Opinion

Novel ecosystems: implications for conservation and restoration

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Many ecosystems are rapidly being transformed into new, non-historical configurations owing to a variety of local and global changes. We discuss how new systems can arise in the face of primarily biotic change (extinction and/or invasion), primarily abiotic change (e.g. land use or climate change) and a combination of both. Some changes will result in hybrid systems retaining some original characteristics as well as novel elements, whereas larger changes will result in novel systems, which comprise different species, interactions and functions. We suggest that these novel systems will require significant revision of conservation and restoration norms and practices away from the traditional place-based focus on existing or historical assemblages.

Why novel ecosystems?

The development of ecosystems that differ in composition and/or function from present and past systems is increasingly recognized as an almost inevitable consequence of changing species distributions and environmental alteration through climate and land use change [1,2]. These new systems are described variously as 'novel', 'emerging' or 'no-analog' [3–5] and have been considered primarily in relation to invasive species or climate change. Change is a normal characteristic of ecosystems in response to disturbance and environmental change, and species distributions have also varied considerably through time [3,6,7]. Hence, all ecosystems can be considered 'novel' when placed in the appropriate temporal context. However, the rapid pace of current change, coupled with the breakdown of biogeographic barriers through the global human transport of species, 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 [5,8].

Although the notion has been canvassed in the literature for some time that novel species combinations will arise through either species invasions or environmental change (or both) [9–11], the relevance of the idea of novel ecosystems as a result of, and response to, increasingly rapid change has only recently been emphasized more clearly [3–6,12]. In addition, more examples of novel ecosystems are being documented [13–17], primarily as new species combinations arising from invasion by non-native species; however, abiotic changes also can be important, and novel combinations of native species have also been noted; for instance, in response to changing land use [17].

Ecosystems have multiple characteristics, such as plant species diversity, ecosystem functions, resistance and resilience, all of which can be altered by changing conditions. Some characteristics, for instance nutrient cycling rates, do not necessarily depend on particular species in a particular location and, hence, substitution of one species by another has little impact. There might therefore be no measurable consequence of invasion of a particular species for ecosystem functions [18]. By contrast, the location of particular species in particular places is a key consideration of what to conserve or restore and where, and has been the prime focus of most conservation activities. Increasing incidence of human modification (Box 1), leading to novel ecosystems, requires serious consideration of where and how such place-based conservation can be maintained.

We consider the development of novel ecosystems in more detail, both in terms of the different types of system likely to exist under different conditions and the implications of the increased occurrence of these systems for conservation, management and restoration. We restrict our discussion to those systems whose characteristics have changed as a result of human modification of 'wild' or 'natural' systems or the abandonment of previously managed systems, particularly abandoned agricultural lands [5,19]. We do not include current intensively managed agricultural or plantation systems.

Possible outcomes of ecosystem change

Does it matter whether the key influences driving particular ecosystems to a novel state are primarily abiotic changes or changing species combinations arising from species invasions and local extinctions? How should these novel states be managed? Until recently, little serious consideration has been given to these issues [12], and yet it seems crucial to explore more comprehensively what is likely to happen to ecosystems in the face of rapid change and what the potential management and legislative responses might be.

We consider ecosystem responses to change in terms of whether the ecosystem remains in, or near to, its historic state, becomes altered into a hybrid state or experiences such a degree of change that it can be considered a novel ecosystem (Figure 1a). The historical ecosystem, traditionally the target for ecological restoration, retains the biota

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Box 1. Living in a human-modified world

Increasing human modification of ecosystems has been noted for some time, but has been reemphasized lately as a result of global assessments of the state of the world's ecosystems [43]. The rate of change of many ecosystem properties has increased rapidly during the past 50 years and the resultant range for many biotic and abiotic variables is greater than in the previous 10 000 years [24]. Direct (e.g. land conversion) and indirect (e.g. long-range transport of pollutants) human influence takes many forms and is difficult to quantify in simple metrics, but global assessments using several available data sets have resulted in analyses such as those presented in Figure I. The Human Footprint Analysis in Figure Ia indicates that large proportions of the global land surface are significantly impacted by human activities; indeed, the analysis suggests that 83% of the land surface of the earth is impacted to some degree (http://sedac.ciesin.columbia.edu/wildareas/). Another analysis shown in Figure Ib identifies the 'anthropogenic biomes' of the Earth and indicates that >75% of the ice-free land shows evidence of human alteration [44].

The analyses in Figure I show slightly different aspects of the same phenomenon but reach the same conclusion regarding the levels of human modification. In addition, sustained human interactions are likely to be an integral part of many ecosystems. Although we focus primarily on terrestrial systems here, equivalent analyses for marine systems also suggest a pervasiveness of human influence in the world's oceans, with 41% being classed as experiencing medium–high impact [45].

Recent studies have indicated a close connection between the intensity of human activity and an array of ecosystem changes, including the incidence of invasive species [46], biotic homogenization [47] and declining diversity. Hence, the general picture given in Figure I is indicative of a probable raft of changes to ecosystem properties that result in new species configurations and ecosystem functioning. Added to the changes illustrated in Figure I are the impacts of climate change already being observed and predicted, which include not only direct impacts, but also synergistic interactions with land use, invasive species and other changes [48]. This all suggests that the development of ecosystems that differ significantly from those found historically is increasingly inevitable and likely to occur over large areas of the world. In addition, there is also increasing debate over the potential for direct human intervention in the facilitation of biotic response to climate change through the agency of assisted migration, or the deliberate movement of species in anticipation of shifting climatic envelopes [49,50].

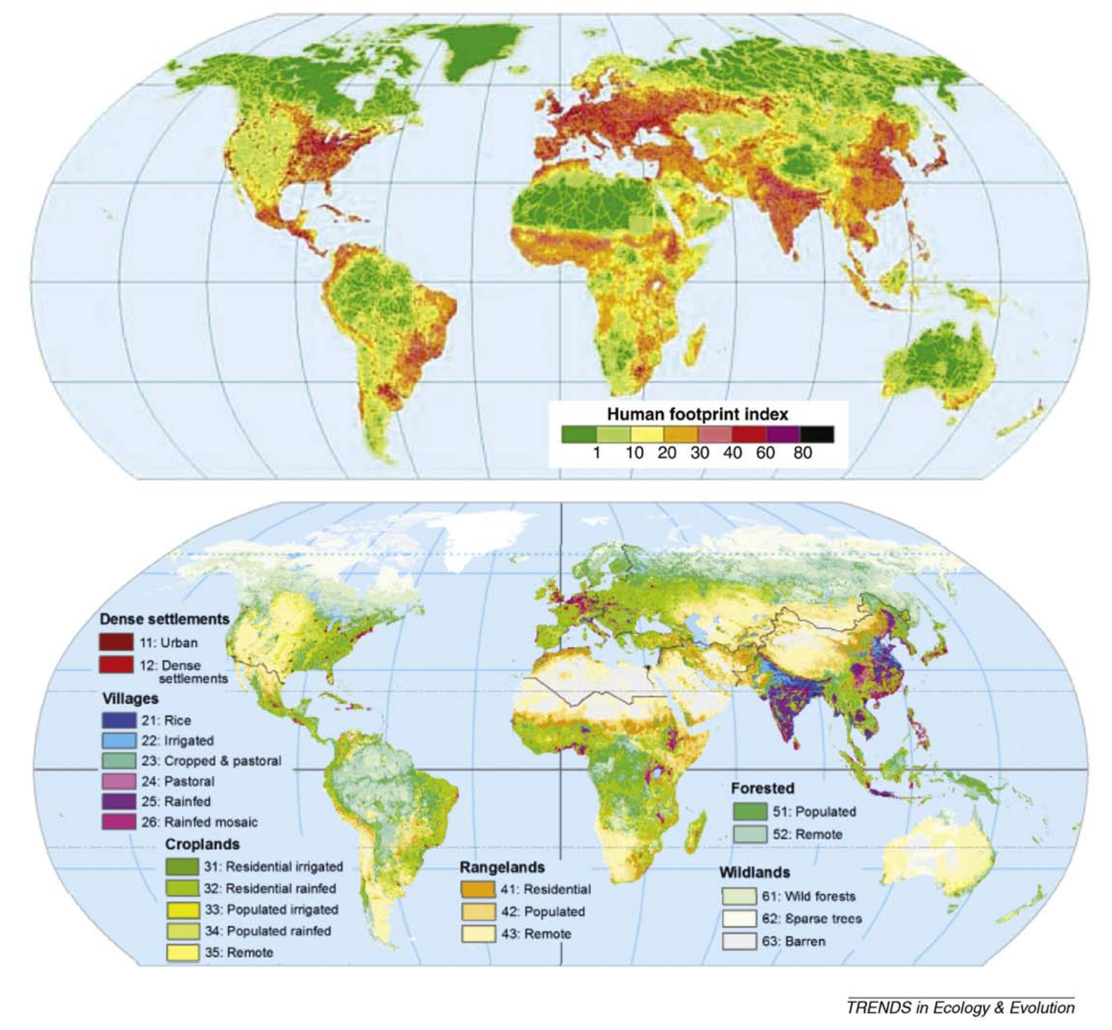

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Figure I. Alternative analyses of the distribution of human impact across terrestrial ecosystems of the earth. **(a)** Intensity of human impact on global terrestrial ecosystems as estimated by the Human Footprint Index (http://sedac.ciesin.columbia.edu/wildareas/). The index is a normalized index produced through an overlay of several global data layers on human population distribution, urban areas, roads, navigable rivers and various agricultural land uses. **(b)** Anthropogenic biomes of the world as derived from global data on human population, land use and land cover [44].

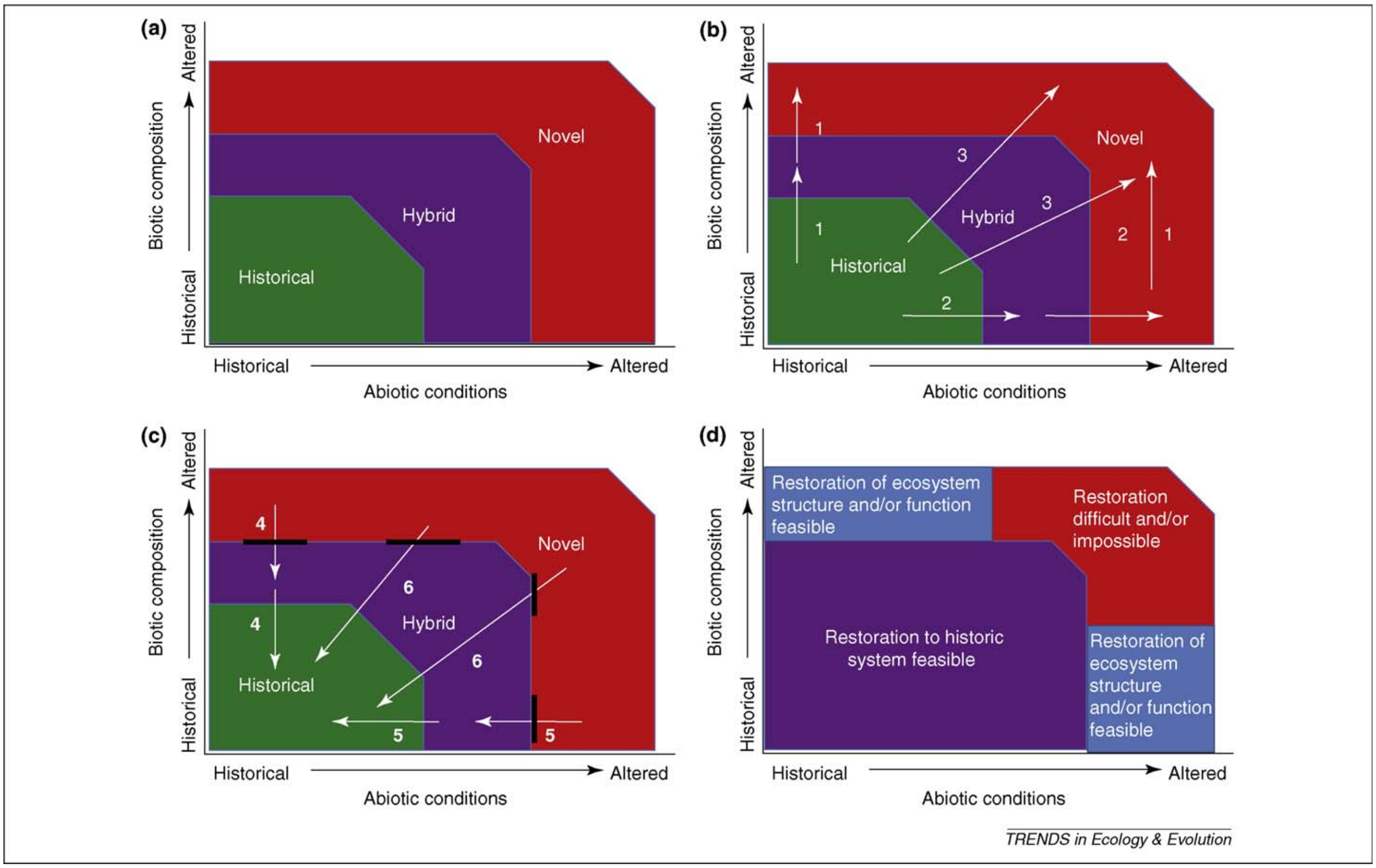

Figure 1. Types of ecosystem that develop under varying levels of biotic and abiotic alteration. **(a)** three main types of system state: (i) historical, within which ecosystems remain within their historical range of variability; (ii) hybrid, within which ecosystems are modified from their historical state by changing biotic and/or biotic characteristics; and (iii) novel, within which systems have been potentially irreversibly changed by large modifications to abiotic conditions or biotic composition. **(b)** Potential pathways of development of ecosystems in the face of changing biotic composition (loss or addition of species) and abiotic change (land use or climate). Pathway 1 is driven primarily by loss of existing species and addition of invasive species (either native or non-native), Pathway 2 by changing abiotic conditions and Pathway 3 by biotic and abiotic changes acting synergistically. **(c)** Reversing the pathways of development in (a) requires removal of invasive species (Pathway 4) and/or amelioration of altered environmental conditions (Pathways 5 and 6). Black lines indicate the presence of potential restoration thresholds that prevent the system moving back to a less altered state without significant management input. **(d)** The state space can be divided into an area within which restoration to a system within the historic range of variability remains feasible (which includes some or most hybrid systems), areas within which restoration of ecosystem structure and/or function can be achieved without a return to historic system characteristics, and an area within which restoration is likely to be difficult or impossible and hence alternative management objectives are required. (Developed from previous conceptualizations from Refs [12,34]).

and ecosystem properties that were prevalent in the past [20]. However, this statement poses many questions currently being debated: which versions of history are important? How far back should we look? How do we know what historic ecosystems were like? How similar to the past configuration does the current configuration need to be to qualify for this definition? Concepts such as the historic range of variability (HRV) [21] are relevant here. We recognize, therefore, that the definitions of ‘natural’, ‘historic’ and ‘altered’ are rarely clear and are often determined in relation to cultural, national, religious or personal experiences and values. It could be argued that few instances of true historical ecosystems remain, owing to the pervasiveness of direct and indirect human influence and changes in species distributions and abundances [22]. Although strictly true, many restoration projects are nevertheless driven by commitment to historical qualities and reestablishing salutary past relationships between people and ecosystems [23].

A hybrid system can be defined as one that retains characteristics of the historic system but whose composition or function now lies outside the historic range of variability. A novel ecosystem, by contrast, is one in which the species composition and/or function have been completely transformed from the historic system: such a system might be composed almost entirely of species that were not formerly native to the geographic location or that might exhibit different functional properties, or both. Clearly, the distinction between the two types is somewhat arbitrary, and the exact point at which an ecosystem is considered novel cannot necessarily be universally applied. The hybrid ecosystem state could be considered the state in which most of the measurable traits of the ecosystem (i.e. nutrient load, hydrology, species diversity, etc.) are the same but most of the species have changed. The novel state would then be defined as when measurable traits are altered from historical ranges.

Several different trajectories of ecosystem change away from the historic configuration are probable based on whether abiotic or biotic alterations occur separately or in concert (Figure 1b). Where the bioclimatic envelope changes but there is no immediate biotic response, and the abiotic infrastructure remains intact, systems can initially remain as relicts of the historic system; that is, a hybrid biotic community remains despite altered abiotic conditions.

Multiple types of abiotic change are possible, including changes in climate, land use, pollution, urbanization and nutrient loads [24]. With further abiotic change, all or some of the biota might be unable to survive or regenerate; in this case, the system is transformed and is thereafter likely to experience significant biotic change into an entirely novel system. The x-axis in Figure 1a is a complex variable and could represent several different contexts: 'abiotic conditions' refers both to the 'biophysical envelope', in particular the temperature and hydrological regime, and to the 'abiotic infrastructure', involving geology, soil, topology and so on. Hence, it is possible for the biophysical envelope to change while the abiotic infrastructure remains the same, or vice versa.

Where only biotic changes are salient, such as significant declines or local extinctions of species and/or significant invasions of species from elsewhere, then a hybrid system will result, comprising pre-existing and new species. As the proportion of new species increases, new combinations of species are likely and a novel system will develop [5,12]. These new species can be non-native (transported by humans accidentally or intentionally) or native species experiencing range shifts; for instance, land-use change in Australia has resulted in bird species that are normally associated with different habitats now combining in novel assemblages [17].

Where both kinds of change occur, novel systems are likely to contain unprecedented (by historical measures) species combinations coexisting under new abiotic conditions. This is, in reality, the most probable scenario because biotic and abiotic factors often change simultaneously and act synergistically. New invading species can have the capacity to modify both the existing biotic assemblage and the prevailing abiotic conditions significantly. For example, broad-scale changes in forest structure and composition are occurring in many parts of North America owing to the increased occurrence of insect pests and pathogens [25]. Such invasions can, themselves, be the result of human-induced landscape changes [26], and there are likely to be increasing levels of synergism among the various drivers of ecosystem change [27]. For instance, abiotic factors can modify trophic interactions, and different species mixes are likely to exhibit different suites of functional traits, which can in turn affect ecosystem function [28].

Implications for conservation and restoration

Increasingly, traditional notions of conserving and restoring biodiversity by direct appeal to historical condition are being reconsidered in the light of rapid environmental change [2,12,29,30]. When retention or restoration of historical ecosystems is no longer possible, or at least no longer feasible given anything short of heroic action and intensive manipulation and management, what other options are there that could be considered as valid conservation and/or restoration goals?

Given the range of potential ecosystem outcomes, there is a variety of options to be considered when managing ecosystems. Generally, conservation aims to reduce or prevent both abiotic and biotic change. Similarly, ecological restoration aims to mitigate abiotic change and reverse biotic change to push the system back towards historical, and more highly valued, composition and function.

Increasingly, conservation managers are unable to remove all non-native species from ecosystems and, indeed, such species are now important components of many systems, providing habitat or resources for other species: for instance, many butterfly species in California now depend on non-native plants for some or all of their food resources [31]. Various authors have also argued that non-native species will have an important role in providing ecosystem services in the future [18,32]. It is likely that a

Box 2. Turkey oaks, gall wasps and tits: new food web or ancient interaction re-established?

The Turkey oak *Quercus cerris* was native to the British Isles prior to the last glaciation (~130 000 – 115 000 years before present), following which it did not disperse naturally, but was re-introduced to the UK during the past 300 years [51]. This could be classified as an 'assisted migration', and there have been concerns raised in conservation circles that the Turkey oak would become invasive, but this does not appear to be the case to date. Furthermore, recent work has demonstrated that the species acts as a reservoir food source for blue and great tits (*Cyanistes caeruleus* and *Parus major*), which are laying eggs earlier in the season in response to climatic cues. The oak also acts as a host for gall wasps (Hymenoptera: Cynipidae, Cynipini, many of which are also non-native but migrating northwards) which provide food for the tit population before the emergence of their normal food sources (Figure I): this is analogous to a multitrophic interaction reported for the last interglaciation, detected in the fossil record [52]. The non-native gall wasps also interact with the native gall wasps, and hence a novel set of interactions have been set up, some of which can be viewed as positive and others potentially negative.

There are several questions arising from this and similar studies: how close are these assemblages to the 'originals'? Should the Turkey oak and its interacting insect species be considered 'native' in the UK? And are there circumstances where assisted migration could have a place in restoration programmes? Further to this, such changing interactions could be expected to become increasingly common with changing environmental conditions and the resulting shifts in species ranges.

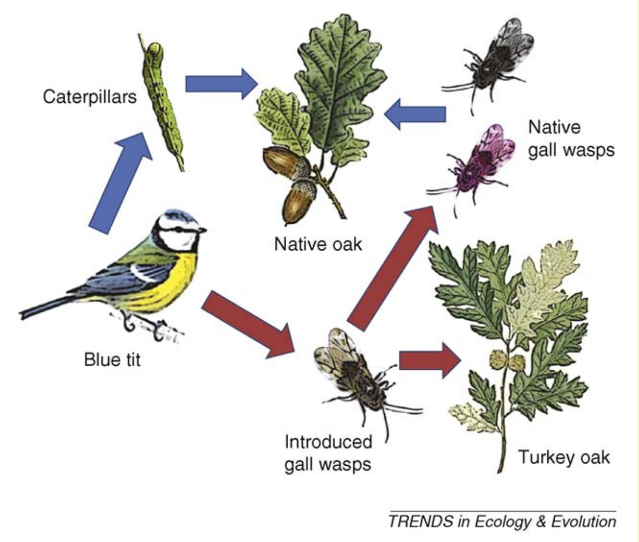

Figure I. Examples of interactions among native and non-native species in the UK, arising from the presence of introduced Turkey oak and the advent of non-native species of gall wasps. Previous interactions are indicated by blue arrows and novel interactions by red arrows. Only selected interactions are shown for simplicity. Derived from Ref. [52].

suitable goal for some systems is their retention in a hybrid state, where some non-native species are accepted as part of the system (Box 2). Clearly, such decisions have to consider both the adverse effects of harmful invasive species and the positive impacts of species that fulfill important roles that might otherwise be lost in degraded systems. Such decisions will depend significantly on cultural values toward nativeness and exoticism and the ways in which such beliefs change in the coming decades [23].

Where systems develop in which the biota are mostly newly dispersed or established in the area, the costs and benefits of trying to redirect the system to a more native composition need to be carefully assessed. Such novel systems can be relatively stable and have high cultural value, particularly if they continue to provide the same, or enhanced, delivery of ecosystem services, such as flood attenuation and habitat provision [18].

Where abiotic conditions change with little accompanying biotic change, hybrid ecosystems might be maintained with continual management intervention. Such systems might persist mainly where the dominant species are long lived and tolerant of large environmental variations or where local communities invest extraordinary amounts of time and energy in maintenance of the system in its current state. However, these systems will be vulnerable to episodic perturbations preventing regeneration. For instance, a fire-dependent system might switch to dominance of invasive plant species following a fire at a different season from that experienced historically. Perhaps a far-fetched idea, we might, in the future, regard historic and hybrid ecosystems in much the same way as we do human historical sites; large investments will be required to restore and maintain the historical character of such sites.

Because of simultaneous biotic and abiotic changes, we might expect increasing incidence of novel systems that have no analog with historical systems, and present novel assemblages and ecosystem functions (as shown in the top right of Figure 1a). The extent to which we can manage these systems or restore them to a state closer to the historical properties and/or restore their ecological integrity is largely unknown. However, it is possible to draw on the growing understanding of ecosystem dynamics in relation to thresholds and state changes [19,33,34] to provide some hypotheses relating to future management options. Figure 1c indicates the potential directions in which restoration and subsequent management could aim to drive systems back from a more- to a less-modified state. It also includes a set of hypothesized restoration thresholds, or circumstances in which the ecosystem has undergone modification that is reversible only with the input of significant management resources and effort [35,36]. Such thresholds can be biotic or abiotic in nature, and their identification and treatment is being used increasingly in restoration to guide the type and level of intervention deemed necessary and appropriate [37]. When mapped on to the state space represented in

Box 3. Novel ecosystem development in southwestern Australian woodlands

Woodlands dominated by *Eucalyptus* species formerly covered large areas of south-western Australia. These have now been extensively developed for agriculture, and remaining patches of woodland are often degraded because of livestock grazing, weed invasion, soil structural change and secondary salinization. Recent studies have focused on the degradation and restoration of such woodlands in the context of threshold dynamics and alternative stable states [53]. Figure I summarizes the different states in which woodland can occur, depending on the extent of biotic and environmental modification experienced. Restoration of woodlands invaded by non-native herbaceous species may be possible if the herbaceous species can be temporarily controlled, regeneration of native species encouraged (using fire or other forms of disturbance) and soil structural changes reversed with mechanical intervention [54].

In old agricultural fields that have been abandoned for decades, novel systems develop that appear to be relatively stable and resistant to restoration management [53]. This results from the combination of land-use legacies, including persistent elevated soil phosphorus, reduced native seed supply and the introduction of invasive species that outcompete native species, especially during the establishment phase. The restoration of the historic ecosystem on old fields would require intense effort and the restored system would continue to be prone to re-invasion [53]. The restoration of a historic ecosystem is not considered feasible in areas affected by secondary salinization because the chemical and physical properties of the soil and the local hydrology are fundamentally altered; alternative ecosystem types might, however, be possible.

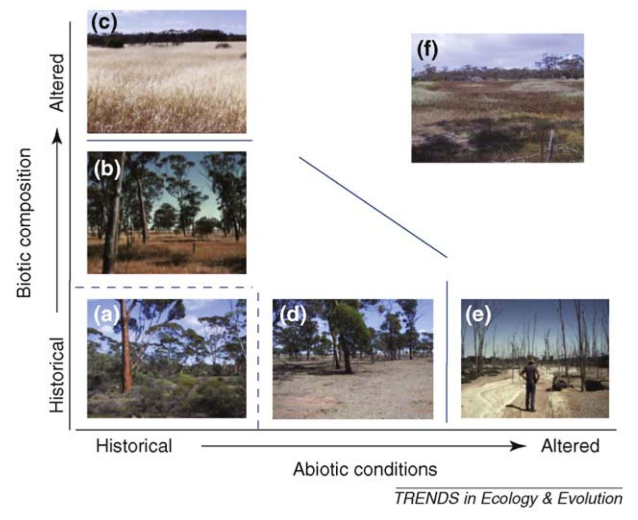

Figure I. The development of novel ecosystems within areas previously characterized by woodlands dominated by *Eucalyptus* species in southwestern Australia. **(a)** Undisturbed woodland with shrubby understorey, patchy tree recruitment and friable soil. **(b)** Woodland invaded by non-native annual herbaceous species, but retaining adult trees. **(c)** Former woodland area cleared for agriculture and subsequently abandoned, now dominated by non-native annual grasses. **(d)** Woodland degraded by long-term livestock grazing leading to removal of understorey and soil structural change. **(e)** Woodland degraded by secondary salinization, caused by rising water tables bringing stored salt to the rooting zone. **(f)** Novel ecosystem that is likely to develop from states (a–e) with persistent change in abiotic factors and invasion of non-native species. Solid lines indicate known 'hard' thresholds, which render system recovery to a previous state highly unlikely; dotted lines indicate 'soft' thresholds, which are amenable to management intervention. This remains a largely conceptual diagram and no attempt has been made to place the system within quantitative axes and exact placement of thresholds.

Figure 1a, such thresholds provide potentially useful insights into where different types of restoration goal might be appropriate and what types of intervention will be necessary (Box 3). Clearly, identifying and locating real thresholds quantitatively in relation to real axes will be a major challenge.

Management options

We suggest that there are three different management scenarios arising in different regions of the state space in Figure 1a (Figure 1d): (i) a region where conservation or restoration of the historic ecosystem might remain a useful and achievable goal, especially if the definition of the historic system is broadened to include a certain amount of modification and/or addition of new species; (ii) regions where (i) is no longer a readily achievable goal but where restoration of key system structures and functions can still be achieved; and (iii) a region where the biotic and/or abiotic changes have forced a transition to a novel system that is unlikely to return to a less modified state because of the presence of restoration thresholds. This might result, for instance, from the novel components developing positive feedback relationships to produce a system that is resilient to further change [38]. Thresholds comprise biotic and abiotic conditions and also financial, cultural and pragmatic considerations (such as cost or technical feasibility). Decisions about how much conservation and restoration investment is appropriate will depend on shifting cultural values about historic fidelity and ecological integrity, sentimentality about ecosystems of the past, local species diversity, priorities for livelihood and sustainability (i.e. historically faithful restorations versus ecosystem services-oriented projects), and designs for resilience. In many parts of the world, primary motivations for ecosystem management relate more to human survival rather than to considerations of historic fidelity.

In the state space where traditional conservation and restoration outcomes are unlikely, a range of options exists that can still result in beneficial outcomes in terms of ecosystem services, biodiversity conservation and ecological integrity [39]. Restoration in the future might need to aim more specifically at novel systems as a way of tackling the unprecedented era in which humans dominate all ecosystems [40]. Indeed, removing the requirement to aim for a historic ecosystem increases the range of options available and could enable reduced investment of effort and resources still to achieve valuable outcomes. However, caution is required: will we be capable of understanding what is best in a rapidly changing world? Will such activities be restoration or evolve into new types of intervention that respond to the rise of novel ecosystems? Restoration will involve a complicated set of decisions rooted in historical understanding and open to many potential trajectories. It will probably change its focus from damage control to ecosystem engineering or ‘designer ecosystems’ [41]. Managers of the future will be tasked with distinguishing between what degrees or types of change could be considered beneficial and which would cause further degradation. In addition, decisions on management and restoration of historic and novel systems will often involve multiple stakeholders who will not always necessarily agree on the best course of action to take.

In this regard, cultural norms of nature, conservation and restoration will evolve alongside changing ecosystems [23], and it is likely that our present beliefs require significant adjustment. Retaining the somewhat static view of ecosystems as particular assemblages in particular places will become increasingly unrealistic and is likely to shackle conservation and restoration efforts to ever more unrealistic expectations and objectives. A more dynamic and flexible approach might not involve throwing out all previously held values and norms entirely, but could require serious consideration of a range of approaches to deal with an increasingly uncertain future. Some progress in this direction is being made, with an increasing recognition of the desirability of initiating a variety of different management activities rather than doing the same things everywhere [42]. A key task will be to determine if and where traditional place- and species-based conservation strategies, which aim to retain local species assemblages, remain appropriate. Where they do not, what are the alternative strategies that need to be developed and implemented? We propose the following criteria as a starting point in considering whether a novel ecosystem is a suitable case for conservation, or a worthwhile target of restoration:

- Is the system maturing, or capable of maturing, along a stable trajectory?
- Is the system resistant and resilient?
- Is the system thermodynamically efficient?
- Is the system providing ecosystem goods and services?
- Is it providing opportunities for individual or community engagement?

Depending on management goals, one or more of these criteria could be used to determine what type of management intervention is initiated. Such criteria highlight the uncertainty faced by managers in setting goals for conservation and restoration. Novel ecosystems produce novel challenges, and it will take some time before a new paradigm will provide secure guidance. In the meantime, it is prudent to respect several delicate balances: between ecosystem services and natural processes, and between ecological integrity and cultural values.

Conclusion

Recent increased recognition of the occurrence and importance of ecosystems with novel species combinations and/or novel abiotic conditions calls for increasing efforts to understand their functioning and the options available for their management. We suggest that, depending on the extent of change, systems can be broadly categorized into those that maintain their historical configurations, those that develop hybrid qualities mixing new and old components, and those that form entirely novel systems. Management options vary depending on the extent of change and on the presence of thresholds that might render a return to historical states difficult. More detailed ongoing examination of novel ecosystems, and how to recognize, quantify and manage them, is required to equip us to deal effectively with the new ecological world order.

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