Matters of Scale

Brian J. McGill

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in the eukaryotic genome. In comparison with prokaryote-prokaryote and prokaryote-eukaryote lateral gene transfers, less attention has been paid to eukaryote-eukaryote lateral gene transfers (*16*). Although such transfer events might have been relatively rare, the recent explosive accumulation of eukaryotic genome information opens a new window to look into unexplored dynamic evolutionary processes.

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ECOLOGY

Matters of Scale

Brian J. McGill

Recognition of the scale dependence of ecological processes helps explain the distribution and abundance of organisms.

In 1687, Newton reported that the same laws could describe Galileo's data on balls rolling down ramps and Brahe's data on planets moving around the Sun (*1*). This observation implied that a finite list of principles could explain our infinite universe. And it inspired a leap across scales: The rules at human scales are not unique. Newton's laws of motion are still the dominant explanatory tool across scales ranging from a few atoms to solar systems. However, over the past 25 years, ecologists have come to realize that, unlike physics, ecology is scale-dependent (*2*–*4*). In a recent paper, Gotelli, Graves, and Rahbek (*5*) highlight the importance of this scale dependence: They show that a process that occurs at small spatial scales, namely competition between individuals, plays an important role even at the large scale of an entire country.

The realization that ecology is scale dependent has recently helped to explain a multitude of seemingly conflicting data in ecology (*6*, *7*). Now consideration of scale is helping to address another key issue in ecology: the question of what controls the distribution and abundance of organisms. For example, why is the scissor-tailed flycatcher (*Tyrannus forficatus*), one of North America's most striking birds, found mainly in Texas and Oklahoma? Four main factors limiting the distribution of species have been hypothesized. Climate explains why the polar bear lives in the Arctic and palm trees grow in the tropics (*8*, *9*). Random dispersal determines who can get somewhere first or in large numbers. Spe-

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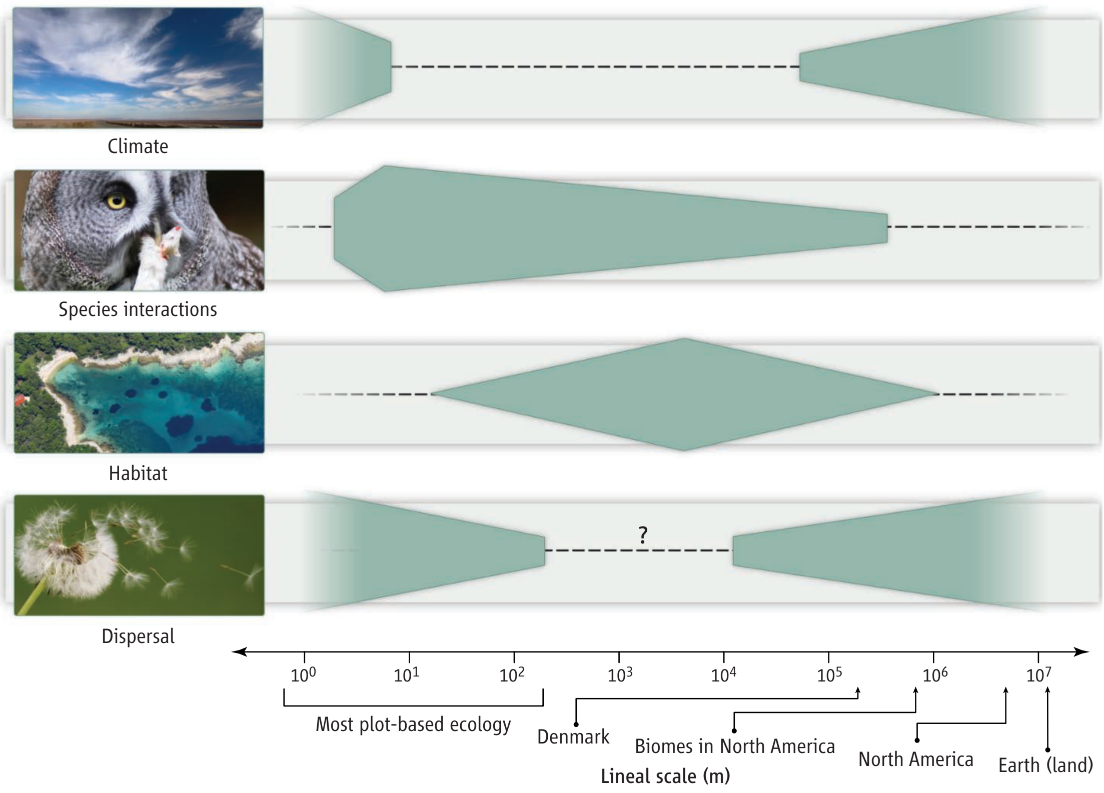

What controls the distribution of species? Four main processes (vertical axis) are believed to control the distribution of organisms; their relative importance changes with scale (horizontal axis). The thickness of the bar for a given factor at a given scale indicates how important that factor is at that scale. Ecologists began drawing such diagrams 25 years ago (*16*), but have only recently begun to perform empirical studies to test the suggested relationships. The question mark at intermediate scales of dispersal indicates that little data exist on this process at these scales. Climate is important for two scales, through two processes: microclimate (such as sun or shade) at small scales and biogeography at large scales. Most ecologists will disagree with some aspect of this figure, but it is the kind of complex, multifaceted, but testable hypothesis that ecology needs.

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cies interactions (competition, predation, and disease) determine whether a species thrives or withers in a given environment (*10*–*12*). The final factor is habitat: Cottonwoods grow throughout the southwestern United States, but only along rivers. Which of these factors are most important?

It is becoming clear that the answer depends on scale. Competition is played out at small scales through interactions between individual organisms (birds in this case). It is difficult to imagine how the interaction between two birds can be influential at large scales, and indeed there is evidence that the role of competition drops off to close to zero at biome or nearly continental scales (*13*, *14*). But there is a big gap between small (up to hundreds of meters) and large (thousands of kilometers) scales. Where exactly does competition disappear?

Gotelli *et al*. assembled an impressive data set on the distribution of birds at the scale of a country (Denmark). Based on the evidence and thinking just mentioned, they expected that competition would no longer be influential at this scale, and that habitat (specifically, the varying types of vegetation) would be most important in controlling where bird species live. Surprisingly, they found that habitat appeared unimportant, but that competition was important in determining which bird species lived where.

The results help to put a band on the scales at which competition is important. Gotelli *et al*. show that at the scale of a few hundred kilometers on a side, competition is important, but we already know (*13*, *14*) that at the scale of a biome (roughly 1000 km by 500 km in the two cases studied), competition is not very important (see the figure). This is an astonishingly precise scale-dependent statement of when competition is important and unimportant.

Thus, Gotelli *et al*. provide an example of how ecology can proceed. Rather than debating which of the four forces is most important in general, ecologists need to ask which force (or forces) is most important at a given scale (see the figure).The first step toward identifying scale dependencies of this kind is to collect more data on what controls species distribution and other variables (such as richness, productivity, and abundance) across scales. However, this will lead to many distinct scale diagrams such as that in the figure, one for each variable to be explained. This raises several new challenges and questions.

What is the minimum number of scale diagrams that we need? Can we, for example, collapse the richness-area and richness-productivity diagrams into one? Given that scale is relative to organisms—forces acting at a scale of 1 m are unlikely to be the same for bacteria and elephants—how can we rescale depending on the organism? Another factor is time. It has been suggested that processes that dominate at large spatial scales usually occur over large temporal scales (*2*). Is this true? And can the importance of different processes (the thickness of the bars in the scale diagram) be measured quantitatively? Statistical techniques and nested sampling designs that tell us how much variation occurs in the variable of interest at each scale could help to address these questions (*15*). The answers will help to put ecology on a more quantitative footing.

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ASTRONOMY

Hidden Growth of Supermassive Black Holes in Galaxy Mergers

Changes in the fraction of quasars hidden by gas and dust over cosmic time helps confirm models of the evolution and merger rates of galaxies.

Joel Primack

Black holes are found at the centers of massive galaxies. Although no light escapes from them, their presence can be revealed by the glow of surrounding gases compressed and heated by the driving force of the black hole's gravitation. This quasar emission ranges from low-energy radio waves to the highest-energy gamma-ray region of the electromagnetic spectrum. Quasar formation can be driven by galaxy mergers, which change the distribution of gas around the black hole. This process can also create stars that supernova and create interstellar dust that obscures our view of galactic centers in the visible to x-ray regions. On page 600 of this issue, Treister *et al*. (*1*) present an analysis of data from several space-based telescopes, showing that a greater fraction of quasars that formed in the early universe were obscured by dust, compared with its later stages. This is consistent with observational evidence on the evolution over cosmic time of gas-rich galaxies and a theoretical model for the rate at which they merge.

Like geologists and evolutionary biologists, astronomers reconstruct the past to understand the present. Landforms erode and only a tiny fraction of organisms fossilize, but all of the energy that was ever radiated by galaxies is still streaming through the universe and can be detected in some form. Some of this radiation is altered. For example, redshifting occurs because the wavelengths of photons stretch as the universe continues to expand, and some short-wavelength photons like x-rays and ultraviolet light are absorbed by dust and re-emitted at longer wavelengths. To figure out what happened in the cosmic past, we must see the entire electromagnetic spectrum, from the high-energy gamma rays to the long-wavelength radio waves. Fortunately, NASA's Great Observatories in space cover much of this wavelength range—x-rays (the Chandra X-ray Observatory), near ultraviolet to the near infrared (the refurbished

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