Trends in
Ecology & Evolution

CellPress

Review

Animal-mediated plant niche tracking in a changing climate

Tristan A. Nuñez [1,2,*,@] Laura R. Prugh,[2,4,@] and Janneke Hille Ris Lambers[1,3,4]

Over half of plant species are animal-dispersed, and our understanding of how animals can help plants move in response to climate change – a process known as niche tracking – is limited, but advancing rapidly. Recent research efforts find evidence that animals are helping plants track their niches. They also identify key conditions needed for animal-mediated niche tracking to occur, including alignment of the timing of seed availability, the directionality of animal movements, and microhabitat conditions where seeds are deposited. A research framework that measures niche tracking effectiveness by considering all parts of the niche-tracking process, and links together data and models from multiple disciplines, will lead to further insight and inform actions to help ecosystems adapt to a changing world.

Highlights

Recent field and modeling studies provide evidence that animals are helping plants track their niches in a changing climate. Key methods include seed tracking (via isotopes or DNA), mapping seed deposition using animal telemetry or simulations, and niche models.

Niche tracking requires (i) seed availability and animal disperser movement toward newly suitable locations to be synchronous, (ii) landscapes that enable movement toward newly suitable areas, and (iii) deposition microsites which support plant recruitment and population establishment.

Niche tracking effectiveness is a framework for assessing the role of dispersers in helping plants track their climatic niches and successfully establish populations in locations newly suitable due to climate change.

Plant and animal traits, together with landscape characteristics, can help predict animal-mediated niche tracking.

Can niche-tracking plants hitch a ride from animals?

Anthropogenic climate change is shifting the climatic niches of plant species across the globe [1,2]. How successful plants are at tracking their shifting niches will affect patterns of biodiversity, extinction, ecosystem function, and the ecosystem services that human societies rely on [3–8]. Because animals disperse over half of plant species worldwide, they are critical to helping plants move in response to climate change [3,9]. As a result, animal **seed dispersal** (see Glossary) will play a key role in shaping the distributions of individual species as well as the composition of plant communities as they reassemble in response to global change [10–14].

Recent research into animal-mediated **niche tracking** – how plants move to occupy newly suitable locations as the climate changes – is shedding light on this process. We provide an overview of the distinct disciplines informing this research and of the need to bridge disciplinary perspectives, and describe and assess the diverse approaches that have been used to study animal-mediated niche tracking. We synthesize and evaluate recent findings, identify challenges and opportunities, and suggest a framework and directions for future work.

Niche modeling, seed dispersal ecology, and movement ecology provide key insights

Insights into how animals help plants move with climate change spring from three distinct fields of research. First, **niche modeling** and range shift projections under scenarios of climate change help identify where plants will need to move. Second, seed dispersal ecology describes the processes and conditions under which seeds are successfully dispersed. Third, animal **movement ecology** provides theory and tools to understand the animal movements that relocate seeds. To advance our understanding of the entire process of animal-mediated niche tracking, better linkages between the new tools and frameworks provided by these fields are needed.

Niche models are trained with historical occurrences and climatic or other environmental conditions, and forecast the locations of suitable climatic conditions under scenarios of future climates

[1]Biology Department, University of Washington, Seattle, WA 98195-1800, USA
[2]School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195-1800, USA
[3]Plant Ecology, Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland
[4]These authors contributed equally to this work.

*Correspondence: tnunez@uw.edu (T.A. Nuñez).
[@]Twitter: @TNunezEcol (T.A. Nuñez) and @LauraPrugh (L.R. Prugh).

[15,16]. Although these projections suffer from uncertainty inherent in climate models and assumptions regarding sampling, dispersal ability, biotic interactions, and projection into novel climates, they provide useful guides about the possible locations of future suitable conditions and can be adapted to specifically model seedling recruitment niches [17,18]. Alternatively, some researchers rely on rules of thumb that species will shift their distributions poleward in latitude or upward in elevation, following major gradients in temperature or precipitation, or on metrics such as **climate velocity** [19].

While niche models tell us where plants need to go, seed dispersal ecology tells us how they get there (Box 1) [20]. Through observational, experimental, and theoretical approaches, seed dispersal ecology has described the core components and key processes involved in animal-mediated seed dispersal (Figure 1A) [21,22]. The field has also established that animals help shape plant distributions, as demonstrated by island colonization studies, landscape genetics of plant populations, and from studies of the spread of introduced species by both birds and mammals [3,4,23–29]. Early observations that trees colonized previously glaciated regions at rates faster than expected from average dispersal distances led to a focus on **long-distance dispersal** [30]. This work suggests that infrequent long-distance dispersal events, rather than the average distance of seed displacements, drive shifts in plant distributions in response to climatic changes [31,32]. Seed transport models predict how far or where seeds are likely to move by incorporating information on plant and animal traits that influence movement, as well as the landscapes through which they move (Box 1).

While seed dispersal ecology approaches seed movement from the plant perspective, movement ecology focuses on the drivers and effects of animal movements, providing an animal perspective on dispersal [33]. Advances in tracking technologies have provided higher resolution movement data for larger numbers of species [21,33]. Movement ecology provides tools to model animals' **behavioral states** from tracking data, allowing identification of the initiation (e.g., foraging),

Box 1. The natural history of animal-mediated seed dispersal and seed transport models

Seed dispersal natural history

The natural history of seed dispersal describes a rich diversity of ways in which seeds are moved. Besides animal-mediated dispersal (also called **zoochory**), wind (anemochory) and water (hydrochory) dispersal are common pathways for seeds, but seeds can also move by gravity (barochory) or ballistic propulsion (ballochory). Within zoochory, seeds can be transported internally (endozoochory) or externally on fur or feet (epizoochory), or by scatterhoarding by seed predators (synzoochory). Secondary seed dispersal (diplozoochory) often involves smaller animals moving seeds deposited by other animals, or even by predators ingesting and moving prey that has ingested seeds (diploendozoochory). Seeds transported internally are deposited not just by defecation, but also in pellets regurgitated by birds, or are spat out (e.g., by primates, or during cud chewing by ungulates). Plants are commonly assigned to **dispersal syndromes** based on inferred adaptation of seed morphology to particular forms of dispersal, and these syndromes form the basis of some models that use traits to predict dispersal distances. However, recent empirical studies have shown that dispersal syndromes are frequently not predictive of the vectors which move the plants, particularly over long distances, suggesting that syndromes should not be treated as rigorous classifications [83]. Birds, primates, ungulates, carnivores, small mammals, fish, and even insects are all important seed dispersers [5,84,85]. Dispersal ecology also provides insights into the effect of ingestion on seed germination rates and whether seeds are deposited in suitable recruitment microhabitats, thus affecting colonization and spread.

Seed transport models

Seed transport models are particularly central to dispersal ecology and model the distance or spatial distribution of seed transport and deposition. These models rely on measures of (i) the amount of seeds carried by an animal, (ii) the velocity or movement tracks of the animal, and (iii) seed retention time (also called gut passage time in the case of ingested seeds) [86]. These models predict the amount of seeds deposited as a function of distance (the **dispersal kernel**), can generate spatially explicit maps of **seed rain** if animal movement tracks are available, and can account for the dispersal kernel generated by entire animal communities [22,52,87].

Glossary

Allometric scaling: the use of general relationships between animal or plant traits (e.g., animal mass, beak size, or wing length for animals and fruit or seed size for plants) and metrics relevant to seed dispersal, such as which seeds animals disperse, how far animals move, and gut passage time.
Behavioral state: the primary activity an animal is engaged in during a specific period of time, for example, resting, feeding, or moving between resource patches.
Climate velocity: the rate or distance of movement needed to maintain a constant temperature under a climate change scenario.
Dispersal kernel: the probability density function of a seed dispersing a given distance from its source.
Dispersal syndromes: the classification of plants according to inferred adaptation of seed morphology to a particular type of dispersal.
DNA metabarcoding: high-throughput sequencing of a specific DNA marker from a mixed sample that enables the identification of multiple species.
Long-distance dispersal: seed dispersal events that are long in distance relative to either a threshold (e.g., distances > 1 km) or in relative terms (e.g., distances > the 95th percentile of a plant's seed dispersal distances).
Movement ecology: the study of the patterns, mechanisms, causes, and consequences of organismal movement.
Niche modeling: quantitative modeling which uses the environmental conditions associated with a species' presence or absence to predict the geographic distribution of a species.
Niche tracking: the process by which species move geographically in order to remain in a favorable environmental (especially climate) space.
Phenology: the timing of a recurring biological event. Examples include fruiting, flowering, leaf flushing, and migration.
Plant-disperser (or plant-vector) pairs: pairs of plants and animals in which the animal disperses the plant.
Recruitment microhabitats: locations containing fine-scale microclimate or other environmental conditions supportive of germination and seedling survival.

movement, and deposition phases of the seed dispersal process [34]. Such models can then be used to simulate movement trajectories that can then be used in seed transport models [21,33]. Animal tracking also reveals migratory behaviors that are especially conducive to long-distance seed dispersal [35].

Seed dispersal: the process by which seeds (used here to mean any reproductive propagule) are transported away from the parent plant.
Seed rain: the spatial pattern of seeds deposited across a landscape by one or more vectors.
Seed retention time: the amount of time it takes for a seed to be deposited (egested or dropped) by an animal after dispersal initiation (ingestion or external attachment). Equivalent to gut passage time for internally transported seeds.
Stopover: a period of localized movements with very low displacements (relative to the whole migration) during a seasonal migration, during which an animal rests or forages.
Zoochory: dispersal of plant seeds by animals.

Recent methodological advances

Recent studies have drawn from niche modeling, seed dispersal ecology, and movement ecology to advance our understanding of animal-mediated niche tracking. These studies draw inference from a diverse array of empirical and modeling methods, which we review here and list in Table 1.

Direct observations of seed movement measure dispersal across climate gradients

Several studies have been able to observe animals moving seeds along climatic gradients, despite the inherent challenges to quantifying seed movement across large distances [30]. For example, isotopic signatures have been used to determine the elevations of parent plants of seeds found in animal scats in Japan [36–38]. Researchers in Spain placed plastic seed mimics in baits that were eaten by foxes (*Vulpes vulpes*) and marten (*Martes martes*), and recorded the elevational shifts of these mimics relocated during scat surveys [39]. Future studies that observe seed movement could either use these approaches or could also use field studies involving continual animal movement and behavioral observations, as is common with some primates [40]. In addition, **DNA metabarcoding** of seed-containing scats, which has been used for identification of both the animal vector and transported seeds, could document seed movement into newly suitable locations along latitude or elevation gradients [23]. Similarly, microsatellite DNA can be used to link specific seeds to parent plants, potentially providing even finer-grain information about seed movement across climate gradients [41,42].

Observations of specific plant-disperser pairs establish the potential for niche tracking

Although studies that document **plant-disperser pairs** are common, few assess the potential of specific plant-disperser pairs to contribute to niche tracking. González-Varo *et al.* [23] established plant-disperser pairs through DNA metabarcoding, identifying both the seeds contained in bird droppings and the bird species responsible for the droppings and evaluated the potential for plant niche tracking from the direction of bird migration at the time of plant fruiting. Similarly, Lovas-Kiss *et al.* [43] documented which seeds migratory birds egest just before or after undertaking long-distance migratory movements both within mainland Europe and between Great Britain and Iceland. Although these studies do not directly establish that seeds are moved into newly suitable locations, they provide evidence for the potential for niche-tracking seed movements [44].

Seed deposition projections can be related to shifting niches

A small number of studies have modeled spatial patterns of seed deposition and linked them to plant range shift projections, or to latitudinal or elevational gradients. Viana [45] projected the distributions of three aquatic plant species into the future at decadal timesteps and assessed the ability of migratory ducks to deposit seeds in the newly suitable locations. Other studies instead have assessed whether seed deposition patterns would allow plants to shift across latitude or elevational gradients [46–48]. There is a need for future work to further connect seed transport models to projections of shifts in plant niches.

Seed transport models linked to empirical or simulated animal movements can quantify the effects of animal behavior and landscape structure on seed dispersal

A larger number of studies have modeled spatial seed deposition patterns but not shifting plant niches. Such studies are still useful for understanding niche tracking by providing insights into the effects of landscape structure and animal behavior on patterns of seed deposition. Some

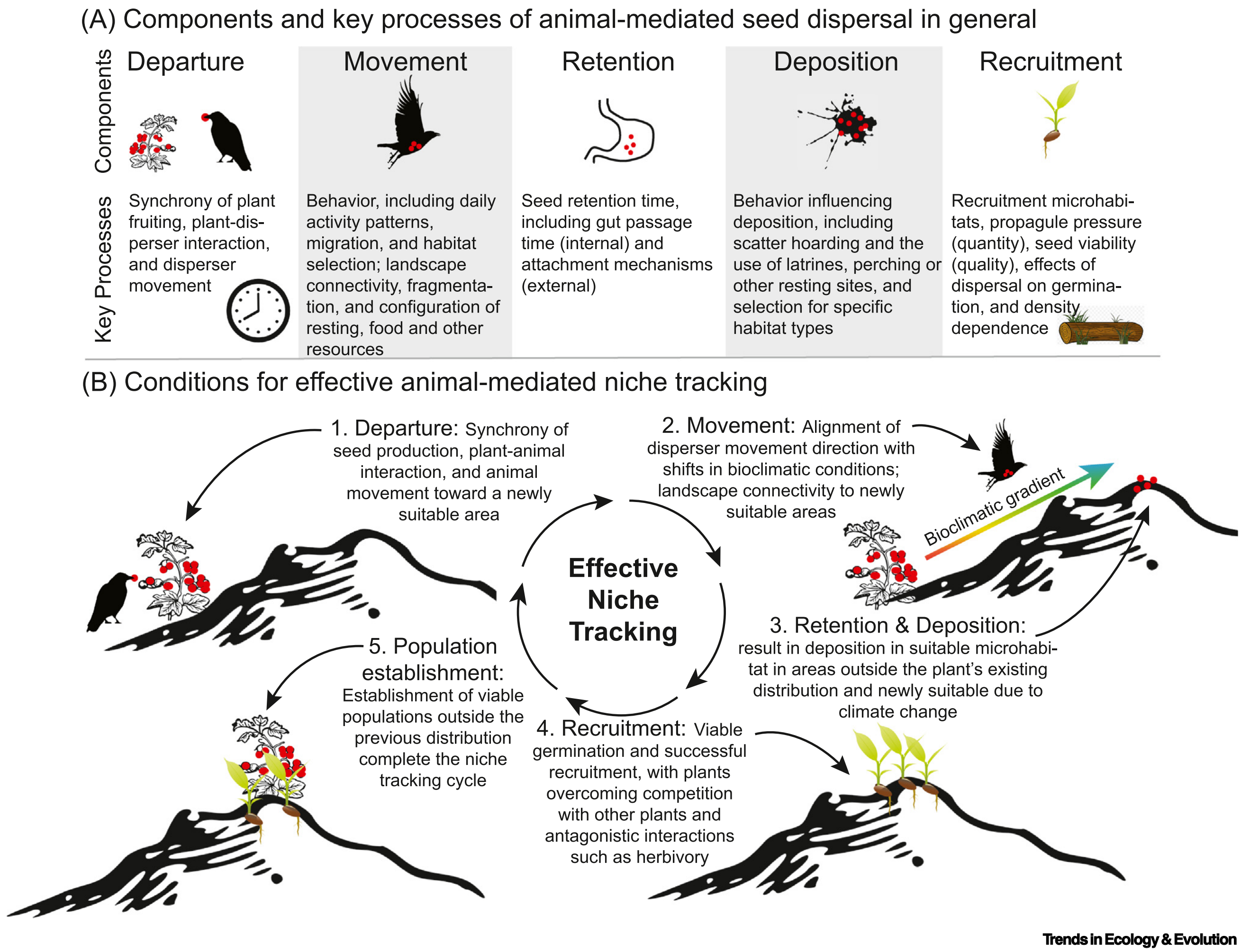

Figure 1. Components of animal-mediated seed dispersal and corresponding conditions required for effective niche tracking. (A) key phenological, behavioral, environmental, and physiological processes influence the effectiveness of seed dispersal for each seed dispersal component (seed departure, animal movement, seed retention, deposition, and recruitment). (B) Specific conditions must be met for each component of seed dispersal in order for niche tracking to be effective, resulting in seed dispersal of sufficient quantity, quality, and alignment with climatic niche movement.

studies use animal movement data to map seed deposition at landscape scales [40,49–51]. These studies typically combine information about the location of seed availability on the landscape, ingestion rates, and retention times to map out where tracked animals ingest and then egest seeds along the observed movement tracks.

A less direct approach is taken by studies that use movement data and models to generate simulations of animal movement, and then use simulated tracks to model spatial seed deposition patterns [52]. These models can incorporate important elements of movement behavior likely to influence seed deposition, such as the probability of stopping at migratory **stopovers** [46]. Also useful are simulations that are responsive to environmental factors within animals' seasonal or home ranges that are likely to shape animal movements and resulting seed dispersal [53,54]. Future animal movement simulations used to model seed dispersal – and particularly for niche tracking – will need to identify the appropriate level of realism without overparameterizing models in such a way that they lose predictive ability [21].

Table 1. Data sources and models informing animal-mediated seed dispersal studies

Dispersal process component	Question addressed	Empirical data source or modeling approach
Plant-disperser pairs	Which animals disperse which plants?	DNA metabarcoding of scat to identify vector and/or seed [23], morphological identification of seeds and scat [36–38,88], collection of scat from bird-species-specific resting or foraging sites with morphologic identification of seeds [43], imputation from plant interaction databases [9]
Temporal seed availability	When are seeds available to be moved?	Literature [23], field observation [23]
Seed retention time	How long does it take for a seed to be egested after ingestion, or dropped after attachment?	Captive feeding and observation [50,89], allometry [9,12]
Germination rates	Are transported seeds viable? How are seeds affected by ingestion?	Imputation from trait databases [9], germination from scat [50,88–91]
Animal movement	How fast (and in which direction) does an animal move after ingestion, and does it prefer to move through some environments more than others?	Bird band recovery [45], GPS telemetry [49,51,89], VHF telemetry [90]
Seed movement	How far has a seed moved from the parent plant?	Stable isotopes [36–38], bait marking [39], microsatellite DNA [41,42], DNA metabarcoding [92]
Climate change	In which direction are suitable conditions for plants moving, and how far are they moving?	Climatic niche projection [45], climate velocity [9], elevation [36–38,47], latitude [23,46]

Trait-based models predict plant-disperser pairs, retention times, and dispersal distances when direct observations are lacking

Instead of using animal movement data directly, other studies have relied on literature, traits databases, or **allometric scaling** to obtain animal movement rates and **seed retention time** parameters to use in models of seed dispersal [55]. Nowak *et al.* [47] used allometric relationships (e.g., between fruit width and bird bill width) to characterize plant-disperser pairs, seed retention time, and movement distances for birds in the Peruvian Amazon. Similarly, Fricke *et al.* [9] imputed seed retention time, movement, and plant-disperser pairs from species traits and phylogenies to predict seed dispersal rates for over 400 species interaction networks, and compared these rates to a climate velocity metric at a global scale [9]. Future niche-tracking research involving large numbers of species or data-poor geographic regions will likely benefit from such literature- and allometry-based approaches to deriving key parameters.

Recent insights into niche tracking

Animal-facilitated plant niche tracking is occurring

Recent studies demonstrate that animals are helping plants move in response to climate change. Isotope and bait-marking studies have documented actual and potential seed movement by mammals and birds toward higher elevations [36,38,39]. Evidence that animals ingest seeds during spring migrations establishes the potential for poleward long-distance dispersal [23,43]. Bird banding data illustrate that migrating mallard ducks (*Anas platyrhynchos*) and Eurasian teals (*Anas crecca*) could allow aquatic plant species in Europe to track modeled shifts in their niches [45]. Movement models and seed retention models indicate that mallard ducks migrating from central Europe's Lake Constance could disperse plant species poleward for hundreds of kilometers [46]. Allometrically parameterized models project that birds and mammals will often, but not always, move seeds poleward or up in elevation to occupy locations made suitable by climate change [9,47]. These studies are promising, but more are needed, particularly those that provide empirical documentation of niche tracking. A global effort to measure animal-mediated niche tracking at the sites of existing studies located on elevation gradients could be especially rewarding [56,57].

Seed presence and animal movements must align to generate niche tracking

For niche tracking to occur, seeds need to be available to animal dispersers when they are moving to locations that climate change has made newly suitable for the plant (Figure 1B). A study of European plant-disperser networks found that the majority of studied plants fruit in autumn and are dispersed by birds that are migrating south, which may prevent these birds from contributing to poleward range shifts of these plant species [23]. This temporal mismatch in **phenology** could act to limit poleward shifts by autumn-fruiting species, while favoring spring-fruiting species (Figure 2A) [23].

The alignment of seed availability with niche-tracking movements also matters for nonmigratory dispersers that redistribute seeds within their home ranges. Empirical studies in temperate forests in Japan found that animals disproportionately move the seeds of early-fruiting plants up elevation gradients, while late-fruiting plants are mostly transported downslope [36–38]. During the early-fruiting period, animals were eating both lower-elevation fruits and young vegetation found at higher elevations, leading to upward seed dispersal; in autumn, animals were eating both higher-elevation wild fruits as well as fruits from agricultural areas found at lower elevations, leading to downward seed dispersal of wild fruits (Figure 2B) [37,38]. Interestingly, these studies suggest that food or other resources (e.g., roosting and denning sites) provide 'movement subsidies' that pull seeds toward or away from newly suitable locations, helping or hindering niche tracking. For example, raccoon dogs (*Nyctereutes procyonoides*) moved seeds from lower elevations to communal latrine sites located at higher elevations [37]. Further studies are needed to understand whether such patterns are found in additional systems.

Animal behavior and landscape structure strongly shape seed deposition patterns and microhabitat quality

Animals' behavioral states and activity budgets structure the amount of time they spend in different locations, shaping where seed deposition takes place [58]. For example, periods of resting or other stationary behavior can result in highly clumped patterns of seed deposition. González-Varo *et al.* [41] found that virtually all bird-dispersed seeds in an agricultural landscape were deposited under perch sites (trees and electrical pylons) and none in the intervening matrix. Similarly, seed dispersal by lesser black-backed gulls (*Larus fuscus*) and mallard ducks largely resulted in deposition occurring either in feeding sites or in resting locations, but not in the intervening landscape [49,51]. This spatial structuring of deposition can have positive effects on seedling recruitment if the recruitment niche of the dispersed seeds aligns with the environmental characteristics associated with the animals' resting, nesting, thermal, latrine, or other behaviors. Alternatively, negative effects may arise if clumping results in intraspecific seedling competition or other forms of negative density dependence, or if seeds are moved to areas that climate change is making less suitable [21,49].

Two-phase seed dispersal – where other animals disperse seeds deposited by the initial disperser – may also influence the interaction of deposition habitat preferences with **recruitment microhabitats** [59]. In an experimental system, a large proportion of the seeds of potential climate refugee species were cached by small mammals in optimal germination sites, increasing the potential for niche tracking [60]. Other seed dispersers also shape microhabitat conditions

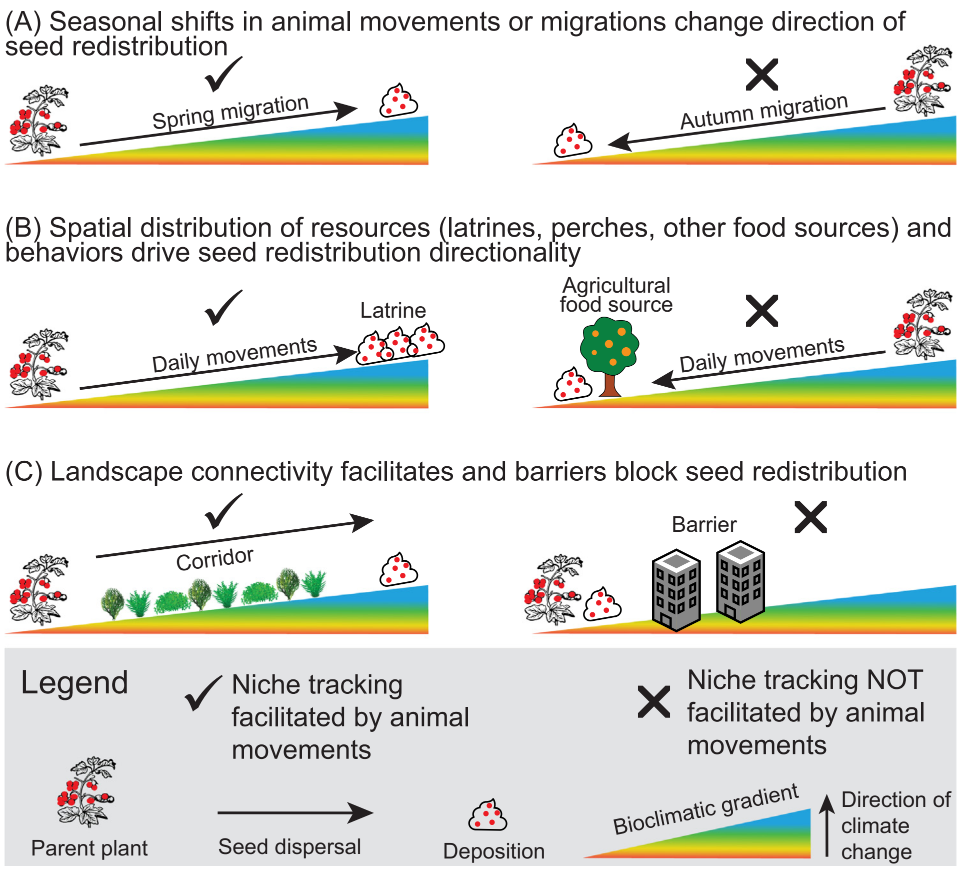

Figure 2. Animal-mediated dispersal can (A) move seeds to locations made newly suitable by climate change if the timing of seed availability coincides with animal movements (both migratory or nonmigratory) in the right direction [23,36], or (B) if key resources pull animals toward newly suitable locations after ingestion [37,39], or (C) if there is sufficient landscape connectivity to facilitate movement to newly suitable locations.

where seeds are deposited (e.g., ungulate trampling and soil disturbance, seed caching by birds and mammals, or ants depositing seeds near their nests), which may influence recruitment success [28,61,62].

Challenges and opportunities on the road forward

Plant niche shifts may not follow rules of thumb

Of the animal-mediated niche-tracking studies we reviewed, only one explicitly modeled and projected plant distributions [45], and most assumed that plant niches were simply moving upward or poleward, or related seed dispersal velocities to climate velocity. However, plant niches may move in ways not coupled to latitude or elevation, particularly if environmental variables other than temperature act to limit the species' distribution [63]. For example, resurveys of historical vegetation transects demonstrate that some plants may instead move downhill with climate change if responding to soil moisture gradients, suggesting the need for caution in applying rules of thumb [64,65]. Moreover, the distances plants will need to move will vary greatly. Plant niches may shift locally, such as from an equatorially facing slope to an adjacent poleward-facing slope, or much farther, such as across continents [66]. While climate velocity provides an elegant measure of how climatic conditions will shift across geographic space, it is sensitive to the variables and spatial grain used [19,67]. Comparing geographically averaged climate velocities to seed dispersal distances is problematic, because climate velocities often vary over many orders of magnitude [68]. Thus, generating spatially explicit projections of suitable conditions for plants may be preferable to relying on climate velocity or rules of thumb, if defensible niche models can be built from extensive species occurrence, physiological, and environmental data.

The spatiotemporal scales of plant dispersal and animal movement tracking often differ

A significant challenge lies in the different spatiotemporal scales in which animal movement and seed dispersal take place, which have influenced the scale of data collection. For example, most animal movement studies record animal locations at greater than hourly or even daily intervals, which is sufficient to understand how animals move within seasons, years, and over their lifetimes. However, when animals disperse seeds, the process (from seed ingestion to deposition) typically takes place in a manner of minutes to hours (and days at most). Behavioral state segmentation techniques require correspondingly high-resolution data to identify the beginning (foraging) or the end (deposition) of the dispersal process [49,51].

A lack of high-resolution data along migration routes may prevent us from understanding behaviors that contribute to seed dispersal, such as migratory stopovers, which are common both in bird and ungulate migrations [46,69]. For example, individual blackbirds (*Turdus merula)* will pause up to 3 weeks at stopover sites during their autumn migrations [70]. Animals may move seeds in many directions at migratory stopover sites as they forage. As a result, during autumn migrations toward the equator, it is possible that birds or mammals still provide some poleward seed dispersal services.

Niche tracking effectiveness provides a framework for further research

The seed dispersal effectiveness framework has shaped seed dispersal research by providing a ‘quantitative framework for estimating the contributions of individual dispersal agents to plant fitness’ [71,72]. It considers both the quantity and quality of seed transport by different dispersers in relation to successful plant recruitment [72]. We believe that extending this framework to ‘plant niche tracking effectiveness’ – the contribution a dispersal agent makes to helping a plant track its climatic niche and to plant fitness in newly suitable areas – would provide similar insights for niche tracking. A niche-tracking metric such as climate fidelity [8] could be used to schematically represent niche tracking effectiveness, alongside the quality and quantity metrics already used in measuring seed dispersal effectiveness. Adopting this framework will require integrating information on each component of the niche tracking process, from seed departure to successful establishment of new populations in newly suitable areas (Figure 1B).

Trait-based hypotheses can help predict niche tracking

Drawing on insights from the empirical and modeling studies described previously, we can hypothesize that specific traits of plants, animals, and landscapes may work to increase or decrease the potential for animal-mediated niche tracking (Table 2) [73]. For example, traits that increase dispersal distances in general (larger body size or movement distances) will also make niche tracking more likely. We suspect that combining plant and animal traits with landscape-level information on shifting plant niches would be even more useful for understanding the factors that directly facilitate movement of plants toward newly suitable niche spaces. For example, animals whose daily movement routines bridge broad climatic gradients may be more likely than others to facilitate niche tracking of those plants whose seeds they disperse. If these animals disperse specific plants whose fruiting period aligns with disperser movements toward newly suitable locations, and they both occur in landscapes with fewer movement barriers, niche tracking is more likely to be successful.

Implications for climate adaptation and conservation

As ecosystems adapt to changing climates, animal-mediated seed dispersal will be a central mechanism through which plant communities shift and reassemble. Some plant species will be better at niche tracking than others, leading to dispersal-driven filtering of arriving species, that in turn affects community assembly [21,23,74,75]. Conversely, seed dispersal biased toward areas made less suitable by climate change may harm the persistence of other species. As land and species managers make difficult decisions about prioritizing resources toward assisted migration or other adaptation efforts, it will be valuable to understand which species may be left behind by natural dispersal processes.

However, it is also important to understand that human influences other than climate change threaten animal-mediated niche tracking. Human activities, livestock, and commerce are dominant drivers of the spread of introduced species that could limit the ability of native species to track their niches [27]. Land use change and habitat fragmentation act to reduce seed dispersal [53,54,76], as does anthropogenic food provisioning (e.g., bird feeders) [77]. Recent defaunation has led to a modeled 60% decline in the ability of plants to move with climate change [9]. Extirpations of animal dispersers as a result of climate change may also reduce the capacity of the plants they disperse to track climate change and may in particular affect specialist seed dispersal mutualisms [3,73,78,79]. Actions that maintain or restore the ability of seed-dispersing animals to move across landscapes can work to counteract these trends (Figure 2C). Focusing connectivity

Table 2. Hypothesized traits that will act to increase animal-mediated niche tracking

Traits	Traits that increase niche tracking	Traits that increase dispersal ability in general
Animals	• Resting, latrine, or other food resources located in newly suitable locations outside the current plant distribution • Migratory movements toward newly suitable locations • More frequent and larger stopovers during migrations	• Larger body size • Larger home range size • Habitat generalists (to transport seeds to new habitats) • Generalist foragers • Higher average daily movement rates • Neutral or positive effects on seed germination rates • Dispersers create favorable microhabitat conditions (e.g., through trampling or seed caching)
Plants	• Overlapping fruiting periods of different plant species across climate gradients • Masting events that attract seed predator-dispersers from far distances	• Longer seed availability windows • Multiple dispersers • Smaller seed size (increases retention time)
Landscapes	• High landscape connectivity across climatic gradients • Vegetation is contiguous across niche boundaries • Steeper climatic gradients	• Highly connected landscapes with few barriers
Plant-animal-climate interactions	• Alignment of direction of animal migrations with the timing of seed availability • Animal migration routes pass through newly suitable locations • Preferred deposition habitats align with plant recruitment niches	

conservation efforts on linkages between current and projected distributions, or across climate gradients generally, may provide the largest contributions to effective animal-mediated niche tracking [80–82].

Concluding remarks

Pioneering studies in animal-mediated niche tracking have used a variety of empirical and modeling approaches and provide a roadmap to a better understanding of how animals can help plants move in response to climate change. Despite this progress, many questions remain about the frequency, magnitude, and nature of animal-mediated niche tracking (see Outstanding questions). Future studies will be able to draw from a range of methods and data sources. Considering all the components of effective niche tracking, from the initiation of dispersal to successful population establishment outside the plant's current distribution, can help organize future work. Finally, trait-based hypotheses can provide a route to useful generalizations and predictions of which plant species will have an easier time tracking climate change, and which ones may be left behind.

Acknowledgments

The authors appreciate helpful suggestions from the editor and two anonymous reviewers, as well as from members of the Prugh and Hille Ris Lambers labs. T.A.N. was supported by the National Science Foundation through a Postdoctoral Research Fellowship in Biology (DBI - 1907348).

Declaration of interests

No interests are declared.

References

1. Franklin, J. *et al.* (2016) Global change and terrestrial plant community dynamics. *Proc. Natl. Acad. Sci. U. S. A.* 113, 3725–3734
2. Freeman, B.G. *et al.* (2018) Expanding, shifting and shrinking: the impact of global warming on species' elevational distributions. *Glob. Ecol. Biogeogr.* 27, 1268–1276
3. Rogers, H.S. *et al.* (2021) Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 52, 641–666
4. Gelmi-Candusso, T.A. *et al.* (2017) Effects of zoochory on the spatial genetic structure of plant populations. *Mol. Ecol.* 26, 5896–5910
5. Godó, L. *et al.* (2022) A global review on the role of small rodents and lagomorphs (clade Glires) in seed dispersal and plant establishment. *Glob. Ecol. Conserv.* 33, e01982
6. Isla, J. *et al.* (2022) Drivers of individual-based, antagonistic interaction networks during plant range expansion. *J. Ecol.* 110, 2190–2204
7. Bello, C. *et al.* (2015) Defaunation affects carbon storage in tropical forests. *Sci. Adv.* 1, e1501105
8. Wang, Y. *et al.* (2023) Plants maintain climate fidelity in the face of dynamic climate change. *Proc. Natl. Acad. Sci. U. S. A.* 120, e2201946119
9. Fricke, E.C. *et al.* (2022) The effects of defaunation on plants' capacity to track climate change. *Science* 375, 210–214
10. Graae, B.J. *et al.* (2018) Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. *Perspect. Plant Ecol. Evol. Syst.* 30, 41–50
11. Pinsky, M.L. *et al.* (2022) Unifying climate change biology across realms and taxa. *Trends Ecol. Evol.* 37, 672–682
12. Pires, M.M. *et al.* (2018) Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. *Ecography* 41, 153–163
13. Fowler, J.C. *et al.* (2022) The geographic footprint of mutualism: how mutualists influence species' range limits. *Ecol. Monogr.* 93, e1558
14. Rosbakh, S. *et al.* (2022) Inferring community assembly processes from functional seed trait variation along elevation gradient. *J. Ecol.* 110, 2374–2387
15. Araújo, M.B. *et al.* (2019) Standards for distribution models in biodiversity assessments. *Sci. Adv.* 5, eaat4858
16. Charney, N.D. *et al.* (2021) A test of species distribution model transferability across environmental and geographic space for 108 western North American tree species. *Front. Ecol. Evol.* 9, 689295
17. Guisan, A. and Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009
18. Copenhaver-Parry, P.E. *et al.* (2020) Multi-scale integration of tree recruitment and range dynamics in a changing climate. *Glob. Ecol. Biogeogr.* 29, 102–116
19. Brito-Morales, I. *et al.* (2018) Climate velocity can inform conservation in a warming world. *Trends Ecol. Evol.* 33, 441–457
20. García, C. *et al.* (2017) Dispersal processes driving plant movement: challenges for understanding and predicting range shifts in a changing world. *J. Ecol.* 105, 1–5
21. Morales, J.M. and Morán López, T. (2022) Mechanistic models of seed dispersal by animals. *Oikos* 2022, e08328
22. Rogers, H.S. *et al.* (2019) The total dispersal kernel: a review and future directions. *AoB Plants* 11, plz042
23. González-Varo, J.P. *et al.* (2021) Limited potential for bird migration to disperse plants to cooler latitudes. *Nature* 595, 75–79
24. Yang, S. *et al.* (2008) Colonization genetics of an animal-dispersed plant (*Vaccinium membranaceum*) at Mount St Helens, Washington. *Mol. Ecol.* 17, 731–740
25. Green, A.J. (2016) The importance of waterbirds as an overlooked pathway of invasion for alien species. *Divers. Distrib.* 22, 239–247
26. King, S.R.B. *et al.* (2019) Potential spread of cheatgrass and other invasive species by feral horses in western Colorado. *Rangel. Ecol. Manag.* 72, 706–710
27. Zhou, Q. *et al.* (2020) Effects of climatic and social factors on dispersal strategies of alien species across China. *Sci. Total Environ.* 749, 141443
28. Kiss, R. *et al.* (2021) Zoochory on and off: a field experiment for trait-based analysis of establishment success of grassland species. *J. Veg. Sci.* 32, e13051
29. Vizentin-Bugoni, J. *et al.* (2021) Ecological correlates of species' roles in highly invaded seed dispersal networks. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2009532118

Outstanding questions

How do climate change and land use change interact to shape animal-mediated plant niche tracking?

Can animal-mediated seed dispersal along elevation gradients be observed at sites across the globe?

Has widespread loss of ungulate and other migrations led to the loss of long-distance dispersal services?

Is the season of seed availability a widespread predictor of the direction of seed dispersal (e.g., are spring-fruiting plants more likely to move uphill or poleward)?

Will animals that support niche tracking for native species also contribute to the spread of introduced, non-native species?

Can animal seed dispersal also help local genetic adaptations track climatic shifts within a species' current distribution?

What is the potential for novel plant–animal pairings? Can we predict niche tracking arising from these novel interactions?

Will directional biases in seed dispersal during climate change-mediated range shifts lead to filtering of species, affecting community reassembly? Can this filtering already be observed at colonization fronts?

Are there 'keystone disperser species' whose outsized seed dispersal services disproportionately increase the potential for effective niche tracking?

Do antagonistic interactions (e.g., herbivory) following dispersal into newly suitable areas act as a barrier to successful population establishment?

How frequently are seeds moved into newly suitable areas as the result of animals utilizing other resources (food, shelter, behavioral) in those areas?

Are seed deposition rates generally proportional to animal time expenditure in a given area?

When simulating animal-generated seed rain, which components of the seed dispersal and animal movement

30. Jordano, P. (2017) What is long-distance dispersal? And a taxonomy of dispersal events. *J. Ecol.* 105, 75–84
31. Clark, J.S. *et al.* (1998) Reid's paradox of rapid plant migration. *BioScience* 48, 13–24
32. Ramakrishnan, A.P. *et al.* (2010) Shifting dispersal modes at an expanding species' range margin. *Mol. Ecol.* 19, 1134–1146
33. Borah, B. and Beckman, N.G. (2022) Studying seed dispersal through the lens of movement ecology. *Oikos* 2022, e08310
34. Gurarie, E. *et al.* (2016) What is the animal doing? Tools for exploring behavioural structure in animal movements. *J. Anim. Ecol.* 85, 69–84
35. Kauffman, M.J. *et al.* (2021) Mapping out a future for ungulate migrations. *Science* 372, 566–569
36. Naoe, S. *et al.* (2016) Mountain-climbing bears protect cherry species from global warming through vertical seed dispersal. *Curr. Biol.* 26, R315–R316
37. Naoe, S. *et al.* (2019) Downhill seed dispersal by temperate mammals: a potential threat to plant escape from global warming. *Sci. Rep.* 9, 14932
38. Tsunamoto, Y. *et al.* (2020) Timing of fruiting rather than topography determines the direction of vertical seed dispersal by mammals and birds. *bioRxiv* Published online May 27, 2020. https://doi.org/10.1101/2020.05.24.112987
39. González-Varo, J.P. *et al.* (2017) Seed dispersers help plants to escape global warming. *Oikos* 126, 1600–1606
40. Tarszisz, E. *et al.* (2018) An ecophysiologically informed model of seed dispersal by orangutans: linking animal movement with gut passage across time and space. *Conserv. Physiol.* 6, coy013
41. González-Varo, J.P. *et al.* (2017) Unravelling seed dispersal through fragmented landscapes: Frugivore species operate unevenly as mobile links. *Mol. Ecol.* 26, 4309–4321
42. Tsunamoto, Y. *et al.* (2020) Different contributions of birds and mammals to seed dispersal of a fleshy-fruited tree. *Basic Appl. Ecol.* 43, 66–75
43. Lovas-Kiss, Á. *et al.* (2019) Shorebirds as important vectors for plant dispersal in Europe. *Ecography* 42, 956–967
44. Viana, D.S. *et al.* (2016) Migratory birds as global dispersal vectors. *Trends Ecol. Evol.* 31, 763–775
45. Viana, D.S. (2017) Can aquatic plants keep pace with climate change? *Front. Plant Sci.* 8, 1906
46. Kleyheeg, E. *et al.* (2019) A comprehensive model for the quantitative estimation of seed dispersal by migratory mallards. *Front. Ecol. Evol.* 7, 40
47. Nowak, L. *et al.* (2022) Avian seed dispersal may be insufficient for plants to track future temperature change on tropical mountains. *Glob. Ecol. Biogeogr.* 31, 848–860
48. Vellend, M. *et al.* (2006) Antagonistic effects of seed dispersal and herbivory on plant migration. *Ecol. Lett.* 9, 319–326
49. Kleyheeg, E. *et al.* (2017) Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*. *J. Ecol.* 105, 1279–1289
50. Oleksy, R. *et al.* (2017) Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. *PLoS One* 12, e0184023
51. Martín-Vélez, V. *et al.* (2021) Spatial patterns of weed dispersal by wintering gulls within and beyond an agricultural landscape. *J. Ecol.* 109, 1947–1958
52. Somveille, M. and Ellis-Soto, D. (2022) Linking animal migration and ecosystem processes: Data-driven simulation of propagule dispersal by migratory herbivores. *Ecol. Evol.* 12, e9383
53. Nield, A.P. *et al.* (2020) The spatial complexity of seed movement: animal-generated seed dispersal patterns in fragmented landscapes revealed by animal movement models. *J. Ecol.* 108, 687–701
54. Tucker, M.A. *et al.* (2021) Human-induced reduction in mammalian movements impacts seed dispersal in the tropics. *Ecography* 44, 897–906
55. Viana, D.S. *et al.* (2013) Allometric scaling of long-distance seed dispersal by migratory birds. *Am. Nat.* 181, 649–662
56. Theobald, E.J. *et al.* (2017) Climate drives phenological reassembly of a mountain wildflower meadow community. *Ecology* 98, 2799–2812
57. Hargreaves, A.L. *et al.* (2019) Seed predation increases from the Arctic to the Equator and from high to low elevations. *Sci. Adv.* 5, eaau4403
58. Spiegel, O. and Nathan, R. (2012) Empirical evaluation of directed dispersal and density-dependent effects across successive recruitment phases. *J. Ecol.* 100, 392–404
59. Enders, M.S. and Vander Wall, S.B. (2012) Black bears Ursus americanus are effective seed dispersers, with a little help from their friends. *Oikos* 121, 589–596
60. Mortelliti, A. *et al.* (2019) Small mammal controls on the climate-driven range shift of woody plant species. *Oikos* 128, 1726–1738
61. Berg-Binder, M.C. and Suarez, A.V. (2012) Testing the directed dispersal hypothesis: are native ant mounds (Formica sp.) favorable microhabitats for an invasive plant? *Oecologia* 169, 763–772
62. Mason, D.S. *et al.* (2022) Passive directed dispersal of plants by animals. *Biol. Rev.* 97, 1908–1929
63. Crimmins, S.M. *et al.* (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331, 324–327
64. Bhatta, K.P. *et al.* (2018) Downhill shift of alpine plant assemblages under contemporary climate and land-use changes. *Ecosphere* 9, e02084
65. Zhang, B. *et al.* (2022) Contrasting plant responses to multivariate environmental variations among species with divergent elevation shifts. *Ecol. Appl.* 32, e02488
66. Ackerly, D.D. *et al.* (2020) Topoclimates, refugia, and biotic responses to climate change. *Front. Ecol. Environ.* 18, 288–297
67. Hamann, A. *et al.* (2015) Velocity of climate change algorithms for guiding conservation and management. *Glob. Change Biol.* 21, 997–1004
68. Corlett, R.T. and Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends Ecol. Evol.* 28, 482–488
69. Wyckoff, T.B. *et al.* (2018) Evaluating the influence of energy and residential development on the migratory behavior of mule deer. *Ecosphere* 9, e02113
70. Packmor, F. *et al.* (2020) Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants? *Mov. Ecol.* 8, 6
71. Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107, 15–29
72. Schupp, E.W. *et al.* (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* 188, 333–353
73. Schleuning, M. *et al.* (2020) Trait-based assessments of climate-change impacts on interacting species. *Trends Ecol. Evol.* 35, 319–328
74. Albert, A. *et al.* (2015) Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. *Oikos* 124, 1109–1120
75. Kraft, N.J.B. *et al.* (2015) Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592–599
76. Teixido, A.L. *et al.* (2022) Anthropogenic impacts on plant-animal mutualisms: a global synthesis for pollination and seed dispersal. *Biol. Conserv.* 266, 109461
77. Sengupta, A. *et al.* (2022) The influence of provisioning on animal-mediated seed dispersal. *Oikos* 2022, e08276
78. Sales, L. *et al.* (2020) Climate niche mismatch and the collapse of primate seed dispersal services in the Amazon. *Biol. Conserv.* 247, 108628
79. Sales, L.P. *et al.* (2021) Climate change reshapes the eco-evolutionary dynamics of a Neotropical seed dispersal system. *Glob. Ecol. Biogeogr.* 30, 1129–1138
80. Littlefield, C.E. *et al.* (2019) Connectivity for species on the move: supporting climate-driven range shifts. *Front. Ecol. Environ.* 17, 270–278
81. Schloss, C.A. *et al.* (2022) "No-regrets" pathways for navigating climate change: planning for connectivity with land use, topography, and climate. *Ecol. Appl.* 32, e02468
82. Anderson, M.G. *et al.* (2023) A resilient and connected network of sites to sustain biodiversity under a changing climate. *Proc. Natl. Acad. Sci. U. S. A.* 120, e2204434119
83. Green, A.J. *et al.* (2021) Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. *Oikos* 2022, e08327
84. Draper, J.P. *et al.* (2022) Frugivory and seed dispersal by Carnivorans. *Front. Ecol. Evol.* 10, 864864

process are critical to include, and which are less important?

How much does long-distance dispersal contribute to the colonization of newly climatically suitable areas, and how does this depend on the rate of climate change, plant traits, animal traits, and landscape features?

Will niche tracking be more effective if seeds grow best in the microhabitats in which animals deposit them?

How do specialist and generalist seed dispersal mutualisms differ in their mediation of plant niche tracking, and in how they are affected by climate change?

85. Mulder, A.J.E. *et al.* (2021) Tracking temperate fish reveals their relevance for plant seed dispersal. *Funct. Ecol.* 35, 1134–1144
86. Nathan, R. *et al.* (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638–647
87. Rehm, E. *et al.* (2019) Animal movement drives variation in seed dispersal distance in a plant–animal network. *Proc. R. Soc. B Biol. Sci.* 286, 20182007
88. Karimi, S. *et al.* (2018) Complementary endozoochorous seed dispersal by large mammals in the Golestan National Park, Iran. *Seed Sci. Res.* 28, 294–302
89. Campos-Arceiz, A. *et al.* (2008) Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology* 89, 2684–2691
90. Bartel, R.D. *et al.* (2018) Endozoochory by mallard in New Zealand: what seeds are dispersed and how far? *PeerJ* 6, e4811
91. Calviño-Cancela, M. *et al.* (2006) Emus as non-standard seed dispersers and their potential for long-distance dispersal. *Ecography* 29, 632–640
92. González-Varo, J.P. *et al.* (2022) Identifying avian seed dispersers through DNA barcoding after rapid field sampling. *Ardeola* 69, 179–190