A journal of the Society for Conservation Biology

POLICY PERSPECTIVE

Seeking International Agreement on What it Means To be "Native"

James J. Gilroy[1,*], Julian D. Avery[2,*], & Julie L. Lockwood[3]

[1] School of Environmental Science, University of East Anglia, Norwich NR47TJ, United Kingdom
[2] Ecosystem Science and Management, Penn State University, PA 16802, USA
[3] Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, NJ 08902, USA

Keywords
Alien; conservation policy; direct introduction; dispersal; facilitation; human agency; invasion; nonnative; novel ecosystems.

Correspondence
Julian D. Avery, Ecosystem Science and Management, Penn State University, PA 16802, USA. E-mail: juliandavery@gmail.com

Received
20 November 2015
Accepted
3 March 2016

*Authors contributed equally to this article.

Author Contributions
JJG and JDA developed the framework and JJG, JDA, and JLL developed the application of the framework and wrote the manuscript.
Editor
Mark Schwartz

doi: 10.1111/conl.12246

Abstract

The management of harmful nonnative species is a priority for governments worldwide. However, confusion concerning what constitutes a "native" species has led to ambiguous or even contradictory wording in adopted legislation. A key issue concerns the treatment of species dispersing beyond their normal ranges in response to global change. Range-expanding species can have negative impacts on the ecosystems they colonize, prompting some authorities to class them as "nonnatives." However, range-shifts are becoming increasingly necessary for species persistence in response to climate and habitat change. Distinguishing these "desirable" range-shifts from other human-driven introductions is therefore a core requirement of legislation. Here, we propose a simplified framework that can be applied unambiguously across the policy arena. We suggest that the "nonnative" moniker should apply exclusively to species transported outside their native range by direct transport (defined herein), leaving species moving via unassisted dispersal as "natives," even if they are responding indirectly to anthropogenic change. We believe that widespread adoption of this simplified approach will facilitate more consistent multinational policies to target problematic invasive species.

Introduction

Nonnative species can cause considerable damage to biodiversity, ecosystems and economies (Lambertini *et al.* 2011; Simberloff 2014), making their prevention and control a priority issue for governments (Avery *et al.* 2013; Simberloff & Vitule 2014). Policies designed to implement such management face a fundamental challenge: how to identify which species qualify as "native" within a given region (Walther *et al.* 2009). This is a surprisingly complex issue, as species regularly colonize new areas via both natural and human-influenced processes.

Wild species are increasingly shifting their ranges in response to environmental change, particularly climate and habitat alteration (Schlaepfer *et al.* 2011; Thomas *et al.* 2004; Willis *et al.* 2009). If such shifts are indirectly driven by human activities, the resulting populations are open to being labelled as "nonnative," particularly when they have negative impacts within newly-colonized ranges (Walther *et al.* 2009). However, dynamic range shifts are also pivotally important for the persistence of wild species in response to global change (Parmesan 2006). The ability to differentiate "desirable" range shifts from unwanted species introductions is therefore a fundamental requirement for any invasive species policy. Projections suggest that climate change could drive up to 90% turnover in some wild communities (Lawler *et al.* 2009), highlighting the sheer magnitude of distributional changes that are on the horizon. It is essential that policy mechanisms keep pace with these changes, ensuring that the right management measures target the right species in the right places.

Table 1 Examples of working definitions of "nonnative," "alien," or "invasive" species used in governmental legislation, together with definitions adopted by key international conservation organizations. We also classify definitions according to our interpretation of whether they consider populations established via direct and indirect human transport to be nonnative

Title / Organisation	Year	Wording of definition	Direct / indirect transport
Australian Government Environment Protection and Biodiversity Conservation Act 1999	1999	"An **invasive species** is a species occurring, **as a result of human activities**, beyond its accepted normal distribution and which threatens valued environmental, agricultural or other social resources by the damage it causes."	Direct and indirect
European Parliament - Regulation on the prevention and management of the introduction and spread of invasive alien species	2014	"**Alien species** means any live specimen . . . **introduced** outside its natural past or present distribution" **"introduction** means the **movement by human intervention** of a species outside its past or present natural distribution""Legislation does not apply to . . . . **species changing their natural range without human intervention**, in response to changing ecological conditions and climate change"	Direct
U. S. Government Executive Order 13112 on Invasive Species	1999	"**Native species** means . . . species that, other than as a result of **an introduction**, historically occurred or currently occurs in that ecosystem."" **Introduction** means the **intentional or unintentional escape, release, dissemination, or placement** of a species into an ecosystem as a result of **human activity**."	Direct
IUCN Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species	2000	**"Alien species** . . . means a species . . . occurring outside of its natural range (past or present) and dispersal potential (i.e., outside the range it occupies naturally or could not occupy without direct or indirect introduction or care by humans)"**"Introduction** means the movement, by human agency, of a species . . . outside its natural range (past or present)."	Direct and indirect
UNEP Convention on Biological Diversity VI/23. Alien species that threaten ecosystems, habitats or species	2006	**"alien species** refers to a species . . . **introduced** outside its natural past or present distribution""**introduction** refers to the **movement by human agency, indirect or direct**, of an alien species outside of its natural range (past or present)"	Direct and indirect
UK Government Infrastructure Bill	2014	"A species is "**nonnative**" if . . . in the case of a species of animal, it is not **ordinarily resident in**, or a **regular visitor to**, Great Britain in a **wild state**."	Direct and indirect

Ambiguity concerning what counts as "native" can lead stakeholders to reach fundamentally different conclusions about the status of a given species or population (Tables 1 and 2; Pyšek *et al.* 2004: Falk-Petersen *et al.* 2006). Newly-arriving colonists that are labeled as "nonnative" are usually considered to have high probability of causing negative impacts, and thus are placed on watch lists, or are actively controlled to reduce or eradicate populations. Colonists that are classed as "native," by contrast, are usually afforded the cover of protective

Table 2 Examples of “nonnative” definitions from the ecological and conservation biology literature. Definitions are classified according to our interpretation of whether they consider populations established via direct and indirect human transport to be nonnative

Reference	Wording of definition	Direct / indirect transport
Pyšek *et al.* 2004	“Alien (exotic, nonnative, nonindigenous) plants . . . are taxa in a given area whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien . . . Human involvement here does not include habitat changes, global warming, atmospheric nitrogen fertilization, acid rain, etc.”	Direct
Prentis *et al.* 2008	“a species that is not native to a region and that was introduced to that region through human activity”	Unclear
Webber & Scott 2012	“Populations of a species have ‘alien’ status when found outside the PDEs (projected dispersal envelope) of populations with native status.”	Direct
Webb 1985	“a native plant (is) one which evolved in these islands or which arrived there by one means or another before the beginning of the neolithic period, or which arrived there since that date by a method entirely independent of human activity. An alien, on the other hand is one which reached the British Isles as a consequence of the activities of Neolithic or postneolithic man or of his domestic animals.”	Direct and indirect
Crawley *et al.* 1996	“Natives: plant species that would be present without human intervention . . . Aliens: species introduced by humans after 500 BC.”	Direct
Manchester & Bullock 2000	“Nonnative refers to a species or race that does not occur naturally in an area, i.e., it has not previously occurred there, or its dispersal into the area has been mediated by humans.”	Direct and indirect
Schlaepfer *et al.* 2011	“We use the term nonnative for species that occur outside of their historic range and invasive for cases in which these species cause biological, social, or economic harm.”	Direct and indirect
Strayer 2012	“I use the term ‘nonnative species’ to describe species that were moved out of their native range by some human action (deliberate or accidental) and established a population in this new range”	Direct
Wilson *et al.* 2009	“Introduced (or alien) species: a species that has shown extra-range dispersal owing directly or indirectly to human activity. Archaeophyte: a plant species introduced to Europe between the development of Neolithic agriculture and the European discovery of the Americas.”	Direct and indirect
Blackburn *et al.* 2014	“Alien species: a species moved by human activities beyond the limits of its native range into an area in which it does not naturally occur. The movement allows the species to overcome fundamental biogeographic barriers to its natural dispersal.”	Direct
Richardson *et al.* 2011	“Those whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (i.e., human-mediated extra-range dispersal)”	Direct

legislation within their new ranges (e.g., ESA 1973). The designation of “native” or “nonnative” therefore precipitates diametrically different policy and management actions for range-shifting species.

Ideally, status designations should be made using a transparent, robust and universally-agreed framework that is applicable to any taxon and region. Given that species ranges transcend political boundaries, there is also a clear need for trans-boundary agreement on species status, requiring an international approach. However, governmental and nongovernmental organizations are increasingly devising their own region-specific policies for invasive species, each involving a set of bespoke criteria to define which species are targeted (Table 1). To be effective, it is essential that these region-specific efforts reinforce one another, rather than contradict one another, in their treatment of shifting populations. Achieving this will require careful and timely input from conservation scientists on the rationale underpinning native versus nonnative species designations (Hulme 2015).

In this article, we review the main areas of ambiguity within existing legislation for nonnative species. We contend that policy-level ambiguity has arisen due to widespread inconsistency in what is considered "native" in the ecological literature (Richardson *et al.* 2000; Blackburn *et al.* 2014). This inconsistency has prevented existing ecological guidelines from being translated into straightforward policy. In particular, we focus on the form of human agency in determining species movements (direct vs. indirect), and the role that this plays in determining the legal status of subsequently established populations. We call for wider agreement among stakeholders, including global conservation organizations, on the precise wording used to define "nativeness." We suggest that this wording should be kept as simple as possible, in an effort to promote applicability and foster broad-scale consistency in the legal treatment of range-shifts. We also discuss how such a framework might be applied at the policy level, highlighting potential difficulties and identifying areas where further research is needed.

A confusion of definitions

Policy-makers have adopted a wide variety of definitions to designate native and nonnative species, with criteria ranging from the pathway of introduction, the extent of species' historical distributions, their dispersal potential, their ability to occupy a given area without human assistance, and the threats they pose to environments and livelihoods (Table 1). Policy wording is often equivocal, and many criteria are extremely difficult to apply on a case-by-case basis. For example, historical distributions are incompletely known for most species (Copp *et al.* 2005), and natural dispersal potential is difficult to quantify or predict over large distances (Lees & Gilroy 2014).

The wording of invasive species legislation is often ambiguous. In some cases, this could allow "nonnative" status to be applied to a wide range of species and scenarios. For example, the UK's recently-proposed Infrastructure Act (www.legislation.gov.uk/ukpga/2015/7/section/23) contains provisions for the control of nonnative species, in this case defined as any species that, although formerly native, is "no longer normally present in Great Britain." Although succinct, this policy would allow species to be redefined as nonnative whenever they go extinct at the national level, precluding future natural recolonizations or reintroduction events (Durant 2014). Moreover, newly arriving colonists would always class as nonnatives under this Act's definition, regardless of whether colonization occurs "naturally" by unassisted dispersal, or by direct human transport.

Such ambiguity in the policy realm is perhaps unsurprising given the often inconsistent terminology used in the invasion biology literature (Shrader-Frechette 2001; Colautti & MacIsaac 2004; Falk-Petersen *et al.* 2006). The concept of nativeness has been defined in many ways (Falk-Petersen *et al.* 2006), and the literature lacks a unified conceptual framework that can be applied across all taxa and ecosystems. For example, many authors conflate nonnative status with the concept of invasiveness (Shrader-Frechette 2001, but see Blackburn *et al.* 2011, 2014). Specific terms have often been used interchangably to refer to different stages and pathways involved in the invasion process, propagating further confusion (Richardson *et al.* 2000). Several recent works have addressed these failings of invasion terminology (e.g., Richardson *et al.* 2000; Blackburn *et al.* 2011, 2014; Heger et al. 2013), but none have directly considered the fundamental question of how "nativeness" itself should be defined, with the exception of Crees & Turvey (2015). This key definition is the cornerstone of any legislation concerning invasive species, and consequently deserves a careful and comprehensive treatment from the conservation science community.

The heart of the problem: direct versus indirect transport

The form of human agency involved in the arrival of a species outside its normal range is the most fundamental point of disagreement in the policy realm (Table 1), as it is in the ecology literature (Table 2) (see e.g., Wilson *et al.* 2009; Richardson *et al.* 2011; Diez *et al.* 2012; Strayer 2012). In some cases, definitions explicitly exclude species moving via natural dispersal in response to indirect human influence, for example the European Parliament's recent bill concerning invasive species (Table 1). In others, the term "nonnative" is applied to both direct and indirect human agency, including the IUCN definition (Table 1). The term "introduced" is often used to specify direct human involvement in the release of individuals, but policy uptake of this term has also been inconsistent (Table 1), as has use across different taxa. In most policy-level definitions, no explicit details are given on what actually constitutes a direct versus indirect human influence on movement (Tables 1 and 2). This is particularly problematic in cases where species move in response to human-driven habitat change, as the degree of human influence in such cases can be difficult to define.

The motivation to label as "nonnative" those species that are shifting their ranges under indirect human influence likely stems from the risk of colonizers having negative impacts following establishment. A prominent case concerns the spread of barred owls (*Strix varia*) into western North America (Livezey 2010), driven by widespread fire suppression and tree planting. Barred owls have significant negative impacts on native populations of spotted owls (*Strix occidentalis*), prompting the implementation of an experimental control program by the U.S. Fish and Wildlife Service (Livezey 2010; Diller *et al.* 2014). This effort has sparked considerable debate about the ethics of controlling species expanding naturally in response to indirect human impacts (Carey *et al.* 2012). Other high-profile examples of range shifts driven by human habitat modification are the inter-basin movements of marine organisms following the creation of the Suez and Panama canals (Galil 2007; Galil *et al.* 2007).

Legislative frameworks that designate these indirectly-driven range-shifts as "nonnative" pose an important problem: how should they treat all the other species that are expanding their ranges in response to anthropogenic change? Humans are continually altering species distributions via three broad classes of indirect mechanism: habitat transformations, climate change, and altered biotic interactions (OSM Table 1). Most of the resulting range-shifts occur with little or no detectable impact within newly colonized areas (but see cases of "invasion debt," Simberloff 2014), and in many cases such shifts are the only possibility for species persistence in response to shifting envelopes of climate suitability (Parmesan 2006). Precautionary definitions that include these indirect forms of human agency within the "nonnative" umbrella, whilst encompassing damaging dispersers (e.g., barred owl), also potentially tar an unknown number of desirable colonizations with the negative associations of the "nonnative" label.

Recently, this issue was addressed in the Convention on Biological Diversity's Strategic Plan for Biodiversity (CBD 2014). To identify nonnative populations (Aichi Target 9), the CBD adopted a framework proposed by Hulme *et al.* (2008) involving the pathways of introduction. Indirect human agency is incorporated via a "corridor" pathway, where populations are considered "nonnative" if they disperse along any habitat corridor opened by human infrastructure (Hulme *et al.* 2008). Little guidance is provided on what classes as "infrastructure," however, making the framework difficult to apply. To arrive at a conclusion on the status of expanding barred owl populations, for example, requires judging whether human-created woodlands represent "infrastructure" (Fig. 1). This framework therefore struggles to resolve the grey area concerning indirectly human-driven range-shifts, and does not address how native but shifting populations should be classified.

A simple concept of nativeness for a dynamic world

To resolve the ambiguity at the heart of most invasive species legislation, we suggest a simple solution: nonnative status should be reserved exclusively for species introduced via direct human transport pathways (i.e., Fig. 2A-C). All species moving via natural dispersal under indirect human influence, including those driven by habitat change and other infrastructure developments, should be considered "native" in their newly-colonized ranges (see e.g., Pyšek *et al.* 2004; Richardson *et al.* 2011). This simplified approach reflects the policy-driven need for clear, unambiguous delimitation between native and nonnative range shifts, avoiding the need for value judgments concerning the magnitude of human influence. This approach also addresses the obvious need for legal protection to be afforded to species that are shifting and expanding their ranges in response to rapid environmental changes in the Anthropocene epoch.

It is important to note that any damaging impacts caused by these "natural" colonists can still be subject to mitigation, via the same policy mechanisms in place to mitigate impacts of other native "pest" species (Côté & Sutherland 1997; Côté *et al.* 2004; Rothstein and Peer 2005; Carey *et al.* 2012). It should never be necessary, therefore, for policymakers to label problematic species as nonnative solely to justify eradication or control.

The direct human transport pathways by which nonnative populations establish include both intentional and unintentional movements of species. Intentional direct transport involves the capture or culturing of individuals from within their native range, and the subsequent transport and release of these individuals outside of their native range (e.g., via the pet and aquaria trade, ornamental or horticultural plant trade, biocontrol programs, fish and wildlife stocking programs, and agricultural or aquacultural programs; OSM Table 2). Unintentional direct transport involves the often haphazard entrainment of individuals by ships, trucks or airplanes; or within the living or nonliving cargo they carry. The commonality across these scenarios is that "colonizing" individuals are received into a location as a direct consequence of human transport. Subsequent spread and dispersal-driven colonization originating from a population established through direct human transport should also be classified as nonnative ("unaided" pathway in Hulme *et al.* 2008).

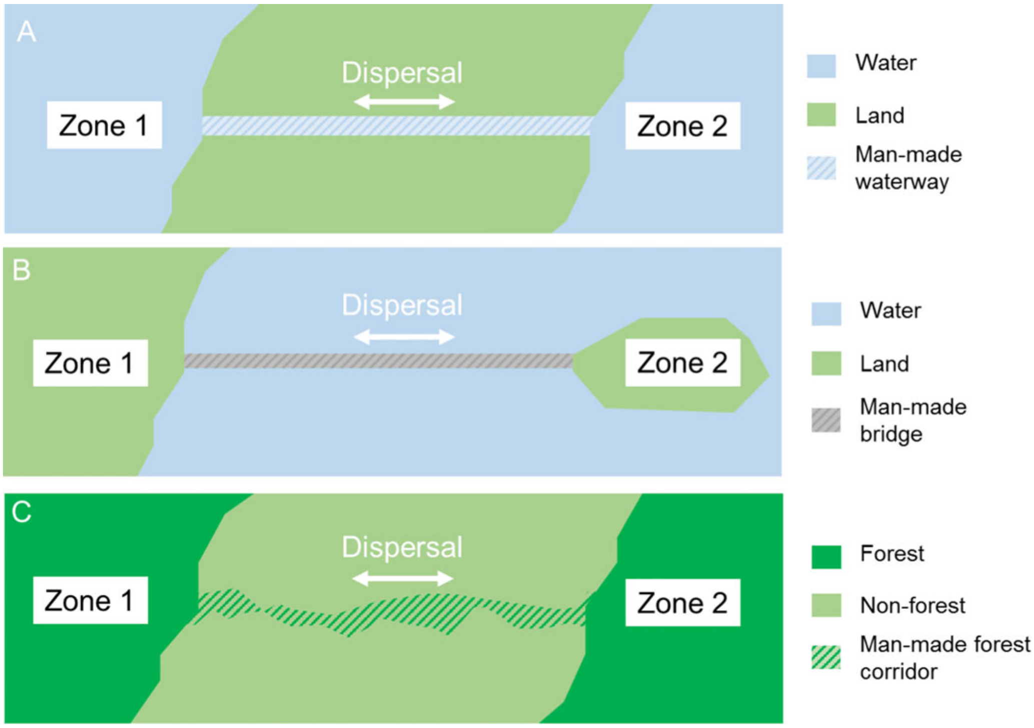

Figure 1 Hypothetical examples illustrating the difficulty of defining "native" dispersal along a corridor pathway. Corridors have been defined as infrastructural developments that allow dispersal between previously isolated biogeographic zones (Hulme *et al.* 2008), for example canals linking ocean basins (A) and bridges linking islands with mainlands (B). However, many other human habitat modifications also create corridors (*sensu* Wilson *et al.* 2009), for example afforestation (C), which is an important conservation tool in facilitating species responses to climate change. At what point do corridors switch from being undesirable drivers of "nonnative" populations to being desirable facilitators of "native" range-shifts?

Guidelines for legislative application

We suggest that this simplified framework would ensure consistency across policy and ecological realms. When faced with evaluating the native/nonnative status of a given population, however, some residual challenges will inevitably persist (OSM Table 2). In particular, status designations may be complicated when organisms make partial use of human vectors during dispersal (Fig. 2). Birds, bats and invertebrates, for example, regularly rest briefly on vessels during overwater crossings, but subsequently resume flight without being transported any significant distance. In these cases, the lines between direct and indirect transport are blurred: do vessels act as static "habitats" that indirectly assist dispersal across oceanic barriers (Fig. 2D)? Or do they act as mobile vectors of direct transport (Fig. 2C)? Transport pathways may also be ambiguous when species colonize areas adjacent to their native ranges, but are also known to be moved via direct transport.

Some tools are available to help resolve these cases, although they are somewhat limited and costly to apply at present. For example, Webber & Scott (2012) recently proposed a method involving the use of potential dispersal envelopes (PDEs), where new colonizers are assessed according to the estimated natural dispersal ability of the species in question. This involves projecting a model-derived PDE around the limits of the focal species' native range, with movements outside that envelope being classed as nonnative. Some authorities, for example the British Ornithologists Union Records Committee, already use assessments of natural dispersal capacity when evaluating extra-limital occurrences (Dudley *et al.* 2006). To use these definitions, however, it is necessary to decide *a priori* which dispersal events should be considered "natural" and therefore included when modelling the species' PDE. This makes the logic underpinning the approach somewhat circular. Furthermore, dispersal capacity is extremely difficult to predict across species. For example, molecular evidence suggests that the thrushes (*Turdus*), a genus dominated by short-distance migrants and residents, have made at least five separate trans-Atlantic colonization events from Europe/Africa to the Americas over recent evolutionary timescales (Voelker *et al.* 2009), underlining the potential for

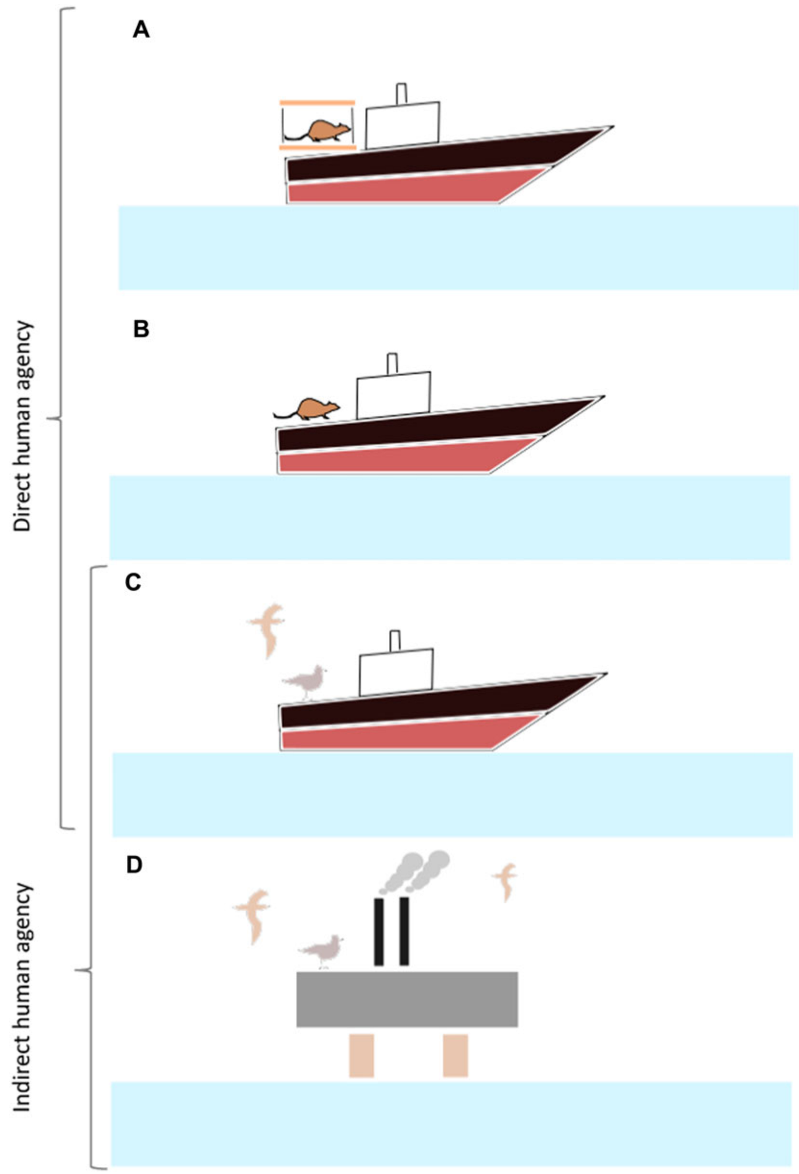

Figure 2 Diagrams illustrating the continuum of human agency in assisting species dispersal across a barrier. When organisms are transported in captivity (A), the degree of direct human agency is readily apparent. In other cases, organisms might remain in a wild state whilst making an entirely human-assisted crossing of a barrier (B). For more mobile organisms, dispersal might be only partially assisted by human transport (C), making the directness of human agency more difficult to assess. The final class of human agency involves purely indirect influences on dispersal (D), whereby human impacts facilitate dispersal or survival to allow species to spread. In this example, stationary offshore installations assist the dispersal of flying organisms across an ocean barrier. This class of human agency could include any habitat alteration that allows a species to expand into a formerly unsuitable area, including anthropogenic climate change.

remarkable extra-range dispersal even in the absence of human involvement.

Given that policy-makers need a framework for species designation that can be applied in a timely and low-cost manner, we advocate a simple approach to the resolution of ambiguous cases, relying on circumstantial indicators of direct human transport (OSM Table 2). For example, organisms with patterns of occurrence that are linked to shipping or airline hubs or road corridors might be precautionarily assumed to arrive via direct transport. This “smoking gun” principle can be applied equally regardless of species dispersive capacity, even amongst those with passive dispersal mechanisms (e.g., wind or water dispersed propagules) - these species are still likely to show a signature of spatial association with human activity when colonizing via direct transport pathways (OSM Table 2).

Some nonnative definitions also specify a timeframe over which “natural” species distributions are assessed (Table 1). Species that re-colonize areas following local extinction are usually considered native, although sometimes a threshold date for contemporary occurrence is applied (e.g., presence within the Neolithic period, Copp *et al.* 2005). Our framework largely obviates the need for these historical date thresholds: colonists are always considered native unless arriving via direct human transport, regardless of past range extents. A residual difficultly in this context is establishing direct human transport if historical records are vague or unavailable (e.g, prehistoric human transport mechanisms). A common, but expensive, solution is to combine available historical records with genetic analyses that can help distinguish populations founded by natural dispersal from those founded by human transport (Avery *et al.* 2013).

Nativeness and "assisted migration"

Many species may lack the capacity to shift their ranges in response to environmental change, either due to dispersal limitation or low productivity within their native ranges (Menéndez *et al.* 2006). This has prompted calls for conservationists to perform "assisted migration," actively establishing new populations in areas where conditions are predicted to become increasingly suitable (Hoegh-Guldberg *et al.* 2008). There has been much debate on the practicalities and ethics of this approach (e.g., Mueller & Hellman 2008; McLachlan *et al.* 2009), but little explicit consideration of how assisted migration fits alongside existing policies related to nonnative species (Schwartz *et al.* 2012).

Assisted migration can be targeted towards areas that lie within the former native range of a species, but where populations are extirpated (i.e., "reintroduction"). For example, the translocation of Florida torreya (*Torreya taxifolia*) to areas 500km north of its current range has been described as a "reintroduction," although it was only present in that area ~65 million years ago (McLachlan *et al.* 2007). In many cases, however, translocation may only be feasible to areas outside the native range of the species. Under our framework, this would result in the establishment of a "nonnative" population, potentially resulting in a conflict with invasive species legislation. On one hand, this could be beneficial in reducing the likelihood of *ad hoc* and poorly-planned independent translocation attempts (McLachlan *et al.* 2009). On the other hand, if invasive species legislation impedes efforts for assisted migration, this could increase the risk of extinction among severely climate-threatened taxa (Hoegh-Guldberg *et al.* 2008; McLachlan *et al.* 2009). This suggests that some legislative flexibility may be necessary in order to deal with particularly acute conservation challenges, although any plans for assisted migration should always be carefully vetted for potential impacts in the new range (Richardson *et al.* 2009).

Conclusions

Management of dynamic populations is more likely to be achievable if policy-makers, ecologists, and conservationists adopt a clear, simple and universal framework that can be applied across all regions and taxonomic groups. This simple measure could greatly enhance our collective capacity to manage and control large-scale species movements, both desirable and undesirable, over coming decades. An important first step in cementing such a framework is agreement between key conservation organizations, for example the IUCN and UNEP, on what constitutes a native population. Such an agreement would increase the probability of widespread uptake by policymakers. Government policies are increasingly proactive towards potential threats (Hulme 2015), and it is important that clear guidelines are provided by the scientific community to avoid law changes that might inadvertently weaken the protection of range-shifting threatened species.

Recently, there have been numerous calls to accept nonnatives as part of emerging anthropogenic ecosystems (e.g., Davis *et al.* 2011), allowing societies to avoid sinking resources into increasingly costly battles against expanding species (Hobbs *et al.* 2014). Proponents argue that our focus should fall on mitigating the negative impacts of species, regardless of their origin, rather than *a priori* screening based on nativeness (Davis *et al.* 2011). However, such screening can significantly improve the success of impact mitigation, as the colonization pathway itself influences the likelihood that nonnative species will bring negative consequences ("origin effects," Buckley & Catford 2016; Fridley & Sax 2014). Human transportation vectors tend to move nonrandom samples of biodiversity, and the characteristics of these species can strongly influence their future ecological and economic impact. Origin and native status can therefore help inform decision-makers about the potential risk of colonizers, alongside other measures of threat (Roy *et al.* 2014, Buckley & Catford 2016). Identifying potentially damaging nonnative species early in the invasion process improves the likelihood of successful control and eradication, underlining the need to carefully screen and classify new species when they first appear in a new region.

In reality, we anticipate that the control of harmful nonnative species will remain a long-term priority for governments worldwide (Paolucci *et al.* 2013; Murcia *et al.* 2014). It is essential that policies use rigorous definitions that can be defended in legal terms, and are carefully tailored to avoid unintended consequences. By adopting a simple, universal criterion to differentiate natives and nonnatives, we believe that stakeholders will face a simplified task in tackling problems and facilitating dynamic ecosystem responses. Moreover, international agreement will make it easier to adapt the framework in response to future changes. Such an adaptive capacity is likely to be critical as the pace of global change escalates, and interventions such as assisted migration become more widespread and necessary. Timely decision-making and effective adaptation are more likely to be achievable if governments and conservation organizations start out on the same page, making an agreement on what it means to be "native" an urgent current priority.

Acknowledgments

We would like to thank MW Schwartz and YM Buckley for their thoughtful suggestions as well as four anonymous reviewers. Publication of this article was funded in part by The Pennsylvania State University Libraries Open Access Publishing Fund.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

OSM Table 1. Indicators of direct transport pathways. Under our definition, only species moving outside their existing ranges via direct human transport should be considered non-native. In cases where the mode of transport is ambiguous, these pathways are still likely to leave a 'signature' in the pattern of occurrence following establishment that can be used as an indicator of direct human involvement. Full references are given in Online Supplementary Material.

OSM Table 2. Examples of indirectly-mediated species distribution shifts. Under our definition, shifts driven indirectly by human impacts such as climate change, habitat change or altered biotic interactions (e.g. predator release), but occurring proximately by natural dispersal from native ranges, should be considered native in newly-colonized areas. Full references are given in Online Supplementary Materials.

References

Avery, J.D., Fonseca, D.M., Campagne, P. & Lockwood, J.L. (2013) Cryptic introductions and the interpretation of island biodiversity. *Mol. Ecol.* **22**, 2313-2324.

Blackburn, T.M., Essl, F., Evans, T. *et al.* (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol.* **12**, e1001850.

Blackburn, T.M., Pyšek, P., Bacher, S. *et al.* (2011) A proposed unified framework for biological invasions. *Trends Ecol. Evol.* **26**, 333-339.

Buckley, Y.M. & Catford, J. (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *J. Ecol.* **104**, 4-17.

Carey, M.P., Sanderson, B.L., Barnas, K.A. & Olden, J.D. (2012) Native invaders—challenges for science, management, policy, and society. *Front. Ecol. Environ.* **10**, 373-381.

Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Divers Distrib.* **10**, 135-141.

Côté, I.M. & Sutherland, W.J. (1997) The effectiveness of removing predators to protect bird populations. *Conserv. Biol.* **11**, 395-405.

Côté, D.D. Rooney, T.P. Tremblay, J. Dussault, C. & Waller, D. (2004) Ecological impacts of deer overabundance. *Ann. Rev. Ecol., Evol., Syst.* **35**, 113-147.

Côté, S.D., Rooney, T.P., Tremblay, J., Dussault, C. & Waller, D.M. (2004) Ecological impacts of deer overabundance. *Ann. Rev. Ecol. Syst.* **35**, 113-147.

Crawley, M.J., Harvey, P.H. & Purvis, A. (1996) Comparative ecology of the native and alien floras of the British Isles. *Philos. Trans. R. Soc. B: Biol. Sci.* **351**, 1251-1259.

Copp, G.H., Bianco, P.G. Bogutskaya, N.G. *et al.*, (2005) To be, or not to be, a non-native freshwater fish?. *J. Appl. Ichtyol.* **21**, 242-262.

Crees, J.J. & Turvey, S.T. (2015) What constitutes a 'native' species?; Insights from the Quaternary faunal record. *Biol. Conserv.* **186**, 143-148.

Davis, M.A., Chew, M.K., Hobbs, R.J. *et al.* (2011) Don't judge species on their origins. *Nature* **474**, 153-154.

Diez, J.M., D'Antonio, C.M., Dukes, J.S. *et al.* (2012) Will extreme climatic events facilitate biological invasions? *Front. Ecol. Environ.* **10**, 249-257.

Diller, L.V., Dumbacher, J.P., Bosch, R.P., Bown, R.R. & Gutierrez, R.J. (2014) Removing barred owls from local areas: techniques and feasibility. *Wildlife Soc. Bull.* **38**, 211-216.

Dudley, S.P., Gee, M., Kehoe, C. & Melling, T.M. (2006) *The British list: a checklist of the birds of Britain*. 7th Edition. Ibis **148**, 526-563.

Durant, S. (2014) Non-native species: UK bill could prompt biodiversity loss. *Nature* **512**, 253-253.

Falk-Petersen, J., Bøhn, T. & Sandlund, O.T. (2006) On the numerous concepts in invasion biology. *Biol. Invasions* **8**, 1409-1424.

Fridley, J.D. & Sax, D.F. (2014) The imbalance of nature: revisiting a Darwinian framework for invasion biology. *Global Ecol. Biogeogr.* **23**(11), 1157-1166.

Galil, B.S. (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Mar. Pollut. Bull.* **55**, 314-322.

Galil, B.S., Nehring, S. & Panov, V. (2007) Waterways as invasion highways - impact of climate change and globalization. Pages 59-74 in W. Nentwig editor. *Biological invasions*. Springer-Verlag, Berlin Heidelberg.

Heger, T., Wolf-Christian, S., & Trepl, L. (2013) What biological invasions 'are' is a matter of perspective. *J. Nat. Conderv.*, **21** 93-96.

Hobbs, R.J., Higgs, E., Hall, C.M., *et al.* (2014) Managing the whole landscape: historical, hybrid, and novel ecosystems. *Front. Ecol. Environ.* **12**, 557-564.

Hoegh-Guldberg, O. *et al*. (2008) Assisted colonization and rapid climate change. *Science* **321**, 345-346.

Hulme, P.E. (2015) Invasion pathways at a crossroad: policy and research challenges for managing alien species introductions. *J. Appl. Ecol.* doi: 10.1111/1365-2664.12470, 1-7.

Hulme, P.E., Bacher, S., Kenis, M. *et al*. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J. Appl. Ecol.* **45**, 403-414.

Lambertini, M., Leape, J., Marton-Lefevre, J. *et al*. (2011) Invasives: a major conservation threat. *Science* **333**, 404-405.

Lawler, J. J., Shafer, S.L., White, D., Kareiva, P., Maurer, E. P., Blaustein, A. R. & Bartlein, P. J. (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology* **90**, 588-597.

Lees, A.C. & Gilroy, J.J. (2014) Vagrancy fails to predict colonization of oceanic islands. *Global Ecol. Biogeogr.* **23**, 405-413.

Livezey, K.B. (2010) Killing barred owls to help spotted owls I: a global perspective. *Northwestern Natur.* **91**, 107-133.

Manchester, S.J. & Bullock, J.M. (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *J. Appl. Ecol.* **37**, 845-864.

McLachlan, J. S., Hellmann, J. J. & Schwartz, M. W. (2007) A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* **21**, 297-302.

Menéndez, R. *et al*. (2006) Species richness changes lag behind climate change. *Proc. R. Soc. Lond. B: Biol. Sci.* **273**, 1465-1470.

Mueller, J. M. & Hellmann, J. J. (2008) An assessment of invasion risk from assisted migration. *Conserv. Biol.* **22**, 562-567.

Murcia, C., Aronson, J., Kattan, G.H., Moreno-Mateos, D., Dixon, K. & Simberloff, D. (2014) A critique of the 'novel ecosystem' concept. *Trends Ecol. Evol.* **29**, 548-553.

Paolucci, E.M., MacIsaac, H.J. & Ricciardi, A. (2013) Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Divers Distrib* **19**, 988-995.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol., Evol., Syst.* **37**, 637-669.

Prentis, P.J., Wilson, J.R.U., Dormontt, E.E., Richardson, D.M. & Lowe, A.J. (2008) Adaptive evolution in invasive species. *Trends Plant Sci.* **13**, 288-294.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* **53**, 131-143.

Richardson, D.M., Pyšek, P. & Carlton, J.T. (2011) A compendium of essential concepts and terminology in invasion ecology. Pages 409-420 in D.M. Richardson editor. *Fifty years of invasion ecology: the legacy of Charles Elton*. Wiley-Blackwell, West Sussex, UK.

Richardson, D.M., Hellmann, J.J. & McLachlan, J.S., *et al.* (2009) Multidimensional evaluation of managed relocation. *Proc. Nat. Acad. Sci.* **106**, 9721-9724.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* **6**, 93-107.

Rothstein, S.I. & Peer, B.D. (2005) Conservation solutions for threatened and endangered cowbird (*Molothrus* spp.) hosts: separating fact from fiction. Pages 98-114 in C.P. Ortega, J.F. Chace & B.D. Peer editors. *Management of cowbirds and their hosts: balancing science, ethics, and mandates*. American Ornithologists' Union, Washington, D.C.

Roy, H. E., Peyton, J., Aldridge, D.C. *et al*. (2014) Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biol.* **20**, 3859-3871

Schlaepfer, M.A., Sax, D.F. & Olden, J.D. (2011) The potential conservation value of non-native species. *Conserv. Biol.* **25**, 428-437.

Schwartz, M.W., Hellmann, J.J., McLachlan, J.M., *et al.* (2012) Managed relocation: integrating the scientific, regulatory, and ethical challenges. *BioScience* **62**, 732-743.

Shrader-Frechette, K. (2001) Non-indigenous species and ecological explanation. *Biol. Philos.* **16**, 507-519.

Simberloff, D. (2014) Biological invasions: what's worth fighting and what can be won? *Ecol. Eng.* **65**, 112-121.

Simberloff, D. & Vitule, J.R.S. (2014) A call for an end to calls for the end of invasion biology. *Oikos* **123**, 408-413.

Strayer, D.L. (2012) Eight questions about invasions and ecosystem functioning. *Ecol. Lett.* **15**, 1199-1210.

Thomas, C.D., Cameron, A., Green, R.E. *et al*. (2004) Extinction risk from climate change. *Nature* **427**, 145-148.

Voelker, G., Rohwer, S., Outlaw, D.C. & Bowie, R.C.K. (2009) Repeated trans-Atlantic dispersal catalysed a global songbird radiation. *Global Ecol. Biogeogr.* **18**, 41-49.

Walther, G.-R., Roques, A., Hulme, P.E. *et al*. (2009) Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.* **24**, 686-693.

Webb, D.A. (1985) What are the criteria for presuming native status? *Watsonia* **15**, 231-236.

Webber, B.L. & Scott, J.K. (2012) Rapid global change: implications for defining natives and aliens. *Global Ecol. Biogeogr.* **21**, 305-311.

Willis, S.G., Hill, J.K., Thomas, C.D. *et al*. (2009) Assisted colonization in a changing climate: a test-study using two U.K. butterflies. *Conserv. Lett.* **2**, 45-51.

Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol. Evol.* **24**, 136-144.

