

Where Tree Planting and Forest Expansion are Bad for Biodiversity and Ecosystem Services

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Misperceptions about the world's grassy biomes contribute to their alarming rates of loss due to conversion for agriculture and tree plantations, as well as to forest encroachment. To illustrate the causes and consequences of these misperceptions, we show that the World Resources Institute and the International Union for Conservation of Nature misidentified 9 million square kilometers of ancient grassy biomes as providing "opportunities" for forest restoration. Establishment of forests in these grasslands, savannas, and open-canopy woodlands would devastate biodiversity and ecosystem services. Such undesired outcomes are avoidable if the distinct ecologies and conservation needs of forest and grassy biomes become better integrated into science and policy. To start with, scientists should create maps that accurately depict grassy biomes at global and landscape scales. It is also crucial that international environmental agreements (e.g., the United Nations Framework Convention on Climate Change) formally recognize grassy biomes and their environmental values.

Keywords: afforestation, carbon sequestration, climate change, old-growth grasslands, REDD+

The world's ancient and biodiverse grasslands, savannas, and open-canopy woodlands (hereafter *grassy biomes*) face immense pressure from human-induced environmental change but are widely perceived to be of low conservation priority relative to forests (Parr et al. 2014, Veldman et al. 2015a). The undervaluation of grassy biomes is reflected in national (e.g., Brazil; Gibbs et al. 2015) and international (e.g., Putz and Redford 2010) environmental policies that inadvertently exacerbate conversion for agriculture, degradation caused by inappropriate management (e.g., fire exclusion), and, increasingly, ill-placed tree planting (Veldman et al. 2015b). Among these threats, tree planting is the most easily avoided, but to understand the environmental costs of tree planting, *reforestation* (i.e., planting trees on deforested land) needs to be differentiated from *afforestation* (i.e., planting forests where they did not historically occur). Similarly, to understand the effects of fire exclusion, *forest regeneration* (i.e., secondary forest regrowth on deforested land) needs to be differentiated from *forest expansion* (i.e., development of forests where they did not historically occur).

Afforestation and forest expansion are of concern because the conversion of grassy biomes to tree plantations or forests comes at a high cost to biodiversity (Bremer and Farley 2010) and ecosystem services (figure 1; Jackson et al.

2005). Dense tree cover is fundamentally incompatible with grassy biome biodiversity, because it severely limits the richness and productivity of light-demanding herbaceous plants (Veldman et al. 2015a) while reducing habitat for animals adapted to open environments (e.g., Araujo and Almeida-Santos 2011). Compared with grasses and forbs, trees require far more water and soil nutrients and have markedly different patterns of above- and belowground carbon allocation (Jackson et al. 2007). Consequently, afforestation and forest expansion can dramatically alter nutrient cycles (Berthrong et al. 2009), reduce soil-carbon storage (Berthrong et al. 2012), and change hydrology (e.g., decrease groundwater recharge and stream flow; Jackson et al. 2005). Despite these high environmental costs, tree planting and carbon sequestration initiatives continue to target grassy biomes, particularly those with seasonally dry tropical and subtropical climates (Parr et al. 2014). In these areas, fire exclusion and/or tree planting can quickly increase aboveground carbon stocks, although the stocks may be quite vulnerable to drought, fire, and timber harvest (figure 1; Canadell and Raupach 2008). In contrast, where grassy biomes are protected, their largely belowground carbon stocks (e.g., Miranda et al. 2014), which store as much carbon as forests do globally (White et al. 2000), are secure.

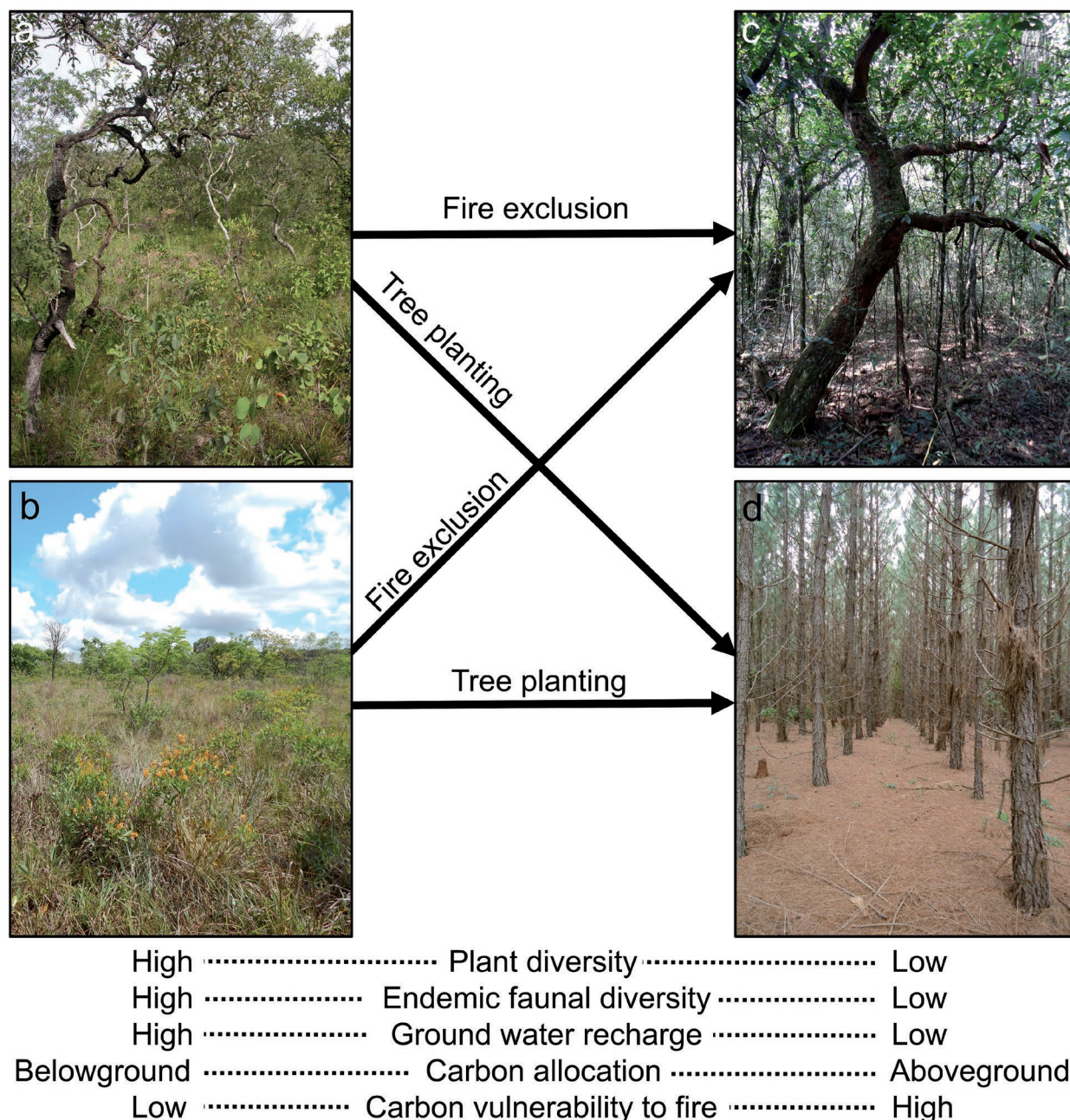


Figure 1. An example from the Cerrado region of Brazil of the causes and consequences of (a) savanna and (b) grassland replacement by (c) forests and (d) tree plantations. As in many grassy biomes, fire exclusion and tree planting in cerrado savanna–grasslands lead to increased tree densities (Moreira 2000), decreased plant (de Abreu and Durigan 2011) and faunal diversity (Araujo and Almeida-Santos 2011), increased transpiration and soil water use (Bucci et al. 2008), a decreased ratio of belowground to aboveground biomass (Miranda et al. 2014), and an increased abundance of fire-sensitive trees (Geiger et al. 2011). Simplified state transitions and their causes are denoted by solid arrows. The qualitative axes of ecosystem attributes are depicted with horizontal dotted lines. Note that in some grassy biomes (e.g., Weigl and Knowles 2014), the exclusion of domestic or native herbivores can also cause forest expansion. Photographer: Giselda Durigan.

Mapping afforestation threats

Many of the world's grassy biomes occur where the climate can theoretically support closed-canopy forests (Staver et al. 2011). Recent scientific advances clearly demonstrate that the extent and distribution of these grassy biomes are

determined not by climate alone but also through interactions with fire, herbivores, and edaphic factors that limit tree growth (Bond et al. 2005, Lehmann et al. 2011). These ecological forces shaped the evolution of grassland species over millions of years and created modern grassy biomes that

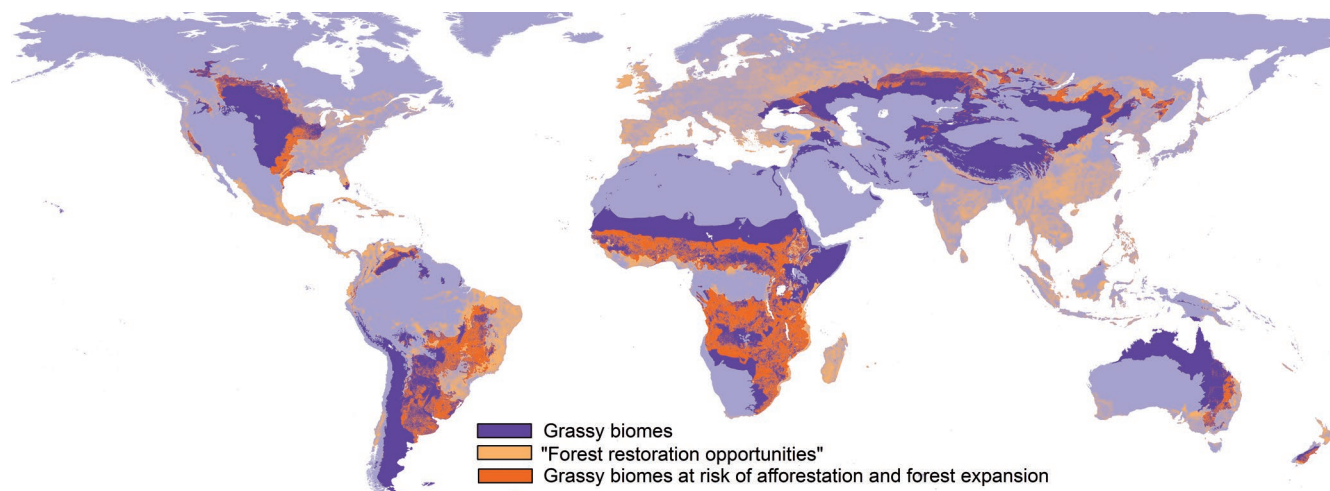


Figure 2. A global map highlighting where 9 million square kilometers of grasslands, savannas, and open-canopy woodlands could be destroyed by misinformed forest restoration projects. Grassy biomes at risk of afforestation and forest expansion are represented by the area of overlap between grassy biomes (see box 1; adapted from Olson et al. 2001) and “forest restoration opportunities” (areas mapped as “wide-scale” and “mosaic restoration” in the *Atlas of Forest Landscape Restoration Opportunities* (WRI 2014).

are ecologically distinct from forests (Ratnam et al. 2011, Maurin et al. 2014) and that include many of the world's biodiversity hotspots (e.g., Noss et al. 2015). But despite overwhelming evidence of their antiquity and richness, the misperception persists that grassy biomes are degraded ecosystems formed as a result of human-caused deforestation (Veldman et al. 2015a).

To illustrate how misperceptions about grassy biomes can lead to flawed science and misguided policy, we assess the *Atlas of Forest Landscape Restoration Opportunities* (hereafter the *Atlas*), an interactive online map published by the World Resources Institute (WRI 2014). The *Atlas* identifies 23 million square kilometers (km²) of the terrestrial biosphere as providing “opportunities” to meet the Bonn Challenge to restore 150 million hectares (ha) of the world's deforested and degraded lands by 2020, a goal that WRI and the International Union for Conservation of Nature (IUCN) describe as “[achievable] through a doubling of current rates of afforestation, forest regeneration, and silvipastoral/agroforestry expansion” (Laestadius et al. 2011). The *Atlas* was produced by WRI and IUCN in collaboration with and/or support from the Global Partnership on Forest and Landscape Restoration (GPFLR), the University of Maryland, South Dakota State University, the Program on Forests, the German Ministry for the Environment, and the Forestry Commission of Great Britain (Laestadius et al. 2011, WRI 2014). The *Atlas* was reviewed by the United Nations Environment Programme–World Conservation Monitoring Center.

Our analysis shows that at the global scale, the *Atlas* misclassifies 9 million km² of grassy biomes as “deforested” or “degraded” and therefore providing “opportunities” for forest restoration (figure 2, box 1); similar errors are also

evident at landscape scales (figure 3, box 2, supplemental appendixes S1–S8). The *Atlas* producers considered any nonforest area where climate could permit forest development to be deforested (Laestadius et al. 2011). This assumption is based on widely held but outdated ideas about “potential vegetation” that fail to account for the roles of fire, large herbivores (native or domestic), and edaphic factors in grassy biome ecology and evolution (Weigl and Knowles 2014, Noss et al. 2015). By applying this assumption globally, WRI and IUCN inadvertently produced a map very similar to the *global distribution of ecosystems in a world without fire* (Bond et al. 2005), albeit with very different conclusions about the nature and value of fire-dependent systems.

Although some ecosystems within grassy biomes may indeed be degraded and in need of ecological restoration, the dense tree planting, fire suppression, and grazer exclusion promoted by IUCN and WRI (2014, ITTO and IUCN 2005) are incompatible with grassland biodiversity and ecosystem functions. In contrast, the restoration of grassy biomes often involves tree removal, prescribed fire, and the planting of grasses and forbs. When trees are planted to restore savannas and woodlands, native fire-adapted tree species should be used and planting densities should be low (Ratnam et al. 2011).

Leakage, or the shifting of environmentally deleterious activities from an intervened area to another, is a serious obstacle to the successful implementation of policies that promote payments for environmental services. Yet leakage from forest conservation projects to the grassy biomes has not been adequately studied by scientists or acknowledged by policymakers. This disregard reflects the lack of recognition of grassy biomes by the United Nations Framework Convention on Climate Change (UNFCCC) and

Box 1. Global mapping analysis.

The lack of a map that adequately depicts grassy biomes globally created a serious hurdle to the assessment of the overlap between the *Atlas of Forest Landscape Restoration Opportunities* (the *Atlas*; WRI 2014) and the world's grassy biomes (i.e., grassy biomes at risk of afforestation and forest expansion; figure 2). We ultimately chose to represent the grassy biomes based on the *Terrestrial Ecoregions of the World* by Olson and colleagues (2001). Unfortunately, that map failed to represent grassy biomes in several regions of the world. For example, the grasslands of Madagascar (Bond et al. 2008), the savannas of India and southeast Asia (Sankaran 2009, Ratnam et al. 2011), the savannas of the North American Coastal Plain (Noss et al. 2015), and many others were not mapped by Olson and colleagues (2001; figure 3). Conversely, there are some natural forests within regions mapped as grassy biomes. For example, gallery forests and forest–grassland mosaics are common in many regions dominated by grassy biomes, including the cerrados of South America and the miombo woodlands of Africa. Based on our experience working in these regions, we expect that any potential overestimate of the global area at risk of afforestation and forest expansion is at least balanced by our underestimation of risk in grassy biomes not mapped by Olson and colleagues (2001). In light of these limitations, we suggest that our global analysis (described below; figure 2) should not be used to determine the restoration status of specific landscapes nor be viewed as an alternative to the *Atlas* (WRI 2014). These considerations underscore the need for accurate, fine-scale vegetation mapping (see the Recommendations for science and policy section).

For the global mapping analysis, we used Esri ArcGIS 10.1 to overlay a shape file of the *Terrestrial Ecoregions of the World* (Olson et al. 2001) and a classified raster image of the *Atlas* (WRI 2014). For the grassy biomes, we included what Olson and colleagues (2001) referred to as tropical and subtropical grasslands, savannas, and shrublands; temperate grasslands, savannas, and shrublands; flooded grasslands and savannas; and montane grasslands and shrublands. For the *Atlas*, we mapped the two restoration classes emphasized by WRI (2014): “wide-scale restoration” and “mosaic restoration.” The *Atlas* producers stated that their map identifies “more than 2 billion hectares” of forest restoration opportunities (i.e., 20 million square kilometers, km²; Laestadius et al. 2011, WRI 2014). Our estimates, based on WRI data, confirm that they mapped 23 million km² of “restoration opportunities,” of which 9.3 million km² (40%) overlap with the grassy biomes.

the program for Reducing Emissions from Deforestation and Forest Degradation (REDD+) and is due in part to the definitions of “forest” used by the United Nations Food and Agriculture Organization (FAO 2010, Putz and Redford 2010). Worse yet, the Clean Development Mechanism (CDM) of the UNFCCC provides carbon credits for both reforestation and afforestation, including the afforestation of grassy biomes. The misinterpretation of grassy biomes as “degraded” by WRI and IUCN demonstrates how the failure to formally recognize grassy biomes, to distinguish afforestation from reforestation, and to differentiate forest regeneration from forest expansion can translate into tree-promoting conservation initiatives that add to the environmental risks of agricultural leakage alone.

On the responses to *Tyranny of trees in grassy biomes*

It was encouraging that in response to our letter in *Science* (Veldman et al. 2015b) in which we raised many of these same concerns, the creators of the *Atlas* (Laestadius et al. 2015) affirmed the importance of protecting ancient grassy biomes from tree- and forest-promoting management interventions. At the same time, they strongly disagreed that their map could contribute to the loss of grassy biomes because “Forest Landscape Restoration (FLR) is a process to regain ecological integrity and enhance human well-being in deforested or degraded forest landscapes” (p. 1210). For further detail on FLR, they cited a report by the International Tropical Timber Organization and IUCN (ITTO and IUCN 2005) that repeatedly described fire

and grazing as “degrading influences” in need of control. Clearly, FLR does not adequately consider the ecology and ecosystem services provided by grassy biomes. Laestadius and colleagues (2015) implied that their map is good because the motivations for its creation (e.g., the implementation of the Bonn Challenge) are laudable and because it achieved global coverage using a big data set. Unfortunately, they conducted no ground validation (Laestadius et al. 2011), and our own assessment shows that 40% of the *Atlas* corresponds to naturally nonforest biomes—that is, places where tree density below “potential” is an unsuitable or unreliable indicator of degradation (box 1, figure 2). Finally, Laestadius and colleagues (2015) suggested that given the “coarseness” of the *Atlas*, national and subnational assessments are needed to determine where and what kind of restoration should occur. Although this disclaimer may sound reasonable, the biomes misidentified by the *Atlas* as “deforested” or “degraded” are already undervalued for their biodiversity and ecosystem services (Parr et al. 2014, Veldman et al. 2015a) and are unlikely to be highly valued in national and subnational assessments. Indeed, in *A Guide to Restoration Opportunities Assessment Methodology*, IUCN and WRI (2014) listed the “first-level priority” restoration options for savannas of eastern Rwanda to include new large commercial woodlots, new industrial timber plantations, and fire management and control. Better safeguards against afforestation and forest expansion in grassy biomes are essential if WRI, IUCN, and GPFLR wish to strengthen the ecological integrity of their restoration initiatives (Suding et al. 2015).

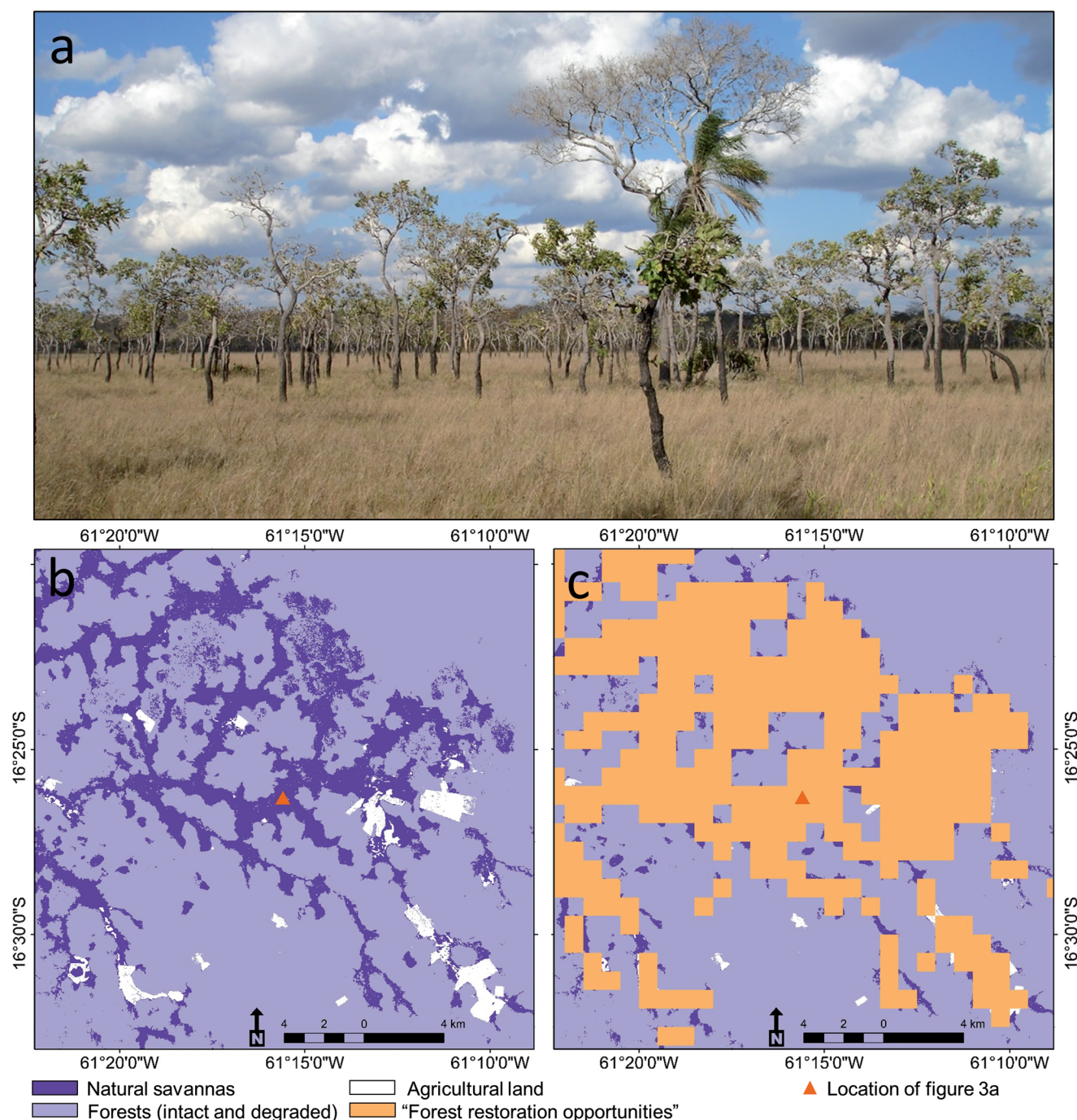


Figure 3. (a) A seasonally wet, fire-maintained, old-growth savanna in eastern lowland Bolivia was misclassified as part of the tropical and subtropical dry broadleaf forest biome in a widely used coarse-scale map of the world's ecoregions (Olson *et al.* 2001) and was mapped as “degraded” by the Atlas of Forest Landscape Restoration Opportunities (WRI 2014). Photographed during the dry season by Joseph W. Veldman. (b) Classified satellite imagery depicts the distribution of natural savannas, forests, and agricultural land in the surrounding 600-square-kilometer area (box 2; adapted from Veldman and Putz 2011). (c) The same map overlaid by “forest restoration opportunities” identified by the Atlas (WRI 2014).

Also in response to our letter (Veldman *et al.* 2015b), the Assistant Director-General for Forestry of the FAO (Rojas-Brales 2015) agreed with our call to conserve grassy biomes and to avoid ill-placed afforestation but wished that we had acknowledged the many grassland-focused activities of the

FAO. To remedy this, he provided references for several FAO grassland projects. Most importantly though, he pointed out a significant area of agreement and our primary concern with FAO policy: grassy biome definitions. The FAO (2010) defined “forests” as land with greater than 10% tree canopy

Box 2. Landscape assessment.

To demonstrate the limitations of low-resolution global vegetation maps (e.g., Olson et al. 2001) and to further assess the *Atlas of Forest Landscape Restoration Opportunities* (WRI 2014), we analyzed a landscape from eastern lowland Bolivia (figure 3). This landscape is an example of an area where grassy biomes are mistakenly identified as “degraded” and “deforested” by the *Atlas* but that are not included in our global estimate of afforestation/forest expansion risk because they are in a forest-dominated ecoregion and were mapped as forest by Olson and colleagues (2001). We adapted the vegetation map prepared by Veldman and Putz (2011), who used field-based samples and satellite imagery (Landsat TM for 1986 and CBERS-2 for 2005; 30 meter \times 30 meter resolution) to distinguish natural savannas from areas of deforestation and severe forest degradation. As such, their map is particularly suitable for evaluating the *Atlas* at landscape scales. We present a 600-square kilometer (km^2) subset of the larger (22,500 km^2) region studied by Veldman and Putz (2011) and simplified the vegetation classes to depict natural savanna, forest land (intact and degraded forests and derived savannas), and agricultural land. We then overlaid this map with the *Atlas* (as in the global analysis; box 1). In addition, to depict the variety of landscapes at risk of afforestation and forest expansion, we compiled a set of example photographs and geographic coordinates (appendixes S1–S8) of grassy biomes misidentified by the *Atlas*.

cover, which encompasses grassy biomes with trees (i.e., fire-dependent savanna-woodlands with as much as 80% canopy cover), despite the fact that they are ecologically distinct from fire-sensitive closed-canopy forests (Ratnam et al. 2011, Parr et al. 2014). Grassy biomes with 5%–10% or less than 5% tree cover are classified as “other wooded land” or “other land,” respectively. At best, these FAO definitions are ecologically uninformative, and, at worst, they contribute to the loss of grassy biomes (Putz and Redford 2010, Parr et al. 2014, Searchinger et al. 2015). Indeed, the use of the FAO’s 10% tree canopy definition by the producers of the *Atlas* (Laestadius et al. 2011, 2015) is a prime example of why these definitions are so important, but other cases can be found in the FAO’s own projects. For example, an analysis by the FAO on agricultural development potential (Alexandratos and Bruinsma 2012) excluded forests—but not grassy biomes with low tree cover—under the mistaken assumption that the agricultural conversion of savanna-grasslands necessarily comes at a lower cost to biodiversity and carbon than the conversion of forests (Searchinger et al. 2015). In light of our shared interest in grassland conservation and ecosystem services (Rojas-Briales 2015), we hope that the FAO will revise its widely used definitions (FAO 2010) to clearly distinguish grassy biomes from forests (Ratnam et al. 2011), to distinguish old-growth grasslands from anthropogenic vegetation (Veldman et al. 2015a), and to clarify the term “natural expansion of forest” to distinguish forest regeneration from forest expansion (Weigl and Knowles 2014).

Recommendations for science and policy

Efforts to conserve and restore forests and efforts to conserve and restore grassy biomes should be integrated. We suggest that scientists, policymakers, and land managers can reconcile the distinct conservation and management challenges posed by forest and grassy biomes by implementing the following recommendations:

(a) Produce accurate, high-resolution vegetation maps that depict grassy biomes at the scales at which ecosystem management is planned and implemented. It is time

to replace the widely used global vegetation maps (e.g., Olson et al. 2001) that neglect grassy biomes in regions where forests are the dominant vegetation type (e.g., figure 3; Weigl and Knowles 2014) or where savannas were historically mistaken for (degraded) forests (e.g., Bond et al. 2008, Sankaran 2009, Ratnam et al. 2010, Noss et al. 2015). Given the limitations of remote sensing to distinguish natural and anthropogenic grasslands (e.g., Wright and Wimberly 2013, WRI 2014), the use of satellite imagery alone is unlikely to permit the accurate global mapping of biologically rich grassy biomes. Instead, maps produced by regional experts at fine spatial scales should be integrated using modern geographic information systems to achieve global coverage. Such an effort would also highlight where further mapping is needed.

(b) Appreciate vegetation heterogeneity and alternative biome states so as to conserve and restore complex landscapes that support both forests and grassy biomes (Staver et al. 2011). Even with accurate maps, the classification of many vegetation types as either grassland or forest will be challenging. Meeting this challenge will require a deep understanding of the distinct ecologies of forests and grassy biomes, as well as vegetation mosaics (figure 3, appendixes S1, S4). In particular, grassy biomes typically require fire and/or herbivory to maintain and restore biodiversity. These same disturbances can degrade forests and hinder reforestation. Rather than risk conserving one biome at the expense of others, nuanced approaches to landscape-level management and restoration of forest and grassy biomes are required.

(c) Finally, formally recognize the value of nonforest ecosystems by, for example, clarifying the provisions of CDM and REDD+ and by revising the forest definitions of the FAO (2010) so as to avoid afforestation, forest expansion, and agricultural conversion of ancient grassy biomes. So long as carbon stored in trees is valued above other ecosystem services, the conservation

values of grassy biomes will remain threatened by agricultural conversion, fire exclusion, and ill-placed tree planting.

Supplemental material

The supplemental material is available online at <http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biv118/-/DC1>.

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References cited

- Alexandratos N, Bruinsma J. 2012. World Agriculture Towards 2030/2050: The 2012 Revision. ESA Working Paper no. 12-03. Food and Agriculture Organization of the United Nations.
- Araujo CO, Almeida-Santos SM. 2011. Herpetofauna in a cerrado remnant in the state of São Paulo, Southeastern Brazil. *Biota Neotropica* 11: 47–62.
- Berthrong ST, Jobbagy EG, Jackson RB. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecological Applications* 19: 2228–2241.
- Berthrong ST, Pineiro G, Jobbagy EG, Jackson RB. 2012. Soil C and N changes with afforestation of grasslands across gradients of precipitation and plantation age. *Ecological Applications* 22: 76–86.
- Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–537.
- Bond WJ, Silander JA Jr, Ranaivonasy J, Ratsirarson J. 2008. The antiquity of Madagascar's grasslands and the rise of C4 grassy biomes. *Journal of Biogeography* 35: 1743–1758.
- Bremer LL, Farley KA. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* 19: 3893–3915.
- Bucci SJ, Scholz FG, Goldstein G, Hoffmann WA, Meinzer FC, Franco AC, Giambelluca T, Miralles-Wilhelm F. 2008. Controls on stand transpiration and soil water utilization along a tree density gradient in a Neotropical savanna. *Agricultural and Forest Meteorology* 148: 839–849.
- Canadell JG, Raupach MR. 2008. Managing forests for climate change mitigation. *Science* 320: 1456–1457.
- De Abreu RCR, Durigan G. 2011. Changes in the plant community of a Brazilian grassland savannah after 22 years of invasion by *Pinus elliottii* Engelm. *Plant Ecology and Diversity* 4: 269–278.
- [FAO] Food and Agriculture Organization of the United Nations. 2010. Global forest resources assessment 2010 main report. FAO Forestry Paper no. 163.
- Geiger EL, Gotsch SG, Damasco G, Haridasan M, Franco AC, Hoffmann WA. 2011. Distinct roles of savanna and forest tree species in regeneration under fire suppression in a Brazilian savanna. *Journal of Vegetation Science* 22: 312–321.
- Gibbs HK, Rausch L, Munger J, Schelly I, Morton DC, Noojipady P, Soares-Filho B, Barreto P, Micol L, Walker NF. 2015. Brazil's soy moratorium. *Science* 347: 377–378.
- [ITTO and IUCN] International Tropical Timber Organization, International Union for Conservation of Nature. 2005. Restoring Forest Landscapes: An Introduction to the Art and Science of Forest Landscape Restoration. ITTO Technical Series no. 23.
- [IUCN and WRI] International Union for Conservation of Nature, World Resources Institute. 2014. A Guide to the Restoration Opportunities Assessment Methodology (ROAM). IUCN and WRI.
- Jackson RB, Jobbagy EG, Avissar R, Roy SB, Barrett DJ, Cook CW, Farley KA, le Maitre DC, McCarl BA, Murray BC. 2005. Trading water for carbon with biological sequestration. *Science* 310: 1944–1947.
- Jackson RB, Farley KA, Hoffmann WA, Jobbagy EG, McCulley RL. 2007. Carbon and water tradeoffs in conversions to forests and shrublands. Pages 237–246 in Canadell JG, Pataki DE, Pitelka LF, eds. *Terrestrial Ecosystems in a Changing World*. Springer.
- Laestadius L, Maginnis S, Minnemeyer S, Potapov P, Saint-Laurent C, Sizer N. 2011. Mapping opportunities for forest landscape restoration. *Unasylva* 238: 47–48.
- Laestadius L, Maginnis S, Minnemeyer S, Potapov PV, Reyter K, Saint-Laurent C. 2015. Sparing grasslands: Map misinterpreted. *Science* 347: 1210–1211.
- Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ. 2011. Deciphering the distribution of the savanna biome. *New Phytologist* 191: 197–209.
- Maurin O, Davies TJ, Burrows JE, Daru BH, Yessoufou K, Muasya AM, van der Bank M, Bond WJ. 2014. Savanna fire and the origins of the “underground forests” of Africa. *New Phytologist* 204: 201–214.
- Miranda SC, Bustamante M, Palace M, Hagen S, Keller M, Ferreira LG. 2014. Regional variations in biomass distribution in Brazilian savanna woodland. *Biotropica* 46: 125–138.
- Moreira AG. 2000. Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography* 27: 1021–1029.
- Noss RF, Platt WJ, Sorrie BA, Weakley AS, Means DB, Costanza J, Peet RK. 2015. How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Diversity and Distributions* 21: 236–244.
- Olson DM, et al. 2001. Terrestrial ecoregions of the worlds: A new map of life on Earth. *BioScience* 51: 933–938.
- Parr CL, Lehmann CER, Bond WJ, Hoffmann WA, Andersen AN. 2014. Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology and Evolution* 29: 205–213.
- Putz FE, Redford KH. 2010. The importance of defining “forest”: Tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica* 42: 10–20.
- Ratnam J, Bond WJ, Fensham RJ, Hoffmann WA, Archibald S, Lehmann CER, Anderson MT, Higgins SI, Sankaran M. 2011. When is a “forest” a savanna, and why does it matter? *Global Ecology and Biogeography* 20: 653–660.
- Rojas-Brales E. 2015. Sparing grasslands: FAO's active role. *Science* 347: 1211–1211.
- Sankaran M. 2009. Diversity patterns in savanna grassland communities: Implications for conservation strategies in a biodiversity hotspot. *Biodiversity and Conservation* 18: 1099–1115.
- Searchinger TD, Estes L, Thornton PK, Beringer T, Notenbaert A, Rubenstein D, Heimlich R, Licker R, Herrero M. 2015. High carbon and biodiversity costs from converting Africa's wet savannahs to cropland. *Nature Climate Change* 5: 481–486.
- Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232.
- Suding K, et al. 2015. Committing to ecological restoration. *Science* 348: 638–640.
- Veldman JW, Putz FE. 2011. Grass-dominated vegetation, not species-diverse natural savanna, replaces degraded tropical forests on the southern edge of the Amazon Basin. *Biological Conservation* 144: 1419–1429.
- Veldman JW, et al. 2015a. Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment* 13: 154–162.
- Veldman JW, Overbeck GE, Negreiros D, Mahy G, Le Stradic S, Fernandes GW, Durigan G, Buisson E, Putz FE, Bond WJ. 2015b. Tyranny of trees in grassy biomes. *Science* 347: 484–485.
- Weigl PD, Knowles TW. 2014. Temperate mountain grasslands: A climate-herbivore hypothesis for origins and persistence. *Biological Reviews* 89: 466–476.
- White RP, Murray S, Rohweder M. 2000. Grassland Ecosystems. World Resources Institute.

- [WRI] World Resources Institute. 2014. Atlas of Forest and Landscape Restoration Opportunities. World Resources Institute: Washington, DC. (1 June 2015; www.wri.org/resources/maps/Atlas-forest-and-landscape-restoration-opportunities)
- Wright CK, Wimberly MC. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences* 110: 4134–4139.

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