

Founder takes all: density-dependent processes structure biodiversity

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Density-dependent processes play a key role in the spatial structuring of biodiversity. Specifically, interrelated demographic processes, such as gene surfing, high-density blocking, and competitive exclusion, can generate striking geographic contrasts in the distributions of genes and species. Here, we propose that well-studied evolutionary and ecological biogeographic patterns of postglacial recolonization, progressive island colonization, microbial sectoring, and even the ‘Out of Africa’ pattern of human expansion, are fundamentally similar, underpinned by a ‘founder takes all’ density-dependent principle. Additionally, we hypothesize that older historic constraints of density-dependent processes are seen today in the dramatic biogeographic shifts that occur in response to human-mediated extinction events, whereby surviving lineages rapidly expand their ranges to replace extinct sister taxa.

Spatial biodiversity shaped by colonization events

The molecular revolution has facilitated detailed spatial genetic analyses of many species, revealing striking geographic partitioning of genetic information over a wide range of geographic scales. Such data have yielded fundamental insights into the processes shaping organismal history, evolution, and ecology. Many of the most distinctive and influential spatial genetic patterns detected to date (e.g., ‘Out of Africa’ [1], postglacial recolonization [2], progression rule [3], and microbial sectoring [4]; see [Glossary](#)) broadly depend on the interplay between dispersal, reproduction, and population density. When a species encounters new opportunities, such as through colonization of new islands, colonization of recently deglaciated areas, or the extinction of a sister lineage, density-dependent processes often become particularly important and can leave long-lasting genetic signatures [5]. Although several different terms have been proposed to explain such density-dependent phenomena (e.g., leading edge, high-density blocking, and gene surfing; [Figure 1](#)), we contend that these are all largely similar and interlinked. Despite their importance for studies of gene spread, phylogeography, competitive exclusion, and biogeography, the potential biological and biogeographic restrictions imposed by

density-dependent processes have often been overlooked in the scientific literature. Such an oversight may result from the focus of many researchers on ‘what has happened?’ rather than ‘what hasn’t happened?’ in ecology and evolution. Perhaps counterintuitively, some of the clearest new evidence of density-dependent effects comes from recent anthropogenic impacts on natural systems, where rapid biogeographic shifts have occurred in response to human-mediated extinction events; that is, lineages that were formerly biogeographically constrained by the presence of sister taxa have been able to expand their ranges, apparently benefitting from the anthropogenic demise of their prehistoric sisters (e.g., [6]). Here, we present a synthesis of these interrelated patterns and processes to highlight both their parallels and their relevance across a range of biological communities, regions, and research fields.

Leading edge colonization of deglaciated regions

Over the past two decades, the genetic study of postglacial recolonization patterns in high latitude regions has

Glossary

Competitive exclusion: the process by which two or more ecologically similar lineages are unable to coexist due to competition.

Gene surfing: the process whereby low-frequency alleles can ‘surf’ on the ‘wave’ at the front of an expanding population. This phenomenon is underpinned by genetic drift associated with ongoing founding events.

High-density blocking: the process by which secondary dispersers arriving in an already colonized, densely occupied habitat fail to become established and reproduce.

Last Glacial Maximum (LGM): the peak of the last Ice Age, approximately 19 000–23 000 years ago.

Leading edge colonization: when a species expands its geographic range, individuals at the front can reproduce rapidly as they colonize vacant habitat; by contrast, individuals in the main body of the population have a slower rate of reproduction.

Lineage patch: a geographic region dominated by one particular biological lineage.

Microbial sectoring: the distinctive ‘wedge-shaped’ morphological or genetic sectors that form within expanding circular colonies of yeasts or bacteria. Distinct sectors are separated by sharp allele frequency gradients.

Out of Africa: the recent geographic expansion of modern humans from an ancestral African source population, as indicated by phylogenetic analysis of uniparental genetic markers.

Postglacial recolonization: biological colonization of formerly glaciated and neighboring, inhospitable, and unoccupied terrain; most commonly referring to latitudinal range shifts since the LGM.

Progression rule: a phylogenetically ordered pattern of biological colonization along an island chain, whereby early lineages colonize old islands, with subsequent colonization of newer islands as they emerge.

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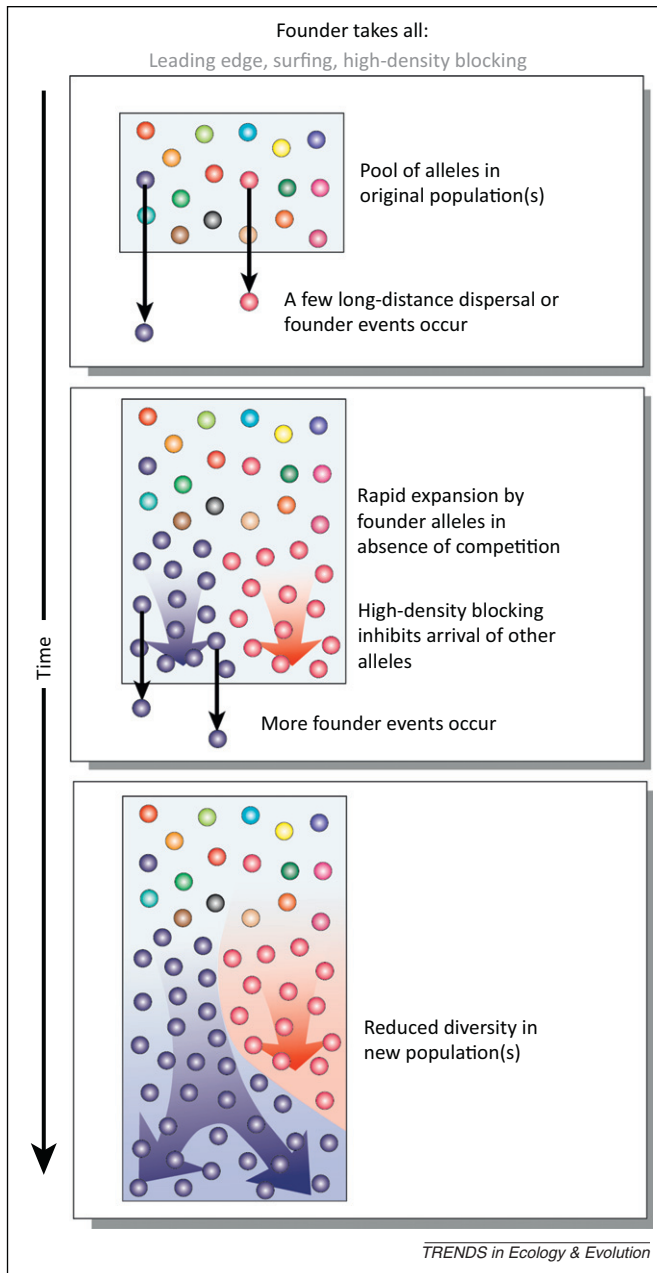


Figure 1. Rapid expansion of founding lineages effectively blocks establishment of latecomers. Different colors represent different genetic lineages. Populations founded by those first able to disperse into new territory can rapidly expand, hindering establishment of later immigrants and leading to a relative lack of genetic diversity in the newer populations.

emerged as a major topic in evolution and ecology. The influential syntheses of spatial genetic data presented by Hewitt [2,7] and Bernatchez and Wilson [8], as well as numerous subsequent studies, have interpreted the genetic homogeneity of numerous high-latitude Northern Hemisphere lineages as a reflection of rapid colonization events following the Last Glacial Maximum (LGM). Similar patterns of high-latitude homogeneity have also been detected in some Southern Hemisphere taxa (e.g., [9–13]). Nonetheless, given the overwhelming evidence for rapid and concerted dispersal by a wide range of species into formerly glaciated terrain, one could reasonably ask why these deglaciated regions are now dominated by just one or a handful of recolonizing alleles and/or genotypes per

species. To resolve this apparent conundrum, Hewitt [7] proposed that ‘leading edge colonization during a rapid expansion would... lead to spatial assortment of genomes’ forming regions of high genetic homogeneity. In some cases, the combination of long-distance poleward dispersal [14] and high-density blocking (i.e., exclusion of subsequent dispersers [15]) can potentially produce longitudinal partitioning (‘sectoring’) of recolonizing genotypes, reminiscent of the microbial colony sectoring recently documented by Hallatschek and coauthors [4] (Figure 2a).

At a subcontinental scale, postglacial colonizers of the Northern Hemisphere are typically divided into lineage patches that are generally larger at higher latitudes. These lineages vary in genetic distance from each other, and in the ages of their divergence, from several million years to the Late Pleistocene [16,17]. Following range contraction into refugia during glacial maxima, these lineages subsequently expanded and met during interglacials, often forming hybrid zones. The rapid postglacial colonization and founder events inevitably reduce within-lineage genetic diversity. The genetic effects of extinction–recolonization are most readily studied for the LGM and subsequent postglacial repopulation of higher latitude regions in the Northern Hemisphere. For populations and lineages that have diverged little, high-density blocking can produce genome patches and sectoring, whereas the contact between more highly diverged lineages will involve high-density blocking and probably some hybrid unfitness. In both cases, the spatial and genetic integrity of the abutting populations, lineages, and genomes is apparently maintained by density-dependent processes. The operation of these processes at different scales can be seen in several well-studied species, such as European hedgehogs (Figure 2b [16,18,19]).

High-density blocking following island colonization

Geological upheaval, such as the formation of new mountains and volcanic islands (Figure 2c), provides dramatic new opportunities for biological lineages capable of long-distance dispersal and colonization. Indeed, newly formed islands (e.g., Krakatau) have been observed to be rapidly colonized by diverse plant and animal taxa [20], implying that oceanic dispersal of many terrestrial taxa might be common over both ecological and geological timescales [21,22]. Island Biogeography Theory incorporates these dispersal and colonization events, as well as density-dependent processes and extinctions, to explain species diversity patterns in isolated ecosystems [23]. As a case in point, the linear and well-dated series of islands comprising the isolated Hawaiian archipelago represents a particularly elegant system for biogeographic research, and attests to the evolutionary importance of biological dispersal [21]. Moreover, recent phylogenetic studies from this archipelago provide strong evidence of concerted, sequential ‘island-hopping’ radiations (dispersal from older to progressively younger islands; Figure 2c) in numerous animal and plant lineages [3,24–26]. However, the finding of linear relationships between island age (geological evolution) and inter-island genetic distance (biological evolution) in several taxa (e.g., [27]) implies that, in some cases, the islands were colonized very rapidly after their geological formation, yet

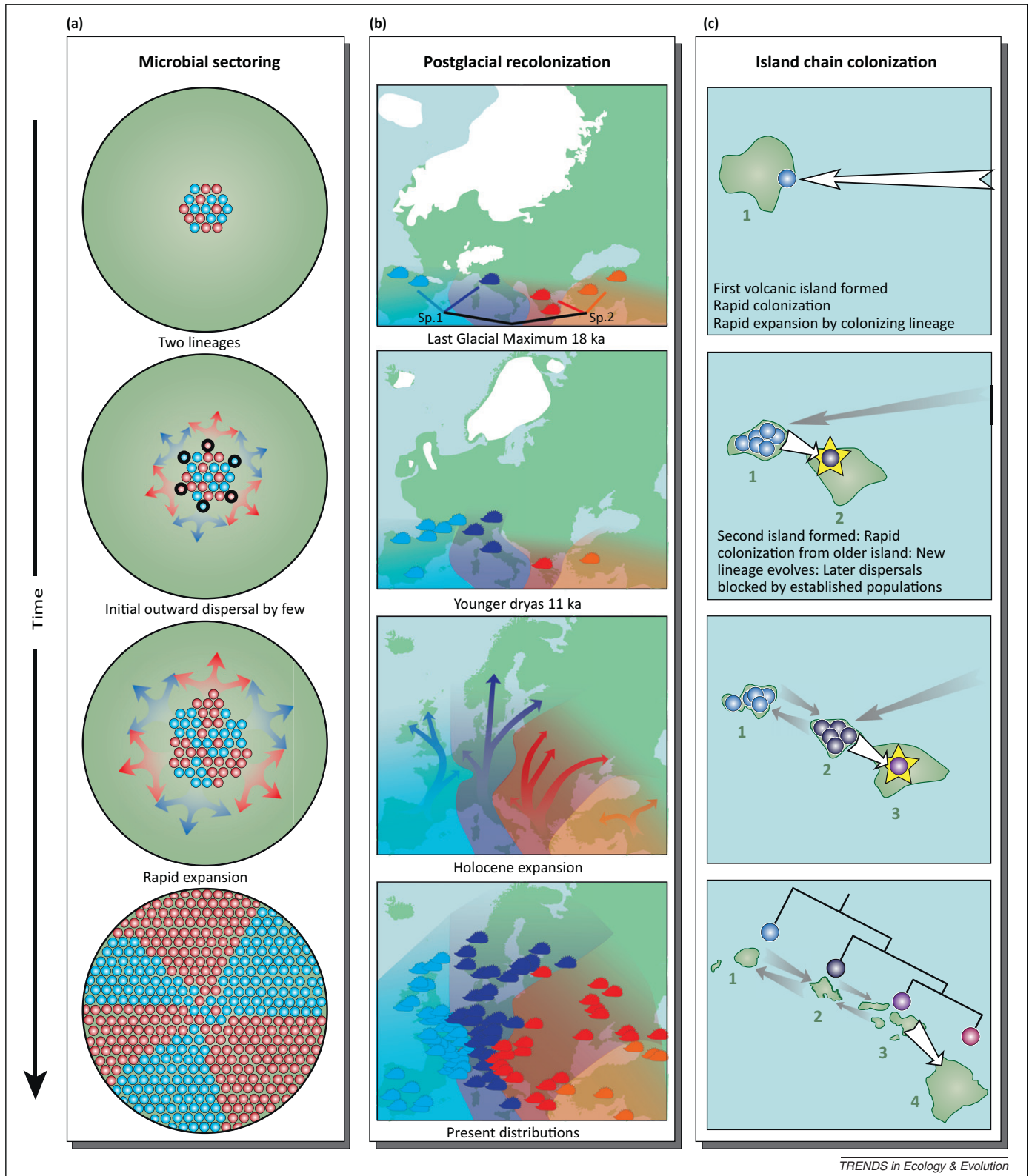


Figure 2. Density-dependent processes operate on various scales. The ‘founder takes all’ principle can explain various biological processes on a range of scales, such as sectoring in microbial cultures, island chain colonization, and postglacial recolonization of continents. **(a)** Microbial sectoring: when bacterial and yeast colonies are grown from an experimental application of two initially well-mixed lineages to the center of an agar plate; lineage sectoring occurs as the first lineage to colonize outwards rapidly multiplies in all unoccupied directions [4]. **(b)** Postglacial recolonization can similarly lead to sectoring of lineages as dispersal into newly available habitat (with poleward recession of glaciers) occurs in all unoccupied directions from leading-edge colonists leaving glacial refugia, and rapid increases in population density prevent colonization by latecomers. This example illustrates sectoring by four main mitochondrial lineages in two species of European hedgehog dispersing from southern refugia after the Last Glacial Maximum (LGM); similar patterns of sectorized expansion from glacial refugia have been observed in a wide range of taxa (e.g., [17]) in Europe, North America, and the Southern Hemisphere. Colored hedgehog symbols indicate the known locations of hedgehog populations at various times based on either dated subfossil remains (upper two panels, [69]) or mtDNA samples (lower panel, [18,19]). **(c)** Taxa inhabiting volcanic island chains, such as Hawaii, have been observed to show phylogeographic patterns consistent with timing of island formation, with older lineages on older islands (the ‘progression rule’). Rapid establishment of the first lineage to arrive at a new island hinders establishment of latecomers. White arrows indicate successful dispersal and establishment; gray arrows represent failed dispersal events; and the phylogenetic tree in the bottom panel schematically illustrates relationships among lineages. Abbreviation: ka, 1000 years ago.

without subsequent follow-up dispersal success. The obvious question arising from these observations is, if dispersal between islands can occur rapidly, why does one typically see genetic evidence of just one colonization event per island (Figure 2c)? In addressing this question, we would argue that additional (perhaps ongoing) interisland dispersal events must indeed occur, but that a 'founder takes all' principle [i.e., high-density blocking by founding lineage(s)] effectively excludes or dilutes the effects of subsequent migrants, enabling preservation of the elegant 'progression-rule' phylogenetic patterns observed across the Hawaiian archipelago.

Comparable island progression patterns (albeit less geographically linear) have also been detected in a variety of Canary Island lineages [28–30], and among *Galapaganus* weevils from the Galapagos [31]. Although the progression rule seems to hold as a general evolutionary phenomenon across island chains, several researchers have also documented exceptions (e.g., some taxa apparently moving from younger to older islands [32,33]). Regardless, the evolution of monophyletic assemblages associated with single oceanic islands is a common feature of island biogeography, with colonization success decreasing as niches are filled [34]. Emerson and Gillespie [34] further suggested that the remoteness of an island increases the time to first colonization, and that this in turn increases the likelihood that subsequent colonizers will be excluded. Overall, we reiterate that island chains around the world represent fertile systems for the study of density-dependent processes that constrain the evolution of ecosystems.

Density-dependent processes in the sea

Local-scale experimental observations and field data both indicate that recruitment of exotic invaders into marine ecosystems decreases with decreasing available open space and, furthermore, that diverse marine communities are sometimes better equipped to withstand exotic invasions than are species-poor communities [35]. We suggest that density-dependent processes are also likely to be important in constraining marine biological dispersal success over much larger biogeographic scales. In particular, such processes may play a key role in determining species and lineage geographic limits for dispersive taxa, even in highly connected ecosystems that would otherwise promote broad panmixia and continuous ranges. For instance, numerous tropical marine taxa show biogeographic turnover across the tropical Indo-Pacific, despite the lack of any contemporary physical barrier between these ocean basins [36–39]. Barber and coauthors expressed understandable surprise that such spatial structure can be maintained despite the high dispersal ability of the taxa involved [36]. A comparable Indo-Pacific disjunction has been detected in temperate seas, along the extensive coastline of southern Australia. Specifically, Waters and colleagues [40,41] documented a marked east–west species turnover between two otherwise widespread and ecologically similar *Nerita* gastropods: *Nerita atramentosa* (Indian Ocean coast of western and southern Australia) versus *Nerita melanotragus* (Pacific coast of southeastern Australia). Despite their strong larval dispersal ability, it seems that density-dependent factors similarly

prevent each species from successfully infiltrating the range of the other. On a global scale, the highly structured biogeography of this particularly speciose genus is best explained by geographic rather than ecological differentiation [42]. As is apparently the case for several widespread marine molluscan radiations (e.g., *Conus*, *Marmarostoma*, *Granulittorina* [43], and cowries [44]), once major lineages become established in new habitats or regions, this severely restricts subsequent opportunities for dispersal success between regions [43]. In some cases, spatial structuring of marine biodiversity is maintained in the face of clear evidence for recent and/or ongoing dispersal across biogeographic transition zones [11,45–47]. In such cases, we hypothesize that dispersal is ultimately ineffective due to density-dependent factors (e.g., high-density blocking; Box 1).

Biogeographic shifts following human-mediated extinction

Ancient-DNA studies showing rapid biogeographic shifts in response to extinction events imply that the ranges of species were formerly limited by the presence of sister taxa; that is, that extinction can promote range expansion. Certainly, the idea that the extinction of one taxon can benefit another has long been attractive to evolutionary biologists. As a case in point, the demise of the dinosaurs is often suggested to have facilitated the subsequent successful radiation of mammals [48,49]. Similarly, in prehistoric North America, the Late Pleistocene demise of a distinct Beringian wolf ecomorph may have played a role in facilitating the subsequent success of the gray wolf (*Canis lupus*) [50]. An even more recent extension of this extinction–replacement hypothesis involves marked biogeographic shifts apparently in response to anthropogenic extinction events in coastal New Zealand, a region colonized by humans as recently as 1280 AD. For instance, the sub-Antarctic penguin *Megadyptes antipodes* apparently colonized mainland New Zealand only within the past few hundred years, shortly after the human-mediated extinction of its prehistoric counterpart *Megadyptes waitaha* [6]. A similar scenario exists for New Zealand sea lions (*Phocarctos hookeri*), with a sub-Antarctic population recently expanding north to mainland New Zealand to replace the prehistoric mainland population that was extirpated by human hunting [5]. It seems clear that recolonizing taxa, such as penguins and sea lions, have always had high dispersal capability, but were previously excluded from mainland New Zealand by the presence of endemic mainland populations.

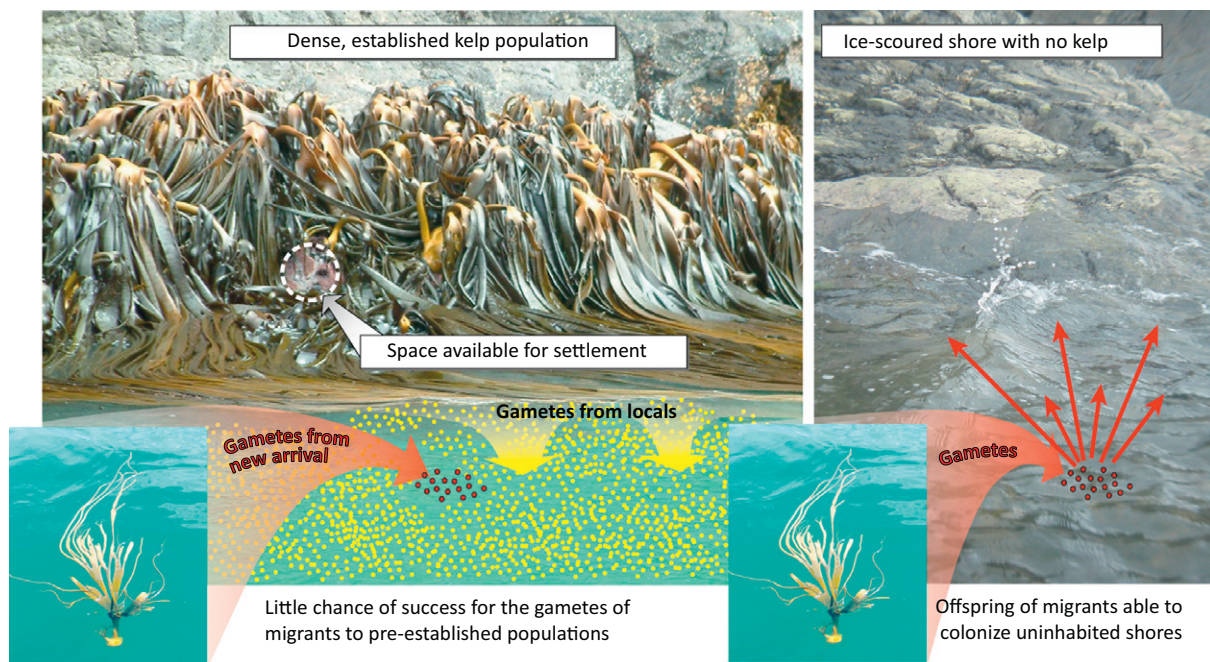
We hypothesize that human impacts on indigenous seabird populations may also explain the recent arrival of an Australian lineage of the little blue penguin (*Eudypula minor*) in southern New Zealand ([51,52] and see [6]). Additional recent biogeographic shifts in mainland New Zealand involve terrestrial bird congeners: the arrival of the pukeko (*Porphyrio porphyrio melanotus*), a dispersive flighted rail, perhaps no more than 400 years ago [53], following the human-mediated functional extinction of the flightless New Zealand endemic takahe (*Porphyrio hochstetteri*); and the arrival of the swamp harrier *Circus approximans*, perhaps a response to the anthropogenic

Box 1. High-density-blocking in southern bull-kelp

Southern bull-kelp (*Durvillaea antarctica*) is a robust, buoyant seaweed species that grows densely along the coasts of New Zealand, Chile, and many sub-Antarctic islands. When plants detach from the shore, they can disperse long distances by rafting, with an estimated 70 million specimens drifting at high latitudes at any time [70]. The kelp, which can grow to up to 12 m and survives for several years, reproduces during the winter months, when male plants release sperm and female plants release eggs. Resultant zygotes rapidly settle on any available, vacant areas of rocky shore.

Despite the vast amount of detached kelp at sea [70], molecular evidence generally shows poor genetic connectivity between temperate coastal populations, even those separated by just a few tens of kilometers [10,11]. This spatial biodiversity is maintained despite direct evidence for frequent dispersal events over 100-km scales [46,47]. The retention of this genetic structure is best

explained by high-density blocking. Specifically, established populations typically offer little vacant habitat for potential new recruits (i.e., just a few small spaces resulting from local disturbances or storms). Thus, it is likely that any eggs or sperm released by drifting, migrant plants will be diluted by the 'soup' of billions of eggs and sperm produced by local plants, and will have little chance of contributing genes to the established population (Figure 1). By contrast, drifting kelp plants that reach unoccupied shores (e.g., high-latitude coasts scoured by ice during the LGM [10]) have a relatively strong chance of colonizing successfully. However, the subsequent rapid growth and reproduction of these founders will quickly blanket the local shores, such that, within a few years, any later migrants would encounter well-established, dense populations, leading to the genetic homogeneity now observed throughout recolonized high-latitude coasts [10].



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Figure 1. High-density blocking by established populations. This example illustrates how density-dependent processes operate in southern bull-kelp (*Durvillaea antarctica*) populations. Inset photograph of detached kelp reproduced, with permission, from Martin Thiel.

extinction of the prehistoric Eyles' harrier *Circus eylesi* [53,54]. We propose that all of these cases highlight the effects of density-dependent exclusion, where an extinction event releases a surviving lineage from the historic constraints previously imposed by the presence of a congeneric or conspecific population, thus promoting range expansion. If this extinction–recolonization model is correct, then we expect future studies to reveal broad evidence for similar biogeographic 'replacement' events in response to human arrival, especially across recently colonized regions where prehistoric records remain well preserved (e.g., islands of the Pacific Ocean).

Density-dependent processes associated with human dispersal

Human ancestry naturally arouses considerable interest, and the availability of thousands of samples of mtDNA (maternal) and Y-chromosome DNA (paternal) sequences has enabled detailed, global-scale research on human

phylogeography. Colonization events, followed by population expansion and high-density blocking, have left marked spatial genetic signatures indicating recent migrations out of Africa, and beyond [1,55,56]. In particular, European genetic data have been interpreted using 'founder analysis', a method for non-recombining sequences that identifies founder types in source populations, and dates derived lineage clusters in settlement populations [55]. This effect clearly depends on founder genomes dominating the population, and has been described as the 'first-come-first-served' principle [56]. Amazingly, three-quarters of modern-day British human sequences represent lineages that apparently colonized Britain shortly after the last Ice Age, from 15 000 to 7500 years ago, before the first farmers, with most having come from northern Iberia. Additionally, it is possible to deduce many details of local colonization and genetic persistence, including survival in reduced populations in Britain throughout the younger Dryas cold reversal, with subsequent re-expansion. Equally surprising is the corollary

that later invasions and conquests (Roman, Anglo-Saxon, Viking, and Norman) each left little genetic legacy. With the greater use of diploid nuclear sequences and more detailed sampling, it will be possible to clarify the effects of drift, lineage sorting, hybridization, and lineage capture, and the signals they produced, in such expanding human populations where founder events have been so important.

In the Pacific (the ‘final frontier’ of human expansion), genetic and linguistic data indicate a rapid human expansion out of Near Oceania and into unoccupied Remote Oceania over the past few thousand years (ultimately reaching the far-flung islands of Hawaii, New Zealand, and Easter Island) [57–60]. These apparently ordered founding events, also detectable as declining genetic diversity over space, seem to contrast with cultural and anthropological evidence for high mobility and bidirectional migrations between populations [61]. It also seems clear that these recent Polynesian expansion events had little impact on already densely occupied regions of Near Oceania [58,61]. We suggest that, in such cases, any apparent conflict between phylogenetic versus archaeological data sets can be explained, once again, by density-dependent processes associated with leading-edge migration. Specifically, severe population bottlenecks associated with initial colonization events, followed by rapid demographic expansions, together with the suggested minimal genetic impact of follow-up migrants, may all combine to retain the phylogenetic signature of the first colonizers (as is also apparently the case for numerous natural biological radiations across the Hawaiian archipelago, for example [25]).

Computational modeling of allele ‘surfing’

Recent studies strongly suggest that the genetic homogeneity of colonizing populations can be explained by density-dependent processes alone (e.g., the founder effect), rather than necessarily requiring the action of selective forces. Specifically, based on computational analyses, Excoffier and Ray [62] noted that rare alleles can ‘surf on the wave of advance of a population range expansion, reaching high frequencies and spreading over large areas’, even in the absence of any fitness-related differences. Similarly, simulation studies by Edmonds *et al.* [63] highlight that this surfing of mutations ‘with the wave front’ (i.e., founder effect) facilitates the reconstruction of historical demographic expansion events. The fact that ‘surfing’ readily applies to selectively neutral variants [64,65] is highlighted by the experimental microbial studies of Hallatschek and colleagues [4,66].

These phenomena associated with alleles surfing on a wave front are comparable to the concepts outlined above (leading edge, high-density blocking, progression rule, competitive exclusion, and first-come-first-served). Although some of these phenomena are supported by laboratory experiments (Figure 2a [4,66]), others can be inferred from ‘natural experiments’ over a range of temporal and geographic scales (Figure 2b). All involve founder colonization with expansion into unoccupied territory, such that establishment of later dispersers is hindered by the high density of successful founder progeny. This basic process simply promotes one allele or genotype to dominate a local area, whether neutral, selectively different, mutant, or

polymorphic. The process continues across unoccupied territory until the expanding front makes contact with another expansion, leading to further blocking, thereby producing the spatial genome patterns seen in microbial sectoring, postglacial phylogeography, island colonization, and human populations (Figure 2). Simulation studies of colonization show that a range of such patterns can be produced depending on the values of the various parameters and expansion models used [62,67,68]. In general, large homogeneous genotype sectors are produced by rare or occasional long-distance colonists, whereas more complex mixtures occur when dispersal events are more frequent (or simultaneous), including occasional small distinct genomic islands, and various patchwork patterns. We suggest that modeling such expansion events using empirically estimated parameters specific to individual species could help to resolve several long-standing biological questions (*cf.* [68]).

Concluding remarks

Broadly, it is clear that density-dependent processes interact to produce informative biodiversity patterns across a great diversity of scales, regions, and systems, emphasizing their general importance in studies of spatial ecology and evolution. Recognition of the similarities among these various concepts that have recently emerged from different fields will surely assist researchers in developing theoretical and empirical analyses that will strengthen understanding of these processes and their wide evolutionary consequences.

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