difference) of about 0.3% oil, and most had a difference of 0.1 to 0.2%. Only about 80% of the QTLs had effects in the same direction as the selection response (38 of 50 inbreds, 33 of 39 hybrids). For the others, the marker allele from the high oil-producing line was associated with low oil—however, alleles of small effect can be fixed by chance in the opposite direction to that of selection if few parents are selected (*5*). The detected QTLs, if segregating independently, could account for about half the genetic variance of the trait in the population and, by summing their effects, about half the divergence between the high and low oil-producing maize lines. The remaining QTLs are likely to have similar or smaller effects on oil concentration because those with large effects were unlikely to be missed given the degree of genome coverage and the size of the experiment.

Similar findings have also been obtained in a recent study on divergent selection lines of poultry. Andersson and colleagues (*6*) analyzed a large intercross of poultry lines that had been selected by Siegel in Virginia (*7*) for high and low body weight (at 8 weeks of age) for 40 generations and that differed in body weight by a factor of about 9. Although 13 QTLs were detected, none individually accounted for more than 3% of the body-weight variance in the F_2 generation, and each of these QTLs contributed only a small part of the divergence between the selected lines. Furthermore, the QTLs mainly had additive effects on body weight, as Laurie and colleagues found in their maize analysis.

In most other studies, however, QTLs of substantial effect have been detected— for example, QTLs for body size in poultry, not only in broiler × layer (*8*) crosses, but also in commercial broiler populations still segregating under intense selection (*9*). Some QTLs exerting large effects on the trait of interest found in mapping experiments have subsequently been identified as a single causative mutation—such is the case with the mutation in the gene encoding insulin growth factor–2 (IGF-2) in the pig, which alters muscle growth in these animals (*10*). Although such effects are real, effects of QTLs declared significant tend to be biased upward, and those of small effect are more likely to be missed (*4*). Models of the underlying distribution of gene effects indicate an exponential form, with numbers increasing as effects get smaller (*11*). Too much variation is therefore usually attributed to QTLs of large effect.

The recent studies of selected maize and broiler lines (*3*, *6*) were extensive, and the QTL effects identified were small. These appear to conform to the infinitesimal model of genes of small effect assumed in much quantitative genetic theory (*4*), which predicts the observed continuous steady responses to artificial selection. It is moot as to what defines a "small" effect, however. A maize line containing 0.2% oil in the kernel represents a difference of almost 1 SD between homozygotes in the maize base population; the largest effects detected in the chickens were almost as big (the variance in the F_2 was much higher than in the base). The continuing responses to selection, therefore, are not likely to be due mainly to continuing tiny changes in gene frequency predicted by the infinitesimal model; instead they may be due to the fixation of genes, including those arising by mutation after selection started (*12*, *13*), which have appreciable effects while segregating. The biological processes leading to oil concentration or chicken growth are obviously highly interactive, but genes that contribute to selection response must differ in effect when averaged over all other segregating genes. This may explain the Laurie *et al.* finding that their detected QTLs had approximately additive effects on oil production in maize. We have yet to discover how such QTLs work, but several of the SNPs associated with oil concentration were at candidate loci (*2*), so there are opportunities to find out. It is a challenge for geneticists to identify the genes and the molecular changes in them that cause these many small but important differences in quantitative traits. It is these small differences that generate variability in populations, providing fuel for change through the action of natural and artificial selection.

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Fig. S1

ECOLOGY

Untangling an Entangled Bank

David Storch, Pablo A. Marquet, Kevin J. Gaston

Biodiversity, the most conspicuous property of life, has fascinated generations of ecologists and evolutionary biologists. Part of this fascination arises from the fact that only a small fragment of this diversity has been described and catalogued, providing endless opportunities to speculate about the rest. Part arises from the sense that any regularities and general patterns in the biodiversity that we see today exist despite, or perhaps because of, the complexity of the processes and interactions that have driven the dynamics of biodiversity through time and space. In the *Origin of Species*, Charles Darwin made a specific appeal to this idea when he wrote his famous description of the complex ecology of a bank covered by dense vegetation: "It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us" (*1*).

Some general patterns in contemporary biodiversity do exist (*2*), and some of them are surprisingly simple. Take the species-area relationship, for example. The number of species increases with the area sampled, often linearly on a log-log scale, suggesting scale invariance. Such invariance is a prime area of investigation among those interested in complex systems. Many phenomena—ranging from the frequency distribution of species extinctions to allometric relationships between body size and rates of various biological processes (*3*)—reveal scale invariance, suggesting that simple rules underlie the structure and function of ecosystems. Some recent discoveries have shed light on the processes that define quantitative patterns in biodiversity. Dissecting these patterns was the goal of an international workshop held recently in Prague and co-organized by the Santa Fe Institute and the Center for Theoretical Study at Charles University (*4*).

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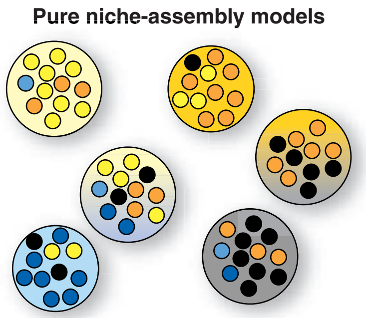
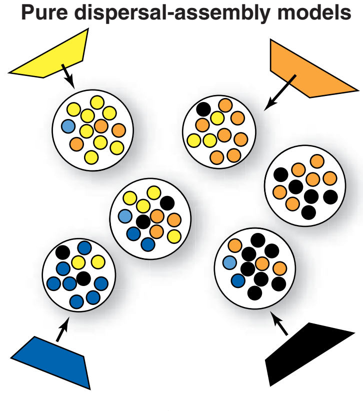
One major challenge is to relate patterns of species richness to the spatial distribution of individual species. Scale invariance of the species-area relationship, for example, has led to the development of models relating this phenomenon to the fractal spatial distribution of individuals, which is characterized by similar spatial patterns over several scales of resolution (*5*, *6*). But two questions arise. First, do species really exhibit fractal distributions? Using sophisticated analytical techniques applied at different scales of observation, Jack Lennon (Macaulay Institute, Aberdeen) and Fangliang He (University of Alberta) concluded that some species really do, but others do not, and that the level of fractality is related in part to the rarity of the species. Second, it is not clear why species' distributions should be fractal. Arnošt Šizling (Center for Theoretical Study, Prague) reported that a distribution that is indistinguishable from a fractal distribution may emerge from random processes of spatial aggregation on several scales of resolution. These findings suggest that fractals are simply a useful and analytically tractable approximation of the complex spatial aggregation of individuals that is responsible for patterns of biodiversity.





Biodiversity, species distribution and community composition. The spatial structure of species' distributions is driven by the availability of suitable habitats and of individuals that can potentially colonize a site. In niche-assembly models of community structure (**above**), suitable habitat is the major force driving species' distributions (background color refers to habitat suitability for species with respective colors). The same pattern of species' distributions and local community composition (**right**) can, however, be interpreted in terms of the spatial distribution of sources of potential colonists of different species (colored polynoms) without the need to consider habitat suitability. These "dispersal-assembly models" give a reasonable prediction of general properties of observed spatial species' distributions and community structure, but fail to predict details about the local species composition of communities. [Adapted with permission from a figure by Jerome Chave, Université Paul Sabatier]

Another widespread observation is a positive relationship between species richness and available energy (*7*). Andrew Clarke (British Antarctic Survey, Cambridge) noted that understanding the connection between species richness and energy has been hindered by ignoring the different meanings of the word "energy" implied in the variety of mechanisms invoked as explanations. One important measure of energy is temperature, which presumably influences species richness by increasing the rates of a variety of biological processes, leading to accelerated speciation (*8*). Although we do not yet have a comprehensive theory (*9*), Andrew Allen (University of New Mexico) suggested that the richness of ectothermic species (which cannot regulate their body temperature) could be predicted from environmental temperature according to fundamental laws connecting body size, temperature, and metabolic rate. Another measure of energy is environmental productivity, which affects the amount of resources available to a population, enabling an increase in the numbers of individuals and the persistence of more species. David Storch (Center for Theoretical Study, Prague) showed how a simple model of spatial dynamics, which assumes that the probability of species occurrence is proportional to productivity, accurately predicts the increase in bird species richness with increasing environmental productivity. Thus, species richness is influenced by available energy in different ways. It is possible that the diversity of ectotherms may principally be driven by temperature, whereas resource availability may be more important for endothermic animals that are able to regulate their body temperature.

The extent to which external constraints limit biodiversity has long been a topic of debate. Typically, those models relating the species-area relationship to the distribution patterns of individual species ignore interspecific interactions or limits to the number of species or individuals that can co-occur in an area. But every ecosystem must have some finite capacity in terms of the number of individuals or biomass that it can sustain. James Brown (University of New Mexico) pointed out that this leads to a zero-sum situation that may affect biodiversity dynamics as well as species distribution. Relationships between environmental energy and biodiversity imply that such limitations do exist, as demonstrated by David Currie (University of Ottawa). He emphasized that large-scale spatial variability of species richness is very well explained by climatic variables, making it unlikely that historical events were the driving force for the current distribution of biodiversity on Earth.

This "zero sum" rule has been assumed in neutral theories of biodiversity that attempt to explain major phenomena concerning species richness, abundance, and distribution in terms of stochastic population growth, migration, and speciation. The original neutral theory formulated by Stephen Hubbell (*10*) can be extended to incorporate realistic dispersal processes (Luis Borda-de-Água, University of Georgia) and can predict many biodiversity patterns—such as the relationship between the richness of native and alien species (Tomaš Herben, Charles University, Prague). However, current neutral models are insufficient to explain observed patterns of species' distributions. Jerome Chave (Université Paul Sabatier) reported that both stochastic spatial processes and environmental heterogeneity (see the figure) contribute to the species distribution patterns of neotropical trees. At least at small spatial scales, the way that species divide resources and habitat is crucial for understanding patterns of biodiversity (Mark Ritchie, Syracuse University).

That said, it is sometimes necessary to sacrifice knowledge about the biological peculiarities of species and communities to make models and theories tractable. Neutral theories, although unrealistic, provide insight into the general processes that govern species richness and distribution. John Harte (University of California, Berkeley) demonstrated that even simple static models without the addition of specific parameters could be useful. His model predicts a variety of patterns in the spatial distribution and abundance of plant species just on the basis of the frequency distribution of total species abundance and a simple probability rule that relates occupancy at one spatial scale to occupancy at smaller scales. Although its biological interpretation is unclear, this approach shows that different patterns are intrinsically linked to one another, and it is important to study these inevitable links, for they can provide the basis for understanding the dynamics of complex ecological networks (Neo Martinez, Pacific Ecoinformatics and Computational Ecology Lab, Berkeley).

As physicist Murray Gell-Mann (Santa Fe Institute) observed, it is interesting how little we actually know. Although sophisticated techniques of data analysis are now available and theory is developing rapidly, macroecology as an exact science is still in its infancy. Many patterns have been documented using only limited data sets, and even some phenomena assumed to be well documented (albeit with a multitude of potential explanations) may look different when examined from another perspective. For some taxa (such as the bacteria or protists), we have only weak evidence about basic patterns (Brendan Bohannan, Stanford University; Jessica Green, University of California, Merced). Obtaining better data across multiple scales and bridging the gap between theory and observation is crucial to achieve a better understanding of quantitative patterns in biodiversity. However, one thing is certain: Darwin's entangled bank is far more entangled than even he thought.

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ASTRONOMY

At the Heart of the Milky Way

T. Joseph W. Lazio and Theodore N. LaRosa

At a distance of just 25,000 light years (2.5×10^{20} m), the center of our galaxy, the Milky Way, provides the foundation for understanding phenomena in other galaxies. The central black hole (*1*) and regions of intense star formation in its vicinity can be probed at 100 times the resolution of even the nearest galaxies. Nonetheless, even the basic properties of a key component of the galactic center, its magnetic field, remain poorly understood.

Magnetic fields have the potential to transform, store, and explosively release energy, to transport angular momentum, and to confine high-energy plasmas into powerful jet flows. They are therefore central to astrophysical activity from stellar to galactic scales.

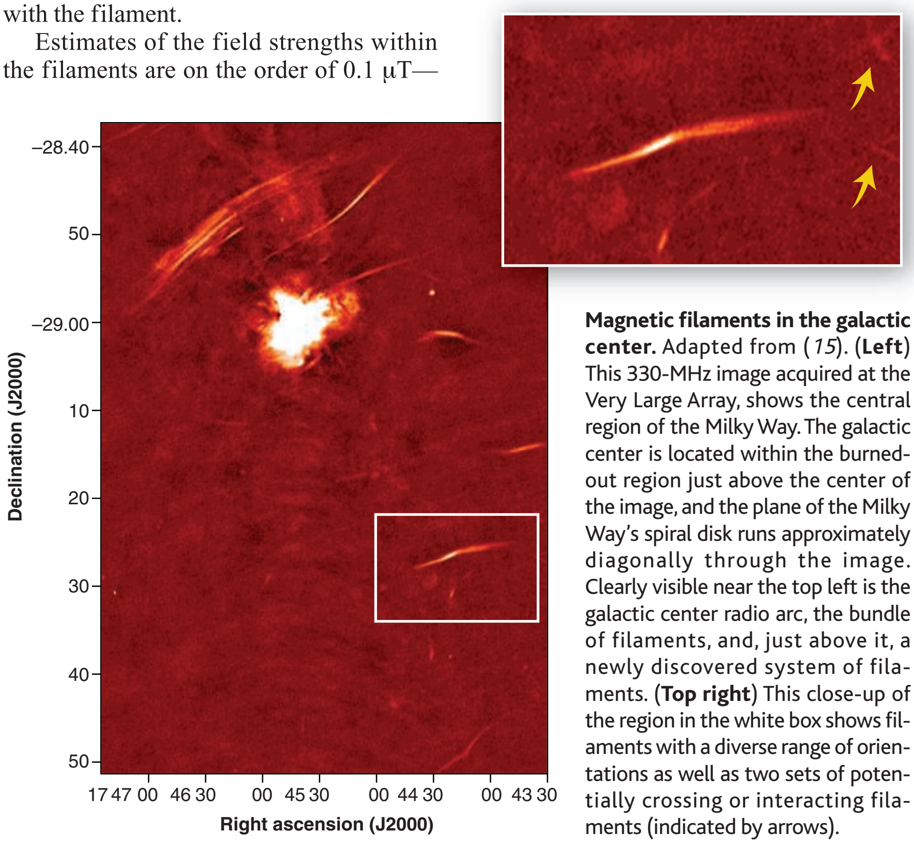
Magnetic fields are found throughout the Milky Way. Measurements suggest that the magnetic field in the spiral disk of our galaxy has two components, one globally ordered and the other random, with approximately equal strengths of ~0.3 nT (*2*); the globally ordered component generally follows the spiral arms of the galaxy. Key questions about the magnetic field in the galactic center are whether it is comparable in strength or much stronger than the field in the disk, and whether it is globally ordered or largely random.

About 20 years ago, the first high-resolution radio images of the galactic center (*3*) revealed numerous magnetic structures that are unique to the galactic center. The most striking of these is the galactic center radio arc, a series of parallel linear filaments, each of which is merely a few light years wide yet more than 100 light years long. Also observed were a number of isolated linear features that were variously referred to as streaks, threads, and filaments. The relation between these isolated filaments and the bundled filaments of the radio arc remains unknown.

These filamentary structures are distinguished by extreme length-to-width ratios (~10 to 100), nonthermal spectra, and a high intrinsic polarization (~30%, and in some cases approaching the theoretical maximum of 70% for synchrotron radiation). The polarization and nonthermal spectra are consistent with the filaments being produced by synchrotron radiation from relativistic electrons spiraling around a magnetic field. Detailed measurements of individual filaments have shown that the magnetic fields are aligned longitudinally with the filament.

Estimates of the field strengths within the filaments are on the order of 0.1 μT—nearly 1000 times the field strength in the galactic disk. In addition, the early studies (*4*) suggested that all filaments are essentially perpendicular to the galactic plane (within 20°). The picture that emerged was of a strong, dipolar magnetic field filling the galactic center. The filaments were explained as magnetic flux tubes, which were "lit up" by relativistic electrons that were accelerated by a local interaction such as magnetic field reconnection (*4*).

However, recent radio and submillimeter observations are challenging this simple picture. New wide-field images at radio wavelengths (between 20 and 90 cm, see the figure) have substantially increased the number of known filaments and have shown that the volume over which filaments occur is much larger than originally thought. With the larger number of filaments has come the discovery of filaments



Magnetic filaments in the galactic center. Adapted from (*15*). **(Left)** This 330-MHz image acquired at the Very Large Array, shows the central region of the Milky Way. The galactic center is located within the burned-out region just above the center of the image, and the plane of the Milky Way's spiral disk runs approximately diagonally through the image. Clearly visible near the top left is the galactic center radio arc, the bundle of filaments, and, just above it, a newly discovered system of filaments. **(Top right)** This close-up of the region in the white box shows filaments with a diverse range of orientations as well as two sets of potentially crossing or interacting filaments (indicated by arrows).

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