that a guild of species preferentially consuming resource A (e.g., herbivores) should, with declining preference, produce a set of consumption vectors of declining bias toward that resource. A second guild preferentially consuming resource B (e.g., granivores) should produce a set of consumption vectors biased to that resource.

When the niche distance between guilds is greater than that within them, the angle between consumption vectors for pairs of species belonging to different guilds will always exceed the angle among any pair of adjacent species belonging

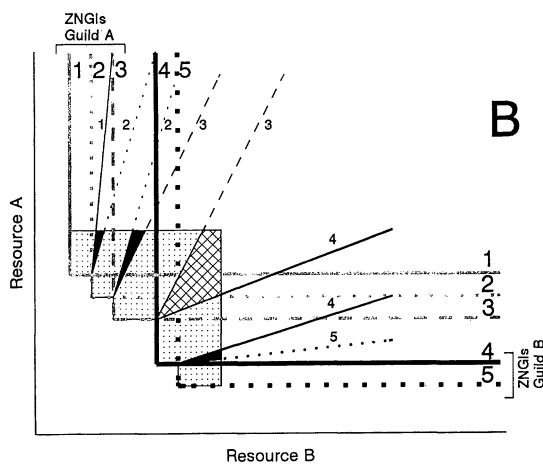
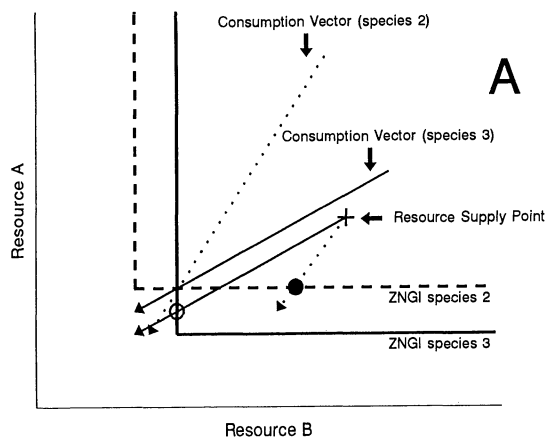


FIG. 1.—The MacArthur-Tilman consumer-resource model of species coexistence. Each species is represented by a ZNGI and a resource consumption vector. In the absence of consumption, resources are renewed to their own carrying capacities (the supply point of the two resources). Each predator's consumption vector counters renewal (population growth) by prey. Renewal and consumption are perfectly balanced (no net change in either resource levels or consumer density) at only one point along the ZNGI. Two consumers coexist at equilibrium when there is no net change in resource supply and in the population densities of the two consuming species, a point defined only where their respective ZNGIs cross. *A*, Filled circle, unstable equilibrium for species 2; new equilibrium for species 3. *B*, Hatched area, Fox state; filled triangles, non-Fox states; stippled polygon, possible sets of one-species assemblies. As drawn, the two resources are essential for each species to exist (the ZNGIs do not contact either axis). We have assumed essential resources for heuristic purposes only; qualitatively identical conclusions hold for various forms of substitutable and hemiessential resources (see, e.g., Tilman 1982).

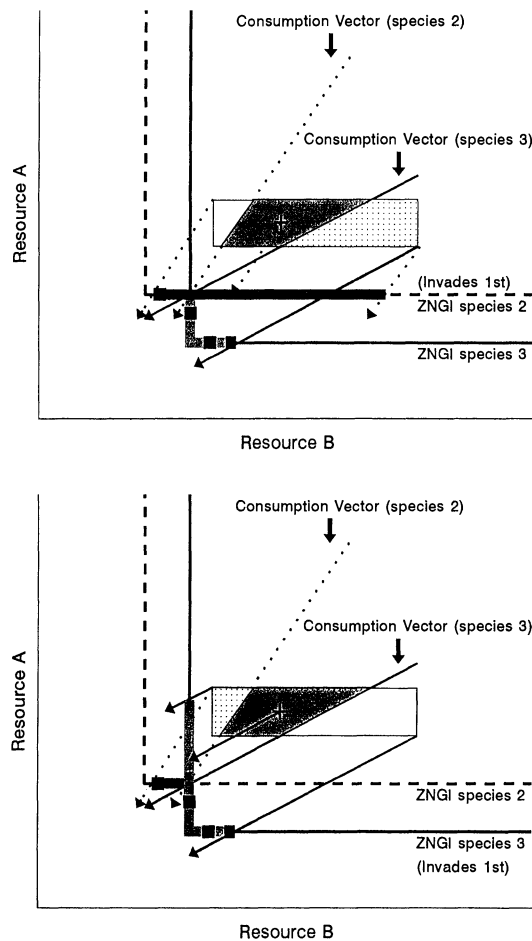


FIG. 2.—An example of priority effects on the probability of successful invasion by two species belonging to a single guild. Each species is represented by a ZNGI and a resource consumption vector as in fig. 1. *Wide dark line*, possible equilibria along the ZNGI of species 2; *wide light line*, possible equilibria along the ZNGI of species 3; *rectangle*, available resource supply points; *shaded polygon*, set of resource supply points in which both species can coexist; *plus sign and associated vector*, harvest of a specific resource supply point; *dark, z-shaped, square-dotted line*, equilibrium resource concentrations when both species are present.

to a single guild (fig. 1B). Thus, the stable coexistence of one species from each guild (a Fox state; *hatched area*) represents a greater proportion of resource space than does the stable coexistence of two species from the same guild (non-Fox state; *filled triangles*) and will occur more frequently in nature. The stippled polygon in the figure indicates the limits of resource values and represents possible sets of one-species “assemblies” on these two resources.

The proportion of resource space occupied by a single species will depend on the degree of resource specialization as well as the value and environmental covariance of resource supply. The species that actually coexist will depend,

similarly, on their specialization and the heterogeneity in the resource supply of the habitat. Each pair can occur in stable equilibrium in a heterogeneous habitat. But Fox's "rule" is more explicit than this. The pattern appears to implicate priority effects in community assembly. Can we generate such mechanisms from consumer-resource dynamics?

Two Species from One Guild

Imagine two species in a single guild invading habitats representing a set of resource concentrations such that both species can, when alone, invade the entire set of habitats (i.e., all resource concentrations are greater than those of either species' ZNGI; fig. 2). The ZNGIs document that species 2 is most limited by resource A; species 3 is most limited by resource B. We wish to investigate how the prior invasion of each species affects the probability of successful invasion by the other.

We evaluate priority effects graphically. We let each species establish and reach equilibrium with its resources, then determine the proportion of resource supply points that the second species can invade. Figure 2 illustrates that if all available resource concentrations were equally represented, and if each species were to have similar colonization potential, the conditional probability of the invasion of one species (e.g., species 3), given that the other (species 2) is present, would often be greater than the conditional probability of the successful invasion of that second species (species 2) in the presence of the first (species 3).

In the top panel, species 2 is assumed to invade first. All available resource concentrations greater than those of its ZNGI will be harvested until they lie along the ZNGI (wide dark line). Species 3 can invade all habitats supporting resource supply points in the stippled area and reduce their concentrations to its own ZNGI (wide light line). The shaded polygon represents the set of resource supply points in which both species can coexist. The plus sign illustrates the harvest of a specific resource supply point. To the right of the shaded polygon, species 3 can harvest both resources to a lower level than the equilibrium concentration for species 2 alone. The equilibrium resource concentrations when both species are present are given by the dark, z-shaped, square-dotted line overlapping the respective ZNGIs. The equilibrium concentrations do not depend on priority effects (cf. the bottom panel, in which species 3 invades first). If all resource concentrations were equally likely, species 3 would have a higher probability of invading a community containing species 2 than the converse (cf. the stippled area of the top panel with that of the lower one).

The proportion of resource supply points that a species can invade depends on its, and its competitors', resource specialization (consumption vectors) and the relative availability of resources. In the example, species 3 is a "better" invader because the range of sustainable resource concentrations is greater for resource B than it is for resource A.

Two or More Guilds

Imagine, now, a community composed of four species belonging to two guilds (fig. 3). Assume, as above, that habitats representing different resource supply points are equally represented. Any single species will be able to occupy those habitat patches whose initial resource concentrations are greater than the joint

concentrations represented by the species' ZNGI. All species can invade the community at any time. The identity of individual species will thereby vary among assemblies. Again, we allow each species to initially occupy the resource space at equilibrium and evaluate the probability of invasion by all others.

The probability of successful invasion will be biased toward the guild most limited by the resource with the greatest range of sustainable concentrations. In the upper left panel of figure 3, in which species 2 invades first, species 3, 4, and 5 all have more or less equal chances of invasion. The combined probability that one member from guild B (species 4 and 5) will invade is about twice that for species 3 (producing a Fox assembly). Another example of Fox's pattern is illustrated in the top right panel. Species 2 can invade a community already containing species 3 in habitat patches located in the vertically lined area of resource concentrations only (where it can occur at equilibrium with species 3). Species 4 and 5, which belong to a different guild, can invade habitat patches representing a much greater range of resource concentrations (*horizontal and stippled regions*, respectively; each can coexist with species 3 in some patches and exclude it from others). The conditional probability for species 4 or for species 5 to invade a community including only species 3 is much greater than that for species 2. The conditional probability of either species invading (the sum of each species' conditional probability) is much greater.

In the lower left panel, species 2, 3, and 5 have about equal opportunities for invasion. The combined probability favors the invasion of a member of guild A (producing a Fox assembly). In the lower right panel, species 2, 3, and 4 have approximately equal chances of successful invasion. The combined probability favors guild A and a Fox assembly. Regardless of which species invades first in these examples, the combined conditional probabilities are always greater for members of the second guild to invade next. Similar mechanisms would tend to regenerate Fox assemblies in stochastic communities undergoing local extinction and recolonization.

Note that the probable sequential invasion of additional members of one guild is lowered not only by reduced resource concentrations but also by the statistical effect of sampling guilds without replacement. Species already present reduce the summed probability of invasion by that guild. The result is that, even with and during stochastic colonization, Fox's pattern should often dominate patterns of guild assembly. Non-Fox assemblies will occur, but with a lower probability.

A TEST

If consumer-resource models of guild assembly are valid, the existence of Fox assemblies should depend critically on habitat heterogeneity (fig. 4). Fox assemblies composed of two or more species from each guild (*large ellipse*) actually contain many different stable states. Subsamples of habitats from Fox assemblies with two or more species in a guild should reveal both Fox and non-Fox states of species coexistence (*small ellipses*).

To make the predictions explicit, imagine that one has sampled the community composed of the seven species belonging to three guilds portrayed in figure 4.

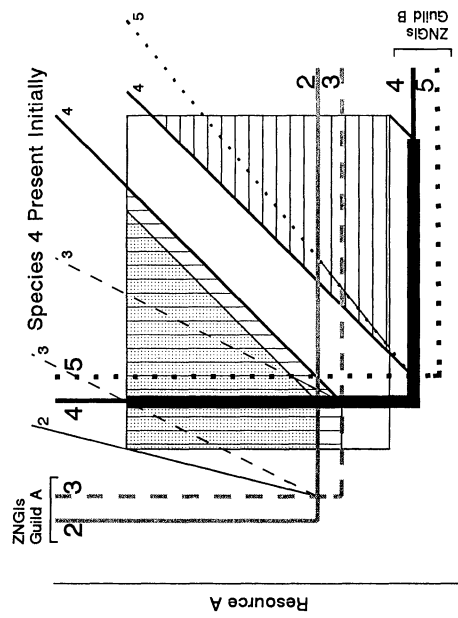
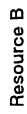
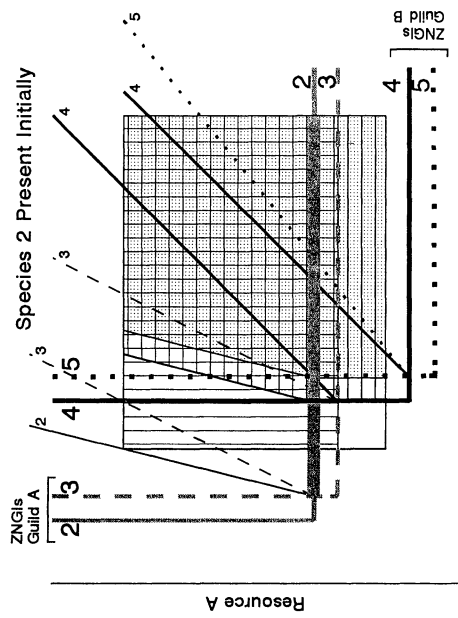
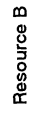
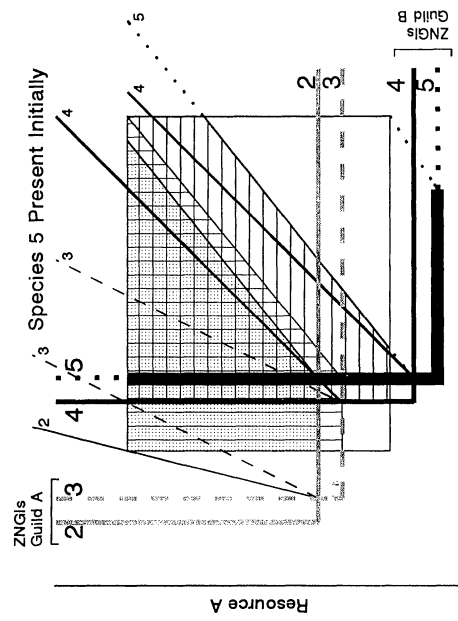
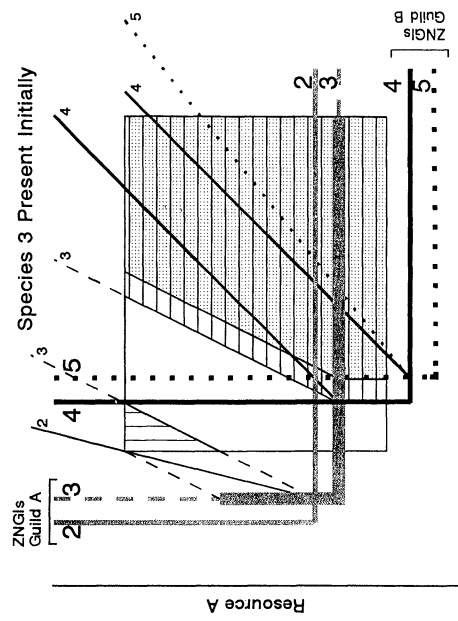
Imagine further that in one pooled sample, species 1, 2 and 3 occupy habitat K, whereas species 3 and 6 occupy habitat L. The pooled sample represents a Fox assembly (two members from guild A and one each from guilds B and C), as does the subsample from habitat L (one species each from guilds B and C). The subsample from habitat K is a non-Fox assembly (two species from guild A, one species from guild B, and none from guild C).

Now imagine that one has sampled a different area. One sample contains species 4, 5, and 6 from habitat K and species 5 and 6 from habitat L (a non-Fox assembly; two species from guild B, one from guild C, and none from guild A). A second sample is composed of species 5 in habitat K and species 5 and 6 in habitat L (a Fox assembly; one species from two different guilds). The non-Fox assembly containing three species should occupy a broader range of variation than should the nested Fox assembly containing two species. To generalize, a non-Fox assembly of i guilds would necessarily occupy a broader range of habitat variation than would any included Fox assembly of fewer guilds.

We tested these predictions by collecting 18 samples of diverse rodent assemblies along 40-station transects in northwestern Ontario. Twenty consecutive stations on each transect were located in regrowing forest cutovers aged from 2 to about 20 yr postharvest. The adjacent 20 stations were located in uncut boreal forest grading from almost pure conifer stands dominated by jack pine (*Pinus banksiana*) and spruce (*Picea glauca* and *Picea mariana*) to more or less pure hardwoods (*Betula papyrifera* [white birch], *Populus tremuloides* [trembling aspen], and *Populus balsamea* [balsam poplar]). Stations were located at 10-m intervals along each transect. Rodents were sampled in 1992 with single Longworth live traps set for 3 consecutive days between July 20 and August 28, the period when rodents at this latitude are approaching their seasonally high population densities and before hibernation by chipmunks and jumping mice. Our scale of sampling (100 km²) was large enough to encompass a range of habitat variation and small enough to ensure that each species had the opportunity to colonize each rodent assembly.

Three microtine herbivores (*Clethrionomys gapperi* [red-backed vole], *Microtus pennsylvanicus* [meadow vole], and *Microtus chrotorrhinus* [rock vole]), two diurnal sciurids (*Tamias minimus* [least chipmunk] and *Tamias striatus* [eastern chipmunk]), two saltating zapodids (*Napaeozapus insignis* [woodland jumping mouse] and *Zapus hudsonius* [meadow jumping mouse]), and one cricetine (*Peromyscus maniculatus* [deer mouse]) defined four rodent guilds. Two additional microtines (*Phenacomys intermedius* [heather vole] and *Synaptomys cooperi* [southern bog

FIG. 3.—Examples of priority effects in a community with two guilds. Each panel displays the initial depression of resource levels following invasion and equilibrium resource harvest by one species (*wide lines*). Areas of resource concentrations where members of guild A can invade are denoted by vertical bars; areas where members of guild B can invade correspond to horizontal bars. Stippling represents the area in which a second member of the alternative guild could invade given that only the initial species is present. Conditions for invasion are given by the intersection of the appropriate consumption vectors with each species' ZNGI.



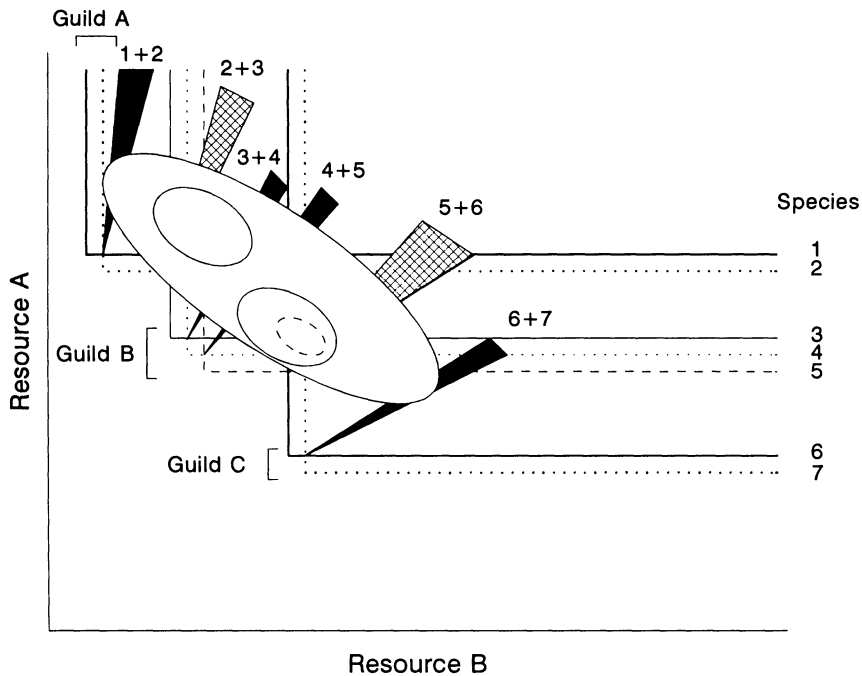


FIG. 4.—A graphical model demonstrating how consumer-resource models generate communities composed of two or more species from each guild. Heterogeneous habitats with a wide range of supply points enable the stable coexistence of more than one species from each guild. Note that Fox assemblies for the entire habitat can degenerate either into non-Fox assemblies or into Fox states representing fewer guilds in habitat subsamples because each includes a smaller range of supply points. *Large ellipse*, Fox assembly; all species coexist. *Small solid ellipses*, non-Fox assemblies; each contains two species from guild B but excludes species from either guild A (*right ellipse*) or guild C (*left ellipse*). *Small dashed ellipse*, Fox assembly; one species from each of two guilds.

lemming]) were sparsely distributed in the area and are excluded from the analyses. Red squirrels (*Tamiasciurus hudsonicus*) were common but were unreliably sampled by our small live traps. The seasonal consumption of conifer seeds by red squirrels and their occasionally carnivorous diet suggest that they represent a guild distinct from that of the two chipmunk species. The exclusion of red squirrels should not affect patterns of Fox versus non-Fox assemblies.

We verified Fox's pattern for the rodent assemblies and then tested the consumer-resource predictions at two scales. First, we examined Fox and non-Fox assemblies at the scale of entire transects. We contrasted these with similar assemblies observed in pure forest and pure cutover subsamples. This partition necessarily reduced the range of sampled habitat variation but maintained a sufficiently large set of stations (20 in each subsample) to census the community.

To test the prediction that Fox assemblies with at least two members in any one guild consist of both Fox and non-Fox assemblies, we contrasted forest and cutover subsamples with the data obtained from the entire transect. But nested patterns could also result from a variety of sampling "errors." Our forest versus cutover

subsampling protocol could, for example, generate non-Fox subassemblies whenever the number of species is a function of sampling effort. We attempted to evaluate sampling bias by contrasting the number of species observed in entire transects with those found in the subsamples. We established controls by counting the number of species found in subsamples comprised of the 20 consecutive stations crossing the habitat boundary (10 stations in each habitat). This protocol matched the number of stations in the forest and cutover segments and controlled habitat variation by maintaining an equal abundance of stations in each of the two habitats.

Estimates of habitat variation were collected in each habitat along all transects. Vegetation was quantified at the third station from each end of the transect and at every fifth station thereafter. The vegetation data were converted into habitat summary variables by principal components analysis (Norušis 1992a; app. A). Variables were transformed where necessary to reduce heteroscedasticity and to improve the fit to a unimodal distribution. We calculated the range of the resulting components to test the consumer-resource prediction that non-Fox assemblies of i guilds should tend to exist over a broader range of habitats than should Fox subsets from fewer guilds. This test assumes that our measures of habitat variation are correlated with either variation in resource supply or physical constraints that modify resource consumption (see, e.g., Tilman and Pacala 1993).

Field ecologists are unlikely to sample a set of supply points equally spaced throughout the possible range of resource values because of some underlying gradient. The more biased the gradient is to one resource, the greater the potential to find coexisting species in a single guild. We tested the biased gradient prediction with our nested subsamples from forest versus cutover habitats. We reasoned that our samples from mature forests would represent different resource gradients for rodents than those from cutovers.

RESULTS

Fox Assemblies Were Much More Frequent than Expected

There were six non-Fox assemblies at the scale of entire transects (fig. 5). Four were composed of two or more microtine species in the absence of one of the remaining guilds; one contained all three microtines plus at least one species from every other guild. Zapodids were absent from four assemblies; sciurids and the cricetine were absent from three each. All 12 Fox assemblies at this scale contained representatives from each of the four guilds.

Analysis at the scale of cutover and forest transects revealed a similar proportion of non-Fox assemblies (13 out of 36 contrasts). Consistent with the reduced habitat variation sampled at this scale, relatively few states included all four guilds.

Only 24 of the 72 possible states of species assembly yield Fox combinations (fig. 5), yet at each scale of analysis roughly two-thirds of all assemblies agreed with the Fox pattern. We counted the number of Fox and non-Fox states represented by assemblies with different numbers of species (fig. 5) and, using each 40-station assembly only once, weighted our counts by the observed occurrences of species richness to generate the expected number of Fox patterns for the 18 transects. Sixteen of the cells in figure 5, for example, correspond to communities composed of four species; only one of these represents a Fox assembly (one

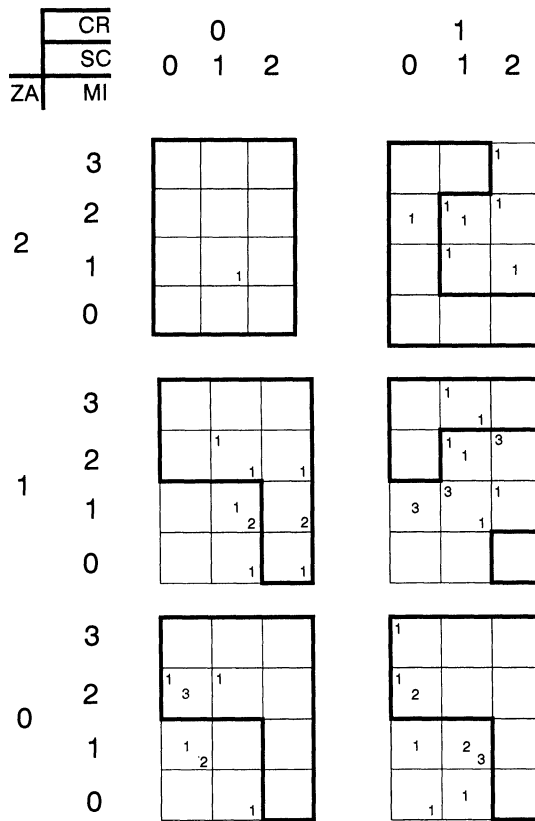


FIG. 5.—Fox and non-Fox assemblies observed in a four-guild rodent community in north-western Ontario. Large numbers reference the number of species in each of the four guilds. *MI*, microtines: *Clethrionomys gapperi*, *Microtus chrotorrhinus*, *Microtus pennsylvanicus*; *SC*, sciurids: *Tamias minimus*, *Tamias striatus*; *ZA*, zapodids: *Napaeozapus insignis*, *Zapus hudsonius*; *CR*, cricetine: *Peromyscus maniculatus*. Non-Fox assemblies are surrounded by a bold border. The top number in each cell refers to the number of observations of each state in 18 transects crossing borders between forest and cutover habitats. The middle number corresponds to the number of observations of each state in forest subsamples; the bottom number corresponds to the number in cutovers.

species from each guild). Five samples contained only four species (three Fox and two non-Fox). The expected number of Fox patterns composed of four species is thus $(1/16)(5) = 0.31$. Expected values were calculated separately for assemblies containing different numbers of species. The separate values were summed to yield the overall expectation of Fox patterns. The observed proportion was much greater than expected to occur by chance alone (cumulative binomial test, expected = 0.284, observed = 0.67, $P = .0008$).

Nested Subassemblies from Fox States Revealed Non-Fox States

At the scale of entire transects, nine Fox assemblies representing all four guilds included two or more species from a single guild (fig. 5). Eight of the nine assemblies included at least one non-Fox state in the subsample obtained from either

TABLE 1
MEDIAN SPECIES RICHNESS OF BOREAL FOREST SMALL MAMMALS
VARIED AMONG SAMPLES

Sample	Stations	Median Richness	Mean Rank	Z-Score
Transects	40	5	50.7	3.32
Controls	20	4	39.2	.64
Forests	20	3	27.6	-2.08
Cutovers	20	3	28.5	-1.88

NOTE.—Analysis was by Kruskal-Wallis k -sample test; $H = 15.12$, $df = 3$, $P = .002$. Controls represented segments of 20 consecutive stations centered on the boundary between forest and cutover habitats.

the forest or clearcut of the same transect (app. B). This differed substantially from the control subsamples, in which only two of the same nine Fox assemblies included non-Fox states.

One reason for differences in the number of non-Fox states between control and forest or cutover subsamples was the difference in species richness (table 1). The median number of species in each transect exceeded the number of species in control subsamples, which demonstrates that species richness depends on sampling effort. But the median number of species in the control subsamples tended also to exceed that in pure forest and pure cutover habitats. Differences in the proportion of nested non-Fox assemblies between control and habitat subsamples appeared to be caused by factors additional to those associated with sampling.

The Range of Habitat Occupied by Non-Fox Assemblies Representing i Guilds Exceeded That of Included Fox Assemblies Representing Fewer Guilds

Two principal components described 57% of the common variation contained in the 12 vegetation variables retained for analysis (app. A). The first component described a gradient from conifer-dominated woodlands with deep moss and/or humus mats and relatively little litter to slash-covered cutovers with shallow mats and a few small trees. The second defined a gradient from cutovers including tall, large shrubs (e.g., *Alnus viridis*, *Corylus cornuta*) with many species of numerous saplings and a good deal of litter to open forest with small, short shrubs (e.g., *Ledum groenlandicum*, *Vaccinium angustifolium*, *Vaccinium myrtilloides*; app. A).

Five of the seven non-Fox assemblies in cutovers contained only microtines, sciurids, and zapodids. Four of the Fox assemblies in cutovers included no more than two of these guilds. Consistent with the theory, the non-Fox states occupied a greater range of habitat variation than did the Fox assemblies (ANOVA; table 2).

Different Guilds Were Biased toward Different Habitats

Forest and cutover samples were biased toward different guilds (hierarchical loglinear analysis [Norusis 1992b], likelihood-ratio $\chi^2 = 15.07$, $df = 3$, $P = .0018$; table 3). Sciurids occurred only rarely in forest habitat but were frequent occupants of cutovers. Deer mice showed the opposite pattern. The remaining two guilds were about equally represented in both habitats.

TABLE 2

RANGE OF HABITAT VARIATION IN CUTOVERS FOR NON-FOX STATES REPRESENTED BY MICROTINE, SCIURID, AND ZAPODID GUILDS COMPARED WITH FOX STATES REPRESENTED BY SUBSETS OF THE NON-FOX ASSEMBLIES

HABITAT VARIABLE	MEAN RANGE		SOURCE	df	SS	F	P
	Non-Fox	Fox					
Including <i>Napaeozapus</i> :							
PC1	1.56	.61	Between states	1	2.18	5.44	.048
			Error	8	3.20		
			Total	9	5.38		
PC2	1.63	.81	Between states	1	1.62	4.1	.077
			Error	8	3.16		
			Total	9	4.78		
Excluding <i>Napaeozapus</i> .*							
PC1	1.75	.61	Between states	1	2.85	9.01	.02
			Error	7	2.22		
			Total	8	5.07		
PC2	1.80	.81	Between states	1	2.20	6.84	.035
			Error	7	2.25		
			Total	8	4.45		

* *Napaeozapus* occurred in one cutover only. All *Napaeozapus* captures in that cutover were at the station adjacent to the forest habitat. The terms PC1 and PC2 refer to the two principal components derived from the vegetation analysis (app. A).

The six non-Fox assemblies in forest habitat were all composed of two microtine species in the absence of sciurids (fig. 5; sciurids existed in seven Fox assemblies in other forest transects). All seven non-Fox assemblies in cutovers contained at least one sciurid, whereas deer mice were absent from six (deer mice occurred in four other cutovers). These data emphasize the point that different guilds were biased toward different habitat gradients.

DISCUSSION

Numerous ecologists have documented nonrandom patterns of species co-occurrence (e.g., Brown 1973; Diamond 1975; M'Closkey 1978; Bowers and Brown 1982; Gilpin and Diamond 1982; Hopf and Brown 1986; Patterson and Atmar 1986; Fox 1987, 1989; Patterson 1990; Patterson and Brown 1991; Fox and Kirkland 1992; Fox and Brown 1993; Kelt et al. 1995). The existence and interpretation of the patterns depend on the assumptions by which one generates the null model of random community assembly (see, e.g., Connor and Simberloff 1979, 1984; Colwell and Winkler 1984; Drake 1990; and others cited in Salt 1983; Strong et al. 1984; Fox and Brown 1995; Wilson 1995). Spurious patterns, and their interpretations, can arise from a variety of causes. Strong tests of nonrandom species assembly require mechanistic explanations whose assumptions and predictions can be evaluated by observation and by experiment. This article demonstrates that mechanisms based on consumer-resource models yield the Fox pattern of guild assembly.

TABLE 3
DEPENDENCE ON HABITAT OF GUILD
REPRESENTATION IN BOREAL FOREST SMALL
MAMMAL COMMUNITIES

Habitat Sample and Guild	Present	Absent
Forest:		
Zapodid	8	10
Microtine	17	1
Sciurid	7	11
Cricetine	13	5
Cutover:		
Zapodid	11	7
Microtine	14	4
Sciurid	15	3
Cricetine	6	12

NOTE.—Hierarchical loglinear analysis (Norušis 1992b), likelihood-ratio $\chi^2 = 15.07$, $df = 3$, $P = .0018$.

A recent version of the theory explicitly incorporates spatial variation in colonization and mortality (the spatial competition hypothesis; see Tilman 1993). We suspect that species belonging to different guilds will be those that are most likely to exhibit the interspecific trade-offs between colonization, longevity, and resource consumption that are necessary for coexistence in this model. If so, the Fox pattern is reinforced.

The theory leads to clearly testable predictions that are consistent with field observations of boreal rodent assemblies in northwestern Ontario. Yet, our preliminary tests are not without problems. Our test of the prediction of non-Fox states nested in Fox assemblies was compromised by sampling. It is likely that our attempt to control sampling effort was only partially successful because it necessarily included consecutive stations in both habitats. Preferences by some species for edge habitat could modify whether or not samples contain Fox or non-Fox assemblies. It is important to note when productivity is held constant, however, that the consumer-resource theory predicts increased diversity whenever there is a concomitant increase in the range of habitats sampled. Forest and cutover subsamples necessarily represented a reduced range of habitat variation relative to that of entire transects and the controls (the control subsamples included equal numbers of consecutive stations in each of the two habitats). The reduced diversity observed in the forest and cutover subsamples confirms the theory's prediction.

It seems unlikely that sampling effects alone could produce the observation that non-Fox states occupied a greater range of habitat variation than did Fox assemblies obtained from samples of exactly the same size. To be fair, differences in habitat preference among species could generate a greater range of habitat variation for non-Fox assemblies, particularly if some guilds typically occupy a greater variety of habitats than do others. But to refute the theory, such differences in habitat selection must have causes other than those directly related to resource consumption (see, e.g., Rosenzweig 1979). The more parsimonious explanation would seem to favor the consumer-resource model.

The final prediction, that different gradients should favor one guild over another, was also confirmed. The guild bias was undoubtedly related to differences in habitat preference, but that is, after all, the point made by the consumer-resource theory. Thus, the theory and current data suggest that competition for limited resources helps to structure communities in such a way that species entering a community are assembled from different guilds until each guild is represented before the pattern repeats (Fox and Brown 1993). The hypothesis awaits rigorous experimental testing.

ACKNOWLEDGMENTS

We thank B. Fox, whose work on guild assembly inspired this contribution and who critically reviewed early versions of this article. B. Fox, J. S. Brown, B. Kotler, and D. Tilman contributed freely to the ideas and their presentation. R. Brassard, R. Jahnke, S. Kingston, K. Lavoie, and R. Madell assisted with field data collection, and S. Hoffstrom assisted with computer analyses. Field research was conducted in the Abitibi-Price-Lakehead University Vidlak Forest. W. Smith coordinated our rental of the Abitibi-Price field camp at Sorrel Lake. We gratefully acknowledge Ontario's Environmental Youth Corps, which helped to fund field personnel, and Canada's Natural Sciences and Engineering Research Council for its continuing support of D.W.M.'s research on species coexistence and evolutionary ecology.

APPENDIX A

TABLE A1

TWO PRINCIPAL COMPONENTS CONTAINING 57.1% OF THE COMMON
VARIATION IN 12 HABITAT VARIABLES DESCRIBING FOREST AND
CUTOVER HABITATS IN NORTHWESTERN ONTARIO

VARIABLE	ROTATED COMPONENT LOADINGS	
	PC1	PC2
Log ₁₀ (conifer basal area + 1)	.91	.04
Square root (number of conifers + 0.5)	.89	-.14
Log ₁₀ (basal area of live trees + 1)	.89	.22
Square root (number of live trees + 0.5)	.81	.06
Percentage cover by decaying nonwood vegetation	-.60	.44
Log ₁₀ (depth of mosses and humus + 1)	.58	-.28
Number of stumps	-.45	-.28
Percentage cover by wood and slash	-.38	-.18
Percentage cover by shrubs > .5 m in height	.03	.80
Square root (number of saplings + 0.5)	.02	.79
Mean shrub height	.13	.79
Sapling species diversity (Simpson's index)	-.02	.60

NOTE.—Sample area = 25 m²; eigenvalues — PC1 = 4.16, PC2 = 2.7. Other variables that had dramatically nonnormal frequency distributions, low frequency of occurrence, or low correlations with other variables were eliminated.

APPENDIX B

TABLE B1

TRANSECTS CONTAINING FOX ASSEMBLIES REPRESENTED BY FOUR GUILDS OF SPECIES WITH AT LEAST TWO SPECIES FROM A SINGLE GUILD PLUS THEIR FOREST AND CUTOVER SUBSAMPLES

SAMPLE AND STATE	OCCURRENCES	NUMBER OF SPECIES IN EACH GUILD			
		Cricetine	Sciurid	Microtine	Zapodid
Transect: Fox	3	1	2	2	1
Subsamples: Fox	1	1	0	1	1
	1	1	1	2	1
	1	1	1	1	0
Non-Fox	2	0	2	1	1
	1	0	2	2	1
Transect: Fox	1	1	1	2	1
Subsamples: Fox	1	1	1	1	0
Non-Fox	1	0	1	2	1
Transect: Fox	1	1	2	1	1
Subsamples: Fox	1	1	0	1	0
Non-Fox	1	0	2	0	1
Transect: Fox	1	1	2	2	2
Subsamples: Fox	1	1	1	1	0
	1	1	2	1	2
Transect: Fox	1	1	2	3	2
Subsamples: Fox	1	1	1	2	2
Non-Fox	1	1	1	3	1
Transect: Fox	1	1	1	1	2
Subsamples: Fox	1	1	0	1	1
Non-Fox	1	0	1	1	2
Transect: Fox	1	1	1	2	2
Subsamples: Fox	1	1	1	1	0
Non-Fox	1	1	0	2	2

NOTE.—Subsamples frequently contained non-Fox assemblies.

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Associate Editor: David Tilman