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 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-
Biological invasions and natural colonisations: are they that different?

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 constraints 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 than 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-
Biological invasions and natural colonisations: are they that different?

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

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![Figure 1](image.png)

*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
Biological invasions and natural colonisations: are they that different?

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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Biological invasions and natural colonisations: are they that different?


Winkler G, Dodson JJ, Lee CE (2008) Heterogeneity within the native range: population genetic analyses of sympatric invasive and noninvasive clades of the freshwater invad-


Biological invasions and natural colonisations are different – the need for invasion science

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Abstract

In a recent Discussion Paper, Hoffmann and Courchamp (2016) posed the question: are biological invasions and natural colonisations that different? This apparently simple question resonates at the core of the biological study of human-induced global change, and we strongly believe that the answer is yes: biological invasions and natural colonisations differ in processes and mechanisms in ways that are crucial for science, management, and policy. Invasion biology has, over time, developed into the broader transdisciplinary field of invasion science. At the heart of invasion science is the realisation that biological invasions are not just a biological phenomenon: the human dimension of invasions is a fundamental component in the social-ecological systems in which invasions need to be understood and managed.

Keywords

Invasion science, invasion biology, definitions
**Something in the way they move**

Hoffmann and Courchamp (2016) argue that human-mediated extra-range dispersal does not differ in terms of processes or mechanisms from natural colonisation, but that all dispersal events sit on a broad but continuous spectrum of species movements. Their rationale is that in both human-mediated extra-range dispersal and natural colonisations, populations have to overcome the same barriers (survival, reproduction, dispersal and further range expansion), and differ only in the “inconsequential” way in which they move from the original to the novel recipient locations (using their own means versus human transportation). Hoffmann and Courchamp (2016) suggest that there are four main reasons why scientists traditionally consider human-mediated extra-range dispersal and natural colonisations separately: (i) propagule pressure is greater for human-mediated extra-range dispersal; (ii) colonisation pressure is greater for human-mediated extra-range dispersal; (iii) genetic diversity is different; and (iv) human-mediated extra-range dispersal is more likely to result in invasions which lead to mass extinctions. They then argue that these differences are not clear-cut, and that even if such differences exist, they are differences of degree (e.g. rate or magnitude) rather than of kind. They conclude that human-mediated extra-range dispersal events “do not represent a distinctly different or change in process, just an acceleration of the colonisation process through multiple mechanisms”.

We agree with Hoffmann and Courchamp (2016) that there is much to be learnt by invasion scientists from studying processes of natural colonisation (and vice versa; ecologists researching colonisation processes may learn from developments in invasion science). The same mathematical and theoretical models of dispersal and establishment can sometimes apply. For example, the concept of hierarchical filters for delineating pools of native species in studies of assemblages of natural communities resembles the concept and stages of the invasion pathway (Blackburn et al. 2011; Karger et al. 2016). In comparing when and where particular models are useful, and how parameter values differ, there can be useful insights for understanding and management.

Nevertheless, we disagree with the rest of their thesis—and note that the arguments made have already been well identified, characterised, and repeatedly rebutted (Cassey et al. 2005; Ricciardi 2007; Richardson and Ricciardi 2013). In particular, the dynamics and processes of dispersal leading to biological invasions are often quantitatively and qualitatively different from dispersal leading to natural colonisation (Wilson et al. 2009a; Wilson et al. 2009b). Wilson et al. (2009b) identified seven key properties of dispersal pathways: propagule pressure, genetic diversity, potential for simultaneous movement of coevolved species, selectivity of what is moved, the duration of the dispersal opportunities, evolutionary distance (time since divergence) between species in the original and new ranges, and the level of human assistance provided in spread and establishment. Hoffmann and Courchamp (2016) examined three of these, but all aspects are important (and there may be others). By focusing on the properties of different types of dispersal it becomes clear that human-mediated extra-range dispersal often varies very substantially in both kind and degree from natural colonisation. There is something in the way humans move species that moves them like no others.
Here, there and everywhere

In some cases, natural and human-mediated extra-range dispersal are qualitatively similar. Hoffmann and Courchamp (2016) provide three examples of this (tsunamis, range-shifts due to climate changes, and Lessepsian migration). Wilson et al. (2009b) categorised such dispersal events as extreme long-distance dispersal, leading-edge dispersal, and corridor respectively. However, there are other types of dispersal that simply never happened before humans evolved and started moving around the world, termed mass dispersal and cultivation (Fig. 1, Wilson et al. 2009b). These pathways are now major drivers of invasions. Such dispersal often results in the movement of massive numbers of individuals of species, that never would have dispersed naturally, to locations where they are provided substantial resources that facilitate establishment and invasion.

Hoffmann and Courchamp (2016) use examples of the colonisation of volcanic islands to argue that organisms move regardless of humans. This is true but disingenuous. Most individuals of most animal species move some distance in their lifetimes, but those distances are constrained at a range of scales. Thus, we can study activity schedules, home ranges, migration routes, and geographic ranges as more or less real entities. At the broadest of these scales, the presence of biogeographic regions shows that there are fundamental barriers to the spread of species that are not normally breached even over evolutionary timescales. If dispersal was not limiting why can we distinguish Gondwanan and Laurasian taxa? The existence of examples like the Great American Interchange (cited by Hoffmann and Courchamp (2016)) simply serve to highlight how rare are major faunal exchanges across such barriers. Biogeographic breaks are hugely important. Some groups might be less restricted by biogeographical features (particularly those groups that can form part of the aerial plankton), but other groups (in particular soil organisms) can be profoundly affected, with the resulting biogeographical breaks hard to distinguish. This is why species that cross such biogeographical breaks (either naturally or through human-mediated means) can occasionally have profound impacts.

The transportation of alien species by human agency across biogeographic barriers that have never historically been crossed before is essentially a daily occurrence now (Seebens et al. 2016). No passerine birds of European origin had colonised New Zealand over the tens of millions of years of the archipelago’s independent existence, but now there is a thriving assemblage of such species that has developed in New Zealand over the last 150 years thanks to human intervention (Duncan, Blackburn & Cassey 2006). The pond slider (Trachemys scripta) is native to the southeast of the U.S.A. and Mexico. The maximum recorded dispersal distance of nesting females is 1.4 km (Steen et al. 2012; Garcia-Diaz et al. 2015). Yet, since the 1960s, the species has been introduced to 77 countries around the world, establishing self-sustaining populations in 36 countries (i.e. a dispersal distance of ~20,000km). Consider the alien fauna and flora of the region where you live. Which, if any, of these organisms could have arrived by natural colonisation? Are these simply differences in rates? Notwithstanding events like the Tohoku tsunami, to view human-mediated extra-range dispersal as simply a difference of degree from natural colonisation is to stretch the concept of degree beyond breaking point.
Human-mediated dispersal and natural colonisation: are they that different? A Stonehenge and B a rocky shore were both created by rolling stones, but they are quite different in origin and these differences are important. A is courtesy of Diego Delso, under the CC BY-SA 4.0 licence, https://commons.wikimedia.org/w/index.php?curid=35323153); B is courtesy of Tim Blackburn.

Even in instances where the differences between natural colonisation and human-mediated extra-range dispersal appear qualitatively similar, the degree can be important. Mass extinctions are “just” extinctions that occur at a higher rate; conservation biology is really only the population biology of species with small or declining populations; epidemiology is “just” the population biology of disease-causing organisms; medicine is “just” the diagnosis, treatment, and prevention of disease in one particular primate species. Are medical doctors basically specialised vets? That they are not is because differences in degree have important implications for the causes and consequences of the processes under investigation. For example, small populations are affected by stochastic events in ways that large populations are not, justifying the distinction between conservation and population biology. Differences of degree also matter because natural systems are frequently non-linear, such that increases in some parameters can lead to step changes in their responses. This is why we worry about humanity’s contribution to atmospheric CO₂, even though this is a natural (and naturally varying) component of the atmosphere, and the concentrations of CO₂ in the atmosphere are well within the levels seen over geological time scales. As a further example, Gaston et al. (2003) compared natural and alien colonisations to Gough Island. Gough has accumulated 28
Biological invasions and natural colonisations are different—the need for invasion science

Indigenous pterygote insect species over its 2–3 million year existence, but a further 71 pterygote species have been added to its insect fauna in the 325 years since humans first landed. Thus, the rate of accumulation on Gough Island has increased by 2–3 orders of magnitude as a result of human transport. This does not represent an acceleration, but rather a step change in species accumulation, akin to the difference between rates of background and mass extinctions (Pimm et al. 2014). Degree matters.

Finally, one of the main reasons such types of dispersal need to be distinguished from natural colonisation is what happens post-arrival. While conceptually the same barriers are present, the resources provided for establishment mean that some barriers are rendered inconsequential. How and where individuals arrive matters a great deal. For example, every year dozens of geese, ducks, raptors, rails, gulls, terns, pigeons, cuckoos, shorebirds, flycatchers, vireos, thrushes, warblers, sparrows, orioles, and other North American bird species arrive in the UK to the immense excitement of birdwatchers. Yet, since naturalists recognised the phenomenon in the early 19th century, none of these species has colonised and established permanent populations in the UK. In contrast, over the same period, the UK has gained well-established breeding populations of at least two North American species (Canada goose *Branta canadensis* and ruddy duck *Oxyura jamaicensis*) as a result of deliberate introductions. The largely stochastic and widely distributed arrival of small numbers of (probably exhausted) birds is extremely unlikely to have the same establishment outcome as concentrated and oftentimes intentional introductions of large numbers of well-provisioned individuals.

**All down the line**

An important emerging lesson in invasion science is that the manner by which species are introduced has long-lasting consequences on invasion trajectories (Donaldson et al. 2014). The invasion process (progression along the introduction-naturalisation-invasion continuum) is different for organisms introduced by humans to the processes associated with establishment and colonisation of organisms that arrive without human assistance (Hulme et al. 2016). Invasions differ from natural colonisation in biogeographical, ecological and anthropogenic dimensions (Rejmánek 2000), and historically too little research has focussed on how species are moved around (Puth and Post 2005). This is changing, and there has been a recent focus on introduction pathways (Essl et al. 2015a; Cope et al. 2016; Faulkner et al. 2016; Ricciardi 2016; Seebens et al. 2016). Moreover, species that have arrived in a new region through human-mediated extra-range dispersal or through natural colonisation can, of course, also co-opt the same dispersal pathways once in a region. This has been acknowledged many times before (e.g. Richardson and Pyšek 2006; Hulme et al. 2008) and is an important part of the reasoning behind the unified framework for biological invasions proposed by Blackburn et al. (2011). This is why there is an important distinction between transport and introduction in this framework, a distinction which is lost in Hoffmann and Courchamp’s unhelpful edits to it.
The terminology of biological invasions that was proposed for plants in 2000 and generalised across taxa a decade later (Richardson et al. 2000; Blackburn et al. 2011) has been accepted by the majority of researchers because it is useful. The scheme has provided the basis for several recent large scale syntheses of the macroecology of invasions in a variety taxonomic groups (e.g. Essl et al. 2015b for bryophytes, Capinha et al. 2015 for gastropods, and van Kleunen et al. 2015 for plants). Such applications highlight strengths and weaknesses, and we welcome such tests of the scheme. As noted by Hoffmann and Courchamp (2016), there is more work to be done on the coding of the different stages proposed in the scheme by (Blackburn et al. 2011), and in particular we need recommendations on how to apply it in practice (Wilson et al. 2014). However, by failing to appreciate the importance of introduction dynamics, the revisions proposed by Hoffmann and Courchamp (2016) reduce the scheme’s general applicability rather than increase it.

Hoffmann and Courchamp (2016) argue for more work on impacts, and we strongly support this call. Despite recent efforts to provide robust insights (Vilà et al. 2011; Pyšek et al. 2012), data on impacts are rare (be they by native or alien species). More information is urgently needed both observational and experimental (Kumschick et al. 2015). However, what data there are strongly suggest that natives are significantly less likely than aliens to be problematic for local ecosystems (Simberloff et al. 2012; Paolucci, Maclsaac & Ricciardi 2013; Buckley and Catford 2016), and that aliens can be extremely problematic. Hoffmann & Courchamp’s suggestion that “with the (dramatic) exception of a few mammals, ants and pathogens,…there is little evidence that exotic species induce species extinctions” flies in the face of the abundant evidence that aliens are a major driver of native species extinction, including alien molluscs, fish and reptiles (Pyšek et al. 2016) – aliens have been the major cause of vertebrate extinctions over the last 500 years (Bellard, Cassey & Blackburn 2016). Even were that not the case, population-level declines (see Pyšek et al. 2016 for examples), introgression and losses of genetic diversity (Munoz-Fuentes et al. 2007), and the loss of community-level identity (i.e. homogenisation; Lockwood and McKinney 2001) are all crucial, and increasingly well documented, impacts of biological invasions. Impact should not be measured solely by species-level extinctions, but by a suite of measure of impacts on people, places and biodiversity. Standardised schemes for categorising environmental impact designed for invasive species (Blackburn et al. 2014) can potentially be adapted for native species, and proposed schemes to classify socio-economic impacts of alien taxa hold much promise for conservation more generally. But understanding where a taxon has come from, and in particular whether it is invasive or not, is often essential to understanding why these impacts occur and how they can be managed.

There are some excellent schemes that provided a basis for how to determine if invasive taxa are different from other taxa (van Kleunen et al. 2010), but in our view, efforts to partition off the “real biological” signal from the influence of humans is not only impractical, but at heart fails to recognise that invasions are intrinsically a human
product. Understanding the processes and mechanisms of biological invasions requires not just ecological studies, but an understanding of how humans move organisms to their new ranges, how they interact with them on arrival, and how they move them around their new ranges. This is why invasion biology has grown and developed into invasion science (Richardson 2011).

No expectations?

Hoffmann and Courchamp (2016) make an attempt at *reductio ad absurdum* with the question: are humans an “invasive” species or not. We agree that this discussion is mostly extraneous semantics, albeit one that can lead to some very disturbing conclusions, but it highlights the essential problem. We cannot extricate humans from invasions or invasions from humans. Invasions provide not only valuable test cases for ecologists, evolutionary biologists, and physiologists, but also important insights for our understanding of humans and their interactions with the environment. Hoffmann and Courchamp (2016) argue that if we want to understand the ecological process of dispersal, then invasion ecology should do more to productively engage with scientists in other fields. That is exactly what invasion ecologists do (in fact most of us learnt our trades in other fields before turning to invasion science). There are plenty of examples of transdisciplinary research on biological invasions produced by collaborations between invasions ecologists and social scientists, economists and evolutionary ecologists, decision scientists and mathematical biologists (Lockwood, Hoopes & Marchetti 2013). These collaborations only serve to highlight the pivotal role of humans.

Neither can we observe any evidence within the field of invasion science of the isolation of researchers working on different taxa. This may have been true twenty years ago, but the last decade has seen rapid development, as data from a broader range of taxa and standardised analytical and conceptual frameworks became available (Hulme et al. 2008; Walther et al. 2009; Blackburn et al. 2014; Essl et al. 2015a). The result has been a series of multi-author collaborations comparing invasion patterns in multiple taxa (Lockwood, Cassey & Blackburn 2005; Pyšek et al. 2010; Vilà et al. 2010; Essl et al. 2011; Aronson et al. 2014; Kumschick et al. 2015).

To conclude, biological invasions and natural colonisations are very often different; sometimes this matters, sometimes it does not. We should clearly focus more on processes and mechanisms, but the null expectation should be that biological invasions are qualitatively and quantitatively different from natural colonisation. Indeed, that is why we are moving from a Holocene period characterised by biogeographic regions with a rich global texture of unique and distinctive biotas, into an Anthropocene characterised by homogenisation, extinction and other massive global changes (Lewis and Maslin 2015). If future civilisations will be able to recognise this change in the geological record, we should be able to recognise it while it goes on around us each and every day of the year.
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When similarities matter more than differences: a reply to Wilson et al.

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Abstract
In our recent Discussion paper, we presented our view that the only real distinction between biological invasions and natural colonisations is the human element. We agree that invasion science is a very important science, not only to better understand the role that human mediation plays for colonisation, but also for many other science fields. We agree with all invasion researchers that the human influence can result in spectacular differences, including in rates of species movement, rates of successful colonisation, the particular species being moved, the biogeography of dispersal pathways and rates of any resulting ecological disturbance and biodiversity loss. Our deep point is that species dispersed by human-mediation or natural colonisation are all subject to the same basic laws and rules of ecology, identical to many other phenomenon that occur naturally and can be greatly influenced by people. The human dimension is merely a mechanistic distinction, albeit important because it exposes insights about the colonisation process that cannot be seen by the study of natural colonisations alone. We provide 10 hypotheses that can be scientifically tested to determine whether biological invasions and natural colonisations are two separate processes or the same process being influenced by different mechanisms.

Keywords
Alien, biological invasion, colonisation, dispersal, exotic, invasion, introduction
Humans have a huge influence on many phenomena

In our recent paper (Hoffmann and Courchamp 2016) we point out that despite many obvious differences between human-mediated biological invasions and natural colonisation, there are also many similarities. Ultimately, yes, they have differences, no one denies that, but are they THAT different? In a reply, Wilson et al (2016) have focused on the differences to argue the point that they are distinct, concluding biological invasions and natural colonisations are very often different; sometimes this matters, sometimes it does not. Here we respond to their arguments, ultimately concluding that biological invasions and natural colonisations are very often similar; sometimes this matters, sometimes it does not. In doing so, we further reinforce that the concepts in invasion ecology should not be artificially dissociated from general ecology.

The deep intent of our original paper was to argue that species dispersed by human-mediation or by natural colonisation are all subject to the same laws of ecology and that overlooking these similarities could slow down scientific progresses in invasion biology. As succinctly put by Lawton (1999) “The most useful scientific laws yield deep insights into the workings of nature: rules are less grand. Mechanisms are weaker still: a mechanism or mechanisms can generate unique phenomena: but general rules require common mechanisms”. Undoubtedly the mechanism of human-mediated dispersal generates the unique phenomenon of modern biological invasions, but species dispersed by the two transport modes are subject to the same ecological laws and rules. To cite Jeschke (2014) “a look at the concepts and hypotheses in invasion ecology reveals that these are deeply connected with those in general ecology.” The two fields have essentially the same hypotheses but with nuanced terminology, (eg invader vs coloniser). Their respective hypotheses, when boiled down to basics, are identical. Would anybody dare argue that hypotheses of propagule pressure, biotic resistance and enemy release only apply to species dispersed by human mediation but not natural colonisation? The fields and their hypotheses are not THAT different, because they focus on the same processes subject to the same biological laws and rules within a general theory of ecology (Scheiner and Willig 2008).

We cannot understate how important research about biological invasions have been to understanding colonisation, because it adds the other side of the continuum that has been studied by island biogeography (MacArthur and Wilson 1967). The commonalities between invasion science and general ecology have long been noted by many (Thompson et al.1995; Davis et al. 2001; Economo and Sarnat 2012). We agree that the human dimensions of biological invasions are pivotal to invasion biology, with clear implications for management and policy. But we are arguing that human-mediation is a mechanism, and thus essentially a biological invasion is a sub-class of the process of colonisation. Equally, natural colonisation is also sub-class of colonisation, and both are subject to the same natural laws.

We agree with Wilson et al. (2016) that scientific testing of hypotheses should determine whether colonisation and biological invasions are truly unique, or just the same overall process initiated by different mechanisms. Naturally there would be huge differences if the focus was at the level of mechanisms such as pathways (i.e. propagule
pressure for most species is undoubtedly statistically significantly different between human-mediated dispersal and self-dispersal). We argue that this is not the correct level for a fundamental scientific distinction, but instead the difference should lie much deeper at the level of laws and rules. As a suggestion of how to test this, we refer to the first 10 hypotheses of general ecology explored in Prins and Gordon (2014). Although specifically written for biological invasions, if the terms for biological invasions and natural colonisations were interchanged in each hypothesis, the hypotheses would be identical for both invasion biology and general ecology.

**Hypothesis 1**: A species will not be able to invade/colonise an area that has abiotic conditions that are outside its physiological tolerance levels.

**Hypothesis 2**: The extent of an invasion/colonisation is negatively correlated to species diversity of functional guild competitors in the invaded environment.

**Hypothesis 3**: An invasive/colonising species will not be able to replace a native species if they occupy the same niche and are in all other ways equal.

**Hypothesis 4**: A species will not be able to invade/colonise an area that harbours pathogens (that cause disease) or predators (that prey on the invading species) that it has not encountered before.

**Hypothesis 5**: A species will not be able to invade/colonise an area if its co-evolutionary species (necessary for parts of the invader’s life cycle) is/are not present in the area.

**Hypothesis 6**: Species that occur at low population densities in their native range will not be invasive/prone to colonise.

**Hypothesis 7**: A species will not be able to invade/colonise an area if it has a lower use efficiency of its limiting resource than a native species that occupies the same location.

**Hypothesis 8**: Species can more easily invade/colonise highly disturbed areas; this disturbance can be either man-made or natural.

**Hypothesis 9**: Species from older lineages are more vulnerable to being replaced by invasive/colonising species that occupy a similar niche.

**Hypothesis 10**: A species will only be able to invade/colonise an area if it has a life-history strategy which is more r-selected (or ‘weedy’) that that of the species which already is occupying the niche.

The testing of the hypotheses for this purpose is not to determine if individual hypotheses should be rejected or not (for an extremely interesting insight into this refer to Prins and Gordon 2014), but instead to determine if there is a difference in the rejection of the null hypothesis for individual hypotheses between the two species movements. If the pattern of acceptance/rejection of these hypotheses is the same between species dispersed by human-mediation vs self-dispersal, then we would have to conclude that species dispersing by the two transport modes are subject to the same process with the same underlying ecological laws.

We agree with Wilson et al. (2016) on the differences of mechanisms (including the degree [rate] at which they occur), as well as their implications, especially for management and policy. But absolutely nowhere have Wilson et al. (2016) demonstrated that the two are subject to a different process. Specifically they give an example
about an apparent difference between the creation of the stones at Stonehenge and the smooth pebbles on a rocky shore. One is obviously human-mediated, the other natural. We agree that the mechanism(s) that gave rise to the rocks being modified into other shapes and configurations is different, but we argue that the underlying laws dictating the erosion process (e.g. laws of thermodynamics and the physics of friction) are identical for both. Indeed humans could create a beach of round pebbles, and there is absolutely nothing in the Laws of Thermodynamics preventing Stonehenge from naturally forming, but the probability (and hence rate) of it occurring is extremely low.

An important point that we want to make clear again is that we by no means are saying that invasion science is redundant. It is a vital science focused on species that are dispersed by people, and forms part of a family of sciences around biology and ecology with wide-ranging linkages with many other sciences including epidemiology and conservation sciences. This seems to be repeatedly lost in arguments by Wilson et al. (2016). For example we fully recognise the fields of conservation biology and population biology. But rather than seeing a black-and-white distinction based on differences of susceptibility of populations to stochastic events relative to population sizes, we instead see that this demonstrates that population sizes follow a continuum, which partly determines population’s relative susceptibility to stochastic events. Our argument is one of a holistic view that whether a population is studied by either science, the process(es) underlying susceptibility to a stochastic event are the same, all that differs is the degree to which a population is susceptible.

Wilson et al. (2016) presented numerous arguments to demonstrate that the magnitude of differences of the two transport modes is an important science distinction, particularly noting that differences are often not just a linear change in rate, but a “step change”. The influence of people on climate change was also provided as an example of such a “step change”, implying some important science distinction. We find the climate change argument presented by Wilson et al. (2016) is instead very pertinent to our argument because of the identical nature of it with the holistic view of colonisation (Figure 1). Are the authors suggesting that the processes that influence global climates will change differently if the CO$_2$ is naturally released or human induced? Climate scientists agree that increasing CO$_2$ levels in the atmosphere is resulting in climate change. Climate scientists agree that there are human-mediated and natural contributions to global atmospheric CO$_2$. Much climate science also focuses solely on the human-mediated component. Despite there being big differences between the rate of CO$_2$ release, the mechanisms by which CO$_2$ is released, and the geography of CO$_2$ release, for the two modes of atmospheric CO$_2$ accumulation no climate scientist would argue that there is some fundamental difference in implications for projected climate changes due to the human-mediated or natural source of CO$_2$. Certainly, whilst there are marked implications for management of the different sources of emissions, none are advocating for a separate science or that there are different processes at play. Similarly, if a significant volcanic eruption somehow induced an atmospheric CO$_2$ step-change, are Wilson et al. (2016) arguing that the laws of chemistry and thermodynamics would influence the climate differently to an identical human-induced step-change? Ultimately, for all of their examples claiming that rates and degree differ, not a single difference in underlying process was given.
We restrict comment about impacts here, just as we did previously, because impacts are not part of the colonisation process, but can be a consequence of it. For this reason, impacts were also not included in Blackburn’s framework (Blackburn et al. 2011). We agree that some invasive species have created much extinction, and have done so spectacularly. The intent of our text was twofold: first to point out that most species moved by people have not been unambiguously shown by science to induce extinction. Indeed, only about 30 taxa are implicated with extinctions (Bellard et al. 2016), and therefore extinction is an exception, not a rule. Second, extinction as a result of colonisation is historically not confined just to species dispersed by people (Bellard et al. 2016), and as also stated by Wilson et al. (2016) nor is it likely “to be just a modern phenomenon”.

We agree with Wilson et al. (2016) that, “at the heart of invasion science is the realisation that … the human dimension of invasions is a fundamental component in the social-ecological systems in which invasions need to be understood and managed.” Naturally, without the human component there could be no human-mediated dispersal. But that is as deep as it gets. Without denying the pivotal role of humans in invasion biology, one must keep in mind that the biological, or ecological, component of it is at least, if not more, important. Even Wilson et al. (2016) wrote “While conceptually the same barriers are present, the resources provided for establishment mean that some barriers are rendered inconsequential.” We couldn’t agree more. Humans override some barriers by overcoming the limitation of the process that affect colonisation - species self-dispersing have to overcome the same barriers by themselves. Invasion science asks the focused question, how do people influence colonisation, and how do those influences change colonisation outcomes?
Ultimately, despite the statement by Wilson et al. (2016) “we strongly believe that the answer is yes: biological invasions and natural colonisations differ in processes and mechanisms” not a single process was presented, there or elsewhere. Let science be the judge. If there is indeed some deep and fundamental science difference between species undergoing range expansion by the two transport modes, then an underlying biological law needs to be found that applies to only one. To conclude along the same lines as Wilson et al. (2016), we believe that future civilisations will recognise from the geological record that at the turn of the Anthropocene, the major mechanisms driving the colonisation process for species globally changed from those that are “natural” and largely random and slow, to those that are driven by a dominant species (humans) and are largely non-random and fast.

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