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State-of-the-art review

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DISPERSAL – LIMITED BIODIVERSITY OF TROPICAL INSULAR STREAMS

ABSTRACT: Numerous species are adapted for colonization of insular fresh waters by using different mechanisms of active and passive dispersal, especially among oceanic islands at low latitudes. Over time, similar animal communities have assembled in many tropical streams and rivers on isolated islands. These freshwater communities are characterized by a relatively low number of species of fishes, decapods, gastropods and insects that typically have complex life cycles including passive, long-distance dispersal. These species often disperse during marine phases with drifting larvae or by rafting and aerial transport of resistant, dormant stages. Active dispersal is sometimes effective for relatively short-distance movements from one island's streams to another island's nearby drainage basin within an archipelago (a "stepping-stones" dispersal pattern). Identifying distinct differences among aquatic communities on "true oceanic" islands of different ages and geologic histories requires a long-term biogeographic perspective including the degree of spatial isolation of populations and differences in rates of speciation. Consequently, the total biodiversity of insular streams is a complex combination of dispersal from multiple sources of species from continents and other islands, as well as evolution of new endemics. Recolonization of streams following natural disturbances and the impacts of introduced species result in dynamic changes in species accumulation and turnover in these insular freshwater ecosystems. Analysis of dispersal to islands provides general perspectives on managing fragmented habitats, especially the effects of invasive species that also shed light on factors affecting the equilibrium composition of animal communities in island-like ecosystems on continents.

KEY WORDS: species diversity, species-area relationships, community assembly, invasive species, island biogeography, disturbance ecology

1. INTRODUCTION

Elton (1958) initially described early changes in insular communities and predicted dramatic changes in the future. He expected that these isolated habitats would be increasingly vulnerable to invasive species because islands generally have relatively fewer species than continents. His original studies continue to stimulate discussion about the importance of species richness, habitat saturation and invasion (e.g. Vitousek 1988, Levine and D'Antonio 1999, Gherardi 2006). Synthesis of current understanding regarding terrestrial communities on islands will provide some useful insights for analysis of freshwater communities. Moreover, additional concepts will likely emerge as many more insular fresh waters are studied and these concepts will have immediate applications in areas of monitoring and managing water quality (e.g. Hughes and Malmqvist 2005) and better understanding of evolutionary biology (e.g. Johnson *et al.* 2000, Kelly *et al.* 2002). Time for these studies may be limited given the rapid human population growth on many islands along with the effects of water diversions, water pollution and increased complexities of land uses. A more sufficient basis for forecasting the consequences of large-scale changes on islands and in island-like habitats is needed to manage these rapidly changing ecosystems in the decades ahead. This review outlines some current literature and emerging ideas that need further exploration and development if insular streams are to better understood and managed.

The first concern is how do these isolated communities become established? Once a species finds the streams, how long can the individuals survive? Do species colonize and re-colonize insular streams from nearby refugia, distant continental sources or from "stepping stones" within archipelagoes? To answer these questions, it is useful to begin with analysis of adaptations for dispersal among the dominant species. The occurrence of certain species in stream communities on isolated tropical oceanic islands is predictable because many freshwater organisms have evolved adaptations for passive dispersal that allow them to be successful colonizers across wide expanses of salt water (Covich and McDowell 1996, Craig 2003, Smith *et al.* 2003). For example, many invertebrate species are well adapted for passive dispersal by producing resistant cysts that remain viable for long periods or by reproducing asexually (e.g. Pointer *et al.* 1993, Harker 1997, Malmqvist *et al.* 1997, Bilton *et al.* 2001, Cottenie and De Meester 2003). Passive dispersal by strong wind storms or by attachment to rafts of floating wood and pumice also results in long-distance dispersal across oceans (e.g. Thiel and Gutow 2005). In some species, a single fertilized live-bearing female or parthenogenetic individual can disperse and begin colonization, as often occurs among some gastropods (Pointier *et al.* 1993) and other invertebrates that are resistant to desiccation (Facon *et al.* 2004). These resistant stages (encased egg masses, dormant individuals) can be carried by other larger organisms, especially birds and fishes, or by strong winds (Bilton *et al.* 2001, Figuerola and Green 2002, Green and Figuerola 2005).

Because all freshwater habitats are subject to drying or filling with sediments over geological and ecological time scales, continental freshwater species have evolved adaptations to disperse passively by developing resistant stages that survive long flights while attached to migratory birds (Darlington 1938, Cáceres and Soluk 2002, Charalambidou and Santamaria 2002) and transported by river flows and floating plant materials along rivers and among lakes (Horvath and Lamberti 1997, Bobeldyk *et al.* 2005). Diapause among crustaceans is another common adaptation for surviving periods of stress that also provides for potential dispersal on continents and across oceans (e.g. Hairston *et al.* 1995, Fryer 1996). In addition, some freshwater species disperse actively by swimming, crawling or flying, but these dispersal movements generally are only effective over shorter distances. These shorter active movements may occasionally occur within island archipelagoes where "stepping-stone" dispersal can accumulate newly arriving species over long distances and long time periods (Gillespie and Roderick 2002). However, predicting the complete assemblage of any particular insular stream community remains difficult because rates of colonization and recolonization (following local extinctions and speciation) vary temporally and spatially across latitudes (Coope 1986, Arthington 1990, Banarescu 1990, Chown *et al.* 1998, Wishart and Davies 2003). In general, insular freshwater ecosystems differ geologically and hydrologically in ways that affect the permanence of freshwater habitats and the biodiversity of stream assemblages (Table 1).

There are partial barriers or "filters" that limit successful colonization of any island or island-like ecosystem. These barriers restrict the number of successful species that are capable of reproducing and persisting as a new population (Fig. 1). Barriers that limit distinct phases of dispersal and reproduction lead to selective colonization by some species

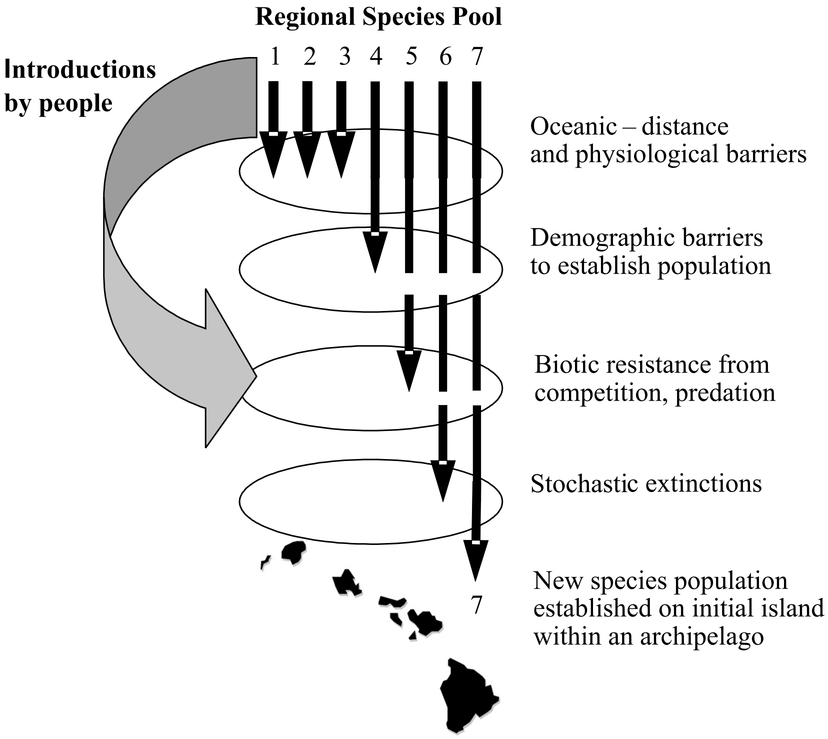

Fig. 1. Barriers for establishing new species on islands and island-like habitats. The small arrows represent 7 species in a source area. They are limited by various barriers to dispersal. Only one species successfully establishes a persistent population on one of the islands in the archipelago. The large arrow on the left side indicates that introductions can by-pass the oceanic (distance and physiological) and demographic (sustained reproduction, population growth) barriers by people transporting sufficient numbers of individuals to the island. Biotic resistance from competing species and effects of predators (as well as parasites and diseases or mutualists, if present) can continue to alter successful colonization. Once on a single island, individuals can move to other nearby islands within an archipelago to expand the species distribution and increase species richness of several islands.

but not others. This serial filtering perspective is modified from that developed by Rahel (2002) in his review of the widespread dispersal of freshwater species. Rapid spread through frequent introductions by humans has indirectly led to extirpations of native species. This "homogenization" of global freshwaters continues, especially as global trade increases in scale (Padilla and Williams 2004). Similar "filters" have been described for fishes dispersing to lakes (Tonn *et al.* 1990), for invertebrates dispersing across landscapes to streams (Poff 1997), and invasive species colonizing new habitats through a series of transitions to new locations (Kolar and Lodge 2001a, 2001b, Gherardi 2006). Freshwater lakes and streams have some island-like attributes of isolation but many have additional degrees of connectivity through linkages within drainage networks. Nonetheless, species dispersing to fresh waters on true geographic islands have some similar barriers to overcome as they do on continents.

Increasing economic activities have caused more species to be actively transported for aquaculture or the aquarium trade throughout the world, and often established in the tropics where warm temperatures provide productive habitats for many introduced species (Fig. 1). Consequently, a high degree of local variability and regional context affects each case study. Long-term data on several parameters including evolution of new endemic insular species, introductions of non-native species, and landuse changes must be analyzed to determine any general patterns (e.g. Barbaut 2003, Bass 2003, Adler *et al.* 2005a). Definition of useful parameters for understanding the relative levels of biodiversity is beginning (e.g. Donaldson 2002, Donaldson and Myers 2002)

Table 1. Attributes and effects on insular freshwater habitats and species diversity.

Attributes	Measurements	Effects
Island age	Time since origin	Older islands accumulate more species from continental and archipelago sources and endemic species from speciation; soil weathering and vegetational succession increases nutrient retention and release to streams
Island location	Distance from source	Close to source(s) increases colonization rates; far from source increases speciation, archipelago formations provide potential increased species richness through temporal and spatial dynamics
Island height	Maximum elevation	Interception of clouds, more rainfall and more runoff creates complex drainage networks and heterogeneous habitats
Island size	Surface area	Larger islands have more total runoff and more heterogeneous habitats with alternative habitats for within inland dispersal
Basin size	River surface area	Local runoff increases with basin size
Basin shape	Width to length	Runoff is slower in wider basins
Drainage network pattern	Reticulate	Runoff is slower in complex drainages
Drainage density	Number channels per unit area	Runoff in high-density networks slows peak flows and reduces washout of food resources and organisms
Channel size	Width	Runoff begins in narrow tributaries with high riparian litter inputs to detritivores. Shading limits light in forested narrow channels and primary productivity is relatively lower than in wide channels

and will assist in predicting biotic responses to many different types of disturbances such as drought (Covich *et al.* 2003), hurricanes (Covich *et al.* 1996, 2006), and habitat degradation (Villa *et al.* 1992, Hau *et al.* 2005).

Although fresh waters generally represent a very small percentage (<0.10%) of the earth's surface, and the total area covered by freshwater habitats on islands is extremely small, the importance of these insular aquatic ecosystems is increasingly recognized. The loss of diverse habitats on islands results from many conflicting pressures to develop catchments and to divert water resources for multiple uses as human populations increase. Despite these losses, many island ecosystems still provide diverse, high-contrast environmental and social conditions. Comparative studies can contribute much needed understanding of how to manage and protect these "living laboratories" (Vitousek *et al.* 1995, Vitousek 2002, Wardle 2003) and island-like, fragmented habitats. Setting aside protected refugia for conservation of species requires understanding how communities respond to changes and their potential for recolonizing habitats following disturbances (Albanese *et al.* 2004). Dispersal by aquatic species among refugia is one of the major traits that must be considered when considering alternative plans to set aside and manage a few large reserves or many small reserves to protect drainage basins. This question of alternative strategies for conservation planning of areas and corridors has been considered primarily relative to terrestrial and marine reserves (e.g. Diamond 1975, Terborgh 1976, Boecklen and Gotelli 1984). However, this analysis is not very often considered when plans are made to protect rare or endemic freshwater species. Much more information derived from studies of dispersal among islands and within drainage networks is needed to better understand how species interact in food webs, where rare freshwater species can be better managed, and how often these aquatic communities can survive disturbances. Given the increasing vulnerability of freshwater communities, there is interest in knowing where and how rapidly the number of co-occurring species is decreasing because rates of localized extinctions are especially high in freshwater ecosystems (Malmqvist and Rundle 2002, Meybeck 2004). Recolonization of freshwaters by both native or by non-native species following disturbances is also increasingly important because more native species are threatened and non-native species are being transported and released (Gherardi 2006).

Understanding the impacts of species loss and recolonization is also essential to identifying the roles of different species in particular ecosystem processes under changing conditions of ecological and hydrologic connectivity (Wallace and Hutchens 2000, Covich *et al.* 1999, Covich *et al.* 2004, Mantel and Dudgeon 2004). Insular tropical streams are especially well suited for comparative studies of the roles of species in ecosystem processes (e.g. Crowl *et al.* 2001, Larned *et al.* 2003). For example, insular food webs are relatively simple in terms of the number of species within a predictable subset of the entire regional biota present in source areas (from continents as well as nearby islands). This nestedness of the widespread subset of a relatively low number of species is open to study on many tropical islands. Biogeographic studies of faunal similarities often use an analysis of nestedness within river drainages and among islands to determine a hierarchy of connectedness (e.g. Boecklen 1997, Cook *et al.* 2004). These comparative approaches provide a strong basis for future field experimental studies because these groups of fishes, gastropods and decapods have some similar life-history traits and means of active and passive dispersal, even if the communities are not in close proximity. Current examples of stream assemblages from the Atlantic to the Pacific Oceans indicate that insular fresh waters share some of these similar attributes despite a very wide range of physical environments and land uses (see Dudgeon 1999, Smith *et al.* 2003 for examples).

Compared to continental streams, only a relatively small number of studies have focused on the colonization, coexistence, and evolution of insular communities (e.g. Spironello and Brooks 2003, McDowall 2005). Few of these insular studies have considered the dynamics of tropical streams (e.g. Covich 1988, Yule 1995, Craig *et al.* 2001, Smith *et al.* 2003, Yam and Dudgeon 2005). This review considers several examples, with an emphasis on case studies from Hawaiian and Caribbean tropical streams. Major biogeographic differences seem to occur at low latitudes among continental and insular streams (Covich 1988). Studies of these differences will likely provide insights for interpreting the generality of current concepts about continental freshwater ecosystems and their responses to disturbances. This comparative approach will also eventually enhance our understanding of overland dispersal because many continental freshwater habitats have island-like distributions in time and space.

2. THE IMPORTANCE OF DISPERSAL TO INSULAR ECOSYSTEMS

2.1. Travel around the globe

How freshwater organisms move around the globe continues to intrigue ecologists and biogeographers (Bilton *et al.* 2001, Malmqvist 2002, Cáceres and Soluk 2002, Bohonak and Jenkins 2003). Despite the many adaptations for dispersal, even widespread species are not found everywhere (Bullock *et al.* 2002). The exception may be among many microbial species (Weisse 2006). Some microbiologists assert that all bacteria are widely distributed and community dominance responds quickly to environmental changes (Finlay 2002, Fenchel 2003). Others, especially among those who study freshwater fungi and invertebrates, note that regional biotas differ in ways that we do not yet fully understand. The durability and transportability of eggs, cysts, ephippia, gemules and other resistant propagules are well known for some species from comprehensive studies of birds' feet and intestinal pathways (e.g. Charalambidou and Santamaria 2002, Charalambidou *et al.* 2005) and crayfish (Pérez-Bote *et al.* 2005).

There are numerous uncertainties regarding the rates and directions of dispersal because of the many species-specific adaptations and uniqueness of diverse taxa among bacteria and metazoans as well as a lack of sufficient long-term data. The time scales that ecologists and evolutionary biologists consider relevant to their studies differ depending on their specific questions. However, in most cases, long-term data over many generations are difficult to collect, yet essential for conclusive interpretations. Nonetheless, there are some robust biogeographic relationships that are widely observed regardless of the taxa being studied. One of the most general relationships is between the increasing size of the habitat and the increasing number of coexisting species that persist over ecological time scales. This positive species-area relationship is commonly observed in the biogeography of many community assemblages (e.g. Williamson 1988, Haynes 1990, Brown and Lomolino 1998, Whittaker 1998, Lomolino and Weiser 2001). Bacterial operational taxonomic units (OTUs) are also found to increase in biodiversity as the size of the ecosystem increases, presumably because the number of specific environmental conditions also increases the number of specific microhabitats used by different OTUs (e.g. Horner-Devine *et al.* 2004a, 2004b, Bell *et al.* 2005, Reche *et al.* 2005). More data are needed from a larger array of habitats to test this pattern's generality. Among invertebrates it is likely that once a population is established in a freshwater habitat, its population will persist for many years in sub-populations or as dormant resting stages in sediments (e.g. Hairston *et al.* 1995). However, great uncertainty lies in knowing if rates of dispersal among different species are relatively fast or slow and if local extinction occurs frequently or rarely.

The null models that assume freshwater species are distributed either universally or randomly avoid some unrealistic assumptions used in strictly deterministic approaches. For example, Hubbell's neutral model provides a different approach for analysis of biodiversity that is now being widely tested for forest communities (Hubbell 2001) and it may prove useful in analysis of freshwater communities. His model of community assembly is "neutral" in that it deemphasizes the general importance of species traits. Differences in niche requirements are minimized in this approach to determine if these species-specific traits are really important. Other models use predictions based on random processes of dispersal that diminish the importance of many specific adaptations and focus on the degree of randomness that might be sufficient to explain some distributions. Stream studies of benthic communities have compared various models based on deterministic or stochastic approaches (e.g. Townsend and Hildrew 1976, Minshall *et al.* 1985, Palmer *et al.* 1996) and on patch dynamics (Pringle *et al.* 1988, Townsend 1989, Thompson and Townsend 2005). Because freshwater organisms have evolved numerous ways to remain in shifting habitats over geological and evolutionary time scales, clear definition of actual community structure is challenging. In any analysis of species richness, accurate predictions often require concepts associated with demographic stochasticity and the temporal variability of chances for dispersal and successful colonization (e.g. Gurevitch and Padilla 2004a, 2004b, Ricciardi 2004, Clavero and Garcia-Berthou 2005, Gillespie 2005, Simberloff 2005).

Conceptual understanding of community ecology and its many inherent evolutionary relationships has benefited enormously from studies of regional insular biotas and the associated dynamical changes in species composition. In addition to speciation as a source of biodiversity, colonization of islands continues to be well studied; centuries of detailed data are available, especially for terrestrial communities. As discussed below, some of the earliest studies of tropical insular streams focused on Caribbean islands (Hynes 1971, Harrison and Rankin 1976). The diverse Caribbean biota often shares evolutionary similarities among major taxa (Woods and Sergile 2001) that result in distinct elevational gradients. On a global scale, species richness among freshwater streams does not reflect latitudinal gradients typically observed among terrestrial and marine communities (Covich 1988, Lake *et al.* 1994, Jacobsen *et al.* 1997, Vinson and Hawkins 1998, 2003, Boyero 2002). The relatively low species richness in tropical streams relative to marine and terrestrial latitudinal patterns may be related primarily to the transient nature of most freshwater habitats and the uneven distributions of freshwaters across continental land masses. The lack of sufficient study of island and mainland freshwater ecosystems is also likely to be a partial explanation.

Understanding evolutionary adaptations for dispersal of rare and endemic species is critical for conservation and management of insular biota (Malmqvist *et al.* 1995, Kaufman *et al.* 1997, Witte *et al.* 2000, Barbault 2003). Formation of isolated freshwater communities is clearly affected by the ages and locations of riverine and lacustrine habitats as well as by specific adaptations for dispersal (e.g. Boxshall and Jaume 2000, Bilton *et al.* 2001, Bohanak and Jenkins 2003, McDowall 2004a). These adaptive relationships need to be better integrated into long-term conservation planning to provide for effective long-term management.

2.2. What constitutes "island" and "island-like" ecosystems?

Biologists have long recognized that islands and archipelagoes provide natural laboratories for comparative studies of evolution and ecology. The large number of islands in Greater and Lesser Antilles and the Hawaiian islands has been especially well studied. The distinct boundaries associated with islands and their freshwater habitats provide convenient opportunities for analysis of species dynamics as well as inputs and outputs of energy and materials in comparable ecosystems. However, studies of insular streams need to define exactly what constitutes the size of an "island" and its various drainage basins. These distinctions are not always simple. For example, the dynamics of changing sea levels often create complex relationships among coastal rivers and lakes, leaving some high and dry for millennia thus altering the sizes of drainage basins over time. Geological history clearly plays a significant role in determining the biotic composition of insular freshwater communities through the long-term changes in positions of the continents and the formation of islands. Even if temporal baselines are clearly established to determine origins of islands, there is no consensus regarding the length of time that isolation is required or the time needed for stream channels to develop into drainage networks. For example, one framework to distinguish true "islands" from "fragments" (those high-contrast, patchy locations that have not been completely isolated) requires that the islands be continuously disjunct for more than 200 years to be considered "old" (Watson 2002). The complex connections among "islands" and "continents" associated with plate tectonics are distinct but relate to earlier concepts of "land bridges". For example, the islands of Trinidad and Tobago are known to have had continental connections with northeastern South America over geologic time scales (Erlich and Barrett 1990). These connections are important for understanding the distributions of freshwater crabs that lack an oceanic larval phase (Rodriguez and Lopez 2003). The geologic history of islands of the Greater and Lesser Antilles (Donnelly 1988, Larue 1994, Curtis *et al.* 2001) provides well-defined time lines for durations of the periods of isolation and opportunities to define "true islands" in order to compare their species richness (Liebherr 1988, Bass 2003).

Four general groups of islands can be defined and ranked in order of expected species richness: 1) geologically younger (>10 000 years of age) islands that are isolated by long distances from sources of colonizing species are expected to have dispersal-limited, low-diversity communities; 2) older islands (>10 000 years of age), closer to continental sources of colonizers are expected to have higher species diversity and competition- or predation-limited communities; 3) older, isolated islands are expected to have higher species diversity resulting from a combination of endemic species (because their longer isolation increases probabilities for speciation) and widespread species (because their adaptations for long-distance dispersal decreases probabilities for speciation); 4) islands that were originally derived from continents are expected to have the highest species diversity reflecting their unique histories. Examples of these different types of islands indicate that geological age and types of origins, as well as area, are important in freshwater community development. The time frame used by most ecologists includes Pleistocene periods but longer periods of earlier geologic relationships may also be needed. However, it is sometimes difficult to resolve the true ages of lakes and rivers on islands. Persistence of these insular freshwater ecosystems over long periods is intrinsically uncertain in light of our incomplete understanding of highly variable climates, complex connections between surface and sub-surface waters, and the often unstudied or unavailable fossil record.

A useful comparative framework can be partially based on varied lengths of time that different locations have persisted in isolation. For example, the North and South Islands of New Zealand are truly distinct islands with different geologic histories, while over a much longer time scale both islands comprise a single entity of a larger, older continental unit. Thus, the well-studied geologic history of New Zealand within the Gondwana paleogeography provides interesting but different definitions depending on when one establishes a baseline for study and how much is known. There is sufficient geological evidence to demonstrate that the earliest formation of New Zealand began when this land mass became disconnected from Gondwana millions of years before Australia and South America (Daugherty *et al.* 1993, McDowall 2003). As another example, McDowall (2005) points out that the Falkland Islands apparently were detached from the southeastern tip of South Africa and then rotated across the southern Atlantic until this unit approached Patagonian South America.

Recently formed islands, whose geologic origins are often very well documented, provide additional clarity in understanding the importance of ages and origins relative to ecologically meaningful definitions of islands. For example, the low-lying coral atolls and high-elevation volcanic islands in the Pacific Ocean provide numerous opportunities to compare assemblages among approximately 25 000 islands, many of which have freshwater wetlands and intermittent or permanent streams. Some islands are still being formed in the Hawaiian Archipelago (Wagner and Funk 1995). Many other archipelagoes with high, volcanic islands in the Societies and Marquesas in the South Pacific (Resh and De Szalay 1995), and Krakatau (Thornton 1996, Bush and Whittaker 1993) are yielding insights regarding the importance of island age as well as area and isolation (Drake *et al.* 2002, DeWit 2003). These island chains are often geologically complex in terms of the sequence of the origins of specific islands. The chronological arrangements of these island chains provide important laboratories for ecologists and others interested in evolutionary biology (Gillespie 2002, Price and Clague 2002, De Queiroz 2004). Relatively young islands can be colonized by species from older islands over time and the relationships between the age of a single island and its biodiversity are sometimes difficult to define. For example, among the current emergent islands of the Hawaiian archipelago, the oldest island is thought to be Kauai (about five million years old). However, submerged islands in this chain are approximately 32 million years old and may once have been a possible source for short-distance dispersal to Kauai if they overlapped in time (Carson and Clague 1995). This serial dispersal within an archipelago could increase biological diversity by extending the length of time for new species to evolve and for sequential land masses to accumulate species from nearby island sources as well as from continents.

These historical perspectives are essential in considering species relationships among islands of different: sizes, areas of catchments, stream network connectivity, and available stream habitats at varied distances from sources for species dispersal. As discussed below, the original MacArthur and Wilson model that included island area and distance from sources of colonists as the main variables was useful for a first approximation to distinguish general relationships of species and area (Williamson 1989, Lazell 2005). However, this approach is not adequate for considerations of temporal changes in dispersal, especially in dynamically changing freshwater habitats where weathering and erosion greatly modify aquatic habitats over time (e.g. Ibáñez *et al.* 1994, Resh and De Szalay 1995, Craig 2003, Smith *et al.* 2003).

3. SPATIAL AND TEMPORAL PARAMETERS FOR UNDERSTANDING DISPERSAL

As previously mentioned, a widely considered, general relationship is that the larger the area of an aquatic habitat (or a drainage basin), the larger the number of species is likely to co-occur. Positive species-area relationships are typically reported in terrestrial communities (Williamson 1988, Reche *et al.* 2005), yet complexities remain regarding means of sampling and analysis (e.g. Schneider 2003). Recently, the time span for sampling as well as the size of the area has been recognized as important in measuring rates of species accumulation in different habitats (Adler *et al.* 2005b). In insular freshwater habitats, sampling time and efficiency can be affected by variations in water depths, topographic complexity, variability in precipitation, and connections among groundwater and surface-water habitats. Catchment-scale, stream habitats are modified by climate, geology, hydrology (Winter 2001, Craig 2003, Cruz 2003, Benda *et al.* 2004) as well as land uses (Dodson *et al.* 2005). These heterogeneous landscapes greatly influence the complexity of freshwater habitats and species diversity, well beyond simply the area of the river basin, the longitudinal profile or the island's surface area (Thorp *et al.* 2006). Studies of how organisms move through this habitat complexity include diffusion-advection models (Skalski and Gilliam 2000) and drainage network analysis (Albanese *et al.* 2004).

This spatial-temporal template also determines how species move through habitats. Habitat structure and species mobility change dynamically in response to natural climatic variability and managed flows. Water diversions, channelization, dam construction, and agricultural and urban land development greatly modify flows of water and materials while potentially reducing species diversity regardless of the insular or continental locations of drainage basins (Pringle 2001, Brasher 2003). The main differences are that insular drainage networks are generally smaller in area and often more linear and less reticulate (Craig 2003, Smith *et al.* 2003).

Although fundamental physical and chemical weathering processes act similarly at global scales to create aquatic habitats, there are definable groups of islands that share general types of geological origins. For example, drainages on islands originating from volcanic activities have distinct fluvial geomorphologies relative to those originating from uplifted islands created by biotic deposition of corals and limestone. Weathering and erosive processes with faulting of strata and slumping of sediments produce dramatic differences locally and affect the formation of drainage networks (e.g. Menard 1986, Louvat and Allège 1998). In general, the physical template is widely comparable across the surface of the globe at multiple scales (Power and Dietrich 2002, Benda *et al.* 2004). Large climatic differences also clearly have important effects on a latitudinal basis that affect the composition of freshwater communities.

3.1. An evolutionary ecological perspective on biogeographical models

Since Darwin, naturalists and evolutionary biologists have examined island communities and recorded remarkable biogeographic examples of long-distance dispersal and resulting speciation following periods of isolation. More than 35 years ago, ecologists developed new concepts of species turnover and equilibrium to generalize how communities assemble over time (MacArthur 1970, Whittaker 1998). MacArthur and Wilson (1967) generated a surge of interest in tests of their graphical model of island biography that resulted in a resurgence of research and theory (e.g. Sauer 1969, Simberloff 1974). That interest continues today along with additional modifications (Gilbert 1980, Lazell 2005) and generation of new general theories (Heaney 2000, Gillespie 2002, 2005). The concept of species turnover on islands (and many island-like habitats) was mostly framed in geographic space (near versus far islands, large versus small islands) and ecological time scales (without speciation involved). This concept of species turnover included dispersal of new colonists who met with ensuing competition for whatever resources were available on the island. The resulting replacement of immigrating species is proposed to offset local extinction and thus to maintain a balance or a dynamic equilibrium of a predicted number of species sustainable by the island's carrying capacity.

This original island biogeographical model has led to many applications and recent modifications regarding dispersal that have been used to provide an ecological basis for conservation biology and management (e.g. Diamond 1975, Higgs 1981, Simberloff and Abele 1982). There are useful and predictable relationships between the number of species on an island and the size (surface area) of the island that are widely reported for bacteria, birds and plants (e.g. Grant 1998, Horner-Devine *et al.* 2004a, 2004b, Bell *et al.* 2005). However, it is also recognized that other attributes such as topographic complexities and ages of islands are important predictors of community composition. Despite the attractiveness of the MacArthur-Wilson model in stimulating discussions, it has often proven to be overly simplistic and insufficient for making predictions. MacArthur and Wilson (1967) originally noted that the emphasis on island area was a convenience and that information on habitat diversity and structural complexity would be needed for a thorough analysis, as would effects of speciation. Much of this information, however, is lacking, especially for freshwater habitats.

The number of species in any "source community" (mainland species richness) typically includes species of very different dispersal abilities so that not all would be able to colonize even nearby insular habitats. The initial concept that immigration rates would start off high initially and then slow until all the source species had colonized is not likely to occur generally. Rates of immigration and successful colonization are highly variable for many species. The initial assumption that extinction rates reflected area alone (and not dependent on habitat quality and complexity) is also unlikely to be as general as needed for analysis of insular freshwater habitats. Thus, the expected equilibrium where extinction and immigration rates are equal is not likely to be sufficiently realistic to provide robust predictions of insular freshwater communities. It is now widely appreciated that fragmentation of insular habitats (resulting from increased land uses and disturbances) is another major variable in limiting dispersal of many species to islands independent of area or distances from sources (Simberloff and Abele 1982).

Rates of extinction in fresh waters are especially difficult to measure because many species are found in distinct microhabitats and are often difficult to sample completely. Moreover, as previously mentioned, certain adaptations for dispersal result in "resting stages" that can remain in the habitat. They develop reproducing populations when conditions change to those environments that support them. In the interim, these "resting-stage species" may be thought to be extinct when they are, in fact, present but inactive and not included in routine sampling results. The challenge for complete sampling in large lakes and rivers is enormous. Thus, determining rates of extinction in insular drainage networks or lakes that are needed in the MacArthur-Wilson model to estimate an equilibrium assemblage typically limits useful applications of the model. Some freshwater examples are provided below that demonstrate that a more complex analysis of dispersal and extinction rates is likely to be needed.

3.2. Freshwater islands as distinct evolutionary assemblages

Stream ecologists have often studied dispersal of species with regard to a single river, lake outflow or local drainage (for review, see MacKay 1992), but studies are also increasingly placing those results into a wider regional or global context with comparisons among isolated locations (e.g. Lake *et al.* 1994, Vinson and Hawkins 1998, Boyero 2002). Hynes (1970) and Minshall *et al.* (1985) indicated the importance of landscape-level, catchment analysis but did not stress connectivity of lake and rivers in regional drainages. Minshall *et al.* (1985) did review the use of island biographic models in studies of species richness in streams as a means to analyze patterns within downstream gradients. They examined aquatic insect distributions using individual rocks as equivalents to oceanic islands. More work has recently focused on freshwater invertebrates in the context of island biogeography (e.g. Resh *et al.* 1990, 1992, Bass 2003, McDowall 2005). Conceptual models of dispersal are also being developed (Bilton *et al.* 2001, Havel *et al.* 2002, Bohanak and Jenkins 2003) and compared among island-like freshwater habitats such as isolated springs, ponds and lakes (e.g. Williams and Williams 1998, Shurin 2000, Shurin *et al.* 2000, Shurin and Allen 2001) and other mainland freshwater habitats. Island and island-like distributional studies include analysis of fish (Angermeier and Schlosser 1989, Angermeier and Winston 1998, Albanese *et al.* 2004, Cook *et al.* 2004, Smith *et al.* 2004, Sorensen and Hobson 2005), aquatic insects (Malmqvist *et al.* 1993, 1995, 1997, Nilsson *et al.* 1998, Crosskey and Baez 2004), decapod crustaceans (Marquet 1991, Fiévet *et al.* 2001, Debrot 2003, Rodriguez and Lopez 2003) and gastropods (Haynes 1990, 1993, Liu and Resh 1997, Haynes 2000, Myers *et al.* 2000, Pugh and Scott 2002, Pointier *et al.* 2005). Several studies on gastropods in continental lakes and ponds have also examined the species-area relationship (Lassen 1975, Økland 1983, Brönmark 1985). Most distributional studies on island biogeography have centered on terrestrial species, and especially vertebrates (Carlquist 1974, Grant 1998, Brown and Lomolino 2000, Woods and Sergile 2001).

A general feature of the biota in insular streams and coastal fresh waters, as previously mentioned, is that many of the dominant species have adapted to these stream habitats from marine origins. For example, the adults and larvae of many species of fishes and invertebrates survive in a wide range of salinities that enhances their dispersal over long distances across marine and brackish waters and results in colonization of streams and rivers on distant oceanic islands (e.g. Waters *et al.* 2000, Fitzsimmons *et al.* 2002, De Bruyn *et al.* 2004a, 2004b, McDowall 2004a, Page *et al.* 2005). Thus, these larvae can drift passively in oceanic and riverine currents from continents to islands and from island to island. Some species continue to use marine habitats as well as freshwater habitats during extended, complex life cycles (e.g. Chace and Hobbs 1969, Anger 1995, Buden *et al.* 2001a, 2001b). Of the nearly 30 animal phyla found in marine waters, 16 have adapted to fresh water and only 7 to terrestrial habitats (Lee and Bell 1999). The very low ionic concentrations of fresh waters create major physiological challenges to the maintenance of osmotic pressures and internal ionic balances. Nonetheless, numerous species have adapted to these highly variable salinities and many of the recent invasive species have been transported to new freshwater locations from marine or brackish waters.

Dispersal of many "freshwater" fish species is enhanced because they are adapted to include a wide range of salinities in different habitats during their entire, complex life cycles (Myers 1949). For example, the young-of-year individuals of anadromous fish species (such as salmonids and sticklebacks) are born in fresh waters and migrate to the ocean where they spend a large portion of their lives before returning to reproduce. These adults can have a major impact on nutrient transport to headwaters as well as on community composition of coastal rivers. Although many of these species have evolved complex orientation mechanisms to return to their natal waters, they are capable of colonizing new locations as climate, land uses and coastal habitats change over time. Of similar or greater impact are the catadromous fish species (such as anguillid eels) that are born in the ocean and spend most of their adult lives in fresh water before returning to the ocean to reproduce. They disperse over very large distances across the ocean, along coastal rivers and they often migrate far upstream in coastal rivers (McDowall 2004a, McDowall *et al.*1998).

In amphidromous species, the larvae require a marine or brackish-water phase of development prior to upstream migration. In some cases larvae are dispersed long distances by ocean currents. Amphidromy is thought to diminish chances for speciation because these species' populations are not sufficiently isolated. Thus, they often lack distinct genetic differences (Zink *et al.* 1996, Chubb *et al.* 1998, Berrebi *et al.* 2005). In some populations, genetic differences among populations are known to occur when sufficient barriers to dispersal have isolated populations (Mashiko and Numachi 1993, Fièvet and Eppe 2002). Fishes and numerous species of gastropods and decapods have amphidromous life cycles. Post-larvae and juveniles migrate over considerable distances from marine waters to reproduce upstream in headwaters (Haynes 1987, 1988a, 1988b, 1993, Covich and McDowell 1996, Blanco and Scatena 2005). Adult fish, such as gobies, reproduce in rivers and many species spend considerable amounts of time in fresh water (Keith 2003, Sorensen and Hobson 2005). Having a larval stage in their life history that includes periods in marine habitats can increase their ability to feed on different resources, and avoid some degree of competition and predation among more specialized species. These complex life cycles also include opportunities for long-distance dispersal by using oceanic currents and passive drift among larvae or juveniles (Calow 1978, Anger 1995, Palmer *et al.* 1996, McDowall 2004b).

A lively debate continues among biogeographers regarding the importance of dispersal mechanisms relative to other factors that control species composition of isolated communities over long periods of evolutionary history and earth processes (e.g. Ebach and Humphries 2003, Ebach *et al.* 2003, Wilkinson 2003). The importance of plate tectonics and movements of islands relative to each other and continental source areas is clearly established. Currently, the relative importance of dispersal and the accumulation of species over various ages of islands (and fossil records from sediments cores or rock deposits of freshwater species) are not yet well defined for most insular streams. In some cases, the reasoning can become complex and potentially circular. For example, Briggs (2003) used the presence of "secondary freshwater fishes" in the categorization used by Myers (1938) as a means to establish transoceanic dispersal of killifishes and cichlids to island habitats because they are adapted to variable salinities. This transoceanic dispersal hypothesis may be correct for explaining these fish distributions in the West Indies or Madagascar. However, the original definition of "secondary freshwater fishes" by Myers was based on the current distributions of these taxa, and some caution is needed in making these interpretations (Sparks and Stiassny 2003, Smith and Bermingham 2005, Sparks and Smith 2005). The geological history (De Wit 2003) and faunal evolution of Madagascar provides numerous examples of the accumulation of species on islands from both dispersal and speciation (e.g. Gattolliar and Satori 2001, Donnelly and Parr 2003, Monaghan *et al.* 2005).

4. CASE STUDIES

In-depth examples help to illustrate the importance of regional and local geographical variables relative to dispersal. Of the many islands and island-like habitats that have been well studied, two regional examples provide some initial comparisons of important interactions among geological history, landscape structure, biological adaptations and ecological processes.

Puerto Rico: The Caribbean Basin includes insular and continental drainages whose warm tropical waters flow into the Caribbean Sea, as well as the Gulf of Mexico. Islands of this region include three archipelagoes: Greater and Lesser Antilles, and the Bahamas. The Greater Antilles are composed of four relatively larger islands: Cuba, Hispaniola, Jamaica and Puerto Rico (Buskirk 1985). The Lesser Antilles comprise a distinct series of smaller islands extending from Grenada to Sombrero, divided from the larger islands by the Anegada Passage (Stock 1986, Larue 1994, Woods and Sergile 2001). Long-term stream research is illustrated by a series of studies on Puerto Rican headwater tributaries (Covich *et al.* 1996, 2003, 2006) and by regional food-web comparisons with other insular streams (Covich and McDowell 1996). Many of these tropical species have complex amphidromous life histories and continue to spend part of their lives as larvae in marine or brackish waters. For example, among the more than 90 species of *Macrobrachium* worldwide, many amphidromous species are distributed in coastal drainages throughout the Caribbean, Gulf of Mexico and southeastern Brazil. Both continental and insular rivers contain some of the same species which have physiologically adapted to fresh waters from marine origins over many years. Consequently, a common riverine fauna and similar food webs are found in many Caribbean coastal habitats that are interconnected by oceanic currents through widely distributed, drifting larvae. These larvae are transported long distances by off-shore currents along insular and continental coasts. Colonization of Caribbean islands by other means, such as island to island flights by insects and by wind transport are also very important (Bass 2003). Once within a group of islands, the upstream and downstream movements of aquatic insects also become important for local dispersal (Bass 2004).

There are few well-established baselines or long-term studies to determine changes in biotic distributions. Even on those species of economic value, such as *Macrobrachium* shrimp which are intensively harvested by local fishermen (Bowles *et al.* 2000, Jayachandran 2001), there are few long-term studies. Nor are the effects of natural disturbances well documented on the distributions of *Macrobrachium* spp. a genus that contains *M. carcinus*, the largest shrimp in Neotropical streams (Covich *et al.* 2006). Five species of *Macrobrachium* (Palaemonidae) occur in Puerto Rican headwaters (*M. carcinus* (L.), *M. faustinum* (De Saussure), *M. crenulatum* (Holthius), *M. heterochirus* (Wiegmann)). The fifth species (*M. acanthurus* (Wiegmann)) is restricted to low elevations, often in saline or brackish estuarine waters (Covich and McDowell 1996, Brailovsky and Galera 1997). Palaemonid shrimps adapt their osmotic and ionic regulatory balances to a wide range of salinities (Freire *et al.* 2003). The total native freshwater decapod fauna of Puerto Rico consists of 14 species of shrimps in three families (Atyidae, Xiphocarididae, Palaemonidae) and one species of crab. Several non-native decapod species, including *Procambarus* sp. from North America and *Cherax* sp. from Australia, are reported to occur from a few unpublished observations. Non-native gastropods and other non-native species have been introduced over several decades. Their rapid dispersal is associated with widespread construction of dams and reservoirs (Holmquist *et al.* 1998, Jobin 1998, March *et al.* 2003) and with land-use changes that have altered runoff and water allocations (Grau *et al.* 2003, Rivera-Monroy *et al.* 2004).

Insular headwater studies have raised a number of yet unanswered questions regarding species distributions within the Caribbean Basin: How widespread are the dominant species in river drainages throughout the region? Can species disperse and recolonize "restored" rivers after major disturbances or improved management of drainage basins? Are headwater habitats being lost because of rapidly growing human populations? Are these well-adapted species vulnerable to over harvesting or to competition from invasive species or to diseases spread by introduced pathogens? Can the sequence of species recolonization after disturbances alter ecosystem processing? Answers to at least some of these questions are emerging from related studies on tropical streams where many of the same genera and species are distributed (e.g. Fièvet *et al.* 2001, Fièvet and Eppe 2002, Debrot 2003, De Souza and Moulton 2005).

It is clear that overharvesting predatory species is likely to increase the abundance of the prey species. Shifts in abundance and/or recolonization of insular streams are also likely to have different effects on ecosystem processes. For example, if various species of detritivores create new conditions by shredding leaf litter, their activities can enhance the production of suspended organic particulates for filter feeders. This indirect mutualism can occur among different pools within drainage basins composed of different detritivorous species (e.g. Crowl *et al.* 2001). These relationships can also be greatly altered by invasions by non-native species through either enhancement or degradation of ecosystem processes (Covich *et al.* 1999).

Panama: The Isthmus of Panama in Central America is a major focus for biogeographic studies because of its location relative to the distinct faunas of the Atlantic and Pacific Oceans as well as North and South American continents. The formation of the Isthmus in the Pliocene allowed for dispersal of aquatic species from North and South America. Dispersal and evolution of freshwater species from these major sources has occurred over millions of years as sea levels changed and entire positions of islands and continents shifted (Zaret 1984, Smith *et al.* 2004, Smith and Bermingham 2005). Fish faunas in these Lower Mesoamerican drainage basins are well studied, especially with regard to the importance of regional dispersal and salinity tolerances (Smith and Bermingham 2005).

Movement of freshwater fishes over recent time scales from one river drainage system to another from opposite sides of the continental divide has continued since the Panama Canal was built (Smith *et al.* 2004). There have been no recorded losses of species in these two distinct riverine faunas. This lack of species extinctions following fish dispersal in both directions indicates that the fish communities in both drainage systems are not yet saturated.

Gatun Lake was created in 1914 as part of the construction of the Panama Canal by damming the Chagres River. The highly irregular and convoluted shoreline is typical of many recently constructed reservoirs. Its water residence time is approximately 1 yr because of the high rainfall and use of outflow to provide use of ship locks at both ends of the lake. Annual lake level is controlled within 2 m of fluctuations to maintain ship traffic through the canal (maximum depth is approximately 29 m, average depth is about 12 m). The biota is a combination of riverine species that adjusted to the reservoir as well as additional species that have colonized or been introduced to the lake (Zaret 1984). The lake food web was dramatically altered in 1967 following introduction of *Cichla ocellaris* (Bloch and Schneider), a large predatory fish from South America that reduced the abundances of most of the native species (Zaret and Paine 1973). Apparently, some 60 fingerlings were introduced to provide sport fishing opportunities and these grew quickly and the population rapidly dispersed throughout the lake. As a predator, well adapted to tropical rivers, it fed on the planktivorous fishes, especially *Melaniris chagresi* (Meek and Hildebrand), and altered the food web. This major alteration is typical of other lakes where rapidly growing populations of non-native predators have been introduced. These changes suggest that a single dispersed species can enter isolated fresh waters and rapidly change the community structure and diversity. Furthermore, multiple introductions of the Chinese grass carp (*Ctenopharyngodon* sp.) have occurred to control invasive aquatic plants. These invasions are likely to continue as the aquatic ecosystem continues to undergo a series of changes. As in other large lakes (Ricciardi and MacIsaac 2000, Ricciardi 2001) with high exposure to shipping traffic, there is the potential for invasive species to change the environment in ways that enhance colonization by other invasive species, resulting ultimately in an "invasional meltdown" through direct and indirect mutualism (Simberloff and von Holle 1999).

5. FUTURE RESEARCH OPPORTUNITIES

Climate change: Historical perspectives are essential in understanding how different stream communities have developed on islands that vary in their ages, sizes, and locations. This perspective is increasingly critical in the management of island ecosystems, especially among small, low-elevation islands where freshwater resources are already limiting human population growth. Of immediate importance is the future persistence of these island drainage systems and their fresh waters as the climate changes and human populations concentrate along coasts (Lal *et al.* 2002). Sea-surface warming and expansion of the ocean's volume is currently causing sea-level rise in many regions. The likely continued increased in sea-level rise resulting from global warming will reduce the size of many low-lying islands and will cause their coastal rivers to change their hydrology.

Small, low-elevation islands generally lack streams but have lens of fresh groundwater and sometimes these form freshwater wetlands around the island perimeter adjacent to mangrove swamps (Drexler and Ewel 2001). Salt-water intrusion during storm surges is likely to increase if hurricane frequency and intensity are projected to increase as a result of warmer sea-surface waters creating a new "baseline" for storm-generating energy (Knutson and Tuleya 2004). Increased frequency of El Niño events may further increase the complexity of these climatic changes (Meehl 1997, Drexler and Ewel 2001). Consequently, intra- and inter-annual variability of salinity in surface and ground waters will also likely increase. Projections indicate that a 1 m rise in sea level would submerge as many as 1190 small islands in the Maldives alone (Pernetta 1992). Many other islands would be reduced in size with elimination of numerous freshwater and estuarine habitats. Atolls, formed by rings of coral reefs surrounding lagoons, are especially vulnerable to sea-level rise, erosion, and storm surges. Groups of atolls in the Maldives, Tuvalu, Kiribati, and Marshall Islands are under study to determine how their lens of fresh water may be contaminated by salt-water intrusion as sea levels rise and storm surges become more intense in many areas (Barnett and Adger 2003).

Non-native species: Previous studies, such as those reviewed from Puerto Rico and Panama, provide an array of documented situations that can continue to be studied to determine rates of changes. Additional baseline studies in many regions will be needed to measure the global impacts of the combined effects, if any, of introduced species on elimination of native species. The cumulative effects of these non-native species, along with the likely increased variability of climatically driven hydrologic drivers, will result in some major changes among insular stream ecosystems.

Because documentation of invasive species is increasing, as well as the frequency of introductions, there are emerging opportunities to study some general relationships of how natural dispersal and intentional introductions compare (Kot *et al.* 1996, Clark *et al.* 2003, Keith 2005). For example, the often encountered assumption that equilibrial assemblages are saturated with species on islands can be tested by current studies on invasive species as well as by other studies on natural communities that continue to increase in species richness (e.g. Maciolek 1984, Ricciardi and MacIsaac 2000, Ricciardi 2003, MacIsaac *et al.* 2004). Many questions remain, however, regarding our current understanding of these rates of change in insular ecosystems.

6. CONCLUSION

This review has examined the adaptations among many freshwater species that are widely distributed on isolated tropical islands and some similarly isolated habitats. The number of tropical stream studies is quite limited relative to similar studies on temperate-zone fresh waters. Many gaps in understanding remain to be explored. Nonetheless, some patterns are evident and can be related to habitat characteristics (e.g. Table 1) and evolutionary histories of the biota that dispersed to these locations independent of human activities. It is not yet clear if these patterns of dispersal will shed light on how isolated habitats at higher latitudes are colonized. Changes in biotic communities located in continental fresh waters are also influenced by various degrees of isolation and colonization from nearby locations. The importance of these broad-scale approaches to evaluating dispersal mechanisms and comparative studies of partially isolated ecosystems (spatially separated to various degrees) may provide new insights for analysis of invasive species. As species disperse widely and establish their dominance, their spread often results in short- or long-term reductions and sometimes in extinctions of otherwise well-adapted local native and endemic species. Some of these recently arrived, non-native species have filled important ecological roles that had been left vacant because of slow dispersal by other species. Currently, we lack sufficient data in most insular fresh waters to predict how each new species will change ecosystem processes and possibly lead to local or global extinctions of species that are essential providers of ecosystem services.

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