

Closing the seed dispersal loop

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Seed dispersal links the end of the reproductive cycle of adult plants with the establishment of their offspring, and is widely accepted to have a profound effect on vegetation structure. Confirming and quantifying this effect, however, has proven to be a challenge. Recent research on animal-mediated seed dispersal has brought us closer to this goal: ecologists have been explicitly examining the processes that mediate seed deposition and seedling recruitment. Exciting new techniques, such as the analysis of stable isotope ratios and molecular genetic markers, are making it possible to relate dispersed seeds and seedlings back to parent plants. Meanwhile, evidence from plant demography research is revealing that seed dispersal might have an important role in determining patterns of tree diversity and distribution. The continued synergy between seed dispersal research and the study of plant demography should help researchers link seed dispersal and adult vegetation structure, closing the seed dispersal loop.

Because SEED DISPERSAL (see Glossary) links the end of the reproductive cycle of adult plants with the establishment of their offspring (Box 1), it is widely recognized as having a profound effect on vegetation structure. Seed dispersal dynamics presumably influence plant processes ranging from colonization of new habitats to maintenance of diversity, with implications for succession, regeneration and conservation. However, for several reasons, establishing the extent of this influence has been difficult, causing one researcher to lament that ‘the implied marriage of animal foraging with plant demography is rarely consummated’ [1].

Why has it been so challenging to link seed dispersal with adult vegetation structure? A primary reason is that the SEED DISPERSAL CYCLE is complex: there are many intermediary steps and processes between seed production and the recruitment of adult trees (Box 1). Historically, researchers have tended to focus on just one or two of the processes and then have tried – and have usually failed – to establish the link by extrapolating over the unstudied processes [2]. A second reason is that traditional seed dispersal studies have been too short: fruit availability and disperser abundance can vary both seasonally and yearly [3–5], almost certainly driving changes in dispersal dynamics on those timescales. Although the short time frame of most seed dispersal studies is probably adequate to investigate seasonal variation, interannual variation and its subsequent effects on vegetation structure are likely to have been underestimated. A final reason is that dispersal can be hard to follow: it is inherently difficult for researchers to track seeds from parent plants to their site of deposition to determine their fates in those locations. The rare – but potentially very influential – long-distance dispersal events are especially hard to measure. All seed dispersal is not created equal: seeds

deposited far from parent plants are likely to have different survival and germination rates than those deposited nearby, and might have a disproportionate influence on the resulting vegetation [6]. However, because these events have been difficult to detect and track, their influence remains largely unquantified.

Recent advances are helping to overcome these challenges. Researchers have addressed the complexity of the seed dispersal cycle by widening the scope of their investigations to examine explicitly some of the previously understudied processes. In addition, longer term seed dispersal studies are now coming to fruition, yielding a deeper understanding of how seed dispersal dynamics fluctuate over time and how that might impact resulting vegetation. The application of new techniques, such as the analysis of molecular genetic markers and chemical isotopes, shows great promise in helping to match dispersed seeds and seedlings with parent plants, allowing easier detection of long-distance dispersal events. Finally, plant demography studies are yielding important results that indicate that seed dispersal can play a crucial role in the creation and maintenance of plant diversity.

Here, we review these advances, and explore how they are contributing to our understanding of the relationship between seed dispersal and vegetation structure. We have restricted our discussion to animal-mediated seed dispersal operating on ecological timescales, but we expect that some of the findings are germane to seed dispersal by other means (wind, water, and/or intrinsic explosive mechanisms). Finally, we suggest directions for future research that will help link seed dispersal and adult plant composition, thus closing the seed dispersal loop.

Linking seed dispersal and seedling distribution

Although scientists as early as Darwin [7] acknowledged the importance of seed dispersal, the scientific study of seed dispersal did not gain momentum until the early 1980s [8]. Initially, researchers tended to start with primary dispersal and work forwards (Box 1): asking how and why fruits were removed from plants and where they were dropped. Consequently, much has been learned about frugivore behavior, including diet choice, fruit removal rates, and tree visitation rates [4,8–10]. Considerable efforts have also been expended in the study of germination of experimentally placed seeds, both in germination gardens [11], and at prescribed distances from parent plants [12,13]. However, few of these studies were able to establish robust empirical

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Box 1. The seed dispersal cycle

It is important to distinguish between the process of seed dispersal, whereby seeds are moved from parent plants, and the seed dispersal cycle, which is a succession of processes (including the process of seed dispersal) whereby seeds produced by an adult plant are moved from the parent plant, germinate to seedlings, and recruit to adult plants, influencing the fruit and seed availability of the next generation (Fig. 1). Although seed dispersal is only one of the many processes in this cycle, we have chosen to call it the seed dispersal cycle to emphasize its role as a 'demographic bridge' linking the end of the reproductive cycle of adult plants with the establishment of their offspring [a]. Not all seeds

are dispersed, and most dispersed seeds do not complete the seed dispersal cycle. However, the parents that produce seeds that successfully complete the cycle pass a disproportionate amount of their genes to the next generation and thus have a disproportionate influence on the vegetation composition of the succeeding generations.

Reference

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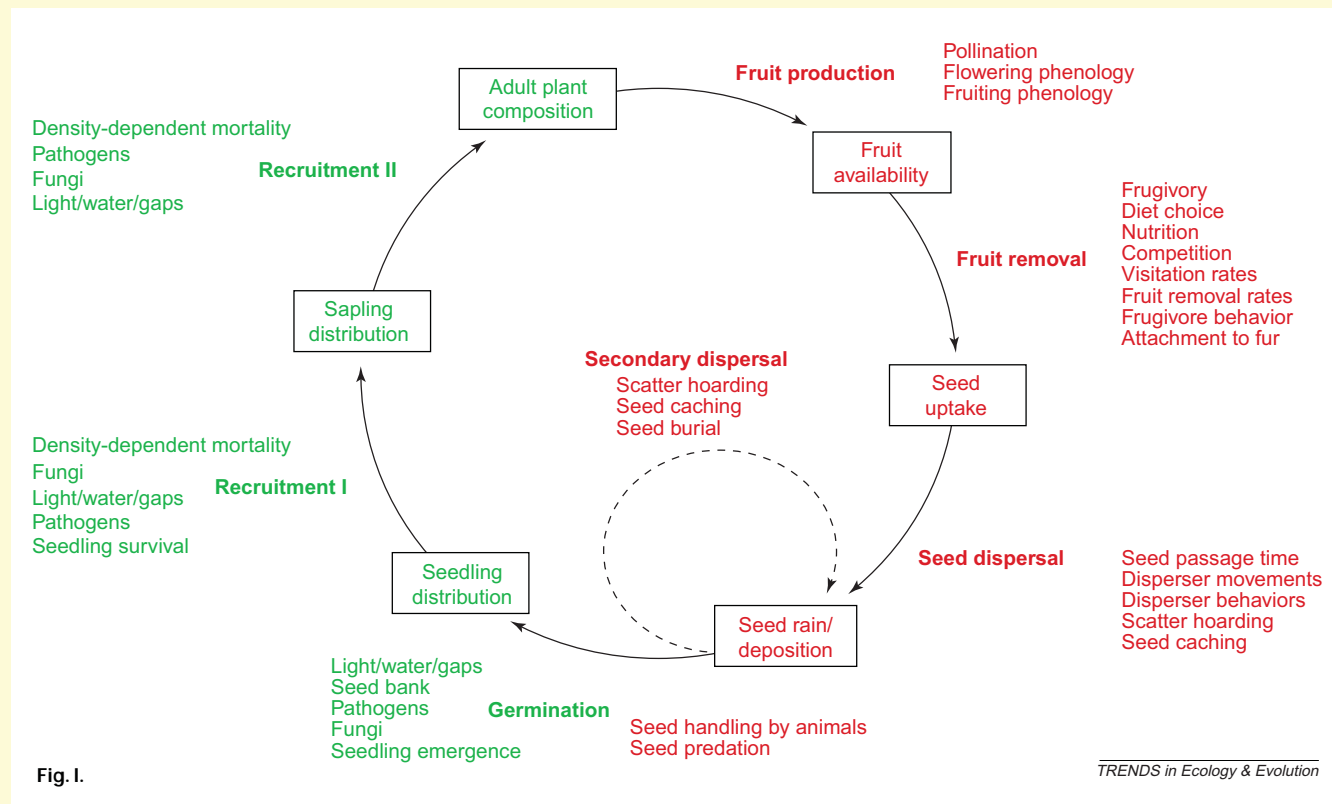


Fig. 1. The two main approaches used to investigate animal-mediated seed dispersal and its consequences: (1) Working forwards entails trying to follow the seed dispersal process in the direction that it happens in nature (in the direction of the arrows). These studies tend to focus on patterns and processes on the right side of Fig. 1 (given in red), and many of them are classified as 'seed dispersal studies'. A major hurdle has been the difficulty of following the dispersers from parent plants to where they deposit

seeds to track the fates of those seeds. (2) Working backwards examines the consequences of the seed dispersal process – seed, seedling, sapling, and adult plant distribution – and tries to deduce the influence of seed dispersal in determining those patterns. These studies focus on patterns and processes on the left side of Fig. 1 (given in green), and many of them are studies of plant demography. Processes (given in bold) generate the patterns (given in boxes) that can be measured.

links between seed dispersal and plant distribution, because: (a) their scope was too narrow, leaving many crucial processes (e.g. SECONDARY DISPERSAL and seedling establishment) understudied; and (b) fates of seeds where they were actually deposited by primary dispersers remained unknown.

The importance of secondary dispersal

In recent times, however, more studies are emerging that explicitly examine the processes that connect seed dispersal with seedling distribution; that is, SEED PREDATION, secondary dispersal and seedling recruitment. Results show that SCATTER HOARDING and other forms of secondary dispersal by rodents and small marsupials are pervasive and potentially

highly influential on vegetation structure [14]. For example, Forget [15] found that in rain forests of French Guiana, 75–100% of *Carapa procera* seeds that were removed were associated with scatter hoarding and secondary dispersal rather than with seed predation. Because many seeds are stored in a single cache, this behavior results in clumped distributions of seeds, and possibly aggregated distributions of seedlings and adult trees [16].

In other systems, this clumping of seeds can be reduced over time. Vander Wall and Joyner [17] tracked individually marked, radioactively labeled (Box 2) seeds of *Pinus jeffreyi* in the mountains of western Nevada, USA as rodents moved them from their initial locations to primary caches. Some seeds

were then moved to second, third, fourth and even fifth caches. With each movement, the number of seeds per cache decreased, the seeds were moved farther from the source area, the distribution of cached seeds became less clumped, and more seeds were placed beneath shrubs, which are nurse plants for *P. jeffreyi* seedlings.

Secondary dispersal is not limited to rodents. Insects such as ants [18,19] and dung beetles [20,21] also perform secondary dispersal, changing patterns of seed and seedling distribution. This creates a 'binary' dispersal system whereby vertebrates, such as birds and monkeys, perform the 'coarse' dispersal away from the parent tree, and insects, such as ants and dung beetles, perform the 'fine' dispersal to the site of final deposition [18,21]. It is becoming increasingly clear that where seeds are initially dropped is often not where they stay, and attempts to correlate the pattern of initial seed deposition with adult vegetation structure can be confounded by this secondary dispersal.

The fate of dispersed seeds

In other systems, secondary dispersal can play a relatively minor role. For example, Wenny [22] tracked the fate of bird-dispersed seeds of the neotropical tree *Ocotea endresiana* in montane Costa Rica, finding that small rodents removed at least 50% of the seeds that were deposited by birds, with no evidence of scatter hoarding or secondary dispersal – removed seeds were probably consumed. This study is particularly comprehensive, explicitly examining all the processes between fruit removal and seedling distribution: seed dispersal, seed predation, secondary dispersal, seed germination and seedling recruitment. Also, this study is one of the first to assess the fate of seeds and resulting seedlings where they were actually placed by the dispersers during their normal activities throughout the landscape. Previous studies determined the fate of seeds where they were experimentally placed by researchers [12] or in areas of high deposition, such as monkey sleeping sites [23], bird nests [24], or ant middens [25]. Over the 12 months of Wenny's study, >99% of the seeds were lost to predation, mediated primarily by rodent activity and disease infestation. And yet, in spite of this high level of seed loss, seed dispersal was important in the system, because fungal pathogens killed more seedlings in the understorey than in gaps. Thus, birds that were more likely to disperse seeds to gaps had a disproportionate influence on recruitment.

Inter-annual variation in seed dispersal systems

Most perennial plant species reproduce over multiple years, and long-term studies are necessary to assess their true impact on the landscape. Recently, more of these longer term studies have been published. Perhaps most notable is Herrera's summary of 12 years of research on the fleshy-fruited plants and

avian frugivores in the Mediterranean montane habitat of southeastern Spain [3,4]. His results revealed large supra-annual differences in both fruit availability and avian frugivore abundance; however, he found little correlation between the fruit supply and the abundance of fruit-eating birds. Furthermore, he found very little agreement between the composition of the diets of the birds and the relative availability of those fruits in the field. Thus, in this system, abiotic factors seem better able to explain annual variations than biotic factors, the long-term dynamics of fruits and their dispersers appear to be decoupled, and the frugivore's diet choice show a 'remarkable 'indifference' to variations in the fruit supply. These results expose the temporal NON-EQUILIBRIUM of this seed dispersal system and illustrate that interannual variation can supercede robust patterns found in shorter term studies. In these instances, overall vegetation patterns might not reflect the seed dispersal patterns that are found in shorter term studies.

Novel techniques for the study of seed dispersal

The aforementioned studies all attempt to look at seed dispersal as it happens in nature; however, researchers often do not have the resources to extensively follow large cohorts of seeds and their dispersers, especially over long periods and distances. Another approach is to look at patterns of seeds and/or seedlings – the consequences of seed dispersal – and work backwards (Box 1, Fig. I), using this information to infer the importance of seed dispersal in generating those patterns. This approach can be especially useful in the study of long-distance seed dispersal, which potentially has profound implications for the persistence of plant populations in fragmented habitats, the colonization of new habitats, the spread of invasive species, and metapopulation dynamics. Better understanding of these processes could help explain migrations of plant species, the effects of global climate change, and the potential of genetically altered crops to 'escape' into natural environments [6]. Although local effects have traditionally been studied using marked and/or individually released seeds (Box 2) and the results used to estimate parameters of mechanistic models [26], long-distance dispersal – the so-called 'tail' of the dispersal curve – has been largely neglected because it is difficult to measure. Some researchers have combined information about movement patterns of frugivores with seed passage times to estimate maximum dispersal distances [27]; however, these estimations are indirect extrapolations. Two emerging new techniques have great potential to facilitate direct measurement of actual dispersal.

Stable isotope analysis

Stable isotope ratios have been analysed to trace nutritional origin and migration in animals (Box 2). Isotopic signatures are intrinsic to the physical

Box 2. Promising techniques for studying seed dispersal

Rapid advances in technologies are enabling researchers to track seeds whilst they are being dispersed and to match them with parent plants after they are dispersed.

Radioactive labeling

Seeds marked by irradiation with high-energy γ radiation (such as Sc-46, half-life 84.5 days) can later be detected with a Geiger counter. The emitted radiation is not harmful to the animals that handle and ingest the seeds. In the case of Sc-46, the decay product is Ti-46, which is nonradioactive [a].

Fluorescent microspheres and/or dust

Small (15 μ m) fluorescent spheres can be attached to fruits and later recovered in fecal material to understand spatial patterns of deposition. Trials with captive cedar waxwings *Bombycilla cedrorum* demonstrated that: (1) percentage recovery of microspheres is high; (2) all defecations containing seeds also contain microspheres; (3) relatively few microspheres are recovered in defecations not containing seeds; and (4) presence of microspheres on fruits does not affect fruit choice. The fluorescence of the spheres aids detection for up to 30 days, even under conditions of full sun and high temperatures [b].

Stable isotope analyses

Stable isotope analyses (primarily $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$, δD , $\delta^{87}\text{Sr}$) have been used to trace nutritional origin and migration of animals ranging from insects to turtles to birds and bats [c]. The tissues of organisms bear foodweb isotopic signatures that vary spatially based on a variety of biogeochemical processes. For example, a recent study of monarch butterflies *Danaus plexippus* found that stable-hydrogen and carbon isotope ratios in the wings of butterflies is highly correlated with the isotopic ratios in the milkweed *Asclepias* sp. (on which the monarchs feed) in their natal regions. These findings strongly suggest that isotope ratios could be used to infer natal origins of butterflies collected on wintering grounds [d]. Isotope ratios might also help match the breeding and wintering grounds of migratory birds [e]. This technique could be applied to seed dispersal studies to infer the location of parents of seeds, seedlings, saplings, and/or adult trees, and could enable detection of low-frequency, long-distance dispersal events.

Molecular genetic markers

A variety of molecular markers can be used to measure gene flow and to match parents and offspring to track both local and long-distance dispersal events. With these methods, the consequences of long-distance dispersal events are studied, rather than the dispersal events themselves.

- Indirect methods – these methods are based on measures of among-population genetic variation (i.e. F_{ST}). More genetic structure

(larger F_{ST}) is an indication of fewer migrants and less gene flow. Genetic structure of groups of offspring plants can be compared with genetic structure of groups of other offspring plants to estimate the gene flow between them. By regressing the geographical distance between the groups against this gene flow estimate and separating seed and pollen mediated gene flow, an 'indirect' estimate of seed dispersal rates can be made [f-h]. Note however, that there are many assumptions when inferring gene flow from estimates of population structure [i]

- Direct methods – these methods use maximum likelihood estimations applied to comparisons of multilocus genotypes to assign offspring to parent individuals or populations. Genomes of offspring and potential parents can be compared 'directly' to measure dispersal and evaluate gene flow.
 - (i) Parentage analysis: used to assign parents to offspring seeds and/or seedlings. Very powerful and direct, but labor intensive and costly, because it requires that potential parents be sampled exhaustively.
 - (ii) Assignment methods: the genotype of an individual seed or seedling is compared with the allele frequencies in potential source populations to assess the likelihood that that individual originated from each of the sampled source populations. Not as precise as parentage analysis, but often more practical, allowing for a wider sampling of potential parent populations [f, j].

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landscape and are incorporated into tissues of plants during nutrient uptake and subsequently passed into the animals that eat them. Thus, these techniques could be used not only to track the long-distance movements of frugivores, but also to match dispersed seeds with their parent populations. The factors that influence the stable isotope ratios of different elements vary on different scales, for example, carbon and nitrogen isotope ratios in plants are influenced by surface geology and the amount of canopy cover and thus vary on a very local scale, whereas hydrogen isotope ratios tend to vary on an altitudinal, regional or continental scale [28]. This allows different resolutions of analysis: when matching seeds to their population of origin, hydrogen isotope analysis may suffice; when matching seeds to specific microhabitats, carbon or nitrogen analysis might be more appropriate.

Molecular genetic techniques

The use of molecular genetic markers also holds great promise for the study of seed dispersal. There are several molecular markers, with differing degrees of variability, which, when analysed, can yield different levels of resolution [29,30]. For many years, so-called 'indirect methods' [29,31], (Box 2) have been successfully used to assess genetic structure of populations and/or subpopulations and infer gene flow between them [32,33], sometimes with important implications for conservation [34]. In plants, gene flow occurs via pollen (containing only paternal DNA) and seeds (containing both maternal and paternal DNA). Thus, analyses of nuclear DNA of seeds or seedlings might tend to overestimate the influence of seed dispersal on gene flow because that DNA reflects both pollen and seed dispersal. However, the cytoplasmic DNA from chloroplasts contains only

maternal contributions and thus reflects only seed dispersal. By comparing the differentiation in nuclear versus cytoplasmic markers, researchers can separate seed-mediated gene flow from pollen-mediated gene flow [6,30,31].

The application of highly variable molecular markers, such as microsatellites, has facilitated the development of so-called 'direct' genetic methods (Box 2); these direct methods have the capacity to revolutionize seed dispersal research. If all the potential parents in a plant population can be sampled, parentage analyses can be performed whereby the parents of individual seeds or seedlings can be determined [35]. This technique, although potentially time and energy intensive, is extremely powerful – it provides a direct method of measuring individual dispersal events. In a landmark study, Godoy and Jordano [36] performed this analysis for *Prunus mahaleb* trees and seeds in the same Mediterranean montane habitat studied by Herrera [3]. By sequencing the woody endocarp of the dispersed seeds (a tissue of entirely maternal origin) and comparing those sequences to the genotypes of all the potential parent trees in the population, they were able to find unambiguous matches for 82.1% of the 95 seeds analysed, concluding that the remaining 17.9% of the seeds came from long-distance dispersal. Up to 62% of the seeds were deposited by their dispersers within 15 m of the parent plant, and measured dispersal distances from these analyses were compatible with estimations of SEED SHADOWS calculated from bird foraging observations at the same site [37].

Even when it is not feasible to sample all potential parents, direct methods can still be applied via assignment tests that assess the likelihood that an individual originated from each of the sampled source populations (Box 2). Although the resolution of these tests might not be as fine as parentage analysis, they do enable sampling across large spatial scales and are useful in detecting low-frequency, long-distance dispersal events [6].

The relevance of plant demography studies

In contrast to seed dispersal studies that attempt to follow the proximate processes of seed movement and the subsequent establishment success of seedlings, plant demography studies examine the ultimate consequences of dispersal – the distribution and diversity of juvenile and adult plants. Thus, we can work backwards from the findings of plant demography research to understand more about seed dispersal and how it affects surrounding vegetation.

Confirming the Janzen–Connell hypothesis

The foundation of most modern seed dispersal research is the JANZEN–CONNELL HYPOTHESIS, which postulates that a main benefit of seed dispersal is that it enables seeds and seedlings to escape the high density-dependent mortality that results from

pathogens, seed predators, and/or herbivores directly under the parent plant [38,39]. Two recent plant demography studies [40,41] from the 50-ha forest dynamics plot (FDP) [42] on Barro Colorado Island (BCI) in Panama provide unequivocal evidence of density-dependent mortality, confirming for the first time that the underpinnings of seed dispersal research are sound. In an analysis of tree diversity and recruitment in different-sized quadrats of the BCI FDP, Wills *et al.* [40] found strong negative density-dependent effects on recruitment of 67 out of 84 of the most common species. Building on this study, Harms *et al.* [41] compared seeds that arrived in 200 seed traps in the BCI FDP with seedlings that established into adjacent quadrats over a four-year period. Their findings corroborate those of Wills *et al.*: for the 53 species of plants that provided enough seeds and seedlings for analysis, strong density-dependent mortality was pervasive. Even when results were corrected for effects of differing germination rates, variation in species-specific mortality, and high densities of seeds near fruiting trees, density-dependent mortality remained a dominant force in shaping seedling composition. These findings are particularly convincing because of the high sample sizes obtained: Harms and his colleagues examined 386 027 seeds and 13 068 seedlings. As Howe points out, 'The Harms paper closes one major chapter [of seed dispersal research] and opens new ones... In short, the field can shift from piecemeal attempts to demonstrate a local advantage of dispersal, to applications of what is now axiomatic' [43].

When dispersal is limited

Another recently published long-term study of plant dynamics from the BCI FDP also suggests a crucial role for seed dispersal in maintaining tree diversity. Hubbell *et al.* [44] examined seedlings and saplings in over 1200 light-gaps that appeared in the plot over a period of 13+ years. Surprisingly, gap disturbance regime did not play a strong role in maintaining tree diversity on BCI. Although gaps did increase seedling establishment and sapling densities, this effect was not specific for any particular tree species or regeneration niche guild (pioneer, shade-tolerant, or mature-phase). Furthermore, species richness per stem (a metric that normalizes data for the increased stem density in the gaps) was identical in gaps and in nongap control sites. Thus, it appears that the main effect of gaps on species richness was a simple area effect. These results suggest that RECRUITMENT LIMITATION (in part because of DISPERSAL LIMITATION) has a much stronger role in maintaining tropical tree diversity than do gap disturbances. This conclusion is supported by ten years of seed trap data involving over one million seeds. No seeds were collected from >50 species having adults in the plot and, when trap locations were analysed separately, an average of 88% of the species did not deliver even a single seed

Glossary

Dispersal limitation: recruitment limitation resulting from the failure of seeds to arrive at favorable sites.

Fruiting/flowering phenology: the timing of the production of flowers and fruits.

Frugivory: consumption of fruits by animals. In this context, a broad definition is used whereby frugivory need not involve ingestion and encompasses all seeds removed from the plant by animals, including seeds in cheek pouches of primates or attached to coats by burs.

Janzen–Connell hypothesis: postulates that a main benefit of seed dispersal is that it allows seeds and seedlings to escape the high density-dependent mortality owing to pathogens, seed predators, and/or herbivory that can occur directly under the parent plant.

Non-equilibrium seed dispersal system: a seed dispersal system in which the relationships between the animal species and plant species vary either in time and/or space. The relative importance of the various subprocesses and constituent factors can also vary seasonally, yearly or spatially.

Scatter hoarding: a primary or secondary dispersal process by which an animal deposits food resources (often seeds) in caches for later use. Unrecovered cached seeds are candidates for germination.

Secondary dispersal: process by which seeds that are already on the ground are moved to other locations; this dispersal is often mediated by ground-dwelling mammals (e.g. rodents, tapirs, and forest antelopes) and insects (e.g. ants and dung beetles).

Seed deposition/placement: process by which seeds carried by dispersal agents are dropped in new locations.

Seed dispersal: movement of seeds away from parent plants, usually by animal agents or by wind, water, or intrinsic explosive mechanisms. Directed dispersal occurs when seeds are deposited disproportionately in favorable locations.

Seed dispersal cycle: a succession of processes whereby fruits produced by a plant are removed by animals that disperse the seeds, some of which might germinate to seedlings and recruit to adult plants, influencing the fruit availability of the next generation (Box 1).

Seed predation: action on seeds that renders those seeds nonviable for germination. Often this predation occurs through ingestion by animals or by infestation of pathogens.

Seed rain: the pattern of seedfall to the ground.

Seed shadow: the area on the ground where the seeds of a single tree either fall to the ground or are placed by dispersers.

Recruitment limitation: the failure of a species to establish in all sites that are favorable to its growth and survival.

maintenance of diversity: the researchers predict that removal of animal dispersers would reduce seedling species richness by 60%. This study provides the first community-wide estimate of active seed dispersal rate in a tropical forest, and serves as a reminder that results of seed dispersal studies have both theoretical and conservation implications.

Conclusions and prospects

Recent developments have brought us closer to the goal of linking seed dispersal and adult vegetation structure. What needs to happen to reach this goal successfully and close the seed dispersal loop?

First, we need to continue to work forwards, looking at seed dispersal in the sequence that it occurs in nature with long-term, comprehensive studies. The seed dispersal cycle has many constituent steps and processes (Box 1); each of these needs to be examined explicitly to gain a full understanding of the effect of dispersal on vegetation structure. Furthermore, the finding that interannual variation can obviate robust patterns found in shorter term studies [3] emphasizes the need to do these investigations over longer timescales.

Second, we need to continue to work backwards, studying patterns of seeds, seedlings, and adult plants, and trying to understand the dispersal processes that generate those patterns. Exciting new techniques, such as the analysis of molecular genetic markers and stable isotope ratios enable researchers to match seeds to parent plants, to detect and measure long-distance dispersal events, to distinguish relative contributions of pollen and seed dispersal to gene flow, and to link offspring to parent populations. Studies of plant demography can help us to understand the importance of seed dispersal in habitats where recruitment appears to be limiting [44] and in habitats where dispersal does not appear to be limiting [45].

Finally, we need to work together. Because seed dispersal and plant demography are inextricably linked, collaboration between researchers of seed dispersal and plant demography will almost certainly be synergistic. To help understand the links between seed dispersal and adult plant composition, seed dispersal researchers should begin to conduct their investigations in sites of ongoing plant demographic research and plant demographers should begin studies at sites of ongoing seed dispersal research. Only when we have information about all parts of the seed dispersal cycle in a single location can we begin to understand how each of these processes influences the others, and impacts the cycle as a whole.

Here, we have presented a conceptual model of seed dispersal that is cyclic (Box 1), allowing us to envision the seed dispersal process as a continuous loop in which fruit availability affects seed dispersal, which then affects adult vegetation structure. This vegetation structure will influence the fruit availability and seed dispersal in the next generation,

to a given location during the decade of continuous sampling [44]. Because of limited seed dispersal and recruitment, superior competitors might not arrive at a particular site, allowing inferior competitors to 'win-by-default'. This could help to explain the proposed nonequilibrium coexistence of arbitrarily large numbers of plant species that have similar resource requirements in species-rich communities, such as tropical forests. In this case, seed dispersal has a very important role, because seeds that are dispersed might be confronted with inferior competitors and thus be afforded a greater chance of germination and establishment.

When dispersal is not limited

In a study of plant demographics that found no evidence for dispersal limitation, Webb and Peart [45] also found a crucial role for seed dispersal in maintaining rain forest diversity. They compared species lists of seedling plots that were nested within 28 previously censused tree plots in the mixed dipterocarp forests of Indonesian Borneo, finding that 68% of the species and 46% of the individual seedlings must have come from active dispersal events. These data were then incorporated into a spatially explicit forest simulation model: results indicated that dispersal limitation might not have a strong role in the maintenance of tree diversity in this forest. However, seed dispersal itself was profoundly important for the

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which will, in turn, influence the subsequent generation of adult vegetation, and so forth. Tracking the fate of a single cohort of seeds remains an important goal; however, ultimately our goal is even more overarching: to discover whether, given all the temporal, spatial, intra- and interspecific variation, the cumulative process of seed dispersal drives community-wide vegetation structure in any detectable and predictable way. How does seed

dispersal affect the vegetation structure after ten turns of the cycle? Or after 50 or 100 turns? These questions might be extremely difficult to answer using direct measurements; however, the application of plant population simulation models [45,46] to seed dispersal systems might provide valuable insights both for our theoretical understanding of seed dispersal and for applied usage in conservation and management.

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Evolutionary genetics of invasive species

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The evolutionary genetics of invasive species has been relatively unexplored, but could offer insights into mechanisms of invasions. Recent studies suggest that the invasion success of many species might depend more heavily on their ability to respond to natural selection than on broad physiological tolerance or plasticity. Thus, these studies stress the importance of genetic architecture, selection upon which could result in evolutionary adaptations and possibly speciation. For instance, epistatic interactions and the action of a few genes could facilitate invasion success. These findings emphasize the utility of genomic approaches for determining invasion mechanisms, through analysis of gene expression, gene interactions, and genomic rearrangements that are associated with invasion events.

INVASIVE SPECIES (see Glossary) and populations pose major threats to biodiversity, ecosystem integrity, agriculture, fisheries, and public health. Economic costs associated with the more publicized exotic invaders, such as weeds, agricultural pests, zebra mussels and plant pathogens, total ~US\$137 billion y^{-1} in the USA [1]. The rapid spread of exotics has received considerable attention within the international community, and has mobilized substantial ecological research. By contrast, evolutionary aspects of INVASIONS have remained relatively unexplored.

Why is evolution integral to the study of invasion biology? Invasions frequently constitute rapid evolutionary events [2], resulting in populations that are genetically dynamic over both space and time. Genetic characteristics of populations have profound impacts on their capacity for range expansions [3–5]. Both natural selection and genetic drift could alter genetic structures of invading populations in ways that modify their tolerance or behavior (see examples below). Invading populations are also capable of inducing evolutionary changes in native species [6,7]. Consequently, incorporating evolutionary genetics is important for revealing characteristics that determine invasion success.

Why is this topic of immediate importance? As impacts of invasions intensify, it is imperative to move beyond treating invasive species as genetic black boxes in mitigation and management strategies. For instance, demographic models that treat invasive species as homogeneous and immutable entities will often fail over extensive spatial or temporal scales. We are in an excellent position to investigate factors that affect invasion success, given recent developments in evolutionary theory and molecular genetics. Technical innovations in GENOMICS (e.g. MICROARRAY TECHNOLOGY and QUANTITATIVE TRAIT

LOCI (QTL) MAPPING) and BIOINFORMATICS offer many opportunities for exploring GENETIC ARCHITECTURE and gene expression patterns of invading populations. Effective application of these tools requires an assessment of the current literature. Thus, here I review recent studies on genetic characteristics and adaptative responses of successful invaders, and recommend topics for future research.

Genetic architecture of invasive species

The importance of natural selection

Biological invasions present interesting evolutionary problems because they are stochastic events often involving small populations that can survive rapid habitat transitions. The classic symposium volume *The Genetics of Colonizing Species* [8] was influential for focusing on evolutionary mechanisms of invasions. In this text, C.H. Waddington asked how genetic architecture might impact the propensity to invade. Mounting evidence supports the importance of genetic attributes for invasion success, such as ADDITIVE GENETIC VARIANCE (AGV) [7,9–11], EPISTASIS [7,12–14], hybridization [4,15], genetic tradeoffs [6,16], the action of small numbers of genes [5,17,18] and, possibly, genomic rearrangements [15,19,20].

Thus, invasion success could be facilitated by the presence of genetic substrate in source populations upon which natural selection could act. In some cases, genetic drift alone has promoted successful invasions [3], but such cases probably represent exceptions rather than the rule. Broad tolerance and PLASTICITY are commonly invoked to explain invasion success [21–23], but often fail upon close examination [24,25]. For example, the copepod complex *Eurytemora affinis* is considered a euryhaline species because it inhabits broad salinity ranges from hypersaline marshes to freshwater lakes [23]. However, certain populations cannot tolerate or acclimatize to the full range of salinities occupied by this species complex, but instead experience strong selection and heritable shifts in tolerance when they invade new habitats [24,26].

Genetic variance

Sufficient AGV is essential for evolutionary ADAPTATION in response to environmental change [27]. Several recent studies have found high levels of AGV within source populations for traits that facilitate invasions [7,9–11]. The observed lag time commonly preceding successful invasions could result from the

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