Metacommunity biology as an eco-evolutionary framework for understanding exotic invasion in aquatic ecosystems

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Abstract

One of the greatest threats to the biotic integrity of native aquatic communities over contemporary time scales is the invasion and rapid geographic spread of exotic species. Whereas dispersal rates of exotic species are documented to affect invasion success, few studies acknowledge the role of dispersal in both exotic and native species in mediating exotic establishment and the evolutionary response of native communities. In this chapter, we suggest that the metacommunity concept may serve as an informative, spatially explicit framework in which to describe dispersal-mediated trajectories of exotic invasion and the associated evolutionary response of native species. We outline ways in which metacommunity biology may enhance our understanding of the spatio-temporal invasion sequence, including exotic establishment, geographic spread, and interactions with native species. The integrative framework is subsequently applied to case studies of eco-evolutionary interactions between exotic and native species within invaded aquatic metacommunities, where dispersal-mediated evolutionary responses in both exotic and native species appear to be important. Finally, we propose a molecular toolkit that may facilitate understanding the evolutionary processes underlying different stages of the spatio-temporal invasion sequence. We suggest that the advances gained from adopting the metacommunity concept may inform conservation strategies by serving to identify native aquatic communities that will resist exotic invasion or evolve in response to the non-native species.

The spread of non-native species among habitats within and across continents has initiated regional mixing of community composition and global biotic homogenization (McKinney and Lockwood 1999; Olden et al. 2004). Biological invasion can result in geographic range expansion of exotic species via establishment and spread and range contraction of native species through local extinction. Thus, exotic species pose a serious threat to global biodiversity and the evolutionary viability of native species and communities. Recent reviews suggest that the establishment of exotic species can affect local species diversity in non-native environments (Bruno et al. 2005) as well as drive contemporary evolution in co-occurring native species (Stockwell et al. 2003; Strauss et al. 2006). Despite the demonstrated importance of dispersal and gene flow in the establishment of exotic species (Lockwood et al. 2005; Suarez and Tsutsui 2008; Dlugosch and Parker 2008), few studies of invasion biology acknowledge the role of dispersal in both exotic and native species in mediating invasion success and the evolutionary response of native species.

In this chapter, we propose the metacommunity as a framework in which to evaluate dispersal-mediated and spatially explicit dynamics of exotic invasion and the associated evolutionary response of native species. The metacommunity concept highlights the role of dispersal of multiple species among local communities in altering species richness and composition across hierarchical spatial scales (Leibold et al. 2004). Recently, the concept was expanded to include the evolutionary consequences of dispersal rates and gene flow among local

communities in an 'evolving metacommunity' framework (Urban and Skelly 2006; Urban et al. 2008). To our knowledge, however, no works to date invoke the eco-evolutionary response of exotic and native species in the metacommunity (regional) species pool. The metacommunity framework presents a useful but largely unexplored approach to describing the process of invasion and the evolutionary response of native species.

In aquatic ecosystems, one of the greatest threats to the biotic integrity of native communities over contemporary time scales is the establishment and rapid geographic spread of exotic species (Ruiz et al. 1999; Roman and Darling 2007; Ricciardi and Kipp 2008). Many aquatic ecosystems show inherent spatial structure and the application of the metacommunity concept may enhance our understanding of exotic invasion and the evolutionary response of native species in these types of habitats. For example, lakes and ponds are often nested within a landscape of terrestrial matrix, where local community composition is jointly determined by regional dispersal rates of component species and local environmental conditions (Fig. 1a,c,e; Cáceres and Soluk 2002; Cottenie et al. 2003; Beisner et al. 2006; Howeth and Leibold 2008, 2010a,b). Estuarine and marine environments additionally exhibit metacommunity structure where habitats are patchily distributed along coastlines (Fig. 1g, Mouillet 2007; Thrush et al. 2008) or as coral reef communities (Fig. 1j, Karlson et al. 2007; Cornell et al. 2008). In these aquatic ecosystems, exotic species often co-occur with native species (e.g., Fig. 1b,d,f,h, j) and can alter their evolutionary trajectory (Strauss et al. 2006). Thus, aquatic environments present model systems for the application of an integrative framework incorporating metacommunity and invasion biology, where a synthetic approach may greatly improve our understanding of exotic invasion and the response of native species.

To begin, we briefly integrate foundational concepts in the disciplines of invasion and metacommunity biology, with an emphasis on the emergent theme of regional and local processes structuring community composition and local evolution of component species over contemporary time scales. We then outline ways in which the synthesis may enhance our understanding of the spatio-temporal invasion sequence, including exotic invasion, geographic spread, and eco-evolutionary interactions with native species. The integrative framework is subsequently applied to case studies of eco-evolutionary interactions between exotic and native species in invaded aquatic metacommunities, where dispersal-mediated evolutionary responses in both exotic and native species appear to be important. Finally, we present a molecular toolkit to apply in future empirical studies employing the integrative metacommunity approach and where different stages of the spatio-temporal invasion sequence are targeted. We suggest that the metacommunity-invasion synthesis may ultimately inform conservation strategies by serving as a framework in which to identify native aquatic communities that will resist exotic invasion or evolve in response to the non-native species.

Integrating metacommunity and invasion biology

Metacommunity and invasion biology acknowledge that both regional and local processes interact to affect invasion and community assembly through predictive theoretical frameworks, including the dispersal-diversity relationships of metacommunity biology (Mouquet and Loreau 2002, 2003) and the diversity-invasibility relationships of invasion biology (Shea and Chesson 2002). These two subdisciplines, however, largely continue to develop independently of each other. Metacommunity biology emphasizes regional processes, notably dispersal and gene flow, in facilitating invasion success and the geographic spread of species (Leibold et al. 2004). Invasion biology, in turn, highlights processes that occur locally within sites, including biotic interactions and abiotic conditions, which influence the establishment of exotic species and the composition of native communities (Shea and Chesson 2002; Melbourne et al. 2007). Integrating metacommunity and invasion biology should therefore provide enhanced mechanistic insight into exotic invasion and spatial patterns of species and genetic diversity.

Four metacommunity paradigms, patch dynamics, species sorting, mass effects, and the neutral paradigm, propose ways in which regional and local processes interact to affect species and genetic diversity, and invasibility at multiple spatial scales (Leibold et al. 2004; Urban et al. 2008). The paradigms differentially weight the relative importance of dispersal and the local environment in structuring the species and genotypic composition of local communities and the regional pool. In this chapter, we address three of the four metacommunity paradigms, patch dynamics, species sorting, and mass effects, and discuss their independent contributions toward understanding the mechanisms of exotic invasion and the response of native communities over evolutionary time scales (Fig. 2). The neutral paradigm (Hubbell 2001) is acknowledged as a null model where speciation and extinction dynamics of ecologically equivalent individuals drive community assembly and species-environment relationships are ignored.

Contrasting the basic features of each metacommunity paradigm facilitates understanding how they may yield different invasion dynamics in the non-native range and metacommunity (Fig. 2). The patch dynamic paradigm originates from Levins' (1969) classic metapopulation model and assumes infrequent dispersal and colonization-extinction processes occurring among homogeneous patch types but may also be extended to heterogeneous patches (Fig. 2a; Holt 1997; Leibold et al. 2004; Shurin et al. 2004). Demographic rates are assumed to be high relative to the dispersal rate and are sometimes linked to trait-tradeoffs in patch dynamic metacommunities (reviewed in Amarasekare 2003). As a consequence, patches can be occupied or empty and the metacommunity is unsaturated and invasible (Smith and Shurin 2006). The species sort-

(a)

(b)

(c)

(d)

(e)

(f)

(g)

(h)

(i)

(j)
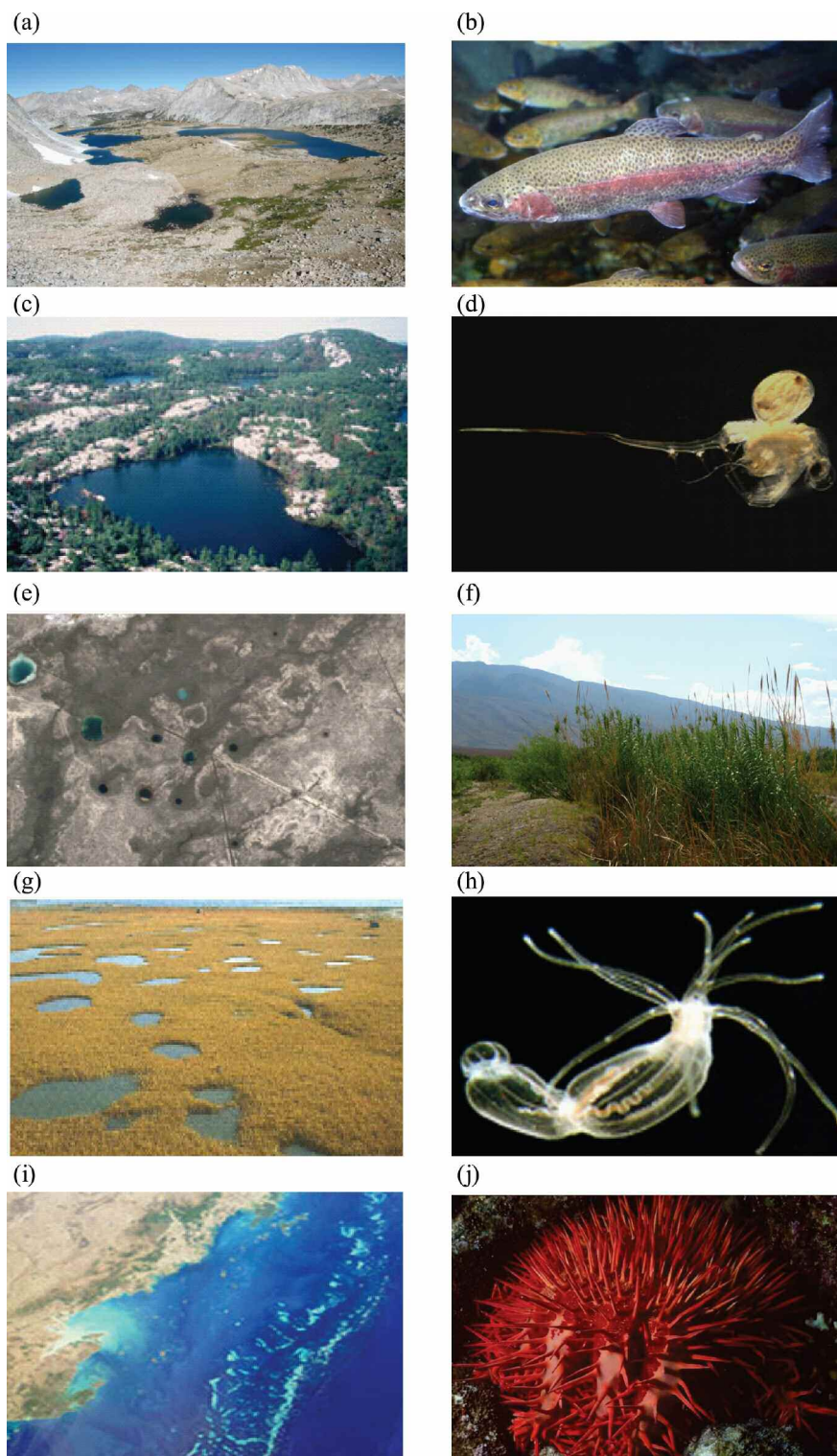
Fig. 1. Metacommunity structure in aquatic ecosystems: (a) lake chains in the Sierra Nevada Mountains of the United States (photo credit: Steven Sadro) have been invaded by (b) rainbow trout, *Oncorhynchus mykiss* (photo credit: United States Environmental Protection Agency 2010) (c) boreal shield lakes in Canada (photo credit: Ed Snucins; Derry et al. 2009) have been invaded by (d) the spiny water flea, *Bythotrephes longimanus* (photo credit: Angela Strecker), (e) spring-fed ponds in Cuatro Ciénegas, Mexico (photo credit: Centro de Investigación Ciéntifica de Cuatro Ciénegas) have been invaded by (f) giant reed, *Arundo donax* (photo credit: Dean Hendrickson), (g) estuaries in Nova Scotia (photo credit: Adam Reitzel) with similar topography to estuaries invaded by (h) the starlet sea anemone, *Nematostella vectensis* (photo credit: Adam Reitzel), and (i) the Great Barrier Reef in Australia (photo credit: National Aeronautic and Space Administration) has been invaded by (j) crown-of-thorns starfish, *Acanthaster planci* (photo credit: Klaus Jost).
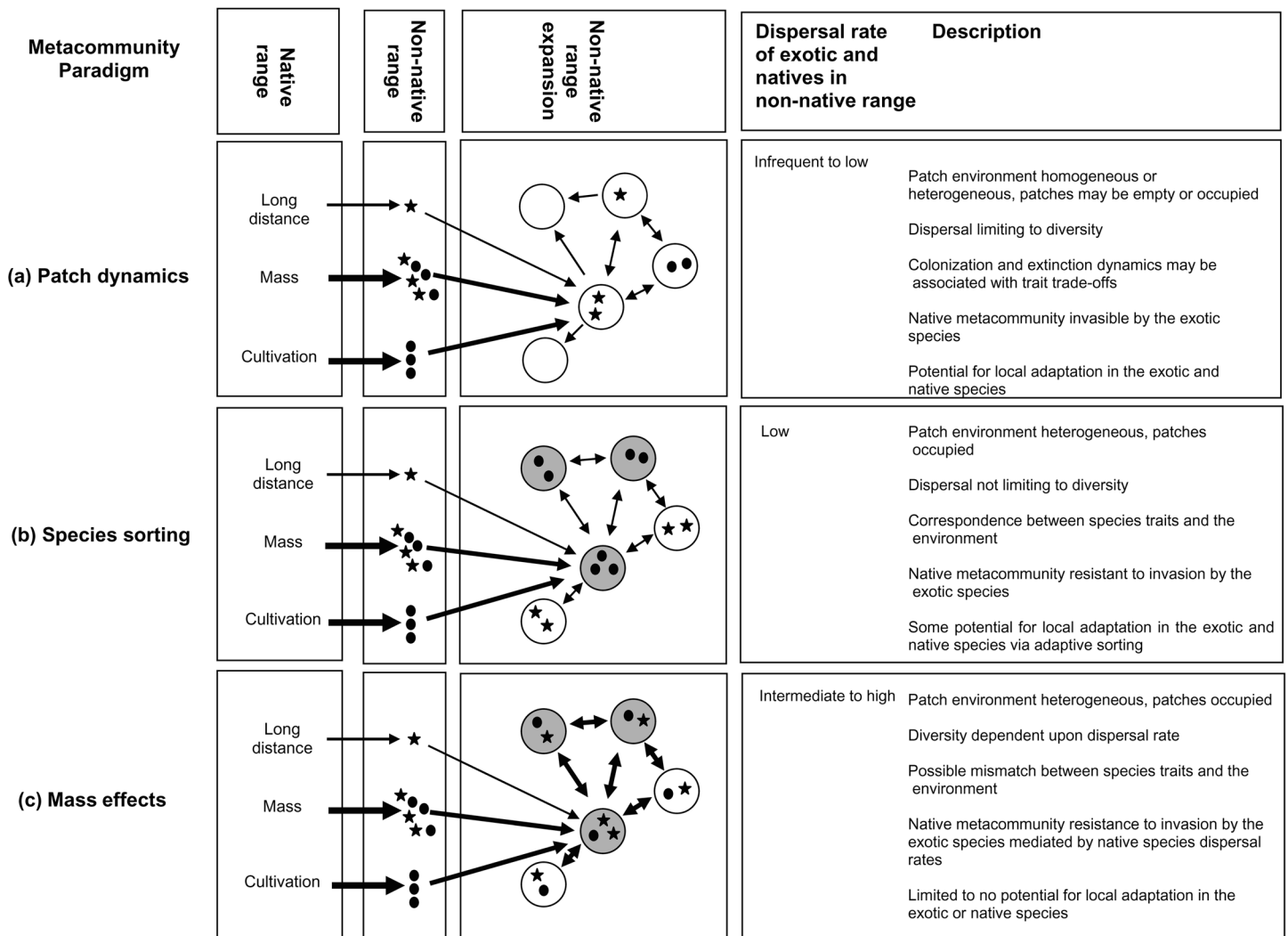
Fig. 2. Exotic introduction to the non-native range and metacommunity, as illustrated by three metacommunity paradigms: (a) patch dynamics, (b) species sorting, and (c) mass effects. For each paradigm, three exotic introduction scenarios differ in the number of individuals and the diversity of intergenotypic traits represented from the native range. Two possible traits for the exotic species are denoted by a circle and a star. In this simplified schematic, exotic introduction to the non-native range may be initiated by three dispersal pathways: (i) long-distance dispersal of a few, potentially diverse propagules (e.g., oceanic rafting), (ii) mass dispersal of multiple, diverse propagules (e.g., hull fouling communities), and (iii) dispersal of multiple, homogeneous propagules from anthropogenic cultivation (e.g., aquaculture species). Circles denote communities of the metacommunity in the non-native range, where shaded circles differ in environment from unshaded circles. Arrows within the metacommunity correspond to the strength of species dispersal, and represent unidirectional (single-headed arrow) or bidirectional (double-headed arrow) movement. Species dispersal rates are assumed to be equal across taxa.

ing perspective suggests that low-levels of dispersal in the metacommunity allows each species in the regional pool to arrive at any given patch but strongly emphasizes the role of niche-based processes in community assembly within heterogeneous patches (Fig. 2b, Leibold et al. 2004). In species-sorting metacommunities, there is a strong correlation between species traits and the environment where dispersal facilitates species compositional tracking of local environmental conditions in space and time (Leibold and Norberg 2004). Finally, the mass effects paradigm acknowledges a broad range of species dispersal rates structuring local community and metacommunity composition in heterogeneous patch environments, with an emphasis on the role of source-sink dynamics operating at dispersal rates that are substantially higher than local demographic rates (Fig. 2c). Incorporating exotic species into these three metacommunity types requires invoking the source of exotic migrants, the number of propagules, and their genetic and associated ecological trait diversity.

Introduction of exotic species to the non-native range and metacommunity can proceed under a variety of extra-range dispersal pathways (reviewed in Wilson et al. 2009). We focus on three of the most common pathways for the introduction

of aquatic species to non-native environments: long-distance dispersal (e.g., intercontinental) and two of its subcategories, mass dispersal (e.g., fouling communities), and cultivation (e.g., aquaculture) (Fig. 2; Roman and Darling 2007; Wilson et al. 2009). Introduction of exotic species to the non-native range via these dispersal pathways can be characterized by a gradient of propagule pressure (Lockwood et al. 2005) and genetic diversity (Suarez and Tsutsui 2008; Wilson et al. 2009). The location of the migrant pool along this gradient will, in part, determine invasion success and the evolutionary trajectory in the non-native range and metacommunity. For example, in long-distance dispersal the migrant pool may be composed of a few individuals in a single introduction event (Wilson et al. 2009), and thus local evolution in the non-native environment may be constrained by low genetic diversity and limited trait variation (Lockwood et al. 2005; Dlugosch and Parker 2008). Conversely, in mass dispersal, the migrant pool represents multiple individuals that are likely to exhibit high intraspecific genetic and trait diversity, thereby increasing the possibility of invasion success and non-native range expansion (Wilson et al. 2009). Finally, in cultivation, the migrant pool may be composed of a few or several individuals exhibiting little to no genotypic or trait variation (Wilson et al. 2009), and therefore, establishment success may be constrained by mismatches between migrant traits and the novel environment. For those species that establish successfully in the non-native range, dispersal from the founding populations initiates non-native range expansion via movement among habitat patches of the metacommunity. Here, we discuss possible invasion dynamics proceeding in the non-native range under each of the three metacommunity paradigms, and from long distance, mass, and cultivated migrants (Fig. 2).

Patch dynamics—The demographic processes associated with patch dynamics may be common during the initial stages of invasion where founding populations are isolated prior to regional establishment. Spatial subdivision among small local founding populations originating from a few migrants (e.g., from long-distance dispersal or cultivation, Fig. 2a) coupled with infrequent dispersal among patches yields potential for maladaptation of the exotic to the novel environment. Demographic stochasticity and genetic bottlenecks may decrease the effective population size and accelerate genetic drift as alleles are lost from the metapopulation, thereby further decreasing genetic diversity and the potential for adaptive evolution (Harrison and Hastings 1996). This scenario can occur at the regional (metacommunity) scale when multiple introductions isolated by space and time prevent gene flow among introduced populations, leading to a geographic mosaic of maladaptation (Dlugosch and Parker 2008). Conversely, large local founding population sizes such as those originating from mass dispersal (Fig. 2a) may facilitate local adaptation of the exotic to the novel environment, even in the presence of restricted gene flow, if there is sufficient genetic variation on which natural selection may act and a stable patch environ-

ment through time. Infrequent dispersal of native species in the metacommunity can mediate the potential for local evolution of natives in response to the exotic (e.g., Strauss et al. 2006). The evolutionary response of native species will depend in part upon the genetic and trait variation represented in the local exotic populations, as determined via initial founder effects and metapopulation connectivity.

Species sorting—Species sorting communities may resist exotic invasion as they are generally assumed to be saturated and at or near equilibrium (Smith and Shurin 2006). However, due to a lack of coevolutionary history between the exotic and natives, exotic establishment may occur (Elton 1958; Colautti et al. 2004). Exotic migrants delivered to the non-native range via mass dispersal will likely have an increased probability of invading species sorting metacommunities relative to long-distance or cultivated migrants, as their relatively high variance in trait diversity maximizes the possibility of matching species traits to the novel environment (Fig. 2b). Environmental heterogeneity in species sorting metacommunities imposes strong localized selection on component species which may result in adaptive sorting among populations along environmental gradients in the region. Adaptive sorting within species matches genotypes and traits with the local selective environment, and occurs in the presence of dispersal rates that are comparable to, or lower than, dispersal rates that facilitate species sorting (Urban et al. 2008). Thus, there is potential for adaptive evolution in exotic and native species in these local heterogeneous communities structured by low dispersal rates (Urban et al. 2008).

Mass effects—Mass effects metacommunity models suggest that the invasibility of a native community will depend upon native species dispersal rates structuring the species and genotypic composition of local communities within heterogeneous patch environments. Mass effects models emphasize the dispersal rate-dependency of species diversity and invasibility relationships. For example, competitive metacommunity models predict a unimodal relationship between species dispersal rates and local species and allelic richness (Mouquet and Loreau 2002; Urban 2006), where intermediate to high dispersal rates can maintain maladapted species and genotypes within sink communities as strong asymmetric gene flow between sources and sinks mutes the strength of selection in sink environments (Urban 2006). Exotic migrants delivered to mass effects metacommunities via mass dispersal will likely have the greatest probability of invasion and spread relative to long-distance and cultivated migrants given their high genetic and trait variation and propagule pressure (Fig. 2c). In a mass effects metacommunity scenario, there is little to no potential for local adaptation of the exotic or native species to local environmental conditions, nor is there potential for co-evolution between the exotic and natives, due to panmixia and genetic swamping (Urban et al. 2008).

As an illustration of the application of the metacommunity paradigms to exotic invasion, we contrast patterns of gene

flow in multiple species that coevolved in their native range and that have invaded the same freshwater environment, the North American Great Lakes, in supplementary Box 1. In the following section, we discuss the potential for dispersal-mediated eco-evolutionary interactions in exotic and native species within the invaded metacommunity and outline empirical evidence for such interactions using case studies.

Eco-evolutionary interactions within invaded metacommunities

Once established in an introduced range and metacommunity, exotic species have the potential to rapidly evolve to adapt to novel conditions encountered in environments where they had no evolutionary experience prior to invasion (Novak 2007; Prentis et al. 2008). Exotic species can also pose considerable potential for driving evolutionary changes in native populations (Strauss et al. 2006; Whitney and Gabler 2008) because non-native organisms become incorporated into novel ecological interactions where they participate with native taxa as predators, competitors, pathogens or parasites, and as mutualists or hosts (Carroll 2007; Whitney and Gabler 2008). As a consequence, unrealized evolutionary potential in native taxa may be expressed following exposure to exotic species that they had not encountered in their evolutionary history (Schlaepfer et al. 2005; Strauss et al. 2006). Over the course of short time scales, native species may be maladapted to the exotic (Schlaepfer et al. 2005) but may evolve in response to the novel selective regime over several generations (Lau 2006; Strauss et al. 2006). Dispersal rates of both exotic and native species in invaded metacommunities may mediate these evolutionary responses by influencing local genetic diversity through gene flow.

The amount of dispersal and gene flow among exotic and native populations in invaded metacommunities can be employed to predict the likelihood of adaptive change and eco-evolutionary interactions between exotic and native species. Population genetics and metacommunity theory suggest that low dispersal rates of exotic species in invaded metacommunities can increase the potential for exotic populations to locally adapt to novel environmental conditions (adaptive sorting; Urban et al. 2008). Low dispersal rates of native species in the metacommunity can also increase the potential of native communities to adapt to the novel selection pressures imposed by the exotic, by maximizing local genetic diversity such that natural selection can operate more efficiently (Urban 2006; Urban et al. 2008). However, intermediate to high dispersal rates may prevent exotic and native species from locally adapting due to genetic swamping (Leger 2008; Urban et al. 2008).

Here, we address case studies of eco-evolutionary interactions between exotic and native species in aquatic ecosystems, where dispersal rates of component species can play critical roles in structuring local communities (Leibold and Norberg 2004; reviewed in Cadotte 2006). We invoke a spatially explicit metacommunity context for interpreting examples of eco-evolutionary interactions between exotic and native species within freshwater and marine habitats, with a focus on two well-studied groups of exotic species that are often cultivated or exhibit mass dispersal: introduced salmonids in freshwater lakes and exotic crabs along marine coastlines.

Freshwater: introduced salmonids—Patch dynamics metacommunities contain species structured by low dispersal rates and trait trade-offs (Smith and Shurin 2006). An example of patch dynamics comes from the intentional introduction of cultivated non-native genotypes that can change the evolutionary trajectory of native species in the metacommunity. Introduced farmed salmonids rarely persist in natural lacustrine environments because they have been artificially selected for traits that boost production in aquaculture, but have fitness tradeoffs in the wild (*Salmo salar*; Fraser et al. 2008). Cultivated strains of rainbow trout (*Oncorhynchus mykiss*) have been anthropogenically selected for high growth rates but use native habitats with high predation risk for foraging when resources are scarce (Biro et al. 2003). As a result, farmed trout have higher mortality rates from piscivorous birds as compared with wild conspecifics (Biro et al. 2004). The absence of avian top predators in the local community will likely favor the introgression of farmed genotypes in native trout with subsequent top-down effects on native species in the freshwater food web.

Exotic species can present novel selective pressures that can alter the evolutionary trajectories of native species structured by low dispersal rates in metacommunities (Urban et al. 2008). The introduction of exotic salmonids into previously unexposed freshwater ecosystems has caused evolutionary responses in native prey species that likely experience limited population connectivity. For example, in New Zealand, brown trout (*Salmo trutta*) induced adaptive changes in the foraging and dispersal behavior of mayflies (*Nesameletus ornatus*) that they fed on (McIntosh and Townsend 1994). Further, in alpine lakes in the Sierra Nevada, U.S.A, populations of *Daphnia melanica* in lakes with a known history of exposure to introduced trout were smaller and more fecund than populations from lakes where trout had not been introduced (Fig. 1a,b; Fisk et al. 2007; Latta et al. 2007). Although dispersal and gene flow have not been characterized for many of these native species, evidence suggests little mixing of mayfly populations among the New Zealand streams that were studied (McIntosh and Townsend 1994). In addition, the isolated nature of alpine lakes likely restricts dispersal of zooplankton such as *Daphnia* sp. (McNaught et al. 1999; Donald et al. 2001; Knapp et al. 2001). Thus, native prey evolutionary responses to exotic predators were likely facilitated by low prey dispersal rates among communities, and therefore, may be described by adaptive sorting occurring in the invaded metacommunity.

Marine: exotic crabs—Eco-evolutionary interactions between exotic crab predators and their native mussel prey

occur in marine metacommunities where native species dispersal rates appear to be infrequent to low. Multiple examples of rapid adaptive sorting in mussels in response to contemporary crab invasions suggest that the evolutionary responses of native species can proceed over short time scales and in the presence of strong exotic propagule pressure. Intercontinental dispersal rates of exotic species have increased due to modern shipping, thereby contributing to the greater number of successful contemporary invasions from mass dispersal as compared with a century ago (Roman 2006). One exotic marine species that has benefited from transport-mediated mass dispersal since its introduction to the Atlantic over a hundred years ago is the green crab (*Carcinus maenas*; Roman 2006). In its introduced range in eastern North America, green crab populations show phenotypic plasticity in claw size over gradients of latitude and temperature (Smith 2004; Baldridge and Smith 2008). In response to predation by this exotic, the native intertidal snail, *Littorina obtusata*, has developed heavier shells, smaller shell openings, and deeper shell withdrawl depths (Edgell et al. 2008). Unlike many marine invertebrates, *L. obtusata* does not release larvae into the water column, but rather deposits egg masses from which juveniles crawl out onto the algal substrate (Schmidt et al. 2007). This life history characteristic may limit gene flow and facilitate an adaptive evolutionary response to the green crab (Schmidt et al. 2007).

Another exotic crab, the Asian shore crab (*Hemigrapsus sanguineus*), was introduced to North America less than 15 years ago and has already elicited adaptive differences in shell thickening among prey populations of blue mussels (*Mytilus edulis*; Freeman and Byers 2006). Interestingly, *M. edulis* can also adaptively respond to predation cues from green crabs by shell thickening. However, in contrast to the response to *H. sanguineus*, blue mussel populations undergo shell thickening in both the presence and absence of green crabs and do not appear to be locally adapted in this defense response to green crabs. The extended larval life history phase of this littoral mussel appears to facilitate the movement of this species over great distances (Wares and Cunningham 2001), and could have homogenized adaptive differences among populations present soon after the initial invasion of green crabs a century ago.
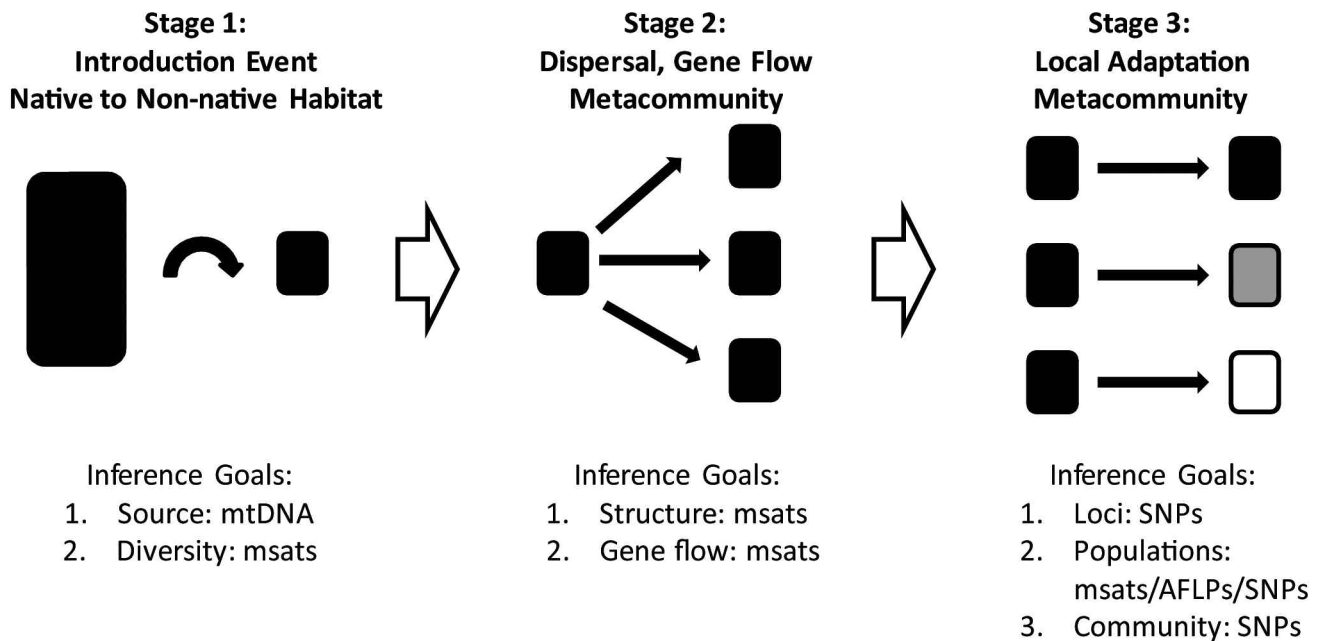
Evolution is a critical component of understanding invasions (Facon et al. 2006; Prentis et al. 2008) and adaptive responses that can occur during invasions can be influenced by the metacommunity context of both the invader and native species with whom it interacts. Evolutionary responses for survival and persistence in introduced populations cannot only help to predict invasive potential for spread (Lee 2002; Lee and Gelembiuk 2008), but also help forecast long-term evolutionary impacts of exotic taxa on native species (Strauss et al. 2006). More work, however, needs to be done to quantify dispersal and gene flow among invasive and recipient native populations to characterize their metacommunity context and predict systems where potential adaptive change is possible.

Molecular tools for understanding invasion in meta-communities

Understanding invasion and eco-evolutionary interactions in a metacommunity requires measuring gene flow and genetic diversity in exotic and native species (Gaggiotti 2004; Hellberg 2006). Processes of establishment, dispersal, and local adaptation of the exotic as well as the potential evolutionary response of native species occur over a broad range of spatial and temporal scales in the metacommunity (Carroll et al. 2007; Dlugosch and Parker 2008). As a consequence, the invasion sequence and associated changes in genetic structure of exotic and native species can be best evaluated with a variety of molecular tools targeting the different spatio-temporal stages. Previous reviews have discussed the relative merits and limitations of the diverse set of molecular markers available for studying population processes (Parker et al. 1998; Sunnucks 2000; Mariette et al. 2002; Brumfield et al. 2003; Diniz-Filho et al. 2008; Brito and Edwards 2009). We have applied these criteria to suggest how these markers are used to understand the invasion process in metacommunities. Here, we present a comprehensive 'molecular toolkit' for addressing the evolutionary response of the exotic and native species over the invasion sequence. We identify molecular markers best-suited for addressing each of three stages of the invasion sequence (Fig. 3): exotic introduction and establishment in the non-native range, gene flow of exotic and native species in the metacommunity, and local adaptation of the exotic and native species.

Exotic introduction to the non-native range and metacommunity (Stage 1)—The location of origin and genetic diversity of the introduced population can help predict establishment success of an exotic species and its ability to spread and locally adapt in the novel environment of the non-native range and metacommunity (Fig. 2, Goolsby et al. 2006; Caldera et al. 2008; Winkler et al. 2008). We suggest that two different genetic markers, on balance, would be the best approach for gaining insight into these two components of exotic introduction.

The source population of introduced species in the native range can be determined with a variety of molecular markers, including mitochondrial DNA (mtDNA), microsatellites, and DNA fingerprinting techniques (e.g., AFLPs, RAPDs; Davies et al. 1999). Among these, sequence-based markers, specifically mtDNA, provide the most useful method for identifying sources of non-native species because they (1) have low convergence but sufficient diversity for discerning population structure in the native range, (2) can be statistically analyzed with phylogenetic techniques (e.g., haplotype networks, nested clade analysis; Templeton 1998) to identify or predict source locations, even if the precise population in the native range is not sampled, and (3) require relatively little investment because there are primers that work well over broad taxonomic groupings making this sequence-based approach straightforward for organisms with little to no previous

Stage 1:
Introduction Event
Native to Non-native Habitat

Stage 2:
Dispersal, Gene Flow
Metacommunity

Stage 3:
Local Adaptation
Metacommunity

Inference Goals:
1. Source: mtDNA
2. Diversity: msats

Inference Goals:
1. Structure: msats
2. Gene flow: msats

Inference Goals:
1. Loci: SNPs
2. Populations:
   msats/AFLPs/SNPs
3. Community: SNPs

Fig. 3. Molecular markers deployed during the study of an introduced species in the non-native geographic range and metacommunity. The figure is organized by the spatio-temporal stages of a simplified invasion sequence from introduction to adaptation by the introduced population in the non-native habitat and metacommunity. For each stage, we list a few inference goals that a researcher may have when applying molecular markers to better characterize the microevolutionary response of exotic and native species. Although a variety of molecular markers have been employed for each of these stages, we provide a recommended marker reflecting a consideration of various strengths and weaknesses of the available markers.

genetic information. High diversity markers such as microsatellites and fingerprinting methods can be useful for comparing genetic diversity to support identification of non-native populations, but frequently are constrained in identifying particular source locations in the native range due to high allelic diversity.

Microsatellites and fingerprinting methods are considerably more useful than sequence-based approaches for quantifying genetic diversity in introduced populations due to large allelic variation as a result of a high mutation rate and the number of loci assessed, respectively. For recently introduced populations, we expect that most loci would show reduced diversity in the introduced populations due to low number of founders (e.g., inbreeding, founding effects) (Davies et al. 1999). Deviation from this expectation would result when individuals from a species have been introduced multiple times, and even more so, from multiple source populations independently (Roman and Darling 2007). These successive introduction events to the non-native range will likely increase genetic diversity in the exotic and potentially exceed the diversity in localized portions of its native range.

Gene flow in the non-native range and invaded metacommunity (Stage 2)—Once a species has been introduced to non-native habitat, the complex patterns of geographic spread are mediated by characteristics of the native community, life history characteristics of the introduced taxa (Sakai et al. 2001; Marchetti et al. 2004), and local adaptation to the novel environ-

ment (Fig. 2, Novak 2007; Prentis et al. 2008). Contrasting patterns of gene flow of introduced species with native species in the metacommunity can be useful to infer population and community connectivity (e.g., comparative phylogeography, Manier and Arnold 2006; Brito and Edwards 2009), community genetics (Wares 2002; Whitham et al. 2006), and landscape genetics (Balkenhol et al. 2009). In addition, quantifying gene flow patterns provides the necessary data for discerning among the metacommunity paradigms (e.g., patch dynamics versus mass effects) because the genetic signatures should be quite different. To do this, we will need to obtain confident assessments of gene flow, which are significantly improved by surveying multiple, independent loci throughout the genome to avoid potential biases introduced by studying single or linked markers.

Because non-native species have been introduced relatively recently, we do not expect numerous novel mutations in DNA sequence and when they do occur, they will be scattered throughout the genome. Thus, higher diversity markers will be necessary to provide the necessary statistical power to discern population genetic structure, particularly over short temporal and spatial scales (Rollins et al. 2009). Of high diversity markers, microsatellite markers have a clear analytical advantage by being co-dominant markers, which permits confident assessment of heterozygosity and tests for deviations from Hardy-Weinberg Equilibrium, but frequently have large ranges in allelic richness and between loci variation resulting in wide

confidence intervals when estimating population genetic parameters including genetic structure (F_{ST} and related measures). In addition, microsatellites vary tremendously among taxa making comparative studies among members of a community difficult to interpret (Chambers and MacAvoy 2000; Barbar et al. 2007). For these and other reasons, recent surveys discussing the utility of genetic markers have emphasized the advantages of single nucleotide polymorphisms (SNPs) for population genetic studies (Brumfield et al. 2003; Morin et al. 2004; Brito and Edwards 2009). Although SNPs have the limitation of lower diversity due to the possibility of only four states and a low mutation rate, SNPs have clear advantages for interpretability at the species and inter-species level. In addition, SNPs can be readily compared among genomes (nuclear, mitochondrial, chloroplast) to use the underlying mutational scales to characterize evolutionary processes including gene flow.

Local adaptation of the exotic and native species (Stage 3)—Introduced species and the recipient community evolve over time in response to local environments, whether they are abiotic conditions or biological interactions. Understanding the evolutionary process and the underlying mechanisms during the introduction process can be critical for predicting the future success of these taxa and their impact on native species (Suarez and Tsutsui 2008). In recent years, there have been tremendous strides to characterize genetic mechanisms underlying ecological and evolutionary relationships among interacting species in a local community (co-evolutionary genetics; Wade 2007). From these studies, it has become clear that individual genetic variation for one species can have large impacts on the evolutionary trajectory of co-occurring species (e.g., Crutsinger et al. 2008). Thus, exotic establishment may alter the genetic composition of native species, including keystone and foundation species, and have community- and ecosystem-level consequences (community genetics; Whitham et al. 2006). The degree of metacommunity connectivity in native species, however, may modulate adaptive responses to introduced taxa because dispersal and gene flow can influence the amount of genetic and species diversity in native metacommunities (Urban et al. 2008). The application of molecular tools to describe adaptive genetic variation in a wide variety of interacting organisms will provide insight about the influence of genetic and species diversity on community composition and ecosystem processes. As a consequence, identifying locally adapted populations and the genetic mechanisms that confer particular selected phenotypes will be imperative for linking ecological and evolutionary changes as a consequence of interspecific interactions in the invaded metacommunity.

To understand the evolutionary responses of the exotic and native species in the metacommunity, ideally we would like to identify loci, and potentially particular polymorphisms, underlying these adaptive changes. We and others (Brumfield et al. 2003; Morin et al. 2004) suggest that SNPs hold the greatest promise to identify regions of the genome undergoing selection, primarily evidenced by an excess or absence of polymorphisms indicating potential diversification or sweeps, respectively, and thus are candidate regions for inferring evolutionary mechanisms (Namroud et al. 2008). The advantage of using SNPs combines the genome-wide assessment of AFLPs with the precise co-dominant, and in the case of a species with a genome, genomic location provided with microsatellites. Knowing the genomic location of polymorphisms is particularly informative in coding regions to identify nonsynonymous mutations (polymorphisms that result in a change of amino acid) that are predicted to affect protein structure, regulation, localization, and/or function that then may impact the phenotype and therefore fitness. For this reason, SNP surveys have already proven useful for identifying mutations involved in human disease and local adaptation (Hoekstra et al. 2006; Gupta et al. 2007). Recent technological advances in DNA sequencing have greatly expanded the opportunity for researchers to amass large panels of SNPs in traditionally non-genetic model species for studying population genetic parameters during the invasion process. Thus, characterizing SNPs can provide insights into the relationship between genotype and phenotype and the adaptive evolution of populations, particularly in species occupying diverse natural environments or in environments undergoing rapid change.

Applications to conservation and management

The integrative metacommunity framework has foundational underpinnings in theoretical ecology yet also has clear applications to the conservation and management of aquatic ecosystems threatened by non-native species. Recent empirical evidence suggests that native species in a community may evolve in response to the establishment of exotic species over contemporary time scales (Strauss et al. 2006; Whitney and Gabler 2008). In this chapter, we suggest that this rapid evolution in native species will depend strongly upon the rate of native species dispersal among local communities and the relative strength of environmental selection in the invaded metacommunity. Regional gene flow and the potential for local evolution in native species will be mediated by the spatial distribution of habitats and the degree of hydrologic connections (e.g., freshwater tributaries, oceanic currents) facilitating landscape connectivity (Leibold and Norberg 2004). As a consequence, predictive invasion models that integrate space and the environment can identify native communities that are targets of invasion (Vander Zanden and Olden 2008), and may detect native community connectivity and forecast the probability of rapid evolution (or extinction) of native species. Thus, there is immense potential for a metacommunity-invasion framework to inform risk and conservation assessments in aquatic ecosystems by generating spatially explicit landscape models that invoke dispersal of both exotic and native species. The potential for dispersal-mediated contemporary evolution in native species in response to exotic invasion will have pro-

found implications for the strength of eco-evolutionary interactions between exotic and native species and the biotic integrity of native communities at multiple scales (Stockwell et al. 2003; Kinnison and Hairston 2007).

Conclusions

In this chapter, we present a relatively novel synthesis of metacommunity and invasion biology that informs ecological and evolutionary mechanisms underlying exotic invasion and the response of native biota in a spatio-temporal framework. We further propose a comprehensive molecular toolkit that will facilitate inquiry into the evolutionary processes underlying different stages of the spatio-temporal invasion sequence in both exotic and native species. The perspectives presented here serve only as a brief introduction to the integrative metacommunity approach, and we suggest that there is tremendous potential for future development of the conceptual framework, the theory, and associated empirical research. We believe that the synthesis may be particularly appropriate for spatially structured aquatic ecosystems where the interaction of regional and local processes plays a critical role in community assembly over contemporary time scales. The conceptual advances gained from additional insight into eco-evolutionary mechanisms underlying the invasion sequence may serve to guide ecologists and evolutionary biologists in a modern approach to the conservation of our most threatened freshwater and marine ecosystems.

Glossary

Adaptive sorting. An evolutionary process by which mechanisms of natural selection match genotypes and traits with the local environment.

Amplified Fragment Length Polymorphisms (AFLPs). Anonymous genetic markers generated through whole genome digest with specific restriction enzymes followed by amplification with restriction site specific primers. AFLPs are referred to as dominant markers because particular bands can only be scored as present or absent with no knowledge of whether the locus is homo- or heterozygous.

Cultivation. Propagules or mature individuals are actively moved by humans (directed dispersal) and receive resources to establish and persist.

Eco-evolutionary interactions. Reciprocal interactions between evolutionary changes in populations and ecological interactions in communities.

Exotic. Refers to a species purposefully or un-purposefully brought into a geographical area where it does not naturally occur (same as introduced).

Gene flow. The transfer of alleles of genes from one population to another.

Genetic swamping. The homogenization or replacement of local genotypes as a result of either a numerical and/or fitness advantage of introduced propagules.

Introduced. Refers to a species purposefully or not purposefully brought into a geographical area where it does not naturally occur (same as exotic).

Local adaptation. Evolution through natural selection of traits that have high fitness in the environmental conditions specific to a population.

Long-distance dispersal. Propagules move beyond the dispersal range observed over ecological timescales (sweepstakes dispersal).

Mass dispersal. A dispersal route is established such that many individuals can move to new sites in the non-native range.

Mass effect. A mechanism for spatial dynamics in which there is a net flow of individuals created by differences in population size (or population density) in different patches.

Mass effects perspective. A metacommunity paradigm that focuses on the effects of immigration and emigration rates on local population dynamics in heterogeneous patches.

Metacommunity. A set of local communities that are connected by dispersal of multiple, potentially interacting, species.

Metapopulation. a set of local populations of a species that are connected by dispersal.

Microsatellites. Short tandem repeats of DNA sequence isolated by PCR amplification with taxon-specific oligonucleotide primers. Microsatellite loci tend to be highly variable due to slippage in the DNA replication. Microsatellite markers are co-dominant markers.

Native. A species that occurs naturally in a particular region, state, ecosystem, or habitat without direct or indirect human activity.

Patch dynamics perspective. A metacommunity paradigm that assumes homogeneous or heterogeneous patches. Spatial dynamics are dominated by local extinction and colonization; patches may be occupied or unoccupied.

Propagule pressure. The number and frequency of individuals released into a region to which they are not native.

Random Amplified Polymorphic DNA (RAPDs). Anonymous genetic markers generated by PCR amplification with randomly constructed oligonucleotide primers. Similar to AFLPs, RAPDs are dominant markers.

Selection. Natural or artificial process that tends to result in the survival and propagation of some individuals or organisms but not of others, with the result that the inherited traits of the survivors are perpetuated.

Single Nucleotide Polymorphisms (SNPs). Single base pair variants at homologous locations in the genome.

Species sorting perspective. A metacommunity paradigm that suggests that heterogeneous patch types cause differences in the local demography of species and the outcomes of local species' interactions. Patch quality and species dispersal jointly affect community composition.

Source-sink effects. A mechanism for spatial dynamics in which the enhancement of local populations by immigration in 'sink' localities is due to the migration of individuals from other 'source' localities.

Trait. An attribute or character of an individual within a species for which heritable differences can be defined.

Box 1. The freshwater metacommunity in the Great Lakes of North America

The metacommunity framework can provide insight into ecological and evolutionary mechanisms underlying invasion and assembly of non-native species in the Great Lakes of North America. The Great Lakes are an invasion hotspot for exotic aquatic species carried in the ballast water of transoceanic ships traveling to Canada and the United States (Grigorovich et al. 2003). Species introduced from the Ponto-Caspian region of Eurasia (Azov, Black, and Caspian Seas) have become widely distributed and abundant, and are having dramatic impacts on the ecology of the Great Lakes ecosystem (Vanderploeg et al. 2002). The success of Ponto-Caspian invaders has been attributed to facilitative interactions between organisms with shared evolutionary histories (Ricciardi 2005), suggesting that an invasional meltdown is underway (Ricciardi 2001; but also see Simberloff 2006). For example, the establishment of zebra mussels (*Dreissena polymorpha*) in shallow nearshore areas and quagga mussels (*Dreissena bugensis*) on sediments in deeper waters (Mills et al. 1993) facilitated the invasion of the amphipod, *Echinogammarus ischnus*, by providing habitat (Bially and MacIsaac 2000). Further, these exotic dreissenids and *E. ischnus* facilitated the invasion of their predators, round gobies (*Neogobius melanostomus*) (Ricciardi 2001). Zebra mussel water filtration has increased water clarity, promoting growth of both native and exotic macrophytes (MacIsaac 1996). A Ponto-Caspian derived community has thus established in the Great Lakes, with numerous ecological interactions occurring among native and non-native species across trophic levels (Ricciardi and MacIsaac 2000; Campbell et al. 2009) in the Great Lakes metacommunity.

The invasion success of multiple coevolved species in the same novel metacommunity provides an opportunity to compare the response of exotic genetic diversity to invasion in a standardized non-native environment. Many Ponto-Caspian invaders show residual signals of genetic bottlenecks associated with founder events that likely occurred during their initial invasion in the Great Lakes (Fig. B1). For example, *Cercopagis pengoi* (Cristescu et al. 2001), *D. polymorpha* (May et al. 2006), *E. ischnus* (Cristescu et al. 2004), *Gymnocephalus cernuus* (Stepien et al. 1998), and *Hemimysis anomola* (Audzijonyte et al. 2008) have reduced mitochondrial DNA (mtDNA) haplotype richness compared to their native populations in Eurasia (Fig. B1a). *Bythotrephes longimanus* (Berg and Garton 1994; Colautti et al. 2005) and *D. polymorpha* (Astanei et al. 2005) also under-

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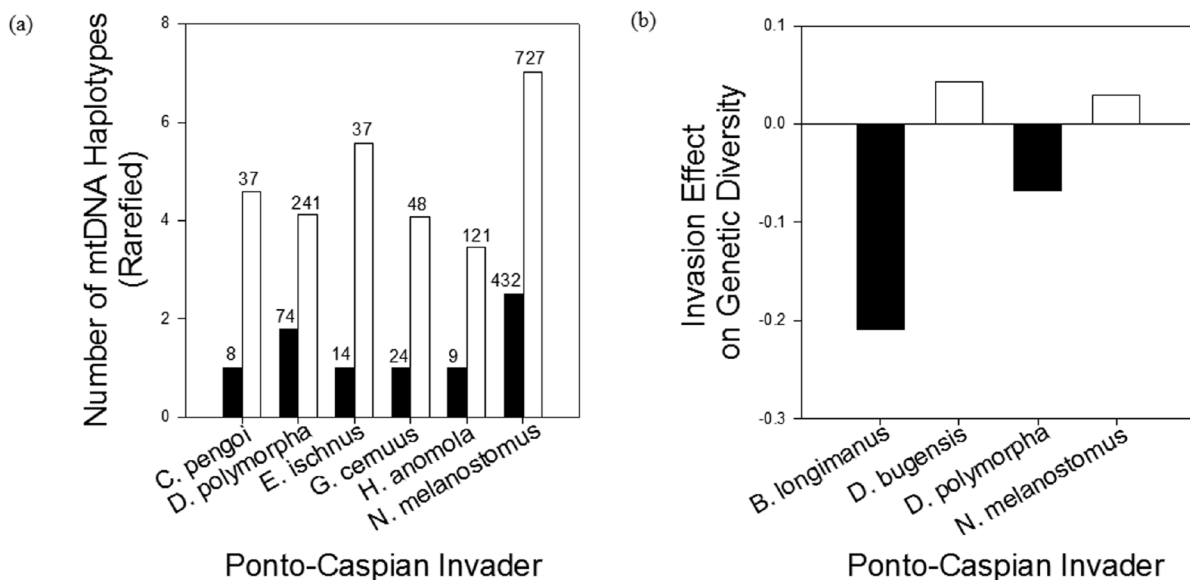
Fig. B1. Residual founder effects in a selection of Ponto-Caspian invaders of the Great Lakes from initial colonization as shown by (a) the number of mitochondrial DNA haplotypes detected in introduced populations in the Great Lakes (black bars) versus native Eurasia (white bars), after controlling for sample size by rarefaction to 8 sequences. Total sample sizes are indicated above the bars. Genes represented are ND5 for *Cercopagis pengoi* (Cristescu et al. 2001), cytochrome b for *Gymnocephalus cernuus* (Stepien et al. 1998), and *Neogobius melanostomus* (Brown and Stepien 2008; Brown and Stepien 2009; Carol Stepien, Univ. of Toledo, pers. comm.), and cytochrome oxidase I for the remaining species: *Dreissena polymorpha* (May et al. 2006; Carol Lee, Univ. of Wisconsin, pers. comm.), *Echinogammarus ischnus* (Cristescu et al. 2004), and *Hemimysis anomola* (Audzijonyte et al. 2008). (b) differences in average observed heterozygosity (Ho) between introduced populations in the Great Lakes and native populations in Eurasia as revealed by microsatellites: *Bythotrephes longimanus* (Colautti et al. 2005), *Dreissena bugensis* (Wilson et al. 1999; Tony Wilson, Univ. of Zurich, pers. comm.; Therriault et al. 2005), *D. polymorpha* (Astanei et al. 2005), and *N. melanostomus* (Brown and Stepien 2009). Black bars indicate a negative effect of invasion on genetic diversity (Ho) relative to native Eurasian populations, and white bars indicate a positive effect of invasion on genetic diversity.

Box 1 Continued

went population genetic bottleneck(s) during colonization, supported by reduced observed microsatellite heterozygosity in Great Lakes populations compared with Eurasia (Fig. B1b). Initial founder events associated with colonization are often offset by high gene flow from Eurasian populations with continued ship ballast discharge. For example, compared with other exotic taxa, a more similar number of mtDNA haplotypes (Fig. B1a) and observed microsatellite heterozygosity (Fig. B1b) have been detected in exotic Great Lakes populations compared with the native Eurasian range in *D. bugensis* (Stepien et al. 2002; Wilson et al. 1999; Therriault et al. 2005) and in *N. melanostomus* (Dillon and Stepien 2001; Brown and Stepien 2008; Brown and Stepien 2009). For these species, there were likely multiple colonization events and a large initial effective population size in the Great Lakes. For the Eurasian spiny water flea (*B. longimanus*), the genetic structure of introduced populations has become more similar to their native source according to allozyme frequencies (Berg et al. 2002) and numbers of rare alleles shared with Eurasia (Colautti et al. 2005). High gene flow among established populations of introduced species within the Great Lakes metacommunity may reduce or eliminate founder effects associated with initial invasion.

   Variation in patterns of colonization and gene flow of Ponto-Caspian aliens in the Great Lakes can be employed to generate hypotheses about metacommunity processes operating among different introduced taxa. Several species, including *B. longimanus* (Colautti et al. 2005), *C. pengoi* (Makarewicz et al. 2001; Therriault et al. 2002), *D. polymorpha* (Stepien et al. 2002),

and *D. bugensis* (Wilson et al. 1999), show mass effects in their introduced ranges through evidence for high dispersal among populations. These taxa are passive dispersers with planktonic life history stages, and show low among-population differentiation compared to their native range (low F_{ST} values; Fig. B2). In contrast, other non-native species of the Great Lakes have relatively low amounts of among-population dispersal, and may be sorted among other dispersal-limited species according to selection. For example, high population differentiation among *N. melanostomus* populations relative to other taxa (Fig. B2; Brown and Stepien 2009) is indicative of low amounts of among-population gene flow and diffusive spread from invasive centers. Low levels of gene flow in ecologically interacting nonindigenous and indigenous species, such as predators and their prey, suggest support for species sorting. For example, species sorting may occur among exotic (*E. ishnus*) and native (*Gammarus fasciatus*) amphipods according to habitat conditions (Palmer and Ricciardi 2004), and this in turn may influence species sorting among exotic (*N. melanostomus*) and native (*Perca flavescens*) fish that prey on these amphipods (Palmer and Ricciardi 2005). Taken together, these patterns of gene flow and species interactions in Ponto-Caspian invaders suggest that mass effects and species sorting predominantly structure the Great Lakes metacommunity.
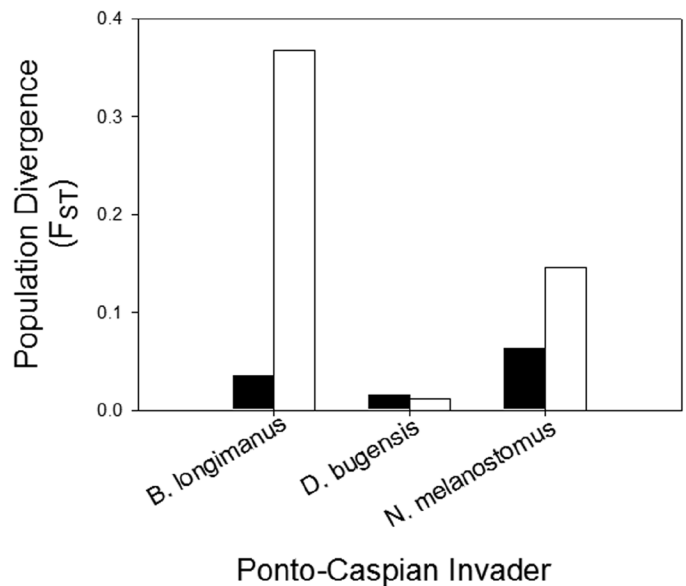
Fig. B2. Population differentiation in a selection of Ponto-Caspian invaders in their introduced range in the Great Lakes (black bars) and in their native range in Eurasia (white bars), as revealed by F_{ST} values that were averaged across microsatellite loci and populations within these ranges: *Bythotrephes longimanus* (Colautti et al. 2005), *Dreissena bugensis* (Wilson et al. 1999; Therriault et al. 2005), and *Neogobius melanostomus* (Brown and Stepien 2009).

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