Island species as models for small population biology and conservation

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Abstract

Islands provide unparalleled natural laboratories for understanding how small, isolated populations persist and evolve. Our synthesis of island population studies reveals that 50–70% report effective population sizes below 100, yet many taxa have sustained such small populations for millions of years. Strikingly, only 4% and 27% of studies examined genetic load and genomic diversity, exposing major blind spots in our understanding of genomic erosion. We argue that island systems offer critical insights into how limited populations retain viability and adaptive potential. Future work should expand taxonomic and geographic coverage, exploit temporal genomic data, and integrate genomic, demographic, and fitness information to link evolutionary resilience on islands to the conservation of increasingly fragmented populations worldwide.

Highlights

- Island populations offer natural experiments for understanding how long-term small population sizes shape evolutionary trajectories, yet their genomic consequences remain underexplored.
- Despite extensive ecological and biogeographic research on islands, studies rarely quantify genetic load or temporal changes in genomic diversity, limiting insight into adaptive potential.
- Many island taxa have persisted for millions of years with extremely small effective population sizes, challenging assumptions about the inevitability of genomic decline.
- Integrating genomic data with life-history traits and demographic histories is essential for predicting vulnerability and guiding conservation strategies for fragmented and declining populations.

Population sizes on islands

The colonization of an island or archipelago typically involves a founder effect, where a small number of individuals establish a new population [1–3]. The often-limited area of islands constrains population sizes, and can increase the likelihood of **inbreeding** [4]. The taxon cycle, in which lineages become increasingly specialized to narrower ecological niches [5], further reduces available suitable habitat. Catastrophic events, such as eruptive volcanic events and massive flank collapses, can further exacerbate these genetic pressures [6]. Collectively, these factors result in the characteristically small population sizes observed in island ecosystems [7].

Small and bottlenecked populations experience reduced efficacy of selection and increased effects of genetic drift and inbreeding, which together promote the fixation of deleterious mutations as purifying selection becomes less efficient [8,9]. Over time, these processes lead to **genomic erosion**, or the progressive loss of genome-wide diversity driven primarily by **genetic drift** and inbreeding [10–12]. Genomic erosion generally manifests as elevated **realised genetic load** (*i.e.*, the component of **genetic load** whose fitness effects are expressed) and maladaptation due to mismatches between genetic variation and the prevailing environmental conditions [11]. As a result, declining genetic diversity diminishes individual fitness and adaptive potential , and reduced population size increases susceptibility to **inbreeding depression** [8,13]. Ultimately, these combined effects heighten extinction risk and may drive populations into mutational meltdown and extinction vortices [14,15]. Consistent with these theoretical predictions, island populations - typically small and isolated - often exhibit signatures of weaker purifying selection [7,14,16], reduced adult fitness [17–19] and morphological abnormalities [20].

Although it has been suggested that island lineages face gradual extinction due to their small population sizes, and the greater ecological turnover dynamics and environmental catastrophes inherent to islands [21], many insular species demonstrate remarkable persistence, surviving for millions of years despite long-term reduced population sizes (N_e) and significant inbreeding [2,4,22,23], while exhibiting substantial genomic variation [24,25]. It may be that smaller and more isolated populations typically face less intense human-driven exploitation compared to larger, less isolated ones [26–28]. However, owing to the taxon-, environment- and population-specific nature of inbreeding depression [29], we argue that these resilient insular populations may offer crucial conservation insights into the evolution and persistence of small populations.

While island systems are well studied in terms of their biogeography, evolutionary history, and ecology, far less is known about their genetic diversity and genomic erosion—the loss of genetic diversity, maladaptation, and accumulation of genetic load. This gap is surprising given that genetic diversity determines adaptive potential and long-term population viability. Here, we explore two interlinked aspects of insular biology: (i) how bottlenecks and long-term small population sizes shape the evolutionary history of island lineages, and (ii) how these demographic histories drive genomic erosion and influence persistence in small populations. We use these dimensions to highlight insular taxa as potential models in informing contemporary conservation strategies. We argue that long-term isolated lineages - sometimes shaped by millions of years of evolution in geographically isolated territories - provide essential insights for safeguarding biodiversity against intensifying anthropogenic threats both in insular and continental contexts.

Fundamental aspects of small population sizes on islands

In many island vertebrates and plants (Box 1) population sizes tend to be smaller than those of their mainland relatives, often as a consequence of founder events and subsequent demographic fluctuations. [1,17–19]. However, this pattern cannot be mistaken as universal, as population size and structure on islands depend strongly on species-specific dispersal abilities, life histories, and spatial genetic structuring within and among islands and continental populations. In any case, the long-term persistence of insular populations offers an opportunity to examine how demographic conditions influence the **purging** of deleterious alleles. Simulations of genomic data suggest that the Channel Island foxes have persisted for millennia through the efficient purging of highly deleterious alleles [23]. Svalbard reindeer maintain adaptive potential despite long-term genetic depletion, successfully surviving in harsh Arctic conditions [30]. These examples align with theoretical predictions that purging can occur in populations with effective sizes (N_e) as small as ≈70 [31] and with empirical evidence that suggests founder effects do not necessarily constrain purifying selection [32]. Collectively, these findings underscore the remarkable capacity of small insular populations to persist despite severe demographic constraints (Box 2).

The severity of inbreeding depression varies substantially among taxa and populations, according to their traits and environmental contexts [29]. Purging of deleterious alleles in lineages on islands may potentially occur through two key ecological mechanisms. First, reduced predator and parasite pressures on islands might lead to more constant demographic dynamics, or a probability of increasing population size, and thus an increased capacity for purging [23]. Indirect support for this comes from increased genetic erosion due to drift following rapid bottlenecks after predator introductions [33]. Second, the dynamics of population demography and connectivity of islands can enable **genetic rescue** via secondary contact between isolated populations. Specifically, oceanic islands often exhibit fragmented habitats resulting from climatic and geological processes, which create fragmented populations and the admixture of these increase genetic diversity and might enable long-term population persistence [34]. In Hawaiian kīpukas or geologically stable areas in the Canary Islands, limited-dispersal organisms accumulate genetic differences across habitat patches isolated by lava flows and massive flank collapses, and subsequent secondary contact could promote heterosis and increased heterozygosity [35,36], potentially masking fixed deleterious mutations [29,37]. In the Chatham Island black robin, historical isolation followed by secondary contact and purifying selection likely purged deleterious alleles, enhancing the species' resilience [38]. Similarly, *Hydrobates* petrels maintain high genetic diversity through inter-colony dispersal [39]. These findings suggest that managed gene flow from nearby populations could be a vital tool for conserving genetically depauperate populations [21], although such interventions must be carefully designed to avoid the risk of outbreeding depression.

Other than demographic and ecological factors promoted by the geographic features of the archipelago, species-specific morphological and behavioural traits can play a crucial role in modulating the purging of deleterious alleles. The Hawaiian hihi maintains population viability and genetic diversity through extra-pair mating behaviors [40], while polyandry and non-random fertilization similarly preserve genetic variation in insular Swedish adders [41]. Hawaiian petrels challenge conventional expectations of conservation biology by maintaining stable and high genetic diversity despite small census population sizes - a phenomenon likely facilitated by their extended generation times and strong dispersal ability allowing inter-colony movement of individuals [42]. These cases reveal an important decoupling between census population size and genetic diversity in long-lived, mobile species, offering critical insights for conservation strategies targeting small populations.

Conservation, genetic load and rewilding

Comparatively small effective population sizes (N_e) of island endemics and native species, in comparison to suitable continental species, may amplify the effect of genetic drift, increasing the risk of deleterious mutation accumulation in island species [7]. This elevated genetic load may erode individual fitness and threaten long-term population viability, raising concerns for *in situ* and captive breeding programs [43,44]. The advent of whole-genome sequencing has positioned genetic load as a critical focus in conservation biology, with whole genome data now enabling a comprehensive assessment of deleterious mutations across all genomic regions [45]. Nevertheless, the lack of standardized methodologies hinders comparative analyses and generalization. Following the framework proposed by [46], we distinguish between **masked load** (deleterious variants in heterozygous state) and realized load (homozygous deleterious variants), assuming that most deleterious mutations are recessive. Computational simulations have become essential tools for quantifying the impacts of such mutations in natural populations [47]. Two major challenges remain for using genetic load in conservation studies. First, accurately inferring the fitness effects of individual variants is difficult, complicating efforts to assess the overall fitness consequences of elevated genetic load [48,49]. Second, more empirical data are needed to quantify the relative importance of masked versus realized genetic load in influencing extinction risk across different timescales [46,49]. Island species, owing to their unique demographic histories, typically small effective population sizes, and limited gene flow, are likely to be especially informative for studying the interplay between purging and the accumulation of deleterious mutations. Well-studied systems such as the Galápagos Islands, Canary Islands, Madagascar, Mauritius, New Zealand, and Hawaii offer valuable opportunities to generate such empirical data, as they have long served as focal points for evolutionary, ecological, and conservation genetics research.

There is growing interest in characterizing deleterious genetic variation and genetic load for the conservation of small and endangered populations. Recent reviews have explored how both selective purging and genetic drift shape the distribution of deleterious mutations during population decline and recovery (*e.g.*, [48]. While strong bottlenecks can facilitate the purging of highly deleterious alleles, weakly or mildly deleterious mutations are more likely to increase in frequency, potentially reducing the overall fitness of the population [50,51]. The balance between drift and selection during demographic decline and recovery thus plays a critical role in shaping genetic load, with important implications for conservation management (see Box 2). In small populations, genetic drift can cause previously masked deleterious alleles to become homozygous and expressed, converting masked load into realized load [52]. Evidence from insular taxa shows elevated realized load due to enhanced drift effects, and illustrates both the accumulation and purging of deleterious variation. For example, passerines on islands tend to exhibit higher genetic load than their mainland counterparts [7,16], while island populations of peregrine falcons show extensive runs of homozygosity and elevated drift load compared to mainland populations [53]. An efficient purging of strongly deleterious alleles following severe bottlenecks seems to occur on islands. For example, the recent population collapse of the Reunion harrier due to anthropogenic pressures exemplifies the complex interplay between genetic drift and purging: while simulations suggest that highly deleterious alleles may have been purged as a result of recent bottlenecks, mildly deleterious mutations persist, likely due to the reduced efficacy of selection [54]. This evidence resembles that of several emblematic island species, such as the San Nicolas Island fox or the Svalbard reindeer, which all show long-term persistence despite high homozygosity and apparent fixation of deleterious variants, suggesting that bottlenecks may lead to purging of deleterious variants and mitigating some of the negative consequences of genomic erosion [23,30,55]. Similarly, distinct demographic histories, including bottleneck and introgression histories, can affect genetic load, as shown in the Anatolian and the Cyprian mouflons [56]. Indeed, the Cyprian mouflon exhibits both lower genetic diversity and genetic load than the Anatolian mouflon, likely because of founder effects, island isolation, introgression from domestic lineages, or differences in their bottleneck dynamics. The San Nicolas Island fox presents a particularly striking example: despite near-complete genomic monomorphism and high homozygosity for putatively deleterious alleles, the population has persisted for decades following a severe 20th-century bottleneck—challenging assumptions that genetic depauperation inevitably leads to extinction [57]. Although few island populations have been the focus of detailed load analyses, existing studies underscore the value of island systems for disentangling the dynamics of deleterious variation, purging, and persistence in small populations (see Box 1). More studies are needed so we are able to draw general conclusions across species with diverse genomic architectures, ecological contexts, and evolutionary histories.

Insular taxa can contribute to valuable insights into the poorly understood relationship between genetic load and fitness. A long-term study of house sparrow metapopulations across eight islands measured fitness as survival probability and lifetime reproductive success, finding that inbreeding consistently reduced individual fitness when compared to mainland populations. Yet, the magnitude of inbreeding depression was similar across populations experiencing different levels of inbreeding [19]. In a small island population of *Glanville fritillary* butterflies, extensive fixation of deleterious alleles contributed to reduced trait performance and elevated genetic load, though inbreeding depression was not observed in recent generations [58]. Recent simulation studies, applicable to both island and non-island systems, highlight how the shape of the distribution of fitness effects (DFE), particularly the prevalence of weakly versus strongly deleterious mutations, can influence both the accumulation of load and its detectability in fitness-related traits. This may help explain why high load does not always translate into observable inbreeding depression [47]. These findings underscore the complex challenges of linking genetic load to immediate fitness consequences. Evidence from islands shows that genomic erosion can constrain future adaptive potential. The Seychelles magpie robin, which underwent historical bottlenecks followed by recent assisted translocations, harbors a high realized genetic load and showcases one of the lowest genetic diversity recorded in endangered birds [59]. Simulations suggest that long-term recovery may require repeated translocations involving large numbers of individuals to mitigate load and restore adaptive potential. The Chatham Island black robin, once reduced to a single breeding pair in the 1980s, has rebounded demographically, with approximately 300 individuals now present in the wild. Genomic comparisons between two extant populations and historical samples predating the bottleneck suggest that some purging of deleterious alleles occurred over time, potentially aided by long-term isolation across multiple islands [38]. However, evidence of persistent inbreeding depression in this species underscores that even when strongly deleterious alleles are purged, mildly deleterious mutations can accumulate and impair fitness [18,60].

Insights from island systems can also inform genetic rescue and rewilding, particularly in the context of species introductions or translocations. The extinction of the dodo on Mauritius, which disrupted seed dispersal for several large-fruited tree species, some of which subsequently declined, is a textbook example of how the loss of key island species can cascade through ecosystems, which calls upon the importance of both rewilding and genetic rescue. Islands have become key testing grounds for rewilding due to their historical loss of ecological actors [61] and fewer sociopolitical barriers to reintroducing megafaunal taxa [62]. For instance, giant tortoise rewilding on Indian Ocean islands demonstrates the potential to restore lost ecological functions, such as seed dispersal and nutrient cycling [62]. However, evidence from islands clearly shows that the genomic legacy of both reintroduced and recipient populations receiving translocated individuals must be carefully considered. Reintroductions from large outbred populations may unintentionally introduce recessive deleterious alleles, as demonstrated in the Isle Royale wolf. In this species, an initial boost in population viability followed the arrival of a single immigrant, but subsequent inbreeding among his descendants led to a population collapse due to the expression of hidden genetic load [63]. While genetic rescue can be a powerful tool, it also carries risks of outbreeding depression, particularly when mixing highly divergent lineages or disrupting local adaptation [55]. For instance, a study on the isolated population of Apennine brown bears endemic to Central Italy showed that introducing individuals from Slovakia would lead to a loss of local ancestry and an increase in genetic load within the Apennine population [64]. Effective rewilding or genetic rescue efforts may therefore require genomic screening to identify individuals with lower realized load, fewer long runs of homozygosity, and higher compatibility with recipient populations.

Conclusions

Earth is undergoing unprecedented environmental transformations fueled by unsustainable economic paradigms that disregard planetary boundaries. This crisis is precipitating biodiversity loss through habitat destruction, decreased size of populations and ultimately species extinction. Within this context, island systems arise as natural and ideal models for studying small population biology. Although small, isolated, insular populations are often assumed to accumulate elevated genetic load, empirical evidence remains limited (only 4% of our literature survey dealt with genetic load). Nonetheless, their long-term persistence, particularly under benign ecological conditions (*e.g.*, reduced predation and competition), highlights these systems as valuable for testing hypotheses relevant to conservation strategies. A critical consideration is the temporal disparity between natural population recovery and human-managed restoration efforts (see Outstanding questions). Natural populations on continents likely experience a genetically sensitive post-colonization phase during bottleneck recovery, a process rarely observed in contemporary island studies since most extant island populations represent long-established systems. This temporal perspective highlights an important gap in our understanding of early-stage recovery dynamics, which may have significant implications for conservation strategies targeting recently founded or reintroduced populations.

Future work should define thresholds at which genetic load compromises viability while identifying buffering ecological contexts, translate island-derived insights into broader conservation strategies for long-term viability of populations, and integrate ecological, genetic, and morphological data to assess fitness consequences across population and individual levels. Expanding studies beyond the current bias toward birds and mammals (Box 1) is essential. Combining demographic and genomic approaches - particularly by linking effective population size (N_e) estimates with direct measures of deleterious variation - will refine population health assessments. Integrating genomic simulations with empirical fitness and genetic load measurements can bridge island conservation genetics with general conservation theory. Additionally, evaluating how human-mediated dispersal influences genetic load and adaptive potential in both native and introduced island species remains crucial. Addressing these priorities will elucidate how isolation, small population size, and demographic history collectively shape the genomic integrity of island biotas.

Outstanding Questions

1. How can we disentangle the relative contributions of demographic history, colonization age, and ecological context to genetic load in island populations?
Understanding how these factors interact is crucial for identifying when purging or drift dominates and for predicting which populations are most resilient to genomic erosion.

2. What comparative sampling designs best capture the temporal dynamics of load accumulation and purging across islands and archipelagos?
Within-archipelago comparisons—among endemic, native, and introduced taxa—offer a promising avenue, but standardized frameworks are needed to separate temporal from ecological effects.

3. To what extent can genomic and demographic data from museum and ancient DNA collections reveal historical changes in load and purging efficiency?
Temporal genomic data remain underused but could uniquely test hypotheses about how small populations recover or decline through time.

4. How can forward-time simulations and variant effect prediction pipelines be integrated to provide robust, comparable estimates of both masked and realized genetic load?
Coupling empirical and simulated data will improve inference by linking specific mutational burdens to demographic processes and fitness outcomes.

5. Which measurable fitness components, such as survival, fecundity, or phenotypic performance, most accurately reflect realized genetic load in wild island populations?
Identifying reliable proxies for fitness will enable more accurate assessments of how genomic erosion translates into ecological performance.

6. How do long-term ecological stability and life-history traits modulate the relationship between effective population size, purging, and extinction risk?
Comparative analyses across species differing in longevity, reproductive rate, and habitat specialization could clarify the conditions that buffer small populations from mutational meltdown.

7. What coordinated research frameworks can unify genomic, ecological, and demographic perspectives to generalize patterns of load evolution in insular systems?
Cross-disciplinary collaborations and shared data standards are essential to move from case studies toward predictive models of genetic load in isolated populations.

Box 1 - Genomic insights from islands: a global synthesis of diversity, bottlenecks, and genetic load

We conducted three literature searches using Web of Science on March 19, 2024, with the following keywords as topics: *(i)* “genetic load” AND “island” (462 entries); *(ii)* “bottleneck” AND “island” (1,379 entries); *(iii)* and “genomic diversity” AND “island” (1,934 entries) (Table S1). We discarded irrelevant publications, for instance, those that focused on ‘genomic islands’ of differentiation across genomes, ending up with 1,063 publications that we carefully reviewed. This included 41, 733 and 289 publications for the 3 different literature searches, respectively. For each of these 1,063 publications, we recorded the geographic focus (*i.e.*, single islands or archipelagos), taxonomic group (*e.g.*, Amphibia, Mammalia, Plantae, Insecta), the minimum reported effective population size (N_e), and the lowest reported individual counts estimated by the authors (if available). For N_e estimations, we only considered cases where N_e was explicitly found in the text, thus discarding the visual inference from plots reflecting N_e changes through time (*e.g.*, PSMC plots). We also noted the biogeographic origin of the lineages (*i.e.*, human-associated dispersal such as invasive species versus native or endemic populations), and whether the study included temporal sampling (*e.g.*, ancient DNA or sampling across multiple years).

The number of relevant publications (1,063 in total) underscores the scientific interest in understanding the genomic consequences of insularity, particularly regarding genetic diversity and the effects of bottlenecks. Nevertheless, only a small proportion of insular genomic studies focused on genetic load (4%), suggesting that very little is known about this topic of growing interest in conservation biology.

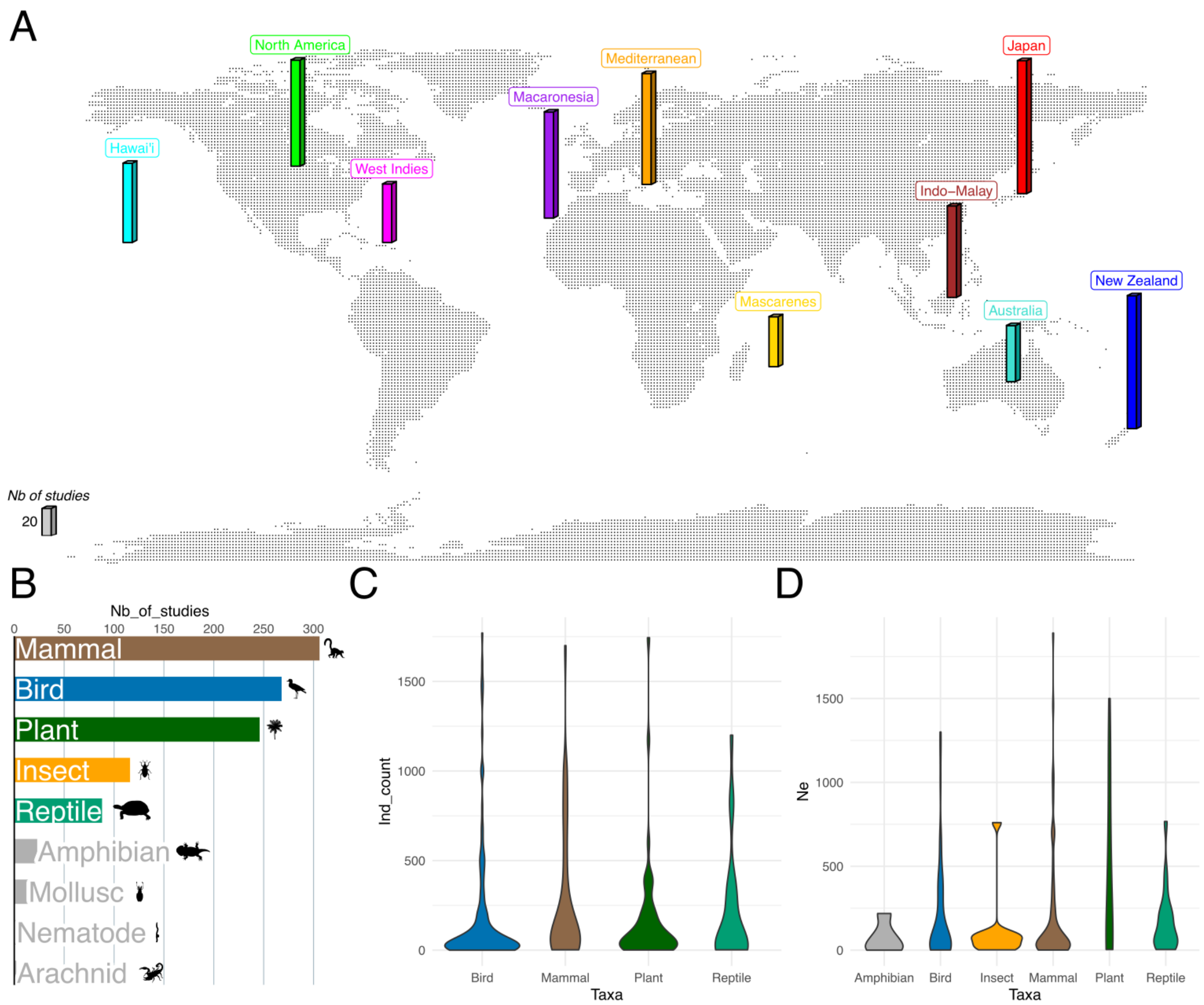

Figure 1 (box 1) Estimated effective population size (N_e) for different taxa across three literature searches. We conducted three separate searches in Web of Science using the following topic combinations: "genetic load" AND "island" "bottleneck" AND "island" and "genomic diversity" AND "island". For each search, we extracted the reported N_e values for each taxon. To highlight the typically low N_e values observed in island populations, we excluded entries with $N_e > 2{,}000$.

The seven most frequently studied regions were: Japan and associated islands/archipelagos (109 papers), New Zealand (109), Mediterranean islands (91), North American coastal and inland islands (87), Macaronesia (86), the Indo-Malay archipelago (75), and Hawai'i (65) (Fig.1A). In terms of taxonomic focus, we identified 306 studies on mammals, 268 on birds, 246 on plants, 115 on insects, 88 on reptiles, 23 on amphibians, 14 on molluscs, 2 on arachnids, and 2 on nematodes (Fig. 1B).

Individual count data were notably low in many cases. For birds, 23 studies reported counts ≤10 individuals, while 100 reported populations effective population sizes of <100 individuals

(70.9% of all studies reporting individual counts). For mammals, 16 studies reported ≤10 individuals while 43 reported <100 (51.2%). For plants, 8 studies had counts ≤10 and 34 had <100 individuals (66.7%). Among reptiles, 9 studies reported counts ≤10, and 15 reported <100 (62.5%) (Fig. 1C). The lowest reported N_e values were 3 for amphibians, 6 for birds, 2 for both insects and mammals, and 4 for both plants and reptiles (Fig. 1D).

Overall, 268 studies focused on lineages introduced through human-associated dispersal, while 816 focused on native or endemic taxa. Only 166 studies incorporated any form of temporal sampling.

Box 2 - Genomic trade-offs in long-term small populations: insights from island species

Island species often have small long-term effective population sizes (N_e), limited gene flow, and persistent isolation. These demographic features may shape their genomes in predictable yet counterintuitive ways, offering critical insights into how small populations persist, and how they may fail.

In some long-term small-N_e populations, including island endemics, inbreeding depression appears weak or undetectable [23,65]. This has often been interpreted as the result of purging of strongly deleterious alleles [23], although it may also result from drift eliminating segregating variation, including mildly deleterious and neutral alleles, giving an illusion of resilience.

Yet this apparent resilience is double-edged. Genetic drift in chronically small populations may fix mildly deleterious mutations, thus elevating drift load and reducing fitness, while also steadily eroding genome-wide diversity, compromising adaptive potential. This genomic erosion is subtle, often going unnoticed in stable ecological conditions, but it may be catastrophic when rapid environmental change occurs [66].

Thus, island species exemplify a fundamental trade-off: they may be buffered against inbreeding depression due to their long-term stable but low N_e, yet this comes at the cost of adaptive flexibility. These two outcomes, reduced inbreeding depression and reduced adaptive potential, are two sides of the same evolutionary coin. Apparent genetic stability may conceal hidden fragility, especially when populations face novel pathogens, invasive species, or climatic shifts. For this reason, island species serve as powerful models for understanding how long-term demography dynamics shapes both persistence and vulnerability in small populations.

Glossary

Genetic drift Stochastic changes in allele frequencies across generations, leading to loss of genetic diversity due to random sampling of alleles, particularly in small populations.

Genetic load The fraction by which the population mean fitness differs from that of a reference genotype (i.e., the genotype with maximum fitness).

Genetic rescue A strategy aimed at improving the genetic diversity and fitness of a small or inbred population through the introduction of individuals from another population.

Genomic erosion Cumulative genetic threats to small populations, including loss of genome-wide diversity, increased genetic load, maladaptation (a mismatch between existing adaptations and the environment), and genetic introgression following hybridization (introduction of non-compatible or maladapted alleles).

Inbreeding Mating between related individuals, leading to increased homozygosity beyond what is expected under random mating (panmixia). Inbreeding is more frequent in small or fragmented populations.

Inbreeding depression Reduction in individual fitness due to increased expression of partially or fully recessive deleterious alleles in homozygous form. While it can facilitate purging of deleterious variants, it may also reduce overall population viability.

Masked load (inbreeding load or potential load) Component of the genetic load whose fitness effects are hidden because deleterious recessive alleles are present in heterozygous form.

Purging Reduction of genetic load via purifying selection against deleterious alleles exposed in homozygous form, often occurring through inbreeding, population fragmentation, or positive assortative mating.

Realized load Component of genetic load representing deleterious alleles that are expressed

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