





Marine Invasion Genomics: Revealing Ecological and Evolutionary Consequences of Biological Invasions



S. D. Bourne , J. Hudson , L. E. Holman , and M. Rius 

Abstract Genomic approaches are increasingly being used to study biological invasions. Here, we first analyse how high-throughput sequencing has aided our understanding of the mechanisms associated with biological invasions. These include the transport of propagules to pre-invaded areas, an exploration of the consequences of hybridisation during range expansions, and the pre- and post-invasion adaptation of colonising populations. We then explore how contemporary genomic methods have been used to probe and monitor the spread of non-indigenous species. More specifically, we focus on the detection of species richness from environmental samples, measures of quantitative traits that may promote invasiveness, analysis of rapid adaptation, and the study of phenotypic plasticity. Finally, we look to the future, exploring how genomic approaches will assist future biodiversity conservationists in their efforts to mitigate the spread and effects of biological invasions. Ultimately, although the use of genomic tools to study non-indigenous species has so far been rather limited, studies to date indicate that genomic tools offer unparalleled research opportunities to continually improve our understanding of marine biological invasions.

Keywords Adaptation · eDNA · Environmental DNA · Hybridisation · Nonindigenous species · Population genomics · Propagule pressure · Transcriptomics

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1 Introduction

Anthropogenic activities are increasingly affecting global biodiversity patterns (Halpern et al. 2008; Williams et al. 2015; Waters et al. 2016), with artificial transport of species away from their native ranges contributing to this change (Simberloff 2013; Boivin et al. 2016). This anthropogenic translocation of species is enhancing the presence of new colonisations by non-indigenous species (NIS) worldwide (Carlton 1999; Mead et al. 2011; Ricciardi et al. 2017; Seebens et al. 2017). In the last few decades, global trade has exponentially increased (Hulme 2009) and with this, marine shipping (Corbett and Winebrake 2008; IMO 2012), which has grown fourfold in the past 25 years (Tournadre 2014). Shipping acts as a vector for marine NIS that are often transported in ballast water tanks (which can carry up to 10,000 species at any one time; Carlton 1999), on ship hulls (Minchin and Gollasch 2003; Drake and Lodge 2007), or inside sea chests (Frey et al. 2014). Further significant vectors include aquaculture (Naylor et al. 2001; Molnar et al. 2008), the opening of artificial channels such as the Suez Canal (Golani and Ben-Tuvia 1989; Golani 1993), and the aquarium species trade (Padilla and Williams 2004). These vectors have been so effective that only 16% of marine ecoregions are recorded as unaffected by NIS (Molnar et al. 2008). NIS are responsible for major changes in the composition and structure of marine ecosystems (Ehrenfeld 2010; Ricciardi and MacIsaac 2010), as well as causing severe impacts on regional and global economies (Pimentel et al. 2005; Williams et al. 2010). This creates an urgent need to understand the phenotypic and genetic attributes that enable their global spread and success in novel ranges.

The publication of *The Genetics of Colonizing Species* (Baker and Stebbins 1965) is considered the beginning of the field of invasion genetics (Barrett 2015). Since then research in the field has been promoted by a dramatic decrease in the cost of DNA sequencing over recent years (NHGRI 2016), driving a rapid growth in the number of studies utilising genetic tools to study marine biological invasions (Rius et al. 2015a). As genetic approaches have recently progressed into more comprehensive genome-wide techniques (Rius et al. 2015b; Viard et al. 2016), researchers are increasingly using a diverse range of genomic tools to study marine biological invasions (Jombart 2008; Zheng et al. 2012; Catchen et al. 2013; Reitzel et al. 2013; Pfeifer et al. 2014). Macro-scale population processes such as connectivity and spread are now being assessed using genomic tools (Wagner et al. 2013; Vera et al. 2016; Narum et al. 2017), as well as studies on adaptation (Stapley et al. 2010, 2015), including marine NIS (Richardson and Sherman 2015; Tepolt 2015; Tepolt and Palumbi 2015; Bernardi et al. 2016; Wellband and Heath 2017). Additionally, new genetic tools allow the genomic analyses of previously-understudied taxa. Genomic studies have been traditionally restricted to the study of model organisms, which represent only a small fraction of total global biodiversity (Sullivan 2015). Recent technological advances have opened up genome-wide analyses to non-model organisms (Ekblom and Galindo 2011; Reitzel et al. 2013; da Fonseca et al. 2016) which are now routinely studied without prior knowledge of reference

genome data (Elshire et al. 2011; Catchen et al. 2013). This increasing accessibility of genomics allows invasion biologists to address a wider set of research questions on any type of taxa.

Here we review current progress in genomic studies of NIS, highlighting studies that use genomic approaches to better understand the mechanisms ruling marine biological invasions. We first focus on how genetic and genomic techniques assist researchers in exploring key mechanisms driving biological invasions, including pre- and post-invasion adaptation and hybridisation of NIS. We then show how methods that invasion biologists use to study NIS have been enhanced by the application of genomic techniques. These include methods to improve early detection of NIS, as well as detailed population-level analyses of NIS. Finally, we show that although the uptake of genomic tools to investigate marine biological invasions has been limited, their recent use to study both aquatic and terrestrial ecosystems suggests that they have great potential for future studies focusing on marine biological invasions.

2 Mechanisms Associated with Biological Invasions

The introduction of species away from their native ranges has been extensively discussed in the literature over the past decade (Rossman 2001; Sakai et al. 2001; Hulme 2009; Lowry et al. 2013), with much work attempting to characterise the invasion process into distinct stages (Williamson 1993; Colautti and MacIsaac 2004; Catford et al. 2009; Blackburn et al. 2011; Tsoar et al. 2011). It is now generally accepted that biological invasions undergo four different stages: transport, introduction, establishment, and spread (Fig. 1). The process begins with survival during transport of NIS; followed by introduction of species and their propagules into a novel habitat, with some individuals establishing to form a small population; and finally thriving to form a self-sustaining population that may spread and cause impacts (Richardson et al. 2000). NIS populations can undergo a lag phase of variable duration (Crooks et al. 1999), which may influence the genetic composition of introduced populations (Gaither et al. 2012). In the following sections we will briefly present the importance of the mechanisms associated with biological invasions considering the different invasion stages.

2.1 *Propagule Pressure*

The number of individuals introduced to a novel environment (propagule size) and the total number of introduction events (propagule number) are important factors determining the invasion success of an incipient population (Roman and Darling 2007; Simberloff 2009; Rius and Darling 2014). Propagule pressure may involve a variety of life-history stages (Fig. 2) and often include larval stages that spread

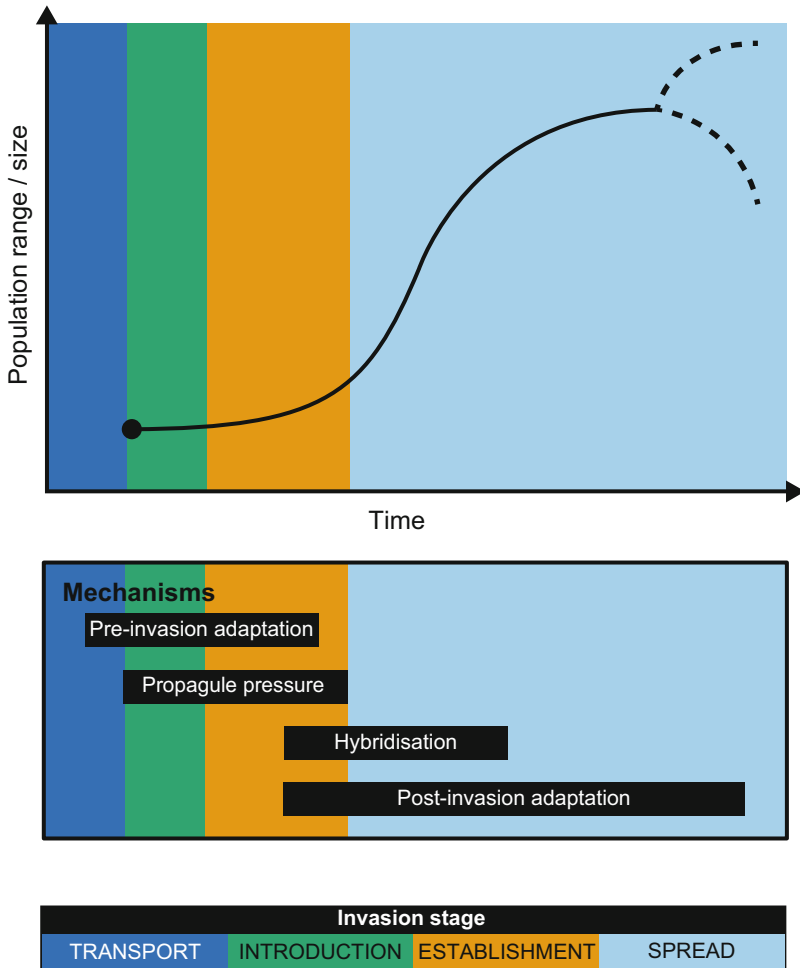


Fig. 1 The invasion stages (different colours) and main mechanisms (black boxes) shaping biological invasions. Dotted lines indicate different trajectories that introduced populations may follow once they become invasive

naturally when released to the introduced range (Johnston et al. 2009). Whilst studies of biological invasions have historically focused on species and recipient ecosystem traits (Blossey and Notzold 1995; Rejmánek and Richardson 1996; van Kleunen et al. 2015), the past two decades have seen an increase in studies assessing the role of propagule pressure on invasion success (Lockwood et al. 2005; Simberloff 2009). When a small number of individuals are artificially transported to a new location, a founder effect may reduce both the number of rare alleles and overall heterozygosity in a given introduced population (Widmer et al. 1998; Allendorf and Lundquist 2003; Roderick and Navajas 2003; Weber et al. 2004; Colautti et al. 2005). In addition, the establishment of a small introduced population may promote

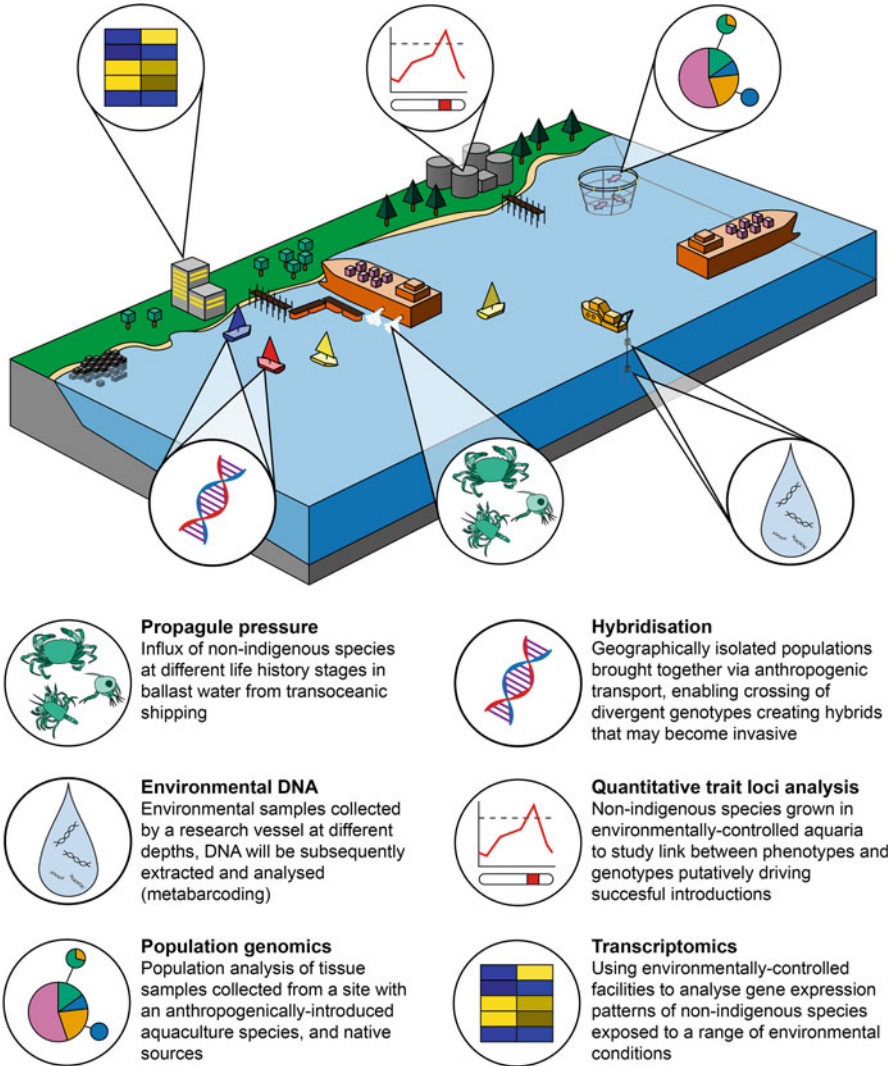


Fig. 2 Generalised schematic showing how marine NIS introductions can be studied in a coastal setting using genomic tools

mechanisms that concentrate alleles at the invasion front, such as allele surfing (Excoffier and Ray 2008; Hallatschek and Nelson 2008), further reducing genetic diversity. If the genetic bottleneck is transient, it would reduce the number of rare alleles present, whilst a longer bottleneck would reduce both levels of heterozygosity within the population and the number of rare alleles. Moreover, this bottlenecked population may be affected by inbreeding (Furlan et al. 2012), further reducing heterozygosity and leading to the accumulation of unfavourable recessive alleles.

This will ultimately affect population fitness in a phenomenon called inbreeding depression (Keller and Waller 2002). Therefore, low propagule pressure can lead to a genetic bottleneck that may limit the ability of an introduced population to establish and spread. Unsurprisingly, increased propagule pressure has been shown to mitigate these bottleneck-related effects, with an increasing number of studies showing similar levels of genetic diversity between native and introduced populations (Kelly et al. 2006; Rius et al. 2012, 2015b).

Roman and Darling (2007) comprehensively discussed how propagule pressure can affect genetic diversity of NIS and reiterated the importance of elucidating the relative contribution of the different components of propagule pressure. For example, it is known that increasing propagule size can benefit introduced populations twofold. Firstly, an increased propagule size will raise the genetic diversity of the introduced population (Suarez and Tsutsui 2008; Simberloff 2009; Wilson et al. 2009), as seen for example in introduced golden mussels (Ghabooli et al. 2013). Secondly, an increased propagule size with large effective population size may be more resistant to hostile conditions in the introduced range (Holle and Simberloff 2005). Regarding propagule number, an increase may improve the resistance of introduced populations to environmental stochasticity (sudden changes in the environment such as natural disasters or freak weather events) (Simberloff 2009). Additional introduction events, from shipping for example, could occur from numerous genetically distinct source populations, increasing genetic diversity in the incipient introduced population (Voisin et al. 2005; Gillis et al. 2009).

The relative role of propagule pressure on invasion success has been studied using experiments under different levels of propagule pressure and controlled conditions. Clark and Johnston (2009) found that on presettled plates, high propagule pressure was needed for NIS recruits to survive past 3 months, but was needed in tandem with disturbance (clearing presettled organisms from a third of each plate) to be successful. Such disturbance was essential to create space for recruits, indicating that high propagule pressure alone is not enough to ensure enhanced recruitment. Another example comes from Hedge et al. (2012), who studied the role of propagule pressure in the recruitment of the Pacific oyster, *Magallana gigas* (formerly *Crassostrea gigas*; Salvi et al. 2014), concluding that small frequent introductions were the most effective method for successful invasion. However, Sinclair and Arnott (2016) demonstrated that propagule size rather than number determined invasion success in the introduced mysid *Hemimysis anomala*.

Propagule size and number can also be strong indicators of an organism's genetic diversity, as Romiguier et al. (2014) showed in their extensive study linking genetic diversity and species ecological strategies. Propagule size was the strongest parameter of all studied ecological strategies to predict the genetic diversity in multiple species and families. Thus, high genetic diversity, ascertained through population genetic techniques, could indicate the presence of high propagule flow. Genomic techniques can also probe propagule pressure, as Narum et al. (2017) showed when they used reduced-representation techniques to genotype two salmonid species between native and introduced ranges. High propagule pressure and associated

mechanisms (e.g. genetic admixture, multiple introductions) maintained high genetic diversity within the introduced range of both species.

Genomic techniques offer the ability to scrutinise genomes to a much finer resolution than genetic approaches (more on this below), allowing a more representative picture of genetic diversity and propagule size to be constructed. Overall, propagule pressure has a major influence in shaping the genetic makeup of NIS, regulating their invasion success. Genetic and genomic techniques are well placed to investigate the genetic constitution of native and introduced ranges, indicating the strength of gene flow within and between them.

2.2 Hybridisation

The spread of NIS provides unprecedented opportunity for previously-isolated genotypes to contact and hybridise (Fig. 2), which can lead to elevated invasiveness (Ellstrand and Schierenbeck 2000). Hybrids may exhibit phenotypic superiority over their parents due to heterozygote advantage – a phenomenon known as heterosis (Lippman and Zamir 2007). In sexually reproducing species, heterosis is seen as transient, affecting only the F1 offspring due to the effects of genetic segregation (Lee 2002). Heterosis can remove inbreeding depression by purging accumulated deleterious recessive alleles (Keller and Waller 2002), enabling a population to “catapult” in size rapidly to overcome disadvantages associated with founder effects (Drake 2006). Crossing between divergent genotypes also provides an opportunity for increasing genetic variation and a larger pool of genotypes on which selection can act (Hegarty 2012). Hybridisation can also promote adaptive variation in NIS (Rius and Darling 2014; Stelkens et al. 2014), as it can occur between native and introduced species (Hänfling et al. 2005; Meilink et al. 2015; Gardner et al. 2016; Oyarzún et al. 2016), leading to displacement of native populations (Huxel 1999). Recent population genomic approaches have found evidence of selection both for and against hybridisation (Saarman and Pogson 2015; Kovach et al. 2016; Jeffery et al. 2017).

Hybridisation can also lead to the genesis of novel genotypes/phenotypes, which may provide a selective advantage due to transgressive segregation (Fig. 3). The generation of phenotypes that are extreme compared to the parental phenotypes and that affect the F2 generation onwards (de Vicente and Tanksley 1993) has been demonstrated in a wide range of organisms. Rieseberg et al. (1999) reviewed 171 hybridisation studies, finding that 155 of them reported at least one transgressive trait. In some cases, transgressive traits provide potential for hybrids to inhabit niches unused by either parent. This is evidenced by the case of *Spartina* spp. in San Francisco Bay, California, where the introduced *Spartina alterniflora* hybridises with the native *Spartina foliosa* (Sloop et al. 2009). Late generation *Spartina* hybrids are larger than either parents and produce more seeds as a result of transgressive segregation. Due to such peculiar gene complexes developed via transgressive segregation, it became detrimental for the hybrid to outcross, leading to selection

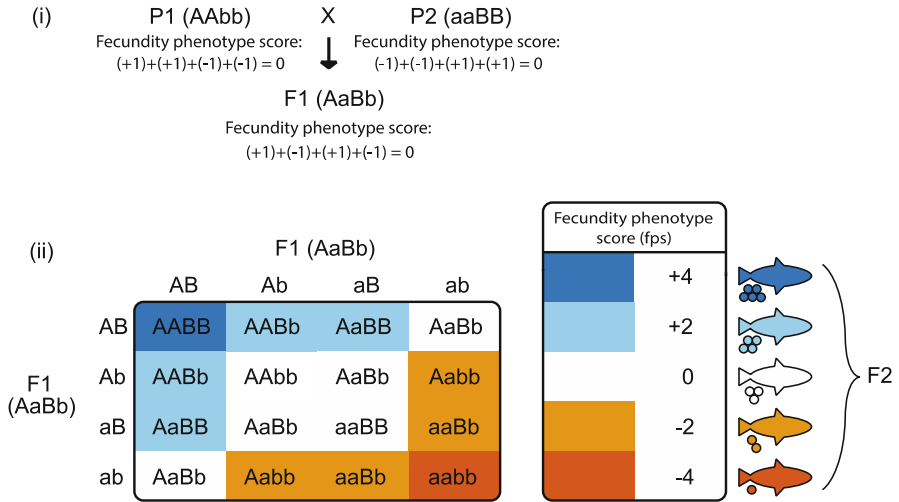


Fig. 3 Transgressive segregation during biological invasions. (i) Two parents, each with a different fixed allele at two unlinked loci. Alleles increase or decrease fecundity phenotype score (fps) by one unit, depending on uppercase (+1) or lowercase (−1). Both parental species are homozygous at both loci, resulting in net score of 0. F1 offspring are all heterozygous at both loci (AaBb), also resulting in a score of 0 ($A + a + B + b = (+1) + (-1) + (+1) + (-1) = 0$). (ii) F2 hybrids' fps range between +4 and −4, indicating varying phenotype fitness. Adapted from Bell and Travis (2005)

in favour of inbreeding (Sloop et al. 2009). Indeed, hybrids can evolve self-fertility, which neither parent nor F1 hybrids are capable of, rapidly assisting colonisation of novel ecosystems (Sloop et al. 2009).

Progeny from the hybridisation of closely-related lineages or species are often infertile, sterile, or inviable – termed hybrid breakdown (Orr and Turelli 2001; Arcella et al. 2014; Stelkens et al. 2015). This hybrid incompatibility is commonly attributed to deleterious epistatic interactions between alleles at different loci of parental genomes (Coyne and Orr 2004), or the breakdown of coadapted gene complexes during recombination, as seen in the copepod *Tigriopus californicus* (Edmands et al. 2009). Hybridisation may also be selected against in introduced populations (Arcella et al. 2014; Saarman and Pogson 2015; Kovach et al. 2016). If recipient and parental environments are similar, hybridisation of ecologically divergent subpopulations (e.g. a preadapted parent with a non-preadapted parent) will disrupt preadapted gene complexes and reduce offspring fitness (Rius and Darling 2014). Additionally, even if hybrids are genetically compatible, reproduction may not occur, or be reduced, due to prezygotic reproductive isolation. For example, hybrid male fur seals (hybridised between Antarctic *Arctocephalus gazella*, subantarctic *A. tropicalis*, and New Zealand *A. forsteri* fur seals) have been shown to exhibit lower reproductive success than pure-species males, putatively due to phenotypic traits affecting mate choice (Lancaster et al. 2007).

Hybridisation may also lead to extinction of native populations (Rhymer and Simberloff 1996; Arcella et al. 2014). An example of this is unfolding with crayfish

(*Orconectes rusticus* and *O. propinquus*) introductions into North American lakes (Arcella et al. 2014). F1 generation hybrids of the native *O. propinquus* and the introduced *O. rusticus* display hybrid vigour (Perry et al. 2001). This dynamic is extirpating native *O. propinquus* populations, as they are outcompeted by F1 hybrids, which then decrease in fitness over subsequent generations and enable the introduced *O. rusticus* to migrate in and outcompete them. As *O. propinquus* is outcompeted by F1 hybrids and *O. rusticus*, it is being removed from lakes in the region.

Genomic approaches offer a strong suite of tools to probe hybridisation (Twyford and Ennos 2012; Payseur and Rieseberg 2016), with population genomics well-suited for marine NIS (Hohenlohe et al. 2011; Hand et al. 2015; Saarman and Pogson 2015; Kovach et al. 2016). Reduced-representation approaches (i.e. sequencing of just a portion of the genome) such as RAD-Seq are particularly useful as the high number of markers returned means they are sensitive to weak levels of hybridisation, allowing them to confidently detect when selection is occurring against hybridisation (Saarman and Pogson 2015; Kovach et al. 2016). Selection against hybridisation may be occurring between native and introduced ascidian species in regions of sympatry. Whilst hybridisation occurs in the laboratory between the native Sea Vase tunicate (*Ciona intestinalis*) and the introduced *Ciona robusta* (Sato and Bishop 2012), genomic analyses indicate that naturally occurring hybridisation is rare (Bouchemousse et al. 2016a; Nydam et al. 2017a).

At the whole genome level, hybridisation can modify the architecture of genomes in complex ways. An F1 individual is essentially heterozygous at all loci, but over subsequent generations selection for coadapted gene complexes and the removal of unfit allelic combinations occurs, resulting in drastic (and rapid) changes in patterns of genomic variation (Ungerer et al. 1998). Important changes in gene expression can also be detected in hybrid transcriptomes using high-throughput sequencing. For example, comparisons of expression profiles of parent species and hybrid individuals show highly-dissimilar gene expression profiles (Wolf et al. 2010). Variation in gene expression can occur with changing ecological conditions (May et al. 2013) and be adaptive (Fisher and Oleksiak 2007), driving adaptation to rapid environmental changes, which may be facilitated by hybridisation (Chown et al. 2015). It is therefore clear that the study of genomes and transcriptomes is key to investigating the genetic basis and consequences of NIS hybridisation.

2.3 *Pre-colonisation Adaptation*

Species traits that have evolved in the native range can sometimes facilitate colonisation success in the introduced range. These are often referred to as preadapted traits (Curnutt 2000) and occur if NIS are introduced to an area that is ecologically or environmentally similar to their native range. Preadaptation may also help NIS more easily withstand environmental challenges in the introduced range (Schlaepfer et al. 2010; Bock et al. 2015; Elst et al. 2016). An example of preadaptation aiding

biological invasions has been detected in the invasion of the European common reed, *Phragmites australis*, in North America. Guo et al. (2014) compared morphological and ecophysiological traits, showing that the introduced genotype was preadapted and outcompeted native congeners due to elevated photosynthetic capacity. A second aquatic example comes from Zhang et al. (2010), who found that a genotype of the water hyacinth *Eichhornia crassipes* that dominates native high-altitude populations monopolised cold parts of the introduced range. Lastly, dominant species of the Red Sea's sandy shores have successfully colonised similar habitats (shallow sandy and muddy shores) in the Mediterranean, suggesting that preadaptation facilitated their establishment into the new range (Golani and Ben-Tuvia 1989; Golani 1993).

Although DNA-based approaches are severely underutilised in studying preadaptation in marine NIS, some studies have inferred preadaptation from genotype distribution (Zhang et al. 2010; Guo et al. 2014). Another approach is to directly use genomic tools to identify the presence of preadapted genes (Ometto et al. 2013; Gleason and Burton 2015; Gleason and Burton 2016a), such as the use of RNA-seq to detect the preadaptation of a whole suite of genes (Wang et al. 2009). These genomic approaches have been effectively used to detect preadaptation in native marine species. For example, Gleason and Burton (2016a) used reduced-representation genomics to probe the marine snail, *Chlorostoma funebris*, finding strong divergence linked to temperature adaptation. RNA-seq revealed that lower-latitude populations were preadapted to cope with thermal stress by employing unique gene expression profiles compared to higher latitude populations (Gleason and Burton 2015). Subsequently, Gleason and Burton (2016b) reinforced these findings by investigating the actual temperatures encountered in the studied populations. They found that lower latitude populations were three times more likely to experience temperatures causing a heat-shock response. These studies show the utility of genomic approaches to identify preadaptation and how this approach can greatly increase our understanding of forces shaping adaptation pre-arrival.

2.4 *Post-colonisation Adaptation*

Post-colonisation adaptation after establishment can also happen when NIS enter a novel ecosystem (Guo et al. 2014; Lin et al. 2017). Studies show that post-colonisation adaptation may occur extremely rapidly (Huey et al. 2000; Dlugosch and Parker 2008; Whitney and Gabler 2008; Moran and Alexander 2014; Stapley et al. 2015) and is often referred to as contemporary evolution (Stockwell et al. 2002). Post-colonisation adaptation is essential for understanding genomic changes that may occur throughout the invasion process.

Rapid adaptation of NIS can be driven by several mechanisms (Gilchrist and Lee 2007), including transposable elements (TE) and epigenetics. Discovered in 1950 (McClintock 1950), TEs are a large group of highly variable loci that are able to move from one location to another on the genome (Pray 2008). They are known to

have a significant role inducing rapid adaptation in response to changes in the environment (Casacuberta and González 2013) and subsequently drive the adaptation of NIS (Schrader et al. 2014; Stapley et al. 2015). TEs are heavily influenced by epigenetics, another mechanism that can drive rapid adaptation in NIS (Ardura et al. 2017). Epigenetics is an umbrella term that refers to a group of heritable effects, such as DNA methylation or chromatin remodelling, that are unrelated to variation in DNA sequence variation (Huang et al. 2017). There is increasing evidence suggesting that epigenetic mechanisms contribute to phenotypic variation in ecologically relevant traits (Bossdorf et al. 2008). This is particularly pertinent to NIS where genetic variation may be very low and population expansion may occur on timescales not conducive to DNA sequence evolution (Dlugosch and Parker 2008). NIS may therefore encounter highly variable conditions to which they are not preadapted and therefore be forced to rely on their epigenetic variation (Pu and Zhan 2017). Current work indicates that the strength of epigenetic signals in NIS overcomes the signal from environmental conditions, supporting the hypothesis that early-invasion NIS, as part of their post-colonisation adaptation, increase phenotypic plasticity as a result of reduced methylation (Ardura et al. 2017). There is still much to study concerning the influence that TEs and epigenetics have on promoting post-colonisation adaptation in NIS. Genomic approaches are well placed to examine them in natural populations (Casacuberta and González 2013; Stapley et al. 2015; Trucchi et al. 2016; Hofmann 2017) as they open up new research avenues such as sequencing both the transcriptome and methylome simultaneously (Hofmann 2017).

Post-colonisation adaptation is known to enable single-source introduction NIS to rapidly respond to local environmental conditions (Dlugosch and Parker 2008; Prentis et al. 2008; Bock et al. 2015) and overcome the negative effects resultant from genetic bottlenecks (Colautti and Barrett 2013). This is often referred to as evolutionary rescue (Gonzalez et al. 2013; Carlson et al. 2014; Lau and terHorst 2015) and is based on the idea that rapid adaptation may aid NIS in mitigating the deleterious effects of low genetic diversity. Pre- and post-invasion adaptation are not mutually exclusive (Sakai et al. 2001; Bernardi et al. 2016), as species may be preadapted before arrival, enabling a successful introduction, and then may undergo rapid post-invasion adaptation to further optimise fitness in the introduced area. This has been reported in the common reed wetland grass (*Phragmites australis*), wherein a more efficient photosynthetic apparatus of a preadapted strain colonised North America and then underwent further post-colonisation morphological and ecophysiological adaptation to maximise fitness and thrive in the introduced area (Guo et al. 2014). This has also been reported in other terrestrial plant introductions (Henery et al. 2010). Introduced species can also induce post-colonisation adaptation in native inhabitants (Carroll 2007; Oduor 2013). The introduction of toxic cane toads (*Bufo marinus*) into Australia induced an adaptation in native snake species (*Pseudechis porphyriacus* and *Dendrelaphis punctulatus*) to restrict their predation of these toxic toads. The snakes adapted morphological traits to lessen risk of consumption and ill effects (decreased gape size, and increased body lengths), whilst snakes that did not prey upon the toads (*Hemiaspis signata* and *Tropidonophis mairii*) exhibited no consistent change after introduction (Phillips and Shine 2004).

NIS introductions also create competition, which can induce morphological changes, as occurred when the native lizard (*Anolis carolinensis*) adapted larger toepads in order to cling to higher perches after the introduction of another lizard – *Anolis sagrei* – (Stuart et al. 2014).

Genetic and genomic techniques provide a strong complement to morphological and ecophysiological analyses to test questions on NIS adaptation. In a study of the introduced Lessepsian migrant bluespotted cornetfish (*Fistularia commersonii*), genomic regions associated with disease resistance and osmoregulation were identified as putatively being under selective pressure in the introduced range (Bernardi et al. 2016). Considering the relatively short time since the introduction of this NIS, it was suggested that both pre- and post-colonisation adaptation may have occurred.

3 Methods Used to Study Marine Invasion Genomics

3.1 Environmental DNA

Organisms naturally shed DNA into the environment in which they live. This environmental DNA (eDNA) can be filtered or precipitated out and analysed to infer the presence or absence of a given organism. Recent work indicates that eDNA is made up of a range of different-sized particles, from very large multicellular fragments (>180 μm) down to extracellular DNA (Turner et al. 2014; Sassoubre et al. 2016). Estimates of eDNA persistence in seawater have been limited to fish (Thomsen et al. 2012; Maruyama et al. 2014; Sassoubre et al. 2016; Andruszkiewicz et al. 2017) and crustacean (Forsström and Vasemägi 2016) species, showing degradation on the order of days. Current eDNA research is progressing from monitoring presence/absence towards quantifying species abundance (Lacoursière-Roussel et al. 2016) – applications that otherwise require large sampling effort. For example, Thomsen et al. (2016) showed that eDNA assessments were comparable to trawling sampling when probing deep-sea fish faunas. Thus, eDNA shows great potential for detecting and monitoring aquatic NIS, in both presence and quantity. eDNA has thus far been used to probe introduced gobies (Adrian-Kalchhauser and Burkhardt-Holm 2016), aquatic plants (Scriver et al. 2015), bullfrogs (Ficetola et al. 2008; Dejean et al. 2012), pythons (Piaggio et al. 2014), carp (Jerde et al. 2013; Mahon et al. 2013; Klymus et al. 2015), crayfish (Larson et al. 2017), bivalves (Ardura et al. 2015a), snails (Goldberg et al. 2013), and turtles (Davy et al. 2015). eDNA has also been used to monitor vectors transporting NIS (Collins et al. 2013; Mahon et al. 2014; Nathan et al. 2015).

Work using eDNA has begun to study the initial stages of colonisation, such as transport and establishment (Fig. 1), where traditional techniques lack the required sensitivity for early detection of both successful and unsuccessful species introductions (Takahara et al. 2013; Forsström and Vasemägi 2016; Tucker et al. 2016; Simpson et al. 2017). Early detection is pivotal for a rapid response to NIS (Pyšek and Richardson 2010) and is more economically efficient than removing a more-

progressed NIS (Williams et al. 2010). For example, the invasion of the black striped mussel (*Mytilopsis salleii*) in 1999 to Darwin harbour, Australia, threatened marine infrastructures, the surrounding environment, and a pearl fishery worth A\$40 million (Bax et al. 2002). A rapid response required chemical treatment of marinas to eradicate the introduced mussel and caused transient mortality in a significant proportion of native fauna. However, the cost associated with eradication (A\$2.2 million) was deemed minimal compared to the potential environmental and economic damage the mussel could have caused (Willan et al. 2000; Bax et al. 2002). eDNA is also a potent tool for ascertaining which NIS are in transit and understanding which shipping routes or ports are prolific transporters, being well-suited to testing ballast water (Egan et al. 2015; Tucker et al. 2016; Darling and Frederick 2017). Current techniques enable detection of eDNA from species at very low densities (e.g. using qPCR; Foote et al. 2012; Bergman et al. 2016), providing a tool to learn more about initial stages of colonisation that previously evaded investigation.

Although eDNA shows great potential in investigating NIS, limitations exist. DNA decays at different rates under varying environmental conditions, biasing the detection of NIS (Barnes and Turner 2016). eDNA is also susceptible to false positives (Ficetola et al. 2016) and negatives (Schultz and Lance 2015), as it can travel long distances (Thomsen et al. 2012; Deiner and Altermatt 2014). Current progress in eDNA research is increasing its accuracy and reliability (Amberg et al. 2015; Ficetola et al. 2016; Lahoz-Monfort et al. 2016; Guillera-Aroita et al. 2017), especially when eDNA surveys are combined with traditional survey approaches (Yamamoto et al. 2016; Sigsgaard et al. 2017).

Innovations in metabarcoding (i.e. using universal primers to amplify and sequence a conserved region in an environmental sample for species identification) are increasingly being applied to marine biological invasions (Ardura et al. 2015b; Zaiko et al. 2015). The metabarcoding of eDNA, when used judiciously (Goldberg et al. 2016), not only allows for the rapid and accurate detection of NIS during introduction and establishment, but also the collection of information on currently nontarget species and community composition.

3.2 *Quantitative Trait Loci Mapping*

A pertinent method for determining the genetic basis of invasiveness and rapid adaptation is the study of quantitative trait loci (QTL) (Stapley et al. 2015). QTLs are genomic regions that correlate with the expression of quantitative traits. Whilst there is not a suite of traits representative of all NIS, quantitative traits such as those that enhance fecundity, growth, and spawning time can play an important role in determining colonisation of novel environments (van Kleunen et al. 2015; McKnight et al. 2017). The main purpose of QTL analysis is to link genotype loci to a phenotype (determining the genetic basis for an observed quantitative trait) and is especially adept at investigating how genomic regions are responsible for adaptive

loci (Pardo-Diaz et al. 2015). QTL analyses have been used to identify the basis of adaptation in introduced terrestrial species (Weinig et al. 2007; Hamilton et al. 2015; Whitney et al. 2015), native marine species (Johnston et al. 2014), and even native's response to NIS (Yu and Andrés 2014). However, much like other genomic techniques, these methods are severely underutilised in the study of marine NIS. QTL mapping could be used to study marine NIS by crossing native and introduced individuals of a marine species that differ in a trait of interest (e.g. size, fecundity, or spawning time). By scoring the phenotype and genotype of the derived individuals, molecular markers linked to QTL will show significant associations with phenotypes, allowing the identification of regions of the genome putatively associated with key traits. QTL mapping may also play an important role in the further study of TEs and their influence on rapid adaptation (Stapley et al. 2015).

3.3 Population Genomics

Population genetics represents a robust approach to assess the demographics and population structure of NIS (Riquet et al. 2013; Rius et al. 2015b; Bouchemousse et al. 2016b; Wrangle et al. 2016; Cordero et al. 2017) – also see boxed case study. The low costs of using mitochondrial DNA and polymorphic markers such as microsatellites, together with the relative computational simplicity of their analyses, means that they are still the dominant approach used in marine invasion genetics (Rius et al. 2015b).

Recent advances in DNA sequencing technology have allowed the transition from population genetics to population genomics (Stinchcombe and Hoekstra 2008; Hemmer-Hansen et al. 2014). High-throughput sequencing approaches on NIS can now return tens to hundreds of thousands of polymorphic markers such as single nucleotide polymorphisms (SNPs) across the genome (Puzey and Vallejo-Marin 2014; Vandepitte et al. 2014; Hand et al. 2015). The ability to sequence large numbers of loci simultaneously enables the detection and categorisation of positive and neutral selection (Luikart et al. 2003). Two general methods exist to identify outlier loci (Hoban et al. 2016): differentiation outlier analyses, which identify loci that are abnormally differentiated between populations, and genotype-environment outliers, in which loci are correlated to local environmental factors (White et al. 2013). The analysis of genotype-environment interactions allows researchers to study how environmental conditions influence adaptation of introduced populations. For example, White et al. (2013), looking at the water vole (*Myodes glareolus*), used geographical distance from the point of introduction as the environmental variable and found that strong signals of selection were affected by rapid range expansion.

The use of a large number of loci also allows greater discrimination of differentiation between populations (Rašić et al. 2014). This is especially important to differentiate native and introduced populations, and to reliably identify source populations of a highly homogenous introduced range. This is clearly shown in a genomic study of the global distribution of the introduced ascidian *Microcosmus*

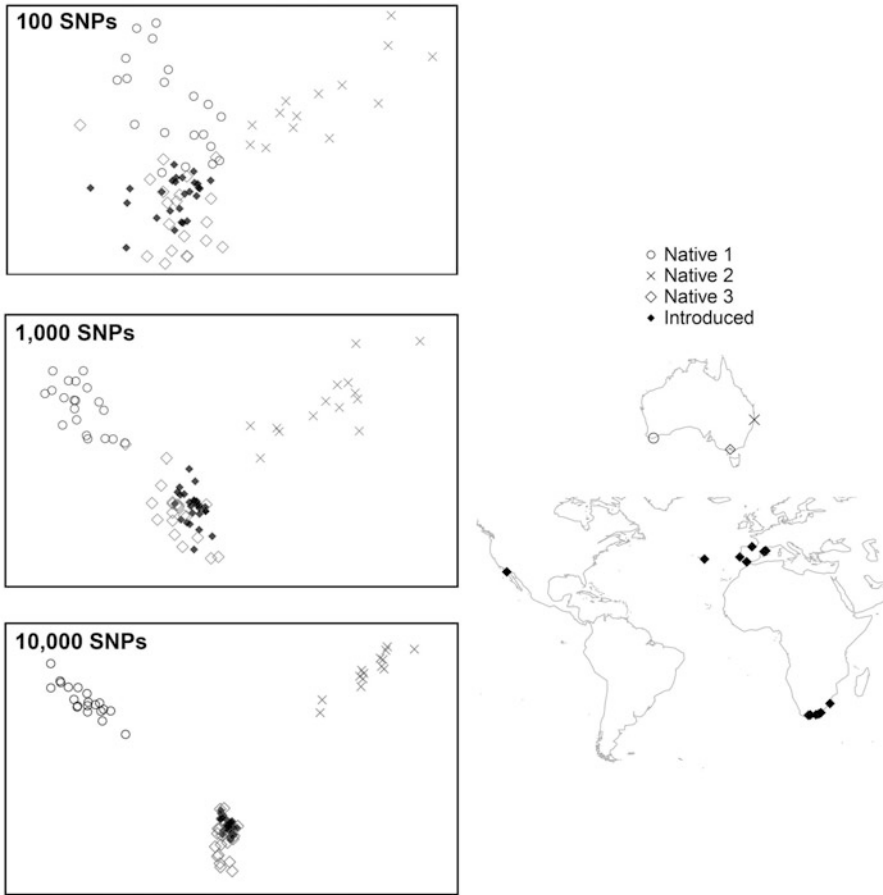


Fig. 4 Discriminant analysis of principal component plots showing how an increase in the number of single nucleotide polymorphism markers for the ascidian *Microcosmus squamiger* (Bourne et al., unpublished) alters the population structure of globally sampled sites. The location of the sampled sites is indicated on the right-side maps, with the native (Australia) and introduced (South Africa, Europe, and Baja California) ranges denoted with different symbols. Note that sites within the native range are genetically divergent, whilst the ones found in the introduced range are panmictic

squamiger (Fig. 4) that shows the beneficial effects of a larger number of markers (Bourne et al. unpublished). A discriminant analysis of principal components shows increasing segregation between native populations as the number of markers increases (Fig. 4). Also clearly elucidated from a higher number of markers is the putative source of introduced populations.

Population genomic approaches are being used with increasing regularity in the study of NIS, having been applied to crabs (Jeffery et al. 2017), salmonids (Narum et al. 2017), toads (Trumbo et al. 2016), mosquitofish (Vera et al. 2016),

trout (Hand et al. 2015; Kovach et al. 2016), and mussels (Saarman and Pogson 2015), finding evidence of reduction or no change in diversity between native and introduced ranges (Vera et al. 2016; Narum et al. 2017). Although these approaches are being incorporated into invasion biology, they are still largely underutilised when studying marine biological invasions (Sherman et al. 2016).

Boxed Case Study



Native to the Indo-Pacific, the lionfishes *Pterois volitans* (Linnaeus 1758) and *P. miles* (Bennett 1828) are highly invasive species. Officially first recorded in the western North Atlantic in 2000 (Whitfield et al. 2002), although observed since at least 1985 in Florida (Florida Fish and Wildlife Conservation Commission 2017), these species have since expanded towards lower latitudes, including South America (Ferreira et al. 2015). Subsequently, they have extensively expanded within the Mediterranean (Golani and Sonin 1992; Azzurro et al. 2017). Thought to be vagrants of the aquarium trade (Hare and Whitfield 2003), lionfish significantly affect invaded ecosystems, including drastically reducing the recruitment (Albins and Hixon 2008) and abundance (Green et al. 2012; Ballew et al. 2016) of native fish species.

Much population genetic work has been undertaken to understand their expansion in the western Atlantic, with Hamner et al. (2007) discovering evidence of a strong founder effect upon colonisation. They also found that the majority were *P. volitans*, with few *P. miles* individuals present. The western Atlantic origin of introduction was found to be the Florida coast by Betancur et al. (2011), who also found that *P. miles* is restricted to northernmost locations, whilst *P. volitans* is much more ubiquitous, with strong population structure evident between northern and Caribbean populations.

(continued)

Valdez-Moreno et al. (2012) reinforced this by finding only *P. volitans* individuals in the Mexican Caribbean and furthermore, after identifying stomach contents, confirmed that they were engaging in cannibalistic behaviour – a first recorded instance in this species. Similarly, only *P. volitans* individuals were found in Puerto Rico by Toledo-Hernández et al. (2014), who also found a secondary founder effect present from the original nonindigenous population. Tracking their spread into South America, Ferreira et al. (2015) used DNA analyses to match individuals to haplotypes found in North America and Mexico, indicating that the nonindigenous population is spreading and that the Brazilian population is not resultant from an independent invasion from the Indo-Pacific, but natural larval dispersal from the invaded Caribbean region. However, a recent DNA analysis has proposed that the invaded region may be the recipient of multiple introductions, and not the single introduction as previously thought (Butterfield et al. 2015), showing that DNA-based approaches can be confounded by the choice of sampled populations. Lastly, comprehensive high-resolution genomic SNP work undertaken by Pérez-Portela et al. (2018) show complete panmixia in the region. Interestingly, this contrasts previous genetic results that found differentiation (Butterfield et al. 2015; Johnson et al. 2016). Pérez-Portela et al. (2018) suggest two reasons for this difference. Firstly, a fundamental difference in findings between genetic and genomic work (or mitochondrial and nuclear DNA), as has been previously-reported (Toews and Brelsford 2012). Or secondly, that high gene flow has eroded the previous genetic signals and created regional homogenisation. Further to the contribution of high gene flow, they also proposed that local adaptation is further contributing to the panmixia.

Genetic work has also identified that hybridisation within the native range may be a contributing factor to the invasion success of nonindigenous populations in the West Atlantic (Wilcox et al. 2018). The invasive lineage may be resultant from hybridisation between the Indian and Pacific lineages, raising the interesting prospect that heterosis may be enhancing the success of the invasive *P. volitans* in the West Atlantic.

The genetics of the nonindigenous Mediterranean population has also been recently probed, with the introduced *P. miles* individuals related to Red Sea populations, indicating a Lessepsian invasion (Bariche et al. 2017). A low genetic diversity also implied the occurrence of another founder effect, though the success to which the Mediterranean has been colonised indicates that low genetic diversity has not proven a barrier to their invasion.

Future genomic studies can assist investigators in mitigating the lionfish expansion. Currently, they must be observed to be recorded in a novel area, but the use of eDNA monitoring could enable conservationists to be more reactive to the lionfish's spread. This in turn allows an accurate picture to be constructed of their nonindigenous range and expanding front, aiding managers in deciding where to allocate their eradication efforts for optimum

(continued)

effectiveness. Future higher-resolution population genomic approaches (see Future Directions), along with more comprehensive sampling, will enable scientists to resolve whether the invaded region has been subjected to multiple introductions or a single expanding front. However, it is possible that the intense homogenisation observed by the high-resolution approach of Pérez-Portela et al. (2018) could mask previous signals of invasion history. If, however, invasion pathways can be elucidated, this would enable investigators to understand where nonindigenous populations are sourced from, again allowing managers to allocate resources to disrupting the pathway supplying the nonindigenous populations. After eradication efforts, further monitoring using eDNA can effectively scrutinise the previous range, confirming the success or failure of such efforts in curbing nonindigenous lionfish populations.

Ultimately, genomic approaches will prove a major contributor in the conservation efforts against lionfish, first enabling scientists and managers to understand their spread, then assisting in their mitigation, and finally monitoring the success of management efforts.

Genomic data may also be used to infer invasion pathways and colonisation histories (Estoup and Guillemaud 2010; Guillemaud et al. 2010; Cristescu 2015). Several methods are available to reconstruct routes of invasion, such as population genetic and genomic inferences using phylogenetic trees (Estoup and Guillemaud 2010; Cristescu 2015). A particularly fruitful approach has been to compare specific invasion scenarios using the approximate Bayesian computation (ABC) method (Beaumont et al. 2002). Multiple software are now available to reconstruct colonisation histories using genetic data and ABC (for review see Estoup and Guillemaud 2010), which have been used extensively in terrestrial studies (e.g. Lombaert et al. 2010; Brown et al. 2011; Boissin et al. 2012; Konečný et al. 2013) and increasingly in aquatic species [ascidians (Rius et al. 2012; Teske et al. 2015; Nydam et al. 2017b), mosquitofish (Purcell et al. 2012), cyprinids (Simon et al. 2011), mussels (Marescaux et al. 2016), red shiners (Glitzbecker et al. 2016), and pike (Pedreschi et al. 2014)]. These studies have found evidence of population bottlenecks (Purcell et al. 2012), secondary introductions (Pedreschi et al. 2014), genetic admixture (Rius et al. 2012; Glitzbecker et al. 2016), and both independent (Marescaux et al. 2016) and non-independent invasions (Rius et al. 2012). These studies have mostly used genetic data, and the few that have used genomic data have quickly overwhelmed computing resources (Marx 2013; Ocaña and de Oliveira 2015). In order to tackle this issue, invasion-inference techniques that use less computing effort are now being developed to handle larger genomic datasets (Pudlo et al. 2016) such as the random forest statistical technique (Breiman 2001). We expect that when coupling these techniques with broadened access to higher computation power (Marx 2013), genomic data will be more commonly used to infer colonisation histories of marine NIS.

3.4 Gene Expression

Transcriptomic approaches have been greatly enhanced by the genomic revolution (Marguerat et al. 2008), providing a useful tool for marine invasion biologists (Fig. 2) (Rius et al. 2015a). The ability to look at gene expression allows researchers to study adaptation of NIS at a more detailed level. Differential gene expression studies across environments can help researchers understand the role of phenotypic plasticity (Aubin-Horth and Renn 2009) in marine NIS (Wellband and Heath 2017). Phenotypic plasticity, or the ability of a genotype to produce different phenotypes in response to environmental conditions (Pigliucci 2001), frequently occurs in NIS (Davidson et al. 2011; Lande 2015; Sassenhagen et al. 2015; Guardiola et al. 2016). Wellband and Heath (2017) compared two introduced goby species, each of varying colonisation success (measured as the extent of geographic spread), finding that success could be related to phenotypic plasticity. The more successful species of the two was more phenotypically responsive to temperature, in both gene transcription magnitude and function. The biological processes altered by the successful goby species were consistent with reported phenotypic gene expression responses to temperature, whereas the less successful goby species exhibited maladaptive phenotypic plasticity. A similar scenario was shown in the mussels *Mytilus galloprovincialis* and *M. trossulus* (Lockwood et al. 2010). *M. galloprovincialis*, which outcompetes *M. trossulus* in warmer habitats (including in the native range of *M. trossulus*), showed an elevated response to acute heat stress, with the most differentially expressed gene between the two being a heat-shock protein. Finally, transcriptomic approaches have been combined with genome assembly to explain the resistance of some introduced marine species to xenobiotic chemicals. An example of this is the highly invasive catfish, *Pterygoplichthys anisitsi*, which has been found to have an expanded defensome (i.e. genes that code for defence mechanisms to chemical environmental stressors), which may assist it in invading polluted areas (Parente et al. 2017).

4 Future Directions

As the cost of high-throughput sequencing is continually decreasing, the inhibitive stage in genomic studies has shifted from data acquisition to storage and analysis, with the vast amount of data generated becoming the new limiting factor on the experiment pipeline (Marx 2013). Indeed, it takes less than a year for the amount of sequence data stored by the European Bioinformatics Institute to double (European Bioinformatics Institute 2012). Researchers must grapple with these new demands, and on a broad scale, the development of associated technology will continue to mitigate the challenges of genomic data storage and analysis, including the introduction of overarching approaches that effectively integrate the four pillars of

genomic studies: data acquisition, storage, distribution, and analysis (Stephens et al. 2015). Progress in this direction will promote a productive future for marine invasion genomic studies.

One approach that is predicted to be especially productive in the future for invasion biologists is eDNA (Barnes and Turner 2016). It has already been applied to the detection of individual NIS, as well as assessing entire community composition (Kelly et al. 2014) or addressing species abundance (Takahara et al. 2012; Lacoursière-Roussel et al. 2016). Other exciting developments include the employment of remote vehicles or stations fitted with eDNA technology (Scholin 2010; McQuillan and Robidart 2017), allowing unprecedented spatial and temporal resolution. Although currently an expensive option, progressing autonomous vehicle development will enable invasion biologists to reliably and regularly sample areas prone to invasion, giving a time-linked genomic profile of the areas and signalling the arrival of NIS. Another exciting future prospect is the use of eDNA to assess population genetic inference of NIS. This concept has recently been proved, with the population genetics of whaleshark populations derived from eDNA-sampled mitochondrial fragments (Sigsgaard et al. 2016). The leading edge of eDNA NIS research involves applying this concept to NIS. It has recently been shown that eDNA can accurately reconstruct the proportion of different genotypes in a water body using qPCR (Uchii et al. 2016). This dramatically increases our ability to understand the distribution of well-studied NIS. Additionally, combining this approach with metabarcoding of variable regions allows researchers to discover previously unknown genotypes (Sigsgaard et al. 2016). Furthermore, it may be possible to infer population parameters using haplotype frequency and diversity data in species where mutation rates are known, which when combined with the added ease of eDNA sampling will prove a robust tool for future invasion biologists.

Another potentially fruitful future concerns the investigation of environmental adaptation in NIS using genomic scans. Genome-wide scans give investigators unparalleled power, as genomic outlier loci can be identified from any genomic region using fixation statistics such as F_{ST} . These outlier loci can then be associated with the environmental conditions in which they are prevalent, such as altitude (Dong et al. 2014), climate (Yoder et al. 2014), salinity, and temperature (Guo et al. 2015). However, Hoban et al. (2016) raise three considerations for which future invasion biologists should be aware of. Firstly, the genomic data must be placed in context with the demographics and population history of the studied NIS. Secondly, the use of reference data will always provide a benefit to genomic projects, and as such efforts should be made to develop reference genomes with high-quality gene annotations. Lastly, concerning experimental design, a priori environmental information should be used to inform sample sites, to broaden our knowledge of the environmental response of the organism. The need for a comprehensive sampling strategy when probing NIS genomics is reiterated by Viard et al. (2016). There is also a pressing need to integrate the current distinct approaches into a single framework, which would prove especially useful when assessing the impact of environment on adaptation in marine NIS (Bragg et al. 2015). When following the

recommendations of Hoban et al. (2016) and Bragg et al. (2015), invasion biologists can reap the rewards of a robust population genomic approach, including the future benefit that will come from full genomes being sequenced for each studied individual. This increasing genomic resolution will enable invasion biologists to disentangle complex invasion histories. Furthermore, a future shaped by a rapidly changing climate will likely see different effects on NIS (Stachowicz et al. 2002; Dukes 2010; Masters and Norgrove 2010; Muhlfeld et al. 2014). Interactions between climate change and NIS can be complex (Kolar and Lodge 2000) and are likely to be context and species dependent, involving multiple factors mediating such interaction (Rius et al. 2014). Greater understanding of the genetic changes of NIS during adaptation to warming is critical for predicting dynamics of future invasions (Somero 2010) and identifying management strategies (Rahel et al. 2008).

Furthermore, the availability of third-generation sequencers is expected to drastically boost evolutionary and invasion research. This new sequencing technology will further promote *de novo* genome sequencing and assembly, leading to genomic resources being developed for more non-model organisms and increasing the genomic repertoire available to invasion biologists. An increase in read length also augments current population genomic approaches as longer reads can be compared between individuals, further increasing extracted information and genome resolution, therefore add a whole suite of tools to the biologists' toolbox (Sedlazeck et al. 2018). Another benefit of the new sequencing technology is the ability to more efficiently probe post-translational modifications (Garalde et al. 2018). The ability to study post-translational modifications opens up many opportunities when examining the occurrence of the rapid localised adaptation frequently accompanying NIS.

5 Conclusions

Biological invasions are one of the greatest threats facing the preservation of global biodiversity, causing vast ecological and economic impacts (Pimentel et al. 2005; Kumschick et al. 2015). In turn, they also provide excellent models for understanding ecological and evolutionary mechanisms (Sax et al. 2005) such as rapid adaptation over contemporary time scales (Huey et al. 2005). The knowledge gained from studying invasion biology in these instances can be pertinent to broadly applicable processes, such as natural range expansions (Colautti and Barrett 2013).

The suite of genomic tools now available to invasion biologists has considerably enhanced the understanding of processes underpinning biological invasions (Stapley et al. 2015; Viard et al. 2016). For example, the role that hybridisation plays in promoting NIS can now be disentangled using genomic approaches, and the study of genomic regions linked to quantitative traits (Dlugosch et al. 2015) is revealing genetic attributes linked to invasiveness (Weinig et al. 2007). NIS can be detected earlier with eDNA (Dougherty et al. 2016), allowing detection of NIS before they cause substantial environmental and economic damage (Williams et al. 2010). The effects of adaptation on marine NIS can be explored (Bernardi et al. 2016) along with

associated mechanisms such as TEs and epigenetics (Casacuberta and González 2013; Stapley et al. 2015; Hofmann 2017). The role of gene expression in marine NIS can be evaluated with transcriptomics (Lockwood et al. 2010; Wellband and Heath 2017), and the ability of marine NIS to thrive in polluted conditions probed (Parente et al. 2017). More fundamentally, genomic resources can be developed for NIS that are unrelated to well-studied model organisms (da Fonseca et al. 2016). Furthermore, the ability to reconstruct recent invasion pathways strengthens our ability to undertake invasion risk assessments. Other genomic applications are also possible, such as the genome-editing technology that is currently under development (Ricciardi et al. 2017) and could alter the genomes of marine NIS. This has the potential to reduce their impact and halt their spread (Esvelt et al. 2014; Webber et al. 2015; Harvey-Samuel et al. 2017). Ultimately, marine NIS can now be studied much more comprehensively than ever before, a result of recent developments in genomic tools.

The current increase in numbers of invasion biology studies using genomic approaches (Barrett et al. 2016) and the reduction of associated sequencing costs (Rius et al. 2015a), show that studies focusing on marine invasion genomics will increasingly help scientists and policymakers better manage this major driver of global biodiversity change.

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