Are Modern Biological Invasions an Unprecedented Form of Global Change?

ANTHONY RICCIARDI

Redpath Museum and McGill School of Environment, McGill University, Montreal, Quebec H3A 2K6, Canada, email tony.ricciardi@mcgill.ca

Abstract: *The uniqueness of the current, global mass invasion by nonindigenous species has been challenged recently by researchers who argue that modern rates and consequences of nonindigenous species establishment are comparable to episodes in the geological past. Although there is a fossil record of species invasions occurring in waves after geographic barriers had been lifted, such episodic events differ markedly from human-assisted invasions in spatial and temporal scales and in the number and diversity of organisms involved in long-distance dispersal. Today, every region of the planet is simultaneously affected and modern rates of invasion are several orders of magnitude higher than prehistoric rates. In terms of its rate and geographical extent, its potential for synergistic disruption and the scope of its evolutionary consequences, the current mass invasion event is without precedent and should be regarded as a unique form of global change. Prehistoric examples of biotic interchanges are nonetheless instructive and can increase our understanding of species-area effects, evolutionary effects, biotic resistance to invasion, and the impacts of novel functional groups introduced to naïve biotas. Nevertheless, they provide only limited insight into the synergistic effects of invasions and other environmental stressors, the effect of frequent introductions of large numbers of propagules, and global homogenization, all of which characterize the current mass invasion event.*

Keywords: biotic interchange, dispersal, exotic species, global change, homogenization, nonindigenous

¿Las Invasiones Biológicas Modernas son una Forma de Cambio Global sin Precedente?

Resumen: *La unicidad de la actual invasión masiva global de especies no nativas ha sido cuestionada recientemente por investigadores que argumentan que las tasas y consecuencias modernas del establecimiento de especies no nativas son comparables con episodios del pasado geológico. Aunque existe un registro fósil de invasiones de especies que ocurrieron en oleadas después de la remoción de barreras geográficas, tales eventos episódicos difieren marcadamente de las invasiones asistidas por humanos en escalas temporales y espaciales y en el número y diversidad de organismos involucrados en la dispersión a larga distancia. Actualmente, cada región del planeta es afectada simultáneamente y las tasas de invasión modernas son varios órdenes de magnitud más altos que las tasas prehistóricas. En términos de su tasa y extensión geográfica, su potencial de disrupción sinérgica y el alcance de sus consecuencias evolutivas, el evento de invasión masiva actual no tiene precedente y debería ser considerado como una forma única de cambio global. No obstante, los ejemplos prehistóricos de intercambios bióticos son instructivos y pueden incrementar nuestro entendimiento de efectos especies-área y evolutivos, resistencia a la invasión y de los impactos de grupos funcionales nuevos introducidos en biotas nativas. Sin embargo, solo proporcionan una visión limitada de los efectos sinérgicos de las invasiones y otros factores ambientales estresantes, del efecto de introducciones frecuentes de grandes números de propágalos y de la homogenización global, que en conjunto caracterizan el actual evento de invasión masiva.*

Palabras Clave: cambio global, dispersión, especies exóticas, homogenización, intercambio biótico, no nativo

Introduction

Are modern biological invasions an unprecedented form of global change, or are they similar in frequency, magnitude, and impact to those that occurred in the distant past? This question is relevant for at least two reasons. First, if human-assisted invasions are comparable to prehistoric invasions, the latter can be used to make useful predictions about the current mass invasion event (Vermeij 2005). Second, it may indicate that invasions are a far more natural phenomenon than is presently believed. Indeed, species dispersal has pervaded the history of life, and it has been asserted that terms such as "non-native" or "invasive" are arbitrary because all species have spread into new territory at some point in their evolutionary history (Sax et al. 2005). Furthermore, it has been argued that the magnitude and impacts of recent invasions are similar to those in the fossil record; thus, the role of humans in the current mass invasion event and concern over its consequences have been overstated (Brown & Sax 2004, 2005; Vermeij 2005).

Natural invasions (i.e., those occurring without direct human influence) are rarely recorded, but are probably not uncommon. Documented examples involve animals undergoing active dispersal by flying (Long 1981) or swimming through connected waterways (McCulloch & Stewart 1998), and undergoing passive dispersal by rafting (Censky et al. 1998) or hitch-hiking on other biota (Green et al. 2005). Natural range expansions might be accelerating in response to global warming (Thomas & Lennon 1999; Perry et al. 2005), as they certainly have done in the past. The fossil record reveals episodes of virtually simultaneous mass dispersal of many species between two adjacent regions that have been isolated from each other for millions of years. Several of these biotic interchanges occurred during the last 25 million years and involved continental and benthic marine biotas (Vermeij 1991*a,* 1991*b*). Such events occurred in response to climate change and the removal of geographic barriers by geological forces (e.g., the formation of a land bridge or the opening of an ocean passage). The best studied of these is the Great American Interchange, in which the spread of species between North and South America was facilitated by the emergence of the Panama isthmus about 3 million years ago. This event had substantial consequences for the subsequent evolution of the respective mammalian assemblages on both continents: 10% of the North American mammalian genera and over 50% of the South American genera are derived from immigrants in the interchange (Webb 1991). It is also thought to have triggered the disappearance of several South American mammals (Webb 1991)— in contrast to most other biotic interchanges, which have left little evidence of extinctions in the fossil record and that appear to have enriched regional biotas (Vermeij 1991*b*).

In sum, prehistoric biotic interchanges occurred throughout the fossil record and their impacts on biodiversity may have been substantial in the short term but largely reversed in the long term. It has been asserted that they are fundamentally similar to human-assisted invasions observed today (Vermeij 2005). Here, I use examples of recent natural invasions and prehistoric biotic interchanges to examine whether the patterns, processes, and impacts of human-assisted invasions are unprecedented in Earth's history.

Differences in Magnitude, Spatial Scale, and Propagule Size

Human-assisted invasions may differ from natural or prehistoric invasions in several ways (Burney 1996; MacIsaac et al. 2001; Cassey et al. 2005; Vermeij 2005) (Table 1). First, it is likely that the geographic extent of modern invasion and the proportion of nonindigenous species in different biotas are unprecedented. Unlike prehistoric biotic interchanges, the current mass invasion is affecting all continents simultaneously. Not a single ocean or landmass is unaffected, including remote and inhospitable regions such as Antarctica, its surrounding islands, and the Southern Ocean (Clarke et al. 2005). Mack (1997) concludes that at least 3% of the planet's ice-free land surface area is dominated by nonindigenous plants—not including the immense area under agricultural cultivation. Primarily as a result of human-assisted introductions within the last 500 years, nonindigenous vascular plants comprise significant proportions of flora on continental regions (median = 10%) and islands (median = 24%). The same is true for nonindigenous fishes (median = 13% for continental regions, 76% for islands) and, to a lesser extent, birds (median = 3% for continental regions, 21% for islands) (Vitousek et al. 1997). Prehistoric biotic interchanges also resulted in increased homogenization of regional faunas, particularly marine faunas, in which the invaders often accounted for substantial proportions of molluscan lineages (Vermeij 1991*b*). But such events usually involved only a pair of neighboring regions and occurred over time intervals of hundreds of thousands to millions of years, which is in stark contrast to the rapid, global homogenization occurring today.

The composition of modern species assemblages strongly reflects idiosyncratic human influence; for example, tropical African grasses dominate large tracts of Central and South America as a result of deliberate introductions by Spanish and Portuguese settlers (Mack & Lonsdale 2001). Several European mammals and birds were introduced to Australia and New Zealand, mostly at the whim of private landowners and acclimatization societies (Long 1981, 2003; Low 2002). As a consequence

Table 1. Differences between prehistoric and human-assisted invasions.

Characteristic	Prehistoric invasions	Human-assisted invasions
Frequency of long-distance dispersal events	very low	very high
Number of species transported per event	low, except during biotic interchange events	high
Propagule load per event	small, except during biotic interchange events	potentially large
Effect of geographic barriers	strong	nearly insignificant
Variation in mechanisms and routes of dispersal	low	extremely large
Temporal and spatial scales of mass invasion events	episodic; limited to adjacent regions	continuous; affects all regions simultaneously
Homogenization effect	regional	global
Potential for synergistic interactions with other stressors	low	very high

of ballast-water discharge from transoceanic ships, the North American Great Lakes have been invaded recently by numerous species from the Black and Caspian seas (Ricciardi & MacIsaac 2000; Ricciardi 2006). Over 25% of the nonindigenous biota in the Baltic Sea is composed of species native to the Pacific and Indian Oceans, largely because of intentional stocking (Leppäkoski & Olenin 2000). It seems unlikely that such profoundly mixed assemblages drawn from remote regions of the planet could have been similarly produced by plate tectonics or any other natural process. Natural processes probably would not have allowed Pacific salmon to establish in the Baltic Sea and certainly would not have transported European mammals to Australia and New Zealand.

Modern invasions also entail an enormous frequency of long-distance migrants. Human vectors commonly involve saltatory transport of organisms between continents or across large water bodies, whereas natural and prehistoric invasions are more likely to involve short-distance dispersal. Natural long-distance dispersal events obviously were sufficient to populate oceanic islands in the past, but are likely orders of magnitude less frequent than human-assisted, long-distance dispersal events. Long-distance dispersal of seeds, spores, and invertebrates by wind and ocean currents (e.g., Scheltema & Williams 1983; Griffin et al. 2002; Munoz et al. 2004) is at the mercy of the vagaries of weather patterns and ocean circulation, but no such constraints apply to human vectors. Some plants produce fruit with seeds that survive passage through the digestive tract of mammals and birds, but the distance over which viable seeds are transported by migratory birds is unlikely to exceed a few hundred kilometers (Clausen et al. 2002). Similarly, certain invertebrates possess traits (e.g., resting eggs) that allow them to exploit bird-mediated transport, which appears to occur frequently over short distances (Figuerola & Green 2002; Green & Figuerola 2005) and may even affect the continental distributions of some invertebrate species (Reid & Reed 1994; Figuerola et al. 2005). However, most propagules would be discharged long before a long-distance flight is completed (Clausen et al. 2002).

An often-cited example of a natural long-distance invasion is the colonization of South America by the Cattle Egret (*Bubuculus ibis*) from Africa, but such colonization events are rare, even though natural dispersal across the Atlantic Ocean and other large water bodies by vagrant birds has been documented frequently. By contrast, hundreds of birds have been introduced successfully by humans into remote regions over the past two centuries (Long 1981). Within the last 150 years a dozen species of British passerine birds became established in New Zealand, well beyond their natural colonization abilities (Cassey et al. 2005). Similarly, during the past millennium numerous nonvolant terrestrial mammals have been introduced onto islands throughout the world that have not been colonized naturally by such species in tens of millions of years (Long 2003).

Native plant distributions in some parts of the globe might be partly explained by wind dispersal (Munoz et al. 2004). Few plant genera, however, are cosmopolitan, reflecting the insufficiency of natural agents to achieve global distributions (Mack & Lonsdale 2001). Furthermore, natural dispersal events typically involve very small numbers of propagules (Figuerola & Green 2002) and therefore should result in lower rates of establishment than human-assisted dispersal because small introduced populations are highly vulnerable to demographic stochasticity and density-dependent effects (Lockwood et al. 2005).

By contrast, human vectors such as transoceanic ships carry an enormous number of propagules (e.g., up to 10^8 invertebrates/ship entering the Great Lakes; Duggan et al. 2005) and are estimated to be transporting >7000 species around the planet on any given day (Carlton 1999). In addition, the movement of diverse communities of fouling organisms on ship hulls has led to the virtual global spread of dozens (potentially hundreds) of invertebrate species in only a few centuries. Most of the coastal species that have been moved on ship hulls have never been found on natural debris drifting on the high seas or associated with any other natural mechanism capable of global transport (Carlton 1999). Modern transoceanic shipping moves

several billion tons of ballast water per year (IMO 2004) and has the potential to transfer entire assemblages of aquatic organisms; it has no natural analogue. Unlike mechanisms of natural dispersal, human-assisted dispersal is far less dependent on time or distance; rather, it is determined almost entirely by the probability of propagule uptake and transport by human vectors. Thus, it permits a high probability of long-distance invasion events over short time intervals (MacIsaac et al. 2001).

So great is the influence of human vectors that it can obscure natural processes. Communities that can resist invasion by small numbers of naturally dispersing propagules are overwhelmed by the large propagule pressure (introduction effort) that typifies human vectors (Von Holle & Simberloff 2005). Whereas the asymmetry of biotic interchanges in prehistoric times is attributed to the diversity and competitiveness of the respective donor pools (Vermeij 1991*b*), modern biotic interchanges are governed primarily by economic activities and trade routes (Levine & D'Antonio 2003; Taylor & Irwin 2004). Processes of natural selection are altered or subsumed by the deliberate transplantations and cultivation of plants and animals (including transgenic organisms) for commercial and aesthetic purposes (Mack 2000; Mack & Lonsdale 2001; Naylor et al. 2001). Substantial proportions, and sometimes the majority, of nonindigenous plant invasions in various regions worldwide were the result of deliberate introductions (Mack 2000). Similarly, transplantations of oysters from the Pacific Ocean and salmonid fishes from North America and Europe have led to the worldwide occurrence of aquatic species (including the parasites and pathogens often associated with intensely cultured stocks) that would not have had the opportunity to achieve global distributions through natural processes alone (Naylor et al. 2001; Ruesink et al. 2005). Hence, the most important factor limiting the large-scale distribution of a plant or animal is whether it possesses a trait deemed valuable by humans for domestication (Mack & Lonsdale 2001; Reichard & White 2001; Ruesink et al. 2005) or, for a species that is not introduced deliberately, whether its traits allow it to be transported by human vectors operating on a global scale (Carlton 1999; Suarez et al. 2001; Ricciardi 2006).

Modern versus Prehistoric Rates of Invasion

One can consider two kinds of invasion rates: the spreading rate of an organism after it has become established in a region and the rate of invasion of a given region. There exist little taxon-specific data on the post-establishment spread of prehistoric invaders. The pollen record from the late Pleistocene suggests that plants spread several hundreds of meters per year in response to climate change (Roy & Kauffman 2001). These rates are inferior to those of modern terrestrial plant invaders, which are on the order of kilometers per year (Mack & Lonsdale 2001; Williamson et al. 2005); however, because the pollen data may reflect a slow advance in response to climate change, it might be inappropriate to compare them with invasions by modern plants moving between climatically favorable regions (D. F. Sax, personal communication). Indeed, it has been asserted (Brown & Sax 2005; Vermeij 2005) that there is no theoretical reason why a species introduced to a region prehistorically should spread across that region at a different rate than do modern invaders. But this assertion too easily dismisses the potential role of humans in facilitating the spread of introduced organisms through disturbance and landscape alteration (Byers 2002; Marvier et al. 2004; Havel et al. 2005) and in supplementing invading populations with additional genotypes through multiple introductions (e.g., Durka et al. 2005).

Nevertheless, a comparison of post-establishment rates of spread ignores differences in the frequency of dispersal events that introduce species to new geographic regions in the first place. A comparison of modern and prehistoric rates of invasion for different geographic regions indicates that modern rates are unprecedented (Table 2). Modern rates are several orders of magnitude higher than prehistoric rates derived from the fossil record. For example, over the past 2 million years, 11 marine gastropod species from the Line Islands in the Central Pacific invaded the Pacific coast of North America and a similar number of coral species from the same region invaded the Neotropical region—both events occurring at the rate of 0.000006 established species per year, or 6 species/million years (Vermeij 1991*b*). The trans-Arctic exchange of marine molluscs following the opening of the Bering Strait 3.5 million years ago occurred at the rate of 50 species per million years (Vermeij 1991*a*). Similarly, the invasion rate for Hawaiian Islands was 30 species/million years (0.00003/year) prior to human settlement. Yet, this rate increased to 20,000 species per million years (0.02/year) after the arrival of the Polynesians and continued to rise during the past two centuries to approximately 20/year, which is nearly one million times higher than the prehistoric rate for Hawaii before human influence (Loope et al. 1988). During the Great American Interchange, 37 genera of mammals dispersed overland between North and South America and became established outside their native range during a period of 1.25 million years (Webb 1991). At least three genera have been exchanged between both continents within the past century (Long 2003), a rate 10,000 times faster than occurred during the prehistoric exchange. An even greater contrast is provided by the history of mammalian introductions to New Zealand: 11 species colonized the islands during the Cenozoic Era (probably starting in the Oligocene period), whereas 35 introduced species became established within the last 1000 years (King 1990). Thus, the natural rate of invasion is 0.33

Table 2. Rates of species invasion (numbers of established species per year) for various regions.[a]

		Modern rates		
Region	*Prehistoric rate*	*long term*	*recent*	*Reference[b]*
Terrestrial regions				
Galapagos Islands	0.0001	1	10	1, 2
Gough Island	0.00001	0.22	–	3
Hawaiian Islands	0.00003	20	–	4
Australia	0.002	13	–	5
Freshwater & marine regions				
Laurentian Great Lakes				
fishes	0.017	0.3	0.2	6
molluscs	0.011	0.09	0.17	7, 8
all biota	–	1.1	1.8	7
Caspian Sea				
invertebrates	0.0002	0.36	0.33	10
Black Sea				
invertebrates	0.0002	0.3	0.4	11
San Francisco Bay	0.05	1.7	3.7	12
Port Phillip Bay	0.08	1.25	2.6	13
Baltic Sea	0.09	0.3	0.7	14
Mediterranean Sea				
flora	–	0.18	1.28	15
Northeastern Atlantic				
flora	–	0.19	0.44	15

[a]*Prehistoric rates are before human settlement and were estimated from the fossil record or by calculating numbers of native species (excluding endemics) that have become established in the region over time. Long-term modern rates are averaged over the past 150–300 years, and recent modern rates are averaged over the past 30–40 years.*

[b]*References: 1, Mauchamp 1997; 2, Porter 1983; 3, Gaston et al. 2003; 4, Loope et al. 1988; 5, Low 2002; 6, Mandrak 1989; 7, Ricciardi 2006; 8, Clarke 1981; 9, Vermeij 1991b; 10, Grigorovich et al. 2003; 11, Grigorovich et al. 2002; 12, Cohen & Carlton 1998; 13, Hewitt et al. 1999; 14, Leppäkoski et al. 2002; 15, Ribera & Boudouresque 1995.*

species/million years, whereas the human-assisted rate is 35,000 species/million years.

A quantitative comparison of modern and prehistoric invasion rates is not without caveats (Roy & Kauffman 2001). Vermeij (2005) argues that calculations of long-term invasion rates based on numbers of species recorded over a given time interval are misleading because opportunities vary with changes in geographic barriers and because such estimates are sensitive to the interval chosen. Prehistoric rates averaged over lengthy time periods may underestimate peak rates of establishment because the removal of a geographic barrier, the formation of a water body, or the creation of a landmass might be followed by a pulse of invasions, the rate of which eventually diminishes due to a limited pool of potential colonists. By contrast, geographic barriers are virtually nonexistent to human vectors, and modern rates are sustained by human activities that have created myriad vectors operating simultaneously to access a virtually infinite donor pool.

Genetic divergence may also be used to estimate the natural incidence of biotic interchange, and such estimates are consistent with those derived exclusively from measured time intervals. The prehistoric invasion rate for invertebrates and fishes dispersing from the Western to the Eastern Pacific coastal regions is estimated to be 50 species/million years (0.00005/year), based on the num-

ber of species occurring on both coasts and the length of time for species to evolve into morphologically distinct forms (A.N. Cohen, memo to California Advisory panel on Ballast Water Performance Standards, 7 August 2005). This estimate is quite similar to that recorded for Hawaii prior to human settlement (Table 2). Sequence divergence of mitochondrial DNA reveals that the modern rate of invasion by European freshwater cladoceran crustaceans in North America is 50,000 times higher than the prehistoric rate (Hebert & Cristescu 2002). And a study combining molecular and paleontological data found that the modern rate of invasion by invertebrates in the Caspian Sea is three orders of magnitude higher than the natural rate occurring over the preceding 2 million years (Grigorovich et al. 2003). Thus, several lines of evidence suggest that modern rates of invasion are enormous compared with prehistoric rates, including rates of biotic interchange.

Impacts of Modern versus Prehistoric Invasions

The magnitude and breadth of impacts of modern invasions might also be greater than in prehistoric times. One major difference is that modern invasions have

opportunities for synergistic interactions with diverse environmental stressors. Synergies with climate change must have occurred in the past, but those that involve interactions with nitrogen pollution and landscape alteration, among a host of other large-scale anthropogenic disturbances, are certainly without precedent. Nitrogen fertilization has increased the invasibility of some terrestrial systems (Dukes & Mooney 1999). Human alteration of disturbance regimes through land clearing has initiated a grass-fire feedback system that prevents forest regeneration and promotes the dominance of exotic grasses over continental areas (Vitousek et al. 1997). River impoundment and fragmentation suppress natural flood disturbance regimes and thereby facilitate invasions of watersheds by nonindigenous fishes, invertebrates, and vegetation (Havel et al. 2005). Habitat fragmentation, with its concomitant loss of refugia, has also rendered native faunas more vulnerable to extinction through antagonistic interactions with invaders (Suarez et al. 1998). Eutrophication and the selective removal of top predators are additional examples of the rapid alteration of selection regimes that place native species at a disadvantage in competitive interactions with nonindigenous species (Byers 2002).

Furthermore, invasions operating over larger spatial scales are more likely to bring introduced species into contact with communities containing no analogous organisms, where they may cause precipitous declines in native species populations (Short et al. 2002; Blackburn et al. 2004; Ricciardi & Atkinson 2004). Novel life forms were encountered by ecologically naïve biotas during prehistoric biotic interchanges, and those encounters have, at times, provoked species loss (Vermeij 1991*b*). But such events are far more frequent in modern times, particularly on islands. Some recent examples involve the brown tree snake (*Boiga irregularis*) introduced to Guam, the rosy wolf snail (*Euglandina rosea*) in the south Pacific, chestnut blight fungus (*Cryphonectria parasitica*) in North America, and the fungus (*Aphanomyces astaci*) that causes crayfish plague in Europe (Vitousek et al. 1997; Mack et al. 2000). Human-assisted introductions of mammalian predators to oceanic islands have caused numerous extinctions of endemic birds around the world (Long 2003; Blackburn et al. 2004).

The global scale of activities of human vectors has also promoted the rapid evolution and spread of new pathogens through hybridization and the recombination of introduced protists and fungi with related resident organisms (Brasier 2001; Slippers et al. 2005). Consequently, human-assisted invasions are a leading driver of modern extinctions and biotic homogenization (Olden et al. 2004; Clavero & Garcia-Berthou 2005). By contrast, invasion-related extinctions have rarely been documented for prehistoric biotic interchange, apart from the Great American Interchange (Vermeij 1991*b*). Homogenization following these episodes added to an overall ge-

ographic pattern of decreasing similarity between biotas with increasing distance, whereas modern invasions tend to homogenize biotas that occur in similar abiotic environments remotely distributed across the world (Burney 1996; Olden et al. 2004).

Given the disproportionate number of species that are carried long distances by human vectors versus those that are carried by wind and water currents, biota transported by human vectors might be more likely than naturally transported biota to include species that can cause strong ecological impacts. For example, none of the plant species that spread commonly by natural long-distance dispersal are considered weedy or detrimental to their new environments (Mack & Lonsdale 2001). Human vectors have also created unprecedented opportunities for synergistic interactions among introduced species. An introduced species can promote the establishment, population growth, and impact of other invaders through mutualistic and commensalistic interactions, with cascading repercussions to the food web (Simberloff & Von Holle 1999; Richardson et al. 2000; Ricciardi 2001). Thus, it is hypothesized that increasing numbers of introduced species can create positive feedback cycles that cause invaders and their effects to rapidly accumulate over time—a phenomenon termed *invasional meltdown* (Simberloff & Von Holle 1999). Nonlinear accumulations of invaders that have been recorded in most systems for which long-term data are available (Ricciardi 2001, 2006) are consistent with the hypothesis, although not conclusive, owing to potential statistical biases (Costello & Solow 2003). If invasional meltdown is a threshold effect of propagule pressure, then one would expect this phenomenon to occur more frequently in a world dominated by human vectors.

Conclusions

Although species invasions have pervaded the history of life and have periodically occurred in waves after geographic barriers have been lifted, such events differ markedly from human-assisted invasions in spatial and temporal scales and in the diversity of organisms involved in long-distance dispersal. These were episodic phenomena involving only neighboring regions and small fractions of the species in either donor pool. By contrast, the current human-driven mass invasion event is global in scale and likely to be continuous through the remainder of human history. Arguably, the role of humans as both dispersers and cultivators of nonindigenous species has been profound enough to surpass natural forces of selection and dispersal. Human interventions, both deliberate and unintentional, often overcome the natural stochastic forces and biotic resistance of recipient biotas that would otherwise repel or remove introduced propagules. Human vectors also create species combinations that would

never have arisen through natural processes and that expose biotas to novel evolutionary pressures (Strauss et al. 2006). In terms of its rate and geographical extent, its potential for synergistic disruption and the scope of its evolutionary consequences, the current mass invasion event is without precedent and should be regarded as a unique form of global change. Prehistoric examples of biotic interchanges are instructive and can increase our understanding of species-area effects, evolutionary effects, community characteristics conferring resistance to invasion, and the impacts of novel functional groups introduced to naïve biotas (Vermeij 1991*b*; Roy & Kauffman 2001). Nevertheless, they provide only limited insight into the synergistic effects of invasions and other environmental stressors, the effect of frequent introductions of large numbers of propagules, and the effect of global homogenization, all of which characterize the current mass invasion event.

Acknowledgments

Literature Cited

Blackburn, T. M., P. Cassey, R. P. Duncan, K. L. Evans, and K. J. Gaston. 2004. Avian extinction and mammalian introductions on oceanic islands. Science **305:**1955–1958.

Brasier, C. M. 2001. Rapid evolution of introduced plant pathogens via interspecific hybridization. BioScience **51:**123–133.

Brown, J. H., and D. F. Sax. 2004. An essay on some topics concerning invasive species. Austral Ecology **29:**530–536.

Brown, J. H., and D. F. Sax. 2005. Biological invasions and scientific objectivity: reply to Cassey et al. (2005). Austral Ecology **30:**481–483.

Burney, D. A. 1996. Historical perspectives on human-assisted biological invasions. Evolutionary Anthropology **4:**216–221.

Byers, J. E. 2002. Impact of nonindigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos **97:**449–458.

Carlton, J. T. 1999. The scale and ecological consequences of biological invasion in the World's oceans. Pages 195–212 in O. T. Sandlund, P. J. Schei, and Å. Viken, editors. Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Cassey, P., T. M. Blackburn, R. P. Duncan, and S. L. Chown. 2005. Concerning invasive species: reply to Brown and Sax. Austral Ecology **30:**475–480.

Clarke, A. H. 1981. The freshwater mollusks of Canada. National Museum of Natural Sciences, Ottawa.

Clarke, A., D. K. A. Barnes, and D. A. Hodgson. 2005. How isolated is Antarctica? Trends in Ecology & Evolution **20:**1–3.

Clausen, P., B. A. Nolet, A. D. Fox, and M. Klaassen. 2002. Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe—a critical review of possibilities and limitations. Acta Oecologia **23:**191–203.

Clavero, M., and E. García-Berthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution **20:**110.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science **279:**555–558.

Costello, C. J., and A. R. Solow. 2003. On the pattern of discovery of introduced species. Proceedings of National Academy of Sciences, U.S.A. **100:**3321–3323.

Censky, E. J., K. Hodge, and J. Dudley. 1998. Over-water dispersal of lizards due to hurricanes. Nature **395:**556.

Duggan, I. C., C. D. A. van Overdijk, S. A. Bailey, P. T. Jenkins, H. Limén, and H. J. MacIsaac. 2005. Invertebrates associated with residual ballast water and sediments of cargo-carrying ships entering the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences **62:**2463–2474.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology & Evolution **14:**135–139.

Durka, W., O. Bossdorf, D. Prati, and H. Auge. 2005. Molecular evidence for multiple introductions of garlic mustard (*Alliaria petiolata*, Brassicaceae) to North America. Molecular Ecology **14:**1697–1706.

Figuerola, J., and A. J. Green. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater Biology **47:**483–494.

Figuerola, J., A. J. Green, and T. C. Michot. 2005. Invertebrate eggs can fly: evidence of waterfowl-mediated gene flow in aquatic invertebrates. The American Naturalist **165:**274–280.

Gaston, K. J., A. G. Jones, C. Hänel, and S. L. Chown. 2003. Rates of species introduction to a remote oceanic island. Proceedings of the Royal Society of London B **270:**1091–1098.

Green, A. J., and J. Figuerola. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. Diversity and Distributions **11:**149–156.

Green, A. J., M. I. Sánchez, F. Amat, J. Figuerola, F. Hontoria, O. Ruiz, and F. Hortas. 2005. Dispersal of invasive and native brine shrimps *Artemia* (Anostraca) via waterbirds. Limnololgy and Oceanography **50:**737–742.

Griffin, D. W., C. A. Kellogg, V. H. Garrison, and E. A. Shinn. 2002. The global transport of dust. American Scientist **90:**226–235.

Grigorovich, I. A., H. J. MacIsaac, N. V. Shadrin, and E. L. Mills. 2002. Patterns and mechanisms of aquatic invertebrate introductions in the Ponto-Caspian region. Canadian Journal of Fisheries and Aquatic Sciences **59:**1189–1208.

Grigorovich, I. A., T. W. Therriault, and H. J. MacIsaac. 2003. History of aquatic invertebrate invasions in the Caspian Sea. Biological Invasions **5:**103–115.

Havel, J. E., C. E. Lee, and M. J. Vander Zanden. 2005. Do reservoirs facilitate invasions into landscapes? BioScience **55:**515–525.

Hebert, P. D. N., and M. E. A. Cristescu. 2002. Genetic perspectives on invasions: the case of the Cladocera. Canadian Journal of Fisheries and Aquatic Sciences **59:**1229–1234.

Hewitt, C. L., M. L. Campbell, R. E. Thresher, and R. B. Martin. 1999. Marine biological invasions of Port Phillip Bay, Victoria. Centre for Research on Introduced Marine Pests Technical report 20. CSIRO Marine Research, Hobart, Australia.

IMO (International Maritime Organization). 2004. International convention for the control and management of ships' ballast water and sediments. Document BWM/CONF/36, 16 February 2004. IMO, London.

King, C. M. 1990. The handbook of New Zealand mammals. Oxford University Press, Melbourne.

Leppäkoski, E., S. Gollasch, P. Gruszka, H. Ojaveer, S. Olenin, and V. Panov. 2002. The Baltic—a sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences **59:**1175–1188.

Leppäkoski, E., and S. Olenin. 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biological Invasions **2:**151–163.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. Conservation Biology **17:**322–326.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution **20:**223–228.

Long, J. L. 1981. Introduced birds of the world. Universe Books, New York.

Long, J. L. 2003. Introduced mammals of the world. CSIRO Publishers, Collingwood, Australia.

Loope, L. L., O. H. Hamann, and C. P. Stone. 1988. Comparative conservation biology of oceanic archipelagoes: Hawaii and the Galapagos. BioScience **34:**272–282.

Low, T. 2002. Feral future. University of Chicago Press, Chicago.

MacIsaac, H. J., I. A. Grigorovich, and A. Ricciardi. 2001. Reassessment of species invasions concepts: the Great Lakes basin as a model. Biological Invasions **3:**405–416.

Mack, R. N. 1997. Plant invasions: early and continuing expressions of global change. Pages 205–216 in B. Huntley, W. Cramer, A. V. Morgan, H. C. Prentice, and J. R. M. Allen, editors. Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota. North Atlantic Treaty Organization ASI series. Springer-Verlag, Berlin.

Mack, R. N. 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. Biological Invasions **2:**111–122.

Mack, R. N., and W. M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. BioScience **51:**95–102.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz, 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10:**689–710.

Mandrak, N. E. 1989. Potential invasion of the Great Lakes by fish species associated with climatic warming. Journal of Great Lakes Research **15:**306–316.

Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat destruction, fragmentation and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis **24:**869–878.

Mauchamp, A. 1997. Threats from alien plant species in the Galapagos Islands. Conservation Biology **11:**260–263.

McCulloch, B. R., and K. W. Stewart. 1998. Range extension and new locality records for the stonecat, *Noturus flavus*, in Manitoba: evidence for a recent natural invasion. Canadian Field-Naturalist **112:**217–224.

Munoz, J., A. M. Felicisimo, F. Cabezas, A. R. Burgaz, and I. Martinez. 2004. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science **304:**1144–1147.

Naylor, R. L., S. L. Williams, and D. R. Strong. 2001. Aquaculture—a gateway for exotic species. Science **294:**1655–1656.

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution **19:**18–24.

Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science **380:**1912–1915.

Porter, D. M. 1983. Vascular plants of the Galapagos: origins and dispersal. Pages 33–96 in R. I. Bowman, M. Berson, and A. E. Leviton, editors. Patterns of evolution in Galapagos organisms. American Association for the Advancement of Science, San Francisco, California.

Reichard, S. H., and P. White. 2001. Horticulture as a pathway of invasive plant introductions in the United States. BioScience **51:**103–113.

Reid, J. W., and E. B. Reed. 1994. First record of two Neotropical species of *Mesocyclops* (Copepoda) from Yukon territory: cases of passive dispersal? Arctic **47:**80–87.

Ribera, M. A., and C. F. Boudouresque. 1995. Introduced marine plants, with special reference to macroalgae: mechanisms and impact. Progress in Phycological Research **11:**187–268.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences **58:**2513–2525.

Ricciardi, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions **12:**425–433.

Ricciardi, A., and S. K. Atkinson. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters **7:**781–784.

Ricciardi, A., and H. J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends in Ecology & Evolution **15:**62–65.

Richardson, D. M., N. Allsopp, C. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions—the role of mutualisms. Biological Reviews **75:**65–93.

Roy, K., and J. S. Kauffman. 2001. Biotic homogenization: lessons from the past. Pages 19–32 in J. L. Lockwood and M. L. McKinney, editors. Biotic homogenization. Kluwer Academic, New York.

Ruesink, J. L., H. S. Lenihan, A. S. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. Annual Reviews of Ecology, Evolution and Systematics **36:**643–689.

Sax, D. F., S. D. Gaines, and J. J. Stachowicz. 2005. Introduction. Pages 1–7 in D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species invasions: insights into ecology, evolution, and biogeography. Sinauer Associates, Sunderland, Massachusetts.

Scheltema, R. S., and I. P. Williams. 1983. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and western Pacific mollusks. Bulletin of Marine Science **33:**545–565.

Short, J., J. E. Kinnear, and A. Robley. 2002. Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in native prey species? Biological Conservation **103:**283–301.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of non-indigenous species: invasional meltdown? Biological Invasions **1:**21–32.

Slippers, B., J. Stenlid, and M. J. Wingfield. 2005. Emerging pathogens: fungal host jumps following anthropogenic introduction. Trends in Ecology & Evolution **20:**420–421.

Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecology Letters **9:**357–374.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology **79:**2041–2056.

Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proceedings of the National Academy of Sciences **98:**1095–1100.

Taylor, B. W., and R. E. Irwin. 2004. Linking economic activities to the distribution of exotic plants. Proceedings of the National Academy of Sciences USA **101:**17725–17730.

Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. Nature **399:**213.

Vermeij, G. J. 1991a. Anatomy of an invasion: the trans-Arctic interchange. Paleobiology **17:**281–307.

Vermeij, G. J. 1991b. When biotas meet: understanding biotic interchange. Science **253:**1099–1104.

Vermeij, G. J. 2005. Invasion as expectation. Pages 315–339 in D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species invasions: insights into ecology, evolution, and biogeography. Sinauer Associates, Sunderland, Massachusetts.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology **21:**1–16.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology **86:**3212–3218.

Webb, S. D. 1991. Ecogeography and the Great American Interchange. Paleobiology **17:**266–280.

Williamson, M., P. Pyšek, V. Jarošík, and K. Prach. 2005. On the rates and patterns of spread of alien plants in the Czech Republic, Britain, and Ireland. Ecoscience **12:**424–433.