Caution against using genetic diversity alone to determine native ranges of aquatic species: the persistence of an old problem

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Abstract

The assumption that elevated genetic diversity in a population directly correlates with its native range is a common but flawed approach in ecological studies. This practice is based on the belief that native populations, having been exposed to local evolutionary pressures over long periods, should exhibit higher genetic diversity, while introduced populations experience founder effects or bottlenecks that reduce genetic variation. However, multiple introductions and genetic admixture in non-native regions can artificially inflate genetic diversity, challenging the assumption that regions with high genetic diversity are the native ranges. This issue, which has been recognized for nearly two decades, remains prevalent in the literature despite strong evidence to the contrary. Studies on a variety of marine invertebrates demonstrate how introduced populations may exceed native ones in genetic diversity. In contrast, bottlenecks in native populations due to environmental stressors can mask the true genetic history of species. This letter argues for an integrative approach when determining native ranges, combining genetic data with historical, ecological and biogeographical analyses. This broader framework helps avoid misinterpretations of genetic diversity, which could lead to inaccurate conclusions about species' native ranges and misinform conservation and management strategies.

Key words: Biogeographic, fossil, haplotype, integrative, invasion, paradox, phylogeography

Introduction

The use of genetic diversity as a tool for inferring the native ranges of species has become increasingly common in ecological studies, particularly when their distributional ranges are well-documented. The rationale behind this approach stems from the expectation that native populations, having existed in their environment over extended evolutionary timescales, will exhibit higher genetic diversity due to the accumulation of mutations, ongoing gene flow, and adaptation to local conditions (Sork 2015; Wadgymar et al. 2022). In contrast, introduced populations are often assumed to undergo founder effects, bottlenecks, or reduced genetic input, leading to diminished genetic diversity (Newman and Pilson 1997; Sakai et al. 2001; Allendorf and Lundquist 2003). Consequently, when elevated genetic

diversity is observed in populations from a specific region, it is often presumed to be the native range of the species. This logic has significant implications for understanding species distributions and informing conservation efforts (Teixeira and Huber 2021). Identifying native ranges is essential for distinguishing natural range expansions from human-mediated introductions, developing management strategies for invasive species, and preserving the integrity of native ecosystems. However, the assumption that genetic diversity directly correlates with nativity overlooks the actual complexities of species introductions.

Processes such as multiple introductions, genetic admixture, and human-mediated dispersal can artificially elevate genetic diversity in non-native regions, potentially obscuring true native ranges. A still-relevant review by Roman and Darling (2007) first highlighted this issue as an explanation for the invasion paradox, emphasizing that multiple introductions often eliminate founder effects, resulting in introduced populations with genetic diversity comparable to or even exceeding that of native populations. Almost two decades later, the reliance on genetic diversity as the sole metric for determining native ranges continues to persist in the literature (Yund et al. 2015; Sun et al. 2017; Taylor and Roterman 2017; Rice et al. 2018; Malan et al. 2020, but see Radashevsky et al. 2023). In this letter, I reiterate the problems of drawing premature conclusions about a species' native range based solely on genetic data while also recommending complementary avenues of inquiry that can provide a more robust and accurate understanding of a species' geographic origins. Aquatic species are a particularly relevant focus due to the frequent occurrence of such repeated introductions through shipping, aquaculture, and ballast water exchange, which often elevate genetic diversity in non-native populations. The high connectivity of aquatic ecosystems further complicates the interpretation of genetic data, highlighting the need for a multidisciplinary approach to accurately determine native ranges.

There is now a growing body of evidence demonstrating how multiple, frequent introductions can lead to elevated genetic diversity in a species' introduced range. Notable examples include the widespread invader *Mytilus galloprovincialis*, which exhibits significantly higher nucleotide diversity in many sections of its invasion range compared to its native conspecifics (Han and Dong 2020). Similar patterns have been observed in other high-profile species, such as the oriental shrimp *Palaemon macrodactylus* (Lejeusne et al. 2014), the invasive mussel *Mytella charruana* (Gillis et al. 2009), and the round goby *Neogobius melanostomus* (Andres et al. 2023). Conversely, bottlenecks in native populations, often caused by habitat loss, overexploitation, or environmental changes, can reduce genetic diversity, masking their true origins. The central problem here is that genetic diversity estimates represent only snapshots of population history and cannot capture the dynamic processes that influence diversity over time. This 'snapshot effect' can lead to false conclusions, such as assigning native status to regions with high genetic diversity due to introductions while overlooking regions with historically stable populations and lower diversity. One key factor in this misinterpretation is sampling bias (see Muirhead et al. 2008; Phillips et al. 2019). Studies of invasive species often focus heavily on introduced populations, while native-range sampling may be limited or uneven (Rius et al. 2014). This can lead to an artificial inflation of diversity estimates in the introduced range while underestimating the full genetic structure of the native range. Additionally, many species exist as metapopulations, where different subpopulations exhibit varying levels of genetic diversity due to local adaptation, genetic drift, or historical bottlenecks. Failing to account for this metapopulation structure may reinforce incorrect assumptions about where genetic diversity is highest. All of this can cause researchers to fall into an interpretational trap, where

genetic diversity is mistakenly equated with nativity, ignoring the complex demographic and ecological forces that shape genetic variation. To contextualize these concerns in practice, I ask readers consider the following hypothetical scenarios:

Scenario A: High genetic diversity leading to misinterpretation

Imagine a species, Species A, native to a region with stable environmental conditions. Over time, this stability results in relatively low genetic diversity as selective pressures optimize genetic composition for long-term environmental stability, leading to a reduction in standing genetic variation at certain loci. Species A is then introduced to a new region with diverse habitats and environmental challenges. To thrive, the introduced populations undergo rapid adaptation, possibly through multiple introduction events from various source populations, leading to increased genetic diversity in the non-native range. Researchers analyzing global populations of Species A might observe higher genetic diversity in the introduced region and, if relying solely on genetic data, could incorrectly conclude that the introduced area is the species' native range.

Scenario B: Bottlenecks in native regions masking true origins

Consider Species B, which historically occupied a vast native range. Due to historical events such as climatic changes, habitat loss, or overexploitation, Species B experiences significant population declines, leading to genetic bottlenecks and reduced genetic diversity in its native regions. Meanwhile, Species B is introduced to a new region where it establishes multiple thriving populations through repeated introductions from various sources, which may include different populations within its native range as well as other introduced populations. These introduced populations might exhibit higher genetic diversity due to the mixing of different genetic lineages. Additionally, incomplete sampling in the native range may underestimate its genetic diversity there, creating a misleading contrast with the introduced range.

Additional avenues of inquiry that can complement genetic diversity to better delineate native ranges should include careful examination of historical records and ecological data, along with biogeographical analyses. Long-term historical data, including records of species distribution over time, can provide relevant context for assessing nativity. For instance, evidence from fossil records or historical documents can help differentiate natural range expansions from human-mediated introductions, which may not always leave clear signatures. Understanding habitat preferences, environmental tolerances, and ecological interactions is also essential. Species thriving in novel environments may exhibit high genetic diversity due to adaptation, but this does not necessarily indicate nativity. Incorporating ecological niche modeling can clarify whether populations are likely to be native or introduced based on their environmental suitability. Finally, geographical and physical barriers such as ocean currents, mountain ranges, or climatic zones play a significant role in shaping species distributions. These factors can provide critical clues about a species' likely native range. For example, patterns of ocean currents, when combined with biophysical modeling, can simulate larval dispersal pathways and help distinguish between natural expansions and introductions via human activities like shipping or aquaculture. Such models can validate genetic data by testing whether observed connectivity aligns with natural dispersal patterns, offering a more robust approach to inferring species origins. A recent study by Radashevsky et al. (2023) provides an excellent example of the pitfalls of relying solely on genetic diversity. The authors identified South

Africa as having the highest haplotype diversity for *Polydora hoplura*, a notorious shell-boring polychaete worm that infests commercially important shellfish such as oysters and abalone. Based on Scenario A, such a finding might suggest South Africa as the native range. However, they questioned this conclusion by referring to additional lines of evidence, including the possibility of multiple introductions through aquaculture and shipping, which could explain the elevated diversity in this region. Furthermore, their study emphasized the importance of integrating genetic analyses with historical (i.e. museum samples) and ecological data (association with human-altered environments such as aquaculture farms) to provide a more accurate understanding of the species' origins.

Needless to say, the complexities of the natural environment in the Anthropocene coupled with the high levels of cryptogenicity in aquatic habitats, especially among invertebrate fauna, highlights the need to consider integrative approaches when inferring native ranges. Without this integrative approach, interpretations risk misrepresenting the ecological and evolutionary dynamics that govern species distributions.

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