service providers, policies that target the protection of whole biotic communities in agricultural ecosystems, rather than just one or a few species, are expected to be more efficient in meeting growing demands for produce while maintaining multi-functional agricultural landscapes. Such measures do not necessarily compete with farmers' profit [9]. They can even be established in areas with lower yield potential but, sometimes, higher conservation value such as river margins or areas with steep slopes. Indeed, in many cases agricultural productivity and/or profit increase as a result of enhanced ecosystem services [3,4,17]. In Table S1, we provide 24 examples of our ten policy targets across at least 14 countries and the EU (27 member states). These examples illustrate the diversity of possible implementation routes. The options available to a particular group of policymakers depend on the political, historic, and environmental context and also on how the target is interpreted, in terms of its precise objective, scale, and magnitude. Given the variety of possible implementation routes and outcomes, it is important that policies implemented in support of ecological intensification include clearly stated objectives, with measurable targets, against which each policy can regularly be evaluated. In our view, the most supportive policies for ecological intensification will consider agriculture as a system that addresses national food security and provides wellbeing to rural populations, through investment in ecological infrastructure and knowledge management.

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Supplemental Information

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Forum

Alternate Grassy Ecosystem States Are Determined by Palatability–Flammability Trade-Offs

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Fire and mammalian grazers both consume grasses, and feedbacks between grass species, their functional traits, and consumers have profound effects on grassy ecosystem structure worldwide, such that savanna and grassland states determined by fire or grazing can be considered alternate states. These parallel savanna–forest alternate states, which likewise have myriad cascading ecosystem impacts.

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Box 1. Alternate Stable States in Grassland Communities

Grass biomass increases with productivity (Figure I; black diagonal), but departures occur when positive feedbacks with fire or grazing entrain communities into tall stature fire-grass (orange line) [4] or low stature grazing-lawn (green line) [6] states. These positive feedbacks arise because the grass traits that 'attract' fire or grazers are associated with traits that also promote competitive ability under these different consumer regimes. This confers stability to each state, with their resilience enhanced by the opposing nature of the traits that attract fire versus grazers: fire-grasses are relatively unpalatable and grazing-lawns are nonflammable. However, critical bifurcations occur when productivity changes: at F_1 grass fuel continuity becomes too patchy to carry fires and at F_2 grazer populations decline due to the low quality of dry season reserves outside of lawns. External factors can also precipitate transitions by reducing the amount of fire (e.g., fire suppression) or grazers (e.g., poaching or disease). Hysteresis occurs due to the different mechanisms that drive state transitions: fire-grasses shade out grazing-lawn grasses, while trampling or concentrated postfire grazing can allow grazing-lawn species to invade the fire-grass state. Transitions from grazing-lawn to fire-grass states (orange broken lines) occur fastest at high productivity, while the slower, more stochastic fire-grass to grazing-lawn transitions (green broken lines) are perhaps most likely at intermediate productivity, where grazers are abundant but the rate of reversion to the fire-grass state is moderate.

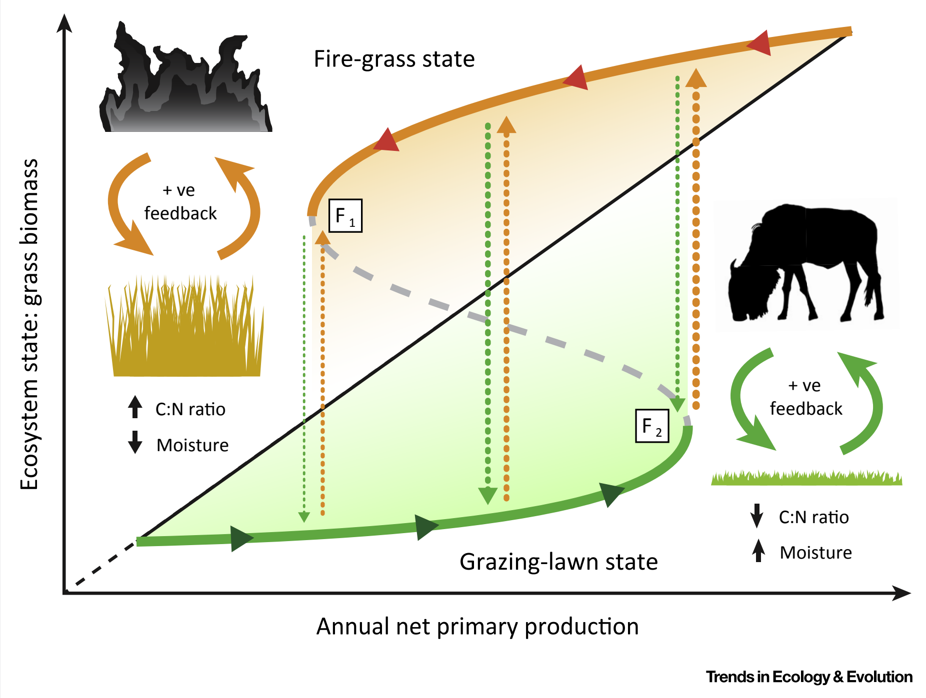

Figure I. Alternate Grassland States. Conceptual diagram of alternate fire-grass (orange unbroken line) and grazing-lawn (green unbroken line) stable states along a productivity gradient. Each state is stabilized by positive feedbacks (filled orange and green arrows) with fire and grazers, respectively, a dynamic underpinned by opposing C:N ratios and leaf moisture traits amongst others. Transitions between states (broken lines) occur when shifts in rainfall exceed critical bifurcation points at F_1 or F_2, or when external factors precipitate changes. Shading represents grasses with higher palatability (green) or flammability (orange), respectively. The black diagonal line represents the general linear increase in grass biomass with annual net primary production.

Positive feedbacks can maintain ecosystems in alternate states, where their structure and function conform to a stable, yet dynamic, ecological regime [1]. Savanna–forest mosaics provide a well-known example of alternate stable states [2], and, because the mechanisms that cause shifts from savanna to forest and vice versa are different, the likelihood, rate, and ecological pathway of transitions are different in each direction. This is evidence for hysteresis (an important property of alternate stable states) and means that initial conditions and lag effects shape how regime shifts occur [1].

Grassy ecosystems also have alternate stable states (Box 1). Within grasses (Poaceae), a family of over 11 000 species, there are numerous life history strategies [3]; yet two strategies stand out for their remarkable ability to drive the 'consumer regime' in parts of a grassland or savanna landscape towards a fire- or grazer-dominated state. On the one hand, there are grasses with trait combinations that make them highly flammable but which also increase their dominance under frequent burning [4]; these 'fire-grasses' are important to maintain the savanna–forest boundary [5]. On the other hand, 'grazing-lawn' grasses are highly palatable and thus sought after by grazers, but the proliferation of these grasses is promoted by regular grazing [6]. These positive feedbacks make it possible for shifts in grass community composition to profoundly affect the ecosystem at large: whether a system is fire- or grazer-driven has implications for soil carbon, nutrient cycling, plant community composition, biodiversity, and habitat structure, among other cascading effects [4,7,8].

Traits and Positive Feedbacks

Light competition underpins the dynamic in grazing-lawn or fire-grass community states. Grazing-lawn grasses are short-statured, often laterally spreading, and vulnerable to being shaded out by the invasion of tall grasses [6–8]. Regular grazing is essential to maintain high light-levels. Grazing-lawns are attractive to grazers because bites consist mostly of densely packed leaf material (i.e., with low C:N ratios and high moisture), which allows for efficient intake of nutritious forage while avoiding low quality stem material; and therein lies the trick: by protecting stem material, roots, and buds, grazing-lawns continue growing largely unchecked by grazing, and are fierce competitors for space and resources when light is not limiting [6,8].

Fire-grasses outcompete other grasses by appropriating the light environment [4]. Their tall, upright stature requires high C:N ratios providing structural support, and this, along with high tannin levels, slows decomposition rates and results in the accumulation of dead biomass [3,9]. Dead biomass obstructs light at ground level while accumulation of a low moisture-dense fuel-bed supports frequent fire [10]. Fire-grasses are well equipped to survive frequent fires, with meristems insulated by layered leaf sheaths and a densely packed plant base. To complete this feedback loop, fire-grasses have rapid postfire regrowth facilitated by high photosynthetic rates, providing little opportunity for other grasses to establish [10]. While fire-grass and grazing-lawn feedbacks have long been established [4,6], their opposing nature and implications for alternate stable states have not been elaborated.

Contrasting Grazing-Lawn versus Fire-Grass and Savanna versus Forest Alternate Stable States

The dynamics of grazing-lawn versus fire-grass alternate states share many properties with savanna versus forest alternate states (Figure 1), despite fundamental differences in how each is formulated. Grazing-lawn versus fire-grass states are underpinned by trait differences within the same plant life form, with each state dependent on positive feedbacks with a consumer (i.e., grazing versus fire). By contrast, savanna versus forest states represent a shift from a tree-grass mixture maintained by fire, to a tree-dominated, resource-limited system (i.e., light competition) [5]. Unsurprisingly, savanna and forest trees require markedly different traits to meet the competitive demands of each system [5].

Fire-grasses and forest trees are both the taller vegetation state, strong competitors for light, and with likely lower belowground investment [10]. Accordingly, these vegetation states tend to dominate under more productive conditions, but are able to expand into grazing-lawns or savanna should grazers or fire be absent for long enough [2,7]. However, resource limitation is likely to constrain how far down the productivity gradient these life history strategies remain dominant. As productivity decreases, grass biomass production decreases, such that fire frequency declines because fuel loads are insufficient for frequent fire, disrupting the fire–grass feedback.

By contrast, grazing-lawn and savanna vegetation states dominate under less productive conditions and depend on grazers and fire, respectively, to maintain an open light environment [2,6]. Opportunities to expand into fire-grass communities or forests occur during brief windows when these taller vegetation types become palatable or flammable: fire-grasses are palatable when regrowing after being burned, and forests become flammable during droughts or unusually hot, dry, windy weather conditions. As productivity increases, grazing-lawns require more frequent grazing, and savannas require more frequent fires, in order to persist. However, associated shifts in forage and fuel properties ultimately constrain how far up the productivity gradient each can occur: grazer populations become limited by declining grass quality outside of grazing-lawns [see below; see Figure I in Box 1 (F_2)] [8], and fire is excluded in wet regions because fuels remain green and are never dry enough to burn [11].

Implications of Spatial and Temporal Constraints on Fire versus Grazers

Fire and grazers are subject to different spatial and temporal constraints, which has implications for the extent and configuration of ecosystem states in a landscape. For example, while grazers can simply walk through unsuitable habitats, fires can be halted by fuel continuity barriers such as roads, and indeed, short-grazed grasses. However, unlike fires, grazers need to survive year-round. Consequently, when grasses stop growing in the dry season, grazers in seasonal environments rely on taller grass reserves outside of grazing-lawns to meet their intake requirements [8]. Grazer populations thus can be limited by grass quality and quantity outside of grazing-lawns (see above).

These differences have consequences for the proportion of landscape that can be maintained in a fire- or grazer-determined state. When conditions are conducive to fire, and if barriers to spread are few, fire can convert entire landscapes into a fire-grass state [4]. However, the maximum proportion of grazing-lawn is contingent upon adequate dry season resources to support grazers [8]. These grazing-lawns can be configured as small, isolated

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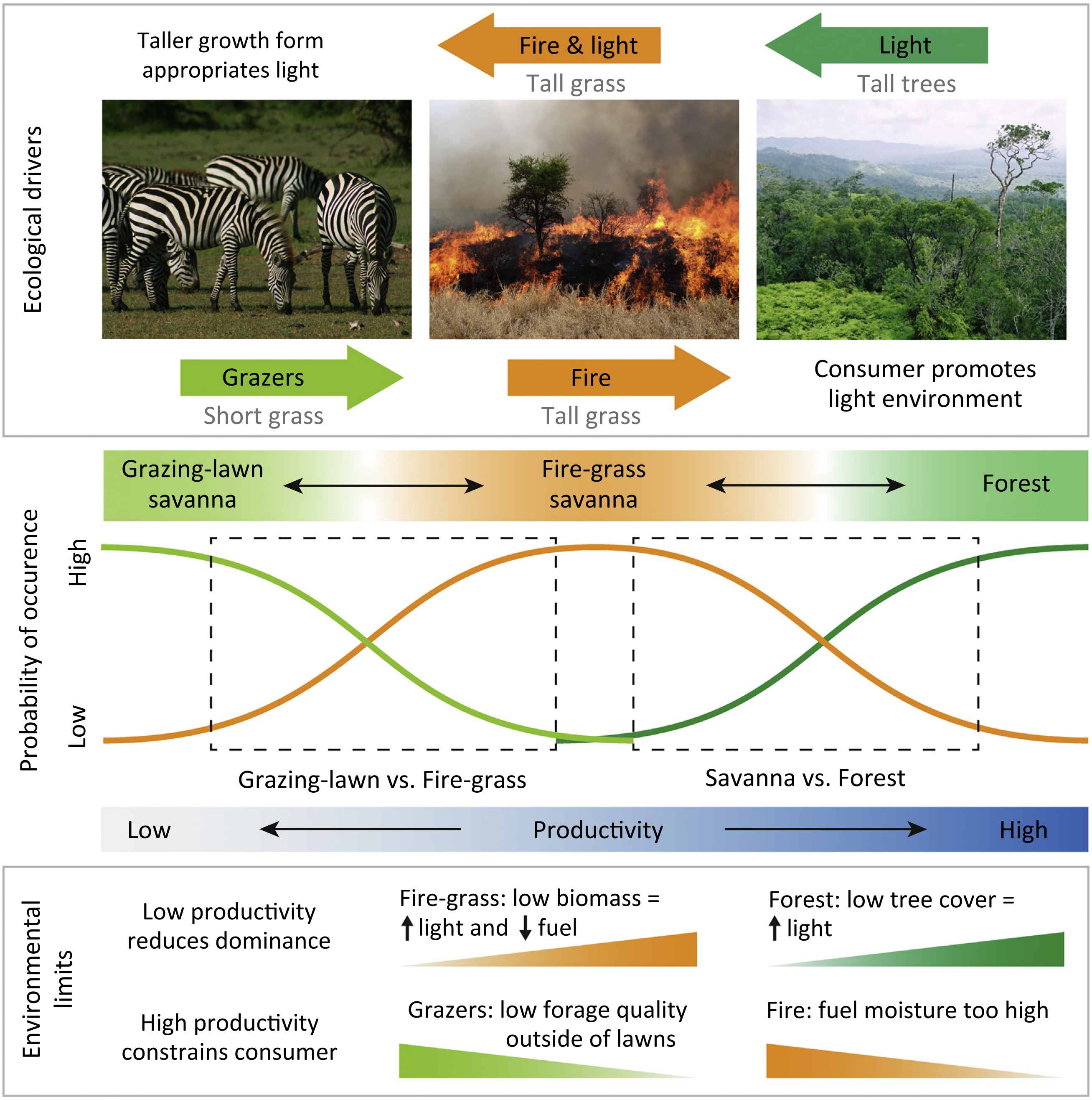

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Figure 1. Grazing-Lawn versus Fire-Grass and Savanna versus Forest Alternate Stable States. The probability of occurrence of grazing-lawn savanna, fire-grass savannah, and forest changes across a productivity gradient (middle panel). This is due to environmental limits on grazers, fire, and biomass production (lower panel), that in turn shape the role that each can play as ecological drivers (top panel), primarily through modifying the light environment. At high productivity, forest can shade out fire-grass savanna, which in turn can shade out grazing-lawn savanna at midlevel productivity. However, positive feedbacks between grazers and grazing-lawn grasses, and fire and fire-grasses, can promote their expansion up the productivity gradient, until these consumers themselves become constrained by environmental limits. These dynamics give rise to alternate grazing-lawn versus fire-grass alternate stable states in savannas, which share parallels with previously described savanna–forest alternate stable states.

patches near water or on nutrient hotspots like termite mounds, or coalesced into large areas that offer additional benefits such as improved predator detectability [8]. The extreme scenario occurs where grazers undertake long-distance migrations between dry- and wet-season ranges, allowing for the formation of vast grazing-lawns (e.g., the short-grass plains of the Serengeti, which support over a million wildebeest in the wet season and almost none in the main dry season [12]). Seasonality should thus be an important predictor of lawn extent in an ecosystem, with a greater proportion of lawn possible in less seasonal systems, or where animals can migrate to track grass phenology.

In the savanna–forest literature, spatial barriers to fire spread have been discussed at two scales: at local scale the forest boundary prevents fire spread if tree density is high enough to reduce surface fuel flammability, while at landscape scale, fire is excluded when forest (nonflammable) patches are extensive enough to prevent fire percolation through the landscape [2,5]. Similarly, at local scale grazing-lawns have traits that make them nonflammable, while at landscape scale grazers can effectively switch-off fire once grazing-lawn extent exceeds the threshold to fire spread [12]. Enhancing our mechanistic understanding of the distribution of ecosystem states along the continuum from grazing-lawn savanna to fire-grass savanna to forest states will require elaboration of the feedbacks to fire and grazer population size at both scales. What appears to be clear, however, is that grasses and their traits are fundamental to orchestrating dynamics in these consumer-controlled ecosystems.

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