

Something in the way you move: dispersal pathways affect invasion success

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Biological invasions are caused by human-mediated extra-range dispersal and, unlike natural extra-range dispersal, are often the result of multiple introductions from multiple sources to multiple locations. The processes and opportunities that result in propagules moving from one area to another can be used more broadly to differentiate all types of extra-range dispersal. By examining key properties of dispersal pathways (notably propagule pressure, genetic diversity and the potential for simultaneous movement of coevolved species), the establishment and evolutionary trajectories of extra-range dispersal can be better understood. Moreover, elucidation of the mechanistic properties of dispersal pathways is crucial for scientists and managers who wish to assist, minimise or prevent future movements of organisms.

Extra-range dispersal

Extra-range dispersal, the movement of propagules of a species from the current range to a new area of habitat, is a process fundamental to the development of biogeographic patterns. Species dispersing naturally to, and colonising into, new habitats can lead to localised mass extinctions, speciation and the formation of new ecosystems. Similarly, the human-mediated dispersal of species to regions beyond their normal range of dispersal (i.e. introduced or alien organisms) has been a major force shaping global biodiversity, especially in the last few centuries.

Some authors have argued that the invasion phenomenon is simply a speeding up of natural extra-range dispersal to rates comparable with past geological events [1]. By contrast, other analyses have suggested that the current rate of species movements is unprecedented – a direct consequence of radical intervention by humans [2]. In this article we focus on the type, rather than rate, of movement, and in the light of recent genetic studies we argue that human-mediated dispersal differs from natural extra-range dispersal in several key aspects.

Relatively few studies in invasion biology have explored the importance of how organisms were introduced [3], but

there is an increasing focus in ecology toward understanding mechanisms of dispersal. In this article, we use the term ‘dispersal pathway’ to refer to the physical type of movement that occurs, which types of organisms are moved and also the manner of that movement, that is from where, to where, when, how often and how much. We have distinguished six general symptomatic types of extra-range dispersal pathways (Figure 1): leading-edge dispersal, corridors, jump dispersal, extreme long-distance dispersal, mass dispersal and cultivation. We describe these pathways and, in the context of the development of human civilisations, discuss how humans have influenced extra-range dispersal. We then identify and discuss the differences between the dispersal pathways in terms of genetic diversity, adaptive potential and enemy release, and highlight essential properties that can be used to define dispersal pathways. We also outline some practical (e.g. classical biological control of invasive species) and theoretical (e.g. the potential for and speed of adaptive evolution in response to new environments) benefits of studying the mechanistic properties of dispersal pathways.

Glossary

Archaeophyte: A plant species introduced to Europe between the development of Neolithic agriculture and the European discovery of the Americas [41].

Dispersal pathway: The combination of processes and opportunities resulting in the movement of propagules from one area to another, including aspects of the vectors involved, features of the original and recipient environments, and the nature and timing of what exactly is moved. The definition thus combines phenomenological and mechanistic aspects.

Extra-range dispersal: Movement of propagules to regions beyond the boundaries of their range occupied over ecological time.

Founder effects: Random genetic drift resulting in changes in population-level allele frequencies when a new population is founded by only a few individuals of the original population.

Genetic bottleneck: Decrease in genetic diversity resulting from a significant reduction in population size for at least one generation.

Introduced (or alien) species: A species that has shown extra-range dispersal owing directly or indirectly to human activity.

Invasive species: An introduced species that has sustained self-reproducing populations and can produce reproductive offspring at considerable distances from parent plants [41].

Long-distance dispersal: Dispersal of propagules over a long distance, defined either by the absolute distance travelled or by a set proportion of all propagules that disperse the farthest [9].

Propagule pressure: The number and frequency of individuals released into a region to which they are not native [15].

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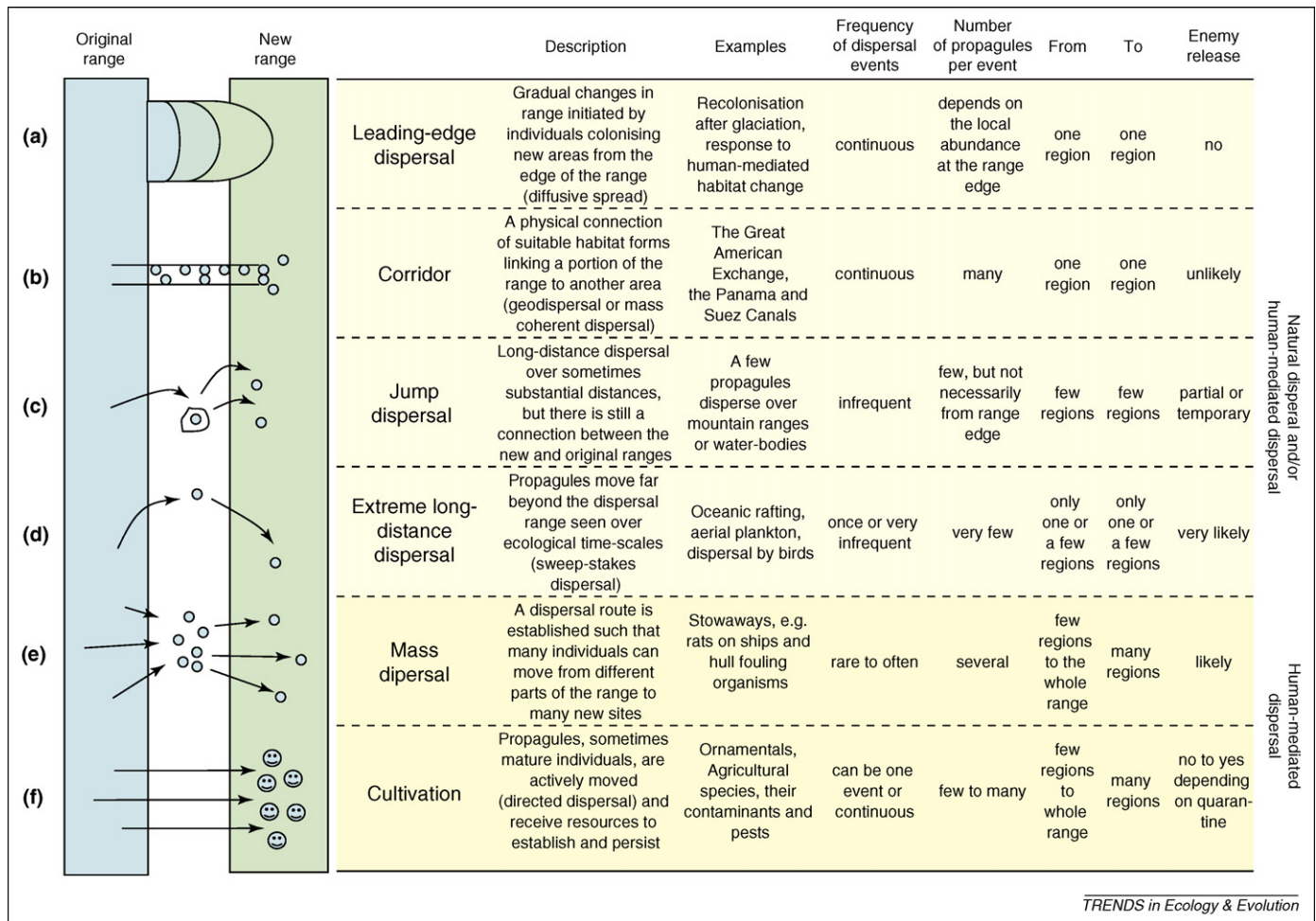


Figure 1. Extra-range dispersal categorised into six types of dispersal pathway. The categories presented are artificially delineated. In most real systems, dispersal is probably intermediate between categories or is a combination of several categories.

Dispersal pathways

The first dispersal pathway we discuss is diffusion (Figure 1a) where, as described by the leading-edge model of range shifts, species distributions expand from the edge of their range according to the normal dispersal distance of their propagules [4]. Such leading-edge range shifts tend to be within a region where the resident biota has a common recent evolutionary history with the organisms that are moving, and a close physical connection between the new and original range is maintained. Mutualists and enemies can, given time, show coinciding range shifts. However, whereas individual species appear to have tracked past climate changes in a predictable way [5], the extent to which assemblages move together or are constantly re-assembled can vary dramatically [6,7].

A special case of leading-edge dispersal occurs where a corridor of suitable habitat forms, linking previously separated potentially suitable areas (Figure 1b). At a regional scale, the biota in the original and new ranges might share recent evolutionary history, allowing secondary contact between divergent populations. But the formation of corridors can also allow a substantial exchange of flora and fauna that were separated since the breakup of Gondwanaland [8]. In contrast to classic leading-edge dispersal, which involves a gradual response to changing conditions,

corridors open up a large area of potentially suitable range that can be colonised rapidly, although the colonisation must happen through the rather narrow connection provided by the corridor.

If a new potentially suitable range is distant from the current range (relative to how far propagules normally disperse), then long-distance dispersal is required for colonisation to occur [9]. We consider two qualitatively different categories of long-distance dispersal based on the potential gene flow between the original and new ranges. With jump dispersal (Figure 1c), there is still the possibility of gene flow between the new and original range over ecological timescales, but there can be a temporary escape from enemies and mutualists during initial colonisation. By contrast, extreme long-distance dispersal (referred to as sweepstakes dispersal in the context of transcontinental and transoceanic dispersal) results in a significant separation between the new and original range [10,11]. Such freak dispersal allows areas to be colonised that are far beyond those typically reached over ecological timescales (Figure 1d). The likelihood of symbionts moving concomitantly or subsequently is very low, and populations in the new range are likely to show strong founder effects and quickly diverge from populations in the original range. Extreme long-distance dispersal has been proposed to

Box 1. Population genetic diversity: natural versus unnatural dispersal

Comparisons between the genetic diversity in native and introduced populations have shown that multiple sources of introduction are common [47,48], and that significantly reduced genetic diversity is relatively unusual in plant invasions [47] (Table 1; although see Refs [49,50], and cases of invasions coming from a single clone [32,48]). However, whereas recent molecular phylogenies linked to the paleo record have highlighted the importance of long-distance dispersal (both jump and extreme) in shaping biogeographic patterns ([12,51] but see Ref. [8]), the amount of genetic diversity introduced via natural dispersal pathways is less easy to quantify. Direct comparisons between donor and recipient populations are usually not possible as a result of uncertainty in determining when and where dispersal occurred, the degree of accumulation of mutations and speciation subsequent to dispersal, and the effect of anthropogenic influences. However, a general trend toward reduced genetic variation can be seen in molecular studies of natural dispersal: range shifts postglaciation result in a lower genetic diversity in recolonised areas

versus refugia (Box 2) [52]; low interspecific genetic differentiation between Asian species of spruce (*Picea*) is thought to be the result of colonisation via the Beringian land-bridge corridor [53]; and a putative single successful extreme long-distance dispersal from South America to Africa led to reduced genetic diversity in Old World *Lycium* species [54]. Long-distance dispersal events in the colonisation of oceanic islands are well studied and known to often result in severe genetic bottlenecks [55], but exceptions exist. For example, nine plant species from an Arctic archipelago showed no significant reduction in diversity compared to their multiple putative source populations [56].

These comparisons between natural and human-mediated species introductions show that although there is much common ground, natural dispersal pathways tend to introduce limited genetic variation from restricted sources over very large timescales, whereas human-mediated pathways tend to introduce larger proportions of genetic variation from more diverse sources over extremely short periods of geological time.

Table 1. Recent studies comparing genetic diversity in native and introduced plant populations

Species	Common name	Native range	Invaded range studied	Molecular marker ^a	Genetic diversity ^b	Probable number of sources ^c	Dispersal pathway ^d	Introduction history	Refs
<i>Aegilops triuncialis</i>	Barbed goatgrass	Eurasia	California	nSSR	–	Multiple ^{e,f} (2)	M, C	Cattle importation contaminant	[57]
<i>Ambrosia artemisiifolia</i>	Annual ragweed	North America	France	nSSR	=	Multiple ^f	C	18th century ship ballast and/or seed lot contaminant	[58]
<i>Centaurea diffusa</i>	Diffuse knapweed	Eurasia	North America	cpDNA	–	Multiple (≥2)	C	Possible alfalfa seed contaminant	[59]
<i>Centaurea stoebe micranthos</i>	Spotted knapweed	Europe	North America	cpDNA	=	Multiple	C	Possible alfalfa seed contaminant	[59]
<i>Cytisus scoparius</i>	Scotch broom	Europe	Australia, California, New Zealand, Chile	cpSSR, nSSR	=	Multiple ^f	C	19th century brewing industry ingredient, ornamental, ship ballast contaminant and dune stabiliser	[60]
<i>Hirschfeldia incana</i>	Hoary mustard	Southern Europe	UK	RAPD	=	Multiple	C?	Unknown	[61]
<i>Hypericum perforatum</i>	St. John's wort	Europe	North America	AFLP	=	Multiple	C	18th century ornamental	[62]
<i>Olea europaea cuspidata</i>	Wild olive	Africa, Asia	Eastern Australia, Hawaii	nSSR, ITS, ptDNA	–	Single (1)	C	19th century horticulture and erosion control	[63]
<i>Olea europaea europaea</i>	Cultivated olive	Mediterranean basin	South Australia	nSSR, ITS, ptDNA	=	Multiple	C	19th century agriculture	[63]
<i>Phalaris arundinacea</i>	Reed canarygrass	Europe	North America	Al	+	Multiple (≥2)	C	19th century agronomy, soil management and water treatment species	[30]
<i>Pueria lobata</i>	Kudzu	China	USA	ISSR	=	Multiple	C	19th century ornamental, erosion control and forage species	[64]
<i>Schinus terebinthifolius</i>	Brazilian pepper tree	South America	Florida	cpDNA, nSSR	=	Multiple ^f (2)	C	19th century ornamental	[65]
<i>Silene latifolia</i>	White campion	Europe	North America	cpDNA	–	Multiple ^f	C	20th century seed or ship ballast contaminant	[29]
<i>Spartina alterniflora</i>	Smooth cordgrass	Atlantic and Gulf coasts of North America	Pacific coast of North America	cpDNA, nSSR	=	Multiple ^f	M	19th century oyster contaminant	[66]

^aAFLP = amplified fragment length polymorphism; Al = allozyme; cpDNA = chloroplast DNA sequences; cpSSR = chloroplast microsatellites; ITS = internal transcriber sequences; ISSR = inter-simple sequence repeats; nSSR = nuclear microsatellites; ptDNA = plastid DNA sequences; RAPD = randomly amplified polymorphic DNA.

^bMeasures describe the invasive range with respect to the native range and are based on the original author's conclusions. + = increased; – = reduced; =, no significant change.

^cThe estimate for the number of source populations is sensitive to the sample design [67] and limited by the extent of the ranges studied.

^dM = mass dispersal; C = cultivation.

^eAdmixture absent.

^fAdmixture present in some areas.

explain range disjunctions between South America and Africa for at least 110 angiosperm genera [12]. The distinction we make between types of long-distance dispersal is relative to the typical dispersal distance of the organism. Consequently, a poor disperser could exhibit the characteristics of extreme long distance dispersal even over quite short distances..

We have also identified two additional types of dispersal pathways; these are essentially subcategories of long-distance dispersal. The regular dissemination of propagules from many sources to many locations over long distances (mass dispersal) increases the potential for introducing high levels of genetic diversity (Box 1). Although mass dispersal resulting in extra-range dispersal is often a result of human activity, it can also be the result of an evolutionary innovation, for example flight (Figure 1e). However, human activity is intrinsically linked to the directed dispersal of propagules over large scales to areas where establishment is facilitated (i.e. dispersal due to cultivation; Figure 1f). Cultivation leads to a sustained propagule pressure in the new range which dramatically increases the chances of finding suitable sites for colonisation and reduces the influence of environmental heterogeneity and Allee effects [13–15].

Invasions throughout human history

Humans began shaping global dispersal pathways relatively recently, and the rise in the number of invasive species corresponds to the development of human civilisation (Box 2; Figure 2) [2,16]. Archaeological, climatological and genetic evidence suggest that most human movement outside Africa started 40 000–60 000 years ago [17]. These early hunter-gatherer societies moved species over relatively short distances, usually between suitable or ecologically matched patches. However, as humans migrated around the world, they took with them those species with which they were most closely associated. These introductions would likely have involved only a few propagules from a single or a limited number of source regions. For example, humans brought dingoes to Australia from a small source population, possibly only once [18]. Dingoes have, until recently, lived isolated from other dog populations. Thus, depending on the importance of the species to hunter-gatherer societies, humans probably moved species in a manner similar to leading-edge, jump or extreme long-distance dispersal (Figure 1a,b,d).

Other more modern human activities have also created dispersal pathways similar to natural pathways. For example, fixed transport infrastructures, such as the Panama and Suez canals, can allow biotic interchange in the same manner as natural corridors (Figure 1b). Human activity can similarly enhance already existing natural dispersal pathways. The massive increase in floating oceanic debris in the past few centuries [19] is likely to facilitate extreme long-distance dispersal (Figure 1d) in a manner similar to historical rafting [20], although the greater abundance and slower decay rate of modern materials might increase the frequency and distance of movement of propagules via this dispersal pathway.

However, cultivation, and to a lesser extent mass dispersal, are distinct types of species movements based on

human activity. These dispersal pathways first came to prominence when the growth in trade routes between settled agricultural communities led to the movement of species in an increasingly organised fashion (Box 2; Figure 2; see <http://www.archatlas.org>). For example, ancient Egyptians traded in living adult plants as early as 2500 BC [21]. The largest increase in human-mediated species movements was immediately after the European Age of Exploration when colonial traders, explorers and surveyors took organisms over major biogeographic barriers – barriers which had previously prevented the dispersal of many, if not most, species. The accidental introduction of brown rats, the deliberate seeding of islands with goats and pigs for food and the dispersal of hull-fouling organisms are the direct and indirect consequences of the sailing ships that once ploughed the world's oceans. Similarly, the planting and tending of large stands of mature plants, such as forestry plantations, ensured that some select species had the best possible opportunity to establish and become invasive.

Although there is a clear link between volume of trade and number of invasive species introduced to a country

Box 2. Genetic consequences of the colonisation of central Europe

The current distribution of the flora and fauna of central Europe is predominantly the result of natural colonisation since the last glacial maximum, but the role of humans in shaping the biota has increased over time. Species movements can be broadly divided into three distinct periods with specific genetic consequences.

Expansion from glacial refugia – no human impact

Postglacial expansion via leading-edge dispersal results in reduced genetic variability in newly colonised areas and increased potential for admixture at suture zones [4]. In line with this, a study of 22 European trees and shrubs found that the level of allelic diversity was highest in refugial populations but heterozygosity was highest at the junction of wave fronts from disparate refugia [68]. However, long-distance dispersal of sufficient frequency, that is jump dispersal, can alleviate diversity loss by maintaining higher levels of allelic variation, thus increasing the potential for migration of genotypes and subsequent heterozygosity throughout the range [69].

Immigration with Neolithic farmers – increased human impact

Archaeophytes and other species associated with Neolithic farming spread westward into Europe from the Fertile Crescent. Leading-edge dispersal from a single source region means that such plants have reduced allelic diversity and heterozygosity owing to founder effects and reduced opportunity for admixture, as is the case for the grass *Bromus tectorum* [70]. Few sources, however, does not mean low propagule pressure, because archaeophyte seeds are thought to have been mixed with crop seeds and consistently planted by Neolithic farmers.

Invasion via global transport network – human-mediated dispersal at unprecedented levels

Global trade has increased the opportunities for organisms to be repeatedly introduced. Recent evidence was found for several sources of introduction in each of three *Heracleum* species invading Europe [71]. Similarly, multiple sources in the invasion of *Erigeron annuus* into France resulted in admixture between individuals from disparate sources, such that levels of allelic diversity and heterozygosity in the native and invaded range are similar [58]. This is contrary to the classic model of genetic bottlenecks resulting from colonisation, and exemplifies the qualitative difference between natural and human-mediated dispersal pathways.

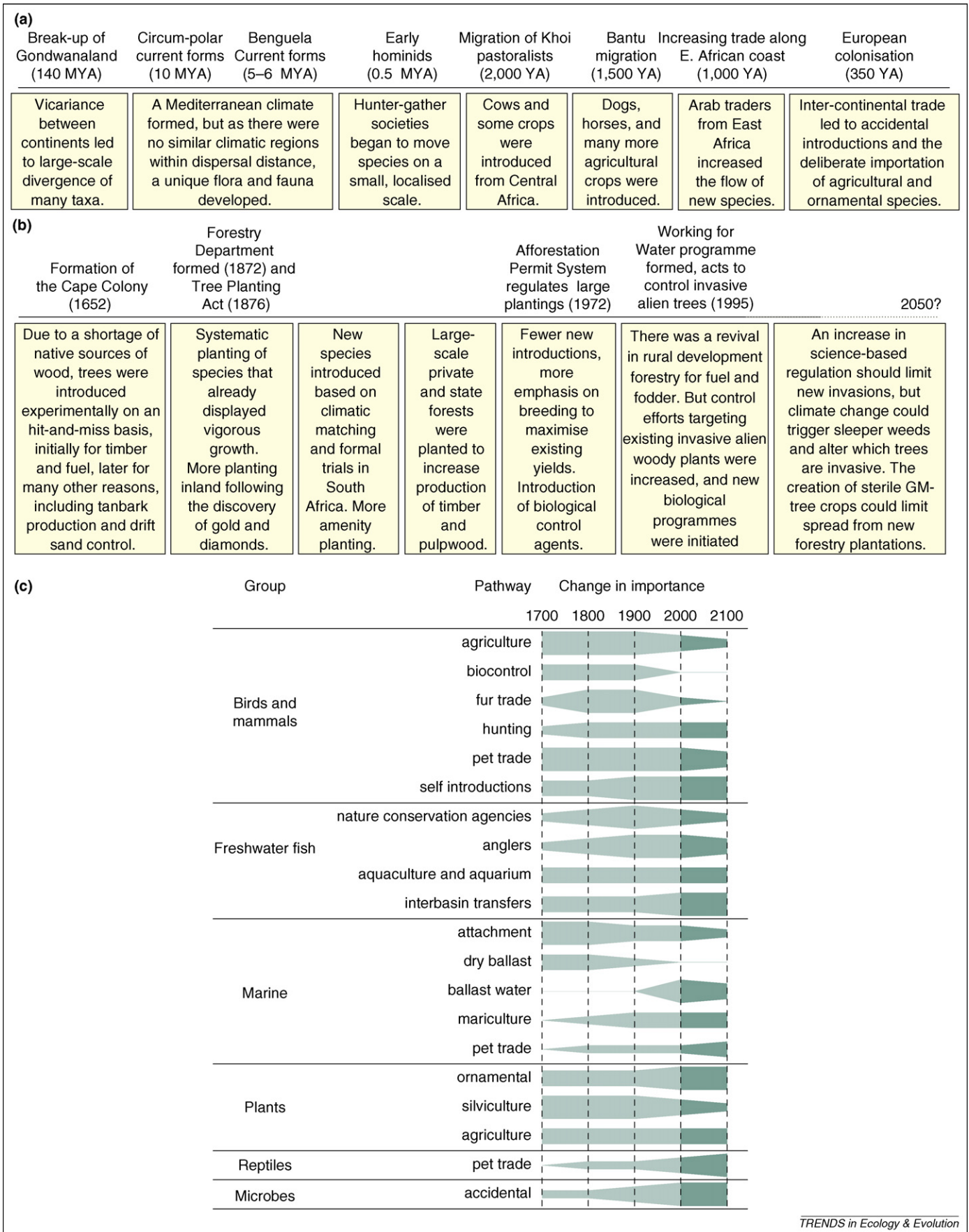


Figure 2. Trends in the introduction of alien species to South Africa. **(a)** The processes affecting South African biota can be divided into two major periods: vicariance from other biogeographic areas has allowed a unique floral kingdom to form, but over the past 2000 years these barriers have been repeatedly overcome by human movement (dates are approximate) [82]. **(b)** The method for selecting alien tree species for forestry has changed markedly over time. Although the potentially undesirable effects of

[22], the number and variety of dispersal pathways created by humans are not static. Dispersal pathways can disappear owing to changes in trade routes, technology or regulation, and new pathways can emerge (Figure 2). For example, the rise in aviation means that organisms with short life cycles (diseases in particular) can move rapidly along trade routes that previously would have been too slow to support viable propagules [23].

Postintroduction spread can also be significantly facilitated by anthropogenic activities. New foci of invasions can be created by species co-opting transport networks (e.g. jump or mass dispersal along and between roads, railways and waterways; Figure 1c,e) [24,25], or by species being actively moved and cultivated at multiple locations [26]. This means that the dispersal rate for most invasive species is much faster than expected from natural dispersal, a factor that must be incorporated in models of invasive spread [27]. Despite such postintroduction assistance to spread, the success of an invasive can still be limited by the properties of its initial introduction pathway.

Properties of dispersal pathways

The dispersal pathways identified here differ in general terms (Figure 1), but they also serve to highlight several important properties that define different dispersal pathways – propagule pressure, genetic diversity, potential for simultaneous movement of coevolved species, selectivity of what is moved, the duration of the dispersal opportunities, evolutionary distance (time since divergence) between species in the original and new ranges, and the level of human assistance provided in spread and establishment. These properties of dispersal pathways have implications both for the management of species movements (Box 3) and the speed of adaptive evolution (Box 4).

An increase in propagule pressure has been shown to increase the likelihood of successful establishment [15]. Propagule pressure and the number of source populations sampled determine what proportion of genetic diversity from the native range is introduced (see Table I in Box 1). Very low propagule pressure, as is expected for extreme long-distance dispersal, is unlikely to sample representative genetic diversity. Conversely, increased propagule pressure, such as mass dispersal, is likely to capture a large proportion of the total genetic diversity of a species. For example, some populations that were introduced to a new area via ballast water have levels of genetic diversity comparable to that of native populations [28].

The genetic diversity sampled by an introduction is also dependent on the structuring of genetic variation in the native range of a species. For example, *Silene vulgaris* and *S. latifolia* were introduced to North America along the same dispersal pathways (cultivation and/or mass dispersal). However, due to differences in mating systems and postglacial colonisation dynamics in the native range, *S. vulgaris* exhibits lower spatial structuring of genetic variation than does *S. latifolia*, whose populations in Europe show strong structuring and low individual genetic diver-

Box 3. Practical consequences of human-mediated dispersal pathways

Risk assessments for invasive organisms

Trade patterns and the nature of particular transport routes are being increasingly used in risk assessment [16,72–74], and to improve quarantine and management [40,75]. Models have included both propagule pressure and the traits of an invader to identify the routes by which particular species are most likely to establish in particular places [72,76]. As propagule pressure, traits of invasiveness and the assistance propagules receive in the new range change in a manner that is predictable from the dispersal pathway, the dispersal pathway becomes an implicit part of such analyses. It might be useful, in the future, to design models that make this link explicit.

Classical biological control

The efficacy of biological control agents used to manage invasive plants is influenced both by the genetic diversity of the introduced population and the origin of the invasive genotype(s). The selection of classical biological control agents has been improved using genetic techniques to identify source populations [77], but where species have been introduced from many mixed sources, a control agent from a single genotype might have limited effectiveness. For example, over 40 different species have been introduced to control the hybrid weed *Lantana camara*, but, to date, any partial control achieved is varietal specific [78]. Where the dispersal pathway limits the movement of symbionts, biological control might be more successful; for example, plants moved as seed without horizontally transmitted endophytes are often more susceptible to disease [79]. It will be interesting to see whether the level of success of biological control programmes is predictable from the genetic diversity of the target species and hence the dispersal pathway.

Climate change response

Species are likely to move in response to climate change in ways similar to natural dispersal: primarily by leading-edge range shifts, but also by jump dispersal and corridors. As such, the lessons from postglaciation should often apply to predicting likely climate change response [80]. We expect biotic resistance to dominate as a process limiting movements, natural enemy release to be negligible (although local release following jump dispersal is a distinct possibility) and the loss of genetic diversity to pose a potentially serious threat to biodiversity. Creating ecological corridors can facilitate more natural processes of range shifts, but we must develop methods whereby attempts to assist migration consider the properties of the dispersal pathway used.

sity. Therefore, the genotypes of *S. vulgaris* introduced in North America represented a relatively complete sample of the genetic diversity of the native range, whereas introductions of *S. latifolia* were associated with a severe genetic bottleneck [29]. Interestingly, however, in the case of *S. latifolia*, the dispersal pathway allowed an opportunity for admixture among previously isolated lineages in the invaded range. Such admixture events have the potential to increase plasticity and invasiveness [30].

In general, because modern invasions tend to be sourced from multiple native populations, recently introduced invasive species (which arrived via human-mediated dispersal pathways) tend to have higher genetic diversity than both species that followed putative natural dispersal pathways and species that were moved by prehistoric humans. Whereas genetic diversity introduced via disper-

invasive alien trees were recognised in the 19th century, concerted efforts to reduce and regulate existing invasions and prevent new ones have only become prominent in the last few decades [83]. (c) The importance of different pathways for introducing species to South Africa has changed and keeps changing. Importance is indicated by the thickness of bars. Post-2000 patterns (pale shading) are speculative [83].

Box 4. Using dispersal pathways to test the speed and potential for adaptive evolution in invasive species

Invasive species that show extra-range dispersal via different pathways (or indeed different introduction events of the same species) can provide an interesting system to test the speed and potential for adaptive evolution [33]. Recent research has shown that natural selection can drive adaptive divergence and cause reproductive isolation between populations on ecological time-scales (<100 generations) [81]. Experimental and empirical evidence also indicate that invasive species can adapt to novel environmental conditions in as little as 20 generations [33]. However, it remains to be tested whether reproductive isolation and speciation can accompany adaptation over such a short time frame. Experiments using controlled crosses between source and introduced populations can start to answer this question.

As invasive species often colonise novel environments, they provide an interesting model to examine the genetic basis of adaptation to different environments. Tests of which genes and proportion of the genome respond to environmental change and novel selection pressures will give insights into the genomic drivers of invasion [33]. A comparative genomics approach would allow a test of whether the same genes are under positive selection in independent invasions of the same species and different species invading the same area.

One of the leading hypotheses in invasion biology, the evolution of increased competitive ability (EICA), states that the invasiveness of a species is based on its evolutionary response to natural enemy release. Specifically, introduced species shift resources that were allocated for defence against natural enemies to traits linked to competitive advantage. Critically, this change must be genetic (i.e. the result of adaptive evolution) rather than due to a transient maternal effect or inherent plasticity. As EICA implicitly depends on the potential for adaptive evolution and enemy release, and both these factors vary according to the dispersal pathway, the applicability of EICA should vary among the dispersal pathways. Comparing the allocation of resources in native and introduced populations in response to natural enemies can provide a test of EICA, although careful consideration of experimental methods is necessary to rule out alternative explanations [47]. Integration of genomic methodologies, by identifying key genes under selection, will also help test EICA scenarios. Consideration of the dispersal pathway will help in identifying putative study organisms for future tests of EICA and shed light on the general applicability of this hypothesis, as well as on the question of how resilient species might be to significant biotic changes [32,33].

sal pathways can be calculated (see Table I in Box 1), the link between this diversity and invasiveness is much more subtle. Repeated introductions from many sources can increase the chance of introducing a preadapted genotype [31], increase the chance that outcrossing species establish [32], increase the standing genetic variation at adaptive loci and increase the likelihood of adaptive evolution [33], all of which might lead to higher rates of spread after colonisation. By contrast, however, some invasive species can be successful precisely because they have low genetic diversity, such as in the case of ants, where low genetic diversity limits inbreeding aggression [34]. Moreover, continuous gene flow, either from repeated introductions or cultivated individuals, can overwhelm the effects of local selection pressures and limit adaptation [33].

The permanency of a dispersal pathway can also affect how likely natural enemies and mutualists are to accompany species movements, with consequences for the success of an introduction [35,36]. Enemy release and, conversely, loss of mutualists are unlikely during leading-edge spread and corridor-type introductions

(Figure 1a,b), although corridors can act as filters in some cases. By contrast, long-distance dispersal processes provide limited connection between the original and the new range. Therefore, natural enemy release is possible for jump dispersal and highly probable for extreme long-distance dispersal (Figure 1c,d). In fact, enemy release might have been a major reason for the success of extreme long-distance dispersal events seen in the paleo record. The degree to which mass dispersal and particularly cultivation result in enemy release depends on the nature of the dispersal pathway. Plants transferred long distances as seed are likely to lose foliar herbivores, whereas the movement of live animals, for example horses, requires careful quarantine procedures to prevent the transmission of pathogens. A fruitful research direction would be to quantify and test the level of natural enemy release provided by different dispersal pathways.

Different types of organisms use different dispersal pathways in different ways. Jump and extreme long-distance dispersal intrinsically select for traits linked to dispersal and, provided that increased dispersal ability has some genetic basis, can exert significant evolutionary selective pressure. Traits that increase dispersal distances, for example a seed morphology that increases adherence to birds, increase the probability of long-distance dispersal [11,37]. Lineages resulting from such dispersal potentially also exhibit the trait, driving future colonisations. Human-mediated dispersal pathways can also exert strong selective pressures both for ruderal traits, and traits unconnected with natural dispersal (such as flower size or morphology). The largest impact of species movement occurs, perhaps, when humans deliberately select organisms with a predisposition to become community dominants (Figure 2). Importantly, the traits selected by humans continue to change over time according to sociological and economic factors (Figure 2) [38], as exemplified by clear differences in traits of archaeophytes and more recent alien plant introductions (Box 1) [39]. In particular, the proportion of introductions stemming from accidental sources increased during the 20th century [40]. Deliberate introductions often receive assistance to establish and spread. Likewise accidental introductions, such as via mass dispersal, often involve the introduction of propagules to highly disturbed habitats, for example ports, roadsides and industrial sites, where unaided establishment is maybe more likely than in habitats with lower levels of disturbance.

The taxon specificity of some aspects of dispersal pathways has already been noted. Propagule pressure often determines the success in vertebrate introductions [15], whereas residence time is a better predictor of plant invasion success [14]. It will be increasingly important not just to appreciate the differences between taxonomic groups, and similarly between natural dispersal and biological invasions, but also to understand and quantify these differences based on the essential properties of the dispersal pathways.

Conclusions and future directions

Recent evidence from genetic studies combined with historical introduction records has shown that most

biological invasions are the result of multiple introductions from multiple sources to multiple locations, in contrast to dispersal and spread through natural processes. Human-mediated dispersal tends to introduce higher levels of within-population genetic diversity, is much more likely to facilitate admixture and results in more rapid increases in range size than natural dispersal, particularly for dispersal over great geographic distances. The novelty and consequence of dispersal pathways created by humans mean that biological invasions differ from natural dispersal and spread not only quantitatively in terms of key dynamics (e.g. propagule pressure) but also qualitatively (e.g. in the kinds of species that can be dispersed). Therefore, the term and concept 'biological invasions,' as a biogeographic phenomenon intrinsically linked to human-mediated dispersal pathways [41], should be separated from considerations of ecological dominance or pest status [42], although these issues are important consequences of dispersal pathways. This clarification in terminology highlights that the differences between extra-range dispersal as seen in the paleo record and human-mediated dispersal pathways will affect how we manage species movements (Box 3).

There has been progress in developing the theoretical aspects of the properties of dispersal pathways. Disturbance can assist colonisation, but too much disturbance can limit establishment [43]. Phylogenetic analyses suggest that the probability of invasive success changes with the degree of evolutionary divergence between the new and the original range [44]. The major mechanisms of long-distance dispersal have been studied and categorised [37], and much progress has been made using mechanistic and statistic models to explore invasive spread within a new suitable range [9,27]. A major challenge in the following years will be to build on these theoretical findings, and, more importantly, to test them by measuring the contribution of propagule pressure and the other components of dispersal pathways to invasive success [45].

Meeting many of the main challenges in applied ecology will rely on our ability to deal with species movements, including areas as diverse as using reintroduction biology for conservation; understanding and managing the impacts of climate change; and assessing the impact of releasing biofuels and genetically modified organisms into the environment. In the same way that the ecological and evolutionary consequences of human-imposed selection pressures have been productively explored in agriculture, forestry and fishery science [46], improving our understanding of the properties and mechanisms of extra-range dispersal of species, and not simply the broad types of dispersal, will help us better manage and understand biological invasions.

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