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Opinion

Tracking Animal Dispersal: From Individual Movement to Community Assembly and Global Range Dynamics

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Dispersal is one of the key processes in shaping distributional ranges and community assemblages, but we know little about animal dispersal at the individual, population, or community levels, or about how dispersal correlates with the establishment and colonization of new areas. This is largely due to difficulties in studying individual movements at the relevant spatiotemporal scale, leading to a gap between the direct study of dispersal and our understanding of the build-up of larger-scale biodiversity. Recent advances in tracking technology make it possible to bridge this gap. We propose a way to link movement, dispersal, ecology, and biogeography. In particular, we offer a framework to scale-up from processes at the individual level to global patterns of biodiversity.

Trends

New tracking technologies allow direct assessments of dispersal.

New tracking methodologies allow direct assessments of diversity build-up.

The Importance of Dispersal in Community Ecology and Biogeography

What determines species diversity is a central question in biology [1–3]. Ultimately, the distribution of diversity through space and time must reflect the net result of speciation, species interactions (i.e., competition, predation, and mutualism), extinction, and **dispersal** (see Glossary). While an understanding of these processes has been pursued for centuries, both independently and in combination, we are still far from a coherent understanding of how diversity patterns are generated. For decades, community ecologists have focused on the effects of species interactions on co-occurrence patterns (e.g., [4–8]), and recent work on speciation and extinction processes has led to significant progress in understanding species diversification (e.g., [9–12]). Dispersal, on the other hand, has proved more difficult to quantify. Nevertheless, dispersal is a key component of spatial ecology, and plays a central role in the redistribution of organisms, contributing to **colonization** of new areas, **range** shifts, and mixing of gene pools within and between populations [1,2,13–17].

This realization is not new. Over a century ago, Darwin [1] noted that variation in dispersal propensities and distances among species was a crucial determinant of their ability to undergo **range expansion**, and later studies have demonstrated how dispersal ability contributes to local abundance [18], range shifts [19], and patterns of species coexistence [20]. Despite this knowledge, dispersal hypotheses continue to be based on *ad hoc* interpretations from indirect evidence (e.g., phylogenies and current species distributions), largely as a consequence of the paucity of suitable empirical data (Box 1). In particular, the rarity and low detectability of ecologically significant dispersal events have impeded research on how species dispersal propensity and distance impact

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 http://dx.doi.org/10.1016/j.tree.2016.01.003

Box 1. Dispersal Assessments So Far

Population Genetic Approach

The majority of dispersal assessments have been and still are largely based on indirect lines of evidence. For example, the generation of molecular data has provided opportunities for determining dispersal. For population-level studies on recent timescales the use of molecular data may lead to direct estimates of dispersal if individuals can be assigned to at least one of their parents or to their population of origin [59]. However, genetic information from individuals is often used without the possibility of tracing the details of the actual movement. Consequently, the estimates of dispersal distances, effective dispersal rates, and effective numbers of migrants only reflect the successful dispersal events [60].

Phylogenetics and Ancestral Area Analyses

On evolutionary timescales, dispersal (often referring to dispersal and colonization combined) inference becomes even more contentious. Several recent attempts to estimate dispersal have relied on molecular phylogenetic analyses coupled with ancestral state reconstructions to trace the origin of particular clades of interest (e.g., [34,61]). This approach provides a way to determine the origin of a clade, and the sequential dispersal and colonization pattern for subclades, but comes with a series of assumptions and limitations. As a minimum, it ignores extinction, which can lead to grave misinterpretations of ancestral areas, origin, and evolutionary dispersal and colonization patterns. Moreover, such approaches can only identify the dispersal events that lead to establishment and colonization, and therefore we do not know if high levels of dispersal lead to higher probabilities of establishment and colonization, nor do we know if dispersal was in all directions but only led to establishment in one direction.

Biogeographic software, which can estimate the likelihood of different models of speciation, extinction, and dispersal (dispersal and colonization combined) simultaneously based on a phylogenetic tree hypothesis, provide a promising method for estimating dispersal [62]. However, such models should be confronted with empirical data and dispersal estimates should be validated by field data. Unfortunately, data on dispersal events are still largely absent hindering validation of dispersal parameters. At present, proxies (e.g., Kipps distance [63] or handwing index [64] for birds) for dispersal are used to identify dispersal ability.

Direct Determination of Movement and Dispersal

Direct evidence of movement and dispersal comes from the fitting of various individual identifiers, ranging from rings and color tags, to satellite transmitters, and even from visual observations following displacement [27,58]. Direct evidence is also generated through observations of birds or butterflies outside their range (vagrants). An additional important insight into the plasticity and evolutionary adaptability of dispersal capacity has been revealed in a series of detailed tracking studies of introduced cane toads in Australia. These studies have shown that dispersal kernels are highly dynamic during periods of range expansion because density effects and spatial assortment by dispersal ability ('spatial selection') drive the evolution of increased dispersal on the expanding front [50,51].

Glossary

Colonization: the outcome of successful dispersal and permanent establishment at the population level outside the range.
Dispersal: the combination of the three types of dispersal, all of which may or may not lead to permanent range expansion.
Dispersal distribution: probability distribution of the dispersal distance. This is synonymous with 'dispersal kernel'.
Establishment/settlement: successful permanent breeding at the population level at a new site outside the range following dispersal.
Long-distance dispersal: movement from birth site or breeding site to a new faraway breeding site. This represents the tail of the dispersal distribution.
Movement: any relocation of an individual in space.
Natal dispersal: movement of individuals from their birth site to their breeding site.
Range: the distribution of a taxon either defined by occupancy or extent.
Range contraction: the decrease in the range of a taxon.
Range expansion: the increase in the range of a taxon.
Seasonal migration: round-trip seasonal movement usually between breeding and non-breeding grounds.
Taxon cycle: the idea that taxa go through phases of range expansions and range contractions.

upon spatial ecology [21,22]. Our ability to test theories about dispersal is now poised for a major revolution. Recent technological advances make it possible to track thousands of organisms directly, from individual to population level, on a global scale [23–27]. These possibilities represent a major step forward for our ability to study dispersal and to understand its impact on the spatial patterns of species distribution and co-occurrence (Figures 1,2).

We focus here on how recent and future advances in direct tracking technologies can provide high-resolution dispersal data that will allow us to answer longstanding questions in spatial ecology (Figure 2). These data can only be obtained by using new technology that makes it possible to follow many individuals from different populations and different regions on a daily, year-round basis. Combining such novel real-time **movement**/dispersal data with other remotely sensed data on vegetation type, greenness, temperature and precipitation, as well as with biological data on life-history traits and phylogenetic relationships among species, we propose to start revisiting research questions in basic dispersal ecology, as well as to assess the evolution of dispersal. In this opinion article we draw heavily on dispersal studies on islands and archipelagos because studies in contiguous populations are much rarer and not as detailed in the understanding of patterns and processes.

The Role of Dispersal in Shaping Communities and Biogeographical Patterns

Historically, biogeography was divided by a major debate between two competing hypotheses to explain disjunct distributions of closely related species: vicariance and dispersal [28]. In the 1970s, cladistics and plate tectonic theory were coupled to give rise to a globally unified theory of