

Distribution and Abundance

SCALING PATTERNS IN EXOTIC AND NATIVE BIRD SPECIES

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Scaling phenomena are at the core of a great variety of ecological processes, ranging from individual physiology to populations, communities and ecosystems, and emerge as the result of the operation of general principles governing their structure and functioning. In this chapter, we assess the generality of scaling relationships in the distribution and abundance of species by comparing exotic and native species recorded in the North American Breeding Bird Survey. We describe scaling patterns in nine exotic species compare them with those in a set of native species chosen to maximize taxonomic and ecological similarity and in a random set of native species. For each set of species, we assess the scaling of the spatial characteristics of range occupancy, the intraspecific and interspecific scaling between distribution and abundance, and the scaling of the abundance frequency distribution. Our results indicate that exotic and native species show similar scaling patterns in their distribution and abundance, which suggests that they are under the influence of similar processes, thus supporting the generality of these scaling relationships. However, exotic species do differ from natives in their ability to reach higher maximum abundances and show a more even abundance-distribution relationship, probably as a result of having broad ecological tolerances, which could be a key to their successful establishment and further spread.

Introduction

By transporting species outside their native geographic ranges, humans have been performing a long-term natural experiment in ecology and biogeography. The main focus of this book, this chapter included, is to take a close look at the results of this experiment with the aim of gaining insights into the structure and dynamics of ecological systems. We are interested here, in particular, in exploring the generality of scaling relationships in ecology.

Scaling phenomena are at the core of a great variety of ecological processes, ranging from individual physiology to populations, communities, and ecosystems. They have become a major venue of inquiry in ecology (e.g., Banavar et al. 1999; Brown and West 2000; Brown et al. 2002; Marquet et al., in press), as they probably emerge as a result of fundamental principles governing the structure and functioning of ecological systems and other complex systems (e.g., Stanley et al. 2000; Brown et al. 2004). Scaling in invasion biology has been explored in two main contexts. The first emphasizes the scaling of the invasion process itself in order to mechanistically understand the spread of exotic species in a new ecological setting. Under this approach, the most commonly reported scaling is that associated with the relationship between spatial spread (measured as the increase in the square root of area occupied from a focal introduction point) and time (Skellam 1951), which is well understood in the context of random dispersal and diffusion (Berg 1983; Okubo 1980; Lubina and Levin 1988; Andow et al., 1990; Hastings et al. 2005). This scaling pattern has also been analyzed in the context of dispersal in heterogeneous landscapes (Johnson et al. 1992) and in considering the effects of different dispersal strategies (Clark 1998; Shigesada and Kawasaki 1997). The second major approach has focused on using exotic species to test scaling relationships predicted by theory, with the aim of ascertaining their generality and the mechanisms underlying their emergence. Representative of this approach is the paper by Keitt and Marquet (1996). These authors used the exotic bird species assemblage of Hawaii to test for the existence of the phenomenon known as self-organized criticality (Bak et al. 1988) in ecological systems, a landmark of which is the existence of a power law relating the frequency or probability of an event to its size. In this case, the events were extinctions of introduced species.

In this chapter, we benefit from both approaches to analyzing scaling relationships as we compare exotic and native species in order to understand the processes that underlie the distribution and abundance of species. Exotic bird species provide an unparalleled opportunity to study the generality of scaling relationships as well as their underlying driving mechanisms. From a theoretical perspective, exotic species that establish self-sustaining populations (i.e., naturalized species) provide us with natural experiments. These experiments can help us to understand the emergence of ecological patterns, as they help to control for the effects of past historical events and evolutionary dynamics (e.g., Sax 2001). This allows us to test for generality in ecological patterns without a need to invoke the action of long-term evolution or selection, focusing instead on the action of general principles that underlie the distribution and abundance of

species. On the practical side, most exotic birds have been introduced during the eighteenth and nineteenth centuries; consequently, there are good records of their distribution and abundance (see review in Duncan et al. 2003), facilitating our ability to use these natural experiments to advance ecological theory.

As pointed out above, in addition to focusing on scaling relationships in the distribution and abundance of species to assess the generality of these patterns, we also want to understand the invasion process itself, as it offers an unparalleled opportunity to understand the dynamics of geographic ranges (e.g., Gaston 2003). While the spatial characteristics of range collapse (i.e., reduction in the range of widespread species) have been the focus of several empirical investigations (e.g., Lomolino and Channell 1995; Channell and Lomolino 2000), we know little about the spatial structure of the opposite process, range expansion or buildup (but see Maurer 1994; Maurer et al. 2001; Gammon and Maurer 2002). Most studies of this process have focused on estimating and/or predicting rates of spread (e.g., Hengeveld 1989; see review in Hastings et al. 2005). Naturalized exotic species provide us with the possibility of understanding the topology of range occupancy for species whose ranges are expanding, mimicking the process that characterizes the dynamics of a species' geographic range from the point of speciation until it becomes widespread.

To understand this process, we first focus on the geometric properties of the spatial distribution of site occupancy by exotic species through time. Our null expectation is that ranges expand following the same basic processes that underlie fluctuations in the occupancy of any species native to a region. To test this hypothesis, we compare the scaling patterns observed for exotics with those characterizing native species. Further, since changes in occupancy are likely to be related to changes in abundance (e.g., Brown 1984; Holt et al. 1997; Newton 1997; Gregory 1998; Gaston et al. 2000), we also compare the intraspecific and interspecific abundance-range size scaling relationship between native and exotic species. As before, our null expectation is that naturalized exotics and natives will not differ, as has already been observed for British mammals and birds at the interspecific level (Holt and Gaston 2003). Finally, we compare the scaling relationship that describes the frequency distribution of abundance for naturalized exotics and native species. Unlike some other relationships, the distribution of abundance has been shown to be affected by factors that include habitat type, body size, phylogeny, and spatial scale (e.g., Magurran 1988; Cotgreave and Harvey 1994; Brown et al. 1995; Gregory 2000; Marquet et al. 2003); thus, we expect that the distribution of abundance may differ among native and naturalized species.

Materials and Methods

Database and general approach

To assess the potential similarities or differences between native and exotic species in their distribution and abundance, we analyzed scaling patterns using data from the Breeding Bird Survey (BBS) (Peterjohn and Sauer 1993; Peter-

john 1994; Sauer et al. 2003), a yearly sampling effort run since 1966 across North America. In Figure 16.1 we show the route coverage in North America for three different years (1966, 1985, 2002) and the total number of routes and area covered by the survey (Figure 16.1D). The number of routes and the geographic area covered have increased rapidly since 1966, but the area sampled leveled off after 1970. To minimize any potential effect of the increase in area sampled, we worked only with the data for censuses after 1970. Details on the species selection procedure are given below.

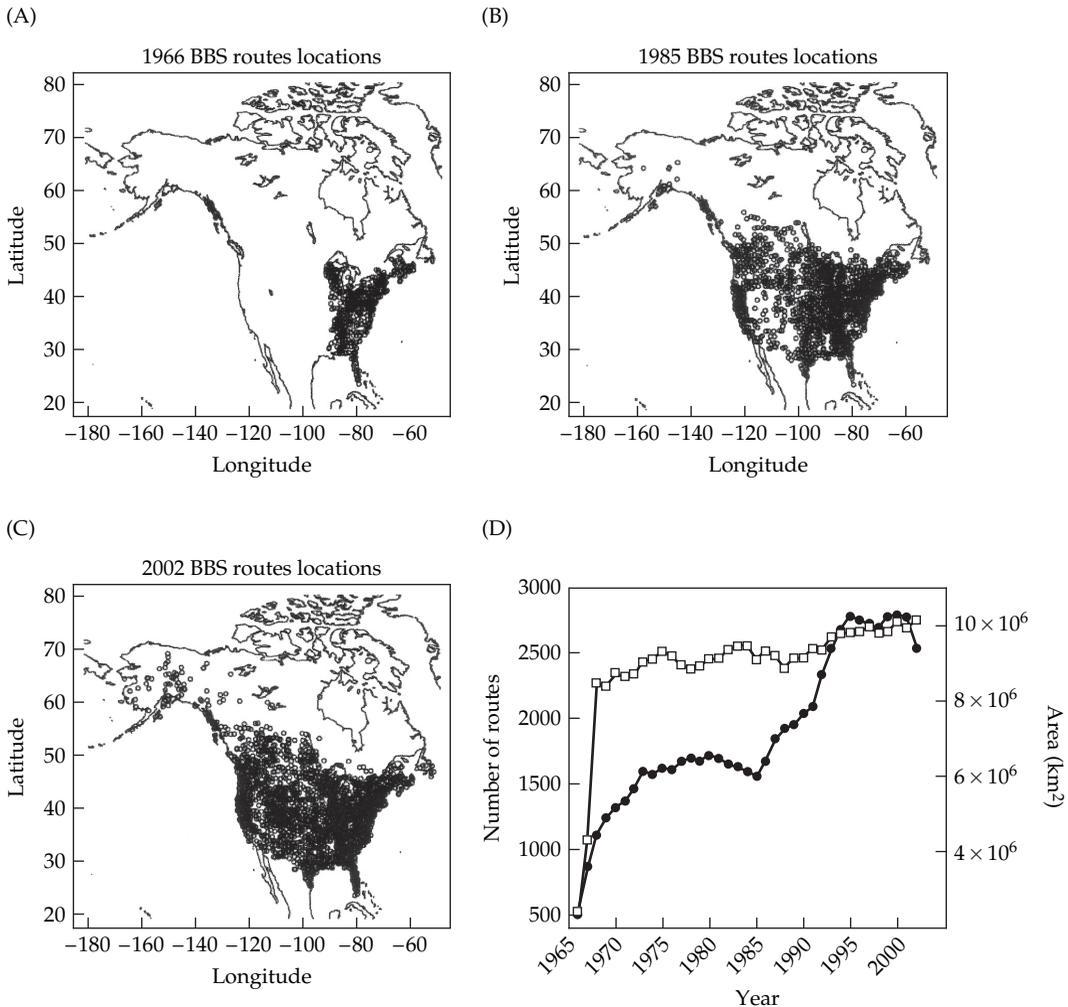


Figure 16.1 Temporal trends in BBS sampling effort. (A–C) Spatial coverage of sampling sites for the years (A) 1966, (B) 1985, and (C) 2002. (D) Temporal trends in total number of routes and in area covered.

Species included in the analysis

After identifying all exotic bird species known for the continental United States, we selected those that had adequate records (more than ten routes) in the North American Breeding Bird Survey. This procedure left us with nine species with adequate spatial and temporal coverage. We called this set of species the “exotic set.” In order to gain insight into the generality of patterns in space use by exotic species, we also included in the analysis a set of ten native species selected to maximize similarity to the exotic species being examined. We selected these similar native species based on phylogenetic relatedness, ecological and life history traits, and body size; the characteristics considered are reported in Table 16.1. The ecological and life history traits used were habitat and diet, respectively. We call this set of native species the “similar set.” The aim of using this group was to assess to what extent the observed patterns could be a result of phylogenetic, ecological, life history, or body size similarities.

We also studied an additional set of ten native species chosen at random from the available North American pool. We called this set of native species the “random set.” As expected, the species in this set show different trends in abundance and encompass a broad spectrum of phylogenetic relatedness, life histories, and ecological attributes (see Table 16.1). The rationale for using this random set of native species was to test for the ecological generality of the observed patterns. Ideally, the patterns should be contrasted against those in a large number of random sets of species; such a task, however, would have been difficult given our computing power, and we believe that this initial set of random species should suffice in the present examination.

Assessing the geometric properties of space occupancy

To assess the geometric properties of species distribution, we used the minimum spanning tree (MST) methodology, which provides a graphic representation of the pattern of occurrences of a species. Figure 16.2A shows a set of points drawn from a uniform distribution in two-dimensional space. These points (or nodes) can be joined in many different ways by lines (or edges), forming a graph. A graph will be defined as connected if there is an edge between any pair of nodes. Figure 16.2B shows one of the many ways to form a connected graph with several circuits or loops. A connected graph containing no circuits is called a tree (Figures 16.2C,D). If a tree contains all the nodes, it is called a spanning tree. The spanning tree that minimizes the total length of connections between nodes is called the minimum spanning tree (MST, Figure 16.2D). Although the number of possible trees for a given data set may be very large, the MST is a unique configuration that reduces the “cost,” or the sum of internodal distances (Gower and Ross 1969; Zahn 1971). However, MSTs will be unique only when there are complex spatial patterns. For simple spatial patterns, it is possible that more than one MST of equal length will exist. It is important to note that this unique network picks out the dominant pat-

TABLE 16.1 *Species in the exotic, similar, and random sets analyzed in this study*

Family	Common name	Scientific name	Body size (g)
EXOTIC SET			
Anatidae	Mute swan	<i>Cygnus olor</i>	11,007
Ardeidae	Cattle egret	<i>Bubulcus ibis</i>	338
Columbidae	Rock dove	<i>Columba livia</i>	355
Columbidae	Eurasian collared dove	<i>Streptopelia decaocto</i>	149
Fringillidae	House finch ^c	<i>Carpodacus mexicanus</i>	21
Passeridae	House sparrow	<i>Passer domesticus</i>	28
Phasianidae	Gray partridge	<i>Perdix perdix</i>	391
Phasianidae	Ring-necked pheasant	<i>Phasianus colchicus</i>	1,278
Sturnidae	European starling	<i>Sturnus vulgaris</i>	83
SIMILAR SET			
Anatidae	Trumpeter swan	<i>Cygnus buccinator</i>	10,701
Ardeidae	Little blue heron	<i>Egretta caerulea</i>	343
Columbidae	Inca dove	<i>Columbina inca</i>	48
Columbidae	Common ground dove	<i>Columbina passerina</i>	30
Columbidae	Mourning dove	<i>Zenaida macroura</i>	120
Fringillidae	American goldfinch	<i>Carduelis tristis</i>	13
Fringillidae	Purple finch	<i>Carpodacus purpureus</i>	25
Phasianidae	Greater sage grouse	<i>Centrocercus urophasianus</i>	2,724
Phasianidae	Blue grouse	<i>Dendragapus obscurus</i>	1,030
Icteridae	Brown-headed cowbird	<i>Molothrus ater</i>	44
RANDOM SET			
Anatidae	Northern pintail	<i>Anas acuta</i>	1,025
Anatidae	Mottled duck	<i>Anas fulvigula</i>	1,013
Anatidae	American black duck	<i>Anas rubripes</i>	1,304
Ardeidae	Tricolored heron	<i>Egretta tricolor</i>	405
Cardinalidae	Painted bunting	<i>Passerina ciris</i>	16
Columbidae	Band-tailed pigeon	<i>Patagioenas fasciata</i>	343
Odontophoridae	Gambel's quail	<i>Callipepla gambelii</i>	167
Odontophoridae	Scaled quail	<i>Callipepla squamata</i>	184
Odontophoridae	Mountain quail	<i>Oreortyx pictus</i>	233
Parulidae	Prothonotary warbler	<i>Protonotaria citrea</i>	17

Source: Diet and habitat data from the BBS and del Hoyo et al. 1994, 1997; body size from Dunning 1993.

^aMinimum and maximum number of routes

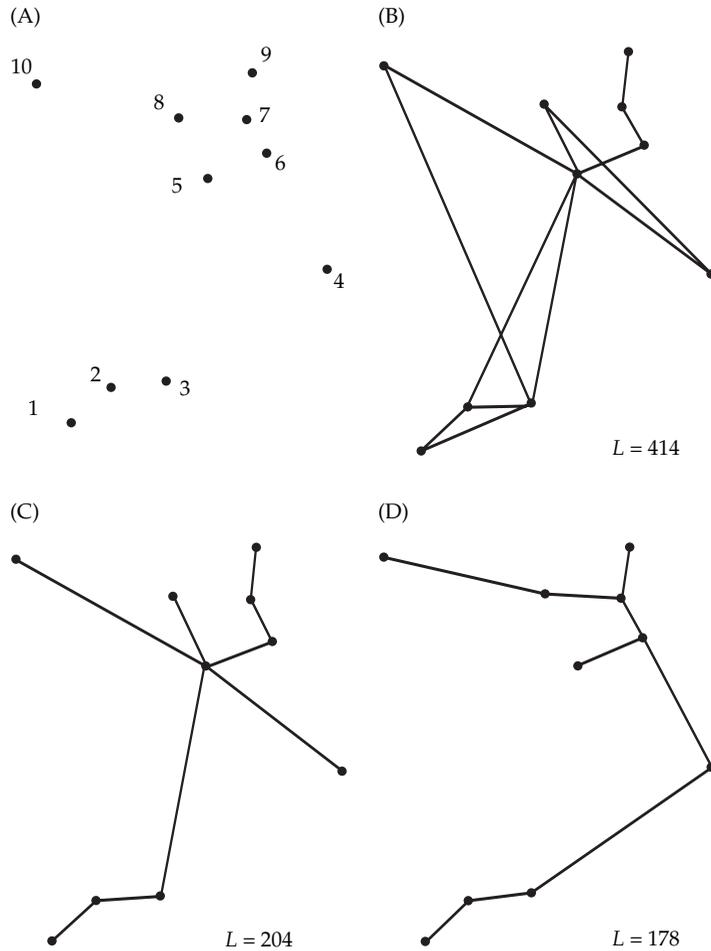
TABLE 16.1 (continued)

Diet	Habitat	Distribution (routes) ^a	Abundance ^b
Plant matter, aquatic invertebrates	Wetland-open water	2–18	5–179
Insects	Wetland-open water	36–307	1,012–17,561
Seeds, plant matter, insects	Urban	280–1,262	4,961–17,858
Seeds, plant matter, insects	Urban	1–134	13–1,287
Seeds, insects	Urban	3–867	10–12,666
Seeds, insects	Urban	493–1,929	44,803–105,318
Seeds, insects	Grasslands	2–104	11–323
Plant matter, insects, worms and snails	Grasslands	127–707	1,249–10,860
Insects, fruit	Urban	507–2250	45,557–117,377
Plant matter, seeds, aquatic invertebrates	Wetland-open water	1–20	1–171
Aquatic invertebrates, fish, reptiles and amphibians	Wetland-open water	50–194	359–1,847
Seeds	Urban	5–74	19–356
Seeds, insects	Successional-scrub	28–129	188–882
Seeds	Urban	454–2,545	11,316–80,294
Seeds, insects	Successional-scrub	411–1,718	5,040–23,624
Flowers, fruit, seeds and insects	Woodland	107–444	519–2,042
Plant matter, flowers, seeds and insects	Successional-scrub	4–38	14–380
Plant matter and insects	Woodland	5–50	28–159
Seeds and insects	Open woodlands, fields	465–2,385	5,433–34,229
Plant matter, aquatic invertebrates, fish, reptiles and amphibians	Wetland-open water	4–182	7–2,099
Aquatic invertebrates, seeds, plant matter, and fish	Wetland-open water	6–33	38–455
Plant matter, seeds, aquatic invertebrates, and fish	Wetland-open water	33–75	97–313
Aquatic invertebrates, fish, reptiles and amphibians	Wetland-open water	12–56	31–535
Seeds, insects	Successional-scrub	10–199	59–2,597
Nuts, fruit, and seeds	Woodland	19–109	196–866
Seeds and insects	Successional-scrub	12–68	175–2,448
Seeds and insects	Successional-scrub	10–87	190–1,142
Seeds, plant matter, and insects	Successional-scrub	4–70	8–729
Insects and snails	Woodland	66–206	163–1,152

^b Minimum and maximum number of individuals

^c Note that this species was examined only in the exotic portions of its range in North America.

Figure 16.2 Examples of point, connected line, and spanning tree graphs. (A) A set of random points in space. (B) A connected line graph showing “loops.” (C) A spanning tree. (D) The minimum spanning tree for the set of points shown in A.



tern of connectedness among the points in a manner that emphasizes their intrinsic linear associations. This procedure has been successfully used in several disciplines, ranging from astronomy (Barrow et al. 1985; Bhavsar and Ling 1988; Adami and Mazure 1999), physics (Dussert et al. 1986; Van de Weygaert et al. 1992; Iribarne et al. 1999; Dobrin and Duxbury 2001), and pattern recognition (Zahn 1971; Hoffman and Jain 1983) to ecology (Cantwell and Forman 1993; Lockwood et al. 1993; Keitt et al. 1997; Bunn et al. 2000; Urban et al. 2001) and biology (Dussert et al. 1987; Jones et al. 1996; Wallet and Dussert 1997).

It is customary to build the MST using Prim’s algorithm (Prim 1957). This procedure starts with a fixed node. One by one, nodes that are the nearest neighbor to the subgraph already built are added to the graph. In so doing, edges that complete a circuit or loop are avoided, since a tree cannot have any circuits. The process stops when there are no further nodes to add. Thus the

minimum spanning tree uniquely connects a set of N nodes with $N - 1$ edges. The MST may be described in many ways, including degree, connectivity, and edge length distributions, among others (Chartrand 1977; Dussert et al. 1987). For the purposes of this work, we will describe the MST by the sum of all the edge lengths, which is a concise descriptor of the way species could connect and fill out space. It can be shown analytically that the expected total length of the MST for N randomly distributed points in a sampling window of area A scales as $(AN)^{1/2}$ (Beardwood et al. 1959; Hammersley et al. 1959; Steele 1988; Jaillet 1995). This result provides the expected pattern under the null hypothesis of random space occupancy by species through time.

Database processing and analysis

For computational purposes, and to minimize errors due to slight changes in route locations across years, we mapped the observed data onto a fixed grid of 30×30 cells per degree of latitude and longitude (with each cell having an approximate area of 15 km^2). This scale was chosen to be similar to the sampling area of a single BBS route (approximately 21 km^2). Using these data, we constructed a MST for each species in each year (from 1970 to 2002) and calculated the total edge length and number of nodes. In order to make scaling relationships comparable across species groups, we normalized MST lengths by dividing them by the square root of the area they cover. The area covered by the pattern of point occurrences in a given year was estimated using a 95% level kernel density estimate contour (Beardah et al. 1996). This procedure eliminates biases in area estimation due to runaway points separated from the densest zone of the geographic range. We call this measure the area-corrected MST. All mathematical procedures were carried out using MATLAB 6.12 (The MathWorks, Inc., Natick, MA), and the R statistical package (R Development Core Team, 2003).

Patterns in distribution and abundance

To assess the scaling relationship between distribution and abundance, we plotted the number of routes where a species was observed in a given year (a measure of distribution) versus total abundance in that year. We examined this relationship for exotic species and for the two groups of native species, both on a species-by-species basis (intraspecific scaling pattern, using total counts of individuals per year from 1966 to 2002) and for each of the three groups as an ensemble (interspecific scaling pattern, in a subset of years: 1970, 1980, 1990, and 2000). Finally, we examined the frequency distribution of abundances for exotic and native species. For each group of species, we plotted the midpoint of each abundance class versus the probability of observing a site in each abundance class (i.e., the number of sites where that abundance class was recorded divided by the total number of sites used in the analyses for that particular group) between 1970 and 2002. We used logarithmic abundance classes and plotted them versus the logarithm (base 10) of their observed probability (see Solow et al. 2003).

Results

Minimum spanning tree scaling

In Figure 16.3 we show the temporal trend in abundance and distribution for selected exotic and native species. As is apparent in these figures, there is substantial variability in both the number of BBS routes where a species was recorded and in its abundance over the study period (1970–2002). Overall, the exotic and similar sets showed an increase in the number of routes occupied by species through time (average linear regression slopes ± 1 S.E. were 13.4 ± 4.0 and 11.7 ± 5.2 , respectively); however, the observed tendency in the random set, although positive, was much weaker (1.3 ± 0.27).

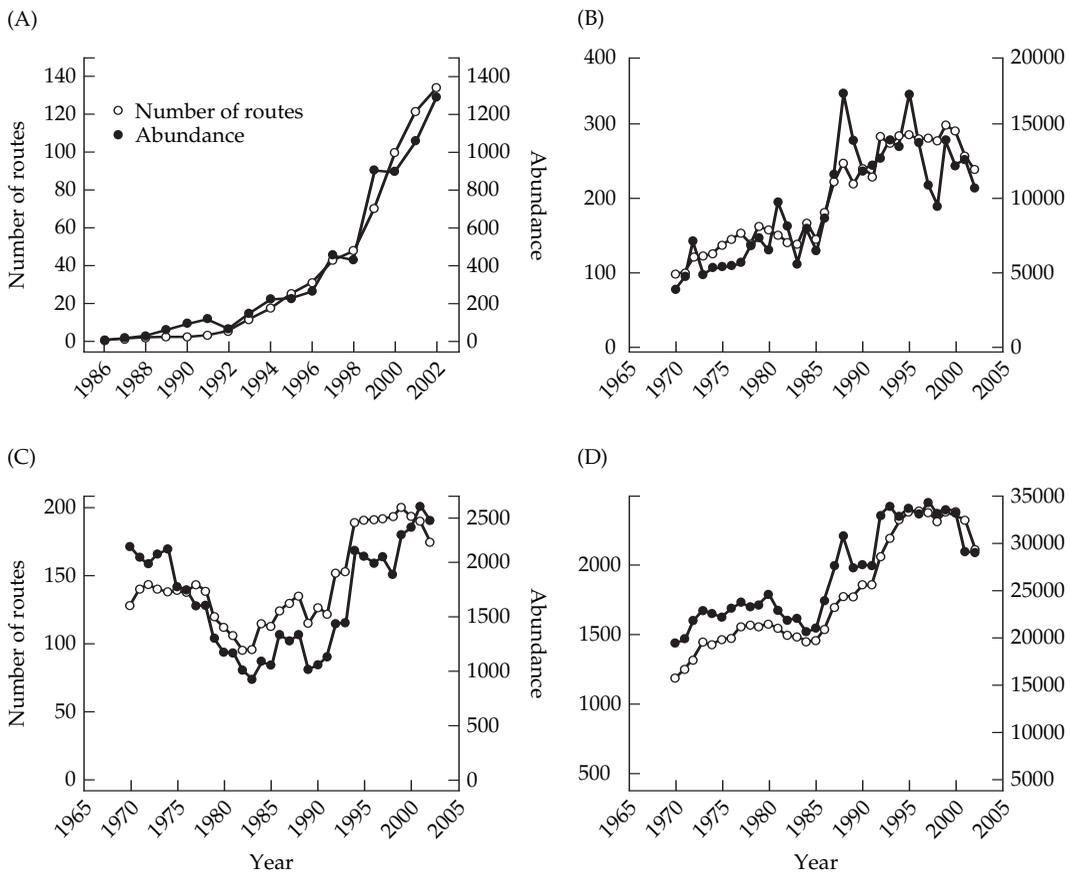


Figure 16.3 Examples of trends in the distributions of exotic and native species. The figure shows the observed dynamics in number of routes and total abundance for two exotic species, (A) Eurasian collared dove and (B) cattle egret, and two native species, (C) painted bunting and (D) brown-headed cowbird.

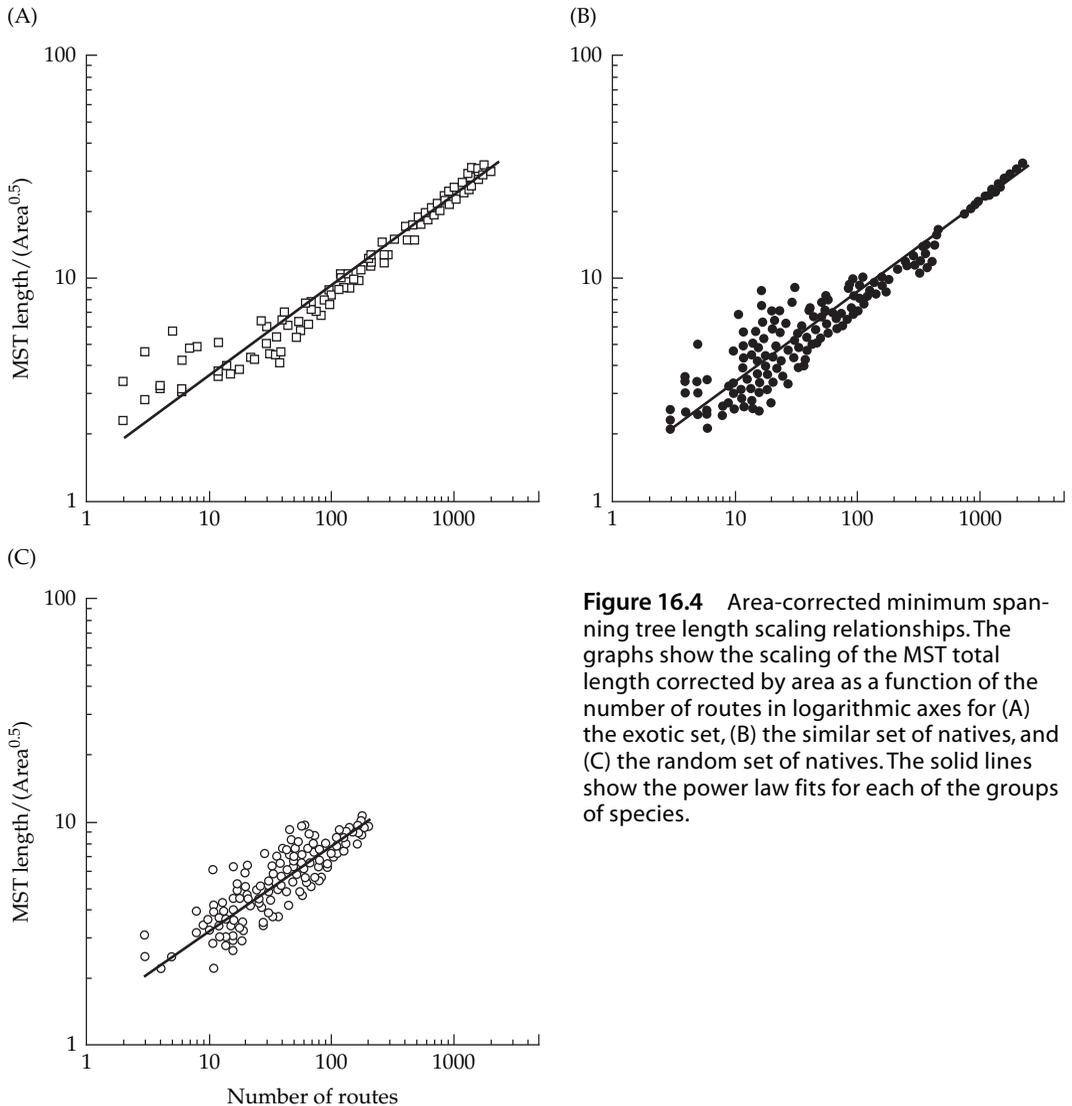


Figure 16.4 Area-corrected minimum spanning tree length scaling relationships. The graphs show the scaling of the MST total length corrected by area as a function of the number of routes in logarithmic axes for (A) the exotic set, (B) the similar set of natives, and (C) the random set of natives. The solid lines show the power law fits for each of the groups of species.

Despite this variation in the number of BBS routes occupied, the total lengths of the minimum spanning trees scale in a similar fashion within the exotic, similar, and random species sets (Figure 16.4A–C). Within each set, species show a tight scaling relationship, even though they show quite different temporal dynamics and spatial patterns of expansion (see Figure 16.3). The average scaling exponent for each of the three groups departs significantly from the null expectation of 0.5. The exponents and standard errors obtained were 0.435 ± 0.006 , 0.444 ± 0.004 , and 0.376 ± 0.013 ($P < 0.001$ for all relationships) for the exotic, similar, and random sets, respectively. [For this comparison, we

TABLE 16.2 *Scaling statistics for the distribution-abundance and area-corrected MST scalings fitted for all species*

Common name	Distribution-abundance scaling				
	Intercept	S.E.	Exponent	S.E.	R ²
EXOTIC SET					
Mute swan	-0.069	0.142	0.550	0.084	0.562
Cattle egret	-0.820	0.156	0.784	0.040	0.917
Rock dove	-1.478	0.229	1.072	0.055	0.915
Eurasian collared dove	-1.377	0.166	1.122	0.071	0.943
House finch	-0.754	0.428	0.637	0.071	0.704
House sparrow	2.219	1.059	0.193	0.216	0.022
Gray partridge	-0.268	0.149	0.921	0.070	0.831
Ring-necked pheasant	-0.242	0.240	0.753	0.061	0.811
European starling	-4.201	0.466	1.492	0.094	0.878
SIMILAR SET					
Trumpeter swan	-0.071	0.122	0.601	0.091	0.591
Little blue heron	0.233	0.152	0.633	0.052	0.810
Inca dove	-0.319	0.088	0.852	0.044	0.917
Common ground dove	-0.039	0.271	0.710	0.100	0.589
Mourning dove	-1.145	0.146	0.924	0.031	0.962
American goldfinch	-0.317	0.279	0.821	0.068	0.808
Purple finch	-0.573	0.382	0.972	0.120	0.653
Greater sage grouse	-0.052	0.113	0.614	0.057	0.776
Blue grouse	-0.393	0.249	0.925	0.134	0.590
Brown-headed cowbird	-1.023	0.168	0.965	0.038	0.948
RANDOM SET					
Northern pintail	0.190	0.177	0.612	0.061	0.742
Mottled duck	-0.086	0.181	0.618	0.083	0.615
American black duck	0.498	0.156	0.553	0.070	0.643
Tricolored heron	0.289	0.110	0.524	0.052	0.747
Painted bunting	-0.291	0.128	0.754	0.040	0.910
Band-tailed pigeon	-0.375	0.277	0.810	0.103	0.653
Gambel's quail	-0.363	0.113	0.672	0.040	0.893
Scaled quail	-0.118	0.369	0.649	0.134	0.410
Mountain quail	-0.119	0.187	0.679	0.073	0.727
Prothonotary warbler	0.910	0.080	0.457	0.029	0.876

Note: The table shows the intercept and slope values with respective standard error estimates (S.E.) as well as the coefficient of determination of the fitted distribution-abundance scaling relationship. Also shown are the scaling exponents for all the species under study. Area-corrected MST scaling exponents that differ from the null expectation (of 0.5) are shown in boldfaced type. C.I. = confidence interval.

TABLE 16.2 (continued)

Normalized MST length scaling		
Exponent	95% Lower C. I.	95% Upper C. I.
—	—	—
0.412	0.354	0.469
0.434	0.397	0.470
0.257	0.182	0.332
0.412	0.387	0.437
0.295	0.231	0.36
0.536	0.433	0.639
0.517	0.468	0.567
0.461	0.422	0.50
0.073	-0.087	0.234
0.449	0.395	0.504
0.322	0.197	0.448
0.469	0.320	0.617
0.487	0.466	0.508
0.395	0.372	0.418
0.033	-0.108	0.174
0.229	0.063	0.553
0.308	0.191	0.425
0.472	0.437	0.507
0.412	0.317	0.507
0.298	0.136	0.460
0.307	0.069	0.545
0.340	0.239	0.441
0.369	0.314	0.425
0.371	0.251	0.491
0.460	0.378	0.541
0.422	0.311	0.530
0.468	0.398	0.537
0.339	0.262	0.416

excluded the mute swan (*Cygnus olor*) because of its restricted pattern of distribution, confined to water bodies in the eastern United States, and because it is present on fewer than 20 routes.] The random set showed a significantly lower exponent than the exotic and similar sets, which are not significantly different. This result suggests that species in the exotic and similar sets fill out space in a less aggregated way than species in the random set. Interestingly, the sampling routes for the BBS show a scaling relationship that is not significantly different from the null expectation, with an observed exponent of 0.506 ± 0.009 . In Table 16.2, we report the statistics of the MST scaling for each species through time. It is interesting to note that most exponents are lower than 0.5, although in each group there are species whose MST scaling is not different from what would be expected under random occupancy.

Scaling of distribution and abundance

In general, the intraspecific pattern (i.e., for individual species among years) in the distribution-abundance relationship was positive and significant within most species (Figure 16.5; see Table 16.2). Exotic species reached the highest abundance for a given number of routes (Figure 16.5) and showed the highest scaling exponent. However, there were no significant differences among average scaling exponents for all three groups. The exponents and standard errors obtained were 0.836 ± 0.1247 , 0.802 ± 0.0473 , and 0.633 ± 0.033 for the exotic, similar, and random sets, respectively. Similarly, intercepts did not differ among sets. These results imply that for a given increase in occupancy, all three sets tend to increase in total abundance in a similar way.

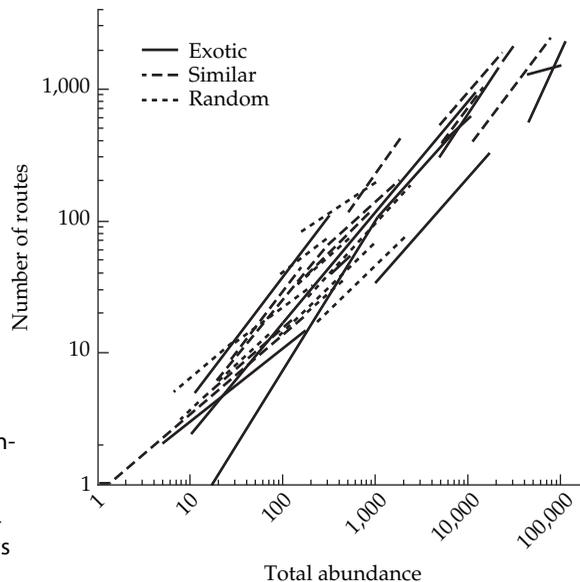


Figure 16.5 Distribution-abundance relationships. The graph shows the fitted scaling relationships for number of routes versus total abundance. Every line represents the relationship for a single species across individual years (i.e., intraspecific scaling).

At the interspecific level (Figure 16.6), the scaling of the distribution-abundance relationship shows that exotic species tend to exhibit higher abundances than natives, particularly at large numbers of routes, while at small numbers of routes they show fewer apparent differences from native species (Figure 16.6). However, there are no significant differences in the average scaling exponents among groups and across years (Table 16.3). A similar pattern is observed when we study the MST length scaling for the same groups over the same years

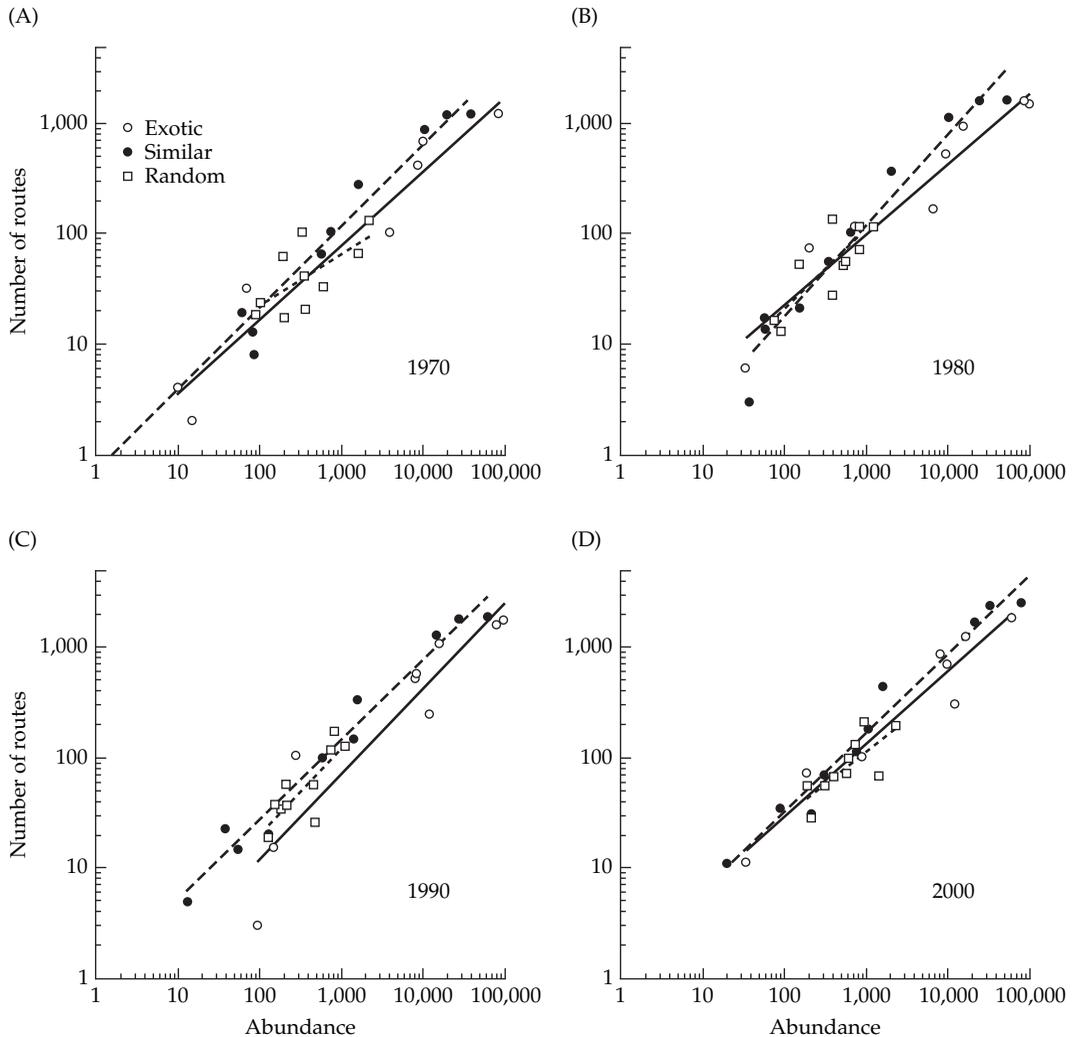


Figure 16.6 Interspecific distribution-abundance relationships for exotic and native species ensembles. Note the trend for exotic species to exhibit higher abundances than natives for a given number of routes, particularly at large number of routes.

(Figure 16.7); there are no significant differences in the scaling exponents among groups and across years (Table 16.3).

Finally, the frequency distribution of abundances for exotic and native species, considering all years and all routes, shows that species in the exotic set have a higher probability of attaining any given abundance than native

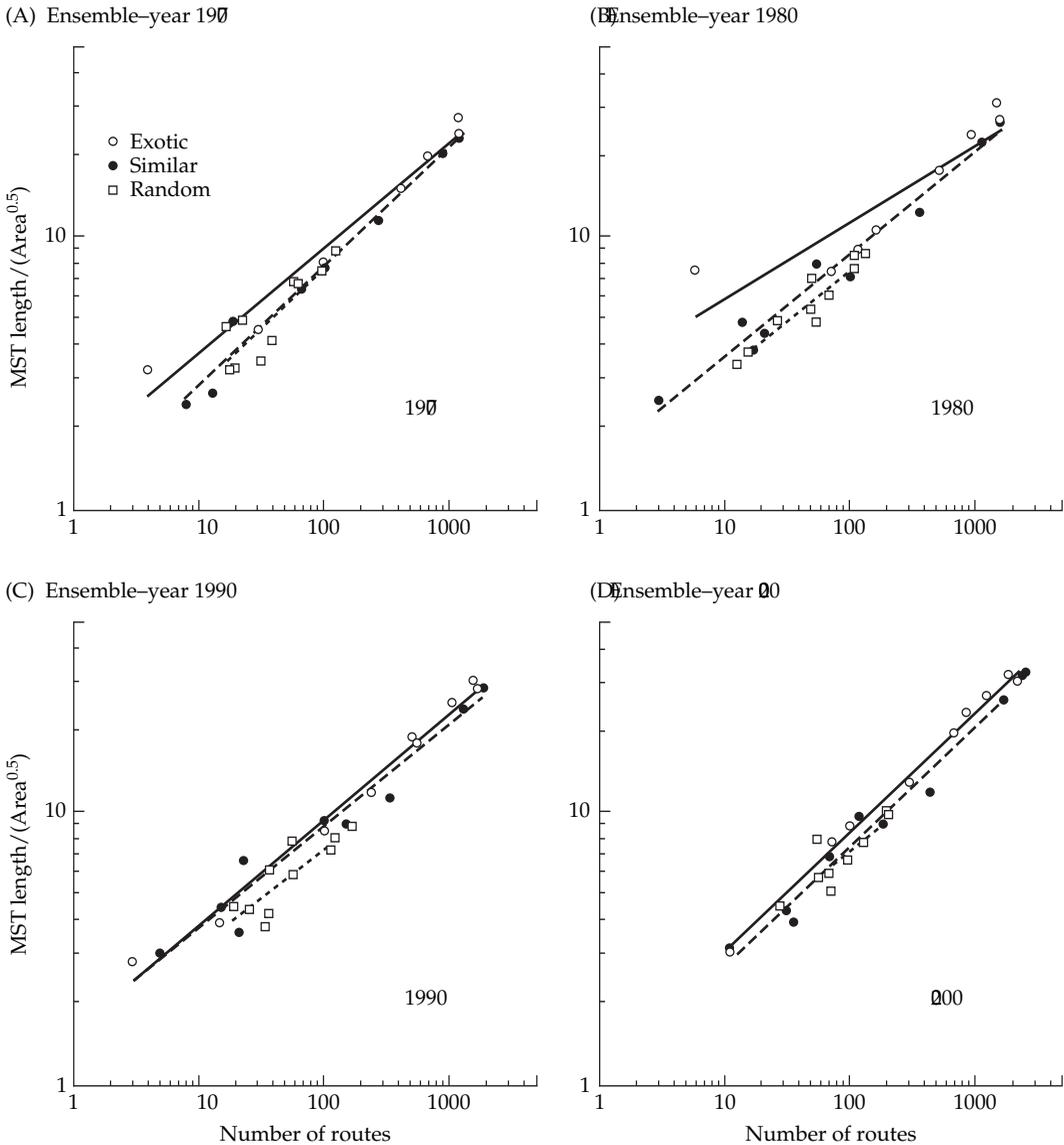


Figure 16.7 Interspecific area-corrected MST length scaling relationship for exotic and native species ensembles present for selected years.

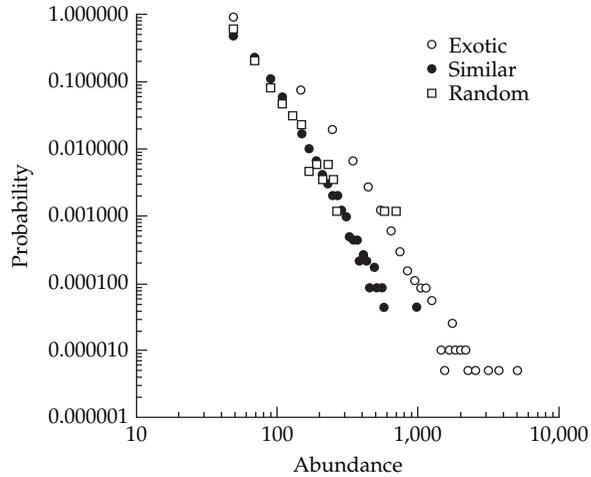
TABLE 16.3 *Statistics for the interspecific distribution-abundance relationship and the area-corrected MST scaling relationship*

Year	Group	Slope \pm S.E. ^a	R ²	P
<i>DISTRIBUTION-ABUNDANCE RELATIONSHIP</i>				
1970	Exotic	0.428 \pm 0.141	0.606	0.023
1970	Similar	0.739 \pm 0.046	0.957	0.000
1970	Random	0.471 \pm 0.180	0.768	0.031
1980	Exotic	0.416 \pm 0.146	0.577	0.029
1980	Similar	0.821 \pm 0.064	0.954	0.000
1980	Random	0.673 \pm 0.176	0.647	0.005
1990	Exotic	0.520 \pm 0.201	0.488	0.036
1990	Similar	0.727 \pm 0.042	0.978	0.000
1990	Random	0.767 \pm 0.194	0.662	0.004
2000	Exotic	0.408 \pm 0.161	0.479	0.039
2000	Similar	0.710 \pm 0.043	0.972	0.000
2000	Random	0.591 \pm 0.021	0.591	0.009
<i>AREA-CORRECTED MST SCALING</i>				
1970	Exotic	0.544 \pm 0.113	0.823	0.005
1970	Similar	0.440 \pm 0.022	0.983	0.000
1970	Random	0.438 \pm 0.086	0.764	0.001
1980	Exotic	0.465 \pm 0.075	0.884	0.002
1980	Similar	0.377 \pm 0.020	0.977	0.000
1980	Random	0.378 \pm 0.048	0.887	0.000
1990	Exotic	0.376 \pm 0.019	0.985	0.000
1990	Similar	0.378 \pm 0.027	0.961	0.000
1990	Random	0.357 \pm 0.080	0.713	0.002
2000	Exotic	0.416 \pm 0.020	0.986	0.000
2000	Similar	0.440 \pm 0.022	0.981	0.000
2000	Random	0.370 \pm 0.078	0.736	0.001

^aS.E. = 1 standard error.

species and show a more even abundance distribution (shallower slopes; Figure 16.8), a pattern that was also observed when the analysis was repeated for years 1970, 1980, 1990, and 2000 (not shown). This pattern is correlated with the fact that only species in the exotic set are found in the highest abundance classes. In general, the scaling relationships observed in the abundance distribution correspond to a power law with an exponent that does not differ when the random and the similar species set are compared (-7.663 ± 0.513 and -7.971 ± 0.295 ;

Figure 16.8 Probability distribution of abundance (individuals per route) for exotic and native species sets calculated over the entire study period (1970–2002) and over all sampling routes. Note the power law scaling shown by all three groups. Regression statistics were estimated for those values in the exponentially decaying tail (i.e., probabilities greater than 0.003).



figures are estimated slopes ± 1 S.E.). However, the scaling exponent for the exotic species set (-5.714 ± 0.288) is significantly different from those of the other two sets.

Discussion

In this chapter, we have explored several scaling relationships characterizing the spatial distribution and abundance of exotic and native species. Our aim was to assess the generality of these relationships and determine whether exotic species show a distinct spatial pattern of occupancy and abundance. As discussed in detail below, on average, exotic and native species (i.e., species in the similar and random sets) do not differ in their geometry of space occupancy and in distribution-abundance scaling; however, important differences in their distributions of abundance were apparent. Further, none of the patterns herein reported were associated with the magnitude of range expansion.

Area-corrected MST scaling

We found that range dynamics for both native and exotic species, measured as the geometry of occupied sites through time, resulted in an area-corrected MST length scaling with an exponent that, on average, is different from random occupancy (i.e., lower than 0.5), implying that the distribution of these species is more clustered than that expected under a random pattern of occupancy. We claim that this result is not a consequence of the topology of the BBS route network across North America, for it follows the scaling pattern expected for a spatial distribution formed by a random process. This claim is supported by the fact that exotic species distributed across nearly all of North America (such

as the rock dove, house finch, and house sparrow) show scaling exponents different from random (see Table 16.2). To further explore the potential effect of the BBS network topology, we used the observed 2002 BBS network to calculate the expected scaling pattern under the assumption that species occupy BBS sites at random. The results of simulating different occupancies (from 10% up to 100% of the total number of routes, in steps of 10%) and using ten replicates of each condition showed an exponent of 0.49 ± 0.004 , $R^2 = 0.99$, which is not significantly different from 0.5. This finding reinforces the notion that the BBS network topology does not cause the observed scaling pattern.

However, there are at least two other potential sources of bias that need to be discussed. First, even if the BBS network is random at the continental scale, it might not be so at a regional scale. Nonrandomness at smaller scales could introduce a bias in the observed area-corrected MST scaling patterns for species found exclusively or predominantly in a particular region. To test for this potential effect, we repeated the analysis of the BBS network scaling, but this time we separated the continent into an eastern and a western half, using longitude 100° as the boundary between the two. The scaling exponents for the two regions were not statistically different from each other (0.458 ± 0.023 and 0.433 ± 0.036 for western and eastern halves, respectively) nor from the expected value of 0.5. Thus, the BBS network appears random, at least at the continental and large regional scales, suggesting that potential biases due to heterogeneity in the topology of the network are not a serious problem.

A second cause for concern is the potential for routes to be located near urban areas and roads in anthropogenic landscapes, which could inflate the pattern of site occupation for species (particularly exotics) associated with anthropogenic habitats (e.g., for the house finch; Gammon and Maurer 2002). The observed randomness in the BBS network suggests that this might not be a general problem. In fact, recent work by La Sorte and Boecklen (in press) has shown that BBS routes tend to be located away from urban areas and are associated with low human activity and moderately low human population densities. Nevertheless, additional work examining differences in occupancy and patterns of abundance across natural-urban gradients would be valuable.

In addition to showing that both native and exotic species do differ from random in terms of their occupancy, we found that there are differences among groups. Exotics and the similar native set showed consistently similar patterns, but both commonly differed from the random native set. Thus, given the same number of sites, the occupancy of exotic and similar native species tends to be less aggregated than the occupancy of species in the random set. This result could be due to a statistical artifact associated with the small number of occupied routes that characterized species in the random set (see Table 16.1), as such a short range in the independent variable, as compared with the other two sets, might affect the estimation of the scaling exponent through regression. However, it seems more likely (given the comparable relationships observed between the exotic and similar sets of species, which were observed despite the small sample sizes of both groups) that such differences between the ran-

dom set of natives and the other two groups reflect the nonrandom characteristics of the species constituting those groups (i.e., a case in which ecological characteristics are driving the observed differences).

Another issue is how accurately the area-corrected MST scaling relationships might reflect the metapopulation dynamics associated with changes in species ranges (e.g., Gammon and Maurer 2002). One way of addressing this question is to carry out spatially explicit metapopulation models and study the relationships between the area-corrected MST scaling exponents and species extinction and colonization probabilities. In fact, preliminary data on this question (F. A. Labra, S. R. Abades, and P. A. Marquet, unpublished data) suggest that there is a connection. In a similar vein, it would be interesting to expand our analysis to a consideration of only routes above some threshold of abundance, as they are more likely to represent the source populations or density hot spots driving the dynamics of space occupancy and expansion (Brown et al. 1995; Gammon and Maurer 2002). This is probably the reason why in all three sets we found species with area-corrected MST scaling exponents that did not differ from random.

The number of sites occupied has been a common measure in ecological theory to describe species distribution. However, it fails to capture significant features of the spatial pattern, because two species with the same number of occupied sites might have very different spatial distributions. In this chapter, we have introduced a new scaling relationship (i.e., the MST length scaling) that captures some aspects of the spatial pattern in the distribution of species. However, we are not alone in these attempts. In fact, a recent paper by He and Hubbell (2003) attempts to quantify the spatial structure in the relationship between abundance and distribution. Although further work on geometric aspects of the distribution and abundance of species (see also Harte et al. 2001) is needed, we believe this work, particularly on scaling laws, will provide invaluable insights into the distribution and abundance of species.

The scaling of distribution and abundance

The distribution and abundance of species are tightly interconnected aspects of their ecology, and most of the time it is almost impossible to think of one without the other. As pointed out by Gaston et al. (2000), in the extreme, a positive interspecific correlation between both variables is almost inevitable, since it can be generated by many different patterns of space occupancy (Holt et al. 2003). This positive interspecific correlation emerges despite controlling for phylogeny, habitat, migration status, and dispersal ability (Gaston and Blackburn 2003) and occurs largely independently of intraspecific relationships (Blackburn et al. 1998).

At the intraspecific and interspecific levels (see Tables 16.2 and 16.3 and Figures 16.5 and 16.6), the average distribution-abundance scaling exponents do not differ among exotic, similar, and random sets. Further, both relationships are always positive and significant (only the house sparrow shows a non-

significant relationship; see Table 16.2). Although our results at the intraspecific level show a consistent pattern of positive relationships, contrary to the patterns observed for British birds (e.g., Blackburn et al. 1998), it remains to be seen whether this pattern holds for the majority of the species in the BBS. Although it has been empirically shown that for some species in the BBS data set, a decline in abundance does not necessarily imply a decline in occupancy, and vice versa (e.g., Gaston and Curnutt 1998; Gaston 2003), our data show that the scaling exponent characterizing this process is similar across native and exotic species; this result points to the existence of a common process or set of processes underlying the scaling relationship between total abundance and distribution for both native and exotic species, reinforcing the conclusions reached by Holt and Gaston (2003) for British mammals and birds.

Unlike most previous studies (but see Keitt et al. 2002), we measured abundance as total number of individuals instead of average abundance. For this pattern, a scaling exponent of 1 is expected if individuals are distributed with equal probability across sites. As a null model, imagine that each population is subdivided into n equally sized, independent subpopulations, and that the number of these subpopulations depends on S , the total abundance. It has been argued by Keitt et al. (2002) that the number of subpopulations does not scale in a simple linear fashion with increasing S , but instead takes the form $n \propto S^{1-\alpha}$ (where α is the exponent of the relationship between local and regional abundance). These authors estimated $1 - \alpha$ to be $3/4$, based on their analysis of the interspecific distribution-abundance relationship for the BBS in 1997. An exponent of $3/4$ is not different from our observed interspecific distribution-abundance scaling exponents reported for years 1970, 1980, 1990, and 2000. Interestingly, our results also show that the same $3/4$ scaling exponent holds, on average, for the intraspecific distribution-abundance relationships observed for the exotic, similar, and random sets. According to Keitt et al. (2002), this is to be expected when there is a positive relationship between regional and local abundance (e.g., Gaston and Lawton 1988). In this context, it is interesting to note that some exotic species show values of α close to zero (rock dove and Eurasian collared dove) and even negative values (European starling), which suggest that for these species, a positive relationship between local and regional abundance should not hold. As suggested by Keitt et al. (2002), the existence of a $3/4$ power law scaling raises the possibility that the processes invoked to explain the emergence of $3/4$ power laws in organismal physiology (e.g., West et al. 1997, 1999) could underlie the emergence of patterns in the spatial structure of metapopulations. However, as yet, there is no formal theory linking individuals to the spatial structure of populations.

Finally, our results show that, on average, exotic species do reach higher maximum abundances than native species and show a higher probability of reaching any given abundance. We are not aware of any study reporting a similar finding. Certainly, this finding deserves further scrutiny, for it points to an ecological pattern for which exotic and native species show differences that might be associated with invading species in general. One potential explana-

tion for this pattern is the purported higher degree of ecological generalization associated with exotic species, which allows them to reach higher abundances within local communities. Although certainly not overwhelming, the existing evidence is consistent with the hypothesis that ecological generalization is related to establishment probability: McLain et al. (1999) showed that successfully introduced species had a greater tendency toward dietary and nest habit generalism; Brooks (2001) found that introduced species categorized as habitat specialists were less likely to be successfully established; and Cassey (2002) found that habitat generalism (among other variables) affected the successful establishment of introduced land bird species. Although it is not known whether those traits that favor establishment also affect spread, the observed correlation between native geographic range and the range achieved after introduction by exotic bird species in New Zealand and Australia (Duncan et al. 1999, 2001; Williamson 2001) suggests that broad ecological tolerances do indeed increase the probability of establishment and subsequent spread (Duncan et al. 2003). Thus, the observed numerical abundance and higher degree of evenness shown by exotics (see Figure 16.8) is probably associated with broad ecological tolerances.

Concluding Remarks

In theory, there are several reasons to expect that exotic species will differ from native species, both in the geometric properties of their spatial distribution and in their distribution and abundance scaling pattern. These differences, usually linked to enemy release, preadaptation to human-modified environments, ecological specialization, and life history, on one hand, make their establishment and success paradoxical (e.g., Sax and Brown 2000), and on the other, make the emergence of patterns in richness (Sax 2001; Sax et al. 2002), and in distribution and abundance, similar to those observed in native species, remarkable. Our results indicate that exotic and native species show similar scaling patterns in their distribution and abundance, which suggests that they are under the influence of similar processes. Although there is still discussion regarding what these processes and their underlying mechanisms are (e.g., Gaston et al. 2000; Harte et al. 2001), our results point to their generality in affecting range dynamics as well as the scaling of distribution and abundance relationships.

It remains to be seen whether other scaling relationships, such as those relating population density and home range size to body size, are the same when exotic and native species are compared, as theory suggests (e.g., Brown et al. 2004). In this context, it would be particularly important to assess how much energy exotic species populations use within local communities, especially considering that empirical evidence suggests that this should be approximately constant across species (i.e., the energetic equivalence rule; see review in Marquet et al., in press). Our results suggest that in at least some places within their range, exotic species reach abundances well above those of similar native

species, which is reflected in the fact that exotics reach higher maximum abundances than natives, and would therefore use a disproportionate amount of available energy. This could be due to a “density compensation” effect, such that exotics occupying sites where few natives are present (for whatever reason) might then utilize a greater proportion of the available energy. Further analyses that examine the use of energy across species, the scaling relationships between distribution and abundance, and the geographic range architecture of both native and exotic species should do much to advance our understanding of the interplay between the complex factors that determine the distribution and abundance of species.

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Literature Cited

- Adami, C., and A. Mazure. 1999. The use of the minimal spanning tree to characterize the 2D cluster galaxy distribution. *Astronomics and Astrophysics Supplement Series*. 134:393–400.
- Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* 4:177–188.
- Bak, P., C. Tang, and K. Wiesenfeld. 1988. Self-organized criticality. *Physical Review A* 38:364–374.
- Banavar, J. R., J. L. Green, J. Harte, and A. Maritan. 1999. Finite size scaling in ecology. *Physical Review Letters* 83:4212–4214.
- Barrow, J. D., S. P. Bhavsar, and D. H. Sonoda. 1985. Minimal spanning trees, filaments and galaxy clustering. *Monthly Notices of the Royal Astronomical Society* 216:17–35.
- Beardah, C. C., and M. J. Baxter. 1996. MATLAB routines for kernel density estimation and the graphical representation of archaeological data. *Analecta Prehistorica Leidensia* No. 28, Leiden University, The Netherlands.
- Beardwood, J., H. J. Halton, and J. M. Hammersley. 1959. The shortest path through many points. *Proceedings of the Cambridge Philosophical Society* 55:299–327.
- Berg, H. C. 1983. *Random walks in biology*. Princeton University press, Princeton, NJ.
- Bhavsar, S. P. and E. N. Ling 1988. Are the filaments real? *The Astrophysical Journal* 331:63–68.
- Blackburn, T. M., K. J. Gaston, J. J. D. Greenwood, and R. D. Gregory. 1998. The anatomy of the interspecific abundance-range size relationship for the British avifauna: II. Temporal trends. *Ecology Letters* 1:47–55.
- Brooks, T. 2001. Are unsuccessful avian invaders rarer in their native range than successful invaders? In J. L. Lockwood, M. L. McKinney, eds. *Biotic homogenization*. Kluwer Academic, New York.

- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American naturalist* 124:255–279.
- Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. *Ecology* 76:2028–2043.
- Brown, J. H., and G. B. West, eds. 2000. *Scaling in biology*. Oxford University Press, Oxford.
- Brown, J. H., V. K. Gupta, B.-L. Li, B. T. Milne, C. Restrepo and G. B. West. 2002. The fractal nature of nature: power laws, ecological complexity, and biodiversity. *Proceedings of the Royal Society of London B* 357:619–626.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Bunn, A. G., D. L. Urban, and T. H. Keitt. 2000. Landscape connectivity: a conservation application of graph theory. *Journal of Environmental Management*. 59:265–278.
- Cantwell, M. D., and R. T. T. Forman. 1993. Landscape graphs: ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecology* 8:239–255.
- Cassey, P. 2002. Life history and ecology influences establishment success of introduced land birds. *Biological Journal of the Linnean Society* 76:465–480.
- Channell, R., and M. V. Lomolino. 2000. Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography* 27:169–179.
- Chartrand, G. 1977. *Introductory graph theory*. Dover Publications, New York.
- Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleo record. *American Naturalist* 152:204–224.
- Cotgreave, P., and P. Harvey. 1994. Evenness of abundance in bird communities. *Journal of Animal Ecology* 63:365–374.
- Del Hoyo, J., A. Elliot, and J. Sargatal. 1994. *Handbook of the birds of the world, Vol. 2. New world vultures to guineafowls*. Lynx Ediciones, Barcelona.
- Del Hoyo, J., A. Elliot, and J. Sargatal. 1997. *Handbook of the birds of the world, Vol. 4. Sandgrouse to cuckoos*. Lynx Ediciones, Barcelona.
- Dobrin, R., and P. M. Duxbury. 2001. Minimum spanning trees on random networks. *Physical Review Letters*. 86:5076–5079.
- Duncan, R. P., T. M. Blackburn, and C. J. Veltman. 1999. Determinants of geographical range sizes: a test using introduced New Zealand birds. *Journal of Animal Ecology* 68:963–975.
- Duncan, R. P., M. Bomford, D. M. Forsyth, and L. Conibeare. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology* 70:621–632.
- Duncan, R. P., T. M. Blackburn, and D. Sol. 2003. The ecology of bird introductions. *Annual Review of Ecology and Systematics* 34:71–98.
- Dunning, J. B. 1993. *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL.
- Dussert, C., G. Rasigni, M. Rasigni, J. Palmari, and A. Llebaria. 1986. Minimal spanning tree: a new approach for studying order and disorder. *Physical Review B* 34:3528.
- Dussert, C., G. Rasigni, M. Rasigni, J. Palmari, A. Llebaria and F. Marty. 1987. Minimal spanning tree analysis of biological structures. *Journal of Theoretical Biology* 125 317–323.
- Gammon, D. E., and B. A. Maurer. 2002. Evidence for non-uniform dispersal in the biological invasions of two naturalized North American bird species. *Global Ecology and Biogeography* 11:155–61.
- Gaston, K. J., and J. H. Lawton. 1988. Patterns in the distribution and abundance of insect populations. *Nature* 331:709–712.
- Gaston, K. J., and J. L. Curruent. 1998. The dynamics of abundance-range size relationships. *Oikos* 81:38–44.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. *Journal of Animal Ecology* 37:39–59.
- Gaston, K. J., T. M. Blackburn. 2003. Dispersal and the interspecific abundance-occupancy relationships in British birds. *Global Ecology and Biogeography* 12:373–379.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Gower, J. C., and G. J. S. Ross. 1969. Minimum spanning trees and single linkage cluster analysis. *Applied Statistics* 18:54–64.
- Gregory, R. D. 1998. An intraspecific model of species' expansion, linking abundance and distribution. *Ecography* 21:92–96.
- Gregory, R. 2000. Abundance patterns of European breeding birds. *Ecography* 23:201–208.
- Hammersley, J. M., J. H. Halton, and J. Beardwood. 1959. The shortest path through many points. *Cambridge Philosophical Society Proceedings* 55:299–327.
- Harte, J., T. Blackburn, and A. Ostling. 2001. Self-similarity and the relationship between abundance and range size. *American Naturalist* 157:374–386.
- Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison, M. Holland, J. Lambrinos, U. Malvadkar, B. A. Melbourne, K. Moore, C. Taylor and D. Thomson. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8:91–101.

- He, F., and S. P. Hubbell. 2003. Percolation theory for the distribution and abundance of species. *Physical Review Letters* 91:198103.
- Hengeveld, R. 1989. *Dynamics of biological invasions*. Chapman and Hall, London.
- Hoffman, R. and A. K. Jain 1983. A test of randomness based on the minimal spanning tree. *Pattern Recognition Letters* 1:175–180.
- Holt, A. R., K. J. Gaston, and F. He. 2003. Occupancy-abundance relationships and spatial distribution: a review. *Basic and Applied Ecology* 3:1–13.
- Holt, A. R. and K. J. Gaston. 2003. Interspecific abundance–occupancy relationships of British mammals and birds: Is it possible to explain the residual variation? *Global Ecology and Biogeography* 12:37–46.
- Holt, R. D., J. H. Lawton, K. J. Gaston and T. M. Blackburn. 1997. On the relationship between range size and local abundance: back to basics. *Oikos* 78:183–190.
- Iribarne, C., M. Rasigni, and G. Rasigni. 1999. Minimal spanning tree and percolation on mosaics: graph theory and percolation. *Journal of Physics A—Mathematical and General* 32:2611–2622.
- Jaillet, P. 1995. On properties of geometric random problems in the plane. *Annals of Operations Research* 61:1–20.
- Johnson, A. R., B. T. Milne, and J. A. Wiens 1992. Diffusion in fractal landscapes—simulations and experimental studies of tenebrionid beetle movements. *Ecology* 73:1968–1983.
- Jones, C. L., G. T. Lonergan, and D. E. Mainwaring. 1996. Minimal spanning tree analysis of fungal spore spatial patterns. *Bioimages* 4:91–98.
- Keitt, T. H., and P. Marquet. 1996. The introduced Hawaiian avifauna reconsidered: evidence for self-organized criticality? *Journal of Theoretical Biology* 182:161–167.
- Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1, no. 1. <http://www.consecol.org/vol1/iss1/art4>.
- Keitt T. H., L. A. N. Amaral, S. V. Buldyrev, and H. E. Stanley. 2002. Scaling in the growth of geographically subdivided populations: invariant patterns from a continent-wide biological survey. *Philosophical Transactions of the Royal Society of London B* 357:627–633.
- La Sorte, F. A., and W. J. Boecklen. In Press. Changes in the diversity structure of avian assemblages in North America. *Global Ecology and Biogeography*.
- Lockwood, J. L., M. P. Moulton and S. K. Anderson 1993. Morphological assortment and the assembly of communities of introduced passeriforms on oceanic Islands: Tahiti versus Oahu. *American Naturalist* 141:398–408.
- Lomolino, M. V., and R. Channell. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. *Journal of Mammology* 76:335–347.
- Lubina, J., and S. A. Levin. 1988. The spread rate of a reinvading organism: range expansion of the California sea otter. *American Naturalist* 131:526–543.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.
- Marquet, P. A., J. Keymer, and H. Cofre. 2003. Breaking the stick in space: of niche models, meta-communities, and patterns in the relative abundance of species. In T. M. Blackburn, and K. J. Gaston, eds. *Macroecology: concepts and consequences*, pp. 64–84. Blackwell Scientific Publications, Oxford.
- Marquet, P. A., R. A. Quiñones, S. A. Abades, F. Labra, M. Tognelli, M. Arim and M. Rivadeneira. In press. Scaling and power-laws in ecological systems. *Journal of Experimental Biology*.
- Maurer, B. A. 1994. *Geographical population analysis: tools for the analysis of biodiversity*. Blackwell Scientific Publications, Oxford.
- Maurer, B. A., E. T. Linder, and D. Gammon. 2001. A geographical perspective on the biotic homogenization process: implications from the macroecology of North American birds. In J. Lockwood, ed. *Biotic homogenization*, pp. 157–178. Kluwer Academic, Plenum Publishers, New York.
- McLain, D. K., M. P. Moulton, J. G. Sanderson. 1999. Sexual selection and extinction: The fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evolutionary Ecology Research* 1:549–565.
- Newton, I. 1997. Links between the abundance and distribution of birds. *Ecography* 20:137–145.
- Okubo, A. 1980. *Diffusion and ecological problems: mathematical models*. Springer-Verlag, Berlin.
- Peterjohn, B. G., and J. R. Sauer. 1993. North American Breeding Bird Survey Annual Summary 1990–1991. *Bird Populations* 1. 52–67.
- Peterjohn, B. G. 1994. The North American Breeding Bird Survey. *Birding* 26:386–398.
- Prim, R. C. 1957. Shortest connection network and some generalizations. *Bell System Technical Journal* 36:1389–1401.
- R Development Core Team 2003. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2003. *The North American Breeding Bird Survey, results and analysis 1966–2002*. Version 2003. 1, USGS Patuxent Wildlife Research Center, Laurel, MD.

- Sax, D. F. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography* 28:139–150.
- Sax, D. F., S. D. Gaines, and J. H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. *American Naturalist* 160:766–783.
- Shigesada, N., and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196–218.
- Solow, A. R., C. J. Costello, and M. Ward. 2003. Testing the power law model for discrete size data. *American Naturalist* 162:685–689.
- Stanley, H. E., L. A. N. Amaral, P. Gopikrishnan, P. Ch. Ivanov, T. H. Keitt, and V. Plerou. 2000. Scale Invariance and Universality: Organizing Principles in Complex Systems. *Physica A* 281:60–68.
- Steele, J. M. 1988. Growth rates of Euclidean minimal spanning trees with power weighted edges, *Annals of Probability*, 16 1767–1787.
- Urban, D. L. and T. H. Keitt. 2001. Landscape connectivity: a graph theoretic perspective. *Ecology*, 82:1205–1218.
- Van de Weygaert, R., B. J. T. Jones and V. J. Martinez, 1992. The minimal spanning tree as an estimator for generalized dimensions. *Physics Letters* 169, 145–150.
- Wallet, F. and C. Dussert. 1997. Multifactorial Comparative study of spatial point pattern analysis methods. *Journal of Theoretical Biology* 187:437–447.
- West, G. B. 1999. The origin of universal scaling laws in biology. *Physica A* 263:104–113.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.
- Williamson, M. 2001. Can the impacts of invasive species be predicted? In R. H. Groves, F. D. Panetta, and J. G. Virtue, eds. *Weed risk assessment*, pp. 20–33. Collingwood, Australia.
- Zahn, C. T. 1971. Graph-theoretical methods for detecting and describing gestalt clusters. *IEEE Transactions on Computers* C 20:68–86.