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For many species, human-induced environmental changes are important indirect drivers of range expansion into new regions. We argue that it is important to distinguish the range dynamics of such species from those that occur without, or with less clear, involvement of human-induced environmental changes. We elucidate the salient features of the rapid increase in the number of species whose range dynamics are human induced, and review the relationships and differences to both natural range expansion and biological invasions. We discuss the consequences for science, policy and management in an era of rapid global change and highlight four key challenges relating to basic gaps in knowledge, and the transfer of scientific understanding to biodiversity management and policy. We conclude that range-expanding species responding to human-induced environmental change will become an essential feature for biodiversity management and science in the Anthropocene. Finally, we propose the term neonative for these taxa.

Keywords: biogeography, biological invasions, climate change, framework, global environmental change, native, range expansion, spread, terminology

Widely accepted definitions of the nativeness of species—or, more generally, of taxa—are based on a dichotomous classification (i.e., native, meaning indigenous, and alien, meaning nonnative, exotic, nonindigenous; Webb 1985, Richardson et al. 2000, Pyšek et al. 2004, Blackburn et al. 2011, Crees and Turvey 2015, Wilson et al. 2016, Essl et al. 2018). Native taxa are those that have arisen through evolution in a region or have colonized a region by their own means of dispersal. Alien taxa are those that have been transported by specific human agency—that is, the anthropogenic movement of propagules or parent organisms, respectively, or the dispersal through human-constructed corridors, such as canals (Essl et al. 2018)—into regions that could not be reached (or could only be reached in very rare cases) by natural dispersal (Pyšek et al. 2004).

Despite considerable debate (e.g., Warren 2007), the basic principles on how native and alien species should be classified have become widely accepted in science (e.g., Richardson et al. 2000, Blackburn et al. 2011, Essl et al. 2018) and environmental policy (e.g., CBD 2002). However, there is ongoing debate on how this dichotomy should be applied in practice, because of the multitude of situations in which human agency may be involved in range expansion and because of the paucity or uncertainties of available taxonomic and biogeographic data (Essl et al. 2018). Less attention has been paid to situations in which range expansion is the result of human modifications of the environment that have led to changes in the distribution of suitable environmental space, allowing a species to disperse naturally to and establish in new areas previously not colonized. The only example we are aware of that systematically distinguished between natural and anthropogenic occurrences—in this case, of vascular plant species—is the New Atlas of British and Irish Flora (Preston et al. 2002).

Human activities increasingly cause environmental perturbations, such as climate change, land-use change, overharvesting, eutrophication, and pollution. The resulting changes in biophysical attributes of the environment affect the distribution of species in different ways (e.g., Pereira et al. 2010, Waters et al. 2016, Pecl et al. 2017). Many species experience population declines or local extinction (e.g., Baker et al. 2018) that result in shrinking ranges or even global extinction (Wessely et al. 2017). Other species track the shifting environmental conditions by colonizing new

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geographical space, at widely varying rates (Chen et al. 2011, Pinsky et al. 2013), and there are many species that react differently to human-induced environmental change in different parts of their ranges (particularly at the northern and southern distribution limits or upper and lower elevational limits, respectively). The phenomenon of geographic range expansion is becoming increasingly frequent (e.g., Lenoir and Svenning 2015), the velocity of range expansion is often increasing (Devictor et al. 2012, Steinbauer et al. 2018), and ongoing rapid environmental change will doubtlessly amplify these processes in the future (e.g., Loarie et al. 2009, Pecl et al. 2017). For instance, recent range expansion into higher latitudes and altitudes have frequently been documented as a consequence of anthropogenic climate change, in particular for mobile species (e.g., Chen et al. 2011, Devictor et al. 2012, Steinbauer et al. 2018).

This situation is blurring the distinction between native and alien species and has fuelled debate on how to classify taxa that respond to human-induced environmental changes by expanding their ranges without any specific human assistance into new regions that are often adjacent to their native range. Some authors have suggested that such taxa should be considered as native (e.g., Webber and Scott 2012, Hoffmann and Courchamp 2016, Gilroy et al. 2017). Others, while agreeing partly with this view, have proposed that alien status may be applied if there is a strong indirect human contribution (e.g., the creation of novel ecosystems such as heated environments—e.g., greenhouses, power plant cooling ponds—in the newly colonized region) that is a prerequisite for such autonomous range expansion (e.g., Essl et al. 2018). Finally, some authors have suggested that all such species should be considered as aliens, because of the underlying indirect human agency and because their range expansion is clearly attributable to human-caused environmental changes (e.g., Ben Rais Lasram and Mouillot 2009) or, at least, cannot be considered native using the current definitions (Pyšková et al. 2016). The classification of such range-expanding species as native or alien has important ramifications for environmental legislation and biodiversity management. This is because, although both groups can cause major effects on communities and ecosystems, they often carry different obligations for responsible authorities.

We argue that there can be substantial differences regarding the spread dynamics and characteristics, as well as the impacts caused, between taxa that are naturally expanding their range solely because of anthropogenic environmental change, native species that have been present in a region since historic times, and alien species that have been directly introduced by humans from another region. The increasing frequency of naturally range-expanding taxa (e.g., Engelkes et al. 2008, Chen et al. 2011, Devictor et al. 2012), and the unclear situation in management and regulations warrants recognizing these species as a special category. In the present article, we elucidate the salient features of the rapid increase in the number of range-expanding species, review the relationships and differences between resident native and alien species, and discuss the consequences for science, policy, and management of expanding taxa in an era of rapid global change. Finally, we consider the pros and cons of introducing a new term (*neonative*) for range-expanding species that track human-induced environmental change.

The temporal dimension of human-induced environmental changes

Indirect human agency has been a driver of species range expansion since the Neolithic Age, in which substantial human modifications of natural environments, through deforestation, onset of agriculture, and anthropogenic changes of the fire cycle are first recorded. Indeed, humans already affected the environment earlier—that is, when hunter-gatherers through their use of fire for hunting stimulated the growth of certain fire-adapted plants that profoundly changed ecosystems or because of the extinction of the megafauna (Alroy 2001). With the onset of agriculture, anthropogenic landscape modifications became a more widespread phenomenon. Around 1500 CE, however, agriculture was still largely confined to a few parts of the world (figure 1; Chini et al. 2014). From the late eighteenth century onward, the beginning of the industrial revolution led to an exponential increase of human population size, agricultural industrial activities and the release of pollutants and fertilizers into the environment, a trend that became particularly pronounced after World War II—the Great Acceleration (Steffen et al. 2007).

Together, the intensifying anthropogenic changes of the environment since the mid-twentieth century have resulted in the current human domination of most Earth's system processes and in widespread substantial modifications of ecosystem properties, such as nutrient and energy stocks and flows, habitat destruction, and in the accumulation of pollutants, man-made substances (e.g., plastic) and structures (e.g., buildings; Vitousek 1997). Concomitantly, humans have become the prime force for redistributing species across the globe, either by direct (transport of propagules) or strong indirect agency (human-made corridors connecting previously separated regions) that have resulted in biological invasions (Elton 1958, Richardson et al. 2000, Blackburn et al. 2011, Essl et al. 2018), or by causing environmental change that has resulted in species latitudinal and altitudinal range reductions as well as expansion.

Do we need a distinct classification for species expanding their ranges as a consequence of environmental change?

Range expansion in response to human-induced environmental changes have become a frequent phenomenon and are likely to continue becoming even more prominent in the future. Because of the profound implications this phenomenon has for biogeography, ecology, policy and management, range expansion involving species that track the changing environmental conditions according to their niche, without specific human assistance, require further elucidation.

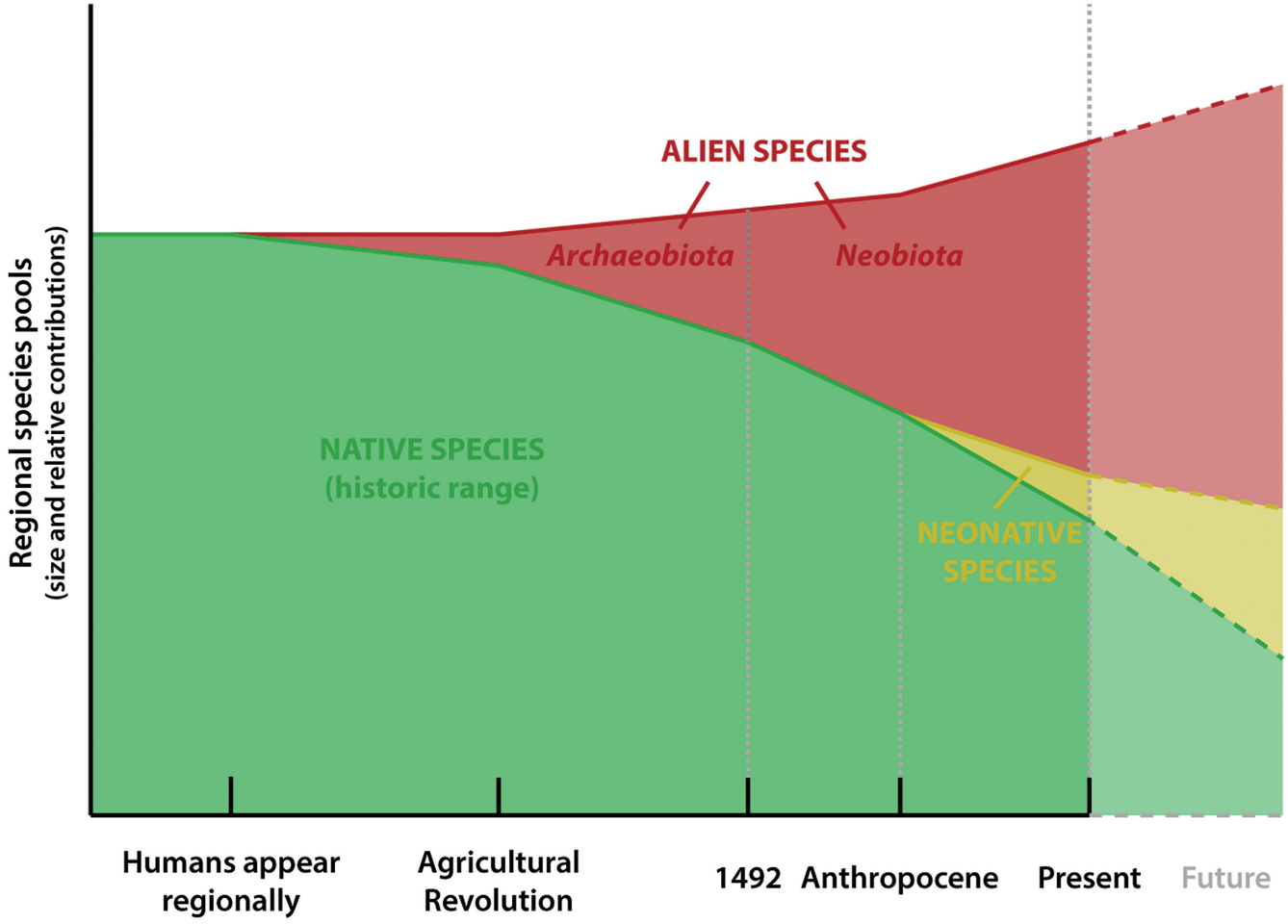

Figure 1. The temporal changes of the composition and size of regional species pools over time from early human history to the present, and with projections of likely future trends into the future (shown with broken lines). Shown are important reference dates or events, and the resulting changes in biogeographically defined regional species pools. The absolute size of regional species pools changes naturally over time because of local extinction, natural immigration and evolution (speciation; not shown in the present figure). The size of regional species pools also changes over time as a result of human activities—that is, because of the regional extinction of native species, and because of the introduction of alien species, and the spread of range-expanding species responding to human-induced environmental change (i.e., neonative species). Note that x- and y-axes are not to scale, nor are the relative sizes of different species groups. The timing of some important events (e.g., the regional appearance of humans, the Agricultural Revolution) differs between regions, and, therefore, no absolute dates are given for these events. Note that we show the approach that uses the onset of the Anthropocene as temporal threshold; if this is relaxed, range-expanding species from earlier times can also be neonative.

First, the processes involved in the range expansion of such species differ considerably from those underlying biological invasions because of the absence of human agency (other than human-induced environmental change), the lack of anthropogenic propagule pressure, and the typically intracontinental pattern of relatively short- to medium-distance spread adjacent to the historical native range (Caplat et al. 2013, but see, e.g., Viana et al. 2016 for intercontinental seed dispersal with migrating birds).

Second, range-expanding species responding to human-induced environmental changes are becoming an increasingly important challenge for conservation and environmental management in many parts of the world. For instance, should such range expansion be facilitated by increasing permeability or connectivity of landscapes (e.g., green infrastructure; EEA 2011) to allow the spread of species to new regions that are presumed to have become climatically suitable? What are the likely impacts of range expansion on resident biota, how can these be anticipated, and do the range expanders need to be managed, and if so, how? Which properties of species and the environment, and which types of environmental change affect the likelihood that a particular species will track the changing environmental conditions? In some cases, facilitating range expansion

(by creating dispersal corridors) may be crucial for ensuring species survival under rapid environmental change.

Characteristic features of range-expanding taxa responding to human-induced environmental change

For a taxon to qualify as range expanding due to human-induced environmental change, we suggest that it has to fulfill the following criteria: Its range has expanded beyond the historic native range, the range expansion has been facilitated by human-induced environmental change, the range expansion is not due to direct human agency (e.g., introduction of propagules), the population status of recent occurrences (i.e., being permanent or ephemeral) outside the historic native reference range, and—optionally—the range expansion has occurred within a timeframe that points to anthropogenic environmental change. We will discuss each of these features in detail and we propose a term for such species (*neonative*) below.

Applying the above-mentioned criteria in practice will often be difficult because of a lack of data (e.g., when did a species expand its range; what are the causal factors underlying the expansion?). Therefore, using expert knowledge and developing practical guidelines and thresholds will be essential for ensuring the usefulness and robustness of assessments of range-expanding taxa. We provide some recommendations on thresholds as a basis for future discussions to reach a widely accepted consensus.

We propose that the historic native reference range of a taxon should be the documented or likely historic range that the taxon has occupied or colonized by natural means before humans began playing a dominant role in landscape or climate modifications. This may include parts of the species' range that have been lost historically (e.g., because of overhunting, or historic anthropogenic habitat destruction), which implies that recolonization into historically lost regions after the causes of decline have been eliminated (e.g., hunting regulations, species management) disqualifies a species from being classified as range-expanding taxon responding to human-induced environmental change (e.g., wolves in Central Europe).

There are arguments both in support of using a temporal threshold to delineate range-expanding species responding to human-induced environmental change or against doing so (i.e., all species fulfilling the other criteria do qualify). We believe that the definition of temporal thresholds warrants further discussion before a consensus on its usefulness can be reached. If a temporal threshold needs to be identified, then restricting the concept of range-expanding species responding to human-induced environmental change to those that expanded their range since the onset of the Anthropocene, which was recently suggested to be the year 1950 CE (Zalasiewicz et al. 2015, Waters et al. 2016), might be a pragmatic temporal reference point. The advantages of using the Anthropocene as a temporal reference are that, in earlier history, the role of human agency on range changes was considerably smaller in most cases (but see Crees and Turvey 2015 for exceptions), whereas the role of naturally occurring changes in the environment were most dominant, and data on range changes are scarce for many regions and taxonomic groups, which makes the reconstruction of historic range changes difficult or impossible in most cases. For those species and regions for which human-induced range expansion that occurred before 1950 CE are well documented, we propose that this reference date may be relaxed, but this should be made explicit. Nevertheless, there are also important arguments for not introducing a temporal threshold; these include that range expansion tracking human-induced environmental change already occurred millennia ago. For example, deforestation in the medieval period in Europe was a strong driver of transformation of the landscapes with vast implications for dispersal opportunities for many heliophilous species, and it is difficult to justify why some events with extreme impacts like this should be included within the concept, whereas others should not. Moreover, identifying the onset of range expansion is often difficult. From this perspective, the most objective approach would be to consider the beginning of Neolithic as a threshold, in the same way as it is applied to the definition of the beginning of biological invasions (Webb 1985, Pyšek et al. 2004). We highlight these different perspectives as a topic that will require further discussion within the conservation community but note that in practice most land or marine managers and conservationists will be concerned with addressing contemporary rather than historical range expansion.

Natural range expansion may occur over vastly different distances and may be driven by different processes, ranging from small-scale fluctuations of metapopulations at range margins to natural long-distance dispersal events. In practice, to qualify a taxon as range expanding, we propose that range expansion should have happened over substantial distances beyond the historic native reference range. What constitutes a substantial distance in this context is difficult to define in absolute terms for a range of taxa and for different regional contexts (e.g., when considering the steepness of environmental gradients), and the mobility of the focal species will play a significant role as well. We believe that agreeing on thresholds of the minimum distances a species has to cross to qualify as range expanding warrants further discussion. However, to initiate discussion, we propose that such minimum distances should exclude marginal range expansion, because, for short distances, it is often difficult to disentangle population fluctuations at the range limits from range expansion. For instance, we propose that for latitudinal range expansion (within the same elevational belt) minimum distances should typically be of the order of at least 100 kilometers (Essl et al. 2018), so way beyond landscape-scale migrations and minor range adjustments. For altitudinal range expansion in mountainous regions, shorter distances of the order of a few hundred meters in elevation will be more appropriate.

To assess the population status of occurrences outside the historic native range requires the assessment of whether

populations are permanent or ephemeral. We propose that the same criteria as for successful naturalizations of alien species should be considered for identifying permanent populations outside the historic reference range—that is, they have to be self-sustaining, persistent, and able to reproduce (Richardson et al. 2000, Blackburn et al. 2011). Temporary occurrences and casual observations beyond the historic reference range should only qualify as neonative when there is evidence that they lead to the establishment of founding populations at the range front of range-expanding species tracking anthropogenic environmental change. Consequently, in the absence of such evidence, short-lived (fluctuating or ephemeral) populations at the limit of the suitable environmental space, isolated long-distance dispersing individuals (e.g., vagrants) and species that expand their range naturally do not qualify as fulfilling this criterion. We believe this is useful, because such ephemeral occurrences of individuals or small short-lived populations do not necessarily indicate range expansion. For example, there are frequent records of individuals of many mobile species such as birds and moths found as vagrants far away from their native range (but see Davis and Watson 2018 for a discussion on the changing role of vagrants for range expansion due to climate change).

Species ranges are inherently dynamic and can fluctuate tremendously over time in response to climatic, tectonic, or oceanographic events. Species ranges are naturally modified through migration and propagule dispersal or often through long-distance dispersal events assisted by wind or water currents (Gillespie et al. 2012), or other organisms, without necessarily involving environmental changes. Human-induced environmental changes may increase the accessibility or suitability of a region for a given species (Chen et al. 2011, Fraser et al. 2018), which may allow for new geographical areas to be colonized. Assessing the contribution of human-induced environmental change to range expansion will mostly be based on circumstantial evidence such as a close match between the ecological requirements of a species and the recent change in the recipient environment brought about by environmental change and attributes of the range expansion process. It is often difficult to ascertain the degree of indirect influence of human agency on species range expansion. However, it is likely that only few species that are currently expanding do so without responding to human-induced environmental change. For practical purposes, we therefore propose that evidence that the spread of a species is due to human-induced environmental change is sufficient to qualify a species to fulfill this criterion (see supplement S1 for examples), whereas evidence that range expansion is not due to human-induced environmental change should be used for identifying species that expand their ranges naturally. However, an estimate of uncertainty of the assessment should be provided. The near ubiquity of anthropogenic impacts in the Anthropocene means that under these circumstances, it may be much harder to distinguish species that are expanding their ranges independently of environmental change.

Finally, the absence of direct human-mediated dispersal for range expansion or the creation of human-made dispersal corridors (e.g., canals) is a prerequisite for a taxon to qualify as range-expanding species responding to human-induced environmental change. Such human agency includes the intentional or unintentional anthropogenic transport of propagules or individuals from the native range (or from a previously colonized alien range) or increasing region accessibility via the construction of corridors (e.g., canals, tunnels, roads, bridges) that connect previously separated regions (e.g., river catchments, seas, islands; Essl et al. 2018). These processes may aid or allow the colonization of regions that have become newly suitable for a species. In many situations, human agency and indirect human-induced environmental change may synergistically enable species-range expansion and attributing their relative importance may be difficult. If human agency (other than human-induced environmental change) is involved, the respective taxon should be considered alien (Richardson et al. 2000, Pyšek et al. 2004, Essl et al. 2018). In addition to these defining characteristics, a range of other features is associated with the phenomenon of range-expanding native species (e.g., ecological novelty).

Range-expanding species responding to human-induced environmental change compared with alien species

Range expansion of species responding to human-mediated environmental change and biological invasions have common features, but they differ qualitatively and quantitatively in key processes. For the former, individuals colonizing new geographic space are usually drawn from the leading edge of the historic native range, with concomitant consequences (e.g., these populations are often genetically less diverse than those in the central part of the range, or they may differ from populations in the central range; Excoffier et al. 2009, Wilson et al. 2009). The individuals driving long-distance dispersal may differ in dispersal-relevant traits from the average values of the population they are drawn from (Darling et al. 2008, Phillips et al. 2010, Hill et al. 2011). Therefore, populations in newly colonized regions may also differ in these traits from the source populations. Range expansion may be driven by widely different numbers of individuals, and if numbers are low (which is often the case), bottleneck and founder effects are frequent and may result in reduced genetic diversity (Excoffier et al. 2009).

In contrast, alien species may be drawn from a wide range of source populations, which are often located in the central parts of their range, and repeated introductions from different source populations are a widespread phenomenon (Shirk et al. 2014). Furthermore, postintroduction evolution in the new range because of different selection pressure and limited gene exchange with native populations has repeatedly been documented (Excoffier et al. 2009, Zhang et al. 2018). This is probably more relevant for alien species, because they typically encounter substantially different selection pressures in

the new region, whereas range-expanding species responding to human-induced environmental change colonize regions adjacent to their historic range with smaller differences in selection pressures. However, it has been shown that native species expanding their ranges in response to climate warming experience less control by natural enemies than long-term resident natives (Engelkes et al. 2008). Therefore, populations of alien species in their new range may be more (e.g., as a consequence of repeated introductions and admixture) or less genetically diverse and substantially different from those in their native range, depending on the direction and strength of the relevant selection processes. However, there are many cases in which alien populations have reduced genetic diversity (Hagenblad et al. 2015). Although range-expanding species responding to human-induced environmental change and aliens are likely to differ in many aspects, comparative studies are needed to determine the character and magnitude of differences between these two species categories.

Typically, range-expanding species responding to human-induced environmental change first colonize regions directly adjacent to the historic native range and may usually only colonize regions further away from the historic range as the expansion progresses. This progression is highly contingent on the maximum spread distance of individuals and the availability of suitable habitats. Range-expanding species responding to human-induced environmental change show denser, more aggregated distributions, reflecting colonization and this link between current distribution patterns and processes of distribution change can be used as indication for identifying range-expanding species (Wilson et al. 2004). In contrast, if alien species are introduced to areas outside their native range but within the same continent, the foci of primary introductions are often not adjacent to the native range, because introductions depend on human agency that helps to overcome dispersal barriers. Subsequent spread across the suitable range is also contingent on the spread potential of the species, but secondary introductions may substantially increase spread (Kowarik 2003).

Ecological novelty is a characteristic feature of species redistribution in the Anthropocene (Saul and Jeschke 2015). Different facets of ecological novelty can be conceptualized, and we argue that these are associated in different ways with range-expanding and alien species (table 1). Specifically, ecological novelty can be inversely measured as ecoevolutionary experience of interacting resident and nonresident species (sensu Saul and Jeschke 2015): Organisms with novel weapons (sensu Callaway and Ridenour 2004) or other novel traits the resident species are not familiar with (i.e., they have a low ecoevolutionary experience) are expected to have stronger impacts than organisms that are similar to resident species (i.e., high ecoevolutionary experience). We would expect that resident species typically have a higher ecoevolutionary experience when interacting with range-expanding species responding to human-induced environmental change than with alien species coming from further away. This is because alien species are frequently more distinct in their morphology, behavior, or other traits and characteristics. Extreme examples are alien mammalian predators introduced to New Zealand (and other oceanic islands) that had a devastating impact on resident flightless birds. Because of the previous absence of such predators on New Zealand, kiwi and other ground nesting bird species became easy prey for cats and mustelids (Blackwell 2005). However, because of evolutionary convergence, aliens sometimes have a lower degree of novelty than range-expanding species. For example, range-expanding plants that track climate change and are expanding into biomes with cooler climates can have profound impacts on nutrient cycling and ecosystem functioning when they introduce novel growth forms (e.g., shrubification of tundra ecosystems, laurophyllisation of temperate forests; Sturm et al. 2001, Walther et al. 2007, Alexander et al. 2018). Similarly, pathogens that spread into new regions because of climate change can have severe impacts on their (new) hosts (Harvell et al. 2002). Future studies are therefore needed to test our prediction that range-expanding species typically have a lower degree of novelty than alien species (e.g., following the procedure proposed by Saul et al. 2013). These will also provide important insights for biodiversity management.

Proposing a term for range-expanding species responding to human-induced environmental change

We note that given the overabundance of terminology in ecology and biogeography, introducing a new term for range-expanding species that respond to anthropogenic environmental change has the potential to exacerbate this unfortunate situation further. However, given the importance of this phenomenon and the absence of a specific term for such species, we believe that suggesting a new term is useful and appropriate. Therefore, we propose that the term *neonative* be applied for range-expanding taxa responding to anthropogenic environmental change (figure 2). We have chosen this term because it succinctly captures the biogeographic status of such taxa—that is, to be present in a region only relatively recently.

Specifically, we propose the following definition for neonatives (see also figure 2, table 2): Neonatives are those taxa that have expanded geographically beyond their native range and that now have established populations whose presence is due to human-induced changes of the biophysical environment, but not as a result of direct movement by human agency, intentional or unintentional, or to the creation of dispersal corridors such as canals, roads, pipelines, or tunnels.

We propose that such taxa should be considered native in the new range, but that there are sound reasons to discriminate them from native species occurring within their historic range and from range-expanding native species that do so apparently without responding to human-induced environmental change. Therefore, taxa may be native, neonative, or alien in different parts of their current range

Table 1. Disentangling relevant features that are associated with the degree of novelty of spreading organisms in a given context and implications for management.

Feature of organismic novelty	Defining characteristics	Major implications on resident species and communities	Relevance and implications for managing expanding species in the Anthropocene	Relevance for neonative species	Relevance for alien species	Selected references
Phylogeny	Evolutionary distance of the spreading organism to the species of the recipient community	Change in phylogenetic composition of the community, hybridization with closely related resident species	Variable. Although functional changes may be considered more relevant to ensure provision of ecosystem functions and services, increasing risks of hybridization and substantial changes in phylogentic composition (e.g., loss of genetic diversity) will remain important	Typically small evolutionary distance that may confer substantial risks of hybridization with native congeners	Often large evolutionary distances confer high impacts on phylogenetic composition	Diez et al. 2009, Excoffier et al. 2009
Functionality	Functional distance (of key traits as life-form, size, diet) of the spreading organism to the species of the recipient community	Change of interactions between species and of physical structure of the community	Increasing. Strong interaction with ecosystem functioning and services.	Variable. Often small, but sometimes large if functionally highly distinct species from adjacent biomes spread into new regions	Variable, including sometimes large functional distance	MacArthur and Levins 1967, Callaway and Ridenour 2004, Ricciardi et al. 2013, Saul et al. 2013
Physiology	Distance in metabolism, tissue quality and compounds produced by the spreading organism to the species of the recipient community	Change in the quantity and quality of organic matter in the community	Likely increasing. Interaction with forestry and agriculture.	Typically small physiological distance	Variable, including sometimes large physiological distance	MacArthur and Levins 1967, Callaway and Ridenour 2004, Ricciardi et al. 2013, Saul et al. 2013
Phenology	Phenological distance (e.g., timing of key life-cycle events as reproduction, flowering period, leaf retention) of the spreading organism to the species of the recipient community	Temporal changes e.g., of resource availability and phenological mismatches	Likely increasing.	Typically small phenological distance, but may be sometimes large if species spread from adjacent biomes	Variable, including sometimes large phenological distance	MacArthur and Levins 1967, Callaway and Ridenour 2004, Ricciardi et al. 2013, Saul et al. 2013
Biology	Distance in biology (e.g., population density, generation time, mating system) of the spreading organism to the species of the recipient community	Change in community composition of the recipient community	Likely increasing.	Typically small biological distance	Variable, including sometimes large biological distance	MacArthur and Levins 1967
Behavior	Distance in ecological behavior (e.g., foraging, habitat use, etc.) of the spreading organism to the species of the recipient community	Change in ecological behavior of interacting species of the recipient community due to competition	Likely increasing.	Typically small ecological distance	Variable, including sometimes large ecological distance	Ricciardi et al. 2013, Saul et al. 2013
Ecosystem processes and functioning	Distance in energy and material flow or retention of the spreading organism to the species of the recipient community	Change in the quantity of organic and inorganic matter (e.g., nutrients) stored in or transported through different compartments of the ecosystem	Increasing. Strong interaction with ecosystem functioning and services.	Typically small distance in energy and material flow or retention	Variable, including sometimes large distance in energy and material flow respectively retention	–

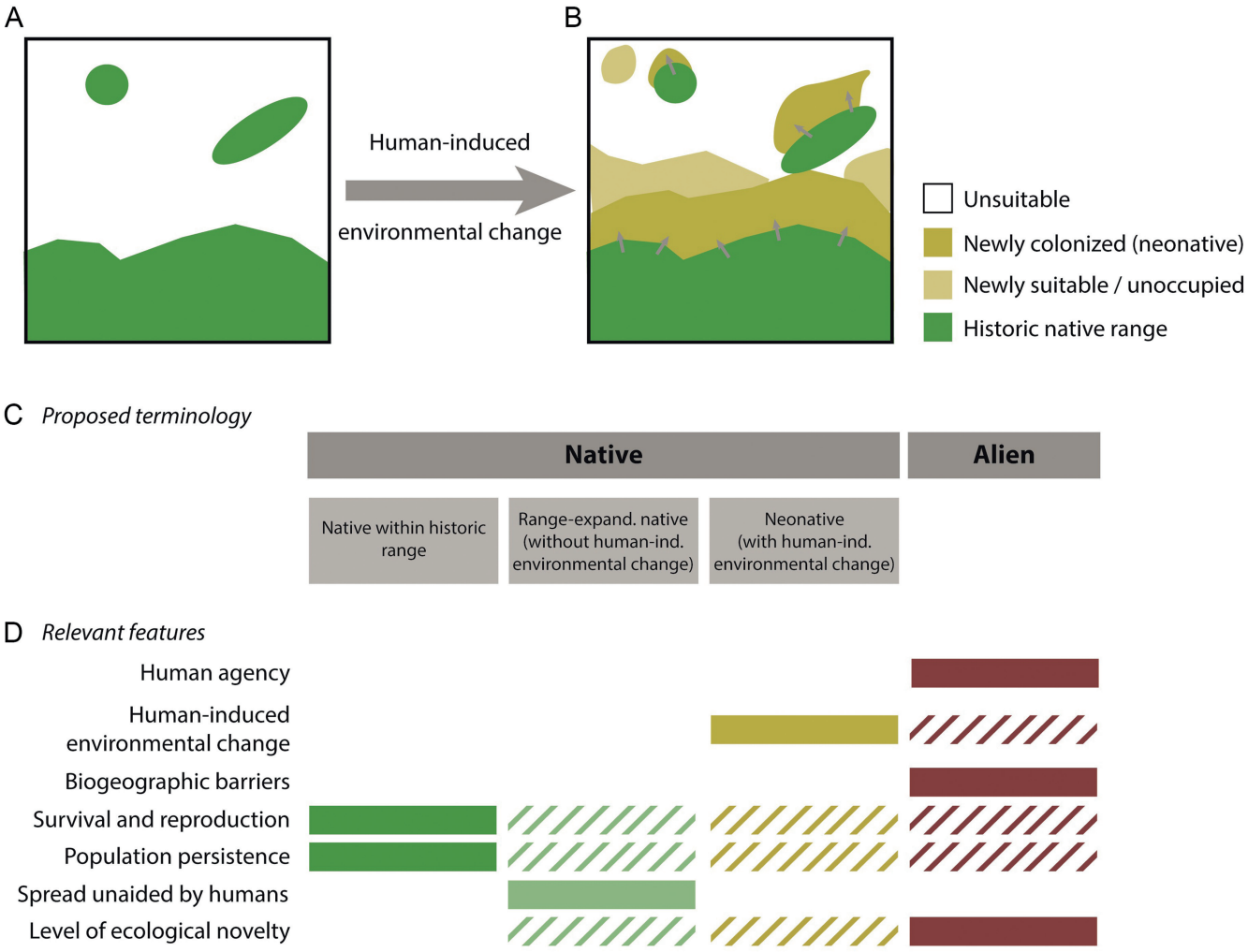

Figure 2. Features relevant for identifying native species, including range-expanding species responding to human-induced environmental change (i.e., neonative species), and alien species. Species respond to human-induced environmental change by expanding from their historic range (a) into formerly unsuitable (or inaccessible) regions (b), often with parts of the newly suitable region being not yet colonized because of colonization lags. The proposed terminology is shown in panel (c), with characteristic features that are relevant for identifying native species in their historic range, native species that expand their ranges without human contribution, neonative species, and alien species that are introduced by human agency (e.g., introduction of propagules; d). The solid lines indicate that a feature applies fully; the dashed lines indicate that it applies partly.

and may even have become extinct in other parts of their former range (e.g., because environmental conditions have become unsuitable there, and their range has subsequently contracted).

The word *neonative* has previously sometimes been used in other contexts. For instance, it has been used in anthropology with regard to colonizing human populations, especially in North America (e.g., Rudy and Farmer 2010). In forestry, the term has been used for discussing the establishment of neonative forest species, including the use of native and alien tree species and nonlocal tree provenances to better adapt forests to future climate conditions (e.g., Millar et al. 2007). We are aware that suggesting a term that has been previously used in related contexts is not ideal, but because previous usage of *neonative* was rare, this should not be a major issue.

Considerations for managing species ranges in the Anthropocene

Although there is broad agreement that alien species in some cases cause substantial impacts on the environment and human well-being (Vilà et al. 2011, Blackburn et al. 2014, Bacher et al. 2018) that warrants management, much less attention is given to the possible impacts of neonative species as defined above. However, there is accumulating evidence that impacts by neonatives can be substantial and even functionally similar to the impacts caused by alien

Table 2. The five characteristic features for defining range-expanding species responding to human-induced environmental change (i.e., neonative species) and proposed suitable evidence that can be used for assessment.

Feature	Description	Suitable evidence for assessment	References
Range expansion beyond historic range	Range expansion of a taxon over substantial distances beyond the historic (e.g., before the onset of the Anthropocene) native reference range which may result in new geographical space becoming available.	Lack of historic occurrence data in a newly colonized region, assuming that the region was adequately surveyed previously. Spread distance to historic native reference range	Parmesan et al. 1999, Devictor et al. 2012, Pateman et al. 2012
Facilitating role of human-induced environmental change	Human-induced environmental changes that increase the accessibility or suitability of a region for a given species, which may cause that new geographic space becomes suitable	Congruence between the known ecological preferences of a species in relationship to the characteristics and direction of environmental change in the newly colonized region. Characteristics of the range expansion process (e.g., colonization expanding from historic native range)	Parmesan et al. 1999, Gilroy et al. 2017
Absence of any other human agency than anthropogenic environmental change	Lack of human agency other than anthropogenic environmental change—that is, a lack of direct or strong indirect human agency for range expansion	Evidence for dispersal without human agency and lack of evidence of anthropogenic transport of propagules or individuals from the native range (or from a previously colonized alien range). Lack of evidence for increasing region accessibility via the construction of corridors (e.g., canals, bridges)	Parmesan et al. 1999, Devictor et al. 2012
Population status of occurrences outside the historic native reference range	The occurrence of permanent self-sustaining reproducing populations or of ephemeral populations at the range front outside the historic native reference range	Evidence for self-reproducing and permanent populations in the newly colonized range. Evidence that ephemeral populations are located at the range front associated with range expansion	–
Timing of onset of range expansion beyond historic native reference range	Onset of range expansion beyond the historic range—for example, after the onset of the Anthropocene (c. 1950); if well documented, this date may be relaxed to earlier dates, or even no temporal threshold may be used	Evidence for start of range expansion in response to changing environmental conditions (e.g., dated historic records, prior absence of species in historic inventories, genetic evidence)	Parmesan et al. 1999

species (Nackley et al. 2017), and that the level of differences to the traits represented in the recipient communities play an important role (Engelkes et al. 2008). For instance, neonatives often encounter closely related species in the newly colonized region, which may make hybridization and genetic introgression a more frequent phenomenon than when alien species invade a new region (Le Roux and Wieczorek 2009, Klonner et al. 2017). Predators and herbivores may switch to closely related prey or plant species as a food resource (Soininen et al. 2007, Pateman et al. 2012). Furthermore, the arrival of neonatives will occur with differential rates of spread, with generalist species likely to spread more rapidly (e.g., Chen et al. 2011, Alexander et al. 2018). Such asynchronous spread may cause boom-and-bust phenomena (Strayer et al. 2017) and an overdominance of generalist species capable of rapidly tracking changing environmental conditions.

Aliens do, but neonatives do not depend on humans as the initial dispersal vector into a new region (although secondary spread of alien species can also be unaided by humans). Consequently, although we can aim to control alien propagule and colonization pressure, there is no easy way to control the arrival and spread of neonatives; management practices can only be post hoc—and they include other risks, because restricting species migration might actually lead to the extinction of the species if the original range becomes unsuitable. The management of neonatives therefore poses challenges that are quite different from the management of aliens (table 1). In fact, the challenge is to manage species turnover, the enrichment or replacement of natives by neonatives such that negative impacts on biodiversity and ecosystem services are minimized or even turned into benefits. There is a critical need to understand how species turnover affects biodiversity and ecosystem services (Hobbs et al. 2013).

Finally, we identify four key challenges for future research and management—namely, assessing the impacts of neonatives on recipient ecosystems, identifying the drivers of rapid range expansion and the specific traits that favor successful range expansion and the different biological and ecological characteristics of neonatives in comparison to resident native and alien species, debating management options and conservation benefits of neonatives, and potentially recognizing neonative species in legislation and policies for management. For these challenges, we provide recommendations for science and biodiversity management of neonatives (table 3). Although some of these challenges address basic gaps in knowledge and understanding, others are aiming to improve the transfer of scientific understanding to biodiversity management and policy.

Conclusions

There have always been species range dynamics, and there will be natural range dynamics in the future. However, we

Table 3. Key implications of range-expanding species responding to human-induced environmental change (i.e., neonative species) for future research and biodiversity management.

Challenge	Rationale	Suitable methods	Implications for research and management
Anticipating and understanding the impacts of neonative species on resident communities, ecosystem functioning and services	The impacts on resident communities may be manifold, and vary widely in terms of strengths and direction, depending on the number and abundance of neonative species, velocity of spread, attributes of the neonative species and recipient communities.	Biodiversity monitoring, field and experimental studies, predictive modeling, meta-analyses	Recognizing and integrating themes on potential impacts of neonatives in research programs, biodiversity assessments and management
Improving the understanding of the characteristics of neonative versus alien and resident native species	Specific traits related to e.g., dispersal, life cycle, ecology and association with humans may facilitate that species become neonatives and these suites of characteristics may separate them from both alien and resident native species.	Field and experimental studies, meta-analyses, individual-based models incorporating functional traits	Risks and opportunities related to characteristics of neonatives in different contexts are understood and integrated in research and management
Advancing the understanding of management options for neonative species, their applicability and usefulness, as well as the associated risks	Improving the understanding of conservation benefits of neonatives, when management should foster or reduce the spread of neonative species, and which risks are associated with these management options.	Testing and evaluating measures that reduce versus increase the spread of neonative species (e.g., establishing or removing dispersal corridors, modifying landscape fragmentation).	Applying scientific results for biodiversity management, spatial planning, and land-use decisions; accounting for neonatives in conservation planning
Recognizing the role of neonative species in biodiversity conventions, guidelines and programs from regional to global scales	Accounting for the increasing importance of neonative species in relevant political documents and biodiversity programs.	Synthesizing and transferring scientific results on neonative species and discussing them with biodiversity managers, NGOs, public institutions, research agencies, and the wider public.	Integrating neonative species into biodiversity policy and management

believe that it is useful to distinguish natural range dynamics from those facilitated by human-induced environmental change. Therefore, expanding the list of currently used categories of biogeographic status to recognize this increasingly important component of regional species pools is warranted and useful for better communication and understanding among scientists, policy makers and managers, which undoubtedly will benefit conservation efforts.

Neonatives are currently treated by most international regulations as natives (e.g., EU Regulation 1143/2014, CBD, IUCN). We support such a classification, albeit as a distinct subcategory from resident natives. Similarly, there will undoubtedly be different opinions on the issue of using temporal and spatial thresholds for identifying neonatives. These issues clearly warrant further discussion among scientists and biodiversity managers.

In any case, we conclude that in the future, neonatives should be explicitly considered in global and regional scenarios for biodiversity management to increase clarity and to decrease undesirable effects. For example, policies aimed at increasing ecological connectivity should give explicit consideration to the potential movements of such species. Research should develop approaches for predicting their potential impacts on ecosystems and human well-being.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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