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Scaling patterns in exotic and native bird species distribution and abundance.

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Abstract

Scaling phenomena are at the core of a great variety of ecological processes ranging from individual physiology to population, community 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 invasive exotics and native species recorded in the Breeding Bird Survey within the North American continent. To do this we compare scaling patterns in nine exotic species (the exotic set) and compare them to a set of native species chosen to maximize taxonomic and ecological similarity (the similar set) and to a random set of native species (the random set). For each set of species we assessed 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 they are under the influence of similar process thus supporting the generality of these scaling relationships. However, exotic species do differ from natives in a key aspect of their ecology; they are able 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 and understanding on the structure and dynamics of ecological systems in general, and on the generality of scaling relationships in ecology in particular.

Scaling phenomena are common in a diverse array of complex systems and have become a major venue of enquiry in ecology (e.g., Banavar et al. 1999, Brown and West 2000, Brown et al. 2002, Marquet et al. in press) as they likely emerge as a result of fundamental principles underlying the complexity 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 one emphasizes the scaling of the invasion process itself in order to mechanistically understand the spread of invasive species in a new ecological setting. Under this approach the most commonly reported scaling is that associated to the relationship between spatial spread (measured as the increase in the square root of area 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, Hasting et al. 2005). This scaling pattern has been also analyzed in the context of dispersal in heterogeneous landscapes (Johnson et al. 1992) and considering the effect 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 and its size, in the case in point, the events were extinction of introduced species.

In this chapter, we benefit from both approaches to analyzing scaling relationships, comparing 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 effect 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, but rather the action of general principles that underlie the distribution and abundance of species. On a practical side, most exotic birds have been introduced during the eighteenth and nineteenth centuries and consequently there are good records on 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 of 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 characteristic of range collapse (i.e. reduction in the range of widespread species) has 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 build up (but see Maurer 1994, Maurer et al. 2001, Gammon and Maurer 2002). For this process, most studies have focused on estimating and/or predicting rate 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. As a point of departure to understand this process we focus on the geometrical properties of the spatial distribution of site occupancy by exotic species through time. Our null expectation is that ranges expand following the same basic process that underlie fluctuations in the occupancy of any species native to a region. To test this, we compare the scaling pattern 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 of species has been shown to be affected by factors that include habitat type, body size, phylogeny and spatial scale (e.g. Magurran 1988, Cotgrave and Harvey 1994, Brown et al 1995, Gregory 2000, Marquet et al. 2003); thus we expect that the distribution of abundance may differ between native and naturalized species.

Materials and Methods

Data base 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 the Breeding Bird Survey (BBS) data (Peterjohn & Sauer 1993, Peterjohn 1994, Sauer et al. 2003). This is a yearly sampling effort run since 1966 across North America. In Figure 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 (Fig 1d). The number of routes and geographic area covered increased rapidly since the beginning in 1966 but the area they cover levels off after 1970. For most of the species we studied, the BBS contains about 46 years of sampling effort, covering the entire area of the USA. Hence, to minimize any potential effect of the increase in area covered shown by the BBS network, we only worked with the data for censuses after 1970. Details on the species selection procedure are given below.

Species included in the analysis

After identifying all exotic bird species known to the continental US, we selected those that had enough records (more than ten routes) in the North American Breeding Bird Survey. This procedure leaves us with nine species with adequate spatial and temporal coverage. We called this set 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 in order to maximize similarity to the selected exotic species; to do so, we took into account, first phylogenetic relatedness and then ecological and life history traits (see Table 1). 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 can be a result of phylogenetic, ecological or life history similarities. Species included in the similar set were chosen so as to maximize similarity in taxonomy, then ecology and finally body size.

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, species in this set show different trends in abundance and encompass a broad spectrum of phylogenetic relatedness, life histories, and ecological attributes (Table 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 a large number of random sets of species; such a task, however, would have been difficult given the capabilities of our computers, 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 geometrical properties of species distribution, we used the Minimal Spanning Tree (MST) methodology that provides a graphical representation of the pattern of occurrences of a species. Figure 2a shows a set of points drawn from a uniform distribution in 2-D 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 2b shows one of the many ways to form a connected graph, with several circuits or loops. On the other hand, a connected graph containing no circuits is called a tree (Figures 2c and d). If the tree of a connected graph contains all the nodes then it is called a spanning tree, and if these connections minimize the total length across the graph, then it is called a minimal spanning tree (MST, Figure 2d). In other words, the MST is the spanning tree of minimum length. 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 only be unique when there are complex spatial patterns, it is possible that more than one MST of equal length will exist for simple spatial patterns. It is important to note that this unique network picks out the dominant pattern of connectedness among the locations 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), pattern recognition (Zahn 1971, Hoffman and Jain 1983), 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 and one by one, adds to the graph those nodes which are closer or the nearest neighbor to the subgraph already built. In so doing we must avoid adding an edge that completes a circuit or loop, since a tree cannot have any cycle to be a MST. The process stops when there are no further nodes to add. Thus the minimal spanning tree uniquely connects a set of N nodes with $N-1$ edges. The MST may be described in many ways, including average degree, connectivity distribution 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, this being 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 holds true for any set of independent random variables with a compact support in any arbitrary dimension greater or equal to 2 (Steele 1988). This result provides the expected pattern under the null hypotheses 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 this data we constructed a MST for each species in every single 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 R12 (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 per year. We examined this relationship for exotic species and 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 also for each of the three groups as an ensemble in specific years (1970, 1980, 1990, and 2000) or the interspecific scaling pattern. Finally, we also examined patterns in the frequency distribution of abundances for exotic and native species. To do this we plotted for each group of species 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 to 2002. We used logarithmic abundance classes and plotted this versus the logarithm (base 10) of probability (see Solow et al. 2003).

Results

Minimal Spanning Tree scaling

In Figure 3 we show the temporal trend in abundance and distribution for a selected groups of exotic and native species. As is apparent in these figures, over the study period (1970-2002) there is substantial variability in number of routes wherein a species is recorded and in its abundance. Overall, the exotic and similar sets showed an increase in the number of BBS routes occupied by species through time (average linear regression slopes \pm 1SE 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). Despite this variability in the number of BBS routes occupied, the total length of the minimal spanning trees scale in a similar fashion among species within the exotic, similar, and random sets (Figure 4a-c). Within each set, species show a tight scaling relationship, even though they show quite different temporal dynamics and spatial patterns of expansion (Figure 3). The average scaling exponent for each the three groups depart significantly from the null expectation of a 0.5 exponent. 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 (from this comparison we 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 in less than 20 routes). The random set showed a significantly lower exponent as compared to the exotic and similar sets, which are not significantly different from each other. This suggests that species in the exotic and similar set 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 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 5, Table 2). Exotic species reached the highest abundance for a given number of routes (Fig.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 do not differ among sets. These results imply that for a given increase in occupancy, all three sets tend to increase total abundance in a similar way.

At the interspecific level (Figure 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 low numbers of routes they show less apparent differences from

native species (Figure 6). However, there are no significant differences in the average scaling exponents among groups and across years (Table 3). A similar pattern is observed when we study the MST length scaling for the same groups over the same years (Figure 7); there are no significant differences in the scaling exponents among groups and across years (Table 3).

Finally, the frequency distribution of abundances for exotic and native species, considering all years and all routes wherein each species was recorded, shows that species in the exotic set have higher probability of attaining any given abundance than native species and show a more even abundance distribution (shallower slopes, Figure 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 distribution of abundance 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 , figures are estimated slopes ± 1 s.e.). However, the scaling exponent for the exotic species set (-5.714 ± 0.288) is significantly different from 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 if 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 the geometry of space occupancy and in distribution-abundance scaling, however important differences in their distributions of abundance were apparent. Further, none of the pattern 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, results 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 their distribution 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 random process in space. This is supported by the fact that exotic species distributed all over North America (such as the Rock dove, House finch and House sparrow) show scaling exponents different from random (Table 2). To further explore the potential effect of the BBS network topology we calculated the expected scaling pattern under the assumption that species occupy BBS sites at random and using the observed 2002 BBS network. 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 different from 0.5. This 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 biases 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, introducing a bias in the observed area corrected MST scaling pattern depending on the area where the

species is currently distributed or was introduced to. To test for this potential effect we repeated the analysis of the BBS network scaling, but this time we separated the continent in an East and a West half using the longitude 100° as the boundary between both. The scaling exponents for both halves were not statistically different between them (0.458 ± 0.023 and 0.433 ± 0.036 for West and East halves respectively) nor from the expect value of 0.5. Thus, it is safe to conclude that the BBS network is 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 problem. Another cause of concern in this analysis is related to the potential for routes to be located nearby urban areas and roads in anthropogenic landscapes, since this could potentially inflate the pattern of site occupation for some species (exotics most likely) 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 density.

In addition to showing that both native and exotic species do differ from random in terms of their occupancy, we also found that there are differences among groups, with the exotic and similar native set showing no differences between them, but both differing from the random native set. Thus, given the same number of sites, the occupancy of exotic and similar native species tend to be less aggregated than those species in the random set. However, this might well be a statistical artifact associated with the small number of occupied routes that characterize species in the random set (Table 1). Such a short range in the independent variable, as compared to the other two sets, might affect the estimation of the scaling exponent through regression. Another issue is how accurately the area corrected MST scaling relationship might reflect the metapopulation dynamics associated to changes in species range (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 exponent and species extinction and colonization probabilities. In fact, preliminary data on this (Labra, Abades and Marquet unpublished results) suggest that there is a connection between both. In a similar vein, it would be interesting to expand our analysis to a consideration of only routes above some threshold 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), instead of giving equal weight to all routes. This is probably the reason why in all three sets we found species with area corrected MST scaling exponents that do not differ from random.

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 paper 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 geometrical aspects of the distribution and abundance of a species (see also Harte et al. 2001) is needed, we believe it will provide valuable insights to understand the emergence of scaling laws in 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, to such an extent that many different patterns of space occupancy can generate it (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 level (Table 2,3 Figures 5, 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 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 if this patterns 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 imply necessarily a decline in occupancy and viceversa (e.g., Gaston and Curnutt 1998, Gaston 2003), our data shows that the scaling exponent characterizing this process is similar across native and exotic species; this 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 $n = S^{1-\beta}$ (where β is the exponent of the relationship between local and regional abundance). These authors estimated β to be $3/4$ based on the analysis of the interspecific distribution-abundance relationship for the BBS in 1997. An exponent of $3/4$ is not different from the 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 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 β close to zero (the Rock dove and the 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 higher probability of reaching any given abundance. We are not aware of any study reporting a similar finding. Certainly, this aspect deserves further scrutiny, for it points out to an ecological pattern for which exotic and native species show differences that might be associated with invading species in general. One potential explanation for this pattern is the purported higher degree of ecological generalization associated with exotic species, which will allow them to reach higher abundances within local communities. Although, certainly not overwhelming, the most direct evidence in favor of this hypothesis reduces to the effect of ecological generalization upon establishment probability; McLain et al. (1999) who showed that successfully introduced species had a greater tendency for dietary and nest habit generalism, Brooks (2001) who found that introduced species categorized as habitat specialists were less likely to be successfully established and Cassey (2002) who found that habitat generalism (among other variables) affected the successful establishment of introduced land bird species. Although, it is not known if those traits that favor establishment will 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) suggest that broad ecological tolerances do indeed increase probability of establishment and subsequent spread (Duncan et al. 2003). Thus the observed numerical abundance and higher degree of evenness shown by invasive exotics (Figure 8) is likely associated to broad ecological tolerances.

Concluding remarks

In theory, there are several reasons to expect that invasive exotics will differ from natives species both in the geometric properties of their spatial distribution as well as in their distribution and abundance scaling pattern. These differences, usually linked to enemy release, pre-adaptation to human modified environments, ecological specialization and life history make, on the one hand, their establishment and success paradoxical (e.g., Sax and Brown 2000), and on the other, the emergence of patterns in richness (Sax 2001, Sax et al. 2002) and distribution and abundance, similar to those observed in native species, remarkable. Our results indicate that invasive exotics and native species show similar scaling patterns in their distribution and abundance, which suggests they are under the influence of similar process. Although there is still discussion regarding what these processes and underlying mechanisms are (e.g., Gaston et al. 2000, Harte et al. 2001), our results point out to their generality in affecting range dynamics, as well as the scaling of distribution and abundance relationships. It remains to be seen if other scaling relationships, such as those relating population density and home range 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 at least in some places within their range, invasive exotics reach abundances well over that 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 other 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, as well as geographical 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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Figure Legends

Figure 1: Temporal trends in BBS sampling effort. The figure shows the spatial coverage of the sampling sites for the years 1966 (a), 1985 (b), 2002 (c). Fig 1d shows temporal trends in total number of routes (filled circles) and area (open squares).

Figure 2: Examples of point, connected line and spanning tree graphs. (a) Set of random points in space. (b) Connected line graph showing ‘loops’. (c) Spanning tree. (d) Minimum spanning tree for the set of points shown in (a).

Figure 3: Examples of trends in the distribution of exotic and native species. The figure shows the observed dynamics in number of routes (open circles) and total abundance (filled squares) for two exotic species: (a) Eurasian collared dove, (b) Cattle egret, and two native species: (c) Painted bunting and (d) Brown-headed cowbird.

Figure 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. A. Exotic species, B. Natives in the ‘similar’ group, and C. Natives in the ‘random’ group (see text for details). The black lines show the power law fits for each of the groups of species.

Figure 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). Exotic species are indicated with black lines and native species by dashed and dotted lines for the similar and random sets respectively.

Figure 6: Interspecific distribution-abundance relationship for exotic and native species ensembles. Exotic species are represented with open circles while the similar and random sets of native species are shown by crosses and filled squares respectively. Note the trend for exotic species to exhibit higher abundances than natives for a given number of routes, particularly at large number of routes. Lines as in Figure 5.

Figure 7: Interspecific area corrected MST length scaling relationship for exotic and native species ensembles present for selected years. Symbols as in Figure 6.

Figure 8: Probability distribution of abundance (individuals per route) for exotic and native species ensembles calculated over the entire study period (1970-2002) and over all sampling routes. Exotic species are represented with open circles. Similar and random sets of native species are shown by crosses and filled squares respectively. Note the power law scaling shown by all three groups. Regressions statistics were estimated for those values in the exponentially decaying tail (i.e. probabilities greater than 0.003). Symbols as in Figure 6.

Table 1: List of species in the exotic, similar and random sets analyzed in this study. Data for distribution and abundance corresponds to observed minimum and maximum number of routes and number of individuals respectively. Diet and habitat data comes from the BBS and del Hoyo et al. (1994, 1997) and body size from Dunning (1993).

Status	Family	Common name	Scientific name	Body size (g)	Diet	Habitat	Distribution (routes)	Abundance (individuals)
Exotic	Anatidae	Mute swan	<i>Cygnus olor</i>	11007	Plant matter, aquatic invertebrates	Wetland-open water	2-18	5-179
	Ardeidae	Cattle egret	<i>Bubulcus ibis</i>	338	Insects	Wetland-open water	36-307	1012-17561
	Columbidae	Rock dove	<i>Columba livia</i>	355	Seeds, green plant matter, insects	Urban	280-1262	4961-17858
	Columbidae	Eurasian collared dove	<i>Streptopelia decaocto</i>	149	Seeds, green plant matter, insects	Urban	1-134	13-1287
	Fringillidae	House finch*	<i>Carpodacus mexicanus</i>	21	Seeds, insects	Urban	3-867	10-12666
	Passeridae	House sparrow	<i>Passer domesticus</i>	28	Seeds, insects	Urban	493-1929	44803-105318
	Phasianidae	Grey partridge	<i>Perdix perdix</i>	391	Seeds, insects	Grasslands	2-104	11-323
	Phasianidae	Ring-necked pheasant	<i>Phasianus colchicus</i>	1278	Plant matter, insects, worms and snails	Grasslands	127-707	1249-10860
	Sturnidae	European starling	<i>Sturnus vulgaris</i>	83	Insects, fruit	Urban	507-2250	45557-117377
Similar	Anatidae	Trumpeter swan	<i>Cygnus buccinator</i>	10701	Green plant matter, seeds, aquatic invertebrates	Wetland-open water	1-20	1-171
	Ardeidae	Little blue heron	<i>Egretta caerulea</i>	343	Aquatic invertebrates, fish, reptiles and amphibians	Wetland-open water	50-194	359-1847
	Columbidae	Inca dove	<i>Columbina inca</i>	48	Seeds	Urban	5-74	19-356
	Columbidae	Common ground dove	<i>Columbina passerina</i>	30	Seeds, insects	Successional-scrub	28-129	188-882
	Columbidae	Mourning dove	<i>Zenaida macroura</i>	120	Seeds	Urban	454-2545	11316-80294
	Fringillidae	American goldfinch	<i>Carduelis tristis</i>	13	Seeds, insects	Successional-scrub	411-1718	5040-23624
	Fringillidae	Purple finch	<i>Carpodacus purpureus</i>	25	Flowers, fruit, seeds and insects	Woodland	107-444	519-2042
	Phasianidae	Greater sage grouse	<i>Centrocercus urophasianus</i>	2724	Green plant matter, flowers, seeds and insects	Successional-scrub	4-38	14-380
	Phasianidae	Blue grouse	<i>Dendragapus obscurus</i>	1030	Plant matter and insects	Woodland	5-50	28-159
Icteridae	Brown-headed cowbird	<i>Molothrus ater</i>	44	Seeds and insects	Open woodlands, fields	465-2385	5433-34229	

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

Table 1 Cont.

Status	Family	Common name	Scientific name	Body size (g)	Diet	Habitat	Distribution (N° routes)	Abundance (N° individuals)
Random	Anatidae	Northern pintail	<i>Anas acuta</i>	1025	Plant matter, aquatic invertebrates, fish, reptiles and amphibians	Wetland-open water	4-182	7-2099
	Anatidae	Mottled duck	<i>Anas fulvigula</i>	1013	Aquatic invertebrates, seeds, green plant matter and fish	Wetland-open water	6-33	38-455
	Anatidae	American black duck	<i>Anas rubripes</i>	1304	Green plant matter, seeds, aquatic invertebrates and fish	Wetland-open water	33-75	97-313
	Ardeidae	Tricolored heron	<i>Egretta tricolor</i>	405	Aquatic invertebrates, fish, reptiles and amphibians	Wetland-open water	12-56	31-535
	Cardinalidae	Painted bunting	<i>Passerina ciris</i>		Seeds, insects	Successional-scrub	10-199	59-2597
	Columbidae	Band tailed pigeon	<i>Patagioenas fasciata</i>	343	Nuts, fruit and seeds	Woodland	19-109	196-866
	Odontophoridae	Gambel's quail	<i>Callipepla gambelii</i>	167	Seeds and insects	Successional-scrub	12-68	175-2448
	Odontophoridae	Scaled quail	<i>Callipepla squamata</i>	184	Seeds and insects	Successional-scrub	10-87	190-1142
	Odontophoridae	Mountain quail	<i>Oreortyx pictus</i>	233	Seeds, green plant matter and insects	Successional-scrub	4-70	8-729
	Parulidae	Prothonotary warbler	<i>Protonotaria citrea</i>	17	Insects and snails	Woodland	66-206	163-1152

Table 2: Scaling statistics for the Distribution-Abundance and the Area corrected MST scalings fitted for all the species under study. 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 of for all the species under study. Area corrected MST scaling exponents that differ from the null expectation (of 0.5) are shown in underlined bold typeface. C.I. = Confidence interval.

Status	Common name	Distribution-Abundance Scaling				Normalized MST length scaling			
		Intercept	s.e.	exponent	se	R ²	exponent	95% Lower C. I.	95% Upper C. I.
Exotic									
	Mute swan	-0.069	0.142	0.550	0.084	0.562	.	.	.
	Cattle egret	-0.820	0.156	0.784	0.040	0.917	<u>0.412</u>	0.354	0.469
	Rock dove	-1.478	0.229	1.072	0.055	0.915	<u>0.434</u>	0.397	0.470
	Eurasian collared dove	-1.377	0.166	1.122	0.071	0.943	<u>0.257</u>	0.182	0.332
	House finch	-0.754	0.428	0.637	0.071	0.704	<u>0.412</u>	0.387	0.437
	House sparrow	2.219	1.059	0.193	0.216	0.022	<u>0.295</u>	0.231	0.36
	Gray prairie	-0.268	0.149	0.921	0.070	0.831	0.536	0.433	0.639
	Ring-necked pheasant	-0.242	0.240	0.753	0.061	0.811	0.517	0.468	0.567
	European starling	-4.201	0.466	1.492	0.094	0.878	0.461	0.422	0.50
Similar									
	Trumpeter swan	-0.071	0.122	0.601	0.091	0.591	<u>0.073</u>	-0.087	0.234
	Little blue heron	0.233	0.152	0.633	0.052	0.810	0.449	0.395	0.504
	Inca dove	-0.319	0.088	0.852	0.044	0.917	<u>0.322</u>	0.197	0.448
	Common ground dove	-0.039	0.271	0.710	0.100	0.589	0.469	0.320	0.617
	Mourning dove	-1.145	0.146	0.924	0.031	0.962	0.487	0.466	0.508
	American goldfinch	-0.317	0.279	0.821	0.068	0.808	<u>0.395</u>	0.372	0.418
	Purple finch	-0.573	0.382	0.972	0.120	0.653	<u>0.033</u>	-0.108	0.174
	Greater sage grouse	-0.052	0.113	0.614	0.057	0.776	0.229	0.063	0.553
	Blue grouse	-0.393	0.249	0.925	0.134	0.590	<u>0.308</u>	0.191	0.425
	Brown-headed cowbird	-1.023	0.168	0.965	0.038	0.948	0.472	0.437	0.507
Random									
	Northern pintail	0.190	0.177	0.612	0.061	0.742	0.412	0.317	0.507
	Mottled duck	-0.086	0.181	0.618	0.083	0.615	<u>0.298</u>	0.136	0.460
	American black duck	0.498	0.156	0.553	0.070	0.643	0.307	0.069	0.545
	Tricolored heron	0.289	0.110	0.524	0.052	0.747	<u>0.340</u>	0.239	0.441
	Painted bunting	-0.291	0.128	0.754	0.040	0.910	<u>0.369</u>	0.314	0.425
	Band tailed pigeon	-0.375	0.277	0.810	0.103	0.653	<u>0.371</u>	0.251	0.491
	Gambel's quail	-0.363	0.113	0.672	0.040	0.893	0.460	0.378	0.541
	Scaled quail	-0.118	0.369	0.649	0.134	0.410	0.422	0.311	0.530
	Mountain quail	-0.119	0.187	0.679	0.073	0.727	0.468	0.398	0.537
	Prothonotary warbler	0.910	0.080	0.457	0.029	0.876	<u>0.339</u>	0.262	0.416

Table 3. Statistic for the interspecific distribution-abundance relationship and the area-corrected MST scaling relationship (s.e.= 1standard error).

Year	Group	Slope±s.e.	R ²	P
Distribution-abundance relationship				
1970	Exotic	0.428±0.141	0.606	0.023
1970	Similar	0.739±0.046	0.957	0.000
1970	Random	0.471±0.180	0.768	0.031
1980	Exotic	0.416±0.146	0.577	0.029
1980	Similar	0.821±0.064	0.954	0.000
1980	Random	0.673±0.176	0.647	0.005
1990	Exotic	0.520±0.201	0.488	0.036
1990	Similar	0.727±0.042	0.978	0.000
1990	Random	0.767±0.194	0.662	0.004
2000	Exotic	0.408±0.161	0.479	0.039
2000	Similar	0.710±0.043	0.972	0.000
2000	Random	0.591±0.021	0.591	0.009
Area-corrected MST scaling				
1970	Exotic	0.544±0.113	0.823	0.005
1970	Similar	0.440±0.022	0.983	0.000
1970	Random	0.438±0.086	0.764	0.001
1980	Exotic	0.465±0.075	0.884	0.002
1980	Similar	0.377±0.020	0.977	0.000
1980	Random	0.378±0.048	0.887	0.000
1990	Exotic	0.376±0.019	0.985	0.000
1990	Similar	0.378±0.027	0.961	0.000
1990	Random	0.357±0.080	0.713	0.002
2000	Exotic	0.416±0.020	0.986	0.000
2000	Similar	0.440±0.022	0.981	0.000
2000	Random	0.370±0.078	0.736	0.001

Figure 1:

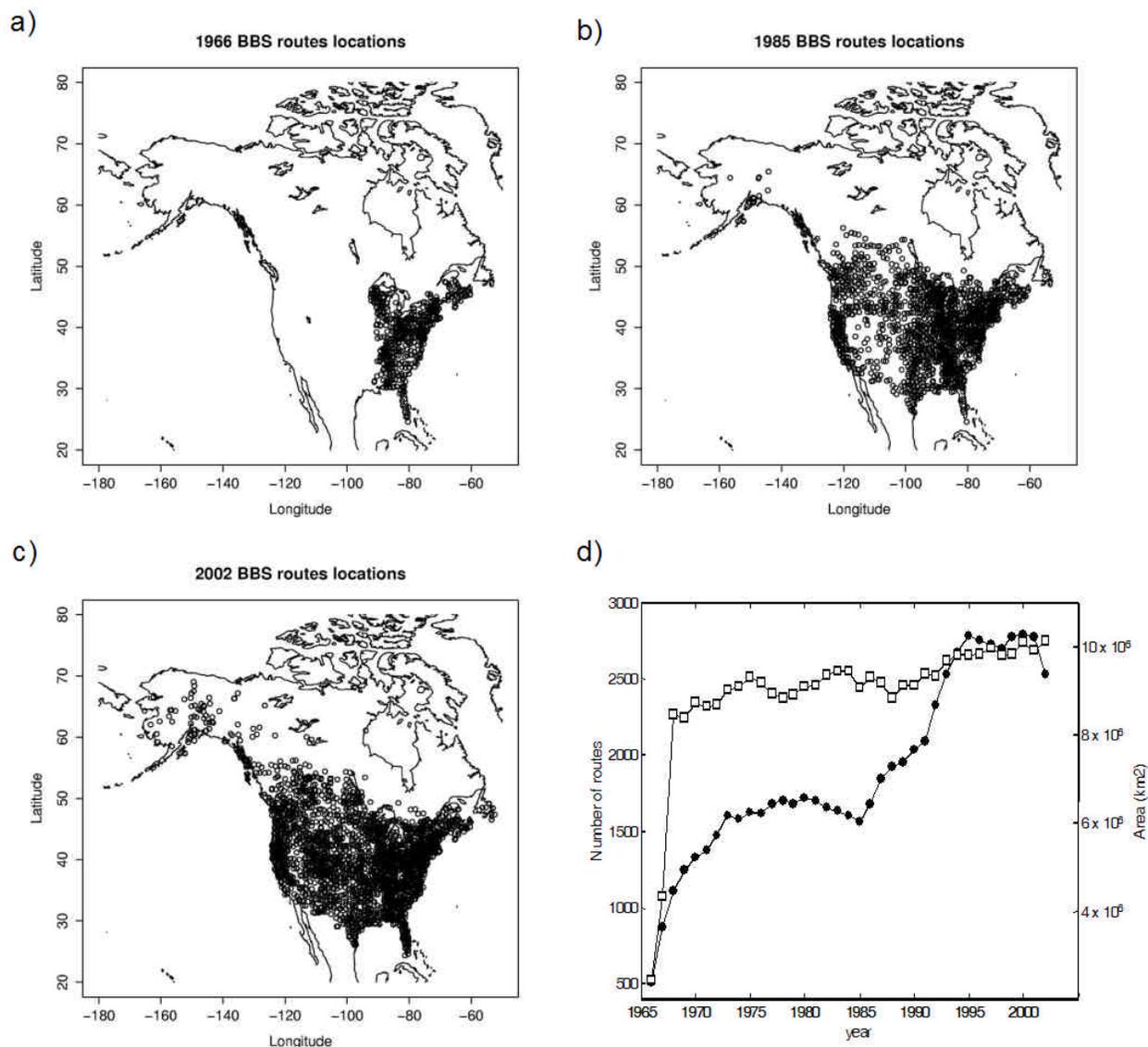


Figure 2:

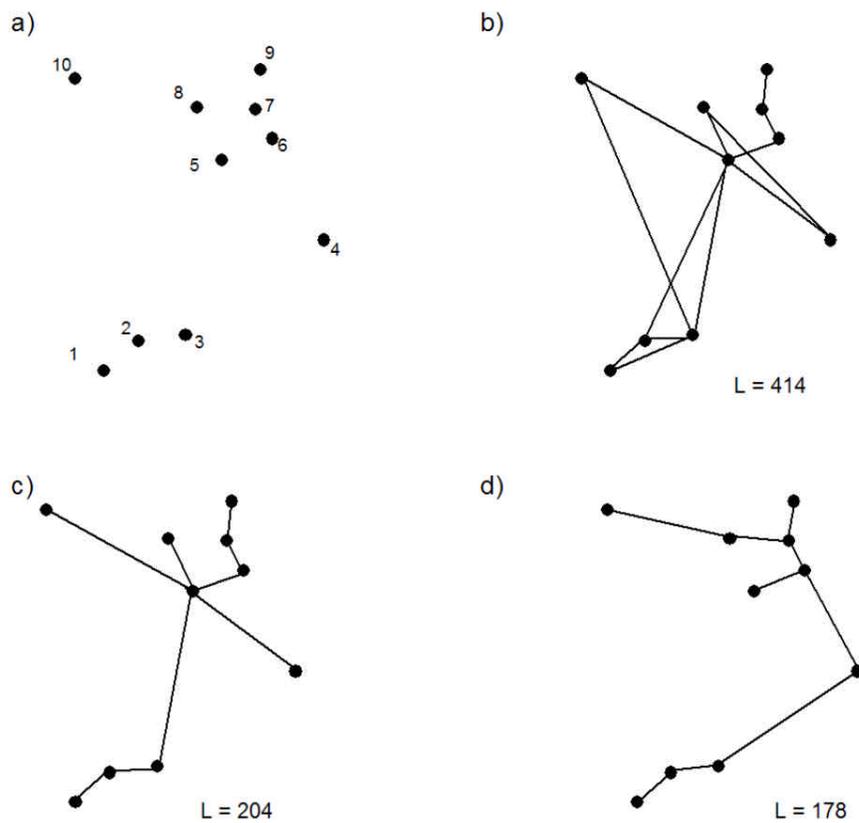


Figure 3:

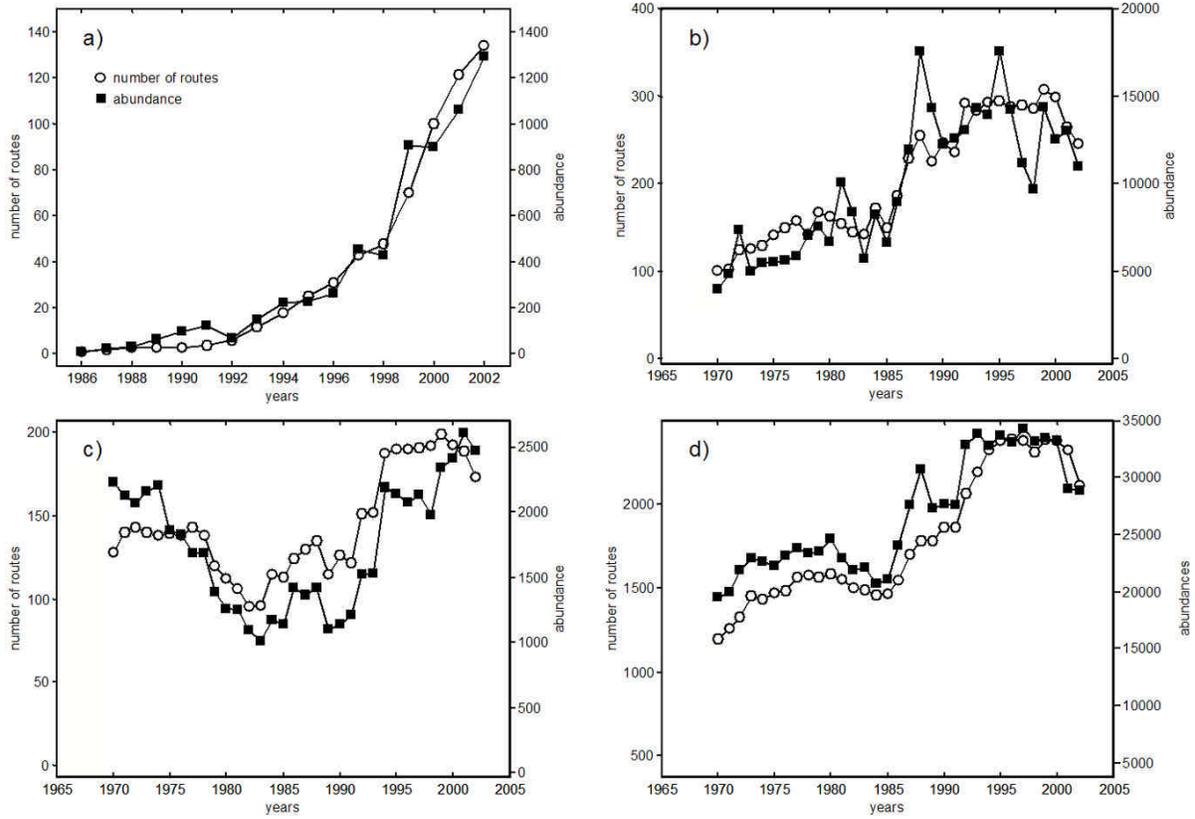


Figure 4:

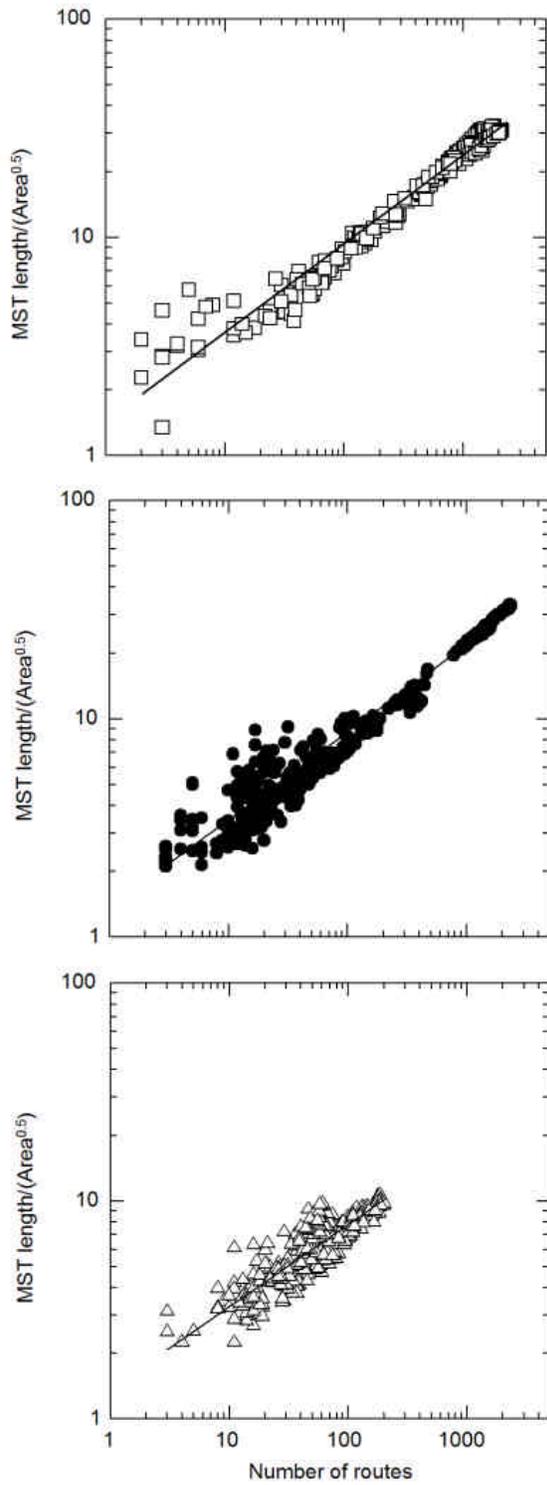


Figure 5:

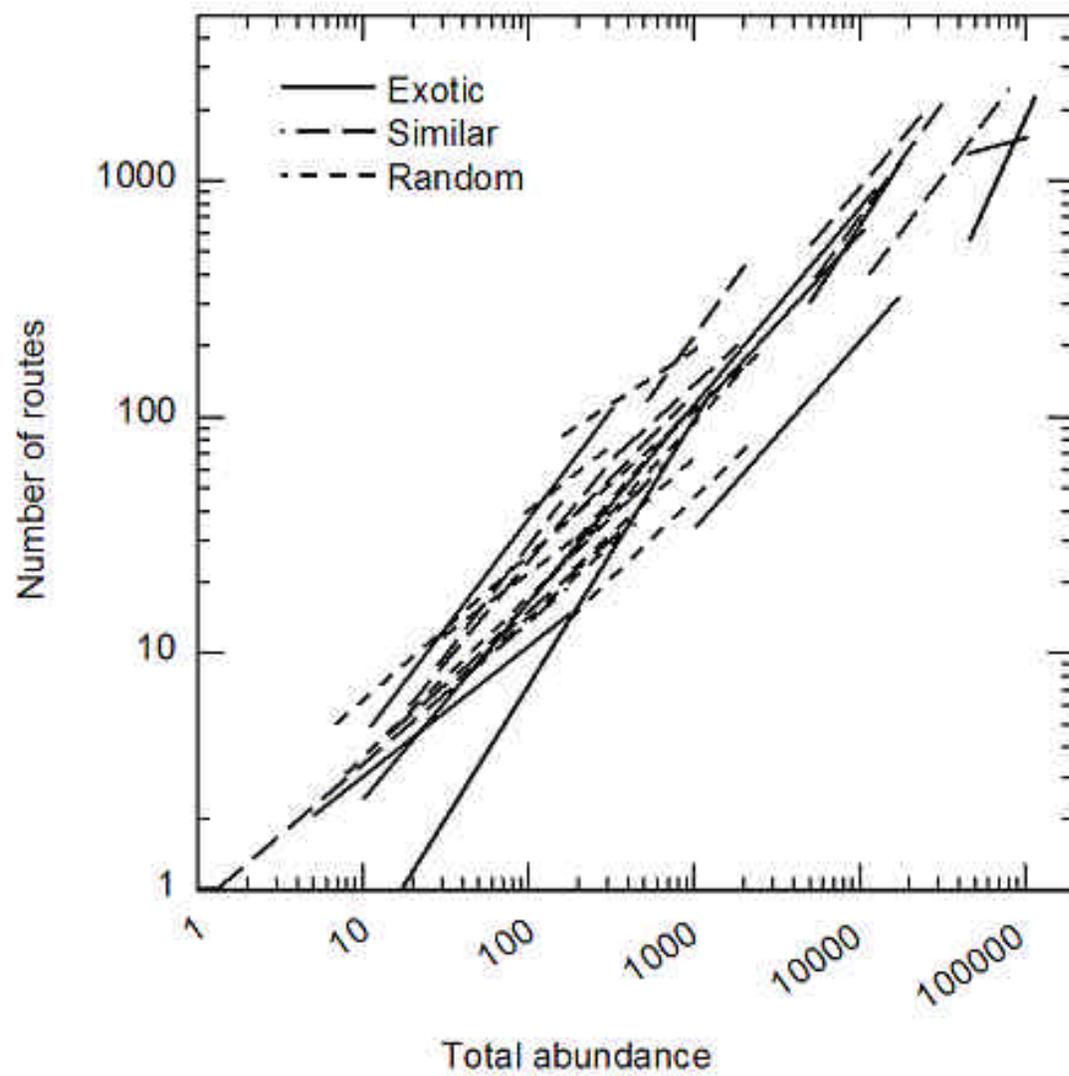


Figure 6:

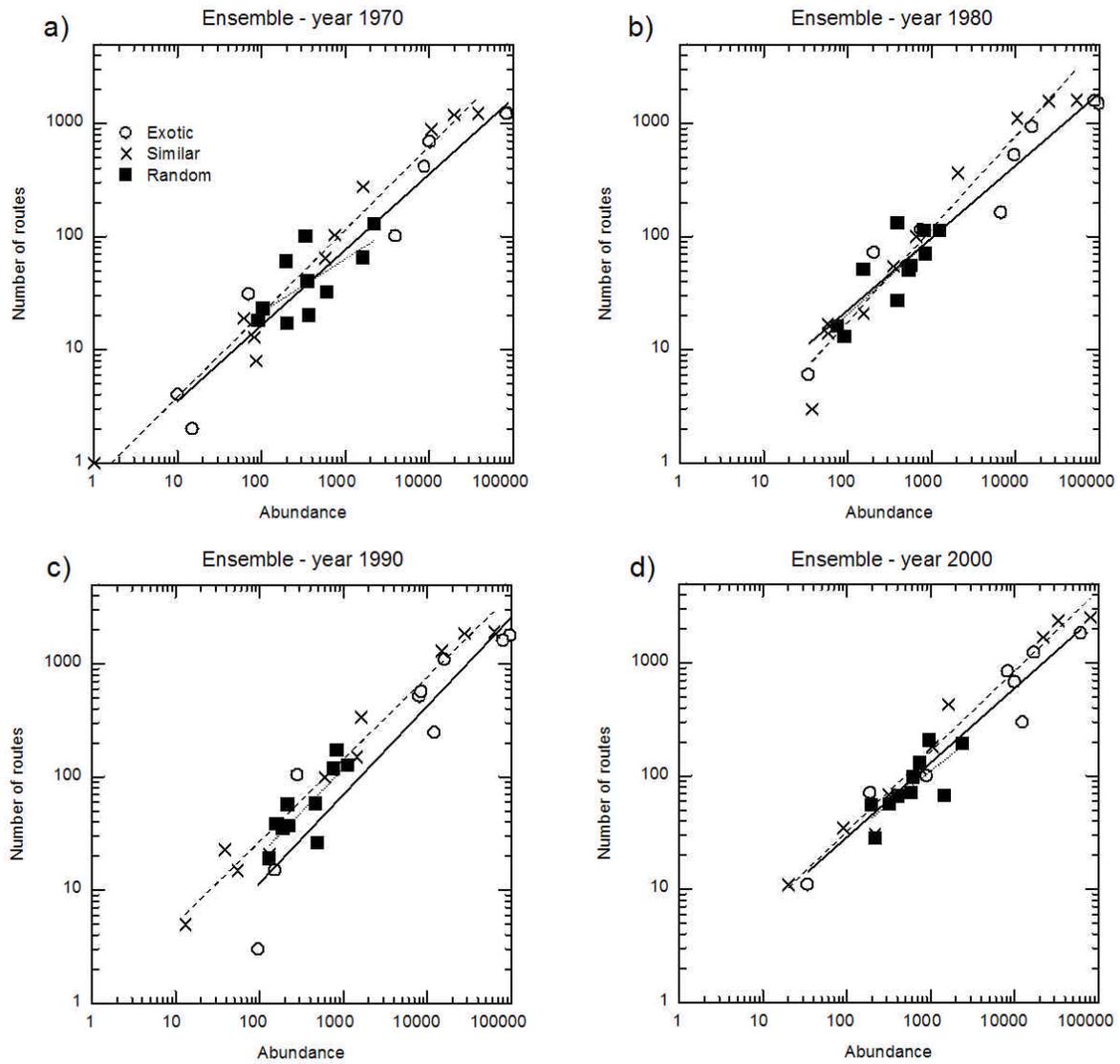


Figure 7:

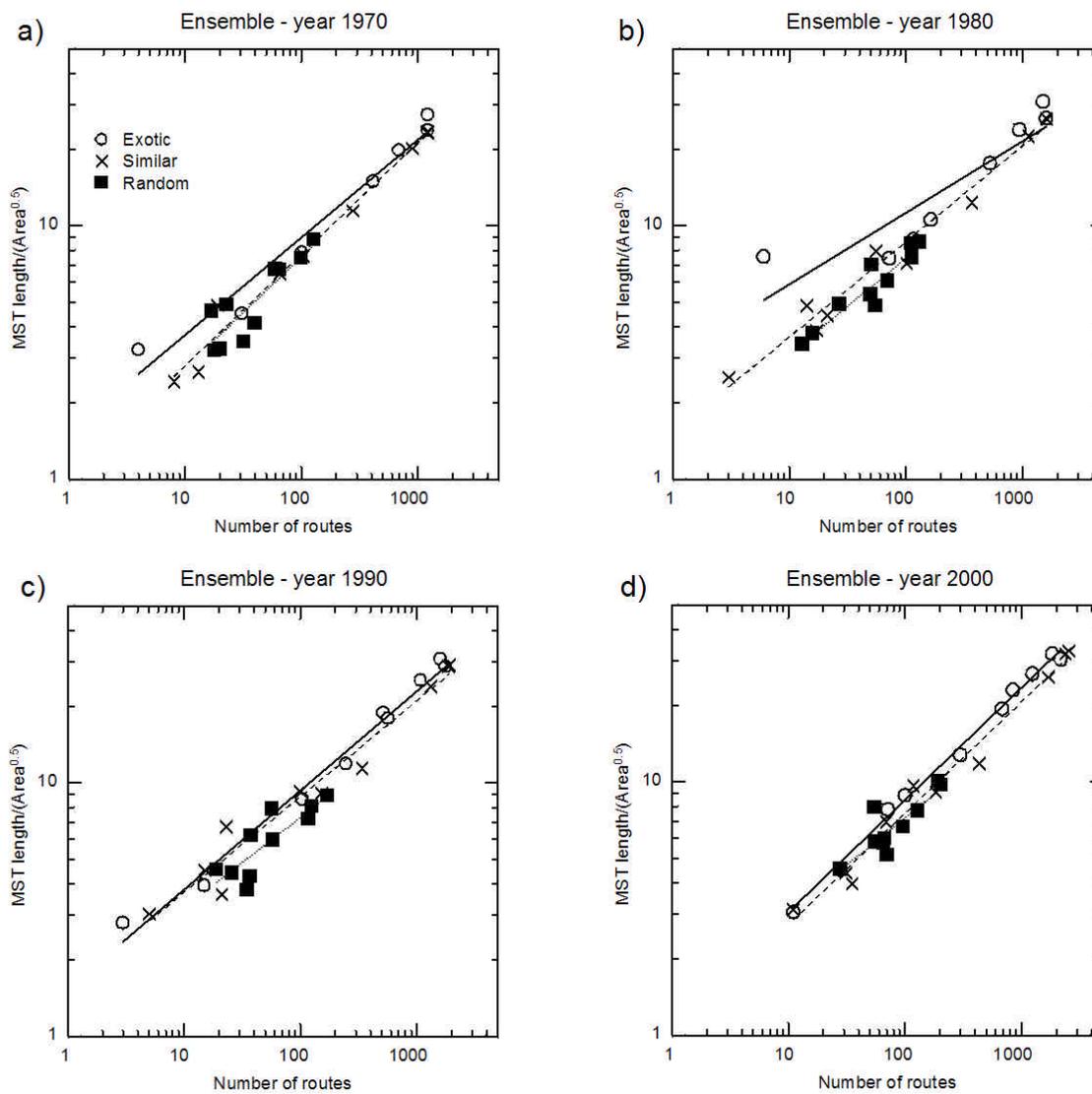


Figure 8:

