Dispersal reduction: causes, genomic mechanisms, and evolutionary consequences

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Abstract

Recent biological analyses indicate that secondary reduction in dispersal ability is a key driver of diversification across numerous lineages. Here we synthesise emerging data to highlight similarities regarding the causes and consequences of dispersal reduction, across taxa and ecosystems, and 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 geographic speciation. Dispersal reduction thus represents a nexus between adaptive and neutral diversification processes, with substantial evolutionary consequences. Recognition of links between these concepts emerging from different fields, taxa and ecosystems is transforming our understanding of the fascinating role of dispersal reduction in the formation of biodiversity.

Secondary 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 has long been recognised as important to the geographic spread and ecological diversification of numerous biological clades [1-4]. Despite the advantages associated with high dispersal capacity, secondary reductions in dispersal (**dispersal reduction**; see Glossary) have occurred repeatedly across the tree of life. This trend is particularly clear within insects, where nearly every order provides examples of multiple losses of flight [5, 6]. Newly emerging data are transforming our understanding of the commonalities and consequences of dispersal-reduction processes across numerous lineages. Here we synthesise recent widespread evidence across a diversity of ecosystems and taxa (see below; Fig. 1) on the causes, genomic mechanisms, and evolutionary consequences of secondary reduction in dispersal capacity. We further explore the role of these shifts within a novel niche-based model explaining patterns of geographic speciation.

Terrestrial ecosystems

Flightless birds on **oceanic islands** (Fig. 1a) represent iconic cases of secondary dispersal reduction. Indeed, flightlessness has evolved repeatedly in numerous avian lineages, with some clades (e.g. ratites [7-9], anatids [10], and rails [11, 12]) showing abundant evidence of repeated flight reduction, particularly on islands [13]. Wings have also been lost repeatedly within nearly all insect orders, and probably thousands of times within the Coleoptera alone [5]. The loss of flight in insects has been regularly linked to particular habitats such as soil and caves [14, 15]. Wing reduction is also widely cited as a feature of island insect assemblages ([16] and Fig. 1b), and there is a similarly substantial literature on dispersal reduction in island plants ([17-19] and Fig. 1c). This repeated association of islands with reduced dispersal capacity in birds, plants,

and invertebrates has captivated the attention of biologists [13], but in the latter case has received only limited empirical assessment (Box 1).

Freshwater ecosystems

Secondary reductions in marine migratory ability and/or salinity tolerance are a widespread phenomenon in diverse freshwater taxa [20-22]. Repeated losses of **diadromy** are particularly well characterised in radiations of salmonid [23], gasterosteid [24, 25], and galaxiid [26, 27] fishes, with many cases of repeated ‘landlocking’ following colonisation of postglacial lakes (Fig. 1d). Rapid reductions in salinity tolerance have also been documented for numerous marine invertebrate lineages entering freshwater ecosystems [20]. Within aquatic insects, wing reduction (as well as eye loss and pigment reduction) is a repeated feature of water beetles colonising subterranean aquifers [28], and multiple studies point to diminished dispersal capacities in species inhabiting running waters compared with related species from standing systems [29-31].

Marine ecosystems

For sedentary marine species that rely on passive transport, loss of buoyancy of larval or adult propagules can substantially decrease dispersal ability [32]. In macroalgae (e.g. *Durvillaea* spp), for example, secondary losses of buoyancy (e.g. transitions from hollow-bladed to solid-bladed adult ecotypes) can drastically reduce potential for trans-oceanic rafting ([33] and Fig. 1e), with non-buoyant lineages typically restricted to single landmasses [34]. Similarly, transitions from planktonic (dispersive) to benthic/brooding (non-dispersive) larval development have occurred in numerous marine invertebrate taxa [35-37], with major implications for biogeography and genetic connectivity ([38-40] and Fig. 1f).

Causes of dispersal reduction

Secondary 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, i.e. the colonisation of isolated (and commonly reduced) habitat patches for a lineage; and (ii) ecological causes, i.e. involving 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 secondary reductions in dispersal ability have been associated with the colonisation of islands [13, 41], and dispersal reduction is indeed one of the most frequently-invoked insular syndromes. Due to the isolated nature of islands, and other patchy ecosystems (e.g. calcrete aquifers [28]), spatial isolation has often been inferred to play a primary role in such dispersal reduction, via direct negative selection against dispersive individuals [42, 43]. 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, that in the case of island birds, reductions in dispersal are significantly associated with island size, but also with decreased predation pressure ([13] and Fig. 2a). Similarly, other researchers have proposed that insular flight reduction is linked to diminished resource availability [44], where secondary dispersal reduction could be the by-product of trade-offs involving selection for other traits (e.g. with juvenile survivorship or competitive ability in the case of insects [19]). In the case of calcrete-aquifer insects, reduced dispersal may also reflect a combination of spatial and ecological causes, with wing reduction partly a side-effect of adaptation to the singular conditions of these fragmented subterranean habitats (e.g. [28]).

Perhaps some of the clearest evidence for ecological causes of secondary reductions in dispersal potential comes from associations between dispersal and habitat variation. In the case of insects, wing reduction events have been frequently attributed to habitat transitions, and linked to changes in habitat features such as stability [5, 45], abiotic stress [46] or habitat discontinuity [28]. Recent examples have provided mechanistic evidence for such processes in alpine insects, where **parallel evolution** of wing-reduction within individual species is associated with repeated adaptation to high altitude habitats ([47-49] and Box 2). For aquatic insect lineages, the contrasting stability of standing (lentic) versus running (lotic) water habitats has been suggested as an ecological driver of diversification in species dispersal capacity [45], even between closely related species [30, 31]. 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 [21]. In the marine realm, reductions in larval dispersal (e.g. transitions from **planktotrophic** to lecithotrophic (yolk-feeding) development, and switches to **viviparity** [35]) are also associated with habitat transitions and linked to habitat features such as ocean temperature [37, 50], habitat productivity and/or environmental predictability [36]. In buoyant seaweeds, for which passive drifting represents an important means of coastal and trans-oceanic dispersal [33, 51], secondary loss of buoyancy may stem from ecological transitions to exploit subtidal niches [34], with dispersal reduction thus an incidental effect of these ecotypic shifts.

Some particular clades seem especially prone to secondary dispersal reduction [52]. For instance, diadromous fish that readily colonise lakes can repeatedly lose their marine migratory larval phases [24], and this may be particularly the case for strong-climbing species that penetrate far inland to reach alpine tarns [53]. Similarly, asterinid sea stars may be predisposed for repeated loss of planktotrophic larval development under environmental gradients [40]. Weak-flying insects such as stoneflies similarly seem predisposed for flight loss in harsh

environments [54]. The apparent propensity of some taxa for such parallel switches may also be partly explained by the **transporter hypothesis** ([55], Fig. 3, and see below). Regardless, while the specific drivers and mechanisms of dispersal reduction may be highly variable among taxa and ecosystems, the similarities that arise from these cases seem to highlight the importance of the interplay between isolation and **ecological selection** in promoting secondary reductions in dispersal capacity (Fig. 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. Recent genomic data imply that dispersal ability has a strong genetic component involving major effect genes (e.g. [56]), and that reductions in dispersal can often evolve rapidly, via genetic changes at both coding and regulatory regions. In assessing genomic shifts in the unique flightless Galapagos cormorant, for example, Burga et al [57] detected mutations that may underpin phenotypic shifts in cilia function and skeletal development. Pan et al's [58] genomic comparisons of several flight-degenerate bird lineages revealed **convergent evolution** of mutations at key genes regulating carbohydrate and lipid metabolism. These authors suggested metabolic switches related to primary energy sources may be important drivers of avian dispersal reduction. Similarly, Sackton et al [9] detected apparently *convergent* regulatory shifts (involving different genes) across independent flight-loss events in ratites. In contrast, Campagna et al [10] identified *parallel* changes at two loci associated with multiple flight reduction events in steamer ducks, with one of these markers having previously been linked to vertebrate skeletal development. In most of the above cases, it seems likely that avian flight diminished gradually over evolutionary time ([10, 13] and Fig. 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 [56], for instance, detected genetic loci, including single loci of major effect, associated with differential timing of marine migration in salmonids. Additionally, genomic analyses of migratory versus resident freshwater fishes are revealing both coding and regulatory loci associated with repeated ecological transitions between convergently-evolved fish ecotypes [24, 59-61]. In genomic comparisons of freshwater versus diadromous stickleback ecotypes, Terekhanova et al [25] detected 18 **genomic islands of divergence**, providing a framework for “rapid assembly of *G. aculeatus* genotypes from pre-existing genomic regions of adaptive variation”. 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 on this standing variation provides a potential pathway to complete loss of dispersal ability [52]. There are also many examples where strictly flighted species have undergone multiple flight loss transitions (e.g. [62]). When selection is strong, such dispersal reduction may be both rapid and complete (Fig. 2b). The developmental-genomic bases of dispersal polymorphisms, however, are only starting to become clear (e.g. [63, 64]). Wing length in some wing-polymorphic insect taxa may be mediated by the expression of the versatile arthropod sesquiterpenoid juvenile hormone (JH) at critical stages of development [65-67]. 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 [68]. In other systems, however, wing-polymorphisms appear to be mediated by the steroid prohormone ecdysone (aphids [69]) or by insulin signalling (planthoppers [63, 70]), suggesting the mechanistic routes for wing loss may vary substantially across insect taxa. However, the

frequently observed bimodal dispersal state in many species suggests that the transition toward flightlessness is likely to occur over much shorter time scales than for avian systems.

Some clades are seemingly genomically-predisposed for secondary dispersal reduction (e.g. [55]), but explaining why (see Outstanding Questions) requires an understanding of the extent to which repeated dispersal reduction events have common versus convergent (e.g. [9]) genomic origins (Fig. 3). Under the ‘transporter hypothesis’ ([25, 55] and Fig. 3), local adaptation is enhanced by the spread of dispersal-reduction alleles via populations of dispersive individuals, with selection acting repeatedly on this pre-existing variation (e.g. suggested by [40]). Increasing support for the transporter hypothesis is emerging from several systems (e.g. [10, 46]), with standing variation facilitating 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. [9] and Fig. 3), although such novel mutations may imply relatively long evolutionary time frames.

Evolutionary consequences of dispersal reduction

Dispersal capacity is a key factor constraining both the geographical range size and genetic substructuring of species [71], and thus influencing the spatial scale of speciation [72]. Hence, secondary reductions of dispersal may increase the sensitivity of lineages to landscape/environmental variation, manifesting as reduced gene flow among populations, potentially driving **neutral evolution** and speciation [73, 74]. Similarly, dispersal reduction can increase extinction risk when habitat is temporally transient and/or spatially disjunct, such that colonization of new habitat patches may be relatively infrequent compared to local population extinction [75]. Along these lines, diverse analyses have linked secondary reductions in dispersal ability to dramatically increased rates of speciation (e.g. [55, 76]), as

well as increased rates of molecular evolution [77, 78], reduced range sizes [79, 80], and increased susceptibility to extinction (e.g. [26, 81])

Loss of dispersal ability among populations can result in drastic consequences over rapid timeframes when strongly reduced gene flow, accelerated genetic drift and loss of heterozygosity lead to rapid geographical speciation [40]. Loss of marine migration, for instance, is considered a key initiator of freshwater fish speciation in many regions of the globe [21, 22, 26, 82]. Such effects are observable both within and among species, with meta-analyses revealing consistently higher levels of intraspecific diversification among freshwater fish populations relative to their marine and diadromous counterparts [83]. Also in the aquatic realm, the higher diversification rates, genetic structure, endemism, disequilibrium with current climate and vulnerability found in insect lineages of lotic habitats have been attributed to the reduced dispersal capacities of these lineages compared with their lentic relatives (e.g. [29, 84, 85])

In some cases, a single loss of dispersal may lead to just a single speciation event (e.g. Galapagos cormorant [57]; *Cryptasterina* sea stars [40]). In other instances, single reductions in dispersal ability can promote the evolution of diverse species flocks (e.g. moa [86]; galaxiid fishes [82]). In the former cases, recent genetic analyses seem to highlight that speciation events (linked to dispersal reduction) can occur very rapidly [40, 48]. Additionally, mutations at genes underpinning such dispersal reduction could perhaps even be seen as ‘speciation genes’ when considered over evolutionary time-frames.

While there is widespread evidence suggesting reductions in dispersal are often key drivers of diversification, it should be noted that in some cases establishing causal links can be

complicated by confounding variables (see Outstanding Questions). As an example, Vogler and Timmermans [87] emphasise that losses of flight and reduced gene flow may both be responses to habitat stability and/or isolation. Thus it may sometimes be difficult to disentangle causes versus effects of dispersal reduction and population differentiation.

The ability of dispersal-reduced lineages to reacquire their former dispersal capacity has long been controversial [6, 88]. Under Dollo's Law [89], loss of dispersal ability should be irreversible — but questions remain about the potential for recently-evolved non-dispersive lineages to reacquire their ancestral dispersal ability. One potential pathway could be via hybridization and introgression of dispersal alleles ([10, 46, 90]; see Outstanding Questions).

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 — as diminished dispersal can be a key driver of subsequent neutral genetic divergence among isolated lineages (Fig. 2). In this way, broadscale patterns of biological diversification, and macroevolutionary biogeographic phenomena (e.g. [79, 80]) may be influenced by allopatric speciation, underpinned by natural selection (see Outstanding Questions). In some cases, even fine-scale microhabitat preferences may substantially influence dispersal ability and rates of neutral genetic differentiation [91]. Broadly, the detection of these interrelated patterns (Fig. 1), across a variety of ecosystems and spatial scales, emphasises their overarching similarities. This model, whereby rates and patterns of neutral divergence are

constrained by adaptive processes, contrasts with Hubbell's [73] strictly 'neutral' theory, but echoes Vrba's [92] 'Effect' hypothesis, whereby immediate adaptation to local ecological conditions (e.g. [93]) can carry incidental yet substantial long-term evolutionary consequences. These data emphasise the general importance of secondary dispersal reduction for explaining macroecological and macroevolutionary patterns (e.g. niche-based latitudinal and altitudinal diversity gradients; changes in neutral diversification rates between closely related lineages; or contrasting vulnerabilities under environmental change; Fig. 2). Recently-emerging genomic data from non-model taxa further highlight the genetic basis of life-history polymorphisms that underpin such repeated ecotypic transitions. These new insights, emerging from diverse ecological, evolutionary and genomic research programmes are revealing the fascinating role of dispersal reduction in the formation of biodiversity.

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Figure captions

Fig. 1. Examples of dispersal reduction. Secondary dispersal reduction has evolved repeatedly across a wide range of taxa and ecosystems, leading to non- or poorly-dispersive lineages. In the schematic examples below, ancestral lineages with higher dispersal potential (connected by gene flow, arrows) are in blue, whereas their dispersal limited (i.e. genetically isolated) derivatives are indicated in red, orange and brown. (a) Flight reduction in island birds (e.g. rails [11, 12]); (b) wing reduction in alpine insects (e.g. *Zelandoperla* stoneflies [48, 54, 90]; (c) increased seed size in island plants (e.g. *Fitchia* sunflowers [17, 18]; (d) loss of marine migratory ability in freshwater fishes (e.g. *Gasterosteus* sticklebacks [24, 25]); (e) transitions from buoyant intertidal to non-buoyant subtidal seaweed ecotypes (e.g. *Durvillaea* kelps [34]); (f) loss of planktonic larval dispersal in marine invertebrates (e.g. *Astrotooma* brittle stars [39]).

Fig. 2. Dispersal reduction is a nexus between ecological selection and geographical speciation. In both schematic examples below, selection along environmental gradients reduces dispersal potential, which in turn increases the probability of population structure 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. [9, 10, 13]); in (b), dispersal ability can be highly bimodal in insect populations, essentially ‘all or nothing’ (e.g. constrained by a simple wing polymorphism; e.g. [46, 48, 64]).

Fig. 3. Evolutionary hypotheses for the widespread occurrence of secondary 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

519 versus multiple losses of dispersal ability (indicated by red stars); (c) distinct evolutionary
520 predictions for dispersal-reduction loci under the ‘transporter hypothesis’ versus ‘independent
521 mutations’ hypothesis. Blue circles represent dominant alleles encoding for dispersal, whereas
522 red and orange circles represent independently evolved recessive flight loss alleles.
523

Box 1. Oceanic islands as drivers of dispersal reduction

The loss or reduction of dispersal ability is usually considered a key feature within the generalised island syndrome [19] that describes directional differences in attributes between island taxa and their continental relatives. This trend has been repeatedly documented in plants, birds and — perhaps most famously — insects, where Darwin [42] speculated that the incidence of flightless species on Madeira described by Wollaston [43] 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, as there is no discernible tendency for oceanic islands to have higher frequencies of flightless species [94]. Alternatively, if islands are more likely to be colonised by flighted species, as would seem plausible, then secondary loss of flight would be needed to explain similar proportions of flightless species compared to continental areas. There are good reasons to expect such a trend, building on Darwin's [42] original argument. Islands are small, but for a habitat specialist, they are even smaller. If the trade-off relationship reported for reduced dispersal investment and higher reproductive investment in insects (e.g. [95, 96]) is broadly generalisable, then there is every reason to expect an island rule for secondary flightlessness in insects, but comparative data are lacking. In the case of birds, a recent comparative analysis does provide evidence for a general trend toward flightlessness in island birds [13]. However, rather than the purely spatial causes which have been suggested to explain flightlessness in insects, this study's results argue for dispersal reduction evolving due to release from predators — an ecological cause. Despite many studies suggesting a general trend toward reduced dispersal ability in island plants (see [97] for examples), it has recently been highlighted that this trend might simply be a passive by-product of selection for large seeds ([19], see Outstanding Questions). There are thus parallels across all three taxonomic groups, with an emerging consensus that, when dispersal loss does occur,

549 it is likely to be helped along — or wholly driven — by indirect benefits to the organism.
550 Particularly with regard to insects and plants, however, more comparative data are needed for
551 a more complete understanding of the relative incidence of dispersal reduction on islands, the
552 selective agents at play, and their relative roles (see Outstanding Questions).
553

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 characterized for montane insect taxa that have secondarily lost their abilities to fly [47-49, 52, 54, 94]. Darlington [98], 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 — with wing-polymorphic insects showing marked increases in wing-reduction over small spatial scales, linked to the alpine treeline [48, 54]. These findings are mirrored by analyses from the mountains of Japan [49] and the Galapagos [47], 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) explain the increasing prevalence of insect dispersal-reduction in montane ecosystems at the species and population levels (Figs 1b, 2b 3). Comparable trends are now emerging also for botanical assemblages, with the majority of plant species in Australia’s alpine flora [99] exhibiting substantially lower seed dispersal capacity than predicted for terrestrial plants more generally [100]. While these macroecological trends might simply stem from the relatively small stature of alpine plants (with lower release height for dispersive propagules), Morgan and Venn [99] 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 above phenomena suggest that purely spatial causes can reinforce dispersal reduction for taxa occupying highly-fragmented (effectively ‘insular’) alpine habitats. The possibility for isolated montane habitats to function as ‘islands’ for dispersal-limited upland taxa has also been suggested for flight-reduced alpine birds which similarly show unexpected phylogeographic

579 diversity [101]. While non-dispersive alpine populations experience rapid rates of genomic
580 evolution ([90] and Fig. 2b), this diversification may be somewhat offset by increased rates of
581 extinction, especially under rapid global change [102].

582

583 **Glossary**

584 **Convergent evolution:** the independent evolution of analogous traits in unrelated lineages.

585 **Diadromy:** life cycles that include movement between freshwater and marine ecosystems.

586 **Dispersal reduction:** secondary decreases in the movement of individuals and reproductive
587 propagules, resulting in diminished gene flow among populations.

588 **Ecological selection:** the operation of strictly ecological processes on the transmission of
589 heritable traits.

590 **Genomic islands of divergence:** small regions of the genome that are tightly associated with
591 adaptation, and resistant to gene flow.

592 **Neutral evolution:** random genetic drift of alleles that are selectively neutral.

593 **Oceanic islands:** islands that do not sit on continental shelf, typically volcanic in origin.

594 **Parallel evolution:** the independent evolution of similar traits in related lineages.

595 **Planktotrophic larvae:** juvenile individuals that drift in the ocean, feeding on plankton.

596 **Transporter hypothesis:** the process by which gene flow transports adaptive alleles to
597 different regions, facilitating parallel selection on standing variation in distinct populations.

598 **Viviparity:** brooding of a developmental stage within the parental body until birth.

1 Outstanding Questions

2 The extent to which selection acts on dispersal for its own sake, as proposed by Darwin, versus
3 being an indirect consequence of selection for other traits, remains contentious, and may
4 potentially vary across both taxa and ecosystems.

5

6 The extent to which dispersal reduction has evolved repeatedly from standing variation
7 (*transporter hypothesis*) — as opposed to convergent genomic mechanisms (*independent*
8 *mutations*) — remains to be revealed for many dispersal-polymorphic groups. While the former
9 hypothesis is receiving increasing support from emerging genomic analyses, further studies are
10 required from a diversity of systems.

11

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

16

17 To what extent does the evolution of dispersal reduction *per se* drive higher diversification or
18 speciation rates? Studies are required that control for other variables that may also explain such
19 differences.

20

21 Can dispersal-reduced lineages reacquire their former dispersal ability? While re-evolution of
22 such complex traits has been considered essentially impossible under Dollo's Law, recent
23 studies hint at the potential for reacquisition of dispersal ability via hybridization and
24 introgression of dispersal alleles.

25

26 To what extent can macroecological patterns of biodiversity be explained by a niche-based
27 model of dispersal reduction, whereby ecological selection accelerates neutral diversification?
28

1 **Highlights**

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

4

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

8

9 The ‘transporter’ hypothesis may provide a key mechanism for the ‘spread’ of dispersal
10 reduction, with widespread parallel evolution revealed by recent genomic analyses of birds,
11 fishes and insects.

12

13 Ecological gradients can drive both gradual (e.g. flight reduction in island birds) and rapid (e.g.
14 wing loss in alpine insects) dispersal reduction.

15

16 Ecological shifts are a key driver of dispersal reduction and subsequent neutral genetic
17 divergence among isolated lineages. Dispersal reduction thus represents a nexus between
18 adaptive and neutral speciation processes.

(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

Figure 2