Which Taxa Are Alien? Criteria, Applications, and Uncertainties

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Human activities such as the transport of species to new regions and modifications of the environment are increasingly reshaping the distribution of biota. Accordingly, developing robust, repeatable, and consistent definitions of alien species that serve scientific and policy purposes has become of prime importance. We provide a set of classification criteria that are widely applicable across taxa and realms and offer guidance on their use in practice. The criteria focus on (a) acknowledging the role of assessment uncertainty, (b) incorporating time since introduction, (c) considering infraspecific taxonomic ranks, and (d) differentiating between alien species whose survival depends on explicit human assistance from those that survive without such assistance. Furthermore, we make recommendations for reducing assessment uncertainty, suggest thresholds for species assessment, and develop an assessment scheme. We illustrate the application of the assessment criteria with case studies. Finally, the implications for alien species management, policy, and research are discussed.

Keywords: biogeography, biological invasions, cryptogenic, distribution range, thresholds

Human activities are increasingly reshaping the spatial distribution of species (van Kleunen et al. 2015, Dyer et al. 2017). Many different activities are involved, including the transport of propagules or live individuals to new regions and modifications of the environment, such as climate change, land-use change, overharvesting, eutrophication, and pollution, which alter the suitability or accessibility to resident and incoming species (Lonsdale 1999, Pecl et al. 2017) and which cause range expansions of species that follow their changing environmental niche. These processes occur with widely different intensities and at varying spatial and temporal scales (Crees and Turvey 2015). Species' ranges are not static and are shaped by natural processes that are independent of human activities and interact with anthropogenic factors (Walther et al. 2009, Pecl et al. 2017), making attribution of the causes of change in species distributions difficult and uncertain in many cases.

As a result, assessing the biogeographic status (native or alien) of species (or more generally, taxa) has become increasingly complicated. Establishing a coherent approach for assessing biogeographic status is essential for several reasons. For scientists, establishing objective criteria that separate native from alien taxa is required if data are to be integrated and communicated. This is a fundamental prerequisite for comparative analyses across taxa, realms, and regions. The issue is also important for conservation managers, policymakers, and the wider public as the numbers of

alien species are increasing rapidly worldwide (Seebens et al. 2017, 2018).

Although the native–alien dichotomy forms the basis for international policies addressing biological invasions (e.g., CBD 2014, EU 2014, IPPC 2017), such policies largely focus on the impact of alien species on the environment, economy, or human health. However, this article does not address the role of potential or actual impacts of alien species, because this is a separate dimension of biological invasions that must be assessed using different criteria and has already received considerable attention (Blackburn et al. 2014, Bacher et al. 2018). Rather, this article focuses on the biogeographic status of species, independent of impact.

The first attempts to define alien species were developed more than 100 years ago, with the plant ecologists de Candolle, Watson, and Thellung being at the forefront (Chew and Hamilton 2011, Kowarik and Pyšek 2012). In the decades following the landmark publications of Lindroth (1957) and Elton (1958), the criteria for defining alien species have been further refined and used ad hoc, leading to a myriad of different terms (Copp et al. 2005, Falk-Petersen et al. 2006) and different interpretations of the same terms. The situation has been exacerbated by the complexity of the phenomenon of biological invasions and the fact that scholars studying different taxa and different environments on different continents and from different disciplines developed their own terms, concepts, and

criteria that invoke different levels of biogeographic resolution and human values.

Substantial conceptual progress has been made in the last two decades in developing criteria for separating native from alien taxa (Pyšek et al. 2004), and especially to determine different stages of the invasion process (e.g., Richardson et al. 2000, Blackburn et al. 2011). Nonetheless, differences remain regarding such criteria and their relevance among scientists and stakeholders with different backgrounds, perceptions, and interests (e.g., Falk-Petersen et al. 2006, Richardson et al. 2011a, Heger et al. 2013). Recently, some authors have proposed accounting for the role of global environmental change that facilitates species range expansions so that only species transported outside of their native range by direct transport should be considered alien (Webber and Scott 2012, Gilroy et al. 2017, but see Hulme et al. 2017). Furthermore, some scientists argue that processes involved in natural colonizations and biological invasions are not that different (Hoffmann and Courchamp 2016), and others are calling for "the end of invasion biology" (e.g., Davis et al. 2011, but see Richardson and Ricciardi 2013 and Wilson et al. 2016). Consistency in defining alien species is pivotal for these discourses and to advance the field of invasion science.

We propose guidelines for assessing the biogeographic status of species on the basis of a set of classification criteria deemed widely applicable across taxa (plants, animals, fungi, and microorganisms), realms (freshwater, marine, and terrestrial), and regions, and we provide guidance for their interpretation and application in practice. These criteria are grounded in biogeographic barriers, human agency, the role of human assistance for survival, and time since introduction. In particular, we consider spatial and temporal criteria and their applicability, the role of assessment uncertainty, and issues related to taxonomic rank. Finally, we discuss the potential implications for research, management, and policy.

Foundations for a harmonized approach to assess biogeographic status

We build on the framework developed by Richardson and colleagues (2000), which Pyšek and colleagues (2004) elucidated for plants and which was later extended to all taxa and elaborated by Blackburn and colleagues (2011). These publications have developed a consensus for the processes associated with human-mediated dissemination of organisms. In essence, these frameworks conceptualize biological invasions as a series of stages separated by barriers. The extent to which species progress along the introduction–naturalization–invasion continuum depends on the ability of individuals to survive, reproduce, and spread after they have been introduced to a new region by human agency.

We call for the explicit acknowledgment of uncertainty in the assessment of the biogeographic status of species. To this end, we provide a map of key concepts (figure 1) and a decision tree (figure 2) to aid in assessing the biogeographic status of species. We further suggest that assessments of the biogeographic status of species across taxa and realms must be transparent—that is, based on a set of criteria (table 1). These criteria have, explicitly or implicitly, already been widely used and can be operationalized to provide a clear link between the research and management of alien species.

In the following section, we review and elaborate the classification criteria that we consider relevant for assessing the biogeographic status of species (figure 1). We discuss features that we consider pertinent to each classification criterion, with a particular emphasis on ambiguous situations and uncertainties, and propose criteria and thresholds for classification (table 2). We then provide recommendations on how each classification criterion should be interpreted to ensure consistency in its usage. Finally, we identify remaining areas of uncertainty and illustrate these with examples.

Criteria for classifying the biogeographic status of species

Subsequently, we present the four classification criteria for assessing the biogeographic status of species.

Criterion no. 1: Crossing biogeographic barriers. Crossing biogeographic barriers is fundamental for separating native from alien species (Wilson et al. 2009). The application of this criterion is straightforward in most situations, but uncertain cases remain (Webb 1985, Pyšek et al. 2004). For instance, uncertainty arises when new occurrences of a species are located very close to, but still outside, the presumed native range of the species and when there is no obvious geographic distribution barrier. Similarly, when species have fragmented or disjunct native ranges, the classification of new occurrences in areas outside the species' core localities can be difficult.

Species are often labeled as alien on the basis of administrative boundaries (e.g., international or subnational borders), although these boundaries often do not match biogeographic boundaries. In such cases, it might be unclear whether species whose native range extends close to the administrative border without obvious biogeographic barriers in between should be deemed native or alien. Conversely, species can be native and alien within the same political entity if that political entity spans more than one biogeographical region. In such situations, a useful approach is to assess the biogeographic status of individual populations of a taxon, as has been done, for example, in some national distribution atlases of vascular plants (e.g., Preston et al. 2002) and in detailed assessments of particular plant taxa (e.g., Australian *Acacia* species; Richardson et al. 2011b). However, assessing the biogeographic status of populations is only feasible when long-term biological inventories have been undertaken or when clear genetic markers are available to assist the identification of original and human-mediated distributions (Sjölund et al. 2017).

This classification criterion is not so easy to apply to species whose native ranges are unknown or highly uncertain or that have evolved as a direct consequence of human activity. The latter include (a) alien species that have hybridized with other alien or native species in the introduced range
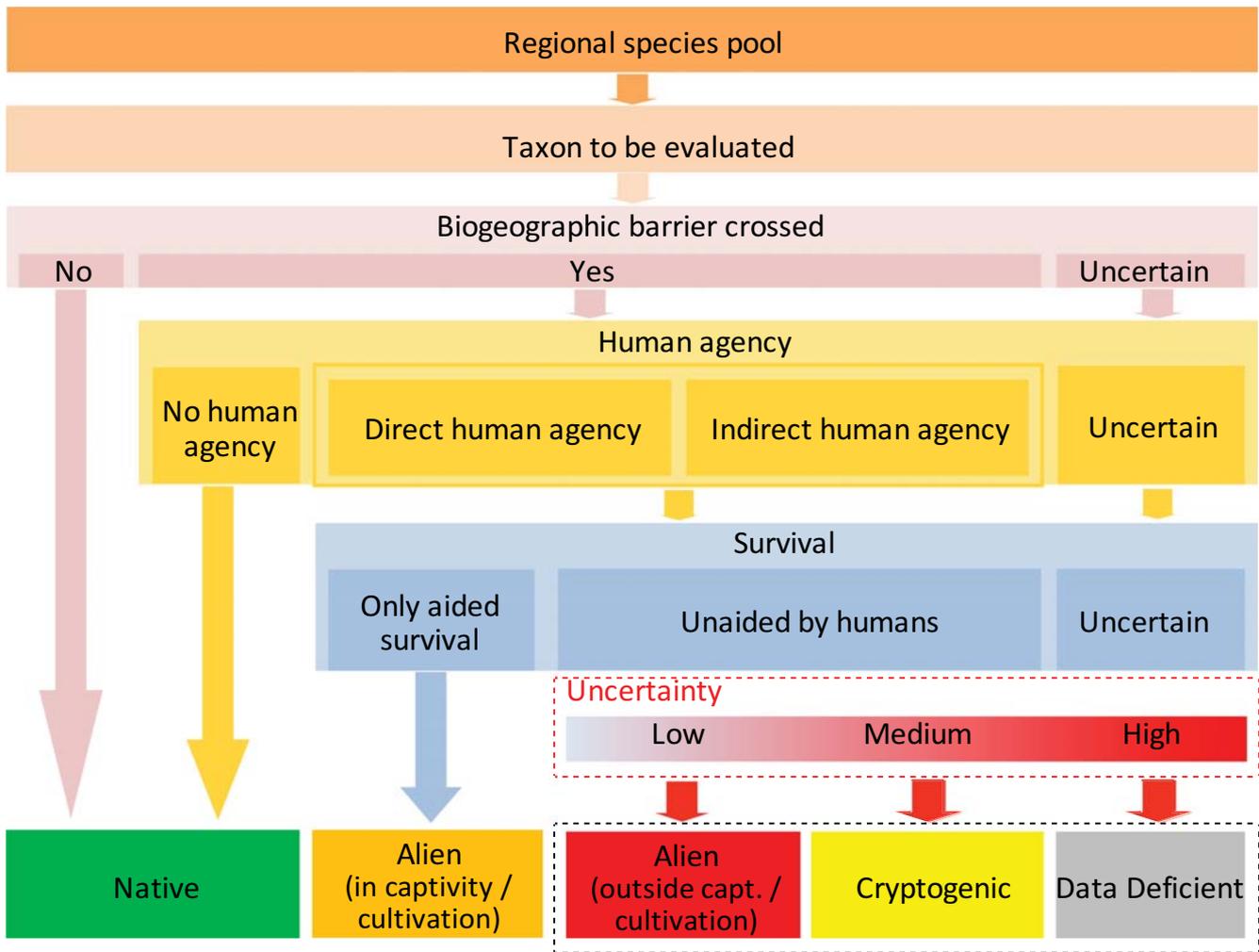
Figure 1. *A conceptual map of the proposed scheme for assessing the biogeographic status of taxa occurring in a regional species pool, showing the four assessment criteria, the levels of uncertainty in assessment, and the resulting assessment outcomes. We propose applying the terms* **cryptogenic** *to taxa of uncertain biogeographic status and* **data deficient** *for taxa for which an assessment of biogeographic status is unfeasible because of the lack of data (see figure 3). For proposed definitions, see table 1. For simplicity, the date of first introduction is not included here.*

(Pyšek et al. 2004) and (b) native species that had originally been ecologically, geographically, or otherwise separated but have been brought into contact by human activity and have subsequently hybridized. Moreover, many plant species cultivated for ornamental or utilitarian reasons have been so strongly modified by breeding that they now represent distinct infraspecific taxa or even species that are distinct from their ancestors. Similarly, some species evolved only in artificial habitats, such as agricultural fields. Both groups of species were termed *anecophytes* by Zohary (1962), a term that only applies to plants. Although this phenomenon is more frequent in plants, cases exist in animals (e.g., domestic cats, dingoes, and the marbled crayfish). These taxa have no native occurrences, because their existence is the result of human activities; therefore, their entire range is alien.

The definition and relevance of biogeographic barriers are also very different for species with different dispersal potential and ecological requirements. For example, dispersal over short distances (e.g., rivers) might not be possible for flightless terrestrial species whose propagules are not dispersed by wind, water, or highly mobile animals. However, species that disperse over long distances by air currents, are good swimmers, survive floating on water, or are occasionally transported by birds might be able to reach oceanic islands (Green 2016, Carlton et al. 2017). In other words, the location and strength of biogeographic barriers are highly contingent on species traits and landscape features, making it unwise to generalize across a wide range of taxonomic or ecological groups.

As a rule of thumb, Richardson and colleagues (2000) proposed that in the absence of knowledge about the transportation mechanism, a distance of at least 100 kilometers between native range and new occurrences should qualify for plant species to be considered as alien (supplemental
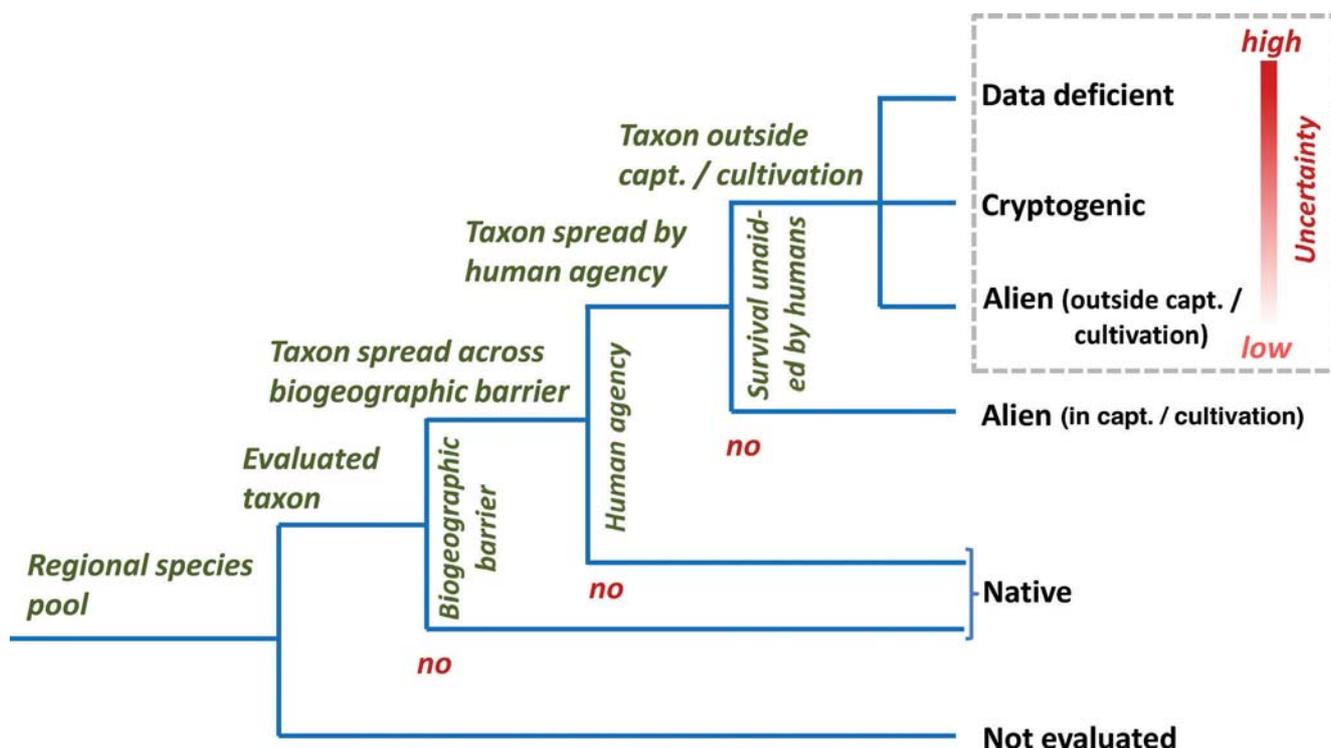
Figure 2. The decision tree for assessing the biogeographic status of taxa occurring in a regional species pool. For proposed definitions, see table 1. Direct and indirect human agency are merged here, because the assessment of these two criteria must be done together in practice. For simplicity, the date of first introduction is not included here.

appendix S1). They added that this threshold should be used critically and fine-tuned to specific situations, such as for islands that are separated from other islands or the mainland by shorter distances. Although not widely applied, we believe that the 100-kilometer threshold is useful in many situations, such as in contiguous continental regions close to the boundaries of biogeographic regions and in large contiguous water bodies such as large lakes, river networks, or coastal regions. However, very steep environmental gradients can still effectively separate native species pools over short distances. Such examples are quite common and include tributaries of separated but neighboring river systems; mountain ranges separated by deep valleys; islands within an archipelago; or ecologically distinct habitats such as caves, springs, and isolated cliffs. Selecting shorter or longer (for highly mobile species) distances as a threshold can be well justified but should be made on the basis of an explicit assessment of the strength of bio geographic barriers.

Criterion no 2.1: Direct human agency. Direct human agency includes the human-mediated physical movement of propagules or individuals, both intentional and unintentional, of any life-cycle stage beyond the native range of the species. There is a wide range of motivations and means by which such movements occur; these can be classified along a continuum from intentional to unintentional. Hulme and colleagues (2008) proposed a classification of pathways that was adopted and further modified by the Convention on Biological Diversity,

with support from International Union for Conservation of Nature (IUCN) Species Survival Commission Invasive Species Specialist Group (CBD 2014). The importance of introduction pathways varies spatially, temporally, and between and within taxonomic groups (Essl et al. 2015b).

The movement of propagules or live individuals involves three processes: (1) collection, (2) transport and introduction into the new region, and (3) subsequent release or escape to sites away from captivity or cultivation. These processes can happen intentionally or unintentionally, but intentional and unintentional collection, transport, and release are multifaceted phenomena that grade into each other (Hulme et al. 2008), and it might be difficult to disentangle human-mediated from natural dispersal (Copp et al. 2005, Wilson et al. 2009). For instance, intentionally introduced individuals are often planted (e.g., trees used in forestry) or held in captivity (e.g., pets), but release of propagules or individuals to areas away from sites of captivity or cultivation can occur accidentally (e.g., by seeds that disperse into adjacent habitats) or intentionally (e.g., by releasing individuals; Hulme et al. 2008). Another important example is the accidental introduction of pathogens with their intentionally or accidentally introduced host species and their subsequent spread to other hosts in the new regions (Roy et al. 2017).

We propose that clear evidence for direct human agency (e.g., documented introductions, releases or escapes, and interceptions with imported goods) as the causal factor for species introduction is needed to fulfill the criterion of a

Number	Criteria	Relevant invasion process(es)	Description	Evidence required	References
1	Biogeographic barriers	Transport, introduction	Crossing of biogeographic barriers between range edge and new occurrence	Evidence for crossing biogeographic barriers (e.g., river catchments, mountain ranges, marine environments separating continents and islands, and persistent oceanographic fronts) between the native and new ranges; the minimum distance between the native and new ranges as a proxy for crossing dispersal barriers.	Richardson et al. (2000, 2011a), Wilson et al. (2009)
2.1	Direct human agency	Transport, introduction, establishment	Direct human contribution to the crossing of biogeographic distribution barriers via the (intentional and unintentional) transport of propagules, gametes, or organisms that may survive and subsequently reproduce	Evidence of direct human agency can include documented introduction events, releases, plantations, and escape events; strong indirect evidence for direct human agency, such as the known association of species with transport pathways, first records in introduction hubs (e.g., ports).	Richardson et al. (2000, 2011a), Pyšek et al. (2004). Hulme et al. (2008, Blackburn et al. (2011), Gilroy et al. (2017)
2.2	Indirect human agency	Transport, introduction, establishment	Substantial indirect human contribution to the crossing of biogeographic distribution barriers via, for example, change in connectivity or the creation of new ecosystems with fundamentally different properties	Evidence for substantial indirect human agency involved in introduction, such as habitat affiliation (e.g., occurrence limited to heavily modified ecosystems), dependence on human-mediated resources (e.g., strongly modified habitats or introduced alien species that are used as essential resource), spread via human-made corridors (e.g., canals or traffic infrastructure).	Richardson et al. (2000, 2011a), Pyšek et al. (2004), Gollasch (2011), Hulme et al. (2008, 2016), Blackburn et al. (2011)
3	Survival without human assistance	Establishment	Survival of individuals without explicit human assistance	Evidence of survival of individuals without explicit human assistance and the time span of survival. It separates alien species that survive unaided outside captivity or cultivation from those that depend on aided survival (e.g., planted in fields, gardens, or greenhouses or held in captivity, such as in zoos or as domestic animals).	Richardson et al. (2000, 2011a), Pyšek et al. (2004), Blackburn et al. (2011)
4	Date of first introduction	All invasion processes	Provides an indication of how long an alien species has been present in a region (ideally both in and outside of captivity or cultivation). In many cases (e.g., Europe), there is a clear and important difference in when alien species were introduced (before or after the start of the European Age of Exploration in 1492)	Year of introduction in confinement (for species introduced on purpose). Year of first record of an occurrence without human assistance (as proxy for year of first occurrence).	Kowarik (1995), Richardson et al. (2000, 2011a), Crees and Turvey (2015)

taxon being deemed alien. However, only in a minority of cases will the introduction and release or escape of a species in the new range be observed and documented. More often, direct human agency is inferred through association of first occurrences with relevant introduction pathways. If such inferences are deemed robust (low uncertainty; see discussion on assessment uncertainty), then such data are sufficient to classify a species as alien outside of captivity or cultivation.

Criterion no. 2.2: Indirect human agency. Besides direct physical movement of individuals from one region to the other, changes in the distributions of species can be the indirect consequence of human actions that change biophysical characteristics of the environment (Crees and Turvey 2015, Lewis and Maslin 2015). These changes might modify the suitability of a region for a particular species via a range of potential mechanisms such as habitat modification, anthropogenic climate change, the creation of novel resources,

Table 2. An overview of the potential changes in region invasibility (**sensu** *Lonsdale 1999*) due to indirect human agency, which may affect the survival, reproduction, and spread of taxa colonizing new regions. Note that we suggest that substantial indirect human agency involved in changes in region invasibility is necessary to qualify a taxon as alien or cryptogenic and that we suggest that several of the mechanisms identified below are not relevant for categorizing taxa as alien (see main text).

Indirect factor	Explanation	Relevance for species spread	Evidence required	Suggested thresholds	References
Land-use change	Human-mediated changes in land use and anthropogenic disturbance regimes affecting ecosystem distribution and quality	Increase in invasibility of the focal region for species adapted to the new ecosystems, decrease for other species	Species ecology (e.g., restriction to heavily modified ecosystems)	Not considered relevant for separating native from alien taxa	Richardson et al. (2011a)
Anthropogenic climate change	Human-mediated change in global to regional climates	Increase in the invasibility of the focal region for species adapted to the new climates	Species ecology (e.g., preferences of warm climates and climatic habitat suitability as predicted by Species Distribution Models)	Not considered relevant for separating native from alien taxa	Devictor et al. (2008), Walther et al. (2009), Webber and Scott (2012)
Change in resource availability	Human-mediated changes in availability of important resources (e.g., nutrients, food, and nesting sites)	Increase in the invasibility of the focal region for species dependent on increased or newly available resources	Interaction of species ecology with human-mediated environmental change	Not considered relevant for separating native from alien taxa	Mack and Smith (2011), Richardson et al. (2011a)
Change in biotic composition and interactions	Human-mediated changes in biotic interactions (e.g., functional loss of guilds as top predators or herbivores) due to selective pressures (e.g., hunting and fishing)	Increase in invasibility of the focal region due to changes in biotic interactions, such as for species released from the competition of native species (e.g., mesopredator release)	Observed range expansions of species after functional extinction of competitors, predators, or pathogens	Not considered relevant for separating native from alien taxa	Snow and Perrins (1998), Lonsdale (1999), Ritchie and Johnson (2009), Richardson et al. (2011a)
Change in connectivity	Human-mediated increase in connectivity between similar ecosystems or realms (e.g., interoceanic and interriver basin canals or terrestrial transport networks such as roads and railways)	Increased likelihood of invasion into the focal region for species from regions with increased connectivity	Existence of human-made corridors that connect previously biogeographically separated regions	Taxa that spread into new regions via human-made corridors that connect previously biogeographically separated regions are alien	Richardson et al. (2011a), Gollasch (2011)

the elimination of native competitors or predators, or, most notably, increasing connectivity via infrastructure corridors (e.g., Gollasch 2011, Crees and Turvey 2015; see our table 2). Many of these indirect human-mediated changes are gradual causing subtle to pervasive changes to a region's invasibility.

The construction of infrastructure corridors has resulted in increased connectivity between regions, thereby facilitating the spread of species across biogeographic boundaries (Wilson et al. 2009). This is particularly true for aquatic organisms that have spread via canals linking seas or river catchments that have been separated for millions of years (Copp et al. 2005, Gollasch 2011). Such taxa can unequivocally be considered alien.

Changes in the suitability of a region may occur for many reasons. The human alteration of landscapes has created new habitats and resources and has facilitated many large-scale range expansions, such as the twentieth-century spread of the Eurasian collared dove (*Streptopelia decaocto*) in Europe

(Snow and Perrins 1998) and the upstream range expansion of fishes in the River Danube and associated invasions of the River Rhine via the Rhine–Main–Danube canal (Copp et al. 2005). The human-mediated extirpation of top predators in many regions of the world has facilitated range expansions of competitively inferior smaller predators (mesopredator release; Ritchie and Johnson 2009). Similarly, ongoing climate change attributable to human activities (IPCC 2013) has become a key driver of the expansion of species toward previously uninhabitable regions (Walther et al. 2009). In particular, mobile taxa, such as birds (Devictor et al. 2008), are already colonizing new regions far from their historic range.

In many such situations, range expansions are only possible because humans provided new essential resources for the expansion of a species in a new region. For instance, the recent spread of the Mediterranean nettle-tree butterfly (*Libythea celtis*) into central Europe (Rabl and Rabl 2015) was made possible by the previous introduction of its food plant,

the nettle tree (*Celtis australis*) for ornamental use, along with climate change that allowed winter survival of the insect.

As a specific phenomenon, mobile debris from humans such as drifting plastic in the ocean may foster the long-distance spread of sessile species; such floating human-made structures may be big in size and colonized by many marine species, as has been shown for debris washed ashore in North America after the tsunami in Japan in 2011 (table 2; Carlton et al. 2017).

However, in the vast majority of cases, the causal factor or factors responsible for such rapid range expansions and the potential human-mediated contribution remain largely unknown. Therefore, attributions are usually best guesses based on often circumstantial evidence and expert opinion. Uncertainty in such situations will remain large. Furthermore, the scale and velocity of global environmental change in the future will likely make range shifts of species a widespread phenomenon (Webber and Scott 2012). In most cases, but not necessarily all, newly suitable regions will be located in proximity to the current ranges of expanding species.

The contribution of indirect human agency to the spread of species is often difficult to authenticate (with the important exception of infrastructure corridors that connect previously separated regions); therefore, doing so is associated with substantial uncertainties. The degree to which indirect human-mediated environmental change should be considered in assigning alien status to a species has become strongly contested, and some authors and legal instruments suggest that it should not be considered at all (Webber and Scott 2012, Gilroy et al. 2017) or only in very specific situations (EU 2014). These authors reason that range shifts of species in response to environmental pressures are an increasingly common phenomenon that is necessary to ensure species survival and that such movements should not be considered as biological invasions. Besides, attributing the colonization of new areas to the underlying factors is often associated with substantial uncertainties for indirect human-mediated contributions to species spread (table 3).

Following the approach advocated by Richardson and colleagues (2000, 2011a), we suggest using a conservative approach for classifying species as alien on the basis of indirect human agency. This ensures that species expanding their range into adjacent territories presumably in response to changing climate, habitat, or resource availability are *not* automatically classified as alien. Therefore, we propose that evidence for substantial indirect human agency that is decisive for a taxon to colonize a new region is necessary for this taxon to fulfill this criterion and therefore be classified as alien. Such substantial indirect human agency might involve the construction of infrastructure corridors that breach biogeographic barriers, such as canals between seas or river catchments (Gollasch 2011, Hulme et al. 2017) or bridges creating new connections with islands; the creation of new ecosystems with fundamentally different properties (e.g., heated indoor environments in cool climates); or the provision of new essential resources (e.g., alien plants that are crucial as food for expanding animal species). We acknowledge that the extent of indirect agency facilitating the spread of a species is in many cases difficult to quantify in practice, so a certain level of uncertainty will remain in such situations, and this needs to be effectively communicated.

Criterion no. 3: Survival without human assistance. This criterion is not necessary to classify taxa as alien, but it is critical to discriminate between aliens that survive only with human assistance and those that survive outside of captivity or cultivation—that is, without explicit human assistance. The latter species pool includes casual, established (naturalized), and invasive alien species (*sensu* Richardson et al. 2000, Blackburn et al. 2011); distinguishing between these advanced invasion stages is beyond the scope of this article. The former species pool includes those alien species for which not only the presence in a region is due to human activities but also their survival and propagation depends on purposeful human assistance (e.g., the sowing and tendering of garden and greenhouse plants or the feeding of animals held in captivity). Such species include pets, zoo animals, garden plants, and species used in forestry, agriculture, and landscaping. This species pool can donate species to the latter over time, because alien species that are dependent on human assistance often only start to spread after substantial time lags (Kowarik 1995). Note that unlike Blackburn and colleagues (2011), we propose the term *outside of captivity or cultivation* rather than *in the wild* because the latter term has proved difficult to implement in practice and has created confusion between different users.

Although the assessment of this criterion is straightforward in principle, the absence of data often precludes its explicit evaluation. Furthermore, in some situations, it is unclear whether an occurrence of a species represents unaided survival. For example, planted or sown plant species used in forestry, landscaping, or growing in abandoned gardens or previously cultivated places may survive for long periods as remnants of cultivation. We suggest that only if there is evidence of further unaided reproduction and dispersal of planted individuals should such occurrences be considered to fulfill this criterion. We note that for cultivated plants, the proposed threshold implicitly invokes sexual or vegetative reproduction as necessary for qualifying a species as alien without human assistance (survival alone only qualifies for being a cultivation remnant; Pyšek et al. 2012) and therefore as an alien dependent (at least at some point in its life cycle) on human assistance.

An important aspect in applying this classification criterion is the time span required for classifying an individual (or a population) as having survived unaided by human assistance. There is a consensus among ecologists that very short-term occurrences (up to a few weeks) are deemed insufficient to qualify a species as fulfilling this criterion (see discussion in Blackburn et al. 2011).

Table 3. Criteria for the delineation of cryptogenic taxa (i.e., those of unknown biogeographic origin, which cannot be categorized as native or alien; Carlton 1996, Richardson et al. 2011a). We propose that several of the criteria have to be fulfilled by a taxon so that a medium uncertainty of the assessment qualifies it as cryptogenic.

Indications of alien status	Definition	Relevant invasion stages	Evidence required	References
Biogeographic barriers	Taxon range suggests human-mediated range expansion	All	Biogeographically anomalous distribution (e.g., disjunctions implausibly caused by natural biogeographic processes)	Söderström (1992), Wilk-Wozniak et al. (2016)
Phylogeography	Taxon most closely related to the focal species occur in distant regions, or genetic population structure within a species suggests human-mediated introduction	All	Geographic genetic population structure (e.g., indication of human-mediated admixture)	Pérez-Portela et al. (2013)
Genetics	Genetic composition of the populations in the new range	All	Indications of recent introduction (e.g., low or absent genetic variability within and among populations as indication for recent founder populations; close genetic relationship with populations from distant regions of the undisputed native range; indication of admixture likely caused by human introduction)	Webb (1985), Pérez-Portela et al. (2013)
Species ecology	Taxon ecology (e.g., habitat affiliation) suggests absence of native populations	All	Restriction of a taxon in the focal region to human-made or highly modified habitats	Söderström (1992), Wilk-Wozniak et al. (2016)
Recording history	Absence of old records	All	Absence of old records of a taxon in the focal region despite historical recording effort	Söderström (1992)
Spread characteristics	Spread behavior of the populations in the new range: rapid expansion and high dispersal rate from existing populations	Spread	Rate of spread of a taxon in the focal region suggests a recent human-mediated establishment (e.g., from a site of introduction, captivity or cultivation)	Webb (1985), Söderström (1992)
Population persistence	Absence of permanent populations	Release, establishment	Populations of a taxon in the focal region are not permanent or dependent on the human-mediated influx of propagules	–
Association with means of introduction	Association of propagules or live individuals with potential means of introduction (e.g., ballast water)	Transport, release	First records of a taxon in the focal region at the likely point of human-mediated introduction (e.g., arboreta, harbors, and railway stations)	Söderström (1992), Hewitt et al. (2004)

Therefore, escapes or releases of pets or zoo animals and introductions of species that were only able to survive up to a few weeks are not considered sufficient to classify them as having survived unaided by humans. Similarly, we recommend that propagules (seeds and dormant stages of animals) introduced to a new region and that remain viable for long time periods do not qualify as fulfilling the criterion of unaided survival if they do not become active (i.e., germinate or hatch).

There is, however, less agreement on the classification of species that survive over many weeks to several months under favorable conditions but that are not able to survive unfavorable periods (e.g., winter months for many tropical species in temperate regions). We suggest that such species should be classified as alien without human assistance but only as casual if the unaided survival is for several weeks to a few months. This approach has already been widely used in many alien species databases and inventories (e.g., DAISIE; *www.europe-aliens.org*). We acknowledge that there is a gray zone and that the minimum period deemed sufficient is dependent on the specific context (e.g., generation time of the focal species) and therefore open to a certain amount of personal judgement.

Criterion no. 4: Date of first introduction. Human-mediated species introductions began many millennia ago (e.g., dingoes occurred in Australia approximately 5000 years ago; Crees and Turvey 2015). There have been massive temporal changes in introduction pathways, propagule pressure, source areas, and invasibility of the target regions. Data generally become scarcer the further back in time we go (Webb 1985, Crees and Turvey 2015).

However, most alien species were introduced relatively recently. In particular, the gradual development of a global trade network following European-led colonization in the fifteenth to eighteenth centuries radically changed the trajectories of biological invasions (Seebens et al. 2017). Some of these regions (e.g., isolated islands) had previously not been colonized by humans, whereas other regions already had human populations that may have introduced alien species prior to European colonization (Hofman and Rick 2017).

How long propagules or live individuals have been resident in an area is an important consideration when seeking to separate old introductions from recently introduced alien species. The residence time can refer either to the time since a taxon was introduced into the new region in a

confined environment (e.g., as cultivated plants in gardens, aquaria, ornamental ponds, plantations, or agriculture) or to the time since they were released or escaped from captivity or cultivation. For biological invasions, the former is relevant to the study of spatiotemporal introduction patterns and processes of spread once propagules have been moved to the new region. The latter is relevant for assessing the residence time of an alien species occurring outside captivity or cultivation and its invasion success; there can be an extended time lag between both processes (Kowarik 1995). It is also important to recognize that propagules and certain life-cycle stages might remain dormant over extended periods after introduction into a new region. Thus, the emergence of a first population can be much more recent than the introduction of propagules. However, the date when dormant life stages were first introduced to a new region is rarely known.

Before the late fifteenth century, the movement of species beyond their native range was in most cases spatially restricted. In the centuries following the discovery of the Americas by Europeans, however, a truly global network of species exchange characterized by high propagule pressure emerged (Seebens et al. 2017). Therefore, using the year 1492 to separate ancient alien species (i.e., archaeobiota) from more recent ones (i.e., neobiota) has become widely accepted (Richardson et al. 2000, 2011a, Crees and Turvey 2015) and proven to be a useful distinction, particularly in Europe (Pyšek et al. 2005) and the Americas. We propose to keep this date as a reference point for distinguishing ancient and more recent aliens while recognizing that it is not always clear whether species have been introduced before or after this date. However, in specific contexts and other regions, different temporal thresholds might be more useful to characterize important regional break points in introduction characteristics. Therefore, the additional use of region-specific temporal thresholds may be useful but should be made explicit. For example, the arrival of the First Fleet to Australia in 1788 marked the onset of introductions of alien species by European settlers, and the opening of the Suez Canal in 1869 sparked a surge of invasions of species native to the Red Sea into the Mediterranean Sea (Gollasch 2011).

We note that archaeobiota are often considered to be important for nature conservation. For instance, in most central European countries, archaeophytes are evaluated in national Red Lists, and threatened archaeophytes such as ruderal and segetal species (mostly of south European or western Asian origin) and some archaeozoa are targeted by conservation action (e.g., Zając et al. 2009). Some of these archaeobiota later followed the European-led colonization of other regions of the world, where they were introduced after 1492 and where they must be considered neobiota. To conclude, in the majority of cases, alien species biosecurity policy focuses implicitly on relatively recently introduced alien species (i.e., neobiota; Seebens et al. 2018) and even on not-yet-introduced species.

Considering assessment uncertainty

The application of assessment criteria is unavoidably associated with uncertainties that arise for several reasons (e.g., incomplete or contradictory data, attributing relevance to different data sets, or linguistic ambiguities). Some uncertainties can be reduced through the acquisition of additional data and new methods, resulting in improved understanding of the species under evaluation, or with better definitions of the criteria (to reduce linguistic uncertainty; Blackburn et al. 2014). However, the unraveling of uncertainty is often not feasible in practice. Indeed, some types of uncertainty can never be sufficiently reduced. Consequently, we suggest the inclusion of uncertainty estimates (i.e., the degree of uncertainty) associated with alien species categorizations according to any of the four criteria above. We suggest a categorization into three levels—high, medium, and low—based on approaches used by the Intergovernmental Panel on Climate Change to classify climate-change uncertainty (Mastrandrea et al. 2011) and adapted by Blackburn and colleagues (2014) and Bacher and colleagues (2018) to classify the uncertainty with which the environmental and socioeconomic impacts exerted by alien species are known.

We propose that *low uncertainty* be assigned when there is direct evidence to support the assessment, when the data are reliable and of good quality, and where all evidence points in the same direction. *Medium uncertainty* should be assigned when there is some evidence to support the assessment but the quality or quantity of the data is insufficient for definitive assessment. We suggest that *high uncertainty* is defined when there is a lack of evidence to support the assessment (e.g., a newly identified species in a region without any information available that allows assessment of the biogeographic status) or data are of low quality or ambiguous. Uncertainty levels correspond to probabilities that the assigned assessment outcome is the correct one (figure 3). *Low uncertainty* means the assessor feels that there is a more than 90% chance that the assessment is correct. *Medium uncertainty* corresponds to a 75%–90% chance of the assessment being correct. *High uncertainty* corresponds to a 50%–75% chance of correct classification and means the assessor concludes that a lack of necessary data renders the assessment highly uncertain. Therefore, an assessment of the biogeographic status of a taxon is impossible, and the assessment outcome is *data deficient*.

The assessment of uncertainty levels can differ among experts because people may assign different relevance and uncertainties to the same data or different people may be aware of different data sources; multiauthor assessments or other forms of group consultation processes are therefore recommended. Uncertainty may also change over time as new data become available. This can result in changes over time of the assessment outcome of a given species in a given region. For instance, for the second edition of the checklist of alien vascular plant species of the Czech Republic, a total of 41 species that were considered to be alien in the first edition were removed from the list because new archaeobotanical evidence resulted in them being reclassified as native (Pyšek
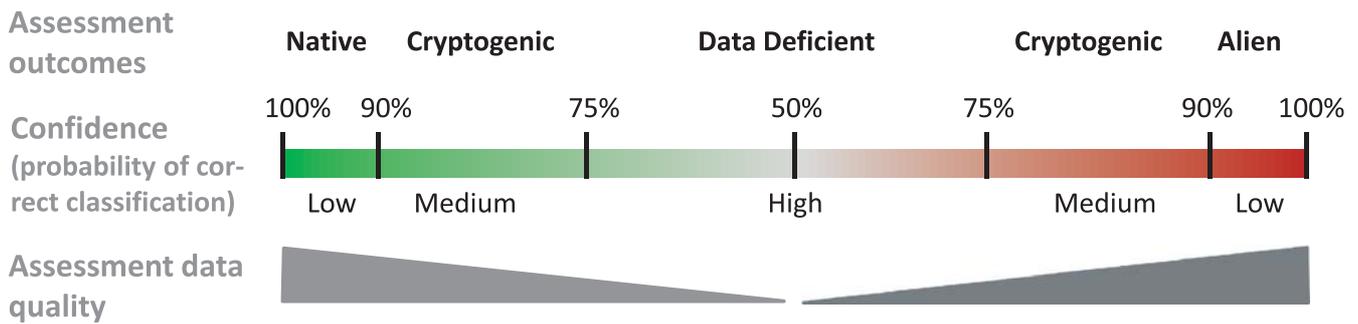
*Figure 3. The recommended classification of uncertainties (i.e., the probability that the assessment result is correct) in the assessment of the biogeographic status of taxa into different uncertainty classes, as well as the corresponding assessment outcomes. In principle, any taxon is either native or alien to a region of interest. Note that a 50% probability of correct classification is equal to a by-chance outcome. Ambiguous, insufficient, or missing data for the assessment may introduce uncertainties. If the assessor assumes that the likelihood that the assessment is correct is more than 90%, the assessment outcome is **native** or **alien**. If the likelihood that the assessment is correct is 75%–90%, the assessment outcome is **cryptogenic**. If uncertainty is even higher, the assessment outcome is data deficient.*

et al. 2012). Using palaeoecological methods, van Leeuwen and colleagues (2008) showed that at least six presumed alien species are, in fact, native to the Galápagos archipelago. A similar example is the freshwater fish crucian carp (*Carassius carassius*) in the British Isles. It was initially believed to be alien (presumably introduced in the 1400s along with common carp, *Cyprinus carpio*) because of a lack of mention of the species in historical literature. It was then believed by some to be native because of the identification of pharyngeal bones from the species at a Roman archaeological site near London. But more recently, it was reclassified as alien with a low uncertainty on the basis of genetic evidence (Jeffries et al. 2017); it was very likely introduced at the same time as the common carp after all.

Identifying cryptogenic and data deficient taxa

Carlton (1996) introduced the term *cryptogenic* to classify species for which indications for alien status in a study region are available but for which definitive evidence is lacking, implying that the species could be native. In the absence of direct evidence, which is often the case for species of taxonomic groups whose native ranges are insufficiently known, definite assessment of the biogeographic status is de facto impossible. Therefore, the identification of probable alien species must be based on circumstantial evidence, taking a range of factors into account (table 3).

Several studies have shown that cryptogenic species can be important constituents in some taxonomic groups and that they may differ from species that are unambiguously identified as alien in several ways (e.g., Peréz-Portela et al. 2013, Essl et al. 2015a, Wilk-Woźniak et al. 2016). For instance, cryptogenic bryophytes differ from alien ones in terms of habitat affiliation (the former are mostly restricted to heavily modified habitats; Essl et al. 2015a). However, even when the biogeographic status of a species is intractable, the assessment of the invasion stage may be done independently and

may yield valuable information. Therefore, we suggest using the combination of cryptogenic and the invasion stage of a species as an additional qualifier (e.g., established cryptogenic species).

We propose that taxa should only be classified as cryptogenic if an assessor judges the focal species to be alien (respectively native) to the focal region with a likelihood of 75%–90% (figure 3). There will be situations in which the lack of data does not allow for an assessment of the classification criteria at all or only permits a very tentative assessment. We suggest introducing the category *data deficient* for such assessment outcomes. This category is analogous to the extinction risk assessment procedure in Red Lists (IUCN 2017).

Taxonomic ranks and biogeographic status

Taxa of all ranks that fulfill the first three proposed criteria can be classified as alien outside of captivity or cultivation. However, in most inventories and databases, only species and subspecies are included, whereas lower infraspecific taxa (e.g., varieties and cultivars) are either excluded or only included if they are morphologically well separated (e.g., DAISIE). This lack of inclusion of lower-ranking infraspecific taxa in part reflects the difficulty in recognizing and identifying them morphologically given the large number of horticultural cultivars. In addition, many varieties or cultivars of popular ornamental plant species lose typical cultural traits when they escape from cultivation. Therefore, dedicated studies are necessary to assess the wide range of cultivars in alien floras (Pergl et al. 2016).

If the cultivars pertain to a species that is also native in the focal region, then the spread of escaped cultivars may lead to introgression with native populations (Pyšek et al. 2013). For instance, *Aquilegia vulgaris* is a popular native garden plant in central Europe. Molecular studies have shown that many native populations of this plant have been affected by introgression (Petit 2004), whereas this phenomenon

is difficult to identify morphologically. There are more examples of species, such as hazelnut (*Corylus avellana*), in which widespread introgression into native populations from cultivated plants is impossible to detect morphologically and can only be detected using molecular methods (Petit 2004). Therefore, although species may be native to a region, infraspecific taxa or genotypes from other regions may have been introduced by human activity. The most prominent example is the spread of European *Phragmites australis* genotypes in North America, where the species is also native but both phylogeographic groups are taxonomically classified as different subspecies (Packer et al. 2017). The subspecies native to Europe qualifies as alien in North America. Similarly, cultivars of native plant species or races of native animal species may have been bred in the native region, and such infraspecific taxa then also qualify as alien.

Another important case in this context occurs when a species is no longer extant in its original native habitats but has colonized human-made habitats. If these populations originate from source populations representing different infraspecific taxa from outside the focal region, then we propose that they should be classified as alien. For instance, in central and western Europe, the native shrub *Cornus sanguinea* is widely planted and often spreads from sites of cultivation. Frequently, planted individuals belong to subsp. *australis*, which is native to southeastern Europe but does not occur in the region of introduction. Accordingly, the occurrences of *Cornus sanguinea* subsp. *australis* are considered alien in central European checklists (e.g., Essl and Rabitsch 2002).

Hybridization can cause the introgression of genes of an alien species into a native gene pool. A prominent example are backcrossings of *Populus × canadensis*—which is a hybrid of the European poplar *P. nigra* and the North American *P. deltoidea*—with *P. nigra* (i.e., with one of their parents). Where *P. × canadensis* and *P. nigra* cooccur (e.g., in central European floodplains), genetic studies have revealed that a substantial proportion of saplings are backcrosses (Smulders et al. 2008). Similarly, native red deer (*Cervus elaphus*) and alien Sika deer (*Cervus nippon*) frequently hybridize in Europe and produce fertile offspring that should be considered alien (Smith et al. 2015). A quantitative picture can be inferred from the Czech alien flora that includes 23 hybrids of archaeophytes and 33 of neophytes with native species (Pyšek et al. 2012).

To conclude, the introduction and spread of low-ranking infraspecific and hybrid taxa is an important phenomenon, and we argue that populations of such taxa should be classified as alien. Therefore, recording infraspecific taxa that can be safely identified in the field is valuable. We also suggest that flagging these taxa in comparative analyses is useful because of the large uncertainties and biases involved. However, if introgression has not (yet) led to the recognition of an infraspecific taxon, then we recommend that such taxa should not be considered alien.

Following established approaches, and although genetically modified organisms (GMOs) do share some commonalities with alien species (Jeschke et al. 2013), we propose that they should not automatically be considered to be alien organisms, except when they fulfill the generally applicable classification criteria.

Applicability across taxonomic groups and realms

The conceptual approach and the recommendations presented here are intended to be applicable across all taxonomic groups. In practice, several issues affect the assessment of the biogeographic status between taxonomic groups.

First, for bacteria, archaea, and many groups of eukaryotic fungi, the species concepts used for macroorganisms are difficult to apply. Therefore, different approaches are used in microbial and fungal taxonomy, and these have changed in recent decades as a consequence of progress in molecular science (Sharma et al. 2015). In the twenty-first century, the microbial species concept that has become most widely accepted is the polyphasic species concept, which is based on combining several characters (e.g., morphology, physiology, biochemistry, and genetics). The species concept used for microbes is still in flux, and new techniques that are currently on the horizon are expected to shape future developments (Sharma et al. 2015). These substantial specificities of microbial species concepts and the severe lack of data on other criteria relevant for classifying the biogeographic status of species (e.g., on native range and the role of human contribution to range extensions) render the classification of microorganisms as native or alien notoriously difficult. However, there is an urgent need to consider them in such classifications, particularly because of their potential devastating effects on biodiversity and humans (Roy et al. 2017).

Second, there are vast differences in biogeographic knowledge between taxonomic groups, and these are exacerbated between regions and realms. Most taxonomic groups (e.g., fungi and microbes), most regions (the tropics in particular), and most species in certain ecosystems (e.g., deep-water marine and subterranean environments) are understudied. These biases in knowledge have important ramifications for the assessment of the biogeographic status of species and the associated uncertainties.

Third, there are specific differences between realms (freshwater, marine, and terrestrial) that are relevant for alien species classification. For instance, for freshwater organisms, the most relevant biogeographic barriers are often those that separate river catchments. For marine species, besides physical connectivity and distance between marine regions, important barriers for species distributions involve gradients in biophysical characteristics of the aquatic medium (e.g., temperature, salinity, and depth of the water body). Over relatively short distances, contiguous marine regions are usually relatively well connected with each other, because marine currents are effective conduits for the dispersal of propagules. Such marine currents may introduce unidirectional connectivity, because dispersal is much easier along a prevailing current than against it.

These specificities of the marine realm must be considered when defining thresholds for the proposed classification criteria.

Applicability in translocations, managed relocations, and reintroductions

Translocations involve the deliberate movement of organisms from one site and release at another, and they have been recognized and applied as a viable conservation strategy under specific but limited preconditions and when applied following specific procedures (IUCN 2013).

From a biogeographic point of view, intentional translocations can be classified into *restocking* (i.e., the introduction of individuals from other populations into a remnant population to increase population size and genetic variation), *reintroductions* (i.e., the planned introduction of a regionally extinct taxon into its former native range), and *managed relocation* (i.e., the planned introduction of a taxon outside its [former] native range; Richardson et al. 2011a, IUCN 2013). Restocking and reintroduction may involve individuals of infraspecific taxa other than those which existed at a site, as has been the case for restocking cougars (*Puma concolor*) from Texas to Florida (Conroy et al. 2006) and for the reintroduction of the European beaver (*Castor fiber*) into many European countries (Frosch et al. 2014). Although such translocated individuals are native at the species level, they are alien at lower taxonomic levels if they belong to an infraspecific taxon that is not native in the target region of the translocation. Similarly, in several cases, organisms have been released outside their native range to perform specific ecological functions of now-extinct species (e.g., translocations of extant tortoises to replace the extinct Mauritian tortoise; Griffiths et al. 2010). The same logic will apply when techniques for resurrecting extinct species from preserved genetic material become available (Seddon et al. 2014).

Managed relocation aims to reduce potential negative effects of global change (especially rapid land-use and climate change) on defined biological units such as populations, species, or ecosystems by moving species from their current areas of occupancy to locations where the probability of future persistence is predicted to be higher (Richardson et al. 2009). In most cases, species earmarked for managed relocation would be classified as alien in the target region, and the risk of such species becoming invasive at that site is a key consideration when deciding whether to undertake the translocation (Richardson et al. 2009). This is analogous to classical biological control. Biocontrol is an important tool in invasive alien species management and so conservation more generally, but the agents used usually qualify as being alien and incur risks that must be assessed before releases are made.

Conclusions

We have reviewed basic criteria and presented guidelines for separating native from alien species and for fine-tuning key concepts that should reduce ambiguity, support cross-taxa analyses, and improve communication among scientists, managers, decision-makers, and the wider public.

Unambiguous terminology is crucial for enforcing policies and legislative tools. In fact, many legal or policy instruments are based on an explicit terminology (e.g., EU 2014), and the criteria and guidelines proposed by the present publication are meant to support a consistent interpretation of concepts and terms that underpin efforts to manage biological invasions. We recommend that national, regional, and international institutions should consider the recommendations proposed here when developing new legislative or policy documents and when enforcing existing ones. We also suggest that based on the criteria proposed in the present publication, a global terminology of biological invasions should be developed and adopted by relevant environmental institutions such as the IUCN and Convention of Biological Diversity in collaboration with the plant and animal health sectors (e.g., IPPC, OIE; IPPC 2017) and should be considered in the post-2020 biodiversity framework. Transferring the concepts presented in this publication to the policy domain will require a dialogue with the key actors, including the standard-setting organizations. This dialogue should combine a rigorous and robust scientific basis with the need to provide a clear and unambiguous terminology, which at the same time does not undermine existing policy tools.

Given the gradual nature of some mechanisms that are relevant to separate alien from native species; the enormous differences between taxa, realms, and regions; and progress in the field, the total harmonization of classification terms is probably an unrealistic aim (Heger et al. 2013). Uncertainties and ambiguities in assessing the biogeographic status of species cannot be totally eliminated. Nonetheless, we hope that this synthesis will be useful for advancing robust definitions of alien, cryptogenic, and native species.

comments from the four anonymous reviewers, the handling editor, and the editor in chief, Scott Collins.

References cited

Bacher S, et al. 2018. Socio-economic impact classification of alien taxa (SEICAT). Methods in Ecology and Evolution 9: 159–168.

Blackburn TM, et al. 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339.

Blackburn TM, et al. 2014. A unified classification of alien species based on the magnitude of their environmental impacts. PLOS Biology 12 (art. e1001850).

Carlton JT. 1996. Biological invasions and cryptogenic species. Ecology 77: 1653–1655.

Carlton JT, et al. 2017. Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. Science 357: 1402–1406.

[CBD] Convention on Biological Diversity. 2014. Pathways of Introduction of Invasive Species, Their Prioritization and Management. CBD. (17 May 2018; *www.cbd.int/doc/meetings/sbstta/sbstta-18/official/sbstta-18-09-add1-en.pdf*)

Chew MK, Hamilton AL. 2011. The rise and fall of biotic nativeness: A historical perspective. Pages 35–47 in Richardson DM, ed. Fifty Years of Invasion Ecology: The Legacy of Charles Elton.Wiley–Blackwell.

Conroy MJ, Beier P, Quigley H, Vaughan MR. 2006. Improving the use of science in conservation: Lessons from the Florida Panther. Journal of Wildlife Management 70: 1–7.

Copp GH, et al. 2005. To be, or not to be, a non-native freshwater fish? Journal of Applied Ichthyology 21: 242–262.

Crees JJ, Turvey ST. 2015. What constitutes a 'native' species? Insights from the Quaternary faunal record. Biological Conservation 186: 143–148.

Davis MA, et al. 2011. Don't judges species on their origins. Nature 474: 153–154.

Devictor V, Julliard R, Couvet D, Jiguet F. 2008. Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B 275: 2743–2748.

Dyer EE, Cassey P, Redding DW, Collen B, Franks V, Gaston KJ, Jones KE, Kark S, Orme CDL, Blackburn TM. 2017. The global distribution and drivers of alien bird species richness. PLOS Biology 15 (art. e2000942). doi:10.1371/journal.pbio.2000942

Elton CC. 1958. The Ecology of Invasions by Animals and Plants. Methuen.

Essl F, Rabitsch W. 2002. Neobiota in Österreich. Environment Agency Austria.(17 May 2018; *www.umweltbundesamt.at/fileadmin/site/publikationen/DP089.pdf*)

Essl F, Dullinger S, Moser D, Steinbauer K, Mang T. 2015a. Identifying alien bryophytes taking into account uncertainties: A reply to Patiño and Vanderpoorten. Journal of Biogeography 42: 1362–1363.

Essl F, et al. 2015b. Crossing frontiers in tackling pathways of biological invasions. BioScience 65: 769–782.

[EU] European Union. 2014. Regulation (EU) no. 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the Prevention and Management of the Introduction and Spread of Invasive Alien Species. EU.

Falk-Petersen J, Bohn T, Sandlund OT. 2006. On the numerous concepts in invasion biology. Biological Invasions 8: 1409–1424.

Frosch C, Kraus RHS, Angst C, Allgöwer R, Michaux J, Teubner J, Nowak C. 2014. The genetic legacy of multiple beaver reintroductions in central Europe. PLOS ONE 9 (art. e97619). doi:10.1371/journal.pone.0097619

Gilroy JJ, Avery JD, Lockwood JL. 2017. Seeking international agreement on what it means to be "native." Conservation Letters 10: 238–247.

Gollasch S. 2011. Canals. Pages 92–95 in Simberloff D, Rejmanek M, eds. Encyclopedia of Biological Invasions. University of California Press.

Green AJ. 2016. The importance of waterbirds as an overlooked pathway of invasion for alien species. Diversity and Distributions 222: 239–247.

Griffiths CJ, Jones CG, Hansen DM, Puttoo M, Tatayah RV, Müller CB, Harris S. 2010. The use of extant non-indigenous tortoises as a restoration tool to replace extinct ecosystem engineers. Restoration Ecology 18: 1–7.

Heger T, et al. 2013. Conceptual frameworks and methods for advancing invasion ecology. Ambio 42: 527–540.

Hewitt CL, et al. 2004. Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. Marine Biology 144: 183–202.

Hoffmann BD, Courchamp F. 2016. Biological invasions and natural colonisations: Are they that different? Neobiota 29: 1–14.

Hofman CA, Rick TC. 2017. Ancient biological invasions and island ecosystems: Tracking translocations of wild plants and animals. Journal of Archaeological Research 26: 65–115. doi:10.1007/s10814-017-9105-3

Hulme PE, et al. 2008. Grasping at the routes of biological invasions: A framework for integrating pathways into policy. Journal of Applied Ecology 45: 403–414.

Hulme PE, Bacher S, Kenis M, Kühn I, Pergl J, Pyšek P, Roques A, Vilà M 2017. Blurring alien introduction pathways risks losing the focus on invasive species policy. Conservation Letters 10: 265–266.

[IPCC] Intergovernmental Panel on Climate Change. 2013. Climate Change 2013: The Physical Science Basis. Cambridge University Press. (1 November 2013; *www.ipcc.ch/report/ar5/wg1*)

[IPPC] International Plant Protection Convention. 2017. Food and Agriculture Organization of the United Nations. (7 February 2017; *www.ippc.int/en*)

[IUCN] International Union for Conservation of Nature. 2013. Guidelines for Reintroductions and other Conservation Translocations, version 1.0. IUCN Species Survival Commission. (17 May 2018; *https://portals.iucn.org/library/efiles/documents/2013-009.pdf*)

———. 2017. Red List of Threatened Specie:. Categories and Criteria. IUCN. (23 January 2017; *www.iucnredlist.org/technical-documents/categories-and-criteria*)

Jeffries DL, Copp GH, Lawson-Handley LJ, Sayer CD, Hänfling B. 2017. Genetic evidence challenges the native status of a threatened freshwater fish (*Carassius carassius*) in England. Ecology and Evolution 7: 2871–2882.

Jeschke JM, Keesing F, Ostfeld RS. 2013. Novel organisms: Comparing invasive species, GMOs, and emerging pathogens. Ambio 42: 541–548.

Kowarik I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. Pages 15–38 in Pyšek P, Prach K, Rejmánek M, Wade PM, eds. Plant Invasions: General Aspects and Special Problems. SPB Academic.

Kowarik I, Pyšek P. 2012. The first steps towards unifying concepts in invasion ecology were made one hundred years ago: Revisiting the work of the Swiss botanist Albert Thellung. Diversity and Distributions 18: 1243–1252.

Latombe G, et al. 2017. A vision for global monitoring of biological invasions. Biological Conservation 213: 295–308.

Lewis SL, Maslin MA. 2015. Defining the Anthropocene. Nature 519: 171–180.

Lindroth C. 1957. The Faunal Connections between Europe and North America. Wiley.

Lonsdale M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536.

Mack R, Smith M. 2011. Invasive plants as catalysts for the spread of human parasites. NeoBiota 9: 13–29.

Mastrandrea MD, et al. 2011. The IPCC AR5 guidance note on consistent treatment of uncertainties: A common approach across the working groups. Climatic Change 108: 675–691.

Packer JG, Meyerson LA, Skálová H, Pyšek P, Kueffer C. 2017. Biological Flora of the British Isles: *Phragmites australis*. Journal of Ecology 105: 1123–1162.

Pecl GT, et al. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355 (art. eaai9214).

Peréz-Portela R, Arranz V, Rius M, Turon X. 2013. Cryptic speciation or global spread? The case of a cosmopolitan marine invertebrate with limited dispersal capabilities. Scientific Reports 3 (art. 3197). doi:10.1038/srep03197

Pergl J, et al. 2016. Dark side of the fence: Ornamental plants as a source of wild-growing flora in the Czech Republic. Preslia 88: 163–184.

Petit RJ. 2004. Biological invasions at the gene level. Diversity and Distributions 10: 159–165.

Preston CD, Pearman DA, Dines TD. 2002. New Atlas of the British and Irish Flora. Oxford University Press.

Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J. 2004. Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. Taxon 53: 131–143.

Pyšek P, Jarošík V, Chytrý M, Kropáč Z, Tichý L, Wild J. 2005. Alien plants in temperate weed communities: Prehistoric and recent invaders occupy different habitats. Ecology 86: 772–785.

Pyšek P, et al. 2012. Catalogue of alien plants of the Czech Republic (2nd edition): Checklist update, taxonomic diversity and invasion patterns. Preslia 84: 155–255.

Pyšek P, et al. 2013. Hitting the right target: Taxonomic challenges for, and of, plant invasions. AoB Plants 5 (art. plt042).

Rabl C, Rabl D. 2015. Die Einwanderung von Libythea celtis (Laicharting, 1782) (Lepidoptera: Nymphalidae) nach Österreich. Beiträge zur Entomofaunistik 16: 3–8.

Richardson DM, Ricciardi A. 2013. Misleading criticisms of invasion science: A field-guide. Diversity and Distributions 19: 1461–1467

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ. 2000. Naturalization and invasion of alien plants: Concepts and definitions. Diversity and Distributions 6: 93–107.

Richardson DM, et al. 2009. Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences 106: 9721–9724.

Richardson DM, Pyšek P, Carlton JT. 2011a. A compendium of essential concepts and terminology in invasion ecology. Pages 409–420 in Richardson DM, ed. Fifty Years of Invasion Ecology: The Legacy of Charles Elton. Wiley–Blackwell.

Richardson DM, Carruthers J, Hui C, Impson FAC, Miller JT, Robertson MP, Rouget M, Le Roux JJ, Wilson JRU. 2011b. Human-mediated introductions of Australian acacias—A global experiment in biogeography. Diversity and Distributions 17: 771–787.

Ritchie EG, Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12: 992–998.

Roy HE, et al. 2017. Alien pathogens on the horizon: Opportunities for predicting their threat to wildlife. Conservation Letters 10: 477–484.

Seddon PJ, Moehrenschlager A, Ewen J. 2014. Reintroducing resurrected species: Selecting DeExtinction candidates. Trends in Ecology and Evolution 29: 140–147.

Seebens H, et al. 2017. No saturation in the accumulation of alien species worldwide. Nature Communications 8 (art. 14435). doi 10.1038/ncomms14435

Seebens H, et al. 2018. Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences. doi:10.1073/pnas.1719429115

Sharma R, Polkade AV, Shouche YS 2015. "Species concept" in microbial taxonomy and systematics. Current Science 108: 1804–1814.

Sjölund MJ, González-Díaz P, Moreno-Villena JJ, Jump AS. 2017. Understanding the legacy of widespread population translocations on the post-glacial genetic structure of the European beech, Fagus sylvatica L. Journal of Biogeography 44: 2475–2487. doi:10.1111/jbi.13053

Smith SL, Carden RF, Coad B, Birkitt T, Pemberton JM. 2015. A survey of the hybridisation status of Cervus deer species on the island of Ireland. Conservation Genetics 15: 823–835.

Smulders MJM, Beringen R, Volosyanchuk R, Vanden Broeck A, van der Schott J, Arens P, Vosman B. 2008. Natural hybridisation between Populus nigra L. and P. x canadensis Moench: Hybrid offspring competes for niches along the Rhine river in the Netherlands. Tree Genetics and Genomes 4: 663–675.

Snow DW, Perrins CM. 1998. The Birds of the Western Palearctic. Oxford University Press.

Söderström L. 1992. Invasions and range expansions and contractions of bryophytes. Pages 131–158 in Bates JW, Farmer AM, eds. Bryophytes and Lichens in a Changing World. Clarendon Press.

Van Kleunen M, et al. 2015. Global exchange and accumulation of nonnative plants. Nature 525: 100–103.

Van Leeuwen JFN, Froyd CA, van der Knaap WO, Coffrey EE, Tye A, Willis KJ. 2008. Fossil pollen as a guide to conservation in the Galápagos. Science 322: 1206.

Vilà M, et al. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702–708.

Walther GR, et al. 2009. Alien species in a warmer world: Risks and opportunities. Trends in Ecology and Evolution 24: 686–693.

Webb DA. 1985. What are the criteria for presuming native status? Watsonia 15: 231–236.

Webber B, Scott J. 2012. Rapid global change: Implications for defining natives and aliens. Global Ecology and Biogeography 21: 305–311.

Wilk-Woźniak E, Solarz W, Najberek K, Pociecha A. 2016. Alien cyanobacteria: An unsolved part of the "expansion and evolution" jigsaw puzzle? Hydrobiologia 764: 65–79.

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM. 2009. Something in the way you move: Dispersal pathways affect invasion success. Trends in Ecology and Evolution 24: 136–144.

Wilson JRU, Garcia-Diaz P, Casey P, Richardson DM, Pyšek P, Blackburn TM. 2016. Biological invasions and natural colonizations are different—The need for invasion science. Neobiota 31: 87–98.

Zając M, Zając A, Tokarska-Guzik B. 2009. Extinct and endangered archaeophytes and the dynamics of their diversity in Poland. Biodiversity Resources and Conservation 13: 17–24.

Zohary M. 1962. Plant Life of Palestine, Israel and Jordan. Ronald Press.

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