Cell Press REVIEWS

Opinion

The Nebulous Ecology of Native Invasions

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In the Anthropocene, alien species are no longer the only category of biological organism establishing and rapidly spreading beyond historical boundaries. We review evidence showing that invasions by native species are a global phenomenon and present case studies from Southern Africa, and elsewhere, that reveal how climate-mediated expansions of native plants into adjacent communities can emulate the functional and structural changes associated with invasions by alien plant species. We conclude that integrating native invasions into ecological practice and theory will improve mechanistic models and better inform policy and adaptive ecological management in the 21st century.

Trends

For much of the 21st century, and before, scientists from around the world have reported the occurrence of populations of native plant species establishing and spreading outside historical plant communities.

In general, native plant invasions were considered small scale and driven by local land use. However, on review of the subject literature it becomes evident that native plant invasions are in fact very widespread, often very large, and often independent of local land-use changes, driven rather by global climate.

Currently, policy for and management of ecological systems focuses on alien invasive plant species, in part because of the widespread awareness of the impacts of alien plant species.

Considerably less attention has been given to invasive native plant species, even when the impacts are structurally and functionally similar to those of invasive alien plant species.

When Endemics Become Epidemic

Invasion science is an ecological subdiscipline that explores the proliferation, spread, and persistence of species transported by human activity to new and potentially distant ranges [1]. Highly contentious topics in invasion science include the utility of origin (i.e., native vs alien) [2,3], 'denial' of impacts [4], and the lexicon used to describe invasions and invaded communities [5–7]. Despite disputes there is nearly universal disciplinary agreement that the role of scientists in studying invasive species should be to gather, interpret, and communicate information as accurately and objectively as possible and that decisions to manage invasive species will require judgments communicated from invasion biologists to policymakers [8]. It is from this common ground that we discuss the challenges of formulating unambiguous native plant invasion science and policy. Whether they are termed 'expansion', 'encroachment', 'colonization', or 'regime shifts', scientists from around the world have documented ecological phenomena that share many characteristics with invasions by alien species. Shared characteristics include changes in population distributions [9,10], ecosystem structure [11], and function [12] as well as impacts on biodiversity [13,14], ecosystem services [15,16], and regional economies [12]. There are concerns that 'artificial distinctions' and a general dissociation by invasion science has created a rift that is impeding policy on and management of native range expansions [17]. If an invasive species is defined as an organism occurring outside its natural past or present range whose presence and dispersal is due to intentional or unintentional human action – and climate change is recognized as being forced by anthropogenic factors – climate-driven range expansions can be considered something other than historical biological colonization. We affirm the collective call for objective science to drive policy [8] and herein advocate for a more inclusive invasion science built on the study of dissemination processes, lag phases, linked invasions [18], and unified classification impacts [19] that embraces a broader consideration of the potential problems caused by species undergoing range expansion, in particular when this is a result of human activity.

Many modern landscapes have experienced exponential transformations since the mid-20th century conception of invasion science. Global environmental change is creating conditions

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that are unprecedented within the typical historical range used to discriminate between native and alien species (i.e., pre-colonial to present). The rapid increase in atmospheric CO_2 concentration and the associated impacts on climate are increasing the likelihood that both native and alien plants will have drastically altered ranges, with expansion in some areas and contraction in others [20]. The existing definitions of native species are increasingly blurred as resident species become poorly adapted to the local environment [21] and competitive balance between co-occurring native species shifts with changing environmental gradients. Now more than ever, expanding transportation networks, technological advances, landscape transformation, climate change, and geopolitical events influence global invasion risks [1]. The breakdown of biogeographic barriers by climate and global human transport also sets the current era apart from previous times in terms of the increasing rate of appearance of novel environments, species combinations, and altered ecosystem function [5].

In many respects expanding native species can be functionally indistinguishable from invading alien species (Table 1). In North America invasive native plant species now represent 10–20% of all invasive plant species [22,23]. However, the appropriate response to invasive native species remains unclear, in part because their importance has been downplayed based on the assumptions that: (i) the majority of native plant invasions are associated with an anthropogenic disturbance; (ii) impacts by invasive native species are less than impacts by invasive alien plant species; and (iii) invasive native species are quite local [22]. However, considering the growing evidence that most invasions, regardless of origin (i.e., native vs alien), result from anthropogenic disturbance, it is an appropriate time to reassess the devaluation of native invasions. Furthermore, biased measures of alien invasive species' impacts [24] and the exclusion of native species from considerations of impact [19,25] may be skewing perspectives, despite the growing evidence that large-scale expansions by native species can also include changes in distributions and/or abundance as well as ecological and economic harm [12]. Last, a preponderance of evidence from ecosystems around the world demonstrates that native invasions are widespread and large-scale [26–32]. For example, in South Africa expansions by native species (Box 1) are occurring at a biome level and affect tens of millions of hectares [10,11,33,34].

Expansions and Invasions

Many ecosystems in Southern Africa and abroad currently resemble the function and composition of historical plant communities and can thus be conserved or restored if historical disturbance regimes (fire and herbivory) are maintained. However, it is likely that these historical plant communities will become less common given that empirical evidence and predictive models suggest that environmental conditions have begun, and will continue, to force shifts of South African vegetation biomes [10,11,35–38]. Nonlinear responses to environmental change have caused existing plant populations to shift at different rates creating novel plant communities. Two primary examples of South African biome shifts are native tree expansion in Savanna biomes and native grass expansion in the Nama Karoo and Fynbos biomes. These structurally different examples tell a common story about the impacts of native invasions on local biodiversity and other important ecosystem functions.

Tree Expansion in Grassy Biomes

Trees and shrubs are on the move in Africa and around the world (Figure 1). During the past 50 years there has been a noticeable and quantifiable increase of trees into global savannas and grasslands [9], which is contrary to the multimillennial trend of grasslands increasing into woodlands and forests [39]. The increasing dominance of trees in grasslands is attributed to modified land use and fire regimes [33,40,41] as well as increasing CO_2 concentrations [11,35,37,38] and altered temperatures and precipitation [38]. Evidence has shown that many savannas occur in climate zones that could support forest [40,42], which suggests that land

Table 1. Traits of Invasive Plants Used in Weed Risk Assessment [61] Are Applied to Two Encroaching Native Trees, *Terminalia sericea* and *Vachellia karroo*, As Well As One Notoriously Invasive Alien Tree, *Acacia dealbata*[a]

Traits of invasive plants		*Terminalia sericea*	*Vachellia karroo*	*Acacia dealbata*
1	Has the species become naturalized where it is not native?	N	N	Y
2	Is the species noted as being invasive elsewhere in the USA or world?	Y	Y	Y
3	Is the species noted as being invasive elsewhere in the USA or world in a similar climate?	Elsewhere in Africa	Elsewhere in Africa	Y
4	Are other species of the same genus invasive in other areas with a similar climate?	Y	Y	Y
5	Is the species found predominantly in the climate that matches those within the region of introduction?	Y	Y	Y
6	Does the plant displace native plants and dominate the plant community in areas where it has invaded? Does the plant over top and/or smother surrounding vegetation?	Y	Y	Y
7	Is the plant a health risk to humans, animals, or fish (toxic tendencies)? Has species been noted as impacting grazing systems?	Y	Y	N
8	Does the plant produce impenetrable thickets, blocking or slowing movement?	Y	Y	?
9	Does this plant reproduce vegetatively via root sprouts, suckers, or stem/trunk sprouts/coppicing?	Y	Y	Y
10	Does this species produce viable seed?	Y	Y	Y
11	Does this plant produce copious viable seeds each year (>1000)?	Y	Y	Y
12	Are this plant's propagules dispersed by mammals/insects or birds or via domestic animals?	Y	Y	Y
Impacts of invasive plants		*T. sericea*	*V. karroo*	*A. dealbata*
13	Formation of dense thickets	Y	Y	Y
14	Increased fuel load	Y	Y	Y
15	Increased H_2O uptake (C_3 vs C_4 and deeper roots)	Y	Y	Y
16	Esthetics degradation	Y	Y	Y
17	Reduced land productivity	Y	Y	Y
18	Reduced seedling establishment	Y	Y	Y
19	Altered soil nutrient pools and microbial composition	Y	Y	Y
20	Altered plant diversity	Y	Y	Y
21	Altered habitat quality	Y	Y	Y
22	Altered faunal community	Y	Y	Y

[a]Alien and native trees are found to have identical traits associated with invasiveness, with the exception of reinforcing tautology (e.g., Question 1). Alien and native trees are found to have identical impacts [25,62] within the ecosystem that they 'encroach' or 'invade'. Inductive reasoning suggests that it is also ecologically relevant to consider native species invasions although at present they are omitted from such evaluations. Management decisions could benefit from more unified measures of impacts [19] applied to native and alien species.

users will have to work much harder than in the past to maintain open grassy ecosystems. Like Africa, North America is replete with observations and research on the spread of native trees into grasslands [14,43], most conspicuously juniper (*Juniperus virginiana*) expansion in Western and Mid-Western States [31,43], mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentate*) invasions in the arid Southwest [43,44], and prairie conversion to woodland

Box 1. Widespread Native Tree Invasion in South African Savannas

Currently, in South Africa agricultural legislation to control 'bush encroachment' is rarely enforced for native species even when, like alien species, native species have invaded well beyond historical ranges, greatly altering plant community structure and composition. In some South African ecosystems, biome shifts from grassland to scrub forest have already been documented (Figure 2) [11]. In particular, the Karoo acacia (*Vachellia karroo*) is a prolific native invader of grasslands in South Africa (Figure 3) [52]. While there are policies to subsidize the control of invasive alien species, surprisingly there is no support or enforcement of the removal of invasive native acacias (e.g., *V. karroo*) or other native South African trees like *Terminalia sericea* and *Colophospermum mopane*, whose 10–20 Mha range expansion across South African grassy biomes [33,34] represents some of the most significant invasions (in terms of area) by any plant species in the country.

(*Quercus garryana* and *Pseudotsuga menziesii*) in the Northwest [28,45]. It is estimated that 330 million hectares of non-forest lands in the USA are being invaded by native woody species [44]. Notably, the majority of these expansions are attributed to human factors such as the absence or increase of fire, grazing, or farming. The scale affected and reinforcing feedbacks from altered abiotic drivers of plant communities (e.g., available soil moisture, nutrient cycles, CO_2 enrichment) suggest that such native invasions may now reflect persistent novel ecological communities.

Altering the relative densities of trees, native or alien, within grasslands and savannas impacts agricultural management, local biodiversity [13,14,46], catchment hydrology, and stand-level carbon and nitrogen cycles [15]. For instance, the expansion of native trees in Africa has been shown to reduce grass productivity and species richness resulting in decreased forage quality [16] and can be a detriment to savanna wildlife [46]. In addition to local and regional impacts, alteration of the competitive dominance of trees and grass can also have large Earth–atmosphere ecological feedbacks [47]. Changes in the composition of savannas is of global significance considering that savannas occupy a fifth of the Earth's land surface, contain some of the most iconic biodiversity, and support livestock grazers as well as wild herbivore populations.

Grasses Invade Shrublands

Native trees are on the move in grassy biomes, but there are also examples of native grass invasions into woody biomes. Notably, South Africa has a high diversity of grasses that possess specific traits to cope with fire, grazing, and disturbance, which makes them more competitive [48]. In general, impacts of grass invasions include altered plant community structure [49], altered nutrient cycling [50], and altered fire regimes [51]. Native grass invasions in Africa are likely to be driven by complex interactions between increasing early-summer rainfall, a reduction in livestock stocking rate, rising temperatures, and altered CO_2 concentrations [36]. Long-term ecological research in the Nama Karoo shrubland biome suggests an increasing dominance of grasses and a loss of shrubs [36,52]. Native grass invasions in the Karoo have significantly altered fire cycles. Now when the system burns, many of the shrubs are destroyed where previously fires did not occur [53]. This change has been widely noted for alien invasive grasses and is now resulting from invasive native grasses. The relationship between grass invasion and fire cycles is also drawing concern in Southern Africa's Fynbos biomes. Non-Fynbos species are able to benefit from elevated CO_2 more than Fynbos species, which have little or no responsiveness to elevated CO_2 [54]. From a functional perspective, the replacement of Fynbos by native grasses is likely to alter nutrient cycling, regional microclimate, and fire frequency. A biome shift from Fynbos to grassland or even mixed shrubland has large implications for the management and conservation of rare and endemic flora and fauna, including specialized avian, insect, and mammalian pollinators associated with the unique Fynbos species.

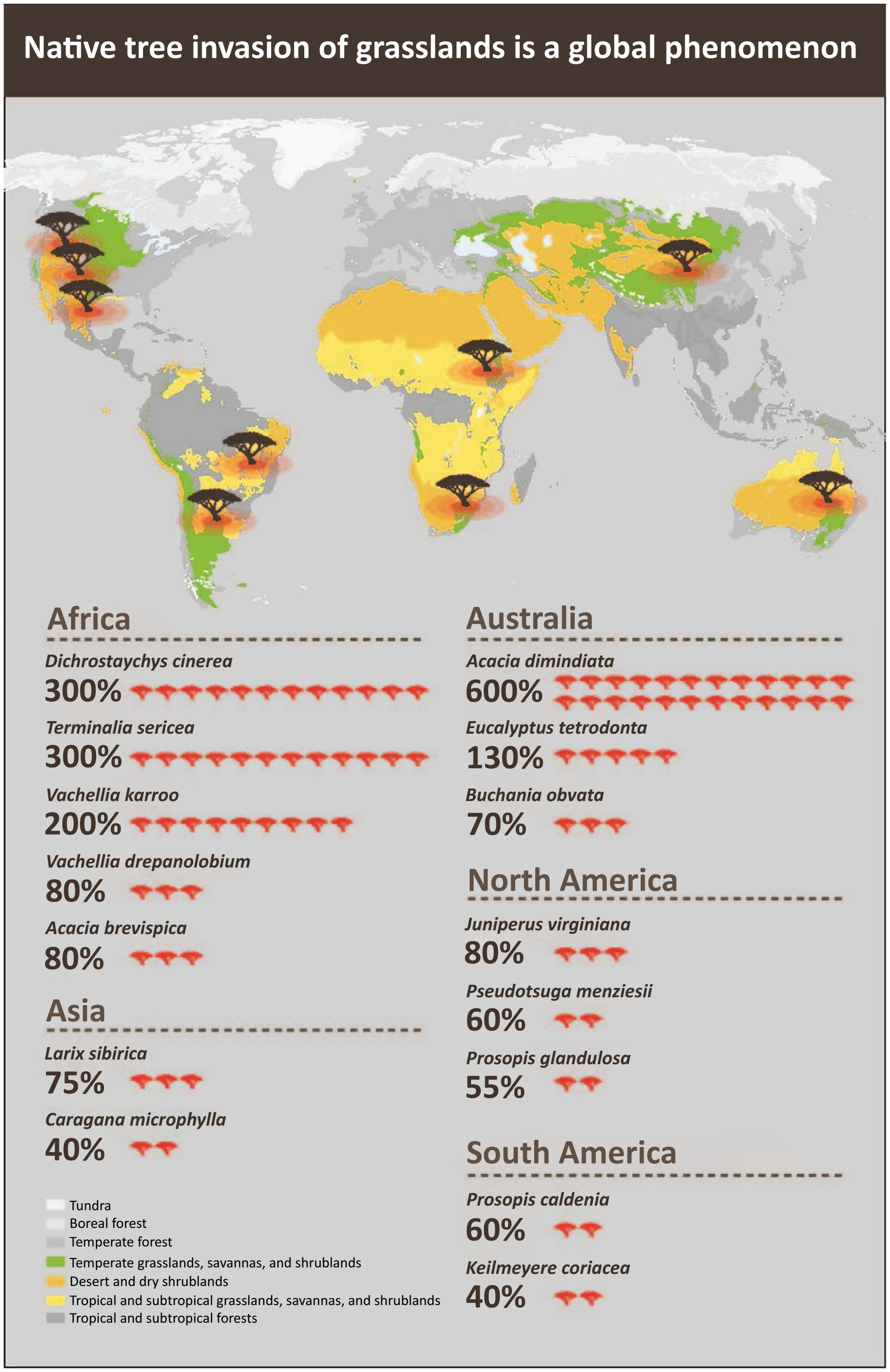

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Figure 1. Evidence of Native Tree Invasions into Grass Ecosystems from Around the World. Percentage increases were calculated from density coverage increase over time. Data collection methods in the source material [16,26–32,35] vary between the studies. Therefore, the percentages can be considered illustrative of a global phenomenon

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The nebulous nature of native invasions is further illustrated in North America where inter- and intraspecific introgression and hybridization have been attributed to the causes of at least two widespread invasions by grasses [55,56]. Hybrid populations are evolutionary variants from historical populations that also represent interbreeding subpopulations. Novel hybrid genetics can quickly become widely dispersed in wind-pollinated grasses. Consideration of active management of invasive native populations, especially for novel subspecies, forces subjective valuation of historical or novel genetics, which seemingly contradicts the disciplinary ethos [8] of informing policies based on objective science.

21st Century Invasion Science: Challenges and Opportunities

Notwithstanding the rich debate about the utility of biotic nativeness [2,3,5–7,17,18], for many national policies addressing invasive species, the potential impact of an invasion is *de facto* judged solely by the origin of the species. Alien plant management has been widely adopted, in part because the objectives are clear and executable (i.e., identify, locate, and remove). Condemning alien plant species is straightforward because it deals with spatial boundaries and temporally defined plant community compositions. Conversely, managing native plant invasions, and novel plant communities, is more complex because the objectives are less clear due to the uncertainty of future environmental conditions. Rather than decreeing whether a species is desirable based on where it existed in the past, novel ecosystem management must be more pragmatic and encompass a certain degree of stochasticity inherent to the variability of biome reconfigurations. A framework proposed to address novel plant assemblages [57] suggests a holistic landscape framework with fewer dichotomous categories (e.g., intact or degraded) that instead reinterprets landscapes as a complex mosaic of ecosystems or 'patches' in varying states of modification. This type of adaptive resource management can be achievable if management methods move away from historical delineations and move towards policies that explicitly define the links between species traits and ecosystem flows as well as ecosystem services.

In South Africa, 'Working for Water', a globally recognized invasive plant removal and social development program, provides an excellent example of how traditional invasive plant management can be adapted to encompass native plant invasions. The South African Department of Environmental Affairs has invested heavily in Working for Water and other programs that address loss of ecosystem quality from impacts by invasive alien trees [34]. Alien tree species were targeted for removal because they possessed traits, which were divergent from indigenous flora, that were negatively impacting catchment (watershed) hydrology. Eradication projects have focused extensively on invasive alien *Acacia* species, *Hakea* species, and *Pinus* species [34]. However, because this program focuses on links between traits and ecosystem function it can be expanded to include invasive native species that also negatively impact ecosystem services.

Managing an Ecosystem Invaded by Native Species: When?

Determining ecologically meaningful baseline conditions for management strategies is difficult in ecosystems that have been highly destabilized by anthropogenic influences, because it applies two contentious theories, novel ecosystems [5] and alternate stable states [40,58], that have both been debated for much of the 21st century. The expanding native African elephant populations in South Africa's Kruger National Park (KNP) provides a telling example of the importance of setting ecologically meaningful baselines in a dynamic system rather than

rather than definitive quantifications of all areas or species affected. The source material was generated by searching the literature for the terms "tree", "invasion", "expansion", "encroachment", "woody", "shrub", "biome shift", "grass", and "savanna". References were selected from the overall search results for each of the major global grassland biomes, if the original methods quantified increased abundance over time.

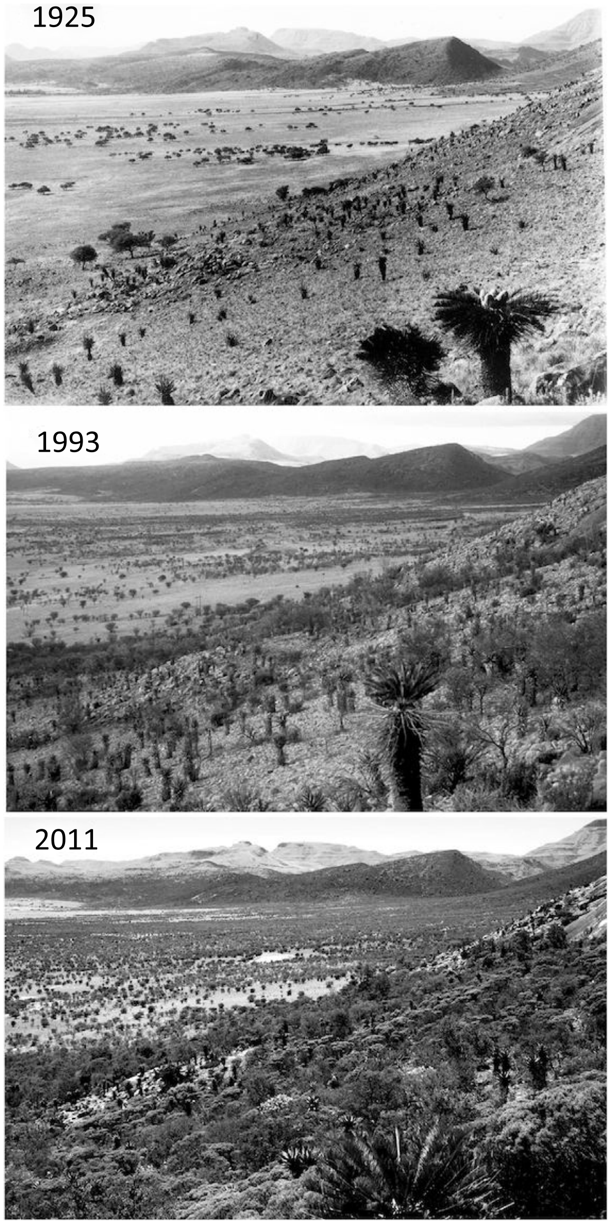

Figure 2. Time-Series Photography from Hillside near Lesseyton in the Eastern Cape Province of South Africa. Top panel from 1925, middle panel from 1993, and bottom panel from 2011. The photographs clearly show the increasing density of *Vachellia karroo* trees moving from a mostly open grassy landscape to a heavily wooded thicket. Photograph credit: Timm Hoffman, University of Cape Town.

managing a static interpretation of the landscape [59]. Infamously, burgeoning elephant populations were perceived as a threat to species diversity and for decades thousands were culled or displaced. However, research suggests that the perceived threats might have been inflated by two factors. First, when KNP boundaries were established, the elephant populations were at a historic low as a consequence of 19th century ivory-trade exploitation; second, the heightened concern about vegetation damage in the 1960s coincided with a 5-year drought that exacerbated the detrimental impacts by elephants on the vegetation [59]. Manipulating one

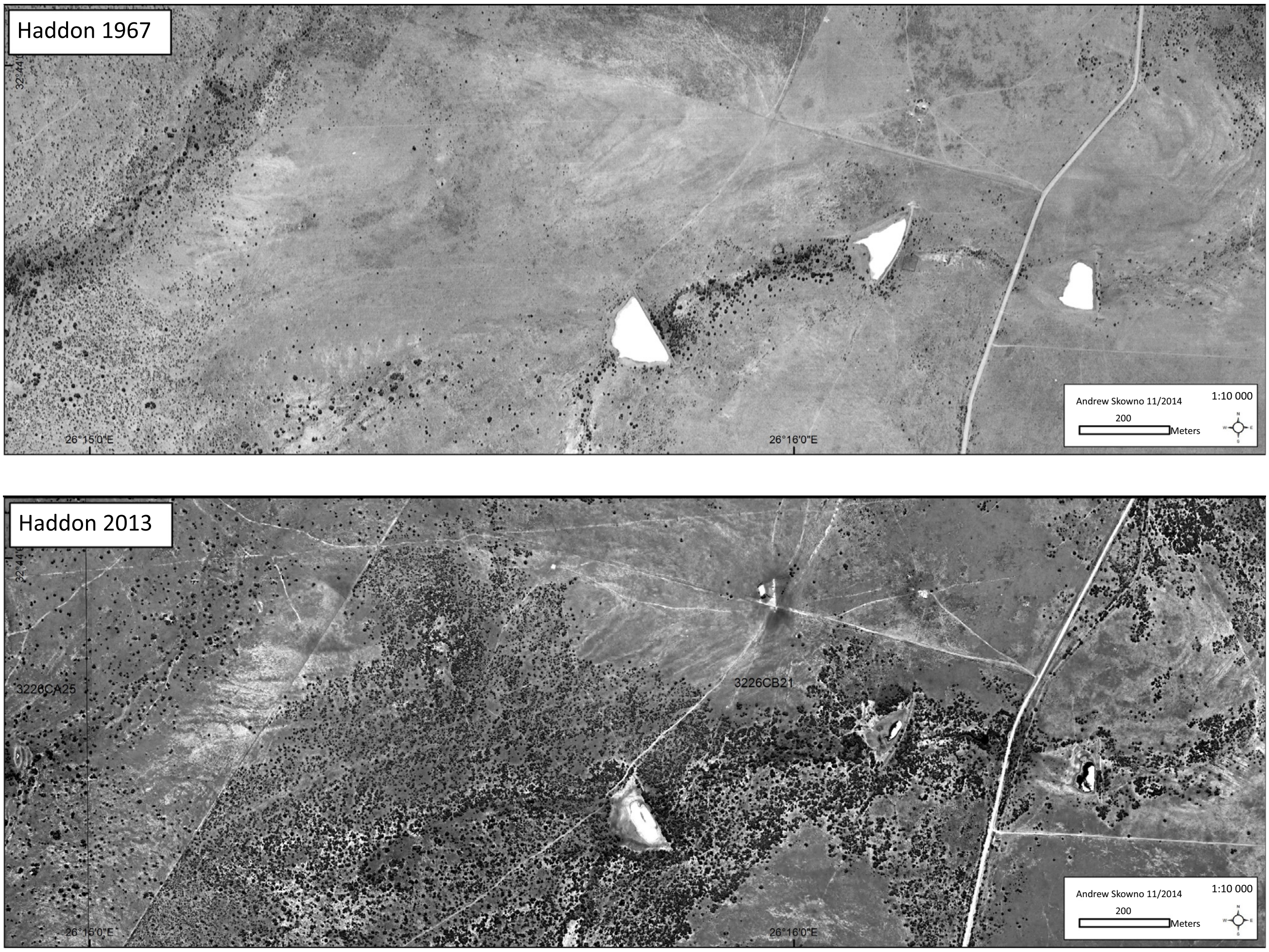

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Figure 3. Aerial Time-Series Photography near Adelaide in the Eastern Cape of South Africa. Top image from a flyover in 1967, bottom image from a flyover in 2013. The images show an invasion by native tree species (the dark dots on the landscape) into open grasslands. Images such as these illustrate that native invasions are not small in scale.

component of an ecosystem, like elephants or invasive alien plant species, is ineffective because it provides no insurance that changes induced by them will be restored when other species or environmental conditions keep a system in the transformed state.

To develop effective management methods for native invasions it is necessary to develop mechanistic models of ecosystem dynamics and, in particular, to explore the extent to which transitions between invaded and non-invaded states tend to be gradual and reversible or abrupt and hysteretic [58]. A difficulty in managing novel plant communities is that restoration of conditions to those before the invasion will not necessarily result in a reversal to the previous, non-invaded plant communities. The likelihood of multiple plant community end points can be highly dependent on the initial conditions [37,40]. It might not be sufficient to focus on current environmental conditions considering that future conditions could be very different (e.g., increased frequency of extreme weather events, land degradation, altered resource availability), which might therefore lead to rapid, nonlinear shifts in ecosystem function that are not predicted by current models. These challenges stress the need to identify and capture the characteristics of resilient ecosystem functions in both predictive models and management guidelines.

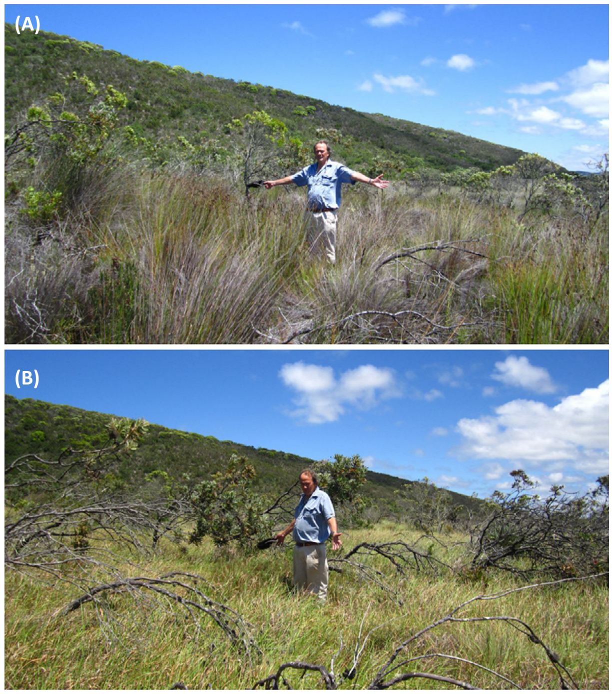

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Figure 4. Alluvial Flats in the Potberg Nature Reserve Fynbos Biome Are Usually Dominated by Species of Restionaceae (A). Increasing observations, never before documented, of invasions by native C_4 grasses (e.g., *Imperata cylindrica*) into Cape Fynbos has local ecological managers concerned (B). Fynbos is one of the most biologically diverse biomes in the world. An invasion by grasses, including native grasses, is alarming given the vast literature showing that grass invasions can fundamentally shift ecosystem function. Although Fynbos is considered a fire-adapted plant community, fires typically occur on decadal or multidecadal cycles rather than the subdecadal or annual burn frequencies associated with grass-dominated plant communities. Increased frequency of fire and flammability would predictably eradicate slower-growing, late-to-maturity Fynbos species. Photograph credit: Edmund February, University of Cape Town.

Managing an Ecosystem Invaded by Native Species: Where?

Novel biological community assemblages are the visual evidence of the varying ability of species to track shifting climate envelopes. It has been predicted that future communities may be dominated by more-dispersive taxa coupled with climate-driven declines in specialists, resulting in increasing homogenization of communities in both natural and anthropogenic landscapes [60]. In this context, management practices addressing the occurrence of invading native species could range from complete eradication to tolerance and even consideration of the 'new' species as an enrichment of local biodiversity [21]. Resistance to global drivers may seem futile if biome shifts become the norm. In the face of such widespread change, a neutral response, in which no action or intervention occurs, may be the most appropriate management decision in landscapes where deleterious impacts are minimal [19]. Unlike national or regional policies for eradication of invasive alien species, the control of native invasions might require local (e.g., watershed) policies. For instance, given the extent of native tree expansion in African savannas, policies can target areas where low abundances of native trees are desirable (e.g., for grazing or ecotourism) rather than decreeing a national-level movement to return all thickets to savanna. Another example is traditional restoration, such as targeted removal programs, which can still be applicable to nascent native grass invasions into the Cape Floristic Region (Figure 4). For such regions of high endemism, where modeled predictions and empirical evidence suggest that biome shifts are likely, the inability of management agencies to directly control global drivers like CO_2 emissions might necessitate the inclusion of *in situ* and *ex situ* conservation strategies.

Managing an Ecosystem Invaded by Native Species: How?

Methods of eradication suitable for alien invasive species might not be suitable for the control of native species that are expanding beyond their historical range. For instance, biological control with introduced predatory insects has effectively decimated populations of invasive alien plant species. Biological control would not be effective for native species, because native species are likely to have evolved with the native predators and the idea of introducing an alien plant pest or pathogen to control a native population would be risky given that biological agents will conceivably travel to non-targeted native populations. Other methods for controlling alien species will be equally as effective for native species. For example, burning, chemical, manual, and mechanical methods have all been highly effective in managing invasive alien plant species and would certainly be applicable for managers targeting invasive native plant populations. Beyond the technical challenges, the redefinition of management strategies to address native species driven to new ranges by anthropogenic climate change will test the theoretical constructs of invasion science by demanding an awareness of the spatiotemporal complexity of ecological interactions.

Concluding Remarks

In the Anthropocene, alien species are no longer the only category of biological organism establishing and rapidly spreading beyond historical boundaries. Climate-mediated expansions of native plant populations into adjacent plant communities are, in many ways, similar to invasions by alien species. Acknowledging the potential impact of native invasions and consequent biome shifts recognizes that environmental conditions are significantly different from the recent past and will continue to change in the future. In a rapidly changing world, we urge ecologists and natural resource managers to base decisions on empirical evidence or mechanistic models quantifying impacts an biodiversity and ecosystem function. Integrating native invasions into a coherent natural resource management strategy better addresses the complex and cascading consequences of the profound ecological changes we are observing in many landscapes.

Outstanding Questions

How great and how persistent must a shift in plant communities be, to be deemed a native invasion?

How do we prioritize restoration efforts if invasions by native species also constitute a threat to ecosystem structure and function?

What are ecologically meaningful restoration targets given that future ecosystems may be fundamentally different from the historical ecosystems?

At what scale should restoration efforts be prioritized? At a global scale, climate change has degraded the resilience of all environments. However, many intact, functioning communities exist at a local scale.

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