# Opportunities for studying propagule pressure using gene flow reveal its role in accelerating biological invasions

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## Abstract

When an alien species establishes at a new location, it must spread to become an invader. The extent to which propagule pressure promotes the spread of invaders, especially at local scales, is often difficult to quantify because it requires a reliable measure of, and variation in, rate of spread, and of propagule pressure across similar areas. In this issue of Molecular Ecology, Mairal et al. (2022) make use an unique system of paired sub-Antarctic islands, one with very infrequent human activities, and another inhabited by scientists, to assess the role of propagule pressure and anthropogenic disturbance in the introduction and spread of a major global invader, Poa annua L., to and on the islands. Genetic admixture between different genetic clusters is virtually absent from the little-visited island, while the inhabited island experienced more introduction events, but also significant admixture between genetic clusters. Detailed distribution maps of P. annua spanning more than 50 years allowed the authors to link genetic diversity to residence time. The nature of the system, and the multifaceted approach used by the authors, allows for new insights into the mechanism by which propagule pressure results in the spread of invasive species.

Invasion biologists have a fairly good idea of what factors allow invasive species to successfully establish in new environments (Van Kleunen et al., 2010). However, much less is understood about the dynamics of the spread of invaders after establishment: what mechanisms allow newly established species to spread? Two predominant theories exist: increased propagule pressure results in increased fitness and thus faster spread of the invading species through more and larger introduction events, which result in rescue effects and higher genetic diversity, which in turn increases population stability and opportunities for adaptation; or the local habitat conditions of the new area are particularly suitable for the invading species through climate-matching or reduced biotic resistance, allowing the species' spread (Bomford et al., 2010; Colautti et al., 2006; Enders et al., 2020).

Disentangling the respective role of propagule pressure against other putative drivers is complex. To quantify propagule pressure, some measure of human connectivity to an area over the time that an invader spreads must be quantifiable. Yet, most places on Earth are now highly influenced by humans, making this difficult. Additionally, an historical record of presenceabsence data is required to quantify spread. Presence data have become increasingly available, mostly from opportunistic surveys, but obtaining reliable absence data, especially through time, remains difficult. Finally, to reliably assess the effect of propagule pressure independent of habitat suitability on spread, areas that face different propagule pressure, but comparable environments with identical native communities, are required. The sub-Antarctic Prince Edward archipelago offers a unique system in which to test the effects of propagule pressure on the spread of invaders (Chown & Froneman, 2008). The archipelago consists of two islands which lie only approximately 21 km apart: Marion and Prince Edward Island. Human impacts on the islands are low and visits well quantified: tourism is prohibited, and in most year only one scientific voyage to the islands takes place. Importantly, human activities on the two islands differ notably. Marion Island houses a South African research station with permanent human habitation with about 22 research and support staff at most times of the year, while the adjacent Prince Edward Island has no research station and is visited very infrequently (at the most by ten researchers for a duration of eight days once every four years). Due to their proximity, both the environmental conditions and native communities of the two islands are similar. Additionally, both islands have elevational gradients that create gradients in habitat suitability. Finally, the islands have a history of rigorous scientific research, which includes detailed presence-absence mapping of plant species across the islands since the 1960s.

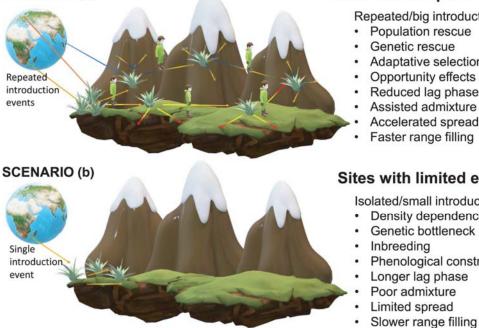
Mairal et al. (2022) employed a multifaceted approach, including presence-absence mapping through time, flow cytometry, microsatellite sequencing and species distribution modelling, to compare the effects of propagule pressure and anthropogenic disturbance on the spread of the invasive grass *Poa annua* L. (Figure 1) on the more frequently-visited Marion Island and the little-visited Prince Edward Island. Originally from the Palearctic region, *Poa annua* is one of the most widespread invaders globally, having invaded regions with a variety of climates, including the Antarctic (Pertierra et al., 2017). Its widespread distribution makes *P. annua* an excellent species on which to test the importance of propagule pressure on spread, as repeat introductions from different localities are likely.



FIGURE 1. A tagged *Poa annua* plant photographed on sub-Antarctic Macquarie Island. (Photograph: L. Pertierra)

Mairal et al. (2022) find several lines of evidence that human activities have played a critical role in the genetic diversity and spreading of *P. annua* on Marion Island, whereas on Prince Edward Island the invasion process was probably slower due to reduced human visitation. Poa annua populations on Marion Island have higher ploidy levels, higher allelic richness per locus, and more genetic clusters than on Prince Edward Island. Almost no admixture exists between genetic clusters on Prince Edward Island, while levels of admixture between genetic clusters on Marion Island suggest a panmictic population structure. On Marion Island, genetic diversity is higher in older P. annua populations. Finally, some P. annua populations on Prince Edward Island were more closely related to Marion Island populations than to other Prince Edward Island populations, indicating rare secondary introductions from Marion to Prince Edward Island with little subsequent admixture. All these results suggest that, on Marion Island, the higher propagule pressure to the island (in this case due to more visits from other land masses to the island), and the higher propagule pressure within the island (due to humans moving around on the island) have contributed to the spread of the species on the island (Figure 2a). In contrast, fewer introduction events and the infrequent and short-term human footprint on Prince Edward Island have resulted in limited spread, and admixture, of the species here (Figure 2b).

#### SCENARIO (a)



Sites with frequent visitation Repeated/big introductions gain:

- Population rescue
- Adaptative selection
- **Opportunity effects**
- Assisted admixture
- Accelerated spread
- Faster range filling

# Sites with limited entries

Isolated/small introductions face:

- Density dependence
- Genetic bottleneck
- Phenological constraints
- Slower range filling

FIGURE 2. Schematic figure indicating how an invasive plant spreads as a result of both propagule pressure and habitat matching on a land mass receiving more humans visitations (Scenario A), compared to its spread on a land mass with very infrequent human visitations (Scenario B)

This study has implications for the future of biodiversity redistribution more broadly. It is well established that areas which would have remained largely unaffected by species introductions due to environmental barriers to species establishment are expected to become more suitable for colonization as a result of the processes of global change (climate shifts and increased habitat disturbances) (Bellard et al., 2013). Now, in addition, the findings of Mairal et al. (2022) suggest that affected sites will also be vulnerable to accelerated naturalization and spread of aliens from recurrent human visitation, even in areas to which human access is highly controlled and which have strict biosecurity measures in place such as Marion Island, but much more so in regions that are readily accessible. Therefore, earth ecosystems conservation

planning should consider inviolate sanctuary sites, where wilderness areas remain. For example, wilderness areas could be designated within existing protected areas. Such pristine sites would not only possess increased biotic resistance since they should remain less disturbed, but would also experience reduced propagule pressure from alien species.

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**Biodiversa ASICS** 

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