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A framework for understanding human-driven vegetation change

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Despite a major research focus on human-mediated reshuffling of plant communities, no coherent framework unites the numerous types of changes in abundances and distributions of native and non-native species that are driven by human activities. Human driven vegetation change can occur through: non-native species introductions; population outbreaks or collapses; range expansions or contractions; and range shifts of both native and non-native species. Boundaries among these different types of floristic changes are not always distinct because of an overlap in the ecological, climatic, and anthropogenic processes that underpin them. We propose a new framework that connects various human-mediated causes of vegetation change, highlights the spatial scales at which drivers act and the temporal scale at which plant assemblages respond, and provides critical insights for identifying and appropriately managing these changes.

Synthesis

Human activities directly and indirectly alter plant communities worldwide, but efforts to link vegetation changes to the full array of possible underlying causes are lacking. Population outbreaks, species range expansion or contraction, range shifts and biological invasions are key ways in which plant communities can be reorganized. We propose a framework that connects various human-driven causes of vegetation change, highlights the spatial scales at which these drivers act and the temporal scale at which plant assemblages respond, and provides critical insights for identifying and appropriately managing these changes.

Human actions have directly and indirectly reorganized the composition of many plant communities worldwide, often by bringing species from different continents or regions together to form entirely new communities (Hobbs et al. 2006). Many researchers are investigating implications of plant community reshuffling for biodiversity conservation and ecosystem functioning (Newbold et al. 2015, Wardle et al. 2011). Vegetation composition is affected by natural disturbances (e.g. floods, extreme climate, wildfires), population dynamics, species interactions, ecosystem processes and plant functional responses in evolutionary time (Franklin et al. 2016). Changes to any of these factors can alter plant community composition and structure. Major components of human-mediated changes in vegetation include: 1) non-native species introductions and establishment, 2) population outbreaks or collapses, and 3) range expansions or contractions and 4) range shifts of native or non-native species (Table 1, Fig. 1). Human-mediated phenomena that affect vegetation types can act at different spatial scales including: 1) local i.e. neighbourhood (e.g. biotic interactions such as plant–animal or plant–microbe), 2) local to regional (e.g. resource availability and land use changes), 3) regional to global (e.g. active human transport and introduction, novel evolutionary advantages), and 4) global (e.g. global environmental changes such as climate change and nitrogen deposition) (Fig. 2, 3; Inderjit et al. 2005, Catford et al. 2009, Gurevitch et al. 2011). These causes of vegetation changes may act simultaneously and result from multiple ecological, climatic, and anthropogenic processes that alter species' geographic ranges and relative abundances.

Previous frameworks for metacommunities identified the importance of patch dynamics, species-sorting, mass-effects, and neutral paradigms in understanding the processes that can influence community assembly (Leibold et al. 2004, Logue et al. 2011) but did not always explicitly discuss human-related drivers of vegetation change. Franklin et al. (2016) provided a framework to highlight the role of anthropogenic drivers – climate change, altered disturbance regimes, non-native invasion, and land use changes – in terrestrial plant community dynamics. However, frameworks that serve to link vegetation changes to the full array of possible underlying human causes are lacking. An assessment of the similarities and differences among these four types of vegetation change, and the processes that drive them,

Table 1. Causes and possible effects of human-mediated vegetation changes.

Vegetation change	Causes	Effects	Examples
Non-native species introduction and establishment[a]	Human transport and global exchange introduce species outside historical ranges, overcoming geographic dispersal barriers and alleviating dispersal limitation	Species expand range by occupying suitable environmental conditions previously unreachable	*Centaurea solstitialis* (Andonian et al. 2011, 2012), *Sequoia sempervirens* (Blair et al. 2010), *Ageratina adenophora* (Inderjit et al. 2011)
Native and non-native species population size change[b]	Increased resource supply (N deposition), increased disturbance, climate warming; biogeographic-evolutionary advantages of non-native species can enable them to reach high abundance	Increase or decrease in relative abundance within historical range	*Calagrostis canesscens, Moliinia caerula, Acer rubrum, Vitus* spp. (Carey et al. 2012, Simberloff et al. 2012)
Native and non-native species range size change[c]	Changes in climate, land use and environmental conditions (e.g. N deposition) causing altered environmental suitability and competitive hierarchies among native species; spread of species outside of historical range leading to high densities because of more favorable ecological conditions	Expansion of species range, possibly coupled with population outbreak, but former range still occupied	*Picea engelmannii* (Jiménez-Moreno and Anderson 2013), *Alliaria petiolata* (Callaway et al. 2008)
Native and non-native species species range shift[d]	Global environmental change (e.g. warming, rainfall, N deposition)	Species' latitudinal or elevational range shifts, with species' distributions tracking suitable environmental conditions	Forest advance (Macias-Fauria and Johnson 2013), *Macropiper excelsum* (Lakeman-Fraser and Ewers 2013), *Acer rubrum* (Leithead et al. 2010)

[a] Movement of a species to new areas outside its native range as a consequence of human actions; that species can then spread to larger areas, attain high abundance, and exert strong impacts in its new environments.

[b] Rapid increases in the local population size of a species that is within its historical geographical range; collapse is the inverse.

[c] Expansion of the range of a native species, where the species still occupies its former geographic range but has an expanded distribution; range contraction is the opposite.

[d] Movement of the entire distribution of a species to track suitable environmental conditions.

is needed to understand the causes of vegetation change (Fig. 2). Many of the observed vegetation changes cannot be fully understood without a framework that highlights their causes. Such a framework is also crucial for predicting the consequences of vegetation change and identifying effective management strategies. Here we present a conceptual framework that identifies similarities and differences among four types of vegetation change.

A framework for understanding human impacts on vegetation change

Human-assisted vegetation changes can involve an overall increase or decrease in native and non-native species' population sizes through introduction and establishment of non-native species (Fig. 2a), increases or decreases in peak relative abundance or dominance (i.e. the proportion of vegetation abundance at a site made up of a given species; Fig. 2b), expansion or contraction of species' range sizes (Fig. 2c), or overall shifts in species' distributions (Fig. 2d). Our proposed framework links these four major types of human-mediated community reorganization with the five key factors driving these changes (Fig. 3). The framework presents the typical spatial scales at which drivers act and the temporal scales at which plant assemblages respond (Fig. 3). Although we distinguish among the four major types of vegetation change, and particularly between the changes that affect species' abundances (Fig. 2b: change occurs along y-axis) versus species' distributions (Fig. 2a, c, d: changes occur along x-axis), we note that the boundaries among them are not stark and changes often occur simultaneously in response to the same external stimuli (Hargreaves et al. 2015, Huang et al. 2015, Louthan et al. 2015). One type of vegetation change can also trigger another because of biotic interactions (Simberloff and von Holle 1999, Kuebbing and Nuñez 2010, Pearson et al. 2016) and the potential for species to alter environmental conditions (i.e. transformer species sensu Richardson et al. 2000).

Following introduction, some non-native species may experience rapid gains in local population size and range expansion (Gurevitch et al. 2011) such that their abundances and distributions in their invaded range exceed those in their native range. We consider such instances as outbreaks or range expansions of non-native species (Fig. 3), rather than an inherent component of non-native species introductions and establishment (Fig. 3), though the latter must necessarily precede the former.

Our framework also highlights the ubiquitous roles of altered biotic interactions, resource availability and land use change, and global environmental change (Fig. 3) in driving all types of vegetation change, but it also identifies factors (Fig. 3) that affect only the abundances and distributions of non-native species. Direct human introduction is a prerequisite for non-native species invasion but is not involved directly in native species' range expansions and shifts, though changes in native species distributions may follow reduction

Figure 1. Human-mediated community reorganization. (a) native species outbreak: flow regulation along the Murray River in southeastern Australia has altered flood regimes, increasing suitability for native *Eucalyptus camaldulensis,* which has increased its local population size by occupying new areas of the floodplain, infilling its former geographic range; (b) native species range expansion: The native species *Picea engelmanii* (dark green in photo) expanded its range near Crested Butte, Colorado, USA owing to climate change; (c) non-native species introduction: *Acacia dealbata, Ageratina adenophora* and *Parthenium hysterophorus* were introduced at different times and in different geographic ranges in India but now co-occur along roadsides and forests in Almora, Uttrakhand, India; (d) non-native species invasion: *Prosopis juliflora*, an aggressive non-native invader, spreads and reaches high densities and suppresses or eliminates local plant species in Shivalik Hills, Panchkula, Haryana, India. Photo credits: Jane Catford (a), Jordan Mayor (b), Inderjit (c, d).

in dispersal barriers. We note that our definitions of the four types of vegetation change classify human-assisted colonization (translocation) of species outside of their historical ranges as non-native species introduction, even when assisted colonization is a deliberate conservation action. Although assisted migration can be a form of species introduction (or reintroduction), discussion of assisted migration of species is beyond the scope of this article.

The framework proposed here highlights similarities in causes and potential consequences of different types of vegetation change (Fig. 2, 3). Yet, there are gaps in our understanding of the commonalities among drivers in explaining various types of vegetation change. For instance, biogeographic–evolutionary processes are largely studied in contexts of non-native invasion but could also be involved in other types of vegetation change. The imbalance in the amount of discussion of the four types of vegetation change reflects the relative availability of evidence for each of them and the amount of research activity that they have each attracted. Below, we expand on each of the four main types of vegetation change depicted in our framework.

Non-native species introduction and establishment

Through global commerce and international travel, humans deliberately introduce plant species to areas outside their historical native ranges (Table 1, Fig. 1d, 2a) (Zhang et al. 2014), where disturbance, resource fluctuations, and high propagule pressure may facilitate their establishment (Fig. 3). Many non-native plant species (≈ 3.9% of the total global vascular flora) have been naturalized globally owing to human actions (van Kleunen et al. 2015). While adequate data on introductions that fail are scarce, it is likely that many introduced species fail to establish viable populations (Jarić and Cvijanović 2012) or are disadvantaged because of maladaptation (Crespi 2000, Sexton et al. 2011). However, a proportion of introduced species form naturalized, self-sustaining populations that do not rely on ongoing propagule introduction (Diez et al. 2009). Most naturalized plant species do not become invasive (Richardson and Pyšek 2012) but instead remain near their sites of introduction at low relative abundance. A small proportion of non-native species reach extremely high abundances in

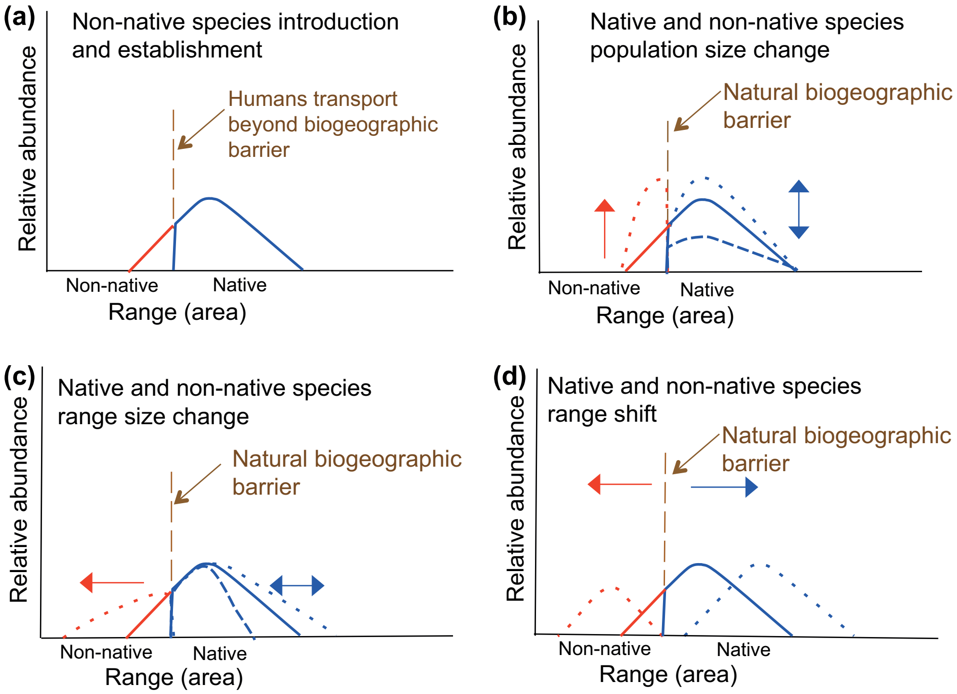

Figure 2. Four scenarios (a–d) showing how species' geographic ranges and relative abundance can change: (a) human transport and introduction of species enabling a species to establish outside its historical native range (i.e. non-native species introduction and establishment), (b) native and non-native species outbreak marked by an increase in species relative abundance within its native and introduced range, and native species population collapse, (c) range expansion and contraction of native species and range expansion of non-native species, and (d) range shift of native and non-native species. Species outbreaks and range expansions often co-occur (as do collapses and contractions), but we have shown them separately here. These vegetation changes can occur simultaneously; for example, non-native species can experience both range expansion and population outbreak in the new range. Native species are in blue; non-native species are in red; solid curve = original range, dashed curve = population collapse or contraction, dotted curve = outbreak, range expansion or range shift.

introduced ranges compared to in their native ranges (Fig. 1c–d, 2a) and can exert important ecological impacts in the new environment (Rejmánek 2011); we address these in the species outbreaks section below. Non-native species that have biogeographic–evolutionary advantages are more likely to establish successfully following introduction (Hierro et al. 2005). Here, biogeographic–evolutionary advantages are represented by evolved relationships (e.g. with consumers, competitors, or mutualists) that can differ biogeographically between native and introduced ranges. These include escape from natural enemies (including release from inhibitory soil biota), the capacity to evolve enhanced competitive ability (Blossey and Nötzold 1995), and possession of novel chemicals that suppress competitors (Gurevitch et al. 2011).

Global environmental change, including climate change, may indirectly facilitate invasion by non-native species (Caplat et al. 2013), highlighting interactions among the drivers of vegetation change. For example, traits such as high resource uptake contribute to invasion by the non-native grass *Agropyron cristatum* in the northern Great Plains of North America, and warmer springs and wetter summers, the frequency of which will increase with climate change, favor its early phenology and help to match its water requirement during summer (MacDougall et al. 2008, Caplat et al. 2013). Each of the five outlined drivers of vegetation change contributes to non-native introduction and establishment (Fig. 3). More research on the relative importance of specific drivers in non-native introduction and establishment in different ecosystems would greatly strengthen our understanding of vegetation change.

Population outbreaks and collapses

At the outset it is important to state that distinguishing native species from non-native species would add value to the proposed framework (Paolucci et al. 2013, Simberloff and Vitule 2014, Simberloff 2015, Buckley and Catford 2016), because non-native species may experience biogeographic–evolutionary advantages in introduced ranges at least in the early phases of introduction, which may help them to establish and become invasive. Non-native species have often been shown to experience biogeographic–evolutionary advantages over native species through a variety of mechanisms such as enemy release, increased competitive ability, novel weapons, positive plant–soil feedbacks, and via invasional meltdown, all providing advantages over native species (Simberloff and von Holle 1999, Klironomos 2002, Funk and Vitousek 2007, Callaway et al. 2011, Gurevitch et al. 2011, Schaffner et al. 2011, Inderjit 2012).

Both native and non-native species can experience outbreaks and collapses in their local abundances and population sizes. We depict such changes as increases and decreases in the peak relative abundance of species in Fig. 2, leading to changes in the area under the curve. Identifying species' outbreaks or collapses would entail comparing their population sizes over an appropriate length of time determined

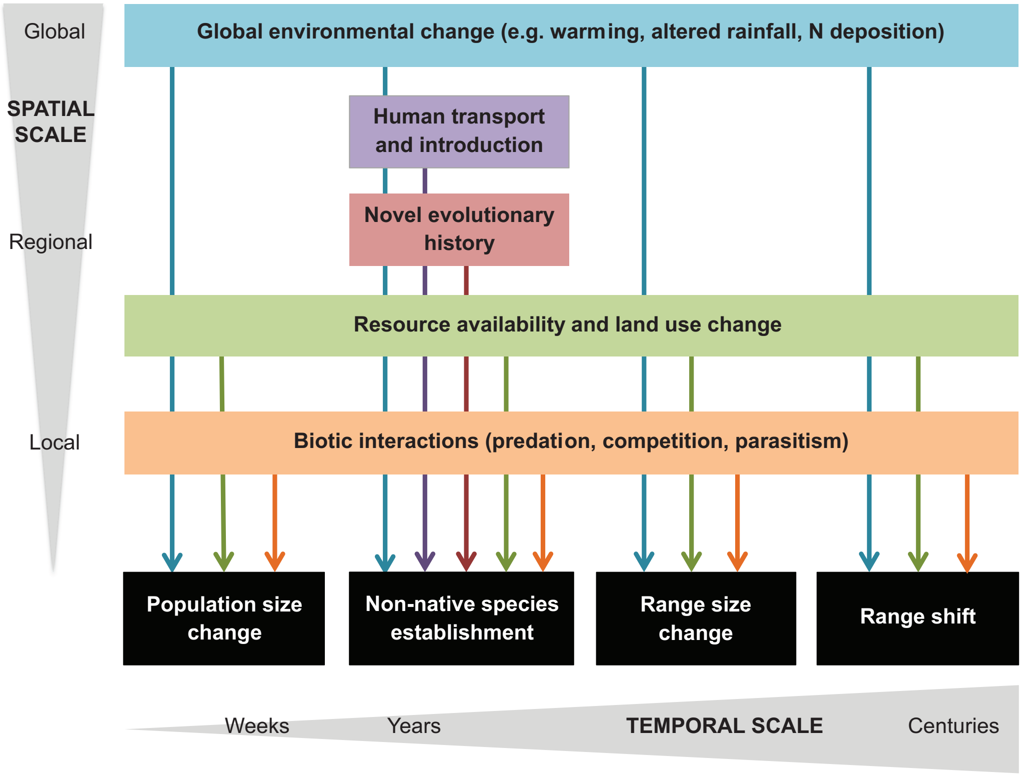

Figure 3. A conceptual framework to illustrate primary drivers (colored boxes) of four major types of human-mediated vegetation change (black boxes), the spatial scales at which drivers act (left grey scale), and the temporal scale at which plant assemblages respond (bottom grey scale); the influence of each particular driver on vegetation change is shown with solid colored lines. Changes in local population sizes include population outbreaks and reductions in abundance. Non-native species introduction and establishment require human actions that directly transport and move species beyond their historical geographic ranges. Range size changes and shifts may involve human changes to the environment and reduction in dispersal barriers, but differ from non-native species introduction and establishment by not involving direct human introduction. Non-native species can become invasive in response to novel-evolutionary advantages in the introduced ranges, strong association with humans, and modified environmental conditions, allowing them to experience both range expansion and population outbreaks. However, although humans govern introduction of non-native species, the establishment of non-native species could be enhanced by the range contraction or collapse of native species. The boundaries among the four different types of vegetation change in the diagram are not stark, indicating some degree of blurring and overlap among these different plant responses to human activities. Further, one type of vegetation change may trigger other forms of vegetation change (interactions not shown for clarity). For example, non-native species invasion may prompt collapse or range contraction of native species and may facilitate invasion by other non-native species.

by a species' generation time, life history, and demography. Population collapses could be due to shifts in the balance between limiting resources, decline in the dispersal vectors across landscapes, or habitat degradation (Ozinga et al. 2009, Harpole et al. 2016). A large difference in population size between the native and invaded ranges of non-native species could also be considered a population outbreak for non-native species (i.e. based on trends in space and time).

Native species abundances within their historical ranges can increase owing to increases in resource availability (e.g. nitrogen deposition), climate change, or anthropogenic disturbance (Table 1, Fig. 1a, 2b) (D'Andrea et al. 2009, Carey et al. 2012, Simberloff et al. 2012, Bocsi et al. 2016). Native species outbreaks include rapid increases in the local population size of a species that is within its historical geographical range. Indeed, in southeastern Australia, river regulation through dams and associated alteration of flooding regimes has enabled native *Eucalyptus camaldulensis* to colonize formerly unsuitable floodplain areas, resulting in an increase in its abundance within its former geographic range (Fig. 1a) (Bren 1992). Humans did not disperse *Eucalyptus camaldulensis* but modified local hydrological conditions, facilitating expansion of a population already present. While population outbreaks like these can be considered a form of range expansion (i.e. into previously unsuitable areas), we classify them as examples of local increases in population sizes as they occur within species' historical geographic ranges. However, outbreaks and range expansion can be interrelated. Whether a species is seen to expand or infill its geographic range is influenced by human perceptions of range boundaries and the spatial and temporal scale at which they are depicted.

Native species do not have novel evolutionary histories that characterize non-native species. Additionally, native species, unlike non-native invaders, remain in the vicinity of their pathogens, herbivores, consumers, decomposers and symbionts. Through similar processes, albeit in the opposite direction, sizes of native species populations have also frequently collapsed because of rapid changes in environmental conditions and resource availability, impacts of non-native species (including those occupying higher trophic levels), and direct human actions like logging, deforestation and land clearance for agriculture (McKinney 2002). Consistent with predator–prey dynamics where enemy abundance may lag behind prey abundance and allow short-term prey population outbreaks (Ryall and Fahrig 2005), native enemies can rein in an expanding population of a native plant species, relatively quickly returning it to its historical size.

Biogeographic comparisons of ecological traits of species and their impacts on native and non-native ranges have aided understanding of why some non-native species experience population outbreaks and suppress local species when introduced to new regions (Fig. 1c) (Hierro et al. 2005, Callaway et al. 2011, 2012, Inderjit et al. 2011, Kaur et al. 2012). Some non-native species may be particularly successful in their introduced ranges because of their novel evolutionary histories, which allow them to persist more readily than native species in modified environmental conditions and which may enable them to outcompete native species (Buckley and Catford 2016). For example, novel chemicals released by exotic species may have adverse allelopathic effects on native species in the invaded community because of the presence of naïve soil communities and susceptible plants that have not evolved in the presence of these chemicals (Callaway and Ridenour 2004, Inderjit et al. 2011).

Non-native ranges to which invasive species have been introduced provide a novel environment in terms of biogeographic–evolutionary advantage (e.g. enemy release, plant–soil feedbacks, novel chemicals), and this novelty may counteract the disadvantages of establishing in a new physical environment and the possible absence of mutualists present in the native range (Table 1). A rapid increase in the abundance of non-native invaders can be triggered by shifts in various population-level interactions. Examples include reduced herbivory (Schaffner et al. 2011, Inderjit 2012, Kalisz et al. 2014), novel chemicals (Inderjit et al. 2011, Svensson et al. 2013, Zheng et al. 2015), plant–soil feedbacks (Inderjit and van der Putten 2010, Inderjit and Cahill 2015), altered physiological allocation (Feng et al. 2011), increased competitive ability (Zheng et al. 2015), disruption of native mutualisms (Traveset and Richardson 2014, Hale and Kalisz 2012), and resulting demographic responses (Gurevitch et al. 2011, Kalisz et al. 2014). Post-invasion evolutionary processes in the non-native species can occur as the invasion proceeds and may result in their eventual decline in abundance (or range contraction) (Iacarella et al. 2015). Conversely, new enemies that have accumulated or soil communities that may have evolved may eventually suppress the invader's population growth.

Range expansion or range contraction

Range expansion refers to the increase in the area occupied by a native species, where the species still occupies its former geographic range but has an expanded distribution; range contraction is the opposite process (Fig. 2c). A native species can expand its range along latitudinal or elevational gradients, but its former range can remain occupied owing to increased geographic extent of suitable environmental conditions and amenable biotic ones (Table 1, Fig. 1b, 2c) (van Grunsven et al. 2010). Site (in)fidelity (i.e. the tendency of a species to return to a previously occupied location, Switzer 1993) and mating system can be important factors in range expansion. Predictive traits such as dispersal ability, persistence in unfavorable climates, ecological generalization, reproductive strategy (vegetative versus sexual), and low competitive ability can aid assessment of the probability that a species will expand its range and colonize new environments in response to climate change (Estrada et al. 2016). Traits of successful non-native invaders may resemble those of native plant species that are expanding their ranges, including natives (Thompson and Davis 2011). For example, physiological traits such as photosystem II thermal tolerance may be similar for both native and non-native plants when water availability is adequate, but non-native species may better tolerate higher leaf temperature than native species, as observed in invaders from Mediterranean-type ecosystems (Godoy et al. 2011).

Several plant species native to North America have experienced range expansion (Simberloff et al. 2012). Likewise, native plants in Australia, including *Sollya heterophylla, Acacia longifolia* and *Leptospermum laevigatum*, became abundant weeds when their distributions increased (Head and Muir 2004). In both instances, whether their expansion is occurring naturally or is being actively mediated by humans often remains unclear. Human-driven environmental changes and habitat modification frequently create conditions that allow native species to spread, which can in turn greatly alter community structure and plant diversity (Carey et al. 2012). Some human-mediated abiotic and biotic changes that trigger increases in native species range size include increased atmospheric nitrogen deposition (e.g. *Calamagrostis canescens* and *Elymus athericus* in Europe, *Molinia caerula* in the United Kingdom), fire suppression (e.g. *Gutierrezia sarathrae, Pseudotsuga menziesii, Acer rubrum, Juniperus occidentalis* in the United States), and increased concentration of atmospheric CO_2 (e.g. *Vitis* species in the United States) (Carey et al. 2012, Simberloff et al. 2012). These are similar to many processes that facilitate non-native species invasion (Fig. 2) (Leithead et al. 2010). Nitrogen deposition, one of the major anthropogenic disturbances, can locally extirpate certain species thereby giving competitive advantage to certain other species and can foster temperate forest expansion into grasslands (Köchy and Wilson 2001, Southon et al. 2013).

Range expansion and contraction are species-specific and depend on local ecological factors such as empty niches or reduced competition from neighbors. Range expansion of red maple *Acer rubrum*, red oak *Quercus rubra* and white pine *Pinus strobus* from Canadian temperate forests into boreal forests occurs when large forest gaps are available, potentially facilitating northward migration of these species (Leithead et al. 2010). This pattern is also seen in several tree species across the prairie–boreal forest ecotone in central North America and is expected to increase owing to climate change (Frelich and Reich 2010). Crown fires common in boreal forests restrict northward expansion of *Pinus resinosa*, a fire-dependent species that tolerates soil surface fires (Flannigan and Bergeron 1998). Many tree species are expanding their ranges in the northeastern US, but others (e.g. *Abies balsamea*, *Betula papyrifera*, *Picea rubens*, *P. grandidentata*, *P. tremuloides* and *Prunus serotina*) are experiencing range contraction (Iverson et al. 2008). Further, at lower latitudes mangroves (*Rhizophora mangle*, *Avicennia* *germinans* and *Laguncularia racemosa*) are expanding their ranges poleward in response to the declining frequency of extreme cold events (Cavanaugh et al. 2014). Across sites in North America, a greater plasticity of some non-native plant species that allows them to shift phenology in response to climate change has resulted in their flowering earlier than native species; thus they can occupy empty niches and expand their ranges (Fridley 2012). However, many non-native species do not expand their ranges after establishment and thus are classified as non-invasive. Three native European herbaceous species of *Centaurea* (*C. solstitialis, C. calcitrapa* and *C. sulphurea*) have established in North American grasslands, but only *C. solstitialis* is invasive there (Graebner et al. 2012). The other two species remain non-invasive largely owing to their lower competitive ability against the invasive congener, which possesses traits that aid its invasiveness, including faster relative growth rate and the ability to outcompete native species (Graebner et al. 2012).

Biotic interactions such as competition, predation, herbivory, and mutualism can influence the impact of climate change on range expansion and contraction (Hellmann et al. 2012, HilleRisLambers et al. 2013). An increase in competitors (i.e. neighbors) or consumers (e.g. herbivores of treeline conifers and alpine plants) and lack of mutualists (e.g. pollinators, bacterial or fungal symbionts, or species that facilitate heterospecific neighboring species in arctic and tree line communities) can eliminate a species from part of its range, leading to range contraction (HilleRisLambers et al. 2013). Geomorphic and lithologic factors (e.g. topography, soil, exposed bedrocks) can retard upward movement of the subalpine tree line in response to climate change (Macias-Fauria and Johnson 2013), as can abundant herbivores at tree species range edges in North America (Fisichelli et al. 2012). The range contraction of the Joshua tree *Yucca brevifolia* in the Mojave Desert is linked to disappearance of megafaunal dispersers that limits its ability to spread northward into new areas (Cole et al. 2011). Clearly, biotic conditions, including natural enemies and dispersers, can influence range expansion or contraction of native species, thus implicating the role of multiple drivers in range expansion or contraction.

Either land use change or climate change alone can result in range contraction of species (Jetz et al. 2007), but the synergistic impact of these two factors can exceed that of either factor alone (Oliver and Morecroft 2014). Further, high-temperature regions are expected to experience greater effects of habitat loss and fragmentation on species ranges, but these effects should be lower in areas that experience an increase in average rainfall. Woody species in Yunnan, China showed contracted ranges owing to both their inability to move northward through unsuitable habitat and the reduction of environmentally suitable habitat in their current ranges (Zhang et al. 2014). In such instances, constructing or retaining north–south migration corridors could mitigate range contraction of species ranges. It should be noted in such cases that range contraction involves not just the inability of a species to expand its range, but also reduction in its existing range.

Like native species, non-native species can both expand and contract their ranges in response to global changes. However, range-expanding native species differ from invasive non-native species because of the greater connection and associated potential for gene flow between populations in the expanded introduced range and original native range. This may result in enhanced genetic diversity in expanding populations that could lead to a greater likelihood of local adaptation (Morriën et al. 2010). Conversely, gene flow can limit local adaptation at the range edge because it may inhibit local adaptation and break up coadapted gene complexes (Levin 2010, Moore et al. 2015, Polechová and Barton 2015, Phillips et al. 2016). Under conditions of environmental constraints to expansion, selection can favor species dispersal traits over competitive ability (Burton et al. 2010, Kubisch et al. 2010). However, using the model plant, *Arabidopsis thaliana*, Williams et al. (2016) showed that experimental populations that rapidly evolve traits including increased plant height, seed dispersal, seed biomass and competitive ability spread further than non-evolving populations.

Some non-native invasive species can expand their ranges rapidly in lower-nutrient habitats relative to native species because of their higher resource-use efficiency (Funk and Vitousek 2007), but in other cases native species outperform non-natives (Daehler 2003). Both native and non-native species can allocate relatively more nitrogen to photosynthetic tissues, which can in turn facilitate range expansion of those species. But the mechanism behind higher allocation of nitrogen to photosynthesis may differ between native and non-native species. For example, *Ageratina adenophora*, a neotropical invader, allocates more nitrogen to photosynthesis in its introduced range than in its native range, resulting in increased growth and vigor (Feng et al. 2011). *Pinus strobus*, a range-expanding evergreen tree native to eastern North America, retains more nitrogen in photosynthetic tissues than do noninvasive deciduous native oak species (Laungani and Knops 2009). Nitrogen (N) retention in plant tissue contributes to the invasive potential of species particularly in N-limiting conditions (Laungani and Knops 2009). Studying nutrient dynamics in central Himalaya forests, Ralhan and Singh (1987) found that *Pinus roxburghii*, which typically grows on infertile soils, translocated higher levels of N from its senescing leaves than *Quercus leucotrichophora*, which typically grows on fertile soils. Further, some non-native species express altered nitrogen allocation patterns with increased nitrogen in photosynthetic tissues and decreased allocation of nitrogen to defense relative to allocation patterns in their native range (Feng et al. 2009, 2011).

Habitat factors combined with new enemies may affect range expansion of non-native species. Non-native species may encounter new enemies in invaded communities and thus experience more herbivore damage (Inderjit 2012, Dostál et al. 2013), particularly in productive habitats (Dostál et al. 2013). For example, the invasiveness of European *Ammophila arenaria* in North America, South Africa, southern Australia, and New Zealand is attributed to the escape of the invader in its introduced ranges from specialist pathogenic nematodes found in the native range (van der Putten et al. 2005). However, the degree of invasiveness of *A. arenaria* varies among its introduced ranges. The presence of generalist pathogenic nematodes in California allows only partial release of *A. arenaria* and limits its invasion there, while abiotic habitat factors such as aridity limit *A. arenaria* in South Africa (Inderjit and van der Putten

2010). Further, human impacts on herbivore densities can render ecosystems more vulnerable to non-native invasion (Carlsson et al. 2009). This may occur, for example, by ungulate herbivores becoming overabundant owing to loss of top predators and through management practices for native ungulates or domestic livestock that favor non-native invaders (Eschtruth and Battles 2009, Kalisz et al. 2014, Shen et al. 2016).

Finally, the inability of native populations to survive or adapt to changing climate conditions may result in their range contraction (Anderson 2015). A species that moves to new locations (e.g. to higher elevations) within the same biogeographic region as a consequence of removal of climate barriers is considered a native species, because this range expansion does not result from direct human introduction and need not bring a novel evolutionary history to the newly occupied sites. Human-mediated dispersal to habitats and locations new to a species but within its native biogeographic range is common (e.g. pines planted outside their climate zone but within the same biogeographic region) (Nuñez and Medley 2011, Gallian et al. 2016). Non-native and native species can exhibit similar evolutionary responses to novel climate, biotic interactions, and empty niches (Moran and Alexander 2014). For example, selection can favor evolution of enhanced dispersal ability when range-expanding species do not encounter natural enemies in a novel environment through re-allocation of energy not used in defense to dispersal traits instead (Caplat et al. 2013). Further, Weber and Scott (2012) proposed the concept of "projected dispersal envelope" to accommodate species movement in spatial and temporal contexts. Both native and non-native species could expand their ranges in new environments, but range-expanding species can be native in their new environments (Weber and Scott 2012). A non-native species may escape from belowground enemies and undergo less negative (or even positive) plant-soil feedback in its new range, and less negative feedback than that experienced by a native species in its new range (Reinhart and Callaway 2004). *Centaurea solstitialis*, a non-native range-expanding species in North America, exhibits this pattern. While it experienced negative plant–soil feedbacks in new range, natives in the same community showed even greater negative plant–soil feedbacks, which likely contributed to the ability of *C. solstitialis* to spread laterally in open areas (Andonian et al. 2011).

Species range shift

As opposed to range expansion (in which species still occupy their former geographic ranges), in a range shift the entire distributions of a species moves to track suitable environmental conditions (Table 1, Fig. 2d). Such shifts often occur along latitudinal or elevational gradients. One major driver of native and invasive species range shifts is climate change (Perkins 2010, Burrows et al. 2014, Riordan and Rundel 2014). However, the role of climate change in range shifts is complex, because temperature, precipitation, length of growing season, and biotic interactions such as herbivory and plant–soil feedbacks (van der Putten 2012, Fisichelli et al. 2012) can all be in play. Further, changes in soil communities along latitudinal or elevational gradients can potentially cause dramatic range shifts of plant species (van der Putten, 2012, Blankinship et al. 2011). However, the direction of plant–soil feedback effects is difficult to predict owing to the complex nature of climate change, and this issue merits further study (Caplat et al. 2013). In response to rising global temperature, species are generally predicted to move to sites that are currently cooler, but range shifts vary among species (le Roux and McGeoch 2008). Louthan et al. (2015) discussed the importance of species interactions in limiting ranges and advanced the species interactions–abiotic stress hypothesis, which predicts that abiotic factors such as climate change are likely the major drivers of range limits in abiotically harsh environments but that species interactions are more important in less stressful environments.

During a range shift, native species can experience enemy release (mainly from herbivores and pathogens) if they are better defended against enemies in their new range (Engelkes et al. 2008, van Grunsven et al. 2010, van der Putten 2012). *Macropiper excelsum*, a New Zealand native, is shifting its range polewards outside its natural range and grows better because it escapes the herbivorous moth, *Cleora scriptaria* (Lakeman-Fraser and Ewers 2013). Resource fluctuations and disturbances in native habitats could favor life-history traits that allow plant species to colonize novel habitats, so that across multiple populations range expansion may differ between disturbed and undisturbed habitats (Lee 2011). Factors driving range shifts can vary greatly among ecosystems. For example, it has been suggested that climate change rather than land use is the main driver of species range shift at high elevations, while at lower elevations impacts of land use changes are difficult to disconnect from those of warming (van der Putten 2012).

Utility of the proposed framework

Several conceptual frameworks have been proposed to describe the reorganization of plant communities or community interactions in the context of climate change (Gilman et al. 2010, Chapin 2003, Shachak and Boeken 2009, Suding et al. 2008, Caplat et al. 2013). For example, Gurevitch et al. (2011) proposed a framework for biological invasions that emphasizes the importance of ecological and evolutionary processes for rapid local population increase, formation of mono-dominant communities, and range expansion of non-native species. This proposed framework is useful because it establishes that boundaries among the four different pathways of vegetation change are not stark, indicative of some degree of blurring and overlapping among them. Further, one type of vegetation change may trigger other forms of vegetation change. For example, non-native species invasion may prompt collapse or range contraction of native species and may facilitate invasion by other non-native species. As Gurevitch et al. (2011) emphasize, there is a need for a conceptual framework that recognizes the interaction among various drivers/causes. Our framework expands these earlier attempts by comparing and contrasting different drivers of vegetation change (Fig. 3) and highlighting interactions among the types of vegetation change. Our framework recognizes the similarities in the causes and potential consequences of multiple types of vegetation change. It thus aids understanding of the relative roles of disturbance, resource fluctuations, climate change, land use changes, and biogeographic–evolutionary processes in driving vegetation changes. It also recognizes that changes in population size, range shifts, and changes in range size of both native and non-native species are driven by biotic interactions, resource availability, land use changes, and environmental changes (Fig. 3).

Certain drivers receive more attention than others when particular types of vegetation change are studied, but unexplored drivers may play key roles. For instance, many studies have identified the importance of novel evolutionary histories in helping non-native species' populations establish, grow, and spread in their introduced ranges (Inderjit et al. 2011, Ricciardi et al. 2013, Taylor et al. 2016). Ecological–evolutionary processes such as enemy release, evolution of increased competitive (EICA) or dispersal ability, development of novel weapons, and plant–soil feedbacks may help explain why a species can become abundant in areas it has not occupied previously. However, the possible role of evolutionary processes in generating changes in native species' abundance and distributions is under-acknowledged and often ignored. Native species can respond similarly to non-native species when released from their enemies, even if the release is only partial. For example, in central New York, herbivore attack on *Solidago altissima,* a native of eastern North America, results in the dominance of understory plants such as *Poa pratensis* (Uesugi and Kessler 2013). To test the validity of the EICA hypothesis, Uesugi and Kessler (2013) studied the competitive abilities of artificially selected *S. altissima* from long-term herbivore-exclusion and control plots. Experimental herbivore-exclusion led *Solidago altissima* to produce greater amounts of polyacetylenes, which allowed it to suppress its main competitor, *Poa pratensis*, more effectively (Uesugi and Kessler 2013). Our framework does not explicitly link changes in the abundance and distribution of native species with species' evolutionary histories (Fig. 3). However, some native species could potentially benefit from biogeographic–evolutionary advantages in the immediate aftermath of a population outbreak, range expansion or range shift, which points to research areas worth exploring.

Understanding how abundances and/or range sizes of species change due to human-mediated ecological and evolutionary drivers remains a major challenge. The proposed framework could also be applied to intraspecific differences, e.g. a southern subpopulation of a species invading the range of a northern subpopulation of that species, which could be due to the crossing a physical barrier to gene flow between subpopulations that foster genetic differentiations between subpopulations (Su et al. 2003). The framework could potentially help conservationists and policy makers to better understand the overlapping causes and consequences of vegetation changes and design appropriate strategies to meet their goals. When an ecologically or economically important species faces threats to its survival owing to environmental change, it can be shifted to suitable ranges or can be replaced by a species with a more suitable gene pool (Carroll et al. 2014). A better understanding of the dynamic nature of the vegetation with increasing human impacts would aid the of design long-term studies on vegetation mapping and predict future vegetation changes.

Although considerable knowledge of the individual types of vegetation change exists, many unanswered questions remain about the general reorganization of terrestrial plant communities. For instance, what is the relative importance of the five drivers – human introduction, evolutionary histories, biotic interactions, resource availability, and global environmental change – in causing the four types of vegetation change that we identify? What are the differences in importance among these components in arctic, boreal, temperate, and tropical ecosystems? Are some of these drivers more important for certain types of vegetation change, and are some easier to manage than others? Which sort of vegetation change is most common, is the easiest to avoid, or is having the greatest impact on biodiversity, and ecosystem structure, function, and services? What lack of knowledge or understanding is limiting accurate prediction of the key drivers and the main consequences of vegetation change? Our framework focuses attention on these sorts of questions, thereby identifying important knowledge gaps.

Concluding remarks

Human-mediated reorganization of plant communities comprises non-native species introductions, population outbreaks and collapses, range size expansions and contractions, and shifts in the geographic distributions of native and non-native species. The underlying drivers of vegetation change – including shifts in dispersal patterns and propagule pressure, environmental conditions, resource availability, and biotic interactions both within and across trophic levels – influence community assembly and vegetation dynamics (Catford et al. 2009) and thus determine the type and extent of vegetation change. Our framework unites the causes and potential consequences of changes in species abundances and distributions and highlights the major drivers behind the anthropogenic reorganization of plant communities. It also emphasizes links that could be strengthened across different aspects of ecological research, including those relating to floristic changes in response to climate change, land use change, and restoration of habitats invaded by non-native species (Fig. 3). Greater empirical evidence gathered from a broader range of ecosystems and across multiple temporal and spatial scales will help elucidate the major causes of human-mediated plant community reorganization, which can then be targeted through management and restoration efforts.

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