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Review

Dispersal Reduction: Causes, Genomic Mechanisms, and Evolutionary Consequences

J.M. Waters,[1,*,@] B.C. Emerson,[2] P. Arribas,[2] and G.A. McCulloch[1]

Recent biological analyses suggest that reductions in dispersal ability have been key drivers of diversification across numerous lineages. We synthesise emerging data to highlight similarities regarding the causes and consequences of dispersal reduction across taxa and ecosystems, as well as the diverse genomic mechanisms underpinning these shifts. Natural selection has acted on standing genetic variation within taxa to drive often rapid – and in some cases parallel – losses of dispersal, and ultimately speciation. Such shifts can thus represent an important nexus between adaptive and neutral diversification processes, with substantial evolutionary consequences. Recognition of the links between these concepts that are emerging from different fields, taxa and ecosystems is transforming our understanding of the fascinating role of dispersal reduction in the formation of biodiversity.

Reductions in Dispersal Ability

A key goal of ecological and evolutionary research is to reveal the processes that generate biodiversity over space and time. The evolution and maintenance of dispersal ability have long been recognised as being important for the geographic spread and ecological diversification of numerous biological clades [1–4]. Despite the potential advantages conferred by dispersal ability (e.g., reduced competition; colonisation of new habitat patches [5]), this strategy also carries substantial energy costs and risks [6]. This tension is highlighted by the fact that major reductions in dispersal ability (**dispersal reduction**; see Glossary) have evolved repeatedly across the tree of life. This trend appears to be clear in birds, and also in insects, where nearly every order provides examples of multiple losses of flight [7,8]. Newly emerging data are transforming our understanding of the commonalities and consequences of dispersal-reduction processes across numerous lineages. We synthesise here recent widespread evidence across a diversity of ecosystems and taxa (later and Figure 1) on the causes, genomic mechanisms, and evolutionary consequences of a reduction in dispersal capacity. We further explore the role of these shifts within a novel niche-based model explaining the patterns of geographic speciation.

Terrestrial Ecosystems

Flightless birds on **oceanic islands** (Figure 1A) represent iconic cases of dispersal reduction. Indeed, flightlessness has evolved repeatedly in numerous avian lineages, and some clades (e.g., ratites [9–11], anatids [12], and rails [13,14]) show abundant evidence of repeated flight reduction, particularly on islands [15]. Wings have also been lost repeatedly within nearly all insect orders, and probably thousands of times within the Coleoptera alone [7]. The loss of flight in insects has been regularly linked to particular habitats such as soil and caves [16,17]. Wing reduction in insects is also widely associated with island [18] and montane [19] (Figure 1B) assemblages, and there is a similarly substantial literature on dispersal reduction in island plants [20–22] (Figure 1C). The repeated association of islands with reduced dispersal capacity in birds, plants, and invertebrates has captivated the attention of biologists [15], but in the latter case has received only limited empirical assessment (Box 1).

Highlights

Dramatic reductions in dispersal ability have evolved repeatedly across diverse taxa and ecosystems.

Dispersal reduction can be driven either by spatial or ecological causes. Repeated losses of dispersal in 'insular' habitats (e.g., island and alpine ecosystems) suggest that both isolation and habitat shifts can underpin loss of dispersal.

The 'transporter' hypothesis may provide a key mechanism for the 'spread' of dispersal reduction, and widespread parallel evolution has been revealed by recent genomic analyses of birds, fishes, and insects.

Ecological gradients can drive both gradual and rapid dispersal-reduction events.

[1]Department of Zoology, University of Otago, 340 Great King Street, Dunedin 9016, New Zealand
[2]Island Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (IPNA)–Consejo Superior de Investigaciones Científicas (CSIC), La Laguna, Tenerife, Canary Islands 38206, Spain

*Correspondence:
jon.waters@otago.ac.nz (J.M. Waters).
@Twitter: @jon_waters_nz

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Freshwater Ecosystems

Reductions in marine migratory ability and/or salinity tolerance are a widespread phenomenon in diverse freshwater taxa [23–25]. Repeated losses of **diadromy** are particularly well characterised in radiations of salmonid [26], gasterosteid [27,28], and galaxiid [29–31] fishes, and there are many cases of repeated 'landlocking' following colonisation of postglacial lakes (Figure 1D). Rapid reductions in salinity tolerance have also been documented for numerous marine invertebrate lineages entering freshwater ecosystems [23]. In aquatic insects, wing reduction (as well as eye loss and pigment reduction) is a repeated feature of water beetles colonising subterranean aquifers [32], and multiple studies point to diminished dispersal capacities in species inhabiting running waters compared to related species in standing systems [33–35].

Marine Ecosystems

For sedentary marine species that rely on passive transport, loss of buoyancy of larval or adult propagules can substantially decrease dispersal ability [36]. In macroalgae (e.g., southern bull kelp, *Durvillaea* spp.), for example, losses of buoyancy (e.g., transitions from hollow-bladed to solid-bladed adult ecotypes) can drastically reduce potential for trans-oceanic rafting [37] (Figure 1E), and non-buoyant lineages are typically restricted to single landmasses [38]. Similarly, transitions from planktonic (dispersive) to benthic/brooding (non-dispersive) larval development have occurred in numerous marine invertebrate taxa [39–41], with major implications for biogeography and genetic connectivity [42–44] (Figure 1F).

Causes of Dispersal Reduction

Reductions in dispersal ability are caused by processes that alter selective pressures on dispersal traits. Causes of dispersal reductions emerging from recent literature can be broadly grouped into (i) purely spatial causes, such as the colonisation of isolated (and commonly reduced) habitat patches for a lineage; and (ii) ecological causes, namely shifts in the abiotic and/or biotic conditions that a lineage experiences. These two causes may act in isolation or jointly. The most paradigmatic examples of reductions in dispersal ability have been associated with the colonisation of islands [15,45], and dispersal reduction is indeed one of the most frequently invoked insular syndromes. Owing to the isolated nature of islands and other patchy ecosystems (e.g., calcrete aquifers [32]), spatial isolation has often been inferred to play a primary role in such dispersal reduction by acting via direct negative selection against dispersive individuals (given their reduced probability of finding a suitable habitat relative to non-dispersers) [46,47]. However, several authors have also highlighted a role for ecological causes of island dispersal reductions, citing changes in biotic and/or abiotic conditions (even without habitat shifts) that are frequently associated with the colonisation of insular settings. It has been demonstrated, for example in the case of island birds, that reductions in dispersal are not only significantly associated with island size but also with decreased predation pressure [15] (Figure 2A). Similarly, other researchers have proposed that insular flight reduction is linked to diminished resource availability and the emergence of conflicting pressures [48], where dispersal reduction could be the byproduct of trade-offs involving selection for other traits (e.g., juvenile survivorship or competitive ability in the case of insects [22]). In the case of calcrete-aquifer insects, reduced dispersal may also reflect a combination of spatial and ecological causes, where wing reduction is partly a side-effect of adaptation to the singular conditions of these fragmented subterranean habitats (e.g., [32]).

Perhaps some of the clearest evidence for ecological causes of dispersal reduction comes from associations between dispersal and habitat variation. In the case of insects, wing-reduction events have been frequently attributed to habitat transitions that are linked to changes in habitat features such as stability [7,49,50], abiotic stress [51], or habitat discontinuity [32]. Recent

Glossary

Convergent evolution: the independent evolution of analogous traits in unrelated lineages.
Diadromy: life cycles that include movement between freshwater and marine ecosystems.
Dispersal reduction: decreased spatial displacement of individuals and reproductive propagules, resulting in diminished gene flow among populations.
Ecological selection: where strictly ecological processes govern the transmission of heritable traits.
Genomic islands of divergence: small regions of the genome that are tightly associated with adaptation and that are resistant to gene flow.
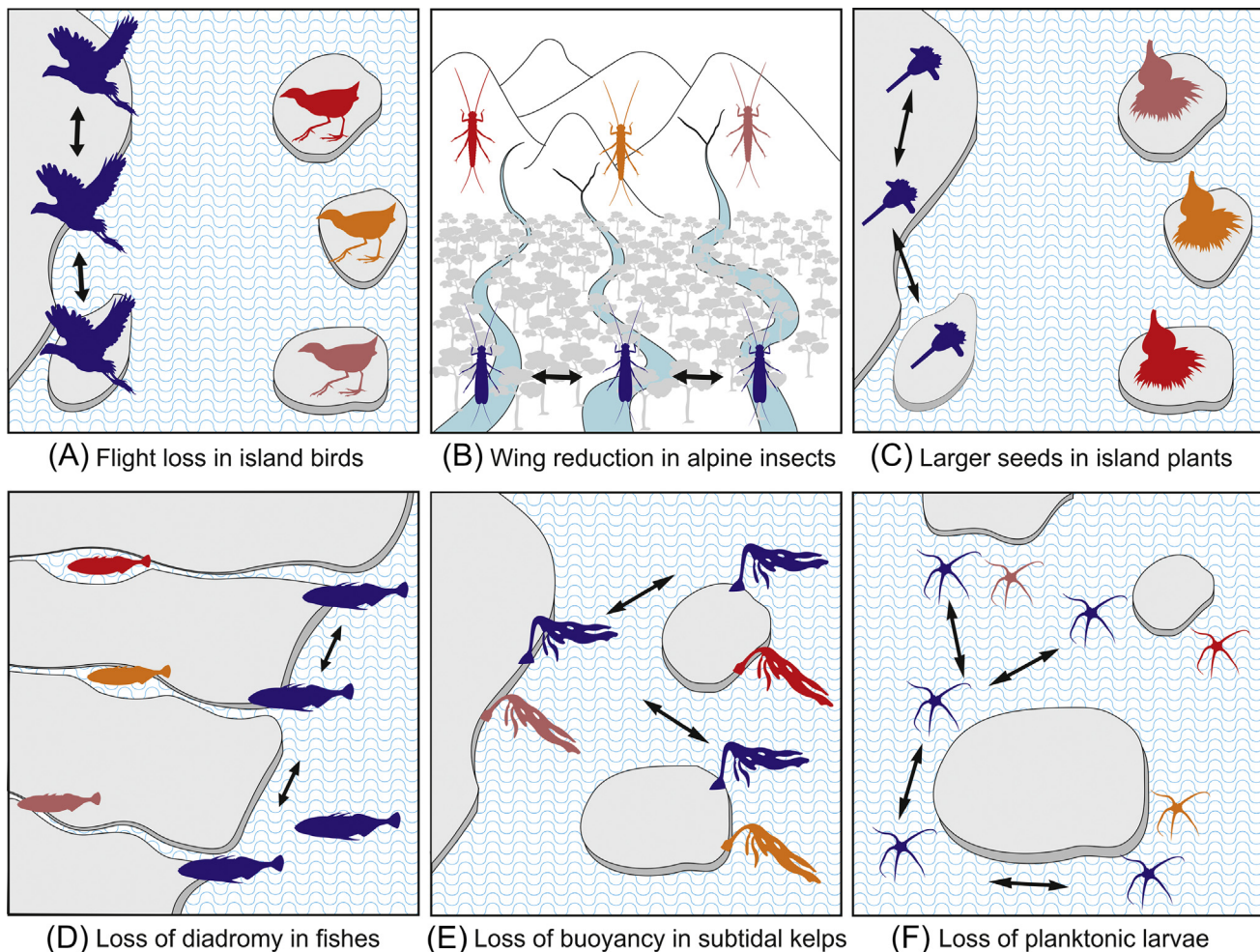**Neutral evolution:** random genetic drift of alleles that are selectively neutral.
Oceanic islands: islands that do not sit on a continental shelf and are typically volcanic in origin.
Parallel evolution: the independent evolution of similar traits in related lineages.
Planktotrophic larvae: juvenile individuals that drift in the ocean, feeding on plankton.
Transporter hypothesis: the process by which gene flow introduces adaptive alleles into different regions, thus facilitating parallel selection on the same adaptive alleles in distinct populations.
Viviparity: brooding of early developmental stages within the parental body until birth.

(A) Flight loss in island birds **(B)** Wing reduction in alpine insects **(C)** Larger seeds in island plants

(D) Loss of diadromy in fishes **(E)** Loss of buoyancy in subtidal kelps **(F)** Loss of planktonic larvae

Trends in Ecology & Evolution

Figure 1. Examples of Dispersal Reduction. Reduced dispersal has evolved repeatedly across a wide range of taxa and ecosystems, often leading to genetic isolation of dispersal-limited lineages. In the schematic examples, ancestral lineages with higher dispersal potential (connected by gene flow, arrows) are in blue, whereas their dispersal-limited derivatives are indicated in red, orange, and brown. (A) Flight reduction in island birds (e.g., rails [13,14]). (B) Wing reduction in alpine insects (e.g., *Zelandoperla* stoneflies [53,59,102]). (C) Increased seed size in island plants (e.g., *Fitchia* sunflowers [20,21]). (D) Loss of marine migratory ability in freshwater fishes (e.g., *Gasterosteus* sticklebacks [27,28]). (E) Transitions from buoyant intertidal to non-buoyant subtidal seaweed ecotypes (e.g., *Durvillaea* kelps [38]). (F) Loss of planktonic larval dispersal in marine invertebrates (e.g., *Astrotoma* brittle stars [43]).

examples have provided mechanistic evidence for such processes in alpine insects, where **parallel evolution** of wing reduction in individual species is associated with repeated adaptation to high-altitude habitats [52–54] (Box 2). For aquatic insect lineages, contrasting habitat stability [e.g., standing (lentic) versus running (lotic) water; tidal versus seasonal marshes] has been suggested as an ecological driver of shifts in dispersal capacity [49,50], even between closely related species [34,35]. In the case of fish lineages, loss of a marine migratory phase seems to be promoted by ecological causes such as drainage geomorphology, habitat quality, and competition [24]. In the marine realm, reductions in larval dispersal {e.g., transitions from **planktotrophic larvae** to lecithotrophic (yolk-feeding) development, and switches to **viviparity** [39]} are also associated with habitat transitions that are linked to habitat features such as ocean temperature [41,55], habitat productivity, and/or environmental predictability [40]. In buoyant seaweeds, for which passive drifting represents an important means of coastal and trans-oceanic

Box 1. Oceanic Islands as Drivers of Dispersal Reduction

The loss or reduction of dispersal ability is often considered to be a key feature within the generalised island syndrome [22] that describes directional differences in attributes between island taxa and their continental relatives. This trend has been repeatedly suggested in plants, birds and – perhaps most famously – insects, where Darwin [46] speculated that the incidence of flightless species on Madeira (as described by Wollaston [47]) could be explained by a selective disadvantage for dispersing individuals that might well perish in the sea. However, comparisons of the incidence of flightless species between island and continental areas have led to the conclusion that no selective arguments are required because there is no discernible tendency for oceanic islands to have higher frequencies of flightless species [19]. Alternatively, if islands are more likely to be colonised by flighted species, as would seem plausible, then secondary loss of flight would be necessary to explain similar proportions of flightless species compared to continental areas. There are good reasons to expect such a trend, building on Darwin's [46] original argument. If the trade-off relationship reported for reduced dispersal investment and higher reproductive investment in insects (e.g., [106,107]) is broadly generalisable, then we might indeed predict an island rule for secondary flightlessness in insects, although comparative data are lacking. In the case of birds, a recent comparative analysis does suggest a general trend toward flightlessness in island birds [15]. However, instead of the purely spatial causes that have been suggested to explain flightlessness in insects, the results of this study argue that dispersal reduction evolves because of release from predators – an ecological cause. Although many studies suggest a general trend toward reduced dispersal ability in island plants ([108] for examples), it has recently been highlighted that this trend might simply be a passive byproduct of selection for large seeds [22] (see Outstanding Questions). There are thus parallels across all three taxonomic groups, and there is an emerging consensus that, when dispersal loss does occur, it is likely to be helped along – or wholly driven – by indirect benefits to the organism. Particularly with regard to insects and plants, however, more comparative data will be necessary for a more complete understanding of the relative incidence of dispersal reduction on islands, the selective agents at play, and their relative roles (see Outstanding Questions).

dispersal [37,56], secondary loss of buoyancy may stem from ecological transitions to exploit subtidal niches [38], and where dispersal reduction is thus an incidental effect of these ecotypic shifts.

Some particular clades appear to be especially prone to dispersal reduction [57]. For instance, diadromous fish that readily colonise lakes can repeatedly lose their marine migratory larval phases [27], and this may be particularly the case for strong-climbing species that penetrate far inland to reach alpine tarns [58]. Similarly, asterinid sea stars may be predisposed to repeated loss of planktotrophic larval development under environmental gradients [44]. Weak-flying insects
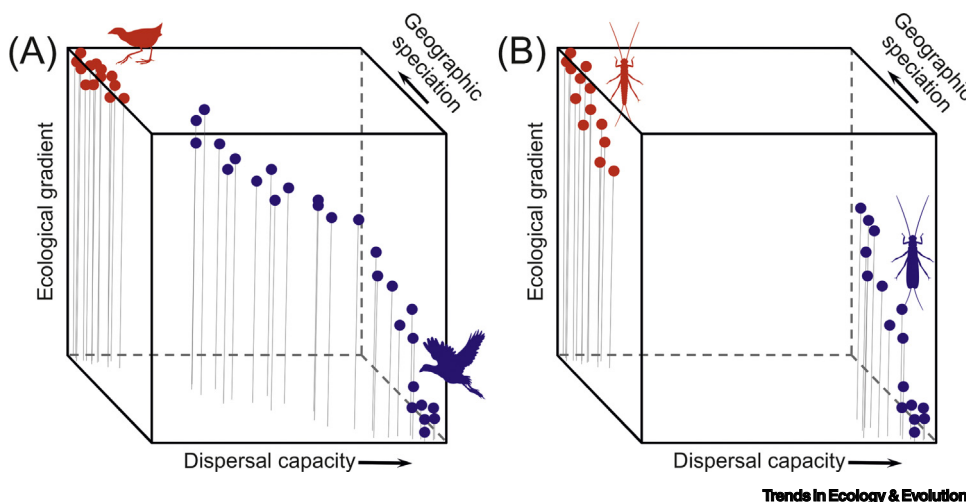

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Figure 2. Dispersal Reduction is a Nexus between Ecological Selection and Geographical Speciation. In both schematic examples, selection along environmental gradients reduces dispersal potential, which in turn increases the probability of population structuring and geographical speciation. (A) Flight reduction in island birds. (B) Flight loss in alpine insects. Flighted lineages are indicated in blue, flightless in red. In (A), flight ability may diminish gradually and predictably in volant birds before being lost completely (e.g., [11,12,15]). In (B), dispersal ability can be highly bimodal in insect populations – being essentially 'all or nothing' (e.g., by being constrained by a simple wing polymorphism; e.g., [51,53,74]).

Box 2. Repeated Dispersal Reduction in High-Altitude Ecosystems

Loss of dispersal potential is a repeated and distinctive feature of high-altitude assemblages, and this phenomenon has been particularly well characterised for montane insect taxa that have lost their ability to fly [19,52–54,57,59]. Darlington [109], for instance, compared diverse beetle assemblages at different altitudes in New Guinea, noting 'Wing atrophy is insignificant among the lowland forms … [whereas] 95 percent of the carabids on the highest mountain-tops have atrophied wings'. Recent altitudinal transect analyses from New Zealand mountains have similarly revealed striking contrasts – even at the intraspecific level – where wing-polymorphic insects show marked increases in wing reduction over small spatial scales linked to the alpine treeline [53,59]. These findings are mirrored by analyses from the mountains of Japan [54] and the Galapagos [52] which similarly reveal parallel evolution of wing-reduced high-altitude insect ecotypes. Together, these compelling data imply that exposure to high-altitude conditions (e.g., winds) explains the increasing prevalence of insect dispersal reduction in montane ecosystems at the species and population levels (see Figures 1B, 2B, and 3 in main text). Comparable trends are now also emerging for botanical assemblages, where the majority of plant species in Australia's alpine flora [110] exhibit substantially lower seed-dispersal capacity than predicted for terrestrial plants more generally [111]. Although these macroecological trends might simply stem from the relatively small stature of alpine plants (with lower release height for dispersive propagules), Morgan and Venn [110] noted that an unusually high proportion of alpine plants also lacked alternative means of long-distance dispersal, contrasting with adaptations that are relatively common in lowland plant communities. Some of the earlier phenomena suggest that purely spatial causes can reinforce dispersal reduction for taxa occupying highly fragmented (effectively 'insular') alpine habitats. The possibility that isolated montane habitats can function as 'islands' for dispersal-limited upland taxa has also been suggested for flight-reduced alpine birds – which similarly show unexpected phylogeographic diversity [112]. Although non-dispersive alpine populations experience rapid rates of genomic evolution [102] (see Figure 2B in main text), this diversification may be somewhat offset by increased rates of extinction, especially under rapid global change [113].
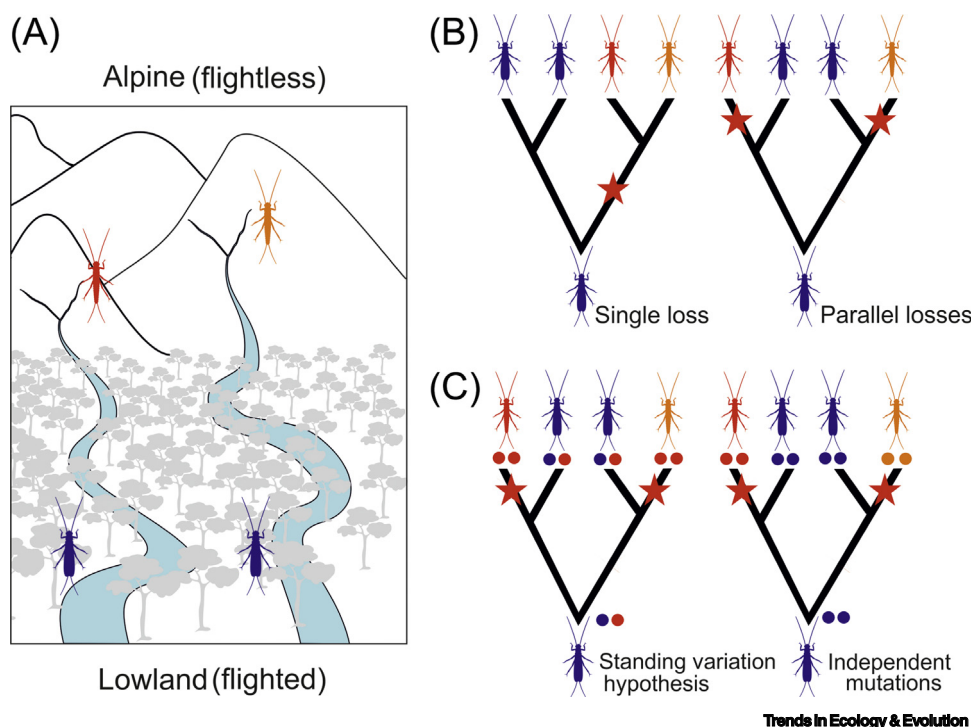

Figure 3. Evolutionary Hypotheses for the Widespread Occurrence of Dispersal Reduction. (A) An example of the distributions of dispersive versus non-dispersive lineages within wing-polymorphic insect taxa. (B) Alternative evolutionary scenarios for single loss versus multiple losses of dispersal ability (indicated by red stars). (C) Distinct evolutionary predictions for dispersal-reduction loci under the 'standing variation' hypothesis (e.g., transporter hypothesis, ancestral variation) versus the 'independent mutations' hypothesis. Blue circles represent dominant alleles coding for dispersal, whereas red and orange circles represent independently evolved recessive flight-loss alleles.

such as stoneflies (Plecoptera) similarly seem predisposed to flight loss in harsh environments [59]. The apparent propensity of some taxa for such parallel switches may also be partly explained by the **transporter hypothesis** [60] (later and Figure 3). Regardless, although the specific drivers and mechanisms of dispersal reduction may be highly variable among taxa and ecosystems, the similarities that arise from these cases highlight the importance of the interplay between isolation and **ecological selection** in promoting reductions in dispersal capacity (Figure 2).

Genomic Mechanisms of Dispersal Reduction

High-throughput genomic sequencing is starting to provide crucial new insights into the drivers and mechanisms of dispersal reduction. In particular, there is a growing literature addressing the genomic and epigenomic bases of animal migratory phenotypes [61]. Although dispersal-related phenotypic variation has been suggested to have complex genetic bases (e.g., [62]), several recent genomic studies conclude that dispersal ability and timing can be heavily influenced by small numbers of major-effect genes (e.g., [63–66]). Furthermore, emerging data imply that reductions in dispersal can potentially evolve rapidly via genetic changes in both coding and regulatory regions [11,67,68]. In assessing genomic shifts in the unique flightless Galapagos cormorant (*Phalacrocorax harrisi*), for example, Burga *et al.* [67] detected mutations that may underpin phenotypic shifts in cilia function and skeletal development. The genomic comparisons of several flight-degenerate bird lineages by Pan *et al.* [68] revealed **convergent evolution** of mutations in key genes regulating carbohydrate and lipid metabolism. These authors suggested that metabolic switches related to primary energy sources may be important drivers of avian dispersal reduction. Similarly, Sackton *et al.* [11] detected apparently convergent regulatory shifts (involving different genes) across independent flight-loss events in ratites. By contrast, Campagna *et al.* [12] identified parallel changes in two loci that were associated with multiple flight-reduction events in steamer ducks (*Tachyeres*), and one of these markers had previously been linked to vertebrate skeletal development. In most of the earlier cases, it seems likely that avian flight diminished gradually over evolutionary time [12,15] (Figure 2A).

Genomic data are similarly increasing our understanding of the genetic basis of variation in fish dispersal ability, including the loss of salinity tolerance. Hess *et al.* [63], for instance, detected genetic loci in salmonid fishes, including single loci of major effect, that were associated with differential timing of marine migration. In addition, genomic analyses of migratory versus resident freshwater fishes are revealing both coding and regulatory loci that are associated with repeated ecological transitions between convergently evolved fish ecotypes [27,31,69–71]. In genomic comparisons of freshwater versus diadromous stickleback (*Gasterosteus*) fish ecotypes, Terekhanova *et al.* [28] detected 18 **genomic islands of divergence**, thus providing a framework for 'rapid assembly of *G. aculeatus* genotypes from pre-existing genomic regions of adaptive variation'. Such genetic shifts probably underpin a broad array of rapid freshwater adaptations, including changes specifically associated with loss of diadromy. In contrast to birds, it would seem that the potential for rapid dispersal reductions may be higher in fish, consistent with the sharp selection gradients between marine and freshwater habitats.

Numerous insect taxa exhibit bimodal intraspecific dispersal polymorphisms, and selection operating on this standing variation provides a potential pathway to complete loss of dispersal ability [57]. There are also many examples where strictly flighted species have undergone multiple flight-loss transitions (e.g., [72]). When selection is strong, such dispersal reduction may be both rapid and complete (Figure 2B). The developmental/genomic bases of dispersal polymorphisms, however, are only starting to become clear (e.g., [73,74]). Wing length in some wing-polymorphic insect taxa may be mediated by the expression of the versatile arthropod sesquiterpenoid juvenile

hormone (JH) at key stages of development [75–77]. Indeed, recent transcriptomic comparisons of sympatric full-winged and wing-reduced stonefly lineages suggest that JH expression may underpin wing reduction in these alpine insect lineages [78]. In other systems, however, wing polymorphisms appear to be mediated by the steroid prohormone ecdysone (aphids [79]) or by insulin signalling (planthoppers [73,80]), suggesting that the mechanistic routes for wing loss may differ substantially across insect taxa. The bimodal dispersal states recurrently observed in many insect species enable rapid responses to fine-scale spatial and temporal environmental heterogeneity [19]. In addition, these extreme phenotypes may suggest the existence of relatively simple developmental/genetic 'switches', and that the transition toward insect flightlessness may occur over shorter timescales than for avian systems.

Some clades are seemingly genomically predisposed to dispersal reduction (e.g., [60]), but explaining why (see Outstanding Questions) requires an understanding of the extent to which repeated dispersal-reduction events have common versus convergent (e.g., [11]) genomic origins (Figure 3). Under the 'transporter hypothesis' [28,60] (Figure 3), local adaptation is enhanced by the spread of dispersal-reduction alleles among regions via dispersive individuals, with selection acting repeatedly on this standing variation (e.g., as suggested in [44]). Increasing support for the transporter hypothesis is emerging from several systems (e.g., [12,51]) where standing variation facilitates rapid, repeated evolution of dispersal-limited ecotypes in a range of taxa. Alternatively, *de novo* dispersal-reduction mutations may arise completely independently in different regions (e.g., [11]) (Figure 3), although such novel mutations may imply relatively long evolutionary timeframes.

Evolutionary Consequences of Dispersal Reduction

Dispersal capacity is a key factor that constrains both the geographical range size and the genetic substructuring of species [81], and thus influences the spatial scale of speciation [82]. Hence, dispersal reduction may increase the sensitivity of lineages to landscape/environmental variation, manifested by reduced gene flow among populations, and potentially driving **neutral evolution** and speciation [83,84]. Similarly, dispersal reduction can increase extinction risk when a habitat is temporally transient and/or spatially disjunct, such that colonization of new habitat patches may be relatively infrequent compared to local population extinction [85]. Along these lines, diverse analyses have linked reduced dispersal to dramatically increased rates of speciation (e.g., [60,86]), as well as to increased rates of molecular evolution [87,88], reduced range sizes [89,90], and increased susceptibility to extinction (e.g., [29,91]).

Loss of dispersal ability among populations can have drastic consequences over rapid timeframes when strongly reduced gene flow, accelerated genetic drift, and loss of heterozygosity lead to rapid geographical speciation [44]. Loss of marine migration, for instance, is considered to be a key initiator of freshwater fish speciation in many regions of the globe [24,25,31,92]. Such effects are observable both within and among species, and meta-analyses reveal consistently higher levels of intraspecific diversification among freshwater fish populations relative to their marine and diadromous counterparts [93]. Also in the aquatic realm, the higher diversification rates, genetic structure, endemicity, disequilibrium with current climate, and vulnerability of lotic insect lineages have been attributed to their reduced dispersal capacities compared to their lentic relatives (e.g., [33,94,95]).

As noted earlier, numerous examples of biological speciation involve splits between dispersive and non-dispersive lineages (e.g., [12,28,31,42,50,53,70,92]), and strong reductions in gene flow seem to be a key driver of such divergence. In some cases speciation occurs despite range overlap and potential for ongoing gene flow among ecotypes, and dispersal reduction perhaps plays a role in the incipient stages of 'divergence with gene flow'. For instance, differential

dispersive behaviour of ecotypes may result in spatial sorting and reproductive isolation (e.g., [50]). Genomic shifts (e.g., islands of divergence [28,96]) may also play important roles in such sympatric diversification scenarios.

Recent genetic analyses highlight that speciation events linked to dispersal reduction can occur extremely rapidly [44,53]. In cases where dispersal shifts initiate divergence, loci controlling dispersal ability could potentially be considered as 'speciation genes' [97]. In some cases, dispersal reduction may be associated with singular (isolated) speciation events (e.g., [44,67]), whereas other dispersal reductions can initiate substantial downstream cladogenesis {e.g., dispersal-limited lineages may be relatively prone to vicariance; e.g., moa (Dinornithiformes) [98] and the *Galaxias vulgaris* fish complex [92]}.

Broadly, widespread evidence suggests that reductions in dispersal can be key drivers of diversification, where rapid divergence is initiated by dispersal reduction [86,92]. However, it should be noted that, in some cases (e.g., in isolated cases when divergence dates are relatively old), establishing causal links between dispersal reduction and speciation can be complex. As an example, Vogler and Timmermans [99] emphasise that reductions in flight could be the effects (rather than the causes) of physical isolation. The Galapagos cormorant, for instance, could have lost flight either before or after its initial divergence from sister taxa. It is increasingly clear that unravelling the precise causes and timeframes of dispersal reduction and divergence requires dispersal-polymorphic systems that are evolutionarily young (e.g., incipient species complexes). Systems exhibiting replicated dispersal reduction have potential as particularly powerful models [51,53].

The ability of dispersal-reduced lineages to reacquire their former dispersal capacity has long been controversial [8,100]. Under Dollo's Law [101], loss of dispersal ability should be irreversible, but questions remain about the potential of recently evolved non-dispersive lineages to reacquire their ancestral dispersal ability. One potential pathway could be via hybridization and introgression of dispersal alleles [12,51,102] (see Outstanding Questions). Future studies of the genomic bases of migration and dispersal promise to shed increasing light on the evolutionary lability of dispersal ability [61].

Concluding Remarks and Future Perspectives

This synthesis highlights that dispersal reduction is both a cause and consequence of ecological and geographical diversification, and can be an important nexus between adaptive and neutral speciation processes. Specifically, reductions in dispersal ability can stem from an array of ecological causes, including immediate ecological conditions (e.g., as evidenced by differential selection across environmental gradients). The consequences of these shifts, however, are substantial because diminished dispersal can be a key driver of subsequent neutral genetic divergence among isolated lineages (Figure 2). In this way, dispersal shifts may even contribute to large-scale patterns of biological diversification and macroevolutionary biogeographic phenomena (e.g., [89,90]) (see Outstanding Questions). In some cases, even fine-scale microhabitat preferences may substantially influence both dispersal ability and the rate of neutral genetic differentiation [103]. Broadly, the detection of these inter-related patterns (Figure 1), across a variety of ecosystems and spatial scales, emphasises their overarching similarities. This model, whereby the rates and patterns of neutral divergence are constrained by adaptive processes, contrasts with Hubbell's [83] strictly 'neutral' theory, but echoes Vrba's [104] 'effect' hypothesis, whereby immediate adaptation to local ecological conditions (e.g., [105]) can carry incidental but substantial long-term evolutionary consequences. These data emphasise the general importance of dispersal reduction for explaining macroecological and macroevolutionary patterns (e.g., niche-based latitudinal and altitudinal diversity gradients, changes in neutral diversification rates between

Outstanding Questions

Does selection act on dispersal for its own sake, as proposed by Darwin, or is dispersal reduction an indirect consequence of selection for other traits? This issue remains contentious, and may potentially vary across both taxa and ecosystems.

The extent to which dispersal reduction has evolved repeatedly from standing variation (either ancestral or transported) – as opposed to convergent genomic mechanisms (independent mutations) – remains to be revealed for many dispersal-polymorphic groups. Although the former mechanisms are receiving increasing support from emerging genomic analyses, further studies from a diversity of systems are required.

Are insect lineages more likely to lose dispersal ability on islands compared to continental areas? Although studies have compared the relative incidence of flightlessness between ecosystems, the question of whether the rate of dispersal reduction is higher on islands remains unanswered.

To what extent does the evolution of dispersal reduction *per se* drive higher diversification or speciation rates? There is a need for studies that control for other variables that may also explain such differences.

Can dispersal-reduced lineages reacquire their former dispersal ability? Although re-evolution of such complex traits has been considered to be essentially impossible under Dollo's law, recent studies hint at the potential for reacquisition of dispersal ability via hybridization and introgression of dispersal alleles. Future genomic studies of migration promise to shed important new light on the evolution of dispersal ability.

Can macroecological patterns of biodiversity be explained by a niche-based model of dispersal reduction, whereby ecological selection accelerates neutral diversification?

closely related lineages, or contrasting vulnerabilities under environmental change; Figure 2). Future ecological genomic analyses of dispersal-polymorphic lineages and complexes promise to further elucidate the fascinating role of dispersal reduction in the formation of biodiversity.

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