

Biological invasions and natural colonisations: are they that different?

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Abstract

We argue that human-mediated invasions are part of the spectrum of species movements, not a unique phenomenon, because species self-dispersing into novel environments are subject to the same barriers of survival, reproduction, dispersal and further range expansion as those assisted by people. Species changing their distributions by human-mediated and non-human mediated modes should be of identical scientific interest to invasion ecology and ecology. Distinctions between human-mediated invasions and natural colonisations are very valid for management and policy, but we argue that these are value-laden distinctions and not necessarily an appropriate division for science, which instead should focus on distinctions based on processes and mechanisms. We propose an all-encompassing framework of species range expansion. This does not detract from the importance of invasion biology as a discipline, but instead will help bring together research being conducted on multiple taxa, and by multiple disciplines, including epidemiology, that are often focused on an identical phenomenon: colonisation.

Keywords

Alien, biological invasion, colonisation, dispersal, exotic, invasion, introduction

Artificial distinctions don't aid science

Ecologists studying human-mediated biological invasions and those studying natural colonisations are essentially working on the same phenomenon (Johnstone 1986; Thompson et al. 1995). Yet, historically, ecological studies on biological invasions and on colonisations have been treated as distinct fields, with too few connections (Davis et al. 2001). Although we agree that the distinction between human-mediated invasions and natural colonisations is very valid for management and policy making, especially for species that have large ecological effects, we argue that this is a value-laden distinction and not necessarily an appropriate division for science, which instead should focus on distinctions based on processes and mechanisms. Current scientific divisions between invasion ecology and ecology is resulting in scientific synergies being inadvertently lost. Species naturally colonising novel environments necessarily go through the same stages of introduction, establishment and spread as species introduced by humans, because they are subject to the same barriers of survival, reproduction, dispersal and further range expansion, and therefore are identical from a scientific perspective (Ricklefs 2005; Jeschke et al. 2013; Rius and Darling 2014; Yek and Slippers 2014). In terms of understanding the processes, mechanisms, and consequences of colonisation, the means of access to new areas is inconsequential. Human-mediated transport merely allows more individuals and more species to arrive in new locations more often and more quickly, ultimately resulting in rates of colonisation being greater than what it is for natural colonisation. Instead what counts are the ecological constraints, the dynamics of species with no common, or a fragmented, evolutionary history, and the intrinsic suitability of the propagule to disperse to and survive in a novel environment. The current artificial polarisation of the respective sciences based on human mediation versus natural colonisation is hindering the progression of our understanding of the underlying mechanisms and processes of range expansions (Davis et al. 2001; Catford et al. 2009; Jeschke et al. 2013; Yek and Slippers 2014).

Following are four examples of the irrelevance of dispersal mode for the science of colonisation. The first is the Lessepsian migration: the dispersal of at least three hundred species from the Red Sea into the Mediterranean Sea following the opening of the Suez Canal. Most species have increased their distributions naturally, as the dominant currents and winds have dispersed their propagules northward (Mavruk and Avsar 2007), but some have also moved through shipping (Galil 2000). Although the ability for species to disperse and colonise was triggered by the removal of a geographical barrier through a human intervention, the act of dispersal has occurred both naturally and with further human assistance. Regardless of opinions about whether these are human-mediated range expansions or not, the science underpinning an understanding of the colonisations, and their ecological as well as evolutionary consequences, is identical.

The second example is the 2011 Tohoku tsunami, which carried about 1.5 million tonnes of debris, vegetation and fauna out to sea. The flotsam was carried across the Pacific where it was also colonised by other marine flora and fauna, and some reached North American coastlines nearly 8,000 kilometres away (Gewin 2013). On the larg-

est bits of flotsam, scientists have identified many Japanese species able to colonise the new continent, some of which may have negative environmental and economic consequences (Gewin 2013). Again, irrespective of opinions of whether these dispersals should be considered natural events to be accepted, or biological invasions to be managed, the science underpinning the understanding of their colonisation and potential effects is identical. Moreover, having two sets of scientific fields and experts to distinctively study colonisers and invaders in this scenario would make no more sense than in the previous example.

A more tangential and arguably extreme example would be the greatest colonisation in global history: humans. Ecologists now accept that people are not disconnected from the environment, and thus scientific understanding of our own spread across the globe cannot be isolated from that of all other species. However, it can certainly be argued that our own dispersal was human mediated, and caused great impact in new ecosystems, which would qualify as an invasion. Yet, certainly in pre-historic times our survival and further spread was fully compliant with, and restricted to, the rules of nature, which would qualify as a colonisation. So did humans naturally colonise the globe, or were we a biological invasion? We argue that the distinction is extraneous semantics: we were both, because both terms describe the same phenomenon.

The last example is the myriad of species undergoing range-shifts due to climate change, which is an issue that is set to result in even less clarity of what is an “exotic” species (Webber and Scott 2012) and what should be managed. One such species is the pine processionary moth, *Thaumetopoea pityocampa*, a major forest pest native to the Mediterranean Basin and now rapidly expanding its range towards higher latitudes and altitudes in response to climate change (Battisti et al. 2005, 2006). Where it becomes newly established should it be seen as an invasive pest or a problematic native species that has naturally and predictably shifted its range? Changes in species distributions are predicted to increase with time as climate change progresses (Thomas 2010), and this mass movement of biota will result in many novel combinations of species. These species will all interact based on the same mechanisms and restraints affecting anthropogenically-dispersed species, some with negative ecological impacts, and others without. Regardless of personal opinions of whether these are “invasions” or not, the science of the range changes is identical.

Arguments separating natural colonisations from human-mediated invasions

Despite several papers over multiple decades highlighting the lack of distinction between “invasions” and colonisations from an ecological perspective (Johnstone 1986; Thompson et al. 1995; Ricklefs 2005), there appears to be great resistance among invasion biologists to acknowledge this artificial separation (Davis et al. 2001). Here we focus on four main arguments that are often presented to argue why “invasions” are different, and we explain why we believe that these arguments are incorrect.

The first argument against ending the artificial separation between colonisation and invasion is that propagule pressure is greater for species dispersed by human mediation, and therefore this represents a difference in process. Propagule pressure consists of the number of individuals arriving in a new location at one time and the number of arrival times. Although we now have good data of accidental human-mediated propagule pressure from the likes of shipping ballast, and cargo freight, the same cannot be said for natural colonisation. As far as we are aware, no attempt has ever been made to compare propagule pressure in any location between natural dispersal events and human-mediated dispersal. But if such a comparison was made, we suspect that on a global-scale, propagule pressure would often be comparable for species dispersing naturally. For example, it has been estimated that 4.5 billion insects were dispersed over the North Sea each summer day from a 30 km coastal strip alone (Edwards 1986b; Heydemann 2008). Elsewhere, quantification of insects aerially deposited on snowfields on 2500 m summit slopes found 24 insects per square metre annually (Edwards 1986a). Indeed, the prevalence of the arthropod fallout globally is so great that many animal communities are dependent upon it for survival, including on high mountains within alpine zones (Swan 1963), oligotrophic lakes, deserts, and deep oceans. Regardless, any difference between the two transport modes merely represents a change of rate, not a change of process.

The second argument is that colonisation pressure (the number of species introduced per colonisation event) is greater for species spread by human mediation, and therefore this is a difference in process. While we agree that such a discrepancy is likely for fauna that clearly cannot easily disperse biogeographically (e.g., lizards, land snails, frogs), the same may not necessarily be so for the bulk of species, the invertebrates, as detailed above. However, such a comparison may not necessarily be meaningful, because natural colonisations appear to occur over continuous periods, not necessarily just individual events (e.g., a cyclone). Just as for propagule pressure, as far as we are aware, there has never been an attempt to compare colonisation pressure in any one location from human-mediated dispersal versus natural dispersal, but disjunct data do exist for comparison. For example, for natural colonisations, within the first two years of the eruption of Mt. St. Helens, USA, in 1980, 43 spider species had ballooned in, including three European species (Edwards 1986b). Similarly, a decade of sampling of arthropod fallout on Mount Rainier, USA, found > 200 species from 17 orders and 140 families (Edwards 1986b; Edwards and Sugg 1993). Within three years of the formation of volcanic Long Island, Papua New Guinea, 20 invertebrate species were found (Thornton 2001). In comparison, meiobenthic assemblages found within residual sediment and ballast water of ships range from an unknown number of species from 6 Classes, including 12 nematode genera (Radziejewska et al. 2006), to 33 taxa from six ships (Gray et al. 2007) and 147 taxa from 32 ships (Duggan et al. 2005). The point we make is that there are no hard data to demonstrate that the number of species being dispersed by people is greater than that of species dispersing naturally, and such data would be highly beneficial. What may be clouding perspectives on this point is that in modern times there has no doubt been a dramatic increase in the rate of species

being moved by human mediation. But, just as for propagule pressure, any potential difference only represents a change of rate, not a change of process.

A third argument is that natural and human-mediated dispersal result in differences in genetic diversity that affect colonisation success, largely being that greater propagule pressure from human-mediated dispersal can result in greater genetic diversity. But there are many documented instances where invasions arose from a very small propagule. For example, the thousands of feral cats that now invade the Kerguelen Islands come from only 2 to 4 cats (Pascal 1980). In addition, although we agree that higher propagule pressure can give rise to greater genetic diversity which can result in a reduced chance of founder effects, species undergoing both natural and human-mediated transport can be successful with highly restricted or highly diverse genetics (Roman and Darling 2007). For both transport modes, where a single propagule (e.g., a queen ant or a seed) is either accidentally transported across a biogeographic barrier by human mediation, or naturally, the genetic restriction, and the Allee effects (Courchamp et al. 2008) potentially affecting colonisation are identical. Likewise, intentional introductions of multiple individuals to increase genetic diversity of the incipient population and natural colonisations that involve the dispersal of many individuals (e.g., a flock of birds in a pulse event or seasonal or continuous fallout of airborne arthropods) both potentially involve equivalent genetic variation that may or may not result in successful colonisation.

We agree that higher propagule pressure increases the likelihood of colonisation success (Blackburn et al. 2013) and also that more important than genetic diversity is the presence of genes suitable for movement to novel locations (Lee 2002; Winkler et al. 2008) and in some instances, genetic admixture (Rius and Darling 2014). Indeed, for species dispersed by either natural or human-mediated transport, and regardless of whether the dispersal is within a region or across a geographic barrier, often only a subset of a species' genetic pool can colonise new locations. This selectivity is a fundamental tenant of the taxon cycle which rightfully makes no distinction between species dispersed by human mediation or not (Ricklefs 2005). Interestingly it appears likely that humans have accidentally, as well as intentionally, acted as a selective filter on genetic-based traits that are suited to colonisation (Hufbauer et al. 2012). But again, such human influence is comparable to the natural selection of species with inherent capabilities for long-distance natural dispersal. Overall, irrespective of the dispersal mode, the distance of dispersal, and the mode by which genetic filtering or admixing occurs, the role of the numerous genetic characteristics to colonisation (Lee 2002) is identical for both dispersal modes.

Importantly for these three arguments, and possibly others, comparisons between species movement by human mediation and natural dispersal must be equivalent comparisons whereby only a single factor varies, but this is often not the case. For example, it is not valid to argue that there are genetic differences when comparing the deliberate introduction of a grass, whereby thousands of seeds with great genetic diversity are brought to an area, with the natural dispersal of a single seed because in this instance genetics is confounded with different levels of propagule pressure.

The fourth argument is that invasions, unlike colonisations, are drivers of mass-extinction. We have four issues with this argument. First, implicit in this argument is that natural colonisations don't have negative impacts, and they are not responsible for localised extinctions. We are unaware of a naturally dispersed species being reported as causing an extinction, but perhaps this is due to the difficulty of demonstrating that a species has indeed self-dispersed and not been spread by human means and then caused an extinction of a native species. Logically, however, throughout evolutionary time, as species have arisen and dispersed, and as species distributions have changed following climates and tectonic movements, they have outcompeted and replaced other biota. For example, placental mammals outcompeted marsupials throughout most of the world. This is particularly well studied in the multiple waves of migrations of mammals between North and South America as the Isthmus of Panama rose c. 3–10 Mio. years ago that resulted in the replacement of most of South America's mammals (Great American Interchange) (Leigh et al. 2014). Moreover, these extinctions would have occurred many more times than modern extinctions from human-mediated colonisations, albeit because of the greater timeframe. Second, although extinction is, arguably, the greatest impact a species can have on co-occurring biota, it remains that impact is a value-laden term that is controversial as a defining term for invasion biology (Blackburn et al. 2011; Jeschke et al. 2014), nor is it an underlying mechanism or processes of range expansion, and frequently species undergoing range expansion are passengers rather than drivers of change (Didham et al. 2005). Third, while it is clear that many species that disperse outside of their native range have significant negative impacts (Mack et al. 2000), with the (dramatic) exception of a few mammals, ants and pathogens, there is little evidence that exotic species induce species extinctions (Gurevitch and Padilla 2004), thus extinction is a relatively rare outcome. Better data are needed to make a conclusive comparison between extinction events resulting from human-mediated vs natural dispersal. Ultimately, this is a management and policy issue that should not make an artificial distinction between colonisation ecology and invasion biology.

A holistic, multi-disciplinary, framework

Many frameworks have been proposed that attempt to display the theoretical processes of biological invasions (Williamson 1996; Richardson et al. 2000; Catford et al. 2009; Saul et al. 2013). The framework for biological invasions proposed by Blackburn et al. (2011), we believe, presents the best effort yet to provide consensus for the processes associated with human-mediated species dispersal. This framework is particularly noteworthy for three reasons. First, it merged theoretical frameworks used by researchers and managers focusing on terrestrial plants and animals, thus the resulting synergy provides a more holistic picture of invasions. Second, nothing in the framework is based on the subjective criteria of impacts. Although we don't dispute that impacts can be very important, this subjectivity is an issue related to terminology, and not fun-

damental to the invasion process itself. Third, the framework excludes species within their native range that undergo population “explosions”, which have been inappropriately called invasions (see e.g., Blondel et al. 2013).

Despite the advance provided by Blackburn’s invasion framework, we believe that it stops short of being more widely applicable for ecology because it solely considers species movements that are human-mediated, and therefore colonisation, even at the biogeographic scale, is excluded (Wilson et al. 2009; Blackburn et al. 2011; Gillespie et al. 2011). We believe that it would be far more scientifically logical and beneficial to consider all species movements under a single framework to provide a more holistic view of species movements, resulting in greater insights for invasion ecology, for ecology in general, island biogeography and for other sciences such as epidemiology. Here, we present such a framework that is slightly but distinctly modified from that proposed by Blackburn et al. (2011) to more holistically encapsulate the spectrum of species colonisations (Figure 1), and that can be utilised by many science disciplines.

Differences of our framework

The framework presented here differs from that in Blackburn et al. (2011) in five main ways. First and foremost, it incorporates natural range expansion as a dispersal mode, and acknowledges that any species in novel environments are subject to the same barriers of survival, reproduction, dispersal and further range expansion, irrespective of how they got there. Second, Blackburn’s Transport and Introduction stages have been

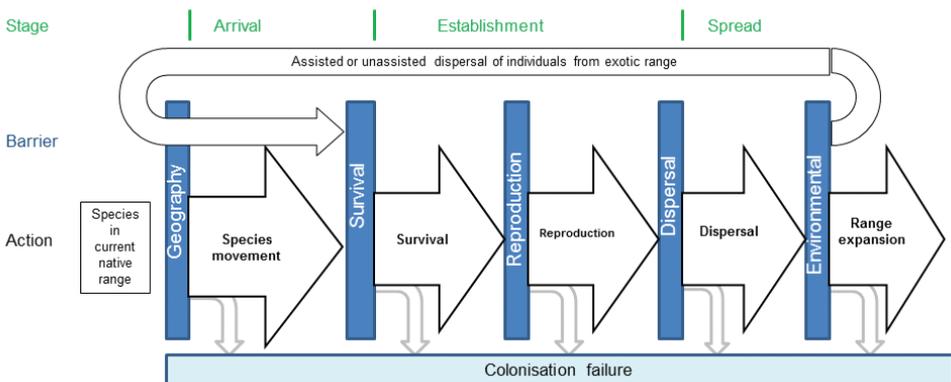


Figure 1. The colonisation framework. This framework considers both human-mediated dispersal and natural dispersal, and acknowledges that any species in novel environments are subject to the same barriers of survival, reproduction, dispersal and further range expansion, irrespective of how they got there. This framework is relevant for epidemiology, simply by changing a few terms (e.g., species movement to infection, dispersal to transmission, invasion to disease spread).

merged into the Arrival stage, and within this the optional “Captivity or cultivation” barrier has been removed. Third, although acknowledged by Blackburn et al. (2011), we explicitly show that the process can be cyclical where the colonisation can be further initiated by dispersal from the exotic range, across another geographic barrier into a new biogeographic region, and can occur as both human mediated (e.g., the intentional introduction and establishment of salmonids into a country outside of its native range, followed by subsequent dispersal into additional aquatic systems (Crawford and Muir 2007)), or self-dispersal (e.g., Eurasian tree sparrows *Passer montanus* flying from Asia to Australia (Chapman 2000)). The fourth change is the use of simplified and descriptive categories. The use of codes to name the movements between the stages in the prior framework was slightly problematic in that these categories were non-descriptive and therefore were inefficient for communication, especially with the wider public. Additionally, from a scientific perspective, there is no need to have multiple categories between each barrier to describe each unique way that a species can move along the colonisation process. Thus we have replaced the many coded categories (e.g., Blackburn’s B1, B2, D1, D2) with single, all-encompassing descriptions between the barriers. Finally we incorporate many other, largely semantic, changes that eliminate focus from human-mediated dispersal. Additionally we have replaced “boom and bust” with “Colonisation failure” because this extreme population cycle does not always occur. The sole importance of this change in state is the extinction itself, not the greatly varying population dynamics that occur prior.

Advantages of the holistic framework

Both with and without the context of climate change, using the framework to detail colonisations overrides subjective issues defining exotics, such as distance away from a species’ historic distribution, recolonisation of extinct populations and colonisation without evolutionary history.

Blackburn’s framework was based on synergies of terrestrial plants and animals. Already the framework has proven applicable for marine animals (Jones et al. 2013). Similarly, our framework is applicable for any biotic phenomenon undergoing dispersal and subsequent range expansion. There is even scope for further synergies, such as with epidemiology, especially for emergent diseases. There appear to be very few frameworks for epidemiology, and those existing appear very rudimentary compared to frameworks for ecology (e.g., Gilligan 2002, but see Jeschke et al. 2013), despite both sciences operating with arguably equally complex environmental settings. Pathogens associated with human, animal and plant health must also disperse, establish within/on a host, reproduce, transmit to a new host and in some instances are able to continue to spread, even globally. Pathogenic spread can be incorporated within our framework with simple word changes for two colonisation *Actions* so that it reads: infection, survival, reproduction, transmission and epidemic (Figure 1). Indeed invasive species management has its roots with pathogen containment, so it is not surprising that the

process of species colonisation would follow an identical framework to that for epidemiology. Epidemiological examples include the accidental emergence and subsequent spread of swine and bird flues (Neumann et al. 2009), the intentional release of rabbit calicivirus in Australia (Bruce et al. 2004), the unintentional spread of pathogenic chytrid fungus affecting amphibians globally (Lips et al. 2006), and the recent epidemics of Ebola (Gire et al. 2014).

Finally, this framework more easily allows the exchange of research ideas and findings across biological disciplines (e.g., conservation biology, invasion ecology, island ecology and biogeography, epidemiology) and for different focal taxa or biomes (e.g., microorganisms, plants and animals, marine and terrestrial organisms) that are often focused on the same phenomenon – colonisation. In particular, for invasion biology, possibly more so than for other science disciplines, the isolation of researchers focused on different taxa or biomes, and researchers from managers, has resulted in the loss of clear definitions and vast inconsistencies in terminology (Heger et al. 2013; Kueffer and Larson 2014). Terminology clarifications and unifications are being repeatedly proposed (Colautti and MacIsaac 2004; Pyšek et al. 2004; Richardson et al. 2011), but they do not necessarily cover all biota, or are not being embraced by stakeholders, partly attributable to the fragmented nature of the science. We have made no attempt here to reconcile these terminological issues, aside from removing all synonyms from the framework. But considering colonisation as a holistic process may help alleviate some of invasion biology's terminology issues.

Concluding remarks: moving towards a holistic view

There is no doubt that dispersal mode greatly influences the opportunity for species to disperse (Wilson et al. 2009; Gillespie et al. 2011), and that human-mediated dispersal of species, both intentional and accidental, has greatly accelerated the rate that species cross biogeographic barriers and colonise novel environments, often with great consequences (Mack et al. 2000). Additionally, the species composition being moved by human assistance is substantially different to the composition that would otherwise move naturally. But we argue that any differences of colonisation seen between species dispersed by human-mediation or not, merely represent different configurations of the same process of colonisation. This is because post-arrival all propagules face the same barriers of survival, reproduction, dispersal and further range expansion. Similarly, irrespective of the dispersal mode, a colonising species may or may not have significant ecological impacts. Indeed species self-dispersing across biogeographic distances via natural dispersal represent some of the greatest biosecurity risks to human interests and environments (Yen et al. 2014), and therefore there is no valid scientific distinction to separate species movements based on dispersal mode.

We argue that climate change biologists, invasion biologists, restoration ecologists, island biogeography biologists, community assembly ecologists and epidemiologists are unnecessarily conducting research in isolation from each other despite essentially

studying the same phenomenon – colonisation. Biological invasions do not represent a distinctly different or change in process, just an acceleration of the colonisation process through multiple mechanisms. The major difference between invasion and colonisation stands, we believe, on ethical ground. This difference should not dictate the science, only management and policy making. For biological invasions, we believe that predictive understanding would benefit most greatly from focusing on (1) determining why so many more species do not manage to successfully colonise new areas (Zenni and Nuñez 2013), and (2) for successful colonisers, determining why some species can establish with a single propagule, whereas others require many propagules. For all of the above sciences, we argue that they would mutually benefit from each other by holistically considering colonisations.

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