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EDITED BY
Jorge Doña,
University of Illinois at
Urbana–Champaign, United States

REVIEWED BY
Kevin Johnson,
Illinois Natural History Survey (INHS),
United States

*CORRESPONDENCE
Aleksandra Biedrzycka
biedrzycka@iop.krakow.pl

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Editorial: Genomic basis of adaptations to new environments in expansive and invasive species

Aleksandra Biedrzycka^{1*}, Anna Fijarczyk², Agnieszka Kloch³
and Ilga Mercedes Porth²

¹Institute of Nature Conservation, Polish Academy of Sciences, Krakow, Poland, ²Laval University, Quebec City, QC, Canada, ³Faculty of Biology, University of Warsaw, Warsaw, Poland

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Editorial on the Research Topic

Genomic basis of adaptations to new environments in expansive and invasive species

Biological invasions are currently one of the most serious threats to worldwide diversity and one of the most difficult issues that must be dealt with by conservation managers. Both human-mediated and natural range colonisations undergo similar demographic and selection-driven processes (Santangelo et al., 2022). Population genomic approaches offer an opportunity for identifying mechanisms underlying evolutionary changes during colonization. Understanding colonization genetics and evolution is central to addressing questions in the biology of expanding and invasive species. By definition, “expansive species” are native species that expand their range and colonize new habitats in a geographic area where they are native (Marcinkowska-Ochtyra et al., 2018). Expansive species have similar negative impacts on ecosystems as invasive species because both can eventually dominate the community and significantly reduce biodiversity (*ibidem*), by competitive exclusion, niche displacement and ultimately the extinction of (other) native species (Mooney and Cleland, 2001).

Introduced populations are primarily geographically isolated, established with varying numbers of founding individuals from potentially different source populations (Dlugosch and Parker, 2008). Further, bottlenecks that are typical for those introduction events cause stochastic changes in genetic diversity. As a result, large differences in allele frequencies or fixation of different alleles may be visible in genomes across the invasive population range. However, many invasive species do not exhibit a genetic bottleneck but maintain high levels of genetic variation in the introduced range. This phenomenon is usually explained by the admixture of genetically differentiated invasive populations (Dlugosch and Parker, 2008; Uller and Leimu, 2011; McGoey and Stinchcombe, 2021). Admixture can increase the adaptive potential of introduced populations (Roman and Darling, 2007; Prentis et al., 2008; Verhoeven et al., 2011; Rius and Darling, 2014; Bock et al., 2015).

Species with poor ability to respond to selection through molecular or phenotypic changes, i.e., low adaptive potential, have lower chances of persistence in a changing environment (Lande and Shannon, 1996; Merilä and Hendry, 2014). On the other hand, invasive species often show a high evolutionary potential that facilitates adaptation to novel conditions and sometimes outperforms native species (Dlugosch et al., 2015). Therefore, species invasions are great models for uncovering evolutionary mechanisms underlying adaptations to new environments (Barrett, 2015; Hodgins et al., 2018). Rapid adaptation is common in invasive populations (Lee, 2002; Rollins et al., 2013) and is proposed to be crucial to their long-term success (Dlugosch and Parker, 2008). Approaches such as genome-environment association studies link specific genomic variants to new environment features and provide indirect evidence for adaptation to a new environment.

This Research Topic gathers a collection of five original research articles and one review that provide the scientific background to understand processes shaping adaptive genomic diversity of naturally expanding and invasive populations, knowledge, which in turn may be useful in (a) planning successful approaches to fight biological invasions, and (b) leading the way for future research necessary to further resolve the genomic basis of adaptation during population expansion. Altogether, these studies underline the need to disentangle demographic relationships between invasive or expansive populations that can be further used to resolve adaptive processes enabling successful survival and spreading of populations under specific environmental conditions.

In their review, Kotlik et al. summarize over two decades of phylogeographic studies on the bank vole. This small rodent becomes a “non-model model organism” to study the complexities of the range expansion from the last glaciation until today. A simple picture drawn from mtDNA was expanded with the use of genome-wide SNPs and whole mitogenomes, revealing cryptic extra-Mediterranean glacial refugia and substantial replacement and mixing of lineages originating from different refugia during end-glacial colonization. The history is not over, as bank vole was introduced to Ireland in the early 20th century, and it has been expanding ever since. The authors introduce the concept of adaptive phylogeography, where local genetic variation within species is attributed to functional differences. Adaptive phylogeography seeks to uncover functional differences between populations that had arisen from adaptations to local conditions and may explain observed phylogeographic patterns in addition to demographic processes.

This aspect of phylogeography is also critically important in studying invasion processes. The study by Sapkota et al. addresses the invasion characteristics of the popular ornamental tree Callery pear, now naturalized in the U.S., which include high mutation rates, high genetic diversity, high gene flow, and lack of a phylogeographic pattern among populations in

the south-eastern United States. Populations were also able to overcome historical founder effects. Overall, the results suggest that the Callery pear populations studied may be part of a much larger community where individuals have been locally introduced multiple times due to human intervention and whose invasion history can be traced back earlier than previously documented.

Despite the absence of population structure, we may observe adaptive divergence in expansive populations. Papa et al. studied the genetic structure and local adaptation in Tarakihi fish in their native marine environments around New Zealand and Tasmania using whole genome re-sequencing data. They identified the New Zealand stock as a panmictic genetic population, indicating its high dispersal potential. The authors also identified genomic clines associated with water temperature gradients. This is an interesting example of adaptive divergence in the absence of neutral genomic structure; such allelic variation could be monitored over time to determine an adaptive response of Tarakihi to changes in ocean temperature due to global change and reveal potential resilience.

The mechanisms underlying local variation in phenotypic traits in invasive starlings were studied by Stuart et al. Using reduced representation sequencing data paired with phenotypic, ecological, and spatial information, they sought to differentiate whether environmental variables or heritable traits play a major role in shaping phenotypic variance of these birds. They demonstrated the important role of elevation. The relationship between allelic frequencies and environmental variables could be attributed to introduction history, later reinforced by environmental gradients during colonization. Taken together, the ecogeographical phenotype trends can be explained by genetics and plasticity induced by environmental differences.

Invasions can lead to unexpected patterns of genetic structure or lack thereof, prompting questions about the source of local adaptation or phenotypic gradients. Eckert et al. tested if epigenetic variation can account for local adaptation or latitudinal gradient in the perennial outcrossing *Solidago canadensis* s.l., an invasive plant in Central Europe. This species has been introduced into Europe since the 17th century and exhibits a clear latitudinal phenotypic gradient that is heritable when reared in common garden settings. The authors used methylation-sensitive AFLP markers to investigate whether epigenetic variation reflects phenotype variation along the geographic cline or fine-scale spatial genetic structure between populations. The authors also looked for genetic and epigenetic loci associated with climate variables or spatial neighborhoods. This study brings us closer to understanding the role of genetic and epigenetic variation in the successful invasion of *S. canadensis* in Central Europe.

The last article in the collection addresses the problem of hybridization of invasive and native species and how it may promote invasion success and adaptation to a novel environment. Wu et al. investigated underlying genomic

signatures for the successful establishment of the creeping herb *Sphagneticola trilobata*, native to South America, through hybridization with its Chinese congener. Expression bias in the F1 hybrid between the native and the invasive *Sphagneticola* species was monitored under cold stress, which was used as a proxy for thermotolerance, an important invasive trait. The authors showed that the transcriptome profiles of the F1 corresponded to physiological responses similar to those of the more cold-tolerant native species and therefore manifested as a transcriptomic shock. Based on these results, it is anticipated that cold-tolerance alleles may be favored if F1 hybrids were to be formed with more northerly native populations, underscoring their potential to form a superweed.

Contributions to this Research Topic reflect the interest in one of the most burning problems of present-day worldwide nature conservation, that is species invasion. Gathered articles prove that using modern sequencing approaches allows us to discover and study rapid adaptations that are crucial for successive invasions. Coupling genetic diversity with phenotype and environmental traits is essential for developing the scientific background to fight species invasion.

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Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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