Review

Human-Mediated Dispersal and the Rewiring of Spatial Networks

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Humans fundamentally affect dispersal, directly by transporting individuals and indirectly by altering landscapes and natural vectors. This human-mediated dispersal (HMD) modifies long-distance dispersal, changes dispersal paths, and overall benefits certain species or genotypes while disadvantaging others. HMD is leading to radical changes in the structure and functioning of spatial networks, which are likely to intensify as human activities increase in scope and extent. Here, we provide an overview to guide research into HMD and the resulting rewiring of spatial networks, making predictions about the ecological and evolutionary consequences and how these vary according to spatial scale and the traits of species. Future research should consider HMD holistically, assessing the range of direct and indirect processes to understand the complex impacts on eco-evolutionary dynamics.

Human-Mediated Dispersal

Dispersal has become increasingly recognised as an essential process in ecology and evolution, and the past 20 years have produced exciting new approaches to understanding dispersal (Box 1). An area of particular interest is the role of dispersal in the ecological and evolutionary responses of species to anthropogenic environmental change [1,2]. For example, dispersal patterns are critical in determining the ability of species to track a changing climate or to survive habitat loss [3,4]. However, humans also affect the dispersal process itself in a variety of ways, the result of which can be characterised as **human-mediated dispersal** (HMD; see Glossary). Here, we distinguish two forms of HMD. **Human-vectored dispersal** (HVD) occurs when humans transport organisms directly. **Human-altered dispersal** (HAD) encompasses the indirect effects of humans on dispersal by altering landscape structure, dispersal vectors, and animal behaviour. Certain aspects of HMD have received much attention, such as human-vectored introductions of non-natives [5] or alteration of landscapes by habitat fragmentation [6]. However, these issues tend to be studied in isolation, and there is a lack of a holistic overview of the different aspects of HMD and how they might interact to drive ecological and evolutionary change.

Here, we show how HMD is expected to have complex effects on **spatial networks** (Box 2) of populations and communities and we demonstrate the benefits of considering the variety of HVD and HAD processes in combination. First, we review the different forms of HVD and HAD and consider the types of organism and community that are affected by these processes. Humans have probably mediated dispersal throughout our history, and there is evidence that early humans and preindustrial societies changed the distributions of species [7,8], and that humans have performed important ecosystem functions more generally [9]. However, human activities are undergoing rapid expansion in scope and spatial extent: the **human footprint**

Highlights

Research into human impacts on biodiversity would benefit from considering HMD as a central process, in particular the wide variety of anthropogenic influences on the dispersal of organisms.

Particular species or genotypes benefit from increased dispersal ability under HMD, including new linkages among areas of suitable habitat; conversely, others suffer from loss of dispersal opportunities and linkages, as well as increased costs.

In total, HMD is expected to rewire spatial networks through the reconfiguration of links among nodes, particularly by changing the distances over which individuals disperse and the creation of highly connected nodes (hubs).

As human impacts on the environment increase, ecology and conservation will benefit from considering rewiring holistically, assessing both the positive and negative impacts of HMD on eco-evolutionary dynamics.

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Box 1. Dispersal Mechanisms and Eco-Evolutionary Processes

Dispersal comprises the movement of individuals or propagules away from their birthplace, leading to reproduction in a new location and generating spatial gene flow. Active dispersal by autonomous movement is governed by the morphology, behaviour, and physiology of an organism. However, organisms can also be dispersed passively by abiotic or biotic vectors, such as animals, wind, or water. In this case, dispersal is determined by traits that affect uptake by the vector and survival during transport. Given that dispersal is an integral part of the life history of an organism, its benefits and costs are correlated with other key life-history traits [39], which can result in dispersal syndromes [91]. Dispersal is often described simply in terms of the probability distribution of where dispersing individuals settle relative to the natal sites (i.e., dispersal kernels; [92]). However, dispersal is a complex process comprising departure (i.e., leaving the natal location), transfer (movement), and settlement (establishment in the new breeding location). While these processes still result in dispersal kernels, their consideration allows a more mechanistic assessment of dispersal rooted in the movement ecology framework (e.g., [93]). For example, departure can be influenced by local densities, transfer by the resistance to movement in the intervening landscape, and settlement by local cues. This leads to a more eco-evolutionary view of dispersal, whereby dispersal processes and patterns are the result of evolving responses to the (changing) ecological environment [94].

A particularly interesting area is that of long-distance dispersal (LDD), which is usually characterised in terms of extreme and rare dispersal events [95]. LDD can connect disparate populations, allowing for connectivity and altering interaction networks (see Box 2 in the main text), meaning that it can have profound effects on eco-evolutionary dynamics. Human activities will affect the kernel through the combined effects of the different aspects of HVD and HAD. For example, HVD by automobiles could increase LDD and bias dispersal towards certain directions, while habitat fragmentation (HAD) could at the same time constrain dispersal, such that many dispersers move very short distances: we give an example of the combined effect of these specific processes in Figure I, which ultimately change eco-evolutionary processes. However, the changes to the dispersal kernel in any particular situation will depend on the type and extent of the HVD and HAD processes taking place.
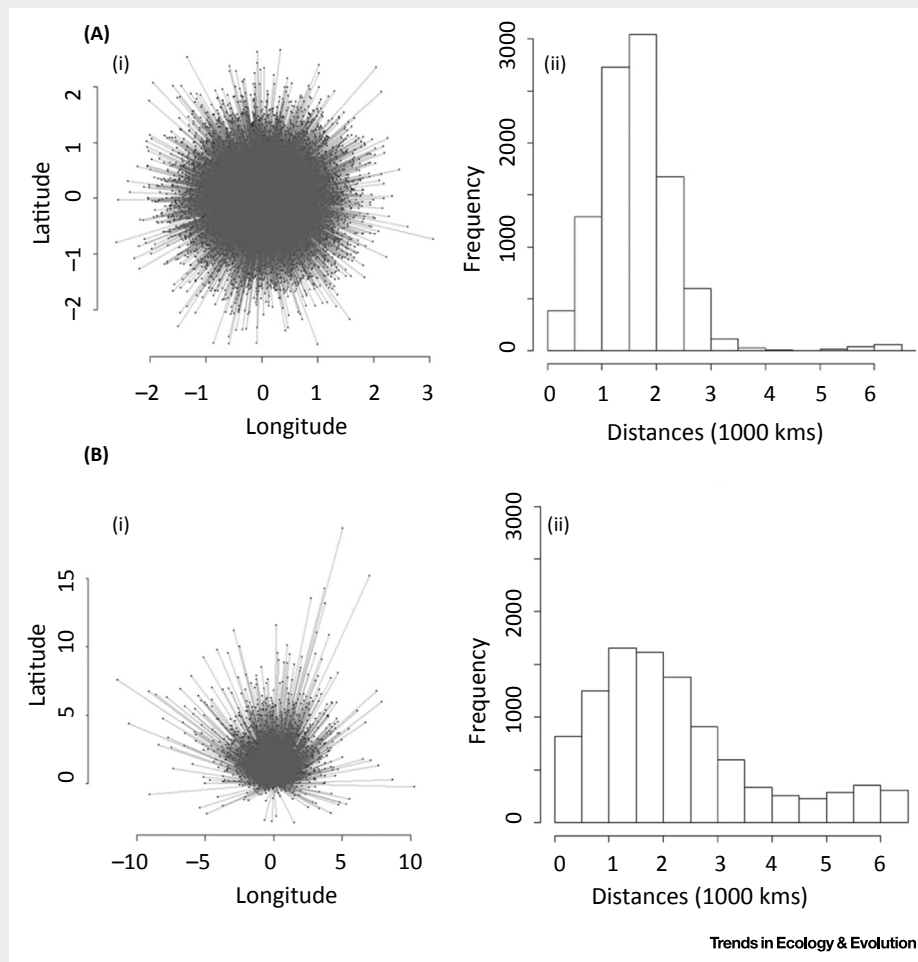

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Figure I. Effects of Humans on Dispersal Kernels. An illustration of a standard dispersal kernel (A), which has moderate dispersal distances with a few long-distance events and equal dispersal in all directions (isotropy), and a representation of a kernel under human-mediated dispersal (HMD) (B). In this example, the kernel is affected by aspects of human-altered dispersal (HAD) and human-vectored dispersal (HVD). By modifying landscape features through habitat fragmentation (HAD), human activities constrain dispersal and so increase the proportion of very short-distance dispersers. At the same time, HVD (e.g., by automobiles) increases the proportion of dispersers travelling very long distances and causes directional bias (anisotropy) by preferentially dispersing individuals to urban areas. The resulting dispersal patterns (i) and kernels (ii) show the combined effect of these HAD and HVD processes.

Box 2. Spatial Ecological Networks

Biological communities can be envisioned as local interaction networks [96], with species represented as nodes and interactions as links and defined within a finite spatial extent (e.g., sites or habitat patches; see Figure 3 in the main text). Antagonistic and mutualistic interaction frequencies depend on both the relative abundances of species (with more abundant species showing higher interaction probabilities) and the matching of traits fostering interactions (e.g., long-tongued insects with long-corolla flowers). The local interaction networks are organised over larger spatial extents by species-specific routine movement (spatial coupling) or dispersal (metapopulations and metacommunities). Spatial coupling occurs within generations and is typically mediated by resource-acquisition strategies, either foraging or mate search. Metapopulation and metacommunity dynamics emerge from dispersal, and generate changes in patch occupancy and abundances at these larger scales. The strength of the spatial interactions are determined by the specific dispersal rates, which generally decline with increased distance and landscape resistance (see Box 1 in the main text), and the abundances of species in the source population. Dispersal determines the presence and/or abundance of local species and gene flow, but local competition, predation, or mutualism interactions in the meta-community will in turn impact dispersal [97]. Therefore, the spatial and local topology of ecological networks is likely to be coupled nonlinearly through eco-evolutionary dynamics.

The dynamical properties of the spatial network are typically analysed using matrix models that combine Lotka-Volterra formulations of species interactions with species-specific among-patch dispersal rates [80] or through aggregated food-chain approaches [98]. Evolutionary dynamics can be integrated by adding gene interaction networks to produce dynamic local trait distributions that determine interspecific interaction strengths. However, the eco-evolutionary approach is still in its infancy because it relies on a comprehensive understanding of the genetic architecture underlying trait distribution and its connection to species interactions [80].

Spatial ecological networks can be altered by both human-driven changes in the local interaction network among species and changes in dispersal interactions among patches. Given that the stability of the spatial interaction network depends on the distribution of interaction strengths [99], any selection exerted by HMD on traits of species and genotypes that mediate interaction strengths will strongly impact this stability. This topological complexity eventually determines the robustness and resilience, and, ultimately, the ecosystem functioning of the entire spatial network. To what degree the hierarchical integration of gene interactions changes this view is currently an open question.

extends over 75% of the global land area [10], and it is intensifying rapidly both on land and in the sea [10,11]. Consequently, below we present evidence that increasing HMD leads to radical changes in the structure and functioning of spatial networks, and causes the **rewiring** of spatial interactions from genes to ecosystems (Figure 1). Considered in this integrated manner, the impact of HMD reaches beyond the introduction of non-native species by also changing ecological and evolutionary dynamics in native regions. We then draw conclusions about the benefits of studying HMD in a holistic manner. We do not cover HMD of human diseases, which has specific attributes and has been the topic of many studies, as reviewed in [12].

Human-Vectored Dispersal

HVD is the direct dispersal of organisms by human actions, either intentionally or accidentally (Figure 2). Intentional HVD not only comprises the transport of organisms for human use in agriculture, horticulture, hunting, biocontrol, ornamental use, or to be kept as pets, but also includes translocation for conservation purposes [13]. Accidental HVD can be by attachment to humans [14] or on and in entities moved physically by humans, such as vehicles [15], pets [16],

Glossary

Dispersal kernel: the distribution of dispersal distances from a source location, expressed as a probability density function.

Green infrastructure: a planned network of high-quality natural and semi-natural areas with other environmental features, designed to protect biodiversity in both rural and urban settings.

Hub: a highly connected node within a spatial network, which has a high number of dispersal events, either departures, arrivals, or both.

Human footprint: extent of human pressures on the environment, in terms of the area of land and water required to produce goods consumed and to assimilate waste generated.

Human-altered dispersal (HAD): a form of HMD, comprising indirect changes in the dispersal of organisms in response to any anthropogenic intervention in the population, community, habitat, or landscape.

Human-mediated dispersal (HMD): alteration of dispersal of organisms caused directly or indirectly by human movement or by other anthropogenic activities.

Human-vectored dispersal (HVD): a form of HMD, comprising movement of organisms carried by humans or on entities moved physically by humans, such as vehicles.

Red infrastructure: high-impact development, such as highways, that hampers partially or totally the movement of organisms.

Rewiring: the alteration of interactions within spatial networks, due to the removal of natural nodes and links, and the emergence of new links between existing or new nodes.

Small-world network: a network topology with low average path length (i.e., the average distance between two nodes in the network) and increased clustering compared with a random graph with the same number of nodes and links.

Soft linear development (SLD): a minor modification of the landscape that does not hamper the movement of organisms, but might instead enhance connectivity. Unpaved roads and firebreaks are examples.
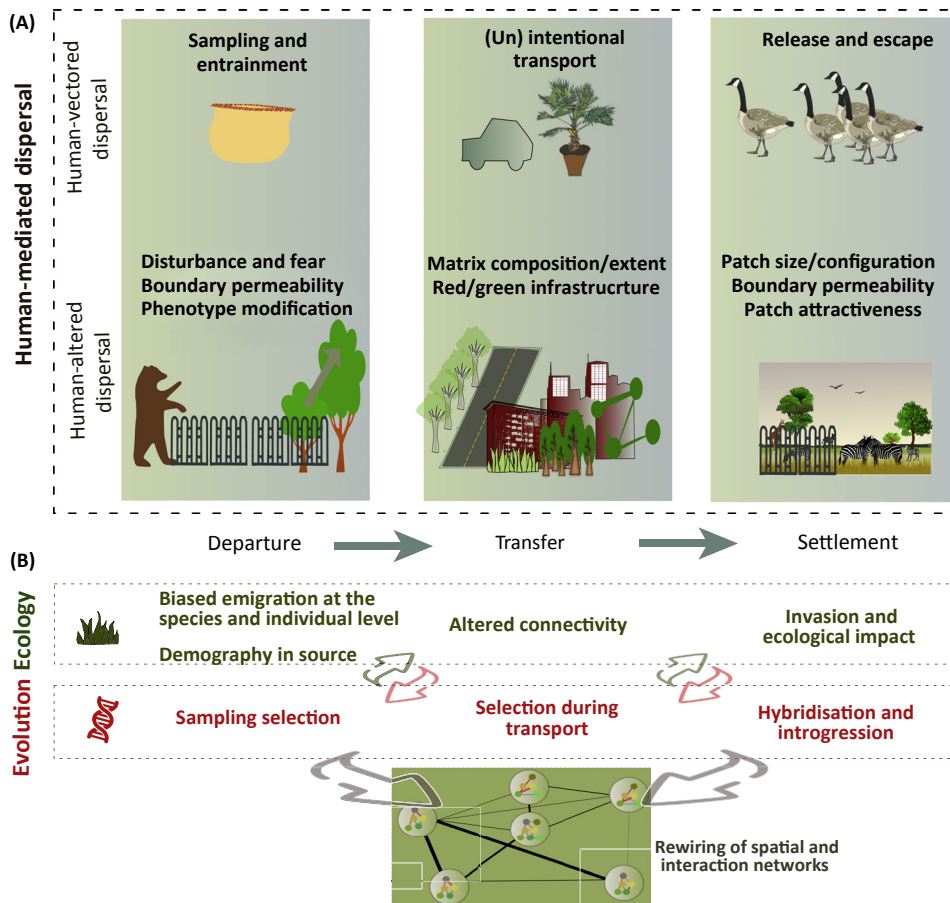
Spatial network: in graph theory, a graph where nodes and links are spatial elements; applied to ecology as a set of spatially distinct populations or communities (nodes) linked by dispersal.

Figure 1. Human-Mediated Dispersal and its Eco-Evolutionary Consequences. (A) Humans mediate dispersal by either actively vectoring movement (by nonrandom sampling, entrainment, transport, and release and/or escape) or by altering the environment so that dispersal will be facilitated or constrained (through altering patch and matrix attributes and/or phenotypes). Dispersal is mediated at the departure, transfer and settlement stages (see Box 1 in the main text).(B) These human-mediated dispersal responses scale up to ecological demographic and connectivity responses. In combination with human-imposed genetic selection during departure and transfer and genetic mixing at the settlement stage, this leads to the rewiring of spatial and interaction networks.

ornamental and cultivated plants [17], livestock [18], human introduction of wild animals [19], and human products and food [20] (Figure 2C). We differentiate the movement of animals by humans (HVD; e.g., livestock herding or pet transport) from the self-willed movement of animals managed or introduced by humans (e.g., free-roaming livestock or escaped introduced species, which is HAD). HVD is most studied in plants and animals, but human transport of other organisms such as fungi [21] and protists [22] has also been demonstrated.

For organisms to undergo HVD, they first need to be exposed to human contact and be taken up (e.g., attached or captured) for departure (Figure 1). Therefore, HVD will only occur in areas where humans are either resident or travelling through. This already encompasses most of the globe [10,11], but as human populations and frequency of movement increase, HVD will become more common, facilitated by a greater number and density of, for example, road

(A) Increasing exposure to human contact increases the likelihood of human-vectored dispersal
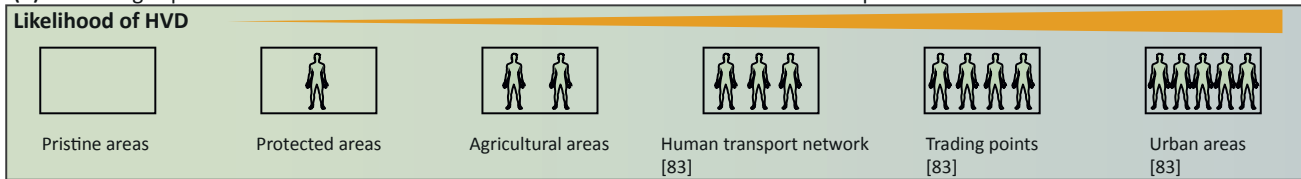
(B) Human dispersal vectors affecting dispersal speed distances
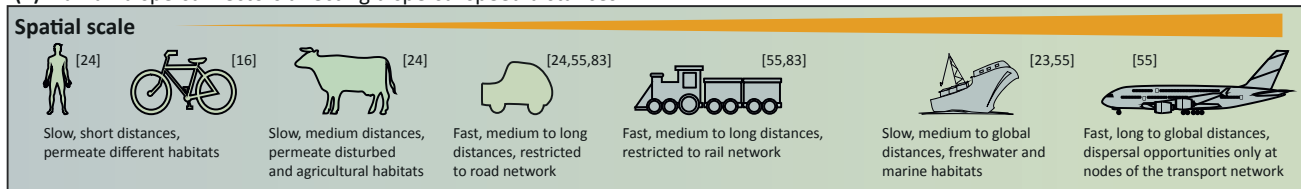
(C) Animal and plant traits that enable human-vectored dispersal
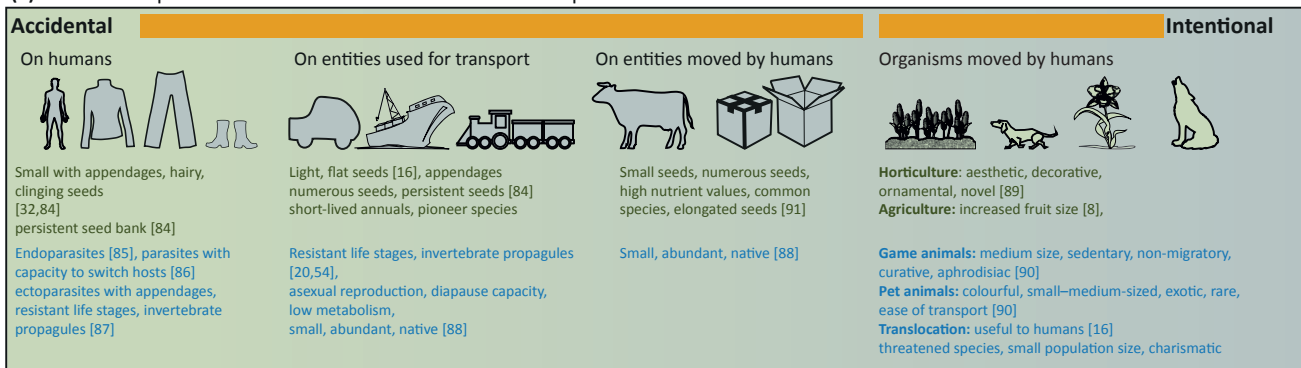
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Figure 2. Factors and Traits that Can Affect the Probability and Effectiveness of Human-Vectored Dispersal (HVD). (A) The likelihood of HVD increases with increasing human population density; we give examples of areas that might correspond to different densities. (B) The speed, travel distance, and mobility patterns of HVD types affect dispersal distances and locations. This panel depicts examples of human dispersal vectors and their associated characteristics along a distance dispersal gradient. (C) Examples of plant (green) and animal (blue) traits that enable dispersal by humans and associated entities, categorised either as accidental or intentional dispersal. Example references [8,16,20,23,24,32,54,55,83–91].

networks, urban areas, and shipping routes [23,24] (Figure 2A). The subsequent patterns of transfer and settlement (Box 1) and, thus, the shape and extent of **dispersal kernels,** will be affected by the specific HVD process. Some forms of HVD permit settlement during human transit, by active or passive deposition of individuals along the transport network. For instance, seeds attached to hikers will generally be transported along walking routes, but could detach at any point on the path. The resulting dispersal kernels often resemble those caused by attachment to animals [25] and patterns along the network will exhibit simple distance decay. By contrast, other forms of HVD have low probabilities of settlement during human transit (e.g., organisms in ballast water or ornamental plants in lorries) and will mainly settle at nodes of the transport network (ports, cities, etc.), causing discontinuous dispersal patterns dominated by long-distance jumps. Furthermore, much contemporary human travel behaviour might best be described as a continuous random-walk process, incorporating long time lags between movements and scale-free jumps [26]. The dispersal kernels resulting from this behaviour are likely to contrast strongly with the unimodal, distance decay form of many natural dispersal

kernels (Box 1). Such dispersal might best be described by gravity models, which can capture how human movement patterns reflect not only distance, but also changed patterns caused by travel between 'attractive' nodes, such as cities [27].

Long-distance dispersal (i.e., the tail of the dispersal kernel) has particularly important consequences for ecology and evolution (Box 1), and several studies have demonstrated longer distance dispersal under HVD than through natural processes. These include seeds travelling over 20 times further by attachment to hiking boots compared with dispersal by wind [14], dispersal of an invasive fish in ballast water 400 times further than the maximum under natural movement [28], and transport of marine invertebrates by shell fisheries ten times further than their maximum distances as plankton [29]. While the characteristics of human movement make it likely that dispersal distances will be increased under HVD, it is not a given that HVD will always lead to long-distance dispersal (Figure 2B). The outcome depends on the HVD process, and the resulting distances can be shorter than under natural dispersal [30].

The propensity of a species for HVD will be determined largely by traits that affect uptake and retention by the human vector and survival during transport. In research on natural dispersal, traits have been used as proxies for dispersal processes and the resulting distances travelled. For example, seeds with hooked appendages are generally dispersed by attachment to animals, while aerodynamic characteristics predict dispersal by wind [31]: the former predicts attachment to humans [32] and the latter the propensity for dispersal in the slipstream of vehicles [30]. Among animals undertaking active dispersal, a larger body size is often associated with greater dispersal distances [33]. However, as with seeds [31], this size–distance relationship is reversed among animals dispersed passively [34], and this same relationship is evident for certain types of HVD (Figure 2C). The critical traits will differ depending on whether HVD is intentional or accidental and whether organisms are transported on humans or on entities moved by humans. In Figure 2, we give examples of these various traits. Given that the types of HVD are wide-ranging, these traits are extremely varied and not necessarily the same as the traits that affect natural dispersal ability. A particular characteristic of intentional HVD is that it can involve life-history stages that are not usually dispersed by natural means. Thus, for plants, HVD can be of entire plants, plant parts or cuttings, as well as seeds and fruits. Similarly, HVD can involve stress-resistant but usually immobile animal life stages, such as eggs, larvae, or pupae in terrestrial animals [35] or sessile adults of marine invertebrates [36] (Figure 2C).

Human-Altered Dispersal
Very different from HVD, HAD occurs where dispersal is altered as an organismal response to anthropogenic changes in communities, habitats, and landscapes. HAD can result from actions designed by humans to enhance dispersal (e.g., creation of **green infrastructure**), while many other human activities can indirectly have unintended effects on dispersal, such as loss of native dispersal agents. While indirect effects of human activities are generally regarded as negative for dispersal, for example habitat fragmentation, we show below that they are not all necessarily detrimental.

Habitat fragmentation involves habitat loss leading to the division of large areas of continuous habitat into smaller patches, isolated from each other by less suitable matrix habitat. It is well documented that this fundamental change to landscapes often has negative effects on dispersal (Figure 1) [37,38], due to avoidance of the matrix and/or increased dispersal costs across less hospitable environments [39]. However, effects vary and, in some cases, dispersal can be unaffected or even boosted following fragmentation, such as where animal vectors move longer distances to access isolated habitat patches [40]. Within fragmented landscapes,

adding green infrastructure can enhance dispersal, while **red infrastructure** can further restrict movement. Green infrastructure includes anthropogenic linear features, such as canals, unpaved roads, and firebreaks {**soft linear development** (SLD) [41]}, which often act as dispersal corridors, for example by allowing the movement of frugivorous animals [41]. SLD might be able to conserve many of the structural features of the original habitat (e.g., extant or planted vegetation along canals and roads [42]).

Red infrastructure includes high-impact developments, such as highways, which can act as physical barriers that impede movement, or as behavioural barriers when animals are reluctant to cross them because they are perceived as a risk [43]. Indeed, the extent of animal movements is typically much reduced in areas with a large human footprint, such as those with a high building density [44]. The level of neophobia (i.e., a fearful response to novelty) of a particular species or individual is an important characteristic that determines how anthropogenic infrastructure affects its movement [45]. For example, while roads act as barriers to some species [46], they are preferred dispersal routes for others because movement is easier than within dense, intact vegetation [47].

Human management and harvesting of populations and communities might also impact dispersal indirectly. Nutrient enrichment of grasslands can decrease the height of wind-dispersed species relative to the sward canopy, reducing wind speed and, thus, dispersal distances [48]. Harvesting can reduce animal emigration by relaxing density dependence [49], but conversely can induce emigration through risk avoidance (landscape of fear [50]). At a broader scale, localised population control or harvesting can induce immigration from non-hunted areas, potentially creating source–sink dynamics [51]. Finally, some species suffer dispersal limitation due to the loss of their natural animal vectors through human activities, such as hunting, cascading effects of biological invasions, or anthropogenic habitat destruction [52,53].

Rewiring of Spatial Networks by HMD

The benefits of integrating HVD and HAD are clear when considering spatial networks of populations and communities and how they are maintained by dispersal [1]. As we have seen, while HVD often increases dispersal distances, different aspects of HAD can increase or decrease dispersal. Thus, HMD does not necessarily lead to higher or lower dispersal propensity or distance moved than in the absence of humans. However, humans can create new movement pathways that lead to the dispersal of organisms from locations, along movement paths, and to destinations that are different to those experienced under natural conditions (Figure 3). HMD is particularly interesting in the way that it can modify dispersal at multiple spatial scales, influencing processes such as population spread, gene flow among populations, the colonisation of unoccupied habitats, and the assembly of local communities [20,22,54]. Thus, in areas with a high human footprint, and so exhibiting multiple aspects of HMD, we might expect local dispersal to be constrained by losses of connectivity caused by HAD, while long dispersal events are boosted by HVD. In such situations, HMD-driven rewiring will have converted geographically constrained spatial networks, where most connections are between neighbouring habitat patches, into spatial networks with fewer local connections (because of fragmentation) and more long-distance connections (Figure 3). These changes can be described in terms of network topology theory [55]. Natural spatial networks can be typified as having nodes linked to nearby nodes with distance decay patterns. By contrast, HMD might lead to **small-world networks** with dispersal shortcuts, whereby any node in the network can be reached from any other node in a few steps, or scale-free networks in which most nodes have few links but a few nodes (**hubs**) have many links. HMD might also decrease the
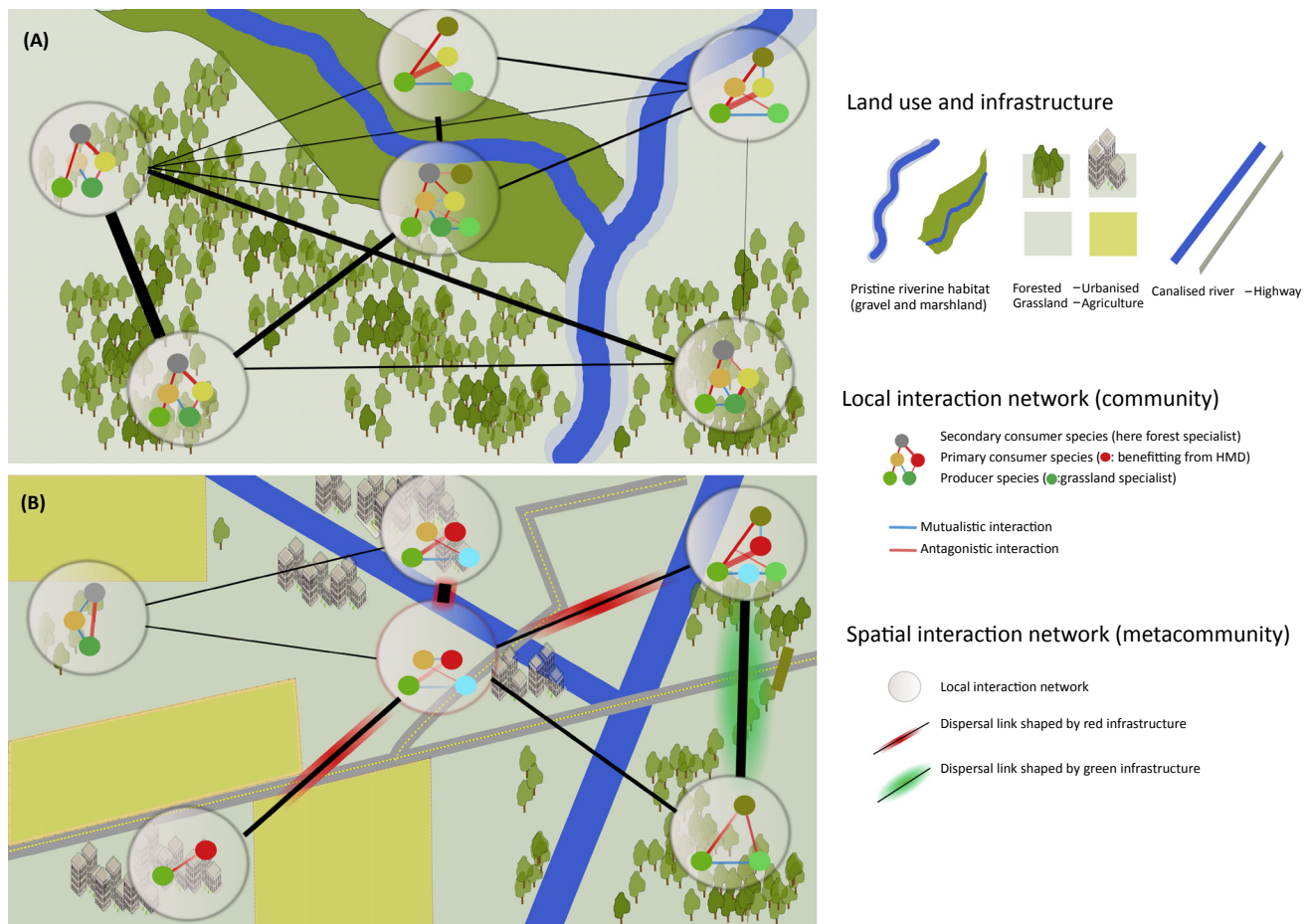
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Figure 3. Rewiring of Spatial Networks by Human-Mediated Dispersal (HMD). (A) A landscape in its pristine state comprising a river valley, and grassland and forested habitat, overlaid with a subset of locations that form a spatial ecological network. (B) Following anthropogenic change, the network is rewired under HMD. A subset of the local interaction networks is represented by different species at different trophic levels that interact either antagonistically or mutualistically. Depending on the species composition, the different metacommunities show different levels of connectivity, as determined by the species traits and the landscape matrix (black links, where the link thickness represents the strength of connectivity). The forests and the grassland habitats have their specialist species (e.g., the middle green producer and grey consumer nodes are forest species). Metacommunity-level dispersal is highest at short distances and with continuous habitat (left link between the two forest nodes), but becomes weaker when the matrix is less continuous (e.g., the upper two local interaction networks are less connected because of the river barrier).

nestedness of the spatial network by promoting the persistence of few highly dispersed species while filtering out others. We predict accidental HVD and HAD to advantage generalists showing weak interactions in the receiving community, which would stabilise local communities. Opposite patterns are anticipated for intentional HVD, for instance through conservation translocations of specialists from higher trophic positions that have strong local interactions.

Ecological Consequences of Rewiring

HMD-driven changes in dispersal patterns within ecological systems can have a wide array of impacts, which might be negative or positive depending on the characteristics of the human activities (Figure 3). While these effects are likely to be multifarious, we can make some predictions at various levels of organisation. For example, we describe above the limitation of dispersal through habitat fragmentation and loss of dispersal vectors. This has been shown

to constrain metapopulation processes, such as rescue effects [56], and to lead to population bottlenecks [57]. We expect that species dispersed by extinction-prone animals, such as large-bodied vertebrates, will be particularly sensitive to these effects. Dispersal collapse might even occur long before vector extinction, particularly when remnant vectors cannot provide sufficient dispersal [58]. Importantly, human activities rarely happen in isolation, and so we expect that, in some cases, these detrimental effects might be compensated for to a certain degree by positive effects of HMD. For example, HVD might increase dispersal rates and distances, which have been shown to benefit certain species by: connecting isolated habitat patches and so increasing metapopulation size [59]; promoting range expansions [60]; and creating dispersal hubs that can maintain metapopulations [61]. However, because increased dispersal in metapopulations might also exacerbate dispersal-driven population synchrony and the likelihood of extinction [1], we anticipate that effects of HMD on metapopulations will vary according to the relative contributions of human-altered and -vectored dispersal (Figure 3). A further consideration is how HVD changes the locations at which individuals settle. Natural dispersal, even when passive, is often directed such that individuals settle at locations that support survival and establishment [62], presumably as a result of dispersal evolution. We predict that HVD will disrupt this process if the new settlement locations are less favourable.

The combined effects of HMD on the individual species in spatial networks will drive local community and ecosystem properties and, ultimately, those of metacommunities and meta-ecosystems [63]. First, in contrast to typical views that human impacts cause foodwebs to become more connected and less modular [64], we anticipate complex changes in local communities because both mutualisms and antagonisms are shaped by both lower and higher-order interactions. These interactions are shaped dynamically by the relative abundances of the different species as determined by human-imposed changes in habitat quality and also increased immigration under HMD. Second, HMD-driven changes in dispersal patterns might eventually change the ecological functions within communities in a nonrandom fashion, for example through network-wide domination by certain species with an homogenising impact on the network structure and local functioning [65]. Here, the correlation between those traits of species promoting the likelihood of HVD, or the filtering effect of HAD, and those shaping interspecific interactions and ecological functions (e.g., body size) will condition the structural and functional consequences of HMD. Finally, we predict that HMD will change metaecosystem processes [63]. Again, depending on the human activities, we can predict different consequences. While colonising species might export nutrients by moving among or switching foraging areas [66], constrained dispersal for large-seeded plants due to the loss of large-bodied animal vectors leads to metacommunities dominated by small-seeded plants with consequences for regional carbon storage [67].

Evolutionary Consequences of Rewiring

Evidence is accumulating of evolutionary changes imposed by human activities [68]. While insights to date derive from theory or observations related to direct impacts of urbanisation, invasions, pollution, harvesting, and climate change, less conspicuous eco-evolutionary changes resulting from HMD are probably at least as important for spatial networks (Figure 1). HMD is likely to be nonrandom among individuals, thus imposing selection [69]; and genotypes with traits associated with a higher sampling probability (i.e., instigating departure; Figure 1) are likely to be moved more than under natural conditions, leading to new evolutionary associations with humans. Increased boldness in animals could, for instance, increase the chances of human-vectored as well as human-altered departure [70]. Such nonrandom sampling and release will, in this respect, not only change patterns of non-neutral gene flow, but we predict that it might also lead to feedback on communities, for instance by imposing changes in the

competitive balance among species [71]. Because experimental studies have demonstrated that these interactions are also subject to evolutionary change [72], we might expect HMD to also change food-web functioning, and eventually to feedback on trait evolution, as shown for dispersal in a theoretical study [73].

Evidence of microevolution following anthropogenic connectivity loss is documented in particular for dispersal-related traits in plants and animals and reproductive strategies in plants [74]. Human extirpation of dispersers can have similar consequences, such as rapid evolution favouring small-seeded phenotypes following the loss of large-bodied avian dispersers [75]. We know of no studies of evolutionary change in traits following connectivity improvement, although physiological selection for stress tolerance during human transfer might provide an example [76]. While microevolutionary changes to settlement processes are less likely, evolution in response to altered sampling and transfer might foster further evolutionary dynamics in human-impacted spatial networks. There is, for instance, a wealth of evidence that HMD impacts patterns of neutral genetic divergence across space, with many studies showing impeded gene flow following disrupted movement in fragmented landscapes [56]. While, in some cases, translocations have induced genetic homogenisation between the source and recipient populations [77], we can also predict that they might fuel evolution in some other circumstances by creating opportunities for hybridisation and, thus, new nodes in the human-impacted spatial network. Indeed, assisted migration or translocation has been implemented to increase the genetic diversity and adaptive potential of threatened populations within their native ranges, although often with mixed success [78,79]. If human activities lead to high rates of dispersal, this might increase genetic diversity and consequently induce stability in rewired spatial networks [80].

Concluding Remarks

We have shown that HMD can profoundly change spatial networks and can have overall beneficial or detrimental effects on species depending on their traits. While HMD can be described in terms of the fundamental dispersal processes of departure, transfer, and settlement, it can completely alter each process compared with the natural state. Within a metapopulation, HMD can change: how many and which individuals, as well as which life stages, disperse; the spatial patterns and distances of dispersal; the number of, and which, individuals survive dispersal and their condition; and the position and habitat quality of locations to which individuals disperse. Similarly, for metacommunities, HMD changes the balance among species of the likelihood of dispersing and how far, and to where, different species disperse. In this way, the many components of HMD can combine to have complex, interactive effects on eco-evolutionary dynamics. Ultimately, we believe that an understanding of the impacts of HMD on spatial networks is important for the following reasons. (1) To account better for growing human impacts on the natural environment. In the near future, the human population is expected to grow rapidly, to extend activities over more natural spaces, to expand urban areas, and to move more in terms of both individuals and trade goods [81]. As we have shown, these processes all modify dispersal in different ways, which we still understand insufficiently (see also Outstanding Questions). It appears clear that HMD will increase in magnitude and extent in the near future. (2) To avoid oversimplifications about human impacts on spatial networks. These include the general characterisation of indirect human impacts on dispersal as negative or, more specifically, the promotion of assisted migration (HVD) to allow species to track climate change. The interacting processes described in Figure 1 illustrate that a change to spatial networks might have ramifications beyond the immediate (perhaps intended) impact. (3) To encourage assessment of new causes and types of HVD and HMD. For example, drone delivery for commercial purposes might become an important means of transport at short to medium distances, to the

Outstanding Questions

How do the positive and negative aspects of HMD play out for individual species and how predictable is this in terms of the traits of species?

Are the spatial dynamics of species other than non-natives and re-introduced natives already driven by HVD?

Given that humans mostly move between human-impacted locations, is HVD taking most species into sink habitats?

Conversely, are there cases where HMD leads to directed dispersal whereby individuals are moved to habitats to which they are pre-adapted?

Are there correlations between traits promoting HMD and those traits affecting ecosystem function (response versus effect traits); how do these compare across and within species?

Do populations and, specifically, dispersal traits undergo evolutionary change following improved connectivity through HVD or HAD?

Does nonrandom sampling of specific genotypes by HMD lead to increasing maladaptation to the local environment?

Does HMD lead to unprecedented evolutionary scenarios?

Is green infrastructure working to counter habitat fragmentation and red infrastructure and, if so, under what circumstances?

How does HMD change the topologies of spatial networks, and is this generally predictable?

Can we identify new emerging hubs for HMD, at local and global scales, and can we demonstrate or even predict how proximity to these hubs alters local ecosystems?

detriment of road transport. Unlike cars, drones are not restricted to a road network and so could lead to new forms of rewiring and extend HVD into new areas. (4) To allow holistic planning of human activities that addresses both HVD and HAD to reduce negative impacts on biodiversity. Specifically, it would be valuable to bring issues such as assisted migration, green infrastructure, dispersal vector loss, and introductions of non-natives into the same discussions and planning activities. For example, construction projects should not only aim to reduce negative impacts, such as fragmentation and red infrastructure, but also plan corridors and protected areas [82]. By separating and characterizing HVD and HAD in this paper, we have provided a structure by which to understand, assess, and ultimately regulate the multiple impacts of human activities on species dispersal and spatial networks.

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