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Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems

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It is difficult to find references to fire in general textbooks on ecology, conservation biology or biogeography, in spite of the fact that large parts of the world burn on a regular basis, and that there is a considerable literature on the ecology of fire and its use for managing ecosystems. Fire has been burning ecosystems for hundreds of millions of years, helping to shape global biome distribution and to maintain the structure and function of fire-prone communities. Fire is also a significant evolutionary force, and is one of the first tools that humans used to re-shape their world. Here, we review the recent literature, drawing parallels between fire and herbivores as alternative consumers of vegetation. We point to the common questions, and some surprisingly different answers, that emerge from viewing fire as a globally significant consumer that is analogous to herbivory.

Parallels between fire and herbivory

Ecologists and biogeographers generally assume that plant distribution, abundance and, therefore, community composition, structure and biomass, are determined largely by climate and soils. This is implicit in current attempts to model species range shifts in response to climate change [1]. However, nearly 50 years ago, Hairston et al. [2] suggested that the properties of ecosystems are instead determined by the regulation of herbivores by predators. In the absence of predators, herbivore populations would proliferate, consuming such large quantities of vegetation that plant communities would be transformed to those tolerant of herbivory rather than those best able to compete for resources. Critics claimed that terrestrial plants are largely inedible so that, even without predators, herbivores could seldom consume enough to transform ecosystems [3]. The effects of fire are, in many ways, analogous to those of herbivory, but have been missing from the trophic ecology literature. Although usually treated as a disturbance, fire differs from other disturbances, such as cyclones or floods, in that it feeds on complex organic molecules (as do herbivores) and converts them to organic and mineral products. Fire

differs from herbivory in that it regularly consumes dead and living material and, with no protein needed for its growth, has broad dietary preferences. Plants that are inedible for herbivores commonly fuel fires.

How does fire, unconstrained by low food quality, fit the predictions of Hairston et al. [2] as an ecosystem consumer that is unconstrained by predators? Here, we discuss the ecology of flammable ecosystems, using the term 'consumer control' for ecosystems in which fire or herbivores significantly alter biomass, the mix of plant growth forms, and species composition in ecosystems. We contend that consumer control is important ecologically, biogeographically and evolutionarily when the consumer is fire.

Fire and consumer control of ecosystems

Polis [3], in a review of the 'green world' hypothesis, argued that terrestrial vegetation is determined largely by climate, locally modified by low-nutrient soils, with consumer control by herbivores sometimes occurring but being localized in space and time. How can the global importance of consumers (herbivores and fires) versus resources (climate and soils) in shaping vegetation be evaluated? A useful alternative to meta-analyses of experimental studies (often limited in space, time, taxonomic bias and reportage counts) is to compare potential versus actual ecosystem properties for a given locality. If an ecosystem differs greatly from its resource-limited potential properties, then it is a candidate for 'consumer control', be it either by herbivory or fire (Figure 1). Frequent fires reduce the height of the dominant plants (Figure 2) and, therefore, the position, but not necessarily the amount, of leaves and canopy photosynthesis. Woody plant biomass, rather than primary productivity, is therefore the more revealing measure of consumer control by fire. The problem is how to measure potential biomass, the 'carrying capacity' of trees at a site, against which actual ecosystems can be measured.

Dynamic global vegetation models (DGVMs) can be used to provide an approximation of climate-limited potential biomass [4]. DGVMs are complex models, analogous to global climate models, which 'grow' plants according to physiological principles using climate and soil physical properties as input [5,6]. The models predict vegetation responses to global change and can simulate

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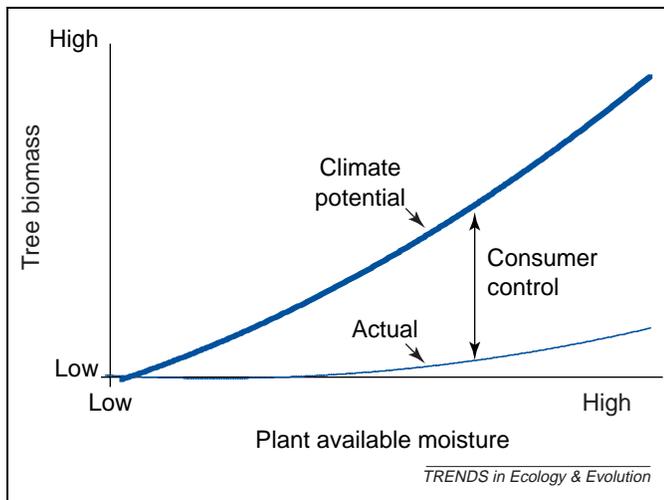Available online 3 May 2005

Figure 1. Assessing consumer control of tree biomass. The extent of consumer control of an ecosystem can be measured as the difference between tree biomass at 'climate potential' and the actual tree biomass. Large differences between potential and actual woody biomass suggest significant consumer control of the ecosystem. 'Climate potential' can be viewed as the carrying capacity of a site for trees.

potential vegetation for any given location (Figure 2). According to these simulations (e.g. Figure 3), vast areas of wooded grasslands in Africa and South America, and smaller areas of grassy ecosystems and shrublands on all vegetated continents, have the climate potential to form forests. Closed forests, which currently cover a quarter of the land surface on Earth, would more than double in extent if world vegetation was as 'green' as it could be [4]. These simulations contradict current perceptions that consumer control is of negligible importance in terrestrial ecosystems [3,7]. The biomes most at variance with climate potential are C4 grasslands and savannas, especially in more humid regions, such as Brazilian cerrados and the wetter regions of Africa. These are the most frequently burnt ecosystems in the world, burning several times in a decade and some burning twice a year [8,9]. Thus, fire is the prime candidate for consumer control of large parts of the world. Past or future changes in the extent of these ecosystems, or species within them, cannot be understood without understanding the ecology of fire.

The implications of Figure 3 are even more significant when it is recognized that the mismatch with climate potential is based only on biomass and not on changes in species composition. The simulations cannot identify those ecosystems in which fires change species composition without significantly altering the biomass of trees, such as conifer forests [10] or Australian eucalypt communities [11]. The full extent of fire-controlled vegetation, defined as ecosystems that are altered in structure, composition and functioning when fire is released or suppressed, is much greater.

Fire and consumer control of species composition

Trophic cascades, measured as large changes in species composition, are an expected consequence of predator removal in ecosystems where consumers have the potential to proliferate in their absence. Although evidence for trophic cascades in terrestrial ecosystems is disputed [7], cascading changes in species composition are commonplace where fire is the consumer. For example, in tropical forests, a single fire can reduce woody plant richness by a third to two-thirds depending on fire severity and can have negative impacts on a diverse array of faunal components [12–15]. Changes in fuel distribution and microclimate after a tropical forest fire increase the probability of more fires and conversion of forest to scrub and grassland [12,15].

By contrast, for ecosystems with a long history of fire, there is concern over the cascading consequences of anthropogenic fire suppression. In tall grass prairies, and comparable grasslands elsewhere, fire suppression has led to the loss of as many as 50% of the plant species [16,17]. Small herbaceous plants with high light requirements for growth and seedling establishment are the worst affected. Changes in faunal composition have also been reported, for example, in dry dipterocarp woodlands, where fire suppression has resulted in a marked loss of termite species [18]. Even greater species losses occur where fire suppression leads to complete biome switches, such as from savannas to forests [19,20]. There is, as yet, no global synthesis of species turnover in different
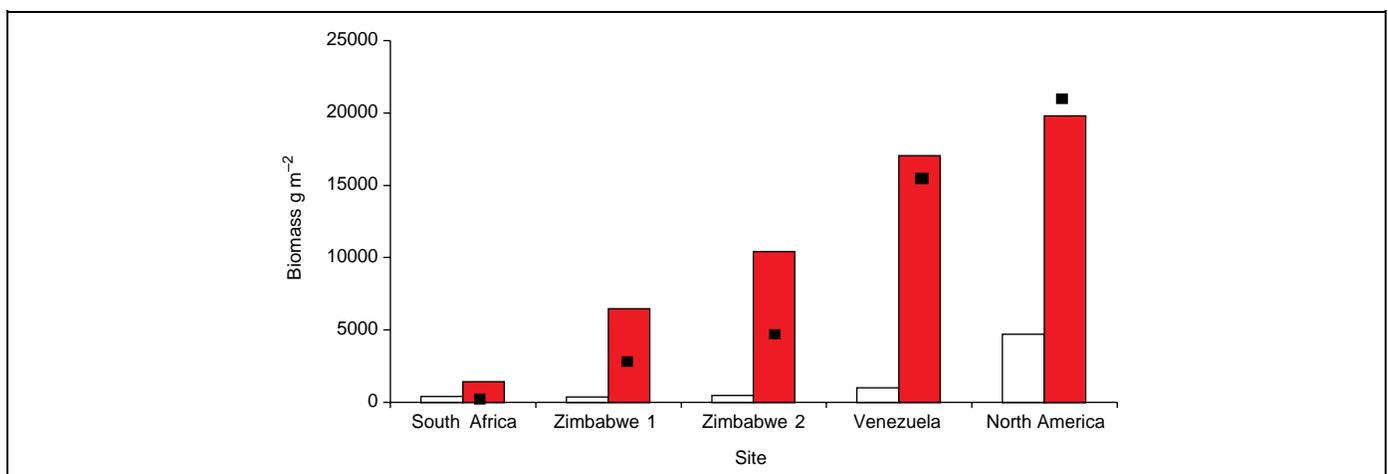

Figure 2. Changes in woody biomass in savanna long-term burning experiments. The unshaded bars indicate aboveground woody biomass in frequently burnt treatments and the shaded bars indicate biomass where fire has been excluded for 35 years or more. Sites are ranked, from left to right, according to increasing plant available moisture. Woody biomass simulated by the Sheffield DGVM for 'fire off' is indicated by the filled squares. Modified, with permission from the New Phytologist Trust, from [4].
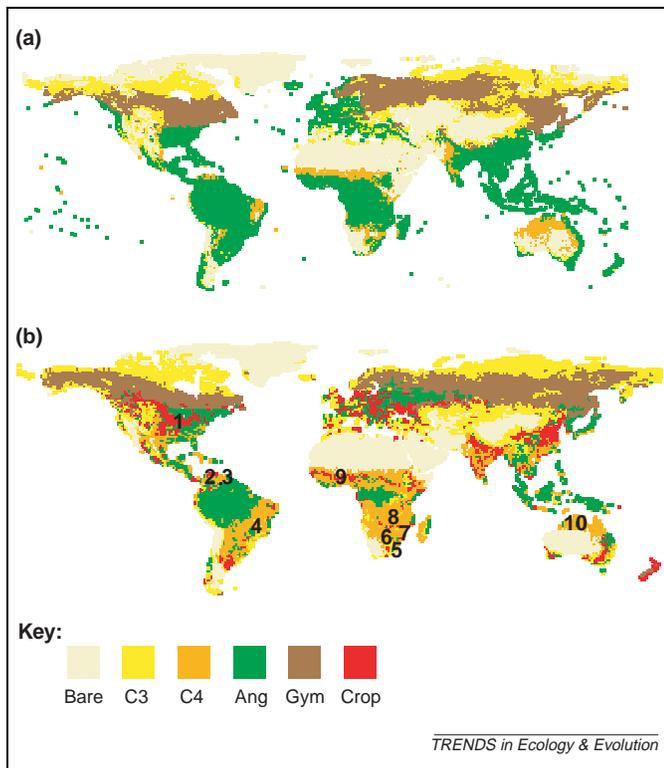
Figure 3. A comparison of global biome distribution at climate potential **(a)** versus actual vegetation **(b)**. Biomes are represented by the cover of the dominant plant functional type: C3 grasses or shrubs; C4 grasses or shrubs; Ang, angiosperm trees; gym, gymnosperm trees (mainly conifers). The numbers indicate sites where fire has been excluded for several decades. All the higher rainfall sites showed a successional tendency to form forest following suppression of fire. The map of potential World vegetation, limited only by climate, was simulated using a DGVM (using global climate and soil databases). The map of actual vegetation was sourced from ISLSCP: (ftp://daac.gsfc.nasa.gov/data/inter_disc/biosphere/land_cover/); reproduced, with permission from the New Phytologist Trust, from [4].

ecosystems and under different fire regimes following fire release or suppression. We would expect a continuum of responses from near-complete species replacement following biome switches to negligible changes in ecosystems where fires, although predictable, are infrequent. The Yellowstone fires of 1988, for example, caused no loss or gain of species in this landscape [21]. Thus, it is not yet possible to draw a global map to show the extent of ecosystems whose species composition would change significantly if fires were suppressed.

The variable nature of fire as a consumer control

Flammable ecosystems include boreal forests, eucalypt woodlands, shrublands, grasslands and savannas. Why, if fire is such an influential consumer, is there such a diversity of growth form mixtures in flammable ecosystems? Fire ecologists have looked first to the diversity of fire regimes for answers. A fire regime includes the patterns of frequency, season, type, severity and extent of fires in a landscape (Box 1). Vegetation consumed and patterns of fire spread vary across landscapes, and different fire regimes produce different landscape patterning and select for different plant attributes. It follows that changes in fire regimes, within a given landscape, should have major ecosystem consequences.

Consider the conifer forests of southwestern North America. In these semi-arid landscapes, forests have long

been shaped by a fire regime of frequent relatively low intensity (low flame height and temperature) surface fires. These forests share attributes with subtropical grasslands in that fires are ignited by frequent lightning strikes at the beginning of the monsoon season, when the fuels are at their driest. However, primary productivity in conifer forests is lower than in mesic savannas owing to their greater aridity and this translates into lower fire frequency, lower fire intensity and greater heterogeneity in 'feeding patterns' of the fire [22]. As a consequence, opportunities exist for the occasional establishment of trees that persist to form low-density forests. Fires exhibit a sort of 'selective herbivory', consuming herbaceous surface biomass but leaving the dominant overstorey trees untouched. Following human settlement during the early 20th century, these conifer landscapes have been managed with a policy of total fire suppression, which is a fortuitous experiment on how fire controls vegetation structure, and has resulted in near-total fire exclusion. Forests that naturally burned at rates of once or twice a decade have now gone unburned for more than a century [23], resulting in major shifts in ecosystem structure and function. Tree density has increased by an order of magnitude or more, with major losses in the herbaceous understorey and species diversity. In addition, the absence of fire has resulted in changes in many ecosystem components. Of profound management importance is the fact that fire suppression has lead to fuel accumulation and this has set the forest on a different trajectory such that, when fires do occur, they now feed as massive forest-consuming 'monsters', rather than in the manner of ground-dwelling herbivores.

Most work on fire regimes is constrained to particular landscapes and ecosystems. There is no global synthesis on what determines fire regimes in world ecosystems. We do not yet understand the synergies and relative importance of ignition, dry periods, the properties of vegetation as fuel, or topographic barriers to fire spread in determining which fire regimes occur where. This seriously undermines our ability to predict the consequences of global change for fire-affected ecosystems or to interpret past changes in the distribution of flammable ecosystems. What is clear is that different fire regimes select for different plant attributes and similar fire regimes select for similar attributes. Savanna ecologists worldwide find similar plant traits with similar fire responses [24]. Ecologists working in Mediterranean-type shrublands find convergent fire-related plant traits on different continents [25,26] but these are different from those of savannas. Transgressing from one fire regime to another seems to be as difficult as finding commonalities between insect and mammal herbivory, because the biology of the 'organisms' is so different.

Fire and community assembly

Hairston *et al.* [2] predicted relatively little competition between plants where herbivores proliferate in the absence of predators, because plant growth would be limited more by consumption than by resources. Instead, community assemblages would comprise species that are best able to persist and thrive in the face of repeated

defoliation. One of the striking features of the fire ecology literature is that there are many studies on life-history traits that enable the persistence of species in a given fire regime (Box 2), but few on resource acquisition and competition. The consistency with the predictions of Hairston *et al.* [2], that competition will be of minor importance in consumer-controlled ecosystems, seems to have gone unnoticed.

The plant traits that are important for fire persistence are different in communities that experience different fire regimes. In crown-fire regimes, where all woody biomass is consumed, there are numerous studies of the mode of recovery from burning (vegetative sprouting or non-sprouting), fire-stimulated recruitment, time to first reproduction and the persistence of seedbanks to the next fire [20,26,27]. These plant traits, together with the patterns of fire consumption, especially its frequency, are widely used for predicting compatible species assemblages [26,28]. However, community membership is seldom attributed to competitive interactions with other plant species, except when those species change the disturbance regime [29].

In surface-fire regimes, such as savannas, fires feed selectively, consuming plants in the grass layer but not trees taller than 2–4 m. The coexistence of trees and grasses has been attributed to niche differentiation, with grasses being the more successful competitors for resources in the soil surface, and trees accessing resources in deeper soil layers [30]. An alternative idea, consistent with consumer-controlled ecosystems, is that tree cover is limited by demographic bottlenecks at different life-history stages in tree growth [30,31]. Fire would be a major cause of these bottlenecks in frequently burnt savannas, reducing seedling establishment and preventing saplings from emerging from the 'fire trap', the flame zone produced by grass fires. Vertebrate herbivores have analogous effects, suppressing seedlings by heavy browsing with rare burst of recruitment when plants are released from herbivory [32]. The niche differentiation hypothesis predicts no changes in tree cover from fire suppression (or herbivore exclusion) because tree cover is limited by resource competition. But many long-term fire exclusion experiments (Figure 2) show that tree cover is limited by fire. In these instances, consumer control, rather than resource competition, determines tree cover [33].

Fire as an evolutionary agent

There are few studies of the evolution of fire-adaptive traits, and many plant traits have been uncritically labeled as 'fire adaptations' without any rigorous analysis either as to the functional importance of the trait, or its phylogenetic origin. For example, post-burn sprouting is often seen as a 'fire adaptation', but sprouting *per se* is a widespread trait in angiosperms. Evolutionary interpretations of the loss or gain of sprouting in different fire regimes make no sense without phylogenetic analysis [34,35].

Among the most compelling new studies are those exploring the evolution of flammability. In a debate echoing that over whether plants have evolved to promote herbivory (and just as controversial), ecologists have asked whether plants in fire-maintained ecosystems

Box 2. Life histories shaped by fire

Of the many traits that can be interpreted as being of functional importance in fire-controlled environments, two have captured most attention: sprouting and fire-triggered seedling recruitment. Sprouting is the vegetative regeneration that occurs following the destruction of living tissues. This can be either from roots or stems following the death of all aboveground tissues, or along stems where branches have been killed. Sprouting is a widespread trait in woody species and is not closely tied to fire-prone environments [35]. One exception is *Pinus*, a genus in which sprouting is rare and apparently derived in crown fire ecosystems [40]. However, sprouting from basal lignotubers that are produced as a normal development stage is a combination much more commonly found in fire-prone Mediterranean-climate ecosystems [25]. Sprouting in the context of other life-history characteristics represents complex patterns that have recently been reviewed elsewhere [35].

Many species in fire-prone environments with stand-replacing fires have seedling recruitment restricted to the first postfire year [20,27]. In flammable southern hemisphere shrublands, many species produce serotinous fruits that open following fire and disperse seeds that readily germinate following the wet season rains [64]. In comparable shrublands of the northern hemisphere, serotiny is relatively rare. In both hemispheres, many species produce seeds that are dormant and accumulate in the soil. Germination is triggered by either heat or smoke (or charred wood) [65]. Heat-stimulated germination is typically in hard-seeded species that have a physical seed coat barrier to water uptake. Germination is triggered by heat shock from fire, or by high soil temperatures on open sites. There is a marked phylogenetic pattern in that certain plant families are associated with either one mode or another; for example, heat-stimulated germination is widespread in Fabaceae, Cistaceae, Convolvulaceae and Sterculiaceae, and smoke-stimulated germination is lacking [65]. Heat-stimulated germination is

globally widespread in numerous fire-prone ecosystems. Chemical stimulated germination is triggered by smoke and/or charred wood. It has, so far, been found to be important in only three Mediterranean-climate shrublands, California chaparral [65], South African fynbos [66] and Australian heathlands [67]. In California, the plant families in which this germination mode is found are generally not the same as in the southern hemisphere shrublands, indicating that this trait might have convergently evolved.

Fire-stimulated flowering is another mechanism for post-burn seedling recruitment [20]. Flowering occurs in the first postfire year on resprouts from bulbs or rhizomes, followed by abundant seedling recruitment in the second postfire year. Most species continue to flower sporadically in later years, thus there is no obligate dependence on fire for flowering. One exception is the South African fynbos geophyte *Cyrtanthus ventricosus*, which germinates within days of a fire, regardless of the season, and remains dormant until flowering is again stimulated by smoke from another fire [68].

Not all species in fire-prone environments have life histories that have been shaped by fire. In Californian and Mediterranean Basin shrublands, many species have seedling recruitment that is restricted to fire-free conditions [69]. They have a suite of reproductive traits, including seed dispersal and seed germination behavior, which are quite distinct from species with fire-stimulated seedling recruitment. In both ecosystems [69,70], these non-fire types are from older lineages and are derived from taxa that had origins under a different climate. It has been suggested that these traits are no longer adaptive and represent historical effects and species sorting processes [70]. An alternative view is that these life-history syndromes are adapted to habitats that still exist in fire-prone landscapes, and the coexistence of fire-type and non-fire types is promoted by natural variability in fire frequency [69].

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have evolved flammability. Are there benefits for flammable plants that outweigh the costs to survival of burning more fiercely? Theory predicts that flammability could, indeed, evolve if fire spread from a flammable plant to kill its neighbors, and if the progeny of more flammable mutants were more likely to recruit into the gaps created [36,37]. In these models, flammability acts as a 'niche constructing' trait [38,39], modifying the local environment to the benefit of the flammable genotype. This hypothesis makes the testable prediction that flammable morphology and fire-stimulated recruitment should be correlated traits, and there is some support for this prediction in pines [40]. In *Pinus*, serotiny (the retention of seed in cones which open after a fire), a fire-recruitment trait, is correlated with dead branch retention, a flammability trait. Plants that retain dead branches are more likely to carry a fire into the canopy than are plants that self prune. Schwilk and Ackerly [41] tested whether these traits showed correlated evolution in pine phylogeny. Using a set of 'supertree' phylogenies, the authors found strong support for the predicted association between serotiny and dead branch retention, and also between these and other 'fire-embracing' morphological traits, such as thin bark, early maturation age and more flammable foliage, which would be expected in these stand-replacing fire regimes [40]. It would be intriguing to explore the evolution of flammability in other taxa and other ecosystems. Has 'niche construction', via the evolution of flammability of common species, played a part in the spread of the flammable formations in which they are contained?

Studies of trait evolution, and the origins of the woody flora of savannas, are hampered by our lack of understanding of the key traits needed to survive in grass-fuelled fire regimes. Traits that are common in crown-fire regimes are rare or absent in savannas [40]. In productive grassy ecosystems, fires are too frequent to provide safe sites for seedlings and fire-stimulated seedling recruitment, including serotiny, seems to be an exception. Fires are too frequent for the evolution of woody non-sprouters and sprouting is the norm [31,42,43].

Trees that survive anthropogenic fires in tropical forests tend to be those that have thicker, insulating bark [12]. Although trees in savannas are often thick barked, regeneration of new plants is perhaps the main obstacle for maintaining populations. Seedlings and saplings face frequent and severe fire damage in mesic savannas. Between fires, seeds have to germinate and seedlings have to acquire bud and root reserves to resprout to survive the next fire. Given that fires occur several times in a decade, seedlings would need to acquire the ability to resprout rapidly. A recent study in Brazil confirms this conjecture [44]. The only consistent differences between seedlings of sister species from forest and savanna habitats was the greater allocation to coarse roots, associated with sprouting, in the savanna species and more plastic light responses [44].

Frequent fires also select for a peculiar sapling growth form, with pole-like stems and swollen underground roots (Figure 4, [45,46]). The pole-like stem facilitates rapid bolting towards a height that is out of reach of surface fires and the roots provide the resources to resprout if the stem fails to reach a fire-proof size before the next burn.

Saplings can be trapped in the flame zone for decades. In longleaf pine, *Pinus palustris*, from the southeastern USA, saplings bolt only once and fire-induced sapling mortality is high [47] presumably because they lack comparably large root reserves. In the polymorphic African tree, *Acacia karroo*, pole-forming saplings occur in frequently burnt savannas whereas plants form cage-like architectures where fires do not occur [46] (Figure 4). The contrasting sapling architectures suggest alternative evolutionary trajectories when plants are exposed to selection by different types of consumer (i.e. fire versus browsers).

Fire and the origin of biomes

The large area occupied by flammable biomes, especially in the tropics and sub-tropics, has often been attributed to anthropogenic burning. Although anthropogenic fires have extended areas of flammable vegetation [48,49], there is now evidence that natural fires occurred long before humans and that flammable ecosystems pre-date anthropogenic burning by millions of years [4,50]. Stable isotope evidence shows that C4 grassy ecosystems, the most extensive flammable formation worldwide, first appeared between 6 million years ago (Ma) and 8 Ma [51]. Cerling *et al.* [51] hypothesized that this was due to decreasing atmospheric CO_2, but recent studies of paleoatmospheres do not support their assumption of low concentrations of CO_2 during the late Miocene [52,53]. The spread of grasses has often been attributed to coevolution with mammal grazers. However it is hard to see how, by consuming grass, grazers would promote the spread of grasslands at the expense of forests. By contrast, grass-fuelled fires are known to promote the spread of grassy ecosystems by carving holes in forests [29]. Strong
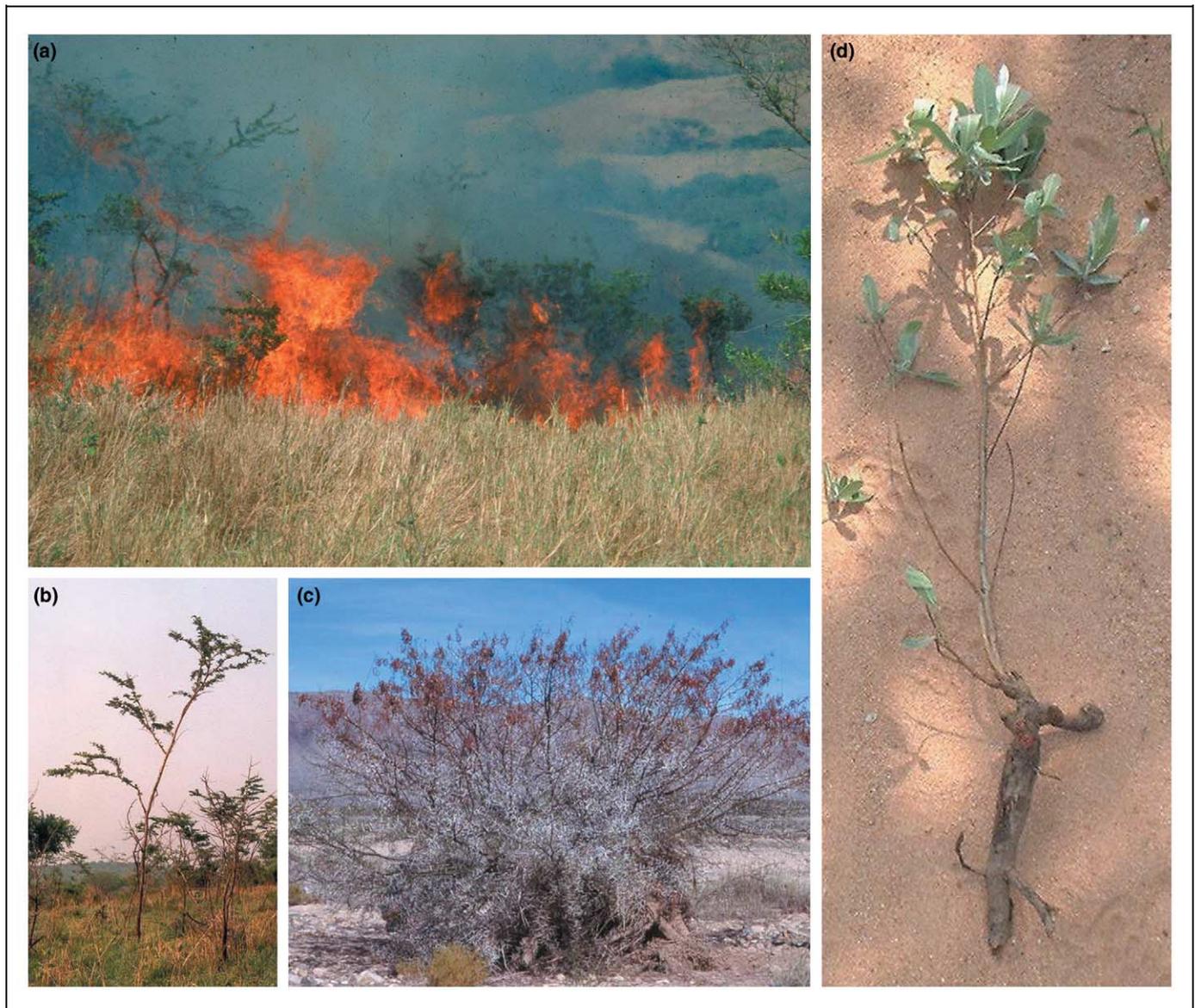
Figure 4. Fire, herbivory and tree architecture in savannas. **(a)** Grass-fuelled fires are very frequent in mesic savannas, posing a problem for the recruitment of tree seedlings and saplings. However, flame heights are too low to cause significant damage to emergent trees. **(b)** Many trees in frequently burnt savannas have pole-like sapling architecture, such as this *Acacia karroo* from a South African savanna. **(c)** The cage-like architecture of *A. karroo* occurs where fires are rare but browsers are common. **(d)** Shows a young sapling of *Terminalia sericea*, a common African savanna tree species The combination of pole-like stems and reserves stored in swollen roots facilitate sapling growth above the flame zone while also ensuring the ability of the plant to resprout after repeated fires.

candidates for feeding the fires are the highly productive and highly flammable C4 grasses of the humid tropics, which began replacing forests from the late Tertiary onwards [54–56].

Recent studies in Australia link fire to the origin and spread of the biomes of that continent. Bowman [11] set out to explain the distribution of the small fragments of 'rainforest' distributed as an archipelago in the vast seas of eucalypt formations. The rainforests are closed formations of fire-intolerant trees with shade-tolerant understorey species. By contrast, the eucalypt formations support shade-intolerant understoreys of flammable grasses or shrubs. Similar anomalous forest patches in a matrix of flammable grasslands are widespread in Africa and South America [4,57]. Generations of ecologists have debated the determinants of these alternative biome types, citing aridity, fire, nutrient-poor soils and anthropogenic burning. Bowman critically evaluated the evidence for all of these for Australia. Both biomes occur across a wide rainfall gradient with 'rainforest' (a misnomer) petering out where rainfall drops below 600 mm y^{-1}. Contrary to popular perceptions, the flammable formations are not 'arid'. Indeed, eucalypts are less tolerant of drought than are many rainforest trees sharing the same climate [11]. Bowman concluded that the only consistent difference between trees of the two formations was in their fire response: eucalypts have a remarkable ability to survive and thrive under frequent fires, whereas rainforest trees are killed by repeated burning [11,58]. The implication is that if you could 'switch off' fires for a long enough period, large areas of Australia would support an entirely different 'rainforest' flora. This process is underway in wet eucalypt formations, where fires have been reduced and rainforests are invading [59]. However, continent-wide replacement is unlikely because the rate of rainforest colonization is slow in drier climates and on nutrient-poor soils compared with the frequency of fires [59].

Recent molecular systematic studies have found that the phylogenetic structure of legumes was caused as much by ecological setting as by tectonic history and the location of land masses [60]. The implication is that speciation and subsequent dispersal of some taxa are confined ecologically, within biomes, as much as by dispersal problems across oceans. The appearance of grass-fuelled fires might be an example of an intra-continental 'vicariance' event, segregating taxa into those that could tolerate fires and those that could not. New molecular tools, coupled with focused ecological studies, promise new insights into the evolutionary history of those parts of the world where fire uncouples biomes from their climate-limited potential.

Conclusions

We have shown major similarities between fire and herbivory and argued for a more-inclusive view of top-down, or, in this instance, consumer control of biomes. We believe that the global extent of fire as a consumer, its many parallels with herbivory, its role in selecting for particular plant traits and in the evolution of biomes, is worthy of much wider attention from ecologists.

There is an added incentive for greater understanding of fire as a globally important consumer. Climate change, habitat fragmentation, the unprecedented transport of highly flammable plants to novel settings, and the ubiquitous overlay of human impacts on fire regimes demand a new level of synthetic understanding for our peaceful coexistence with this charismatic beast.

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