Linking temporal and spatial scales in the study of an Argentine ant invasion

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Abstract

Our long-term study of an invasion of Argentine ants (*Linepithema humile*) in a 481-ha biological preserve in Northern California links multiple spatial and temporal scales. We have investigated, at local spatial scales of tens of meters, how nests spread and contract seasonally and from year to year. Microsatellite analysis shows population genetic structure on the scale of about 100 m. At the landscape scale, we have surveyed the spread and impact of Argentine ants in the biological preserve since 1993, and have found high variability both seasonally and from year to year. Here, we describe how seasonal patterns in nesting behavior at the local scale help to explain how the location of the invasion edge changes. Thus, the growth and spread of nests on the scale of tens of meters, from season to season, produce the dynamics of the invasion from year to year at the scale of hundreds of meters.

Introduction

Ecological processes at one scale may determine patterns at another (Wiens 1989; Levin 1992). Here we consider the relation between the local behavior of an invasive ant on the scale of meters and its spread on the scale of hectares. Local seasonal patterns in nesting behavior produce year-to-year changes in the location of the invasion front.

The Argentine ant, *Linepithema humile*, has invaded ecosystems worldwide, particularly in Mediterranean climates. Traveling from Argentina by boat with sugar and coffee cargo in the late 19th and early 20th century, it is now established on six continents and many oceanic islands, including the Mediterranean coastline, the coast of South Africa, Hawaii, Australia, the southeastern United States and the California coastline (Suarez et al. 2001). Because the ants tend homopterans, the Argentine ants are considered agricultural pests (Markin 1970). Wherever they become established, they reduce populations of native ants and other arthropods (Ward 1987; Cole et al. 1992; Cammell et al. 1996; Human and Gordon 1996; Human and Gordon 1997; Holway 1998; Suarez et al. 1998; Sanders et al. 2001, 2003). Despite the ubiquity and impact of Argentine ants, surprisingly little is known about their population ecology.

Argentine ants are unicolonial: a colony contains many queens distributed among many interconnected nests and aggression is rare among conspecifics (Suarez et al. 1999; Tsutsui et al. 2000). This differs from the more typical ant species, in which each colony has a single nest and ants react antagonistically toward all non-nestmates. Reproduction in Argentine ants is also not typical. In most ant species, colonies reproduce when winged sexuals fly to a mating aggregation, and then the newly mated queens

found new colonies (Hölldobler and Wilson 1990). In Argentine ants, by contrast, reproduction occurs by budding. Some workers and queens leave an existing nest and walk to a new nest. At global and regional scales, the distribution of Argentine ants depends on jump dispersal events by means of human transport (Suarez et al. 2001). But once the ants have been introduced to a particular area, spread occurs largely by budding.

Little is known about interactions among neighboring nests of Argentine ants. Workers appear to move freely among neighboring nests at distances less than 60 m (Markin 1968; Ripa et al. 1999; Krushelnycky et al. 2004). To learn how workers from different nests interact, many researchers have relied on aggression bioassays (Suarez et al. 1999; Giraud et al. 2002; Roulston et al. 2003; Buczkowski et al. 2004). In these tests, ants from one nest are introduced to ants from another. If the ants fight, they are considered to belong to different associations of nests, or 'supercolonies'. If the ants do not fight, they are considered to belong to the same supercolony. Aggression tests have led some to conclude that Argentine ant colonies cover vast spatial regions, such as the state of California (Tsutsui et al. 2000) and the Mediterranean coastline (Giraud et al. 2002). The lack of intraspecific aggression at such large spatial scales may make it easy for propagules transported by humans to become established. However, the apparent lack of aggression at large distances is not relevant to processes of local spread, which depends on interactions at distances that ants can travel to meet other ants.

Here we argue that associations among neighboring nests on the scale of tens of meters within supercolonies have important effects on the dynamics of the local spread of Argentine ants. We draw on data from 11 years (1993–2004) of an ongoing study of the invasion of Argentine ants in the Jasper Ridge Biological Preserve (JRBP) in northern California. Seasonal changes in the distribution of local nest associations, at the scale of tens of meters, produce a fluctuating invasion edge at the landscape scale of many hectares. This leads to a fluctuating impact on native species at the invasion edge.

Local scale

Nest associations

Maps of Argentine ant nests reveal that the nests are not distributed evenly in space. In patches with many nests, the nests are often connected by trails. Trails do not usually connect nests more than 10 m apart. Instead distant nests are connected only through a series of intermediary nests. This results in clusters of interacting nests varying in radius from about 10 to 100 m. Thus, supercolonies are sub-divided into many smaller colony units. Nests may be considered to belong to the same supercolony if, when ants from those nests are placed together by an experimenter, the ants do not fight. By contrast, nests belong to the same colony only if they are connected by trails.

The nesting behavior of Argentine ants changes seasonally (Newell and Barber 1913; Markin 1970). The location, number, size, connectedness, and spatial pattern of colonies differ in the summer and winter (Figure 1; Heller and Gordon, in prep.). During the cool, wet winters typical of Mediterranean climates, the spatial range of the colony is contracted, as the nests associated with
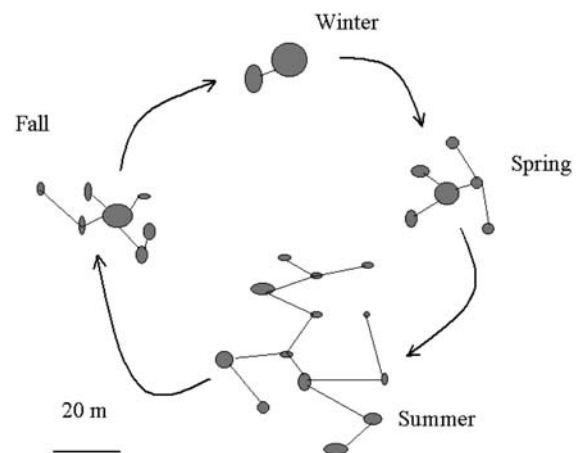

Figure 1. A schematic illustration of the seasonal accordion cycle of the colony. Gray circles represent nests; the size of the circle indicates the nest size. Lines indicate trails. Within each colony, nests are large and contracted in the winter. In the spring, ants begin to disperse and spread out into smaller nests. By summer the spatial extent of the colony has increased, with many, small dispersed nests. In fall, the ants begin to return to old winter nesting sites and the spatial extent of the colony contracts.

each colony join into one or more large aggregations. During the spring, aggregations are slowly abandoned and the ants disperse, budding into many smaller nests. In the hot, dry summers, population size increases and the ants are very active (Krushelnycky et al. 2004) moving nest sites frequently (Benois 1973) and continuing to spread, by budding, into new areas. These newly budded nests remain linked together with trails. As a result, the colony covers a larger area in the hot, dry season than the cool, wet season. In the late fall, as temperatures drop, the ants move back to nest aggregation sites from the previous winter.

The seasonal colony cycle of nest aggregation in the winter, and nest dispersion in the summer, like an accordion expanding and contracting each year, seems to be common in Argentine ants. Two studies, one in New Orleans, USA, and one in southern France report similar seasonal dynamics (Newell and Barber 1913; Benois 1973). Seasonal shifts in nest sites and nest number may track environmental conditions and food availability (Benois 1973; Holway and Case 2000). Argentine ants usually nest in the top 35 cm of the soil (Markin 1970; Heller 2004), so nest temperature and humidity can be highly variable. Argentine ants die rapidly when exposed to low levels of humidity and high temperatures (Tremper 1976; Holway et al. 2002), and as conditions become unfavorable, they will move to find more favorable sites (Markin 1970; Holway and Case 2000; Walters and Mackay 2003). Ants may aggregate in the winter to increase nest temperatures. Summer dispersion may function to increase the foraging range of the colony during periods of high protein demand because of brood production (Markin 1970; Benois 1973).

Genetic structure

We analyzed variation in microsatellites to evaluate the structure of Argentine ant populations in JRBP (Ingram and Gordon 2003). The results show significant genetic differentiation on the scale of tens of meters. Thus the spatial scale of genetic structure, about 100 m, is the same as the scale of colonies, clusters of nests visibly connected by trails. This analysis indicates that

queens, who do not fly, are dispersing less than 100 m. It appears that new nests at the invasion front bud off from nests near the invasion edge, not from nests far inside the invaded area.

Microsatellite analysis at the local scale further shows that mixing among nests decreases over the course of the years that the Argentine ants occupy an area and become more established (Ingram and Gordon 2003). It seems that as local interactions between the nests of a single colony determine how that colony spreads, so too the rate and duration of spread in turn affect the extent of interaction among local nests. Since density tends to increase over time once an area has become occupied by Argentine ants (Ingram 2002), the decrease in mixing over time suggests that at higher densities, ants move less between nests.

Landscape scale

Since 1993, we have monitored the distribution of the ground-foraging ant fauna at JRBP. Each May and September, we visit about 250 permanently marked locations (sample plots) and record the ant species present (for details see Human and Gordon 1996; Human et al. 1998; Sanders et al. 2001; Sanders et al. 2003).

Argentine ants are invading the preserve from the surrounding agricultural and residential areas (Human et al. 1998; Sanders et al. 2001), and have increased their range size at JRBP by 14 ha in 11 years, though there is considerable seasonal and yearly variation in this rate. The average rate of spread from 1993 to 1999 was about 5 ha/yr (Sanders et al. 2001), but decreased from 2000 to 2004. Other studies from California report rates of spread along one dimension ranging from 0 to 300 m/yr (reviewed in Suarez et al. 2001).

In some years the range of Argentine ants in JRBP increased, and in others it decreased. The most dramatic shifts occurred between 1998 and 2000, following an El Niño event (Figure 2). The variability in the rate of spread illustrates the importance of long-term data; short-term measurements may lead to misleading predictions (Wiens 1989).

Measures of Argentine ant distribution also depend strongly on season. Each year more sample plots are invaded in the September survey, at
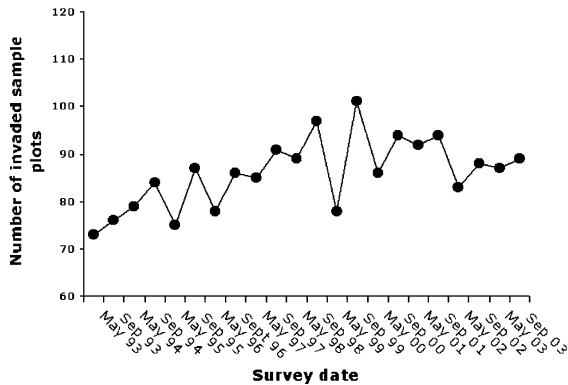
Figure 2. The number of invaded sample plots in 22 surveys over 11 years. The graph includes only the data from the 127 sample plots that were surveyed in each May and September survey since 1993.

the peak of the hot, dry season, than in the May survey, at the end of the cool, wet season (Sanders et al. 2001) (Figure 2).

From year to year, the location of the invasion front fluctuates. At sample plots where the Argentine ants were already established when the survey began in 1993, they have almost always remained. However, at sample plots where the ants have invaded more recently, they have often abandoned the site and native ants have returned (Figure 3). Over the last 11 years, 80% of sample plots invaded have alternated in status, from only Argentine ants (average of 25% surveys) to only native ants (average 52% surveys) to
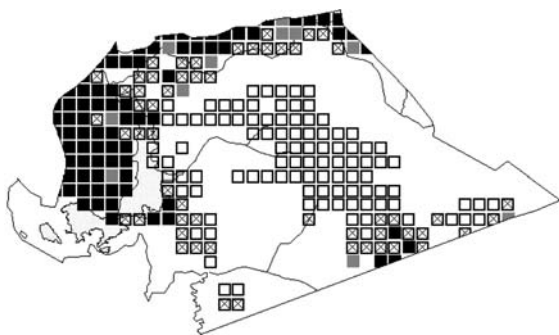

Figure 3. Map of JRBP with the invasion status of sample plots indicated. Each square represents a 1-ha sample plot. Black lines inside the preserve boundaries indicate streams, and a lake and wetland area are shown in gray dots. Black represents Argentine ants found in every survey since 1993; light gray represents Argentine ants invaded since 1993 and established immediately; X represents Argentine ants and native ants alternating; open represents no Argentine ants. The Xs depict the fluctuating edge of the invasion.

Argentine ants and native ants (average 23% surveys).

Both the seasonal and year-to-year shifts in distribution contribute to the apparent rate of spread. Figure 4 shows the change in numbers of sites occupied by Argentine ants over time. Data for May and September are shown separately. The May data, when the Argentine ant range is more contracted, show a steady increase. The September data, when the Argentine ants are more dispersed, show a sharp increase in 1998 and 1999 and more recently a decline.

Linking local and landscape scales

Seasonal changes in the distribution of Argentine ants are probably due to the seasonal colony cycle in nesting behavior. Areas that appear to be empty of Argentine ants during the cool, wet season, when nests gather into winter aggregations, are likely to be occupied by nests when it is hot and dry. As a result we find ants in more sites in the fall than in the spring.

The yearly rate of spread is a combination of expansion in the dry season and retraction in the
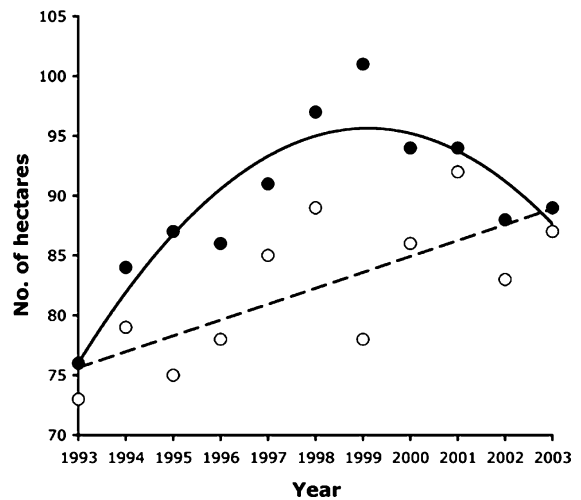

Figure 4. The distribution of Argentine ants at JRBP in northern California over 11 years. The data come from the 127 sample plots surveyed in each survey since May of 1993. Filled circles represent data from the September surveys and open circles represent data from the May surveys. The solid line is the best fit line of the September data ($r^2 = 0.83$, $P < 0.001$) and the dashed line is the best fit line of the May data ($r^2 = 0.52$, $P = 0.01$).

wet season. Even in Hawaii, where seasonal differences in climate are less pronounced than in other parts of the Argentine ant's introduced range, spread tends to occur in the summer and fall (Krushelnycky et al. 2004). *Pheidole megacephala*, another unicolonial, invasive ant, shows a similar seasonal dynamic in the rate of spread, with expansion in the dry season and contraction in the wet season (Hoffman et al. 1999).

Year-to-year changes in the range of Argentine ants in JRBP suggest that there is more variation in the extent of summer dispersal than in the distribution of winter aggregation sites. There is a steady increase in numbers of sample plots occupied in our data collected in May when nests have just begun to disperse from winter aggregations (Figure 4). The data from September at the peak of the hot, dry season show a different pattern. There was a large increase in range in 1998 and 1999. Perhaps summer dispersal was especially high in the years following the unusually wet winters related to the El Niño event. However, in those years the ants still contracted their range in the winter, so high water availability did not increase the overall rate of spread.

Year-to-year fluctuations in the range of Argentine ants may depend in part on which native ant species are present in newly invaded sites. As in other areas where Argentine ants have invaded, when Argentine ants spread to a new site at JRBP, they dramatically alter species composition and community structure (Human and Gordon 1996; Sanders et al. 2001, 2003). However, there is some suggestion that high native species richness (Kark et al. unpublished manuscript) or the presence of particular taxa, such as *Prenolepis imparis* and *Formica moki*, may prevent Argentine ants from becoming established at the edge.

Each native species' response to changing environmental conditions may influence the intensity of its competition with Argentine ants (Shea and Chesson 2002). Argentine ants are active in a wider range of abiotic conditions than most native species at JRBP (Human et al. 1998). However, Holway et al. (2002) found that in laboratory colonies, Argentine ant foragers were more active and experienced less mortality when reared under warm, moist conditions than under hot, dry conditions. At the edge of the invasion front at JRBP, abiotic conditions probably interact with the suite of native ant species to limit the establishment of *L. humile* nests.

Seasonal patterns in Argentine ant colony structure may also be important in their interactions with native ants. In our survey, we observe that the impact of Argentine ants on native ants is greater in the fall than in the spring. Argentine ants and native ants overlapped significantly more often in the spring than in the fall (Sanders et al. 2001). This may be due to the seasonal accordion behavior of Argentine ant colonies. For example, *P. imparis* has often been observed to coexist with *L. humile* in California (Ward 1987; Suarez et al. 1998; Sanders et al. 2001). *P. imparis* is most active in the winter, at the time when Argentine ants are less active and contracted into winter aggregations, which may facilitate the coexistence of the two species. Native species that peak in activity in the summer, when Argentine ants are more dispersed and more active (Benois 1973; Holway 1998), are likely to encounter Argentine ants more frequently. Since Argentine ants tend to be aggressive in encounters with native ants (Human and Gordon 1999), frequent encounters may force native ants to retreat.

Conclusions

Our long-term study of the Argentine ant invasion in a preserve in northern California shows interesting dynamics across multiple temporal and spatial scales. First, the rate of spread and distribution of Argentine ants is highly variable both within and between years. Second, our data suggest complex links between spatial and temporal scales. Processes at the local scale, which are mediated by climatic variability, determine the dynamics of spread and impact at the landscape scale.

A connected cluster of nests, or a colony, aggregates in the winter and disperses in the summer. This alters the location and spatial extent of colonies on the landscape, and thus produces a fluctuating invasion front. Invasion is not a one-way diffusive process; rather it is a shifting, seasonal movement of nests forward and backward, and

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the overall rate of spread is the result of movement in both directions. Annual variation in climate affects the amount of expansion, relative to contraction, of each colony. For example, in years of heavy rainfall, summer dispersion may be great because increased soil moisture has increased the number of suitable nest locations. However, in years of heavy rainfall, nests may aggregate into a smaller number of areas because fewer locations are sufficiently dry and warm for nests. Interactions with native species also influence the seasonal and annual movement of Argentine ant nests. Many native ant species persist at the fluctuating invasion edge. We find these native species most active in the spring when Argentine ant colonies are more contracted. In the hot, dry season, as Argentine ant nests disperse, their expansion may sometimes be limited by competition with native ants. Native ants probably limit Argentine ants most in years when climatic conditions favor the foraging activity and thus population growth of native species.

In conclusion, annual and seasonal shifts in climate, and native species diversity, interact with the spatial organization of Argentine ant colonies to produce the invasion dynamics that we observe at Jasper Ridge.

References

Benois A (1973) Incidence des facteurs écologiques sur le cycle annuel et l'activité saisonnière de la fourmi d'argentine *Iridomyrmex humilis* Mayr (Hymenoptera, Formicidae), dans la région D'Antibes. Insectes Sociaux 20: 267–296

Buczkowski G, Vargo E and Silverman J (2004) The diminutive supercolony: the Argentine ants of the southeastern United States. Molecular Ecology 13: 2235–2242

Cammell ME, Way MJ and Paiva MR (1996) Diversity and structure of ant communities associated with oak, pine, eucalyptus and arable habitats in Portugal. Insectes Sociaux 43: 37–46

Cole FR, Medeiros AC, Loope LL and Zuehlke WW (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology 73: 1313–1322

Giraud T, Pedersen JS and Keller L (2002) Evolution of supercolonies: the Argentine ants of southern Europe. Proceedings of the National Academy of Sciences of the United States of America 99: 6075–6079

Heller NE (2004) Colony structure of the invasive Argentine ant in native and introduced populations. Insectes Sociaux 51: 378–386

Hoffman B, Andersen A and Hill GJE (1999) Impact of an introduced ant on native rain forest invertebrates: *Pheidole magacephala* in monsoonal Australia. Oecologia 120: 595–604

Hölldobler B and Wilson EO (1990) The ants. Harvard University Press, Cambridge, MA

Holway DA (1998) Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia 116: 252–258

Holway DA and Case TJ (2000) Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. Animal Behaviour 59: 433–441

Holway DA, Suarez AV and Case TJ (2002) Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. Ecology 83: 1610–1619

Human KG and Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105: 405–412

Human KG and Gordon DM (1997) Effects of Argentine ants on invertebrate biodiversity in Northern California. Conservation Biology 11: 1242–1248

Human KG and Gordon DM (1999) Behavioral interactions of the invasive Argentine ant with native ant species. Insectes Sociaux 46: 159–163

Human KG, Weiss S, Weiss A, Sandler B and Gordon DM (1998) Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). Environmental Entomology 27: 822–833

Ingram KK (2002) Plasticity in queen number and social structure in the invasive Argentine ant (*Linepithema humile*). Evolution 56: 2008–2016

Ingram KK and Gordon DM (2003) Genetic analysis of dispersal dynamics in an invading population of Argentine ants. Ecology 84: 2832–2842

Krushelnycky PD, Lloyd LL and Joe SM (2004) Limiting spread of a unicolonial invasive insects and characterization of the seasonal patterns of range expansion. Biological Invasions 6: 47–57

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943–1967

Markin GP (1968) Nest relationship of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae). Journal of Kansas Entomological Society 41: 511–516

Markin GP (1970) The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* in southern California. Annals of the Entomological Society of America 635: 1238–1242

Newell W and Barber TC (1913) The Argentine Ant. US Department of Agriculture, Bureau of Entomology Bulletin 122: 1–98

Ripa R, Rodriquez F, Rust MK and Larral L (1999) Distribution of liquid food and bait in colonies of Argentine ant

(Hymenoptera: Formicidae), pp 225–229. In: The 3rd International Conference on Urban Pests, July 19–22, Czech University of Agriculture, Prague, Czech Republic

Roulston TH, Buczkowski G and Silverman J (2003) Nestmate discrimination in ants: effect of bioassay on aggressive behavior. Insectes Sociaux 50: 151–159

Sanders NJ, Barton KE and Gordon DM (2001) Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. Oecologia 127: 123–130

Sanders NJ, Gotelli NJ, Heller NE and Gordon DM (2003) Community disassembly by an invasive ant species. Proceedings of the National Academy of Sciences of the United States of America 100: 2474–2477

Shea K and Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17: 170–176

Suarez A, Bolger D and Case T (1998) Effects of fragmentation and invasion on native ant communities on coastal southern California. Ecology 79: 2041–2056

Suarez A, Tsutsui N, Holway D and Case T (1999) Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. Biological Invasions 1: 43–53

Suarez A, Holway D and Case T (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. Proceedings of the National Academy of Sciences of the United States of America 98: 1095–1100

Tremper BS (1976) Distribtuion of the Arentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. Dissertation. University of California Berkeley, California, USA

Tsutsui ND, Suarez AV, Holway DA and Case TJ (2000) Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences of the United States of America 97: 5948–5953

Walters AC and Mackay DA (2003) An experimental study of the relative humidity preference and survival of the Argentine ant, *Linepithema humile* (Hymenoptera, Formicidae): comparisons with a native *Iridomyrmex* species in South Australia. Insectes Sociaux 50: 355–360

Ward P (1987) Distribution of the introduced argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia 55: 1–16

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3: 385–397