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Clarifying the confusion: old-growth savannahs and tropical ecosystem degradation

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Ancient tropical grassy biomes are often misrecognized as severely degraded forests. I trace this confusion to several factors, with roots in the nineteenth century, including misinterpretations of the nature of fire in savannahs, attempts to reconcile savannah ecology with Clementsian succession, use of physiognomic (structural) definitions of *savannah* and development of tropical degradation frameworks focused solely on forests. Towards clarity, I present two models that conceptualize the drivers of ecosystem degradation as operating in both savannahs and forests. These models highlight how human-induced environmental changes create ecosystems with superficially similar physiognomies but radically different conservation values. Given the limitation of physiognomy to differentiate savannahs from severely degraded forests, I present an alternative approach based on floristic composition. Data from eastern lowland Bolivia show that old-growth savannahs can be reliably distinguished by eight grass species and that species identity influences ecosystem flammability. I recommend that scientists incorporate savannahs in tropical degradation frameworks alongside forests, and that *savannah* be qualified as *old-growth savannah* in reference to ancient grassy biomes or *derived savannah* in reference to deforestation. These conceptual advances will require attention not only to tree cover, but also to savannah herbaceous plant species and their ecologies.

This article is part of the themed issue 'Tropical grassy biomes: linking ecology, human use and conservation'.

1. Introduction

A great deal of confusion exists over the ecology and conservation values of tropical savannahs. In recent literature, this confusion is attributed to several interrelated causes, including misperceptions of savannahs as successional vegetation [1], the outdated, but still influential, idea of *potential vegetation* [2], use of physiognomic rather than functional or floristic definitions of *savannah* and *forest* [3], failure to distinguish natural savannahs of native species from grasslands resulting from deforestation [4] and undervaluation of savannah biodiversity and ecosystem services [5]. This confusion hinders savannah conservation efforts [1], obscures biodiversity losses due to agricultural conversion, afforestation and forest expansion [6,7], impedes scientific advances [8,9], and threatens people who depend upon savannahs for their livelihoods [10,11].

With so much at stake, we must be clear: tropical savannahs are ancient, biodiverse, and provide critical ecosystems services, including livestock forage and provisioning of water [5]. And yet, the notion persists that savannahs are degraded ecosystems created by human-caused fires and deforestation. For this reason, unless otherwise qualified, I will only use the term savannah to refer to *old-growth savannahs* [9]: ancient ecosystems with a continuous herbaceous-stratum of 'grassy' plants (i.e. graminoids and forbs; [1]), including treeless tropical grasslands as well as grassy ecosystems with fire-tolerant trees (thus encompassing many systems commonly referred to as *woodlands* or *open forests*) [3]. I will also focus primarily on *mesic savannahs*, which occur across vast regions of the tropics where savannahs and forests are alternative biome states determined by interactions among climate, vegetation, fire, herbivores and edaphic factors [12–16].

Misinterpretations of savannahs as young, successional vegetation degraded by fire are not scientifically supported. Instead, palaeoecological evidence suggests that savannahs originated millions of years ago [17,18], long before humans began clearing forests. Indeed, in several places, savannahs once thought to be anthropogenic have proven to be ancient [19–21]. Millions of years of frequent fires and herbivory [22] selected for savannah floras composed of graminoids with basal meristems, forbs that invest in underground storage organs [23,24], and trees with thick, fire-resistant bark [25]. When savannahs composed of these fire- and herbivore-adapted species are destroyed, what is lost goes unnoticed: extensive roots and underground stems [26,27]. The loss of these *underground forests* [28] warrants the level of concern given to deforestation, but plants that hide much of their biomass from fire and herbivores are hidden from human eyes as well, leading to undervaluation by scientists and policymakers.

In this paper, I seek to answer the question of why, despite evidence of their antiquity and conservation values, savannahs are commonly mistaken for severely degraded forests. I begin by looking back to the ways savannahs were described in the ecological literature and how ecosystem degradation has been conceptualized in the tropics. Two key themes emerge: (i) savannahs are absent from influential conceptual models of tropical ecosystem degradation. When savannahs were forced into models developed for forests—into which neither savannahs nor fire fit—ecologists often misdiagnosed them as degraded forests. (ii) Such misinterpretations have been reinforced by the tendency to adopt physiognomic definitions of savannah and forest, i.e. definitions based on vegetation structure, rather than floristic composition, ecosystem functioning, and/or ecosystem age. This is not to say that certain structural attributes of vegetation are never useful, but that the most commonly used physiognomic definitions of forests (based on tree cover [29]) and of savannahs (based on a combination of tree and herbaceous cover [8]) are inadequate for distinguishing old-growth savannahs from *derived savannahs*—the low-diversity grass-dominated vegetation that results from human-caused deforestation [3,4]. With these causes of confusion identified, I present two conceptual models of ecosystem degradation that integrate both savannahs and forests. These models include savannah and forest ecosystem states that have similar physiognomies but very different conservation values. In support of these models, I present data on the relationship between tree cover and herbaceous cover, as well as grass species composition and biomass, from old-growth and derived savannahs in eastern lowland Bolivia. The results demonstrate the failure of physiognomy and the utility of basic floristic information to clearly distinguish old-growth savannahs from severely degraded forests.

2. Origins of confusion

Ecological accounts of tropical savannahs from the late nineteenth century (e.g. by Thode, Pechuel-Lösche, Warming and Schimper [30]) emphasized plant species and their characteristics, and generally lacked language about human-caused degradation. In these accounts, savannahs were observed in their place, a place they were thought to occupy because of climatic factors (e.g. seasonal drought) or edaphic conditions that limited water availability [30]. It was clear that savannahs were flammable and that fire was a common occurrence, but these accounts did not emphasize fire as important to the existence of savannahs or as a factor associated with degradation. Indeed, Warming [31] rejected the idea that savannahs were created through the destruction of forests by fire [32]. Nonetheless, the idea that humans could create savannahs, or influence the dominance of grasses over trees, did exist [10]. Writing in 1898, Schimper [30, p. 162] asserted that ‘In districts which . . . possess neither a decided woodland climate nor decided grassland climate, the action of mankind suffices to start the struggle’. As evidence that humans could promote grasses over forests, Schimper [30] referenced the expansion of cogon grass (*Imperata cylindrica*) on former forest lands in eastern Java, though it is not clear if he considered this example of grass-dominated deforested land to be *savannah*. But overall, these early ecological accounts describe savannahs that were floristically rich and that occurred where climate and soils, not humans, dictated.

In the early to middle twentieth century, the ideas of Clements [33,34] forced ecologists to explain the existence of savannahs in climates where forests could develop [35]. Whereas before the concept of the *climatic climax* savannahs could be observed and described, their existence now required explanation. This legacy of Clements persists today, with a great deal of savannah ecology framed around the question of why savannahs are not forests—the *savannah problem* [35]. In hindsight, this is not a problem at all, but rather a dissonance between reality (i.e. the existence of savannahs) and overly simplistic climate-based models of vegetation distributions that did not incorporate fire [14]. Indeed, even before Clements, the incongruence between climate and vegetation was evident, exemplified in Schimper’s unconvincing attempt to explain the distributions of savannahs and forests in the same landscapes in relation to ‘slight changes of climate’ [30]. So, although this savannah–climate dissonance existed previously, it was the popularity of Clements’ ideas that brought the savannah problem into focus.

Beard’s 1953 monograph [32] on neotropical savannahs lends insight into how successional theory and savannah ecology intermixed. For Beard, the existence of savannahs could not possibly be determined by climate alone, as he described the wide range of climates and soils that supported savannahs. In trying to reconcile savannahs and the successional paradigm, he wrote [32, p. 213]: ‘All types of savannah may be swept by regular fires and the vegetation is so adapted as to be fire resistant. The herbaceous vegetation does not, however, depend upon fire for its maintenance and the savannah is an edaphic climax, i.e. it is determined by soil and site conditions’. As with earlier ecologists, Beard described savannahs that were floristically rich and presumably ancient, but went further to distinguish *natural savannahs* from *fire grasslands* that formed due to the cutting and burning of forests by people. Despite the importance of this distinction, Beard’s dichotomy—i.e. natural savannahs as edaphic climax and fire grasslands as anthropogenic—did not recognize the existence of natural fire-dependent savannahs. This misreading of the ecology of fire allowed others, e.g. Budowski [36], to argue that because fire exclusion permits forests to replace savannahs, and because humans set fires, tropical savannahs must therefore be products of deforestation.

Despite the challenge posed by the existence of savannahs, climate models have strongly influenced tropical ecology; a prime example is the Holdridge Life Zone System [37,38]. In its simplest form, the system is a model for classifying climate zones on the basis of precipitation and temperature. When first published in 1947 [37], Holdridge labelled low elevation, low latitude zones with 500–1000 mm of precipitation *savannah or dry forest*, apparently in recognition that tropical savannahs and forests can both occur in the same climatic zone. In later versions [38], Holdridge completely removed savannahs from the model and labelled the life zones by the presumed climatic climax vegetation. Within life zones, he further described *associations*, which he attributed to atypical environmental factors related to, for example, soils, drainage and precipitation patterns, but apparently not fire. Continuing with this hierarchical approach, he described actual vegetation based on its successional stage within an association. Holdridge only mentioned fire as an agent of soil degradation and deforestation. Thus, it is difficult to read Holdridge [38] without concluding that he viewed savannahs as fire-degraded forests (i.e. a successional stage, rather than an edaphic association, in his life zone system).

Holdridge's perspectives on fire and soil degradation were parallel to the influential work of Nye & Greenland [39], published in 1960, on nutrient cycling and shifting cultivation in the tropics. Their monograph described the factors that impoverish tropical soils, including colonization of agricultural fallows by certain grasses and volatilization of nitrogen during grass-fuelled fires. Nye & Greenland must have recognized the difference between old-growth savannahs and grass-invaded agricultural fallows (e.g. they refer to *savannah regions* in West Africa as distinct from forest regions and even mention *old savannah* in contrast with *mature forest*), but for the most part they used *savannah* in the physiognomic sense, without any clear distinction among different types of grass-dominated vegetation. Consistent with the successional paradigm, they classified savannahs as a *secondary formation*. The notion of savannahs as young vegetation, successional to forest was reinforced by their observations that agricultural fallows in 'savannah' were quickly recolonized by grasses and developed into a grass-dominated *fire-climax* within 20 years; perhaps their conclusions about the rate of savannah recovery would have been different had they observed how long it took for the full savannah herbaceous plant community to re-establish [27,40], rather than just the dominant grasses. In presenting their case for how low intensity traditional cropping systems could be sustainable, Nye & Greenland also raised concern over deforestation. Of particular note, they discussed how poor management can convert forests to derived savannah, dominated by a few grass species and maintained by recurring fires. In sum, the work of Nye & Greenland illustrates how successional theory and physiognomic definitions contributed to the idea that savannahs were degraded forests, and that forests, not savannahs, were of primary conservation concern.

Concerns over tropical deforestation led to the development of degradation frameworks that either did not consider savannahs, or conceptualized them as degraded. Initially, these frameworks, influenced by succession and the Holdridge life zone system, focused on basic terminology and established old-growth tropical forests as the reference state (e.g. [41]). More recently, these degradation frameworks expanded to clarify the many drivers of forest degradation [42] and to suggest how such frameworks could be applied to ecosystem management [43]. Unfortunately, though, when savannahs are interpreted in the context of forest-focused degradation frameworks the diagnosis of 'degraded' is all too common [7]. The risk of confusion is particularly high in frameworks where 'savannah' is listed as a degradation state and fire is only conceptualized as a degrading force rather than a natural process (e.g. [43], but see discussion on savannahs in [42]). This confusion over savannahs, fire, grasses and forest degradation has been further reinforced by decades of literature on the *savannization* of forests, a term applied to the process of forest degradation via fire and grass invasion (i.e. the formation of derived savannahs, e.g. [44]), misapplied to some savannahs in Africa [10], and probably misapplied also to several neotropical savannahs (e.g. [45–47]). I suggest that continued use of the term savannization perpetuates confusion over the substantive differences between tropical savannahs and severely degraded tropical forests. That confusion, with roots in the nineteenth century, persists today [48].

3. Integrating savannah and forest degradation frameworks

There is a critical need to expand forest-focused conservation agendas to encompass grassy biomes [5,7,49]. In particular, forest ecologists should better recognize the ecological attributes and conservation values of savannahs, and savannah ecologists should consider adopting terminology that would foster communication with foresters. Better integration of savannahs into tropical degradation frameworks is a key step toward these goals. Such integration should not diminish the importance of forest conservation, but give similar prominence to the contribution of savannahs—maintained by fire and megaherbivores—to tropical biodiversity. Of particular importance, degradation frameworks should clearly distinguish old-growth savannahs from degraded forests and recognize the similarities and differences among drivers of savannah and forest degradation (figures 1 and 2).

Recognition of the drivers of tropical savannah degradation is important to improve their conservation. Most savannahs are dependent on frequent fires and/or megafaunal herbivory, forces that are part of the internal ecological dynamics of savannahs, rather than externally imposed disturbances [9,50]. Although in pre-human history, savannah fires were ignited by lightning strikes, in most of the world's savannahs, humans are now the primary sources of ignitions [2,51,52]. Similarly, most savannahs support populations of native and/or domestic herbivores, often under human management [11,53]. When fires are excluded (often because they are viewed as unnatural or destructive) and/or herbivores are improperly managed, woody plants may rapidly increase in abundance. With chronic fire exclusion, mesic savannahs are replaced by low-diversity forests (i.e. *forest-encroached savannahs*; [7,54–56]). There is also growing evidence that woody encroachment is accelerating globally [57,58] (but see [59]) as elevated atmospheric carbon dioxide concentrations shift the balance between C_4 grasses and woody species with C_3 photosynthesis [60].

A clear contrast exists between the role of fire in savannahs and its role in most tropical forests: savannah biodiversity depends on frequent fires, whereas forests are typically degraded by fire [3,9]. As such, an apparent conflict exists between savannah and forest conservation, with the potential

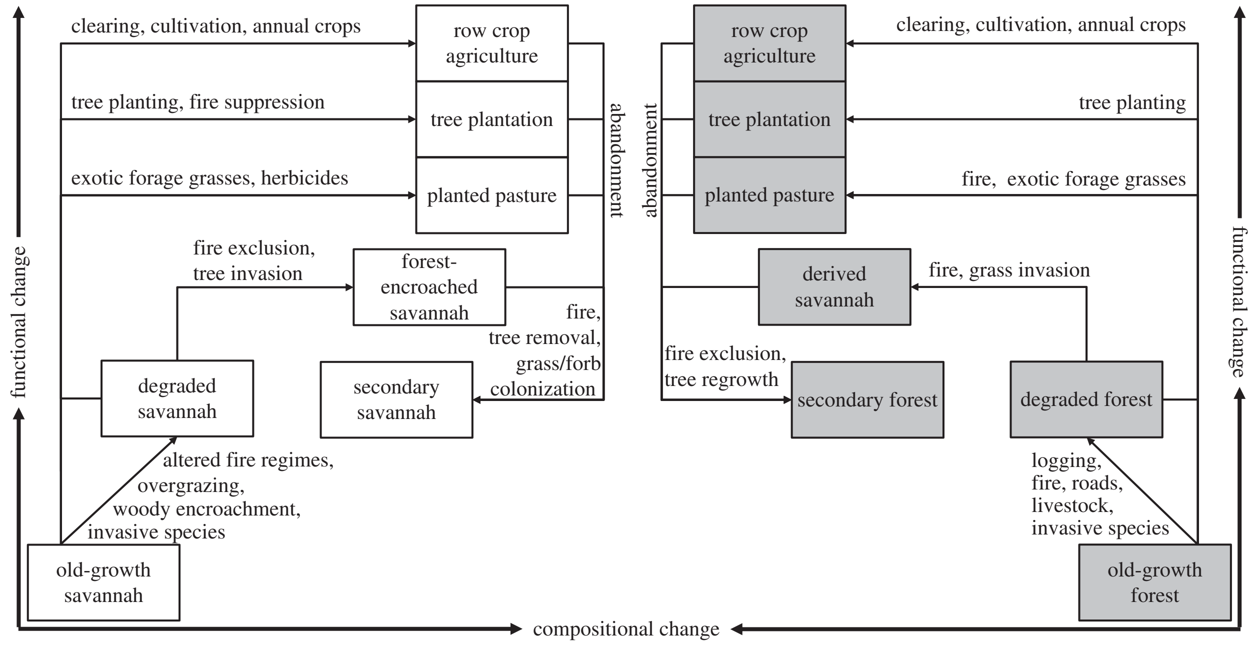

Figure 1. Common ecological states (boxes) and transitions (arrows) created by human-induced environmental change in the tropics. States and transitions are depicted in relation to two reference states: old-growth savannah (white) and old-growth forest (grey). For simplification, only transitions that can occur over short timescales (i.e. years to decades) are depicted. The axes of functional and compositional change depict divergence from the reference states and convergence toward biological simplification.

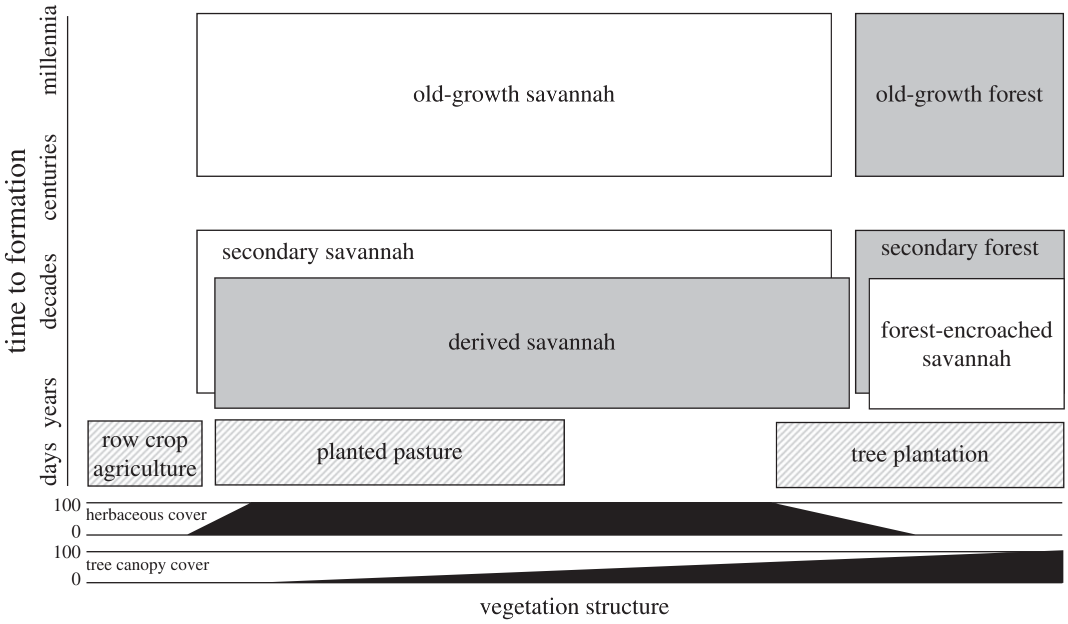

Figure 2. Physiognomy (i.e. vegetation structure) and antiquity (i.e. time to formation) of common ecological states in the tropics. States that originated as old-growth savannah or forest (figure 1) are white and grey, respectively; states with grey and white stripes can originate from either savannah or forest. Note that the axis of vegetation structure does not include all possible combinations of tree and herbaceous cover.

for fire management to degrade one ecosystem to maintain the other. But in reality, across vast areas of the tropics, savannahs and forests form relatively stable mosaics of fire-dependent and fire-sensitive ecological communities [12]. This is in part because savannah–forest boundaries are reinforced by differences in the flammability of savannah and forest fuels [61], functional differences between savannah and forest trees [3,55], and seasonality of fire (i.e. savannahs often burn during seasons when forest fuels are too moist) [51]. In sum, fire–vegetation dynamics at the boundaries between old-growth savannahs and old-growth forests [62] appear to be quite different than those observed at forest edges created by human-caused deforestation [44]. Better recognition of old-growth savannahs as distinct from derived savannahs is essential to identify landscapes where fire enhances tropical biodiversity (e.g. ancient savannah–forest mosaics) versus fragmented forest landscapes, where fire is a novel and destructive disturbance [63,64].

In addition to their distinct responses to altered fire regimes (i.e. changes in the frequency, seasonality and/or intensity of fires), savannahs and forests face the common threat of conversion for agriculture and tree plantations [65]. Such conversions result in a dramatic loss of biodiversity that is irreversible over short timescales [6,9]. While the ecological outcomes may be similar once savannahs and forests are converted (i.e. ecosystem states converge with agricultural and silvicultural intensification, figures 1 and 2), rates and spatial patterns of conversion can be very different. For example in Brazil, from 2004 to 2012, conservation policies with a forest bias [49] had very different consequences for forest and savannah biomes: Amazonian deforestation decreased dramatically during this period, while agricultural conversion of Cerrado remained steady, surpassing Amazonian deforestation rates by 2012 [66]. In Colombia, expansion of agriculture and tree plantations in savannahs of *Los Llanos* has displaced traditional cattle ranching and contributed to deforestation for planted pastures elsewhere [67]. In Africa, mesic savannahs but not forests are being targeted for large-scale agricultural conversion under the misperception that these savannahs support little biodiversity and store little carbon [6].

The development of policies to promote carbon sequestration may further complicate the interrelated nature of savannah and forest degradation [68] and exacerbate biodiversity losses [69]. In particular, carbon payment schemes focused on forests and trees, combined with inadequate definitions of *forest* (e.g. definitions used by the United Nations Food and Agriculture Organization [70]) [7,42] and associated challenges to the assessment of forests and deforestation [29,71], risk creating a future in which deforestation for agriculture is offset by afforestation and forest expansion in savannahs. Under current monitoring methods, the world could achieve no net deforestation, even as losses to biodiversity and ecosystem services are substantial [7,42]. In sum, because the causes and consequences of savannah and forest conversion to agriculture and tree plantations are interrelated, degradation frameworks that integrate both forests and savannahs are essential to improve tropical ecosystem science and conservation.

To promote the integration of forest and savannah conservation agendas, I present two conceptual models (figures 1 and 2) that together depict savannah and forest degradation in relation to vegetation structure and ecosystem age. These models include two reference states (old-growth savannahs and old-growth forests) and focus on major ecological transitions that are driven by human-induced environmental change over short timescales (i.e. years to decades, rather than millennial-scale dynamics, e.g. [72]). For the forest portions of these models, ecological states, associated terminology and causes of degradation are well established [42]. For savannahs, degradation terminology is less clearly established, in part because fire-dependent savannahs have only recently begun to be conceptualized as non-successional systems [1,9,50]. To facilitate communication among forest and savannah ecologists, the terminology I use for savannah ecosystem states (figure 1) reflects analogous forest degradation terms and the savannah conservation literature. Of particular note is the concept of *secondary savannahs* [27]—the grassy vegetation that forms following agricultural or silvicultural conversion of savannahs and subsequent abandonment—as distinct from both old-growth savannahs and derived savannahs. Studies of secondary savannahs suggest that, like regenerating forests, they are very slow to return to an old-growth state [27,40]. Because of the very long periods of time involved [9,73] and uncertainty about the conditions under which a return to the reference state is possible [27,74], I do not depict the full recovery of degraded ecosystems in figure 1 (e.g. from secondary to old-growth savannah). Note also that, for simplicity, I used discreet boxes to represent ecological states that may be better conceptualized as a continuum (figures 1 and 2), and not all possible states or transitions are depicted (e.g. a forest-encroached savannah could be cleared for agriculture, figure 1).

One of the most important reasons to place savannahs and forests in the same degradation framework is to clarify which ecosystems are not degraded. To help conceptualize the physiognomic overlap between ecological states that differ in conservation values, figure 2 depicts savannah and forest degradation in relation to vegetation structure and ecosystem age (i.e. time to formation). This model emphasizes the long periods of time required for savannahs and forests of high conservation value to develop. Of key importance, the model shows that on the basis of tree and herbaceous cover, recently formed derived savannahs are indistinguishable from old-growth savannahs.

4. Importance of species

Given that physiognomy is inadequate for distinguishing old-growth savannahs from derived savannahs—let alone describing their salient ecological characteristics—I suggest that we look to herbaceous plant community composition to delineate ecological states. Among the many different savannah definitions used in ecology [8,35], the presence of herbaceous plants (i.e. graminoids and forbs) is a common feature [1]. Furthermore, these herbaceous plants account for most old-growth savannah plant diversity [5,9] and are critical to fire regimes [61]. Savannah trees are also ecologically important [3], but a reliance on trees can be problematic at the grassland end of the savannah tree-density spectrum (figure 2). Typically, a full complement of information on floristics and land-use history is needed to move from the sorts of general degradation models that I propose (figure 1) to operational degradation frameworks (i.e. ecological reference models) that can guide restoration and management of specific ecosystems [75–77]. In tropical savannahs, species of the herbaceous plant community should play a critical role in the development of such operational definitions of degradation.

To demonstrate the importance of the species that comprise savannah herbaceous plant communities, I present data from eastern lowland Bolivia that show: (i) physiognomy cannot distinguish old-growth savannahs from derived savannahs, (ii) grass species (Poaceae) can serve as ecological indicators of old-growth savannahs, and (iii) grass species range widely in aboveground biomass in ways that influence ecosystem functioning (e.g. fuel loads). I collected these data (electronic supplementary material, data) in Chiquitania, Bolivia (16° S 62° W), a region that supports mosaics of savannahs (Cerrado) and forests (Chiquitano dry forest) [78]. Given that these Bolivian ecosystems have high floristic and ecological similarity to other neotropical savannahs and dry forests [78–80] and are subject to the drivers of environmental change and ecosystem degradation that operate throughout the tropics (figure 1) [81], results are probably generalizable to other mesic savannah regions, at least in the Americas.

The field sampling methods were previously described [4], but briefly: I used satellite imagery of a 22 500 km^2 area to detect physiognomic shifts in vegetation over two decades. Based on this analysis, I randomly selected a subset of old-growth savannahs and derived savannahs (i.e. areas where forest tree cover had declined substantially, but excluding large-scale agricultural deforestation). Thus, the old-growth savannahs and derived savannahs had similar physiognomies and spectral signatures, but differed in age and whether they

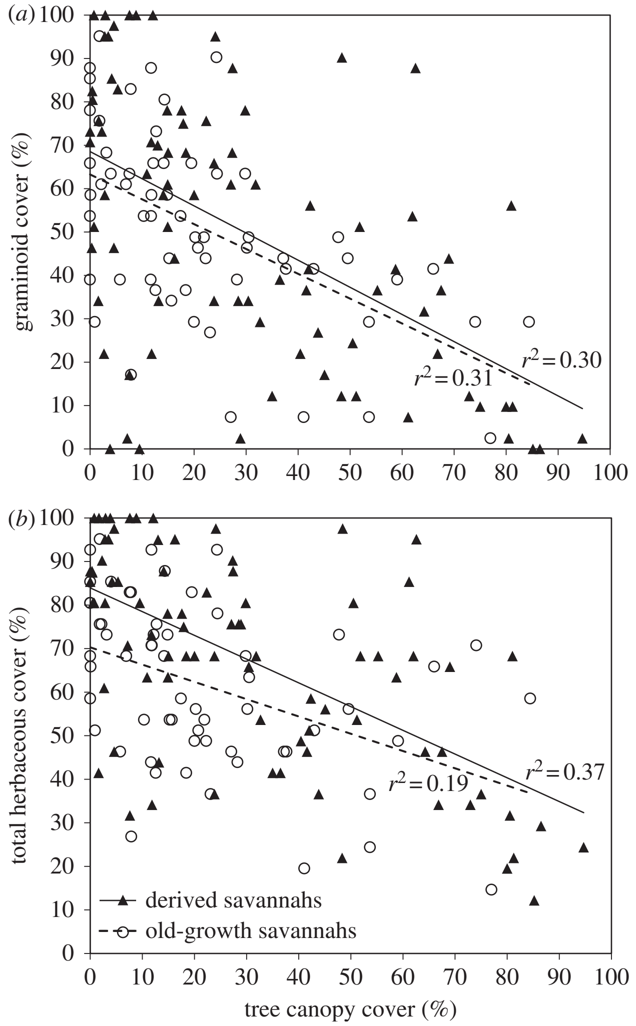

Figure 3. Relationship between tree cover and (*a*) graminoid cover and (*b*) total herbaceous cover along 145 20 m transects in 12 old-growth savannahs ($n = 60$) and 17 derived savannahs ($n = 85$) in eastern lowland Bolivia. All linear regressions significant at $p < 0.001$.

were historically savannah or forest. To sample grass and tree communities, I established five 20 m transects in each of 12 old-growth savannahs (60 transects) and 17 derived savannahs (85 transects). Mean distance between transects within sites was 270 m for derived and 640 m for old-growth savannahs. Although not statistically independent, I used the 20 m transects as the unit of replication for analyses where site-level means would obscure substantial local-scale variation. For comparison, NASA Landsat pixels are 30 × 30 m. Along each transect, I measured tree canopy density, cover of herbaceous plants, grass species presence and standing grass biomass by species in three 0.25 m^2 clip plots (1 m^2 clip plots were used for the fire-adapted bamboo *Guadua paniculata*).

These data demonstrate that old-growth savannahs and derived savannahs are not distinguishable based on tree cover, herbaceous cover or structural tree–grass relationships (figure 3). At the 20 m scale, old-growth and derived savannahs in Bolivia displayed wide and highly overlapping ranges of tree canopy cover, and correspondingly wide ranges of graminoid and total herbaceous cover (figure 3). The negative linear relationships between tree canopy cover and both graminoid and total herbaceous cover were also quite similar for the two ecosystem types (figure 3). (Note that some authors consider graminoid cover to be the salient feature of savannahs, e.g. figure 3*a* [35], and others emphasize all herbaceous cover over 10%, e.g. figure 3*b* [8].) Old-growth and derived savannahs not only had physiognomic similarities, but they also had very similar spectral signatures [4]; improved remote sensing methods are urgently needed that can reliably distinguish these two ecosystem states. In the meantime, this example from Bolivia demonstrates the serious shortcomings of physiognomy for assessments of tropical savannah and forest degradation (figures 2 and 3).

The good news is that many grass species can be used to distinguish old-growth savannahs from derived savannahs (table 1). Of 77 grass species that I encountered, 36 occurred exclusively in old-growth savannahs [4]. Many of these species were uncommon, so I looked for a set of indicator species that had high fidelity to old-growth savannahs (i.e. at least 95% of occurrences were in old-growth savannah transects) and occurred with high frequency (i.e. were present in at least 20% of old-growth savannah transects). Eight species met the criteria, including *Axonopus barbigerus*, *Elionurus muticus*, *Ichnanthus procurrens*, *Paspalum erianthum*, *Paspalum stellatum*, *Schizachyrium sanguineum*, *Thrasya petrosa*, and *Trachypogon spicatus* (table 1, nomenclature follows [79]). Excluding old-growth bamboo thickets of *Guadua paniculata*, at least one of these indicator species was present in 95% of the old-growth savannah transects. There were also 24 grass species with high fidelity to derived savannahs. Several of these species might be suitable indicators of derived savannahs (e.g. *Digitaria insularis*, *Leptochloa virgata* [4]), but more data would be required. Forage grasses of African origin [82] were common in derived savannahs, including *Megathyrsus* (*Panicum*) *maximus*, *Urochloa* (*Brachiaria*) *brizantha*, and *Urochloa* (*Brachiaria*) *decumbens* (see [83] for revised nomenclature). Despite their high fidelity to derived savannahs in my data (table 1), *Urochloa* spp. are increasingly sown into or invade (e.g. figure 4*b*, [84]) old-growth savannahs and are thus unreliable indicators of whether an area was historically savannah or forest.

Grass species should not be viewed simply as a tool for identifying ecological states in a degradation framework, but as entities that reflect the ecological history of a place and influence its contemporary ecology. Put simply, grass species are not ecologically equivalent, even though grasses are often treated as a monolithic functional group in ecological models. Of particular importance, grass species differ radically in their ability to invade forests and promote intense fires through high biomass production [4,44,85,86]. Among the grass species I measured in Bolivia, there were 1000-fold differences between the maximum standing biomass of the most and least productive species (table 1). In general, the most productive species occur with greater frequency in derived savannahs (table 1), where soils are more fertile [4]. Interactions among grass species, soil fertility and ecosystem age apparently result in large differences in grass species diversity and productivity [4]. Consequently, derived savannahs support twice the standing grass biomass of old-growth savannahs: 361 ± 77 and 165 ± 41 g m^{-2} (mean ± s.e., $n = 17$ and 12, respectively, $p = 0.03$). Given the importance of grass biomass to ecosystem flammability [61] and the importance of plant diversity to buffer ecosystems from environmental variability [87], I suggest that greater attention to species identity and community composition could help distinguish old-growth savannahs from derived savannahs while also leading to greater insight into the future of environmental change in tropical ecosystems.

Identifying herbaceous plant species that are diagnostic of old-growth savannahs will require effort on the part of local

Table 1. Frequency and maximum biomass of 31 grass species along 145 20 m transects in 17 derived ($n = 85$) and 12 old-growth savannahs ($n = 60$) in eastern lowland Bolivia. Standing aboveground biomass was measured in three 0.25 m^2 clip-plots per transect; only species clipped in at least four transects are shown. Old-growth fidelity equals the frequency in old-growth savannah transects divided by the sum of the frequencies in both old-growth and derived savannah transects.

	derived savannahs		old-growth savannahs		
grass species	**freq. (%)**	**max. biomass (g m^{-2})**	**freq. (%)**	**max. biomass (g m^{-2})**	**old-growth fidelity**
Elionurus muticus[a]	—	—	57	222	1.00
Trachypogon spicatus[a]	—	—	40	197	1.00
Schizachyrium sanguineum[a]	—	—	28	166	1.00
Paspalum erianthum[a]	—	—	27	27	1.00
Thrasya petrosa[a]	—	—	25	112	1.00
Ichnathus procurrens[a]	—	—	20	76	1.00
Digitaria dioica	—	—	13	16	1.00
Gymnopogon spicatus	—	—	12	34	1.00
Aristida riparia	—	—	10	4	1.00
Leptocoryphium lanatum	—	—	8	177	1.00
Panicum quadriglume	—	—	8	85	1.00
Axonopus canescens	—	—	8	48	1.00
Paspalum stellatum[a]	1	—	37	68	0.97
Axonopus barbigerus[a]	1	—	27	158	0.96
Schizachyrium microstachyum	1	—	20	65	0.94
Axonopus chrysoblepharis	1	—	15	26	0.93
Andropogon selloanus	1	—	13	6	0.92
Andropogon fastigiatus	1	—	10	5	0.89
Paspalum plicatulum	4	—	22	236	0.86
Hyparrhenia rufa[b]	8	132	18	67	0.69
Imperata brasiliensis	14	1382	13	41	0.49
Guadua paniculata	35	4324	17	1251	0.32
Setaria scandens	11	179	3	—	0.24
Urochloa (Brachiaria) brizantha[b]	34	822	2	—	0.05
Digitaria insularis	14	460	—	—	0.00
Urochloa (Brachiaria) decumbens[b]	6	379	—	—	0.00
Megathyrsus (Panicum) maximus[b]	8	288	—	—	0.00
Setaria vulpisetia	6	92	—	—	0.00
Leptochloa virgata	12	82	—	—	0.00
Panicum trichanthum	5	75	—	—	0.00
Panicum trichoides	11	14	—	—	0.00

[a] Old-growth indicator species.

[b] Non-native species.

and regional experts [9]. I suggest that these efforts begin by looking into published floras, which often include observations of species habitat preferences (e.g. [79]), and to ecological studies that describe species assemblages in old-growth savannahs (e.g. [88]). Where such information on savannah herbaceous plant communities is lacking, new research to compare old-growth savannahs to other ecosystem states (e.g. secondary and derived savannahs) should be prioritized. It is promising that in addition to the Bolivia example, studies in other floristically rich grassy biomes have also identified grass and forb species that are diagnostic of old growth [27,76]. Ideally, future research on savannah indicator species will be part of broader efforts to map the biodiversity and ecosystem services of old-growth savannahs [7]. Among research questions, it will be important to determine the relative influence of vegetation structure, plant species composition and ecosystem antiquity [9] on animal habitat preferences (e.g. [89]), ecohydrology, fire regimes, nutrient cycling and carbon storage.

5. Conclusion

Within ecology, confusion over the substantive differences between old-growth savannahs and severely degraded forests

Figure 4. Examples from eastern lowland Bolivia of the superficial similarities in vegetation structure between old-growth savannahs and severely degraded ecosystems: (*a*) old-growth savannah with high herbaceous species diversity and fire-tolerant trees, (*b*) planted pasture of exotic forage grasses and remnant savannah trees in formerly old-growth savannah, (*c*) derived savannah formed by repeated forest fires and exotic grass invasion and (*d*) planted pasture of exotic grasses on deforested land.

has existed for well over a century, in large part due to misperceptions over the ecological role of fire in the tropics and the persistent idea that climate is the primary determinant of tropical ecosystem distributions [14]. To help clarify this confusion, I propose that tropical degradation frameworks be expanded so that forests and savannahs are conceptualized side-by-side (figure 1), thus achieving models that reflect the heterogeneity of tropical biomes. This conceptual advance must be accompanied by a reassessment of how physiognomy is used to classify vegetation and infer degradation—simple vegetation structure (e.g. tree cover) cannot differentiate old-growth savannahs from severely degraded forests (i.e. derived savannahs, figures 2 and 3). Instead, plant community composition needs to be considered in combination with historical information to assess ecosystem degradation and antiquity. Nonetheless, physiognomic definitions are unlikely to be abandoned, and so *savannah* should be clearly qualified as *old-growth savannah* in reference to ancient tropical grassy biomes, *derived savannah* in reference to severely degraded forests, and *secondary savannah* in reference to the grassy vegetation formed after agricultural conversion of old-growth savannahs and subsequent land abandonment.

Conceptual models that include savannahs (and other non-forest ecosystems [49]) are essential if we are to broaden the scope of tropical conservation agendas. Yet critically, the real-world effectiveness of the changes I propose will depend not only on the availability of location-specific ecological knowledge [77] and the strength of socio-economic forces that alter fire regimes [90], but also on existing political and professional biases [91]. Currently, conservation agendas are largely being set by foresters for forests, without consideration of the importance of fire, herbivores and low tree cover to savannah biodiversity and ecosystem services [5,7,9,56]. Indeed, the Paris Agreement adopted by the Conference of Parties to the United Nations Framework Convention on Climate Change [92] includes language on forests and carbon, but no mention of savannahs or other grassy biomes. Similarly, policies and financing to promote large-scale restoration of tropical ecosystems are gaining momentum [93], but these initiatives continue to focus on forests without adequate consideration of savannahs. Confusion about savannah ecology and conservation values has deep roots in western European culture, which viewed fire as a force of ecosystem degradation [10]. Given what we now know about the important role of fire in creating and maintaining tropical biodiversity, it is time to re-evaluate our concepts of tropical ecosystem degradation and fully acknowledge the place of savannahs and fire in the tropics.

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