Alternative Biome States in terrestrial ecosystems

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There is growing interest in the application of alternative stable state (ASS) theory to explain major vegetation patterns of the world. Here, we introduce the theory as applied to the puzzle of nonforested (open) biomes growing in climates that are warm and wet enough to support forests (alternative biome states, ABSs). Long thought to be the product of deforestation, diverse lines of evidence indicate that many open ecosystems are ancient. They have also been characterized as 'early successional' even where they persist for millennia. ABS is an alternative framework to that of climate determinism and succession for exploring forest/nonforest mosaics. This framework explains not only tropical forest–savanna landscapes, but also other landscape mosaics across the globe.

Forests and 'Nonforests'

Traditionally, the distribution of different vegetation types across the world was thought to be driven by climate [1,2], while soil interactions (e.g., competition for resources) were considered the main assembling process [3,4]. One of the clearest arguments suggesting that soil and climate cannot fully explain vegetation distribution is the existence of mosaics of strikingly different vegetation in the same environment [5–7]. Many regions of the world can support forests (as indicated by forest patches and forestry plantations) yet are covered by 'nonforest' ecosystems, such as grasslands, prairies, shrublands, or open woodlands (collectively called '**open ecosystems**', see Glossary). This mismatch between climate and vegetation has long puzzled ecologists [8–10].

One common explanation is that open ecosystems are the result of anthropogenic deforestation, especially through human use of fire and that, given enough time, these 'early successional stages' will transform to a higher biomass ecosystem (forest) as trees shade out smaller growth forms (Table 1). A prominent alternative idea is that open and **closed ecosystems** share the same landscape because of divergent soil conditions influencing plant growth, with forests growing on soils conducive to tree growth, and open ecosystems on soils hostile to tree growth. A prediction is then that forests cannot develop on grassland soils, for example. However, as we will see later, diverse lines of evidence have cast doubt on the generality of both sets of explanations.

A third idea is that open ecosystems are maintained by ecological processes that consume trees, preventing succession to a closed forest. Fire is a prominent and widespread **plant consumer** with many analogies to large vertebrae herbivory. Both wildfire and large vertebrates can reduce tree cover, either by killing established trees or by inhibiting their recruitment. Open (consumer-controlled) ecosystems would be predicted to switch to closed forest if the consumer was excluded from the system for long enough for forest trees to grow. Contrary to succession theory, open ecosystems can be maintained for millennia if the feedback between the plants and the consumer persists.

Highlights

There are many ancient open vegetation formations worldwide that maintain a high diversity of shade-intolerant species where the climate is suitable for forests.

Fire and herbivores are ancient consumers of plant biomass that maintain open ecosystems and shape shade-intolerant species.

Therefore, open ecosystems are not necessarily either produced by deforestation or early successional, but have been maintained by consumers as ABSs to forests.

ABSs are not only found in tropical environments, but also in temperate and Mediterranean conditions.

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We currently know that both the open ecosystems and the consumers that maintain them are many millions of years old. Paleoecological [11–16] and phylogenetic [17–20] evidence indicates that fires and large herbivorous tetrapods have been consuming plants for hundreds of millions of years; their impact on ancient ecosystems is currently an active area of research [11,14,18,19,21,22]. The sudden dominance of C_4 grasses during the Miocene is among the most dramatic examples of the assembly of an open ecosystem in the geological record [23–25]. Further evidence for the ancient origin of open ecosystems is the richness and endemism of their biota. Global biodiversity hotspots include open grasslands, shrublands, and savannas rich in endemic shade-intolerant plants and animals, and subject to regular fires or herbivory [26–30]. The existence of a species-rich open habitat biota contradicts the idea that open ecosystems are recent products of deforestation, but supports the evidence that they are persistent stable habitats [31].

ASS theory has recently emerged from being a theoretical backwater to becoming a major hypothesis for explaining mosaics of open and forested ecosystems around the world. Here, we introduce readers to ASS theory by exploring its utility in explaining mosaics of forests and nonforest **biomes** (ABSs). We discuss why ABS is considered an important contender for explaining the distribution of tropical grassy biomes, and why it may explain many of the forest/nonforest mosaics elsewhere. We also note points of contention that cause vigorous debate, discuss conservation implications of ABS, and indicate new directions and questions raised by the ABS theoretical framework.

Alternative Biome States: The Concept

The biome concept was first introduced to characterize structurally similar vegetation types in similar climates around the world. Climate classifications, such as that of Koppen, use annual and seasonal means of precipitation and temperature to categorize climates that encompass different biomes. The biomes, then, are supposed to represent distinct climate zones. The circularity of this definition (vegetation and climate are indistinguishable) narrowed our understanding of the processes behind vegetation patterns.

The problem was recognized, and structural definitions of biomes were developed independent of climate or location. Biomes were instead based on the shared dominance of particular major growth forms within a vegetation type, but with different growth forms among biomes [32]. Consequently, ABSs refer to the potential dominance of different growth forms (and, thus, different biomass, leaf area, shade tolerance, and community structures) under the same environment, with each state (**open versus closed biome**) persisting over generations. ABS is a special case of the more general theory of ASS [33–38], which has been applied to a range of biological systems, from cells to oceans [36]. In such systems, each state returns to the same state (stable state) after small disturbances (**resilience**) thanks to the existence of stabilizing feedback processes [39–41]. However, occasional strong stochastic events (**perturbations**) or gradual shifts in environmental drivers (see [42] for a detailed distinction) can push the system from one state to the other (a biome shift); the new state remains stable, while the intermediate situations are unstable. Removing the driver that induced the state change may not necessarily cause the system to switch back to the previous state (**hysteresis**).

Here, we first introduce the case of ABS in the tropics, because it is there where it has been best documented; we then examine the difficulties in testing the ABS and review ABS beyond tropical environments. As feedback mechanisms, we focus on fire and vertebrate herbivory (plant consumers), which have been most widely studied as the major drivers generating ABS at broad scales. Other processes have been proposed as candidates for regime shifts (e.g., freezing,

Glossary

Basin of attraction (attractor): range of conditions in which an ecosystem can oscillate due to disturbances, without changing state (see 'Resilience'). Each basin of attraction corresponds to a stable state. It is typically represented by a cup, with a ball (ecosystem) oscillating inside it.

Bimodal (multimodal): a frequency distribution with two (or more) peaks. In relation to vegetation mosaics, it refers to peaks in the frequency distribution of a vegetation indicator (e.g., tree cover, basal area, biomass, or tree density) in a given landscape or region (i.e., intermediate values are rare).

Biome: grouping of vegetation types with the same dominant growth form (s) that remains stable over generations. Open and closed biomes (see later) can be alternative stable states.

Consumers (plant consumers): agents that consume plant biomass generating feedback to the vegetation by influencing their own regime; consumers include herbivores and fire, and consumed-controlled systems include many grasslands, savannas, and shrublands. Consumers convert complex organic compounds into simpler by-products. Note that physical disturbance agents (wind, flood, landslide, etc.) do not consume or convert plant matter, neither is their disturbance regime altered via feedbacks with vegetation.

Encroachment (woody encroachment): the increasing dominance of woody plants in a grass-dominated system.

Hysteresis: difficult-to-reverse shifts because the two pathways of change between ASSs differ. For instance, grazing may maintain a savanna, and removing grazers may drive the system to a forest, but the savanna is not recovered by just adding back grazers in the forest.

Landscape anachronism: those landscapes that are best explained by extinct animals and are currently maintained by human intervention. Many European landscape mosaics are anachronistic because they include species-rich grasslands currently maintained by livestock or mowing.

Open versus closed biomes: open biomes are those dominated by shade-intolerant plants; they can include some trees, but tree density and leaf area is low enough to allow abundant

drought, and cyclone damage [43,44]); however, these are typically of local importance and do not generate feedbacks that maintain one of the states; thus, they are not considered here.

Alternative Biome States Explain Tropical Forest–Savanna Mosaics

The striking differences and sharp boundaries between tropical forests and tropical grassy biomes (savannas and grasslands; Figure 1) led to early suggestions that they were ecological examples of ABS. ABSs are maintained over generations by stabilizing feedback processes that enhance the conditions required for a given state while hindering the conditions for the other state. For forest–savanna systems controlled by fire (Figure 2), the main stabilizing feedback processes are as follows [39,40,45–48]: in the low biomass state (savanna), frequent fires keep the system open and enable a dominance of shade-intolerant flammable grasses that enhance frequent fires. In the higher biomass state (forest), shade limits the growth of flammable (shade-intolerant) grasses, and the higher humidity and the lower wind speed inhibits fire spread while enhancing the growth of forest trees (which further inhibits flammable conditions). Under extreme weather (dry, hot, and windy) conditions, fire may spread from savannas into the forest and open the canopy beyond a light threshold that allows the colonization of flammable grasses, potentially causing a shift to an open stable state [10,49]. By contrast, a long fire-free interval may enable tree colonization of the open state, causing eventual exclusion of shade-intolerant trees and flammable grasses and their replacement by shade-tolerant forest trees [45,47]. The regime shift to forests is stabilized by changes in microclimatic conditions and the loss of flammable grasses (Figure 2). The two rates of change are different (i.e., the basins of attractions are asymmetrical). In general, closed ecosystems cannot easily switch to open ecosystems because forests may be insufficiently flammable, or because the size of the woody species may have exceeded the threshold at which they become fire and/or grazing resistant. Thus, the switch requires an infrequent disturbance event (a perturbation, e.g., a long El Niño/La Niña event; Figure 2 [10,49,50]). This difficulty in reverting the state (hysteresis) is a characteristic of many ABSs. The savanna-to-forest switch is slower, but well within the lifespan of a tree, with a tipping point when difficult-to-ignite bush clumps exceed the threshold at which fire no longer 'percolates' through the landscape and the system switches to a nonflammable forest state [51]. The

shade-intolerant species. Typical examples are grasslands, savannas, and shrublands. Closed biomes are forests, that is, tree-dominated ecosystems in which the density and leaf area is high enough to exclude shade-intolerant plants in the understory. Closed biomes typically have higher plant biomass than open biomes. Open biomes are often maintained by plant consumers.

<u>Open versus closed ecosystems</u>: as for biomes, but in more general terms (i.e., open ecosystems are those dominated by shade-intolerant plants while closed ecosystems are dominated by trees that exclude shade-intolerant plants in the understory). Open versus closed ecosystems should not be confused with open/closed as used in thermodynamics and system theory.

<u>Perturbation</u>: disturbance (often infrequent) that shifts the state of a system; also called extrinsic disturbances or destabilizing factors. Note that not all disturbances generate a perturbation of the system.

<u>Resilience</u>: ability to return to the reference state after disturbance (i.e., to fluctuate within the basin of attraction), and maintain functions, structure, and feedback processes. 'Elasticity' is the speed of the return.

<u>Threshold</u>: point where a small gradual change in conditions lead to large changes (discontinuous jumps) in system state variables (e.g., biomass, number of individuals, or cover).

Table 1. Comparison of the Three Main Dynamic Processes Assembling Disturbance-Prone Communities and Landscapes[a]

Characteristics	Succession	Autosuccession	ABS
Mechanisms	Facilitation	Resprouting, seeding	Positive feedbacks
Stable states	1	1	2 (or more)
Changes in spatial structure (boundaries)	Gradual	No	Abrupt[b]
Temporal changes	Gradual	No	Abrupt[b]
Community trajectory	Unidirectional	Low, nondirectional	Multidirectional
Disturbance	External property	Inherent property	Inherent property
Predictability of composition	High (temporal sequence)	Very high	Low
Key plant traits	Height, leaf and root traits, shade tolerance	Bud and seed banks	Shade tolerance, leaf area index, bud bank, flammability, palatability
Typical examples	Post volcano, oldfields	Chaparral-type shrublands	Forest–savanna mosaics[c]

[a]The three processes compared are: classical (facilitation) succession, autosuccession, and ABSs. Under the ABS framework, autosuccession is understood as a mechanism that maintains an alternative state.
[b]Abrupt relative to the tree longevity. Note that, in aquatic ecosystems, abrupt changes are faster than in terrestrial ecosystems due to the different generation times of the organisms.
[c]See also Table 2 in the main text.
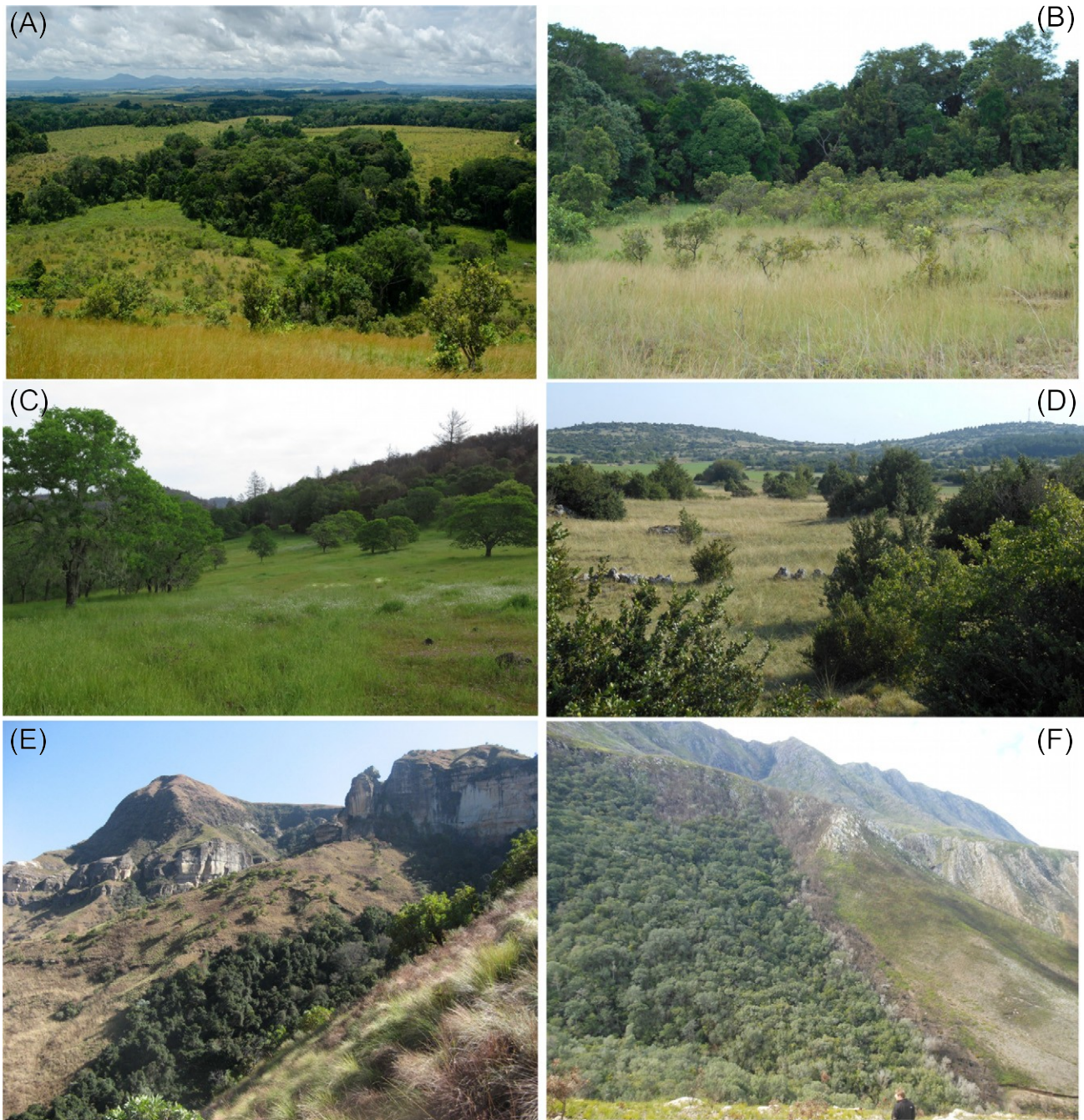
Figure 1. Examples of Multibiome Landscape Mosaics Where Closed Forests Alternate with Open Biomes (Grasslands and Shrublands) That Are Maintained by Mammal Herbivory and Fire. These examples include tropical (A, B, E); temperate (D); and Mediterranean climates (C, F). Locations: (A,B) Lope, Gabon; (C) Sonoma county, CA, USA; (D) Larzac, France; (E) Drakensberg mountains, South Africa; (F) closed forest and adjacent burnt Cape fynbos, South Africa, showing fire stopping in the forest. Photos by W.J. Bond.

contrasting fire regimes and responses between the two states lead to divergent functional characteristics of the woody plants, as observed in several studies: forest trees typically have thin bark and exposed buds and, thus, are sensitive to grass fires, while trees and shrubs from
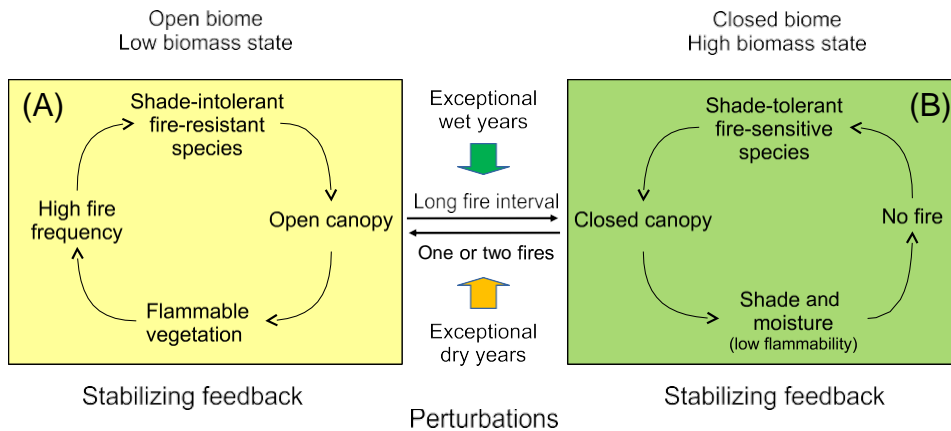
Figure 2. Generalized Feedback Processes in Fire-Prone Landscapes Where Open and Closed Biomes (e.g., a Grassland and Forest) Are Stable States Maintained by Stabilizing Feedbacks, While Perturbations Generate Abrupt Transitions among States (Destabilizing Factors). In open ecosystems (A), with lower moisture and higher fire frequency, woody plants have less leaf area and invest in fire-resistant mechanisms (thick bark and insulated buds), while in closed canopies (B) with higher shade and moisture, trees shade and inhibit understory plants. In the closed state, one or two consecutive fires (a pulse perturbation) may kill some fire-sensitive trees, open the canopy, and allow the colonization of flammable vegetation, which may surpass the flammability threshold that led to stabilizing the low biomass state. This is a sudden and quick transition. In the open state, a long period without fires (perturbation) may allow the invasion of fast-growing fire-sensitive trees that close the canopy beyond a threshold that generates enough shade and moisture to stabilize the closed canopy state. This shift may be slower. The open state (A) can also be maintained by herbivory, enhancing palatable vegetation (grazers) while inhibiting woody vegetation (browsers). Herbivory exclusion may drive the system to a closed woody state, while browsing and fire may revert to the savanna state [7,39,64].

flammable open ecosystems have either thick fire-resistant bark [45,46,52] or a high resprouting ability from either insulated epicormic buds [53–55] or underground bud banks [20,56].

While fire has been extensively studied as a global consumer maintaining open ecosystems, the same is not true for large vertebrate herbivores; the spatial extent and environmental conditions favoring herbivore-maintained open ecosystems are still not well known. Large vertebrate herbivores, similar to fire, can generate feedbacks by consuming woody vegetation (browsing) while favoring grasses [5,57–59]. Herbivore exclusion favors the establishment of woody vegetation [14,60,61]. Herbivory may maintain grasslands [7,62–64], but a biome switch from woodlands to grasslands may require fire [10,49,65]. While both herbivory and fire compete for the same resource (biomass), their relative importance in a landscape varies depending on a range of factors (e.g., herbivores require more fertile soils [64]). For instance, in Africa, there is a relatively abrupt shift from herbivory- to fire-controlled systems along a precipitation gradient [7,64,66]. Semiarid savannas and nutrient-rich soils support heavy grazing, whereas humid savannas with leached soils support unpalatable vegetation (high C/N), thereby inhibiting herbivory and promoting fire [64,67]. In southern South America, the density of cattle modulates fire activity along the precipitation gradient [68]. In other regions, fire may have increased in importance as a plant consumer, after the extinction of large herbivores [11,69,70].

Given that abrupt transitions among biomes are related to time-dependent processes (e.g., intervals between disturbances and plant growth rate; Figure 2), environmental conditions can influence the dynamics among states by controlling the speed at which the system reaches thresholds. Thus, climate influences the probability of finding alterative biome states, with very wet tropical climates having high probabilities of closed forest, whereas very dry tropical climates

generally only support grasslands [7,64]. Similarly, spatial heterogeneity in microenvironmental conditions can influence the dynamics among states. Thus, patches of higher soil fertility, deeper soils, or small topographic depressions enhance the transition towards the closed state, while patches of unproductive environment favor open states [71,72].

Testing Alternative Biome States

Despite conceptual and modeling advances in ASS theory, experimental ecologists have had difficulties demonstrating the existence of ABS, particularly because of the high bar set by theoretical ecologists (Box 1) and the problem of demonstrating stability in systems with long-lived organisms [40]. ABS theory differs from traditional succession theory in predicting that the open states are stable and not early successional (Table 1). However, the states are also dynamic and, thus, the capacity to switch from one state to another must also be demonstrated. Experimental ecologists would need several decades to convincingly demonstrate that a tree can recruit and grow to maturity in a grassland, but several centuries to convince themselves that an experimental forest can stably occupy the 'grassland' site. Since rigorous long-term experiments are difficult to perform in complex terrestrial ecosystems [38,40,73] (Box 1), many ecologists have overlooked ABS and rely on bottom-up (resource) explanations for biome mosaics [74,75]. The pervasive idea that forests are ancient and nonforests are derived (by human deforestation) has been an additional hindrance to unbiased research on the causes of ABS, in which natural disturbances can switch between alternative biomes [21].

More recently, field ecologists have suggested protocols for testing ABS, emphasizing different features of the theory. For example, a recent protocol emphasized the dynamism of the alternative states [76] and included demonstrating stability over time using paleoecological and historical data, then searching for field evidence of dynamism (e.g., tree growth rates and biome boundary movements), and finally testing it with natural or designed experiments supplemented with simulation models. However, much of the recent surge of interest in ABS emphasizes pattern, not dynamics, especially thanks to new global remote-sensing information [6,7,64,77–80]. These studies reveal that tree cover across a precipitation gradient is multimodal and tends to be either high or low, with few intermediate values. This is consistent with tree densities falling into different basins of attraction, and strongly supports the ABS theory. Subsequent studies have shown

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Box 1. The Difficulties of Testing Alternative Biome States in Terrestrial Ecosystems

The criteria for recognizing ASSs were hotly debated during the 1980s and became strongly restrictive. The proposed protocol was as follows [35,38]: (i) identify potential alternative states; (ii) apply a range of perturbation levels hypothesized to switch states; (iii) perturbations should mimic natural regimes; (iv) perturbation should not be maintained (pulse disturbance); (v) the monitoring should be long enough for the alternative state to develop; (vi) perform the reverse experiment, preferably in the same site; and (vii) if the two experiments are performed in a different site, then both experiments need to be well replicated. We could even add: (viii) atmospheric conditions (climate, CO_2, or nutrient deposition) during the experiment should reflect the natural regime. This protocol is difficult to accomplish (if even possible) when studying terrestrial ecosystems and long-lived plant species.

Using these criteria, very few studies have demonstrated the existence of alternative states in natural systems [38,73], let alone the existence of alternative biomes. The criteria emphasize experimental studies, and this possibly leads to a failure to recognize patterns consistent with ABS theory at regional and continental scales. Fire and grazing exclusion experiments are probably the closest approach for testing whether environmental heterogeneity maintains distinct states. Although many such experiments have been maintained for decades, they are still relatively short in relation to plant longevity, and none were designed for testing ABS [75]; stabilizing disturbance and perturbations often do not mimic natural processes. The existence of tree plantations in open landscapes is a useful indirect evidence in support of ABS in demonstrating that environmental conditions (soils and climate) are not responsible for excluding forests. Thus, an analysis of patterns should form part of the criteria for recognizing ABS as a global phenomenon (see Box 2 in the main text). A large and randomized sampling may be needed to overcome some of the shortcomings when concluding processes from patterns.

similar patterns using ground-based analyses of basal area, a surrogate for biomass [7]. By contrast, a unimodal distribution of tree importance would be expected if tree populations were controlled by resource availability.

In parallel with the development of remote sensing for broad spatial-scale analyses, the emergence of new paleoproxies provides strong temporal evidence for both stability of states and their potential to shift [10,14,76]. For example, there is isotopic evidence that current forests replaced savannas in southern Africa [81]. Savannas persisted for thousands of years before being replaced by forests, which have now persisted for at least 2000 years [82]. Both states are stable and both occupy soils that can be occupied, and have been, by the other state [82]. Such studies have made it feasible to demonstrate both stability and regime shifts on timescales far beyond what is practical in field experiments.

However, manipulative and opportunistic experiments are important tests of whether each biome state can occupy the domain of the putative alternative state. For instance, forest plantations in landscapes dominated by grasslands, prairies, savannas, and shrublands are evidence that the environment is warm and wet enough to support forests. Multidecadal burning experiments show that fire exclusion can transform grasslands to shrublands [83] or closed forests [84–86], while recurrent fires continue to maintain open ecosystems and savannas. Fire exclusion policies at landscape scales have also shifted open ecosystems to closed forests in both tropical and temperate environments [87–89]. Grazing exclusion experiments show a clear increase in woody biomass [14,60,61], while browsers and mixed feeders reduce woody biomass and favor savannas [39]. However, the level of grazing needed to suppress fire, and the growth rate of trees needed to escape browsing and fire thresholds, depend on system productivity and, thus, in most tropical systems, fire, grazing, and rainfall interact in determining the dynamics of the ABS [39,64,66,68]. There are also instances where, after decades, fire and/or herbivory exclusion do not trigger shifts to an alternative biome state [90,91]; these are likely caused by edaphic constraints on tree growth, but no synthesis has yet been made. Understanding in which conditions shifts do occur, and in which they do not, is a major research challenge.

In summary, there are different ways to test the different assumptions of the ABS theory (Box 2), and current research suggests that the ABS is the most likely explanation for many of the tropical savanna–forest mosaics. There is now growing evidence that ABS also operates beyond tropical systems [92].

Alternative Biome States Beyond the Tropics

Among the earliest attempts to understand landscape mosaics were those of Wells in central California [93] and Jackson in Tasmania [94] during the 1960s. They provided pioneering analyses of multiple stable states in what we would now consider an ABS framework. Both proposed that the complex mosaics of grassland, shrublands, and forests were explained by divergent fire regimes, rather than by soils and substrate differences. There is increasing evidence that different biomes in temperate and Mediterranean climates (grasslands, shrublands, broad-leaved forests, and coniferous forests) can overlap in the environmental space, co-occur in the landscape, generate sharp boundaries, and alternate over time in each climate (Table 2, Figure 1). Long-term human impact may blur natural patterns, particularly in Eurasia, hindering our understanding of the drivers shaping temperate landscapes; however, ABS still leaves traces in modern landscapes. For instance, large areas of mountain grasslands in eastern USA and temperate Europe are maintained by grazing, occasionally with fire, and the cessation of grazing can initiate

Table 2. Examples of Likely ABSs from Nontropical Ecosystems[a]

Closed biome: higher biomass state	Perturbations (closed to open)[b]	Open biome: lower biomass state	Maintenance of the open biome[b]	Examples[b]	Refs
Evergreen broad-leaved forest	Fires in extreme weather	Shrubland	Short FRI, grazing	S Europe	[102]
Serotinous conifer forest	Infrequent very short FRI	Shrubland	Short FRI	S Europe	Personal Observation (Pausas, 2019)
Tall (nonserotinous) coniferous forest	Infrequent high intensity crown-fire	Shrubland	Frequent crown fires	S Europe	[30,101]
Deciduous broad-leaved forest	Infrequent severe fires	Shrubland	Short FRI	Patagonia	[92,107]
Broad-leaved forest	Infrequent crown-fire	Coniferous savanna	Short FRI, other disturbances	SE USA	[109,110]
Forests (conifers, broad-leaved)	Climate extremes (glaciations)	Mountain grasslands	Grazing (and fire)	E USA, CE Europe	[95]
Tundra (including forest tundra)	Pleistocene grazing, Pleistocene low-CO_2	Steppe	Grazing, trampling	Eurasia	[97]
Woodlands	High FI	Grasslands and/or shrublands	Short FRI	Great Plain, USA	[83]
Forest	Fire, herbivory	Wood pastures	Mammal herbivory	Europe	[57]
Shrubland	Short FRI and grazing	Grassland	Short FRI and grazing	Great Plain, USA	[135]
Forested wetland	Fire	Nonforested wetland	Low transpiration and interception; water-logging	Tasmania, AU	[10]
Forest	High FI	Sedgeland/shrubland	Short FRI	Tasmania, AU	[76,94]
Forest	Browsing + Fire	Oak savanna	Browsing	Canada	[63]
Broad-leaved deciduous	Long FRI, accumulation of peat	Conifer forest	Predictable FRI of low FI	Boreal	[113,114]

[a]Open and closed biomes represent two ASSs. Perturbations switching the closed state to the open state, and the processes maintaining these open lower biomass states are also shown based on the examples indicated. Perturbations related to fire are often tied to infrequent extreme weather and/or climate events, but the main direct (mechanistic) effect is fire and not drought. This is not an exhaustive list.
[b]Abbreviations: CE, central-east; E, east; FRI, fire return interval; S, south; SE, south-east.

encroachment by trees [95,96]; this suggests that forests and temperate grasslands are ABSs. Similarly, large areas of cold steppes are maintained by grazing, and a decrease in grazing drives the system to a tundra state with some trees [97]. Although temperate grasslands are currently mainly maintained by livestock or mowing, there is evidence of a long history of grazing in these ecosystems [14,57,62,67,98]. Megafauna collapse coincided with the arrival of early human populations, but many herbivores (e.g., elk, deer, bison, horses, and wild cattle) remained at significant densities, as reproduced in the wall of numerous Paleolithic caves in Europe, and reported by early travelers in America [95]. Thus, domestic livestock may have replaced Pleistocene grazers in maintaining ancient open ecosystems [57,98]. In some regions, it is likely that the loss of the Pleistocene megaherbivores would have led to a substantial reduction in grasslands and plant diversity in favor of forest and tundra [67,95,97,99]. In fact, fossil dung beetles in Europe indicate that vegetation was more open during the last Interglacial than after the megafauna extinctions [15]. Thus, sharp grassland–forest boundaries currently maintained by livestock or mowing may be a **landscape anachronism** of a previous natural system.

A relatively well-documented ABS is the oak savanna and forest in temperate North America [61,63]. Many of these oak savannas are maintained by deer browsing, which suppresses forest tree regeneration. This favors unpalatable species, some of which are highly competitive under high light incidence, and this further suppresses tree regeneration. In addition, the openness makes large forest trees more susceptible to windstorms. These feedbacks maintain open savannas as stable states; a reduction in deer populations is usually insufficient to cause a regime shift to a forest [61,63]. Similar processes (feedback and hysteresis) have been documented in areas with introduced browsers [100].

In many nontropical environments, forests alternate with shrublands that have a radically different species assemblage (Table 2). While in temperate and cold environments, ABS appears to be driven by herbivores (above), in warmer Mediterranean conditions, species-rich chaparral-type shrublands are often maintained by regular fires [30,101,102]. For instance, in South Africa, patches of evergreen forest occur in landscapes dominated by flammable fynbos shrublands on some of the most nutrient-poor soils in the world [102–104]. Here, the ABSs have major effects on the chemistry of quartzite-derived soils, with forests enriching the soil and fynbos maintaining very low nutrient concentrations [104], reinforcing the divergence of the two states. Mediterranean shrublands are among the most species-rich ecosystems in the world [30,105], yet they grow in environments that can sustain high biomass forests, including tall eucalypt (Australia) and redwood (California) forests, as well as vast forest plantations. In these Mediterranean conditions, extreme changes in fire regime can drive a coniferous forest to a shrubland. Such is the case under a reduced fire return interval in serotinous trees, or after an increased fire intensity in nonserotinous tree forests. Once the system has shifted to a shrubland, it can remain stable under relatively frequent fires of high intensity (traditionally termed 'autosuccession'; Table 1) with a species-rich shade-intolerant flora with high postfire regeneration capacity [30,106]. These fire-dependent forest–shrubland mosaics also occur in colder environments [92,107,108].

The alternation of fire-maintained open vegetation and fire-resistant broad-leaved forests is also well known in temperate warm ecosystems, especially in the eastern USA (Table 2). Frequent grass-fueled fires maintain pine and oak savannas, while fire suppression promotes closed broad-leaved forests with contrasting shade, fire regimes, and feedbacks [88,109,110]. In boreal ecosystems, these forest mosaics may be driven by ungulate browsing and budworm outbreaks [111,112] or changing fire regimes [113]. Studies in Alaska have shown that needle-leaved (conifer) boreal forests switch to broad-leaved (angiosperm) forests after intense fires when

these convert organic to mineral soils [114]. Besides suggesting the potential for extremely rapid vegetation change in the future [113], these studies also suggest the possibility of ABS if the broad-leaved forests are maintained for long periods (a century or two); otherwise, the switch back to a conifer-dominated ecosystem would be an example of classic succession.

Implications for Conservation in a Changing World

Open ecosystems harbor a huge diversity of light-demanding species and species that require large open habitats [115]; most of these species cannot live in forests. In addition, many biodiversity hotspots are savannas and shrublands maintained by fire; indeed, fire is a strong driver of biodiversity [116]. Thus, the ABS provides a framework for the conservation of landscape mosaics where different alternative states coexist in an ecologically and evolutionary dynamic way. Classical succession theory suggests markedly different (narrower) conservation priorities because open ecosystems are considered transient (immature, nonoptimal), and fire and herbivory are viewed as processes that delay succession towards the optimum. Thus, an ABS perspective on conservation management can be seen as promoting fire as essential for conserving the open state, whereas a succession approach is more likely to suppress fire as a process preventing succession to a forest climax.

Global warming is increasing the probability of heat waves and intense fires and, thus, it may enhance the tendency towards open ecosystems. However, increasing atmospheric CO_2, the abandonment of rural activities (e.g., livestock), and strong fire suppression in some ecosystems are promoting woody encroachment worldwide and threatening ancient open habitats [117,118]. Afforestation of open ecosystems for CO_2 sequestration has been widely promoted and is a growing threat to their future [119]. This is despite great uncertainty as to the effectiveness of afforestation as a carbon sink and the disruptive social, economic, and ecological consequences of landcover change over enormous areas [119–121]. Anthropogenic defaunation of large herbivores (e.g., poaching or habitat fragmentation) is another threat to ABS landscapes. Managing these landscapes should include the management of consumer regimes because they can alter biome trajectories and even alleviate some of the effects of global change [28,122–125]. Prescribed fires and wildfire management are becoming key options in many ABS landscapes [126]. Rewilding [127] is another management option increasingly considered for restoring landscape mosaics, although its application is still limited. The ABS framework also provides an indication of when management strategies can make significant changes for conservation (e.g., close to the thresholds) and when they would fail [128].

ABS has also implication for species distribution modeling under climatic change, because this technique often assumes that species respond individualistically to climate. Given that plants in ABS landscapes respond within a biome, changes in species distribution are not expected if the biome does not change. Thus, in ABS landscapes, predictions based on individual species response to environment are likely to be poor.

Overall, ABS provides the appropriate framework for the conservation of the different alternative states, and the processes that maintain them.

Concluding Remarks

Despite the difficulties in performing rigorous long-term experimental tests to demonstrate terrestrial biome shifts under a given environment (Box 1), there are diverse lines of evidence suggesting that ABS are common in the tropics and beyond. However, the relative importance of ABS versus successional processes or fixed soil constraints on vegetation distribution remains to be quantified in different regions and environments (see Outstanding Questions). ABS theory provides a

valuable alternative framework for understanding spatial and temporal vegetation patterns that differ from those based on gradual changes (e.g., gradient analysis and succession), and suggests that multistability in a given environment is common. This view has some startling implications: for example, instead of asking how organisms fit the environment, we need to ask how the organism can change the environment to fit the organism (niche construction). While classic succession theory suggests that communities change as species modify their environment, making it more favorable for later successional species, the ABS perspective is that species modify their environment, making it more favorable for their own continued occupancy (Table 1, Figure 2), which is better aligned with a Darwinian view of nature.

One of the advantages of the ABS is that disturbances (plant consumers) are well integrated into the system in contrast to classical successional theory (based on facilitation and competition), where disturbance is an external factor that reverts succession (Table 1). The ABS framework highlights fire and vertebrate herbivory as the key processes promoting ABS since both affect the plants growing in a community and, in turn, the plants influence the activities of both consumers (feedback). The relative role of each consumer requires further research (see Outstanding Questions), but is likely to depend on historical contingencies and productivity; for instance, fires dominate at intermediate productivity [129] and where herbivores were decimated (e.g., Pleistocene overkill); and herbivores tend to be important where fires are limited (too dry or too moist). There is growing evidence that disturbance regimes affect plant biomass and select for distinct strategies. Thus, ABS also provides the appropriate context for the evolution of contrasting functional traits in plants [19,46,130,131] and animals [29,132]. Of particular importance to the idea of consumer control and feedbacks between the consumer and the ecosystem is whether plants have evolved to promote the consumer and the associated disturbance regime (see Outstanding Questions). For example, there is considerable interest in whether plants have evolved flammability, promoting fire, or palatability, promoting increased grazing, with feedbacks to ecosystem properties [133,134].

Thus, is it not time to broaden the idea found in most biogeography textbooks that climate controls the major vegetation formations of the world to the richer notion of consumer control? Working within climatic and edaphic constraints and depending on the plant species pool, consumers can produce vastly different ecosystems from the climate potential and have done so for millions of years.

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