

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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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].

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

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.

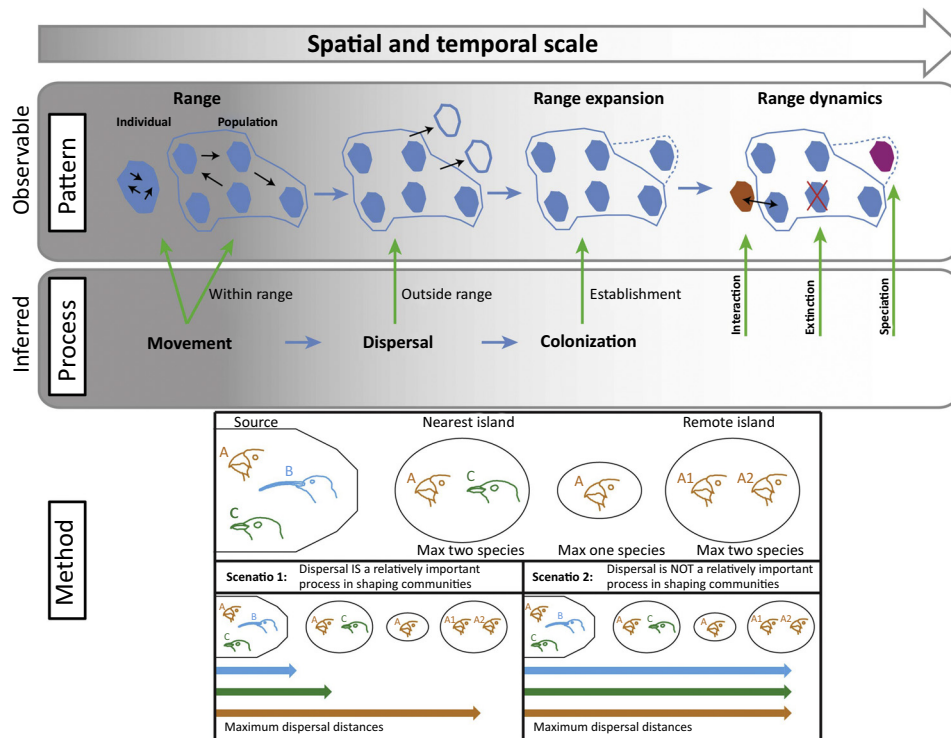
Range: the distribution of a taxon either defined by occupancy or extent.

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.



Trends in Ecology & Evolution

Figure 1. Conceptual Visualization of the Pattern, the Process, and the New Methods (Simplified Here and in More Detail in Figure 2) Proposed Here To Elucidate Dispersal From Small (Left) to Large (Right) Spatio-temporal Scales. Recent advances in direct tracking technologies make it possible to quantify dispersal via life-long global tracking of large numbers of individuals. Such high-resolution dispersal data will allow us to determine the relative importance of dispersal in shaping community assembly. For example, one can determine if dispersal is limited for some species, thereby limiting colonization of remote islands (scenario 1), or if all species disperse with equal probability and distance, in which case dispersal capacity is not the limiting factor for colonization. Instead, species may be limited by reduced ability to establish, for example owing to competitive interactions (scenario 2).

biogeography based exclusively on vicariance. By contrast, explanations that relied on dispersal across geographic barriers were considered unscientific because they could be invoked *ad hoc* to explain almost any given species distribution [29]. Dispersal has recently been resurrected as an explanatory process in historical biogeography, especially in the case of oceanic islands [30], and the previously polarized debate has adopted a more pluralistic approach [31,32]. While dispersal in this context is merely a debate about whether range expansion took place before or after the formation of a barrier, it is relevant because the debate at its core is also about the relative importance of dispersal in the formation of species and the shaping of communities.

Incorporating dispersal explicitly has already led us to question some well-established truisms in biogeography. For example, indirect evidence of dispersal and colonization in island systems suggests substantial movement of species both between continents and islands, among islands, and even re-colonization of continents (e.g., [33–35]). This challenges the traditional view that island taxa are sedentary and reluctant to cross water [36], and that islands are evolutionary dead-ends. There is compelling evidence that high levels of dispersal can lead to increased differentiation and high net diversification in insular systems [37,38]. However, Mayr and Diamond [39] suggested that a combination of intermediate dispersal coupled with high abundance (a measure of persistence) led to the highest levels of differentiation across archipelagos. This makes intuitive sense because high levels of dispersal may lead to continuous

Box 2. Darwin's Finches on Daphne Major Island

Darwin [1] suggested that the many species of finches on the Galápagos Islands originated from a single colonization event and subsequent adaptive evolutionary divergence. While it is clear today that his idea was largely correct, exactly how such diversification occurs remains difficult to answer. A long-term study of Darwin's finches on Daphne Major Island (where *Geospiza fortis* and *G. scandens* breed) in the Galápagos Archipelago, initiated in 1973 by Peter and Rosemary Grant [65], has provided many important insights into the dynamics pertaining to dispersal and speciation. Most individuals (>95%) on this island have been genotyped and color-marked, allowing detailed understanding of the movements and fates of individual finches.

Knowing the individual fates of finches on the island has allowed Grant and Grant [65] to discover how an immigrant medium ground (*Geospiza fortis*) finch arrived on the island, and after a period of 28 years resulted in a single reproductively isolated lineage. The immigrant was larger than the conspecific on the island and was not a pure medium ground finch (carrying some *Geospiza scandens* alleles). Song is culturally transmitted, and the immigrant sang an aberrant song that led individuals of this line mate with each other during a severe drought when large-billed mates were rare. Thus, divergence was initiated in allopatry and, during the secondary contact phase, speciation was aided by several stochastic elements that could only be revealed with genotyping combined with morphological features requiring individual recognition.

Over 18 years, only four immigrants bred. They were identified using genotyping, but how immigrants interact with the local population requires long-term individual following. The Grants had knowledge of individuals from color-marking, but not all individuals were marked and certainly only a small part of their life was mapped. Imagine if they had access to information on where each bird went and with whom it mated unsuccessfully. Perhaps even more important: how often individuals actually flew to different islands and in which cases successful colonization resulted. This knowledge is necessary if we want to understand the processes of dispersal, colonization, and ultimately also speciation.

mixing of populations, thereby restricting differentiation. On the other hand, high abundance, which is considered equivalent to persistence, is equally important because it allows sufficient time for population to differentiate. Recently, Weeks and Claramunt [40] used the handwing index of birds as a proxy for dispersal capacity to demonstrate that dispersal has inhibited avian diversification in Australasian archipelagos, and generally ambiguous results have emerged from the studies to date that relied on anecdotal evidence and indirect assessments of the recurrence and frequency of dispersal. This ambiguity has clouded our understanding and interpretation of biogeographical patterns.

At the scale of community ecology, on the other hand, the importance of dispersal is widely accepted, although attempts to directly quantify dispersal are rare (Box 2 gives an example of how detailed knowledge of dispersal in a community has shed light on species interactions and speciation). In recent years, studies of community assembly have had an increased focus on the role of regional species pools (which we define as the set of species that could potentially disperse to a local community over ecological time) and on how environmental filters must interact with the species pool to shape the species composition of local communities [5–7]. However, while dispersal is recognized as important for the build-up of communities, conclusions about dispersal have generally been based on indirect inference, and little data on the direction and prevalence of dispersal events are available.

Armed with high-quality direct dispersal data, we can revisit longstanding questions in ecology and biogeography. For example, Diamond [4] investigated the distribution of birds across the Bismarck Archipelago, and suggested that the composition of species assemblages was a direct result of competitive exclusion, based on the observation of 'checkerboard' distributions where closely related taxa never occupy the same island. Connor and Simberloff [41] rejected Diamond's evidence by demonstrating that checkerboard distributions are predicted to be common even under a null model assuming random distributions of species. This led to a longstanding debate on the role of species interactions in community assembly that was never fully resolved. With multiple movement tracks over the lifetime of individuals, it will be possible to tease apart dispersal and colonization (e.g., dispersal may be frequent but colonization infrequent) and also to assess the relative importance of dispersal and colonization versus species

Observable pattern of distribution on three islands	Without knowledge of dispersal one might conclude:
<p>(A) Equal dispersal probability – assuming dispersal to an island with open space leads to colonization</p> <p>Source Nearest island Remote island</p> <p>Max two species Max one species Max two species</p>	<p>(i) Species B is a great disperser of remote islands (ii) Species C is a poor disperser and can only reach nearest island (iii) Species B and C cannot coexist</p>
<p>(B) Unequal dispersal probability: $A > B$; $A > C$; $B = C$ – assuming dispersal to an island with open space leads to colonization</p> <p>Source Nearest island Remote island</p> <p>Max two species Max one species Max two species</p>	<p>(i) Species A is superior to other functional groups (ii) Species B and C cannot coexist (iii) Only species A can colonise and persist on remote islands</p>
<p>(C) Unequal dispersal probability: $A > B$; $A > C$; $B = C$ – assuming dispersal to an island with open space leads to colonization With sufficient time island populations may speciate</p> <p>Source Nearest island Remote island</p> <p>Max two species Max one species Max two species</p>	<p>(i) Species B does not disperse (ii) Species A and C outcompete species B (iii) Species A is superior to other functional groups</p>
<p>(D) Equal dispersal Unequal colonization probability: $A > B$; $A > C$; $B = C$</p> <p>Source Nearest island Remote island</p> <p>Max two species Max one species Max two species</p>	<p>(i) Species A is the best disperser (ii) Species B and C cannot coexist (iii) Only species A can colonise and persist on remote islands</p>
<p>(E) Equal dispersal – assuming dispersal to an island with open space leads to colonization Dispersal distance matters – stepping stones</p> <p>Source Nearest island Remote island</p> <p>Max two species Max one species Max two species</p>	<p>(i) Species C is the best disperser (ii) Species B is a poor disperser (iii) Species A and C outcompete species B</p>
<p>(F) Equal dispersal – assuming dispersal to an island with open space leads to colonization species A and B cannot co-occur random extinction</p> <p>Source Nearest island Remote island</p> <p>Max two species Max one species Max two species</p>	<p>(i) Species B cannot disperse (ii) Species C is a great disperser (iii) Interaction between species A and C is mutually beneficial</p>

Trends in Ecology & Evolution

Figure 2. New Technology Aimed at Tracking Dispersal, as Outlined in this Paper, Can Enable the Collation of Data To Tease Apart Dispersal And Colonization, Thereby Allowing Us To Disentangle the Relative Roles of the Processes that Underlie Observed Distributions, and Ultimately Answer Some Outstanding Questions in Ecology And Island Biogeography. To the left in each panel is a source with three species, which can colonize the three islands to the right, which have different diversity capacities. (A) All birds can disperse to any island with equal probability. For simplicity it is assumed that dispersal to an island with open space leads to establishment and colonization. Data on direct dispersal would allow us to determine if all species have equal dispersal probabilities, if dispersal probabilities are the same irrespective of the distance to an island, and whether dispersal to an island does lead to establishment. Without knowledge of dispersal one might conclude differently. (B) Species A has a higher probability of dispersing than species B and C. For simplicity it is assumed that dispersal to an island with open space leads to establishment and colonization. Data on direct

interactions, ultimately allowing us to disentangle the relative roles of processes in generating the observed distributions (Figure 2).

Tracking Dispersal Directly

New technology allows large numbers of individuals to be tracked [24]. We focus on opportunities to utilize these innovations to obtain direct measures of dispersal: specifics about the technological advances are described in detail elsewhere (e.g., [23,27]). We propose that direct tracking approaches at different spatial scales will provide data that can be used to address questions pertaining to the spatiotemporal evolution of species ranges. We generally focus on animals that have high dispersal potential as models for studying dispersal and colonization. Because questions related to dispersal and colonization are population-level processes, it is advantageous to study large numbers of individuals, and that the generation times of the species studied are not too long. Shorter generation times allows individuals to be followed more easily throughout their lifetimes to determine if there are differences between juveniles and adults, and how dispersal capacity changes over several generations. Of course, tagging of animals has ethical implications, especially when conducting larger-scale studies as we suggest. For useful inference from tracking, it is of paramount importance that any effects on individuals are minimal. Thus, great care must be taken to establish tagging methods with minimal impact.

Local and Regional Movements

Obtaining local movement data is a necessary starting point to determine large-scale dispersal. Local movement data provide basic knowledge of movement patterns of different individuals and sexes, as well as across seasons. Moreover, this approach provides contextual data on the timing and direction of movement, and the potential effect of varying weather conditions (e.g., [42,43]). To assess local movements, radio telemetry (for example by automated receiver units, e.g., [44]), or GPS data-loggers using GSM systems (global system for mobile communications) are ideal. The latter is so far limited to larger species (>500 g), while traditional radio telemetry can be operated on relatively small organisms (down to 10 g) [23,43]. Potentially, the beacon or transponder tags that can be detected by weather radars [23] could be used to study continental-scale dispersal if extended to a larger network of radars. Location-based tracking systems generally do not follow the fate of individuals dispersing out of the study area. For this purpose, we need long-term global tracking of tagged individuals.

Global Movements

Except for the excessive cost, detailed global tracking is possible today for a wide range of larger species [23,24]. However, to study long-distance movements and dispersal of smaller animals, the best commercially-available tracking devices are light-weight (5 g), durable (years) satellite

dispersal would allow us to determine if species have different dispersal probabilities, and if a higher dispersal capacity also leads to a higher probability of colonization. Without knowledge of dispersal one might conclude differently. (C) Species A has a higher probability of dispersing than species B and C and, with sufficient time, a species may diverge on an island. Because species A is a better disperser and colonizer, it becomes dominant across the islands. Without knowledge of dispersal and colonization abilities one might conclude differently about the underlying processes that determine community assembly. (D) All three species disperse with equal probability but species A is better at establishing. This leads to the same distributional pattern as in scenario B. Direct data on dispersal would tease apart dispersal and colonization. (E) All three species have the same probability of dispersing. For simplicity it is assumed that dispersal to an island with open space leads to establishment and colonization. However, distance matters, and it is easier to disperse to an island that is close to the source than to a remote island. Once species A and C have colonized the closest island, there is a higher probability of those two species dispersing to and colonizing the more remote islands. Direct dispersal data would provide such insights. (F) All species disperse with equal probability and, for simplicity, it is assumed that dispersal to an island with open space leads to establishment and colonization. However, in this scenario species A and B cannot coexist. We also introduce random extinction. With competition and extinction the introduced distribution patterns become more complex to interpret, but with knowledge of dispersal and establishment probabilities it may be possible to determine the relative importance of extinction and competition in shaping communities.

receivers, based on relay systems where data are collected and retrieved by satellites, that can transmit data directly in real-time (e.g., [45,46]). The accuracy of location estimates of these tags is generally within kilometres, which is presumably often precise enough to estimate dispersal. These methods are costly, leading to sample sizes often far below what is needed to estimate dispersal. With costs expected to decrease, however, these tags are becoming accessible to researchers. This represents a new dawn for animal tracking because these tags can provide data for local, regional, and global movement, and most crucially they collect data for dispersal events that do not lead to **establishment** and colonization [24]. Many tags are solar-powered with the potential to transmit locations throughout the lifetime of an animal. Such lifelong tracks will make it possible to detect short-term changes in distributional ranges. However, the continued challenge will be to bridge the gap between individual movements and population dispersal events up to global-range dynamics on evolutionary timescales.

Scaling from Individual Dispersal to Global Evolution

By integrating dispersal data with other existing data (e.g., phylogeny, distribution, **seasonal migration**, greenness, temperature, and precipitation), we will be able to answer fundamental questions about how dispersal governs various aspects of geographical species ranges, such as (i) size, (ii) shape, (iii) boundaries, and (iv) geographical position. In addition, we will also be able to shed light on how dispersal affects species ranges over time (i.e., how points i–iv change temporally), for example, via continuous range expansions and **range contractions** (i.e., **taxon cycles**).

It is currently uncertain how common dispersal, establishment, and colonization of new areas (i.e., range expansions) are, and whether a high dispersal capacity often leads to range expansion. The complexity of processes involved in species range dynamics is shown schematically in Figure 1. The dispersal distances of individuals collectively form a probability distribution, where longer dispersal events tend to be progressively less likely. In addition, whereas dispersal events within the central part of the probability distribution are somewhat predictable [47], the rare events in the tail of the dispersal kernel are difficult to predict [48]. Nevertheless, **long-distance dispersal** events from the long tails of a **dispersal distribution** are generally thought to be important determinants of colonization dynamics and genetic connectivity [49].

The new tracking developments make it possible to follow large numbers of individuals through their entire lifetime, and thus allow improved estimation of these rare dispersal events. For example, with enough individuals, relatively rare dispersal and establishment outside the current range (i.e., colonization) can be tracked. Furthermore, by tracking the individual offspring of these new colonizers, we can monitor the persistence of newly established populations and changes in broad distribution ranges. It will also be possible to determine the movement between occupied communities to reveal the role for dispersal in meta-community dynamics.

Range contractions and expansions are generating increasing interest because they are important for understanding how species shift distributions in response to climate change. Tracking individuals from different parts of a species range (e.g., center and perimeter) will allow us to document and understand these dynamics in unprecedented detail. For instance, we will see whether dispersal ability of individuals is expressed differently when a population is stable, expanding, or contracting. This elucidates the lability of dispersal and the speed at which ranges can change both on average and in extreme cases [50,51].

At the largest scales, these new technologies pave the way towards understanding the evolutionary origin and determinants of dispersal ability itself. Individuals and species differ in the traits that determine dispersal ability and propensity (e.g., [52,53]), as well as in the traits underlying establishment [54]. Consequently, our understanding of the role of natural selection in

shaping dispersal remains limited [13,55,56]. In the future, dispersal capacity will be quantified directly and mapped onto phylogenies, and we will be able to account for changing dispersal capacities associated with functional traits and short-term variation in climate and habitat. Another promising application of these data will be to simulate the evolutionary dynamics of ranges using real dispersal data, which will help to clarify the gradual build-up of communities at local and regional scales.

Quantifying Dispersal and Its Influence on Range Dynamics – How Can It Be Done?

Comparative tracking studies should be explicitly designed for testing hypotheses in biogeography and would allow us to quantify spatiotemporal dispersal patterns for species with different attributes. We provide here two comparative examples of how direct dispersal data will allow an informed discussion of the underlying processes that are responsible for the generation of diversity patterns (see also Figure 2).

Do Individuals of a Young Widespread Species Have Higher Dispersal Capacity than Individuals of an Old Single Island Endemic Species

Without knowledge of dispersal one would assume that a young widespread species has dispersed widely, thereby colonizing a large area within a short time-frame. Thus, such a species is expected to have a high dispersal capacity. By contrast, an old species that is restricted to a single small island must have either been restricted to this particular island for a long time or its range has contracted over time. Thus, this species is assumed to have a low dispersal capacity. However, it may be that the single island endemic does disperse widely but then fails to establish in new areas, for example due to competition. Conversely, the widespread species may not disperse as much as expected but may be very good at establishing when it does disperse, perhaps because of particular advantageous functional traits. Direct dispersal data would give us the answer.

Are Generalists Better Dispersers and/or Colonizers than Specialists?

Generalists are intuitively thought to be better colonizers than specialists because their flexible diet allows the exploitation of many different food resources in new environments. However, specialists such as frugivores may be better dispersers because they must continuously move to find their preferred food. In 1961, Edward Wilson [57] proposed that island communities are shaped through taxon cycles. Taxon cycles are generally described as consisting of four main stages: an initial expansion stage (i) in which a taxon colonizes all islands within an archipelago, but largely confined to coastal habitats. In the next stage (ii) geographic expansion slows down and phenotypic differentiation takes place. At this stage differentiated populations become more specialized and start to inhabit higher elevations. In the next stage (iii) populations on the smallest islands become extinct, and in the final stage (iv) the distributional range has contracted dramatically and only populations on a few (or single) large and topographically high islands persist. The question is: do generalists disperse more than specialists, or are they simply better at establishing new populations? Does dispersal capacity change over generations? How plastic is dispersal capacity? Direct dispersal data would give us the answer.

By obtaining life-long tracks from individuals and their offspring it will be further possible to elucidate when dispersal is most likely to take place during a lifetime and, equally importantly, when during a lifetime is dispersal more likely to lead to establishment. For example, a species may disperse mostly during its first year (**natal dispersal**) and less when it is adult. However, the probability of establishment may be positively correlated with age and thus negatively correlated with dispersal. Long-distance dispersal may be equally likely for juveniles and adults, but perhaps only leads to successful establishment for generalists. It is also possible that species inhabiting coastal areas are more likely to be exposed to long-distance dispersal than birds that

inhabit interior forest but, in the rare event that an interior forest bird is relocated to another interior forest via long-distance dispersal, that this is more likely to lead to establishment than when the coastal species gets relocated via long-distance dispersal to a faraway coastal locality. Direct dispersal data would allow us to tease apart the relationship between dispersal, establishment, and colonization.

One promising avenue is translocation experiments, which would allow us to follow the fate of individuals after an ‘artificial dispersal event’. Displacement events could be simulated by relocating individuals and tracking their subsequent response (e.g., [42,58]). With this we can look for different vulnerabilities to such events among range-restricted specialist taxa and widespread generalist taxa, which we might expect to respond differently. Moreover, there is the possibility of following particular ecological and geographical conditions in parallel with tracking individuals, which will provide information as to how individuals follow particular environmental conditions [24].

Clearly, multiple factors influence establishment and colonization, but until we know about dispersal, we are searching in the dark for the underlying mechanisms that determine community build-up. For birds where good data on phylogenies and distributions exist, it is possible to test community build-up hypotheses for several closely related species with different distributional attributes. For example, within genera there may be both widespread and range-restricted taxa. Extending this further, one could investigate differences in dispersal capacity between species with different life-history traits and functional traits. A detailed understanding of the differences in movement between species, and how these relate to dispersal and successful colonization, will provide important information as to the predictability of dispersal and the influence on the build-up of diversity.

Concluding Remarks: Bridging the Gap between Individual Movement and Global Range Dynamics, and Further Implications

New tracking technologies provide a way forward by allowing detailed mapping of the movements of thousands of individuals over their entire lifetimes. As a first step, this makes it possible to generate realistic dispersal kernels and provides an understanding of directionality and the extent of the tail of the dispersal distribution (i.e., the recurrence of long-distance dispersal). This will provide important parameter estimate with variance estimates which can be used in modeling frameworks.

Even more importantly, we believe that a significant leap forward can be gained in ecology, evolution, and biogeography from tracking dispersal directly, as is currently underway in the field of seasonal migration research. Such approaches will help us elucidate the processes behind the patterns (Figure 1) and will bring us closer to resolving longstanding paradoxes and conundrums pertaining to the evolution and redistribution of life on Earth (Figure 2). Ultimately, this will move the study of dispersal ecology and dispersal in biogeography away from anecdotal and indirect evidence, and towards a field based on high-resolution empirical evidence.

Finally, we note that current climate change alongside global land-use changes will alter living conditions for life on Earth within the next century, and dispersal is one of the few possible ways for species to adjust to these changes. Therefore, achieving a better understanding of dispersal is crucial for the success of current and future conservation initiatives.

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References

- Darwin, C. (1859) *The Origin of Species by Means of Natural Selection*, John Murray
- Wallace, A.R. (1876) *The Geographical Distribution of Animals; with a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*, Macmillan
- Pennisi, E. (2005) What determines species diversity? *Science* 309, 90
- Diamond, J.M. (1975) Assembly of species communities. In *Ecology and Evolution of Communities* (Cody, M.L. and Diamond, J.M., eds), pp. 342–444, Harvard University Press
- Lessard, J.P. et al. (2012) Inferring local ecological processes amid species pool influences. *Trends Ecol. Evol.* 27, 600–607
- Mittelbach, G.G. and Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends Ecol. Evol.* 30, 241–247
- HilleRisLambers, J. et al. (2012) Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Syst.* 43, 227–248
- Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
- Höhna, S. et al. (2011) Inferring speciation and extinction rates under different sampling schemes. *Mol. Biol. Evol.* 28, 2577–2589
- Purvis, A. (2008) Phylogenetic approaches to the study of extinction. *Annu. Rev. Ecol. Syst.* 39, 301–319
- Ricklefs, R. (2007) Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* 22, 601–610
- Morlon, H. et al. (2011) Reconciling molecular phylogenies with the fossil record. *Proc. Natl. Acad. Sci. U.S.A.* 108, 16327–16332
- Clobert, J. et al., eds (2012) *Dispersal Ecology and Evolution*, Oxford University Press
- MacArthur, R.H. and Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387
- MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- Simpson, G.G. (1940) Mammals and land bridges. *J. Washington Acad. Sci.* 30, 137–163
- Wiener, P. and Tulljapurkar, S. (1994) Migration in variable environments: exploring life history evolution using structured population models. *J. Theor. Biol.* 166, 75–90
- Holt, R.D. (1985) Population dynamics in two-patch environments: some anomalous consequences of optimal habitat distribution. *Theor. Popul. Biol.* 28, 181–208
- Dytham, C. (2009) Evolved dispersal strategies at range margins. *Proc. R. Soc. B* 276, 1407–1413
- Holyoak, M. et al., eds (2005) *Metacommunities: Spatial Dynamics and Ecological Communities*, University of Chicago Press
- Nathan, R. (2001) The challenges of studying dispersal. *Trends Ecol. Evol.* 16, 481–483
- Koenig, W.D. et al. (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.* 11, 514–517
- Bridge, E.S. et al. (2011) Technology on the move: recent and forthcoming innovations for tracking migratory birds. *Bioscience* 61, 689–698
- Kays, R. et al. (2015) Terrestrial animal tracking as an eye on life and planet. *Science* 348, 6240
- Hussey, N.E. et al. (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348, 1256–1262
- Tottrup, A.P. et al. (2012) Drought in Africa caused delayed arrival of European songbirds. *Science* 338, 1307
- Wikelski, M. et al. (2007) Going wild: what a global small-animal tracking system could do for experimental biologists. *J. Exp. Biol.* 210, 181–186
- Zink, R.M. et al. (2000) The shifting roles of dispersal and vicariance in biogeography. *Proc. R. Soc. B* 267, 497–503
- Nelson, G. and Platnick, N.I. (1981) *Systematics and Biogeography: Cladistics and Vicariance*, Columbia University Press
- de Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol. Evol.* 20, 68–73
- Ronquist, F. (1997) Dispersal–vicariance analysis: a new approach to the quantification of historical biogeography. *Syst. Biol.* 46, 195–203
- Heaney, L.R. (2007) Is a new paradigm emerging for oceanic island biogeography? *J. Biogeogr.* 34, 753–757
- Filardi, C.E. and Moyle, R.G. (2005) Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* 438, 216–219
- Jönsson, K.A. et al. (2011) Major global radiation of corvid birds originated in the proto-Papuan archipelago. *Proc. Natl. Acad. Sci. U.S.A.* 108, 2328–2333
- Jönsson, K.A. and Holt, B.G. (2015) Islands contribute relatively high amounts of evolutionary diversity in passerine birds. *Nat. Commun.* 6, 8538
- Diamond, J.M. (1981) Flightlessness and fear of flying in island species. *Nature* 293, 507–508
- Fritz, S.A. et al. (2012) Diversification and biogeographic patterns in four island radiations of passerine birds. *Evolution* 66, 179–190
- Moyle, R.G. et al. (2009) Explosive Pleistocene diversification and hemispheric expansion of a ‘great speciator’. *Proc. Natl. Acad. Sci. U.S.A.* 106, 1863–1868
- Mayr, E. and Diamond, J.M. (2001) *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography*, Oxford University Press
- Weeks, B.C. and Claramunt, S. (2014) Dispersal has inhibited avian diversification in Australasian archipelagos. *Proc. R. Soc. B* 281, 20141257
- Connor, E.F. and Simberloff, D. (1979) The assembly of species communities – chance or competition? *Ecology* 60, 1132–1140
- Thorup, K. et al. (2007) Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18115–18119
- Thorup, K. et al. (2011) Juvenile songbirds compensate for displacement during migration. *PLoS ONE* 6, e17903
- Kays, R. et al. (2011) Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *Comput. J.* 54, 1931–1948
- Klaassen, R.M.G. et al. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J. Anim. Ecol.* 83, 176–184
- Willems, M. et al. (2014) Narrow-front loop migration in a population of the common cuckoo *Cuculus canorus*, as revealed by satellite telemetry. *PLoS ONE* 9, e83515
- Lowe, W.H. and McPeck, M.A. (2015) Is dispersal neutral? *Trends Ecol. Evol.* 29, 444–450
- Vellend, B.M. (2010) Conceptual synthesis in community ecology. *Quart. Rev. Biol.* 85, 183–206
- Cain, M.L. et al. (2000) Long-distance seed dispersal in plant populations. *Am. J. Bot.* 87, 1217–1227
- Lindström, T. et al. (2013) Rapid shifts in dispersal behavior on an expanding range edge. *Proc. Natl. Acad. Sci. U.S.A.* 110, 13452–13456
- Perkins, T.A. et al. (2013) Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecol. Lett.* 16, 1079–1087
- Harrison, R.G. (1980) Dispersal polymorphisms in insects. *Annu. Rev. Ecol. Syst.* 11, 95–118
- Sorensen, A.E. (1978) Somatic polymorphism and seed dispersal. *Nature* 276, 174–176

54. Clobert, J. *et al.* (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* 12, 197–209
55. Levin, S.A. *et al.* (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Evol. Syst.* 34, 575–604
56. Ronce, O. (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* 38, 231–253
57. Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95, 169–193
58. Moore, R.P. *et al.* (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecol. Lett.* 11, 960–968
59. Manel, S. *et al.* (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends Ecol. Evol.* 20, 136–142
60. Broquet, T. and Petit, E.J. (2009) Molecular estimation of dispersal for ecology and population genetics. *Annu. Rev. Ecol. Evol. Syst.* 40, 193–216
61. Matzke, N.J. (2014) Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* 63, 951–970
62. Goldberg, E.E. *et al.* (2011) Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst. Biol.* 60, 451–465
63. Kipp, F.A. (1959) Der Handflügel-Index als flugbiologisches Mass. *Vogelwarte* 20, 77–86
64. Claramunt, S. *et al.* (2012) High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc. R. Soc. B* 279, 1567–1574
65. Grant, P.R. and Grant, B.R. (2014) *40 Years of Evolution: Darwin's Finches on Daphne Major Island*, Princeton University Press