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SYNTHESIS

Distribution mapping of world grassland types

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ABSTRACT

Aim National and international policy frameworks, such as the European Union's Renewable Energy Directive, increasingly seek to conserve and reference 'highly biodiverse grasslands'. However, to date there is no systematic global characterization and distribution map for grassland types. To address this gap, we first propose a systematic definition of grassland. We then integrate International Vegetation Classification (IVC) grassland types with the map of Terrestrial Ecoregions of the World (TEOW).

Location Global.

Methods We developed a broad definition of grassland as a distinct biotic and ecological unit, noting its similarity to savanna and distinguishing it from woodland and wetland. A grassland is defined as a non-wetland type with at least 10% vegetation cover, dominated or co-dominated by graminoid and forb growth forms, and where the trees form a single-layer canopy with either less than 10% cover and 5 m height (temperate) or less than 40% cover and 8 m height (tropical). We used the IVC division level to classify grasslands into major regional types. We developed an ecologically meaningful spatial catalogue of IVC grassland types by listing IVC grassland formations and divisions where grassland currently occupies, or historically occupied, at least 10% of an ecoregion in the TEOW framework.

Results We created a global biogeographical characterization of the Earth's grassland types, describing approximately 75% of IVC grassland divisions with ecoregions. We mapped 49 IVC grassland divisions. Sixteen additional IVC grassland divisions are absent from the map because of the fine-scale distribution of these grassland types.

Main conclusions The framework provided by our geographical mapping effort provides a systematic overview of grasslands and sets the stage for more detailed classification and mapping at finer scales. Each regional grassland type can be characterized in terms of its range of biodiversity, thereby assisting in future policy initiatives.

Keywords

Conservation biogeography, conservation policy, division, ecoregion, ecosystem, ecosystem management, formation, highly biodiverse grasslands, International Vegetation Classification, vegetation mapping.

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INTRODUCTION

Grasslands have historically been an area of expansion for human land use (White *et al.*, 2001), and much of the world's highly productive grassland has been converted to crops, mixed farming and artificial pastures (Suttie *et al.*, 2005). In temperate grasslands, this conversion occurred prior to the 1950s (Millennium Ecosystem Assessment, 2005), and the percentage of protection for this biome is lower than for all other biomes (Hoesktra *et al.*, 2005). A

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current wave of agricultural expansion is occurring in the tropics, with many tropical savannas and grasslands undergoing change (Gibbs *et al.*, 2010). Growth of agricultural sectors in South America (Gavier-Pizarro *et al.*, 2012), southern Africa (Maeda *et al.*, 2010), North America (Landis & Werling, 2010), and Asia (Qiu *et al.*, 2010) heralds new pressures on global grassland ecosystems. Future threats to grasslands also appear high, given a need to feed a rapidly growing human population (Foley *et al.*, 2011).

These threats challenge governments, business and civil society to develop policies that address conversion pressures on global grassland ecosystems and seek to balance development with conservation. However, decision-makers currently lack a framework within which to monitor global grassland biodiversity for both biological uniqueness and total historical distribution. One promising initiative is the International Union for the Conservation of Nature's (IUCN) proposed Red List of Ecosystems, where the likelihood that an ecosystem will persist into the future is assessed (Rodríguez *et al.*, 2010). However, the projected completion date of the global Red List assessment is 2025 (Rodríguez *et al.*, 2012; Keith *et al.*, 2013), and policies are being implemented today. For example, the European Union's Renewable Energy Directive (EU RED) restricts imports of biofuels feedstock harvested from areas containing significant biodiversity and/or carbon stock (European Commission, 2009). A clear intent of this policy is to conserve grassland biodiversity, but the policy cannot be operational on a global basis without a global grassland distribution map as a foundation.

To address this gap, we present a framework for defining world grassland types and a methodology for mapping their geographical distribution. We propose the combination of two systems: the International Vegetation Classification (IVC), to give clarity to the definition of grasslands (Faber-Langendoen *et al.*, 2014), and Terrestrial Ecoregions of the World (TEOW), to provide an initial global geospatial characterization (Olson *et al.*, 2001). By combining these two systems, we generate a systematic, spatially explicit framework that broadly accounts for grassland biodiversity (as vegetation types) and the spatial ecological complexes (as ecoregions) within which grasslands occur. This approach provides a better platform for decision-makers to advance grassland conservation.

Defining grassland: challenges in developing a common framework

A primary obstacle to developing and implementing effective grassland conservation policies is the wide spectrum of grassland definitions. Unlike forests, for which the United Nation's Food and Agriculture Organization (FAO) provides a clear definition (5 m in height, 10% or more canopy cover, > 0.5 ha, and not under agricultural or other non-forest land use; FAO, 2010), grasslands are variously defined (e.g. Gibson, 2009; and see the FAO's compilation of definitions http://www.fao.org/agriculture/crops/thematic-sitemap/theme/spi/gcwg/definitions/en/). This profusion of definitions may be due to the greater difficulty in characterizing the limits of grasslands, a less persistent canopy structure, more frequent disturbance regimes, and their occurrence within a physiognomic continuum between forests and deserts.

Grasslands might well be expected to be dominated by grasses, but the term often has a broader meaning when set in the context of defining a comprehensive set of ecological vegetation types (such as grassland versus forest, desert, tundra or wetland). In that context, the concept still emphasizes dominance by grasses or grass-like plants (graminoids) and the lack of trees, but the full suite of growth forms may include grasses, other narrow-leaved grass-like herbs (i.e. non-woody graminoids) and even forbs (broad-leaf herbs). Perhaps the more technically appropriate term is 'herbland' [similar to UNESCO's (1973) 'Herbaceous Vegetation'], but 'grassland' is the most popular, given that grasses are by far the most typical component and because forbs are often mixed within or patchily distributed among grasses (Davies *et al.*, 2004). In his comprehensive review of major grasslands regions of the world, Coupland (1979, p. 22) defined 'grassland' as referring to 'ecosystems in which the dominant vegetative component is comprised of herbaceous species'. Sometimes the term grassland is used even more inclusively to encompass herbs and shrubs (White *et al.*, 2001); grasses and shrubs can form intricate mixes, and dominance may alternate between the two within the span of years or decades. In some cases, grasses may overtop shrubs (Faber-Langendoen *et al.*, 2012).

Here, we consider the various concepts of grasslands and provide a synthesized definition based on previous work. First, we clarify the term 'grass', which we define broadly as an herbaceous monocot with narrow leaves, sometimes referred to as a graminoid. Raunkiær (1934, in Mueller-Dombois & Ellenberg, 1974, pp. 458–459) defines 'grass' as 'a caespitose or reptant hemicryptophyte life form'. Box (1981, p. 162) defines it as graminoids that are, 'narrow-leaved herbs…growing from generally well-developed underground rootstocks which may be either perennial (e.g. rhizomes) or annual…classified as bunched (cespitose), or spreading (sward-forming), and rooting'. The primary taxonomic members are Poaceae, but they may also include Cyperaceae, Restionaceae and other narrow-leaved monocots. We consider grasslands to be dominated by these members, while often containing, and sometimes dominated or codominated by forbs. A dominant or co-dominant is any species or growth form with at least 10% cover (Faber-Langendoen *et al.*, 2012). Grass dominance is clearly expressed when grasses have greater than 25% grass cover (Kucera, 1981) but may be as low as 10% cover if they exceed that of all other growth forms. Shrub cover in grasslands is typically < 25%.

Second, we distinguish largely native or natural grasslands from cultural grasslands. Natural grassland ecosystems are thought to have had a global distribution for at least 15 million years (Jacobs *et al.*, 1999). The widespread expansion of C_4 grasses, which developed with seasonal climatic aridification and/or atmospheric change and which grow exclusively in open terrestrial areas, is seen in the macrofossil and pollen record as far back as the Miocene. Additionally, herbivore dental morphology has been shown to have co-evolved with the newly available C_4 grasses, substantiating the existence of widespread climax grassland ecosystems prior to the Anthropocene (Coupland, 1992; Jacobs *et al.*, 1999; Edwards *et al.*, 2010). Grasslands today range from strongly cultural, human-created systems, such as exotic grass pastures, to those largely shaped by more natural ecological processes of climate, fire and native grazers (FAO, 2005). For example, Mongolian grasslands have been managed as pasturelands since before the days of Genghis Khan (Li *et al.*, 2006). In Australia, native grasslands are recognized by their component species, distinct from recently introduced exotic pasture grasslands (Lonsdale, 1994; Ash *et al.*, 1997). But, the distinction between natural and cultural grasslands is not always black and white: the western North American grasslands are often referred to as rangelands (which include both shrublands and grasslands) and are often managed as such, but currently they form a continuum of natural (native), semi-natural (naturalized exotic), and cultural (intensive pasture) grasslands. For our purposes, we define native or natural (including semi-natural) grasslands, as those where non-human ecological processes primarily determine species and site characteristics. In other words, the vegetation is composed of a largely spontaneously growing composition of plant species shaped by both geophysical (site) and biotic processes (Küchler, 1969; Westhoff & van der Maarel, 1973). Natural vegetation forms recognizable groupings that can be related to ecological site features. Human activities influence these interactions to varying degrees (e.g. logging, livestock grazing, fire, introduced pathogens), but do not eliminate or dominate the spontaneous processes (Westhoff & van der Maarel, 1973). As with forests in the FAO definition, we exclude cultural grasslands, which are primarily planted and maintained for agricultural reasons (pasture, hay, intensive livestock production). Although these distinctions can sometimes be problematic, they are also consistent with the approach of the Ecosystems of the World project, which provided separate descriptions of natural (Coupland, 1992) and managed grasslands (Breymeyer, 1987–1990).

Third, we clarify the limits of grassland along an ecotone from grassland to woodland. We set a literature-based threshold for grassland with respect to tree cover, beyond which trees become a co-dominant and/or diagnostic part of the plant community concept, exerting disproportionate influence on competition for canopy cover and subsurface resources (White, 1983; Scholes & Hall, 1996; Scholes & Archer, 1997; House *et al.*, 2003; Lock, 2006; Bucini & Hanan, 2007). In the temperate region, tree savannas are more restricted in area and often closely related to or included within the concept of woodlands (Faber-Langendoen *et al.*, 2012). When tree cover exceeds 10% in temperate regions, we exclude it. In the tropics, tree savannas are extensive and overlap with open savannas or grassland. The canopy cover threshold is notoriously variable for tropical wooded grasslands or tree savannas, and varies from low (25%) (UNESCO, 1973; Mueller-Dombois & Ellenberg, 1974), to high (75%) (Mucina & Rutherford, 2006). We used a 40% canopy cover threshold to distinguish between tropical grassland (including wooded grassland) and tropical woodland, with tropical wooded grasslands having a continuous grass layer, trees < 8 m in height, a simple two-layer structure, between 10 and 40% canopy cover, and open grassland having < 10% tree cover. Similarly in need of differentiation are shrublands, defined as where shrubs > 0.5 m tall have > 25% shrub cover (or if < 25% cover, shrubs have at least 10% cover and exceed herbaceous cover), and tree cover is < 10% (Faber-Langendoen *et al.*, 2012) (see Table 1 for a comparison with definitions provided by Lock, 2006).

Finally, wetlands are excluded where graminoids and other herbaceous vegetation occur in a matrix with wetland species, including aquatic plants, forbs and mosses. We suggest that although these wetlands may technically meet certain aspects of the grasslands definition, they are typically composed of a range of non-grass vegetation and better treated as part of global wetland definitions, such as that of the Ramsar Convention (Matthews, 1993).

In summation, we propose the following definition of grasslands for global application. A natural or semi-natural grassland is defined by the following characteristics: (1) a non-wetland formation; (2) vascular vegetation has at least 10% cover; (3) graminoids have at least 25% cover (but if < 25% cover, graminoids exceed that of other herbaceous and shrub cover); (4) broad-leaved herbs (forbs) may have variable levels of cover and dominance; (5) shrubs have < 25% canopy cover; (6) and trees: (i) in temperate zones, typically have < 10% canopy cover, are < 5 m tall and single-layered, or (ii) in tropical regions, typically have < 40% canopy cover, are < 8 m tall, and are single layered.

Beyond this basic physiognomic definition of grassland, reference can be made to the floristic composition of a division and lower levels of the IVC hierarchy. For example, decisions about how to classify wooded tropical grasslands with > 40% cover could factor in the degree to which specific grassland species are dominant in the ground layer.

Characterizing ecosystems

Natural grasslands occur around the world and have been characterized using a number of methods (see Appendix S1 in Supporting Information). For global characterizations, the methods can be grouped into four types: vegetation composition; ecological and economic assessment; ecosystem mapping; and remote sensing classification. The vegetation approach stresses the importance of species and growth forms as a primary expression of a terrestrial ecosystem and uses plant species assemblages to classify stands into plant community types (e.g. 'associations', 'alliances') and, combined with physiognomy, into broader vegetation types (e.g. classes, divisions, formations) (UNESCO, 1973; Ellenberg, 1988; DiGregario & Janssen, 1998; Faber-Langendoen *et al.*, 2014). The ecological and economic assessment approach

Table 1 Adapted version of Lock's (2006) table comparing intercontinental (African and South American) variations on the definition of savanna. Our grassland concept includes these three grassland types.

Recommended term	Environment and structure	African term(s)	Approx. equivalent South American term(s)
Wooded grassland	Single dry season > 4 months. Trees with crown cover < 40%, > 10%. One tree layer. Grasses narrow-leaved, tussock-forming and xeromorphic. Single dry season > 4 months. Fires regular, often annual. Tree-dominated vegetation; crown cover at least 40%. Usually only one main tree layer. Woody climbers and epiphytes absent or very scarce. Grasses narrow-leaved, tussock-forming, often xeromorphic.	Scattered tree grassland, wooded grassland	Campo cerrado, sabana arbolada*
Bushed grassland	Single dry season > 4 months. Bushes (multi-stemmed, short stature) < 40%, > 10%. One shrub layer. Grasses narrow-leaved, tussock-forming and xeromorphic.	Open bushland, bushed grassland, savanna bushland, bush savanna	Campo sujo, sabana arbustiva
Grassland	Single dry season > 4 months. Woody plants with canopy cover < 10%. Grasses usually tussock-forming and xeromorphic, at least in Africa. Fires regular. Natural grasslands often in sites with seasonal waterlogging, shallow soil or high metallic ion concentrations.	Grass savanna, savanna grassland	Campo limpo (no large woody plants), camp sujo, sabana abierta, sabana lisa

*Our review of the cerrado literature suggests that 'cerrado *sensu stricto*' also fits with wooded grassland, but may have canopy cover up to *c.* 70%. Thus, *contra* Lock (2006), we would not equate all of the cerrado *sensu stricto* as 'woodland'. Similar issues may exist in Africa where e.g. Lock places both Miombo woodland and Miombo savanna in the woodland category.

characterizes global grassland ecosystem health through an analysis of pressures exerted on the ecosystem, and also reports on the connection to human well-being (Coupland, 1979; White *et al.*, 2001; Suttie *et al.*, 2005). The ecosystem mapping approach emphasizes the geographical or landscape delineation of ecosystem boundaries based on patterns present in biophysical factors, such as climate, landform and, sometimes, floral and faunal evidence (Holdridge, 1967; Uvardy, 1975; Walter & Box, 1976; Schultz, 1995; Bailey, 1996; Olson *et al.*, 2001). The remote sensing method uses the vegetation approach in combination with satellite imagery to create global land cover datasets describing generalized spatial patterns in vegetation, abiotic and anthropogenic features on the Earth's surface (Defries *et al.*, 1995; Loveland & Belward, 1997; Bontemps *et al.*, 2011).

We chose to develop our map of global grassland distribution using a combination of the vegetation approach, represented by the IVC, and a spatially explicit landscape-based approach, as manifested in the TEOW framework. Both systems offer a robust, hierarchical approach to describing global grassland biodiversity.

MATERIALS AND METHODS

We evaluated each ecoregion within the TEOW framework for grassland characteristics and integrated IVC grassland divisions to develop a global distribution map of world grassland types, and reported IVC grassland types if they currently occupy, or historically occupied, at least 10% of an ecoregion (Fig. 1). The IVC is a non-spatial vegetation-based classification system that describes a hierarchy of terrestrial ecosystems using the EcoVeg approach, as described in Faber-Langendoen *et al.* (2014). This technique uses a combination of physiognomic, floristic, ecological and biogeographical patterns to organize vegetation patterns into an eight-level hierarchy, and has been used as the basis for a vegetation classification standard in several countries and continents (Baldwin & Meades, 2008; Federal Geographic Data Committee, 2008; Faber-Langendoen *et al.*, 2009; Navarro, 2011; Sayre *et al.*, 2013). For the purposes of this study, we focused on two of the higher levels of the IVC hierarchy: the formation and the division (Table 2). In the IVC, a formation represents combinations of dominant and diagnostic growth forms reflecting macroclimatic factors incorporating elevation, seasonality, substrates and hydrological conditions (Faber-Langendoen *et al.*, 2014). Nested within each formation is a set of divisions, which describes broadly uniform growth forms and a broad set of diagnostic plant species at large biogeographical scales, reflecting continental gradients in climate, geology, substrates, hydrology and disturbance regimes (Faber-Langendoen *et al.*, 2014). At both the formation and division levels, the ecological and vegetation types include a range of tree savanna, shrubland and grassland types. For example the IVC division Patagonian Grassland & Shrubland includes reference to both grassland and shrubland. Grassland and shrubland are grouped together at the

Table 2 Comparison of our two classification methods for ecosystems – one based on vegetation and ecological pattern without spatial constraints, the other based on biodiversity and ecological pattern with spatial constraints. See also Fig. 1.

International Vegetation Classification: *vegetationally* constrained hierarchy	Terrestrial Ecoregions of the World: *spatially* constrained hierarchy
Formation Combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions (Federal Geographic Data Committee, 2008; cf. 'formation-type' and 'biome-type' of Whittaker, 1975; Lincoln *et al.*, 1998), e.g. • Tropical Grassland, Savanna & Shrubland • Temperate & Boreal Grassland & Shrubland	*Major Habitat Type/Biome* Vegetation structure, ecological dynamics and environmental conditions (Wikramanayake *et al.*, 2002), e.g. • Tropical & Subtropical Grasslands, Savannas & Shrublands • Temperate Grasslands, Savannas & Shrublands
Division Combinations of dominant and diagnostic growth forms and a broad set of diagnostic plant species that reflect biogeographical differences in composition and continental differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes (Federal Geographic Data Committee, 2008).	*Ecoregion* Relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land use change (Olson *et al.*, 2001).
Macrogroup A vegetation unit defined by 'moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographical differences in composition and sub-continental to regional differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes' (Federal Geographic Data Committee, 2008) cf. Pignatti *et al.* (1994), Brown (1982).	

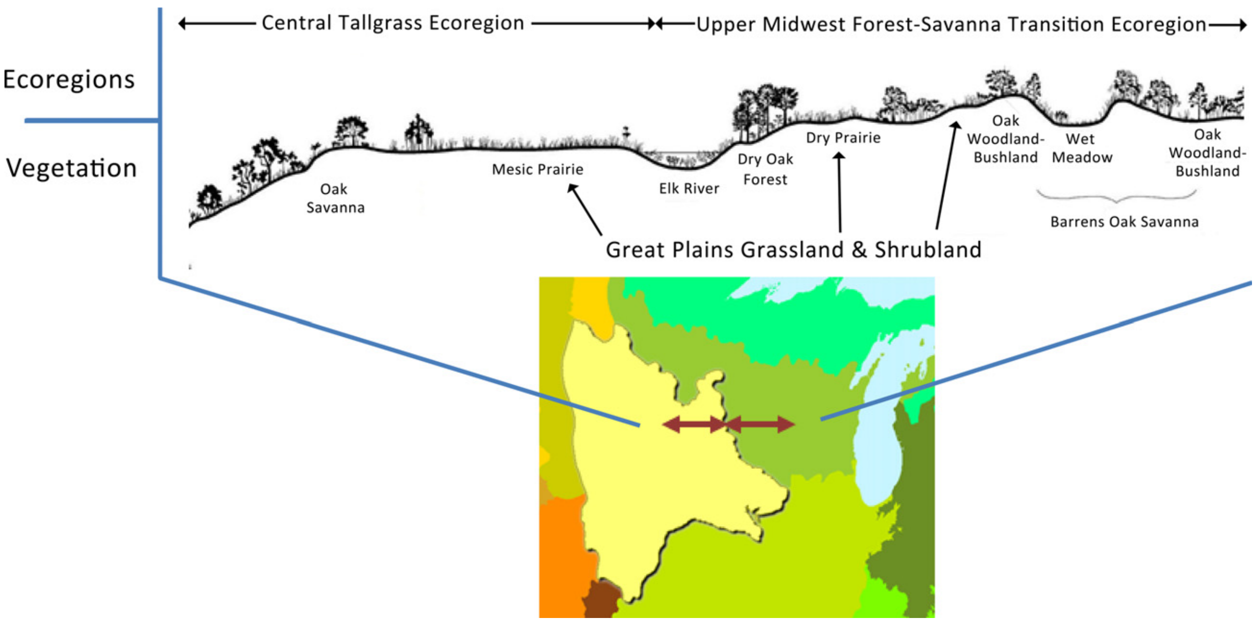

Figure 1 Example of how the International Vegetation Classification (IVC), a non-spatial classification system, and Terrestrial Ecoregions of the World (TEOW), a spatial system, are used together to report the geographical distribution of world grassland types. The Great Plains Grassland & Shrubland Division is a dominant part of the Central Tallgrass Ecoregion, with the ecoregional boundaries shaped by this type, but it is a minor component (less than 10%) of the Upper Midwest Forest–Savanna Transition Ecoregion, defined by the dominant forests, woodlands and savannas. (Figure adapted with permission from Wovcha *et al.*, 1995).

IVC division level because they strongly overlap in floristic composition, growth forms and biogeography. However, within the hierarchy, a lower level distinction is eventually made between the grassland component and other components. Faber-Langendoen & Josse (2010) drafted a set of formation and division levels that contain grasslands, but in preliminary form and without geographical distribution information. Here we build on that study, providing an updated version of the global divisions that contain grasslands.

TEOW is a spatial system of 867 ecoregions nested within a set of 14 global biomes. An ecoregion is a large complex of ecosystems with roughly equivalent biophysical characteristics and species compositions. Importantly, ecoregions are bounded at a regional scale, with boundaries synthesized from previous ecosystem delineation efforts and from the use of biophysical and remotely sensed data (Olson *et al.*, 2001). The TEOW framework separates broadly distinct sets of ecosystems, and includes detailed ecological characterizations describing grassland composition. We found TEOW to be a comprehensive dataset that can describe grassland distribution globally.

To provide an ecologically based geographical distribution of the IVC grassland types provided by Faber-Langendoen & Josse (2010), we listed all ecoregions where the grassland component of an IVC division occupied at least 10% of the given ecoregion. The linkage of TEOW to IVC was completed through an iterative process of comparing and contrasting ecosystem characteristics. A review of TEOW characterizations (http://worldwildlife.org/science/wildfinder/), literature review, outreach to regional grassland experts, and consultation of geographical datasets assembled from remotely sensed data, ecosystem delineations and ecological characterizations was completed to resolve the grassland characteristics of each ecoregion and determine to which IVC division it belonged (see Appendix S2).

Here, we provide an example of the synthesis between TEOW and IVC for the IVC division Eastern Eurasian Cool Semi-Desert Scrub & Grassland. The division is described as extending 'from Kazakhstan to China, including Mongolia and central China. It is dominated by perennial bunchgrass, ranging from forest steppe to semi-desert steppe and into the montane regions of Tibet' (Faber-Langendoen & Josse, 2010, Appendix B 'Division Description and Richness Sum'). The characterization of each ecoregion in the TEOW framework was reviewed for comments on the types of ecosystems present as well as dominant and diagnostic plant species. If there was a lack of clarity on either herbaceous cover or grass species presence, external datasets were consulted. The map of *Ecosystems of Mongolia* (Guinin, 2005) was used to determine the grassland/desert ecotone of northern China and southern Mongolia, as well as clarify the presence of grassland in the Altai montane forest and forest steppe. Data from the Econet project from WWF-Russia (Pereladova, 2002) were used to evaluate dominant/diagnostic grass species occurrence throughout the central Asian region. Finally, data from Globcover 2009 (Bontemps *et al.*, 2011), Sun (1989) and Zhao & Herzschuh (2009) were used to evaluate the presence of grasslands in the Qiadam Basin semi-desert ecoregion just north of the Tibetan Plateau. The remotely sensed data and literature review indicated that a majority of the ecoregion contains arid desert with little herbaceous cover; however, the eastern section contains enough herbaceous cover (10% grass cover) with grass species present to qualify under the grasslands definition.

Although we typically excluded wetlands from our study, we did include several divisions in the tropical freshwater marsh formation in South America (found in the Pantanal, Humid Chaco, and Guayaquil flooded grasslands ecoregion) because these divisions contain a complex of upland grassland types or grasslands flooded during a short period of time, in enough proportion (at least 10% of an ecoregion contains grassland) so as to qualify as a grassland ecoregion.

Our approach identifies all ecoregions where IVC divisions contain grassland types that form a dominant component of the ecoregion. In a few cases, the original ecoregion boundary was altered because the ecoregion encompassed an overly broad geographical range of vegetation types (grassland and other vegetation). For example, the northern half of the Canadian Aspen forests and parkland ecoregion was removed to isolate the grassland-dominated southern half. The Montana Valley and Foothills ecoregion was split in half to recognize the cool semi-desert climate in the Montana valley as distinct from the temperate mixed grass vegetation and climate of the Montana foothills.

RESULTS

We matched TEOW with IVC divisions and identified 49 taxonomically and spatially distinct grassland types, creating a new global biogeographical representation of Earth's grassland types. Our review led to several additions and refinements to grassland IVC divisions. Faber-Langendoen & Josse (2010) originally described 56 IVC divisions. In this new analysis, 20 IVC divisions were either refined or added to reflect new ecosystem information obtained throughout the analysis. The new or updated IVC divisions reflected climatic differentiation or a more accurate geographical nomenclature (i.e. Pampean Grassland & Shrubland, or semi-arid Pampa). Of the resulting 65 IVC divisions (nested within the nine IVC formations), grassland components were extensive enough in approximately 75% (49/65) (Table 3, Fig. 2) to be displayed within the TEOW distribution map. These IVC divisions were aggregated from 145 ecoregions (Fig. 3). The remaining approximately 25% (16/65) of IVC divisions with major grassland components were not mapped (Table 4) onto TEOW, either because of the patchy and diffuse nature of grasslands in the IVC division, or because the scale of grasslands in the IVC division is smaller than the regional scale at which the ecoregions were drawn. These were frequently Pacific island grasslands, high elevation grasslands, or continental grasslands occurring in a much larger matrix of non-grassland.

The distribution and variety of grasslands that are dominant in at least one ecoregion is highly variable across the world. South America and Africa have the highest number of mapped dominant grassland divisions, with 16 and 12, respectively. North America and Oceania have the lowest numbers, each with four mapped divisions, and each had six and five divisions, respectively, that were not mapped because, to the best of our knowledge, they are not dominant in any ecoregion (Table 5). Eurasia contains nearly double the number of total grassland ecoregions of the other continents, with those ecoregions aggregated into nine divisions, and with two more divisions that were never dominant

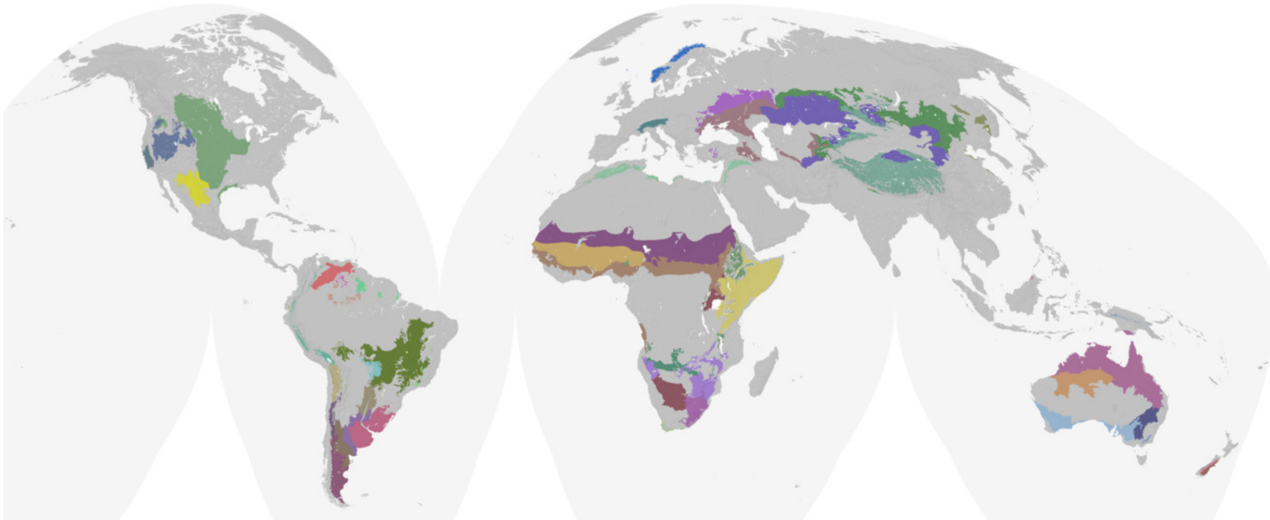

Figure 2 International Vegetation Classification (IVC) divisions with dominant grassland types. The IVC, a non-spatial vegetation classification, was matched with the spatially explicit Terrestrial Ecoregions of the World (TEOW) to produce a map of global grassland distribution. A total of 49 IVC divisions are displayed on this map; however, 16 other IVC divisions remain unmapped due to the fine-scale nature of their distributions.

within an ecoregion, and therefore were not mapped. Many of the unmapped grassland divisions may have historically only occurred as small patches within the ecoregion, and may only be dominant at very local landscape scales, such as dry hillslopes, glades and rocky grasslands in an otherwise forested landscape.

Some IVC divisions are more diverse ecologically than others, as nearly half of ecoregions identified as grasslands occur in just seven IVC divisions. These seven IVC divisions contained 72 ecoregions. The remaining set (42) of the IVC divisions corresponded to the other half of the total (73) ecoregions, indicating that most IVC divisions roughly correspond to a similar scale ecoregions are delineated (Fig. 4).

The IVC division with the largest area, North Sahel Semi-Desert Scrub and Grassland (3,040,000 km^2), is composed of only one ecoregion (Sahelian Acacia Savanna) (Table 6), although not all of the area is, or was, grassland. The second largest grassland IVC division is the Great Plains Grassland & Shrubland, which is an aggregation of 15 ecoregions that cover a total land area of approximately 2,980,000 km^2. The smallest grassland IVC division is the African (Madagascan) Montane Grassland and Shrubland, which is found in only one ecoregion, with a total land area of 1273 km^2.

DISCUSSION

We mapped global grassland ecosystems by linking IVC divisions with their distribution in one or more ecoregions. The TEOW were originally drawn to represent natural communities prior to major land use change (Olson *et al.*, 2001). We suggest that an advantage to using this historical approach of geographical distribution is that it clearly outlines total potential geographical distribution of the individual grassland divisions. Further, the historical approach provides the boundaries needed to complete spatial analyses quantifying total grassland loss, degradation and protection of each division. This spatial information can also be used to evaluate current and historical status of grasslands and their ecosystem processes, including but not limited to hydrological flow, energy cycling, disturbance regimes and ecosystem services.

Our approach capitalizes on the existence of both the IVC and TEOW to develop a platform for global grassland conservation policies. Furthermore, describing grasslands and their spatial distribution through a hierarchy of ecological and vegetation types provides decision-makers with robust information on global grassland biodiversity patterns.

We have demonstrated that an important threshold in spatial scale occurs at the division level, given that species differentiation emerges here. The formation level does not include species, and is only based on climate and distinctive combinations of growth forms. For example, within the temperate grassland formation, there is little to no species overlap between the Eastern Eurasian Grassland & Shrubland division and the Great Plains Grassland & Shrubland division. It is thus at the division level that biodiversity indicators such as species richness, abundance and endemism may begin to be used, facilitating management and policy decisions (Faber-Langendoen & Josse, 2010). However, development of the level below division, that of macrogroup (Faber-Langendoen *et al.*, 2014), would greatly enhance the specificity of the grassland types, because it is more comparable to types used by other widely used classifications. For example, the macrogroup is comparable to the Braun-Blanquet 'class' widely used in Europe and elsewhere (Rodwell *et al.*, 2002).

Table 3 International Vegetation Classification (IVC) formations and divisions with substantial grasslands showing distribution by Terrestrial Ecoregions of the World (TEOW). TEOW where grassland occupied < 10% of the ecoregion are not shown.

IVC Formation	IVC Division	TEOW
Alpine Scrub, Forb Meadow & Grassland	Australian Alpine Scrub, Forb Meadow & Grassland	Australian Alps montane grasslands
	Central Asian Alpine Scrub, Forb Meadow & Grassland	Altai alpine meadow and tundra
		Altai montane forest and forest steppe
		Central Tibetan Plateau alpine steppe
		Eastern Himalayan alpine shrub and meadows
		Karakoram-West Tibetan Plateau alpine steppe
		North Tibetan Plateau-Kunlun Mountains alpine desert
		Northwestern Himalayan alpine shrub and meadows
		Qilian Mountains subalpine meadows
		Sayan Alpine meadows and tundra
		Southeast Tibet shrublands and meadows
		Tian Shan montane steppe and meadows
		Tibetan Plateau alpine shrublands and meadows
		Western Himalayan alpine shrub and Meadows
		Yarlung Tsangpo arid steppe
	European Alpine Vegetation	Alps conifer and mixed forests
	New Zealand Alpine Scrub, Forb Meadow & Grassland	South Island montane grasslands
Boreal Grassland, Meadow & Shrubland	Eurasian Boreal Grassland, Meadow & Shrubland	Faroe Islands boreal grasslands
		Scandinavian Montane Birch forest and grasslands
Tropical Montane Shrubland, Grassland & Savanna	African (Madagascan) Montane Grassland and Shrubland	Madagascar ericoid thickets
	African Montane Grassland and Shrubland	Angolan montane forest-grassland mosaic
		East African montane moorlands
		Eastern Zimbabwe montane forest-grassland mosaic
		Ethiopian montane grasslands and woodlands
		Ethiopian montane moorlands
		Jos Plateau forest-grassland mosaic
		Rwenzori-Virunga montane moorlands
		Southern Rift montane forest-grassland mosaic
	Brazilian-Parana Montane Shrubland and Grassland	Campos Rupestres montane savanna
	Guianan Montane Shrubland and Grassland	Pantepui
	Indomalayan Montane Meadow	Kinabalu montane alpine meadows
	New Guinea Montane Meadow	Central Range sub-alpine grasslands
	Southern African Montane Grassland	Highveld grasslands
		Drakensberg alti-montane grasslands and woodlands
		Drakensberg montane grasslands, woodlands and forests
	Tropical Andean Shrubland & Grassland	Central Andean wet puna
		Cordillera Central páramo
		Cordillera de Merida páramo
		Northern Andean páramo
Tropical Freshwater Marsh, Wet Meadow & Shrubland	Parana-Brazilian Freshwater Marsh, Wet Meadow & Shrubland	Pantanal
	Chaco Freshwater Marsh and Shrubland	Humid Chaco
	Colombian-Venezuelan Freshwater Marsh, Wet Meadow & Shrubland	Guayaquil flooded grasslands

Table 3 Continued

IVC Formation	IVC Division	TEOW
Tropical Lowland Shrubland, Grassland & Savanna	Amazonian Shrubland & Savanna	Rio Negro campinarana
	Australian Tropical Savanna	Arnhem Land tropical savanna
		Brigalow tropical savanna
		Cape York Peninsula tropical savanna
		Carpentaria tropical savanna
		Einasleigh upland savanna
		Kimberly tropical savanna
		Mitchell Grass Downs
		Trans Fly savanna and grasslands
		Victoria Plains tropical savanna
	Brazilian-Parana Lowland Shrubland, Grassland & Savanna	Beni savanna
		Cerrado
	Colombian-Venezuelan Lowland Shrubland, Grassland & Savanna	Llanos
	Eastern and Southern African Dry Savanna & Woodland	Kalahari xeric savanna
		Victoria Basin forest-savanna mosaic
	Guianan Lowland Shrubland, Grassland & Savanna	Guianan savanna
	Miombo and Associated Broadleaf Savanna	Zambezian Baikiaea woodlands
		Western Zambezian grasslands
	Mopane Savanna	Angolan Mopane woodlands
		Southern Africa bushveld
		Zambezian and Mopane woodlands
	North Sahel Semi-Desert Scrub and Grassland	Sahelian Acacia savanna
	Sudano Sahelian Dry Savanna	West Sudanian savanna
	West-Central African Mesic Woodland and Savanna	Angolan scarp savanna and woodlands
		East Sudanian savanna
		Guinean forest-savanna mosaic
		Saharan flooded grasslands
Mediterranean Scrub, Grassland & Forb Meadow	Australian Mediterranean Scrub	Coolgardie woodlands
		Esperance mallee
		Eyre and York mallee
		Mount Lofty woodlands
		Murray-Darling woodlands and mallee
		Southwest Australia savanna
		Swan Coastal Plain scrub and woodlands
	California Grassland & Meadow	California Central Valley grasslands
		California interior chaparral and woodlands
	Mediterranean Basin Dry Grassland	Mediterranean dry woodlands and steppe
		Middle East steppe
	Pampean Grassland & Shrubland (Semi-arid Pampa)	Espinal
	South African Cape Mediterranean Scrub	Lowland fynbos and renosterveld
Temperate Grassland, Meadow & Shrubland	Australian Temperate Grassland & Shrubland	Southeast Australia temperate savanna
	Eastern Eurasian Grassland & Shrubland	Daurian forest steppe
		Gissaro-Alai open woodlands
		Kazakh forest steppe
		Mongolian-Manchurian grassland
		Nenjiang River grassland
		Terai-Duar savanna and grasslands
		Selenge-Orkhon forest steppe
		South Siberian forest steppe

Table 3 Continued

IVC Formation	IVC Division	TEOW
	Great Plains Grassland & Shrubland	Canadian Aspen forests and parklands
		Central and Southern mixed grasslands
		Central forest-grasslands transition
		Central tall grasslands
		Edwards Plateau savanna
		Flint Hills tall grasslands
		Montana Foothill grasslands
		Nebraska Sand Hills mixed grasslands
		Northern mixed grasslands
		Northern short grasslands
		Northern tall grasslands
		Palouse grasslands
		Texas blackland prairies
		Western Gulf coastal grasslands
		Western short grasslands
	New Zealand Grassland & Shrubland	Canterbury-Otago tussock grasslands
	Northeast Asia Grassland & Shrubland	Amur meadow steppe
		Bohai Sea saline meadow
		Suiphun-Khanka meadows and forest meadows
		Yellow Sea saline meadow
	Pampean Grassland & Shrubland	Humid Pampas
		Uruguayan savanna
	Patagonian Grassland and Shrubland	Patagonian steppe
	Western Eurasian Grassland & Shrubland	Central Anatolian steppe
		East European forest steppe
Cool Semi-Desert Scrub & Grassland	Eastern Eurasian Cool Semi-Desert Scrub & Grassland	Altai steppe and semi-desert
		Badghyz and Karabil semi-desert
		Eastern Gobi desert steppe
		Emin Valley steppe
		Great Lakes Basin desert steppe
		Kazakh semi-desert
		Kazakh steppe
		Kazakh upland
		Ordos Plateau steppe
		Qaidam Basin semi-desert
		Sayan Intermontane steppe
		Tian Shan foothill arid steppe
	Mediterranean and Southern Andean Cool Semi-Desert Scrub & Grassland	Southern Andean steppe
	Patagonian Cool Semi-Desert Scrub & Grassland	Low Monte
	Tropical Andean Cool Semi-desert Scrub & Grassland	Central Andean dry puna
	Western Eurasian Cool Semi-Desert Scrub & Grassland	Alai-Western Tian Shan steppe
		Eastern Anatolian montane steppe
		Kopet Dag woodlands and forest steppe
		Pontic steppe
	Western North American Cool Semi-Desert Scrub & Grassland	Great Basin shrub steppe
		Montana Valley grasslands
		Snake-Columbia shrub steppe
		Wyoming Basin shrub steppe
Warm Semi-Desert Scrub & Grassland	Australia Warm Semi-Desert Scrub & Grassland	Great Sandy-Tanami desert
	Eastern Africa Xeric Scrub and Grassland	Masai xeric grasslands and shrublands
		Northern Acacia-Commiphora bushlands and thickets

Table 3 Continued

IVC Formation	IVC Division	TEOW
		Southern Acacia-Commiphora bushlands and thickets
		Somali Acacia-Commiphora bushlands and thickets
	North American Warm Desert Scrub & Grassland	Chihuahuan desert

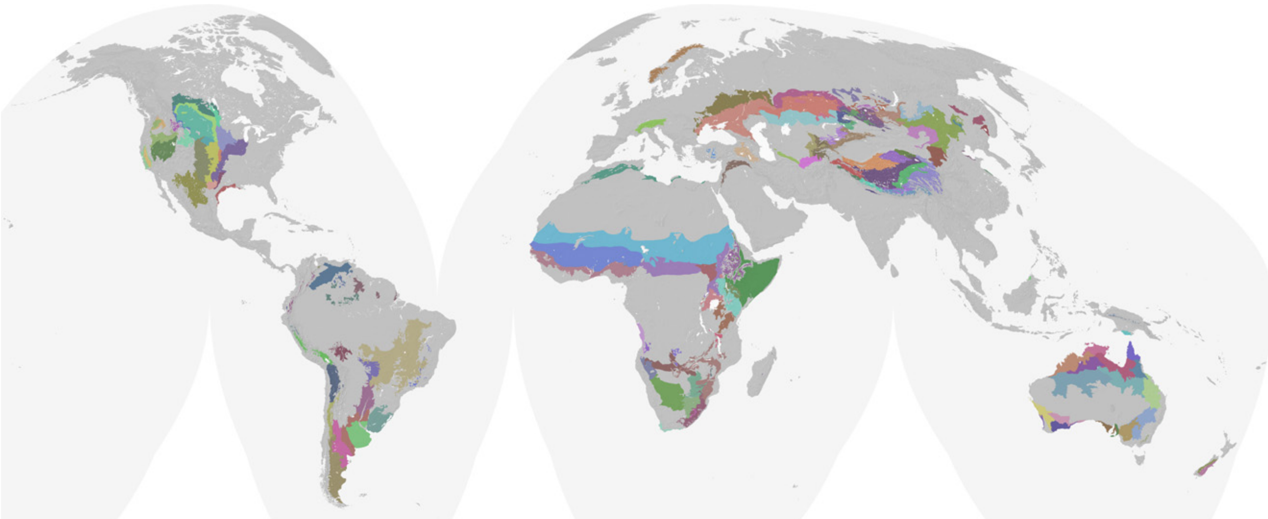

Figure 3 Terrestrial Ecoregions of the World (TEOW) containing at least 10% of the total area dominated by grassland types. A total of 145 ecoregions were determined to contain dominant grassland types described by the International Vegetation Classification (IVC).

Our criterion of excluding ecoregions with < 10% grassland cover meant that ecoregions where grasses may be common but within woodland systems are omitted. Such ecoregions include the Canadian Aspen forests and parklands at the northern reach of the North American Great Plains division, the Mediterranean dry woodlands and steppe, and the South American dry Chaco. The criterion also led to the exclusion of some semi-deserts, where aridity and edaphic conditions may limit the potential for vegetation growth, but allowed for inclusion of open semi-desert grassland in the North American Chihuahuan desert and the South American Patagonian steppe, and the high montane grasslands of the South American Puna, since at least 10% of their total area corresponds with our grassland definition.

The criterion for trees to have no more than 10% (temperate) or 40% (tropical) cover, and be typically greater than 5 m (temperate) to 8 m (tropical) was critical to evaluating African and Latin American savannas, especially those surrounding the forests of the Congo basin. It resulted in the exclusion of some woodlands that contain a substantial grassland layer, for example African miombo, southern Congolian woodlands, and South American Caatinga, each containing tropical seasonally dry forest or scrub as the dominant vegetation. We included the Cerrado, which historically contained many areas with greater than 40% tree canopy cover, but at least 10% of the ecoregion probably had < 40% tree canopy over 8 m tall with a dominant grass layer, thus qualifying it for inclusion as a grassland ecoregion.

Meanwhile, in the temperate region, many forest–savanna transitional areas, such as the Midwest forest–savanna transition of North America were excluded as grasslands because of the threshold of 10% tree cover with 5 m height. Similarly, the dehesas and montados of the Iberian peninsula (Marañón, 1988; Joffre & Rambal, 2006) were excluded because they contain semi-natural and cultural grassland components in an open woodland matrix, and probably had higher tree canopy cover historically. Nevertheless, a lack of information on the extent and composition of these ecosystems prior to major land use change makes current assessments a challenge.

The IVC places many of the wetland complex/river delta ecosystems in the wetlands formations, resulting in the exclusion of the Nile delta flooded savanna and the Everglades, where grasses may occasionally be dominant. Conversely, there are also grassland types that, while they occur largely

Table 4 International Vegetation Classification (IVC) formations and divisions containing grassland types without a corresponding Terrestrial Ecoregion of the World (TEOW) due to their fine-scale, patchy distribution. The IVC formations are italicized, while the IVC divisions are regular type.

Alpine Scrub, Forb Meadow & Grassland
Southern African Alpine Vegetation
Eastern North American Alpine Scrub, Forb Meadow & Grassland
Western North American Alpine Scrub, Forb Meadow & Grassland
Tropical Montane Shrubland, Grassland & Savanna
Caribbean and Central American Montane Shrubland and Grassland
Polynesian Montane Shrubland, Grassland & Savanna
Eastern Melanesian Montane Shrubland, Grassland & Savanna
Tropical Lowland Shrubland, Grassland & Savanna
Indomalayan Mesic Savanna and Grasslands
Polynesian Lowland Shrubland, Grassland & Savanna
Eastern Melanesian Lowland Shrubland, Grassland & Savanna
Mediterranean Grassland & Forb Meadow
Mediterranean Basin Montane Grassland & Scrub
Temperate Grassland, Meadow & Shrubland
Vancouverian and Rocky Mountain Grassland & Shrubland
Eastern North American Grassland, Meadow & Shrubland
Western North America Interior Sclerophyllous Chaparral Shrubland
Southeastern North American Grassland & Shrubland
European Grassland & Heath
Boreal Grassland, Meadow & Shrubland
North American Boreal Grassland, Meadow & Shrubland

Table 5 The distribution of International Vegetation Classification (IVC) grassland types per continent. We describe 49 global IVC grassland divisions, with the Mediterranean Basin Dry Grassland IVC division occurring in both Africa and Eurasia.

IVC divisions with dominant grassland types per continent	
South America	16
Africa–Madagascar	12
Eurasia	9
Australia	5
North America	4
Oceania	4

within wetland complexes, contain sufficient historical upland grassland communities to be considered grassland by our definition, for example the Guayaquil flooded grasslands in north-western South America.

Thirteen IVC divisions were too limited in distribution to be effectively mapped with our approach, owing to differences in scale between the IVC and TEOW. In some cases, there was no correspondence of TEOW in IVC divisions in montane and alpine elevations, as well as island ecosystems, as small glade or grassy openings in otherwise forested landscapes, or as locally specialized substrate-based ecosystems (e.g. serpentine grassland). Yet because the vegetation types in these places are taxonomically distinct, they warrant a unique IVC division. These divisions highlight the need for a

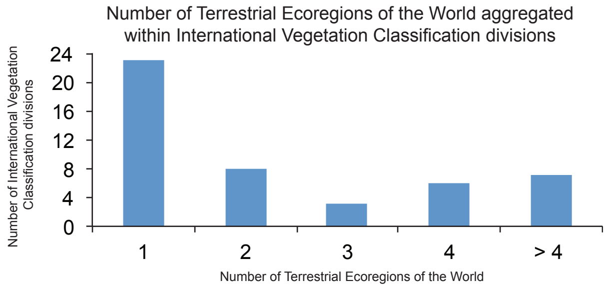

Figure 4 Distribution of Terrestrial Ecoregions of the World (TEOW) with dominant grassland types described by International Vegetation Classification (IVC) divisions, demonstrating that most IVC divisions correspond to four or fewer ecoregions. Seven IVC divisions were an aggregation of more than four ecoregions. For example, the Great Plains Grassland & Shrubland is an aggregation of 15 ecoregions.

spatial refinement of TEOW, which is a spatial representation of ecosystem expression in a two-tiered hierarchy (biome, ecoregion) nested within biogeographical realms (Olson *et al.*, 2001). The IVC, on the other hand, is a non-spatial vegetation-ecological approach that allows for eight levels of ecological vegetation types. When distinctive combinations of physiognomy, composition and ecology are found to diverge, the IVC is capable of creating a lower level in the hierarchy. As we have demonstrated here, there are significant correspondences between IVC and TEOW with 75% formation/biome and division/ecoregion levels matching when grasslands are dominant components of the landscape. The correspondence decreases where grassland ecosystems occur as small patches or on sites atypical of the TEOW ecosystem regionalization process.

This first approximation of our mapping effort will benefit from further resolving grassland types at finer biogeographical scales. This will take considerable more effort but can build on efforts such as *The vegetation of Africa* (White, 1983), *The vegetation of South Africa, Lesotho and Swaziland* (Mucina & Rutherford, 2006), *A new map of standardized terrestrial ecosystems of Africa* (Sayre *et al.*, 2013), the *Ecological systems of Latin America and the Caribbean* (Josse *et al.*, 2003), and the *Ecological systems of North America* (NatureServe, 2009). As noted above, these efforts help establish more detailed concepts at the macrogroup mid-level to attain levels of grassland type specific enough to guide global assessments such as the IUCN Red List of Ecosystems (Keith *et al.*, 2013). Our approach can help set the stage for this work in terms of distribution and definition, as has been done for other major formations, such as tropical dry forest (Miles *et al.*, 2006). A refinement of our analysis of global grassland types could adjust the current spatial boundaries incorporating remote sensing, and spatial analysis to capture the finer scale IVC units at the desired hierarchical level.

Validation of these maps is an important next step. Increasingly detailed land cover and ecosystem maps are becoming available across the globe [e.g. Sayre *et al.*, 2013,

Table 6 Land area of each International Vegetation Classification (IVC) division with dominant grassland types.

IVC Division	Area (km^2)
North Sahel Semi-Desert Scrub and Grassland	3,042,404
Great Plains Grassland & Shrubland	2,982,562
Eastern Eurasian Cool Semi-Desert Scrub & Grassland	2,853,283
Central Asian Alpine Scrub, Forb Meadow & Grassland	2,803,147
Australian Tropical Savanna	2,151,165
Eastern Eurasian Grassland & Shrubland	2,115,940
Brazilian-Parana Lowland Shrubland, Grassland & Savanna	2,035,627
West-Central African Mesic Woodland and Savanna	1,837,498
Eastern Africa Xeric Scrub and Grassland	1,701,057
Sudano Sahelian Dry Savanna	1,631,860
Western Eurasian Cool Semi-Desert Scrub & Grassland	1,351,143
Mopane Savanna	827,443
Australia Warm Semi-Desert Scrub & Grassland	820,767
Eastern and Southern African Dry Savanna & Woodland	751,888
Pampean Grassland & Shrubland	751,051
Western Eurasian Grassland & Shrubland	750,819
Western North American Cool Semi-Desert Scrub & Grassland	723,332
Australian Mediterranean Scrub	719,191
Patagonian Grassland and Shrubland	554,804
North American Warm Desert Scrub & Grassland	508,892
Mediterranean Basin Dry Grassland	424,371
Southern African Montane Grassland	399,718
Colombian-Venezuelan Lowland Shrubland, Grassland & Savanna	375,787
African Montane Grassland & Shrubland	354,878
Patagonian Cool Semi-Desert Scrub & Grassland	353,640
Australian Temperate Grassland & Shrubland	321,999
Pampean Grassland & Shrubland (semi-arid Pampa)	298,735
Miombo and Associated Broadleaf Savanna	297,444
Chaco Freshwater Marsh and Shrubland	291,590
Tropical Andean Cool Semi-Desert Scrub & Grassland	254,929
Eurasian Boreal Grassland, Meadow & Shrubland	246,322
Northeast Asia Grassland & Shrubland	174,343
Brazilian-Parana Freshwater Marsh, Wet Meadow & Shrubland	170,501
Tropical Andean Shrubland & Grassland	161,602
European Alpine Scrub, Forb Meadow & Grassland	149,871
Mediterranean and Southern Andean Cool Semi-Desert Scrub & Grassland	124,779
California Grassland & Meadow	119,712
Guianan Lowland Shrubland, Grassland & Savanna	104,496
Amazonian Shrubland & Savanna	95,986
New Zealand Grassland & Shrubland	53,594
New Zealand Alpine Scrub, Forb Meadow & Grassland	40,006
South African Cape Mediterranean Scrub	32,744
Guianan Montane Shrubland and Grassland	27,534

Table 6 Continued

IVC Division	Area (km^2)
Brazilian-Parana Montane Shrubland and Grassland	26,247
New Guinea Montane Meadow	15,503
Australian Alpine Scrub, Forb Meadow & Grassland	11,999
Indomalayan Montane Meadow	4,320
Colombian-Venezuelan Freshwater Marsh, Wet Meadow & Shrubland	2,924
African (Madagascan) Montane Grassland and Shrubland	1,273

for Africa; and LANDFIRE for the USA (LANDFIRE, 2013)] and could be used to document the current extent of grasslands. In addition, teams of division-based grassland experts could be formed to create models of grassland extent prior to major land use change.

CONCLUSIONS

We believe that our approach of linking vegetation with ecoregions provides a timely framework for policy use. Our global grassland map could support the environmental management goals advocated in the Millennium Ecosystem Assessment (2005), and it may serve as a tool to help convince policy makers and land managers of the conservation value of grassland ecosystems, especially those with high rates of conversion. The definition of grassland that we offer provides a set of criteria that policy makers can use to guide conservation decisions, such as setting sustainability criteria for maintaining native grasslands. The definition also sets the stage for describing the diversity of grasslands around the world through ecosystem mapping, illustrated by the broad-scale distribution map that we provide here.

An analysis of grassland conversion within the mapped IVC divisions is an important next step. Remotely sensed Earth observation data can be used to document explicit rates of conversion due to agricultural activities, such as cultivation of commodity crops and grazing (Ramankutty *et al.*, 2008; Miles *et al.*, 2006).

We hope that the integration of ecoregions and grassland classification will assist ecosystem management efforts through the current period of global economic expansion and population growth. This new map can contribute to improving other quantitative metrics of biodiversity, such as species richness, endemism, abundance, and ecological integrity in relation to the spatial extent where they occur, allowing decision-makers the ability to evaluate species and ecosystems as part of a larger biodiversity matrix of landscape function and process (Noss, 1990, 1999). These metrics may be custom-tailored to the diverse set of grassland types present around the world. Within each grassland division, we can work towards specifying minimum areas of ecological integrity to ensure the persistence of these broad-scale ecosystems in the face of anthropogenic stressors. Finally, combining our dataset and the World Database on Protected Areas (IUCN & UNEP, 2010) can potentially allow us to assess current levels of protection, which would be of value in ensuring that grasslands can continue to provide a variety of high-value ecosystem services.

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REFERENCES

Ash, A.J., McIvor, J.G., Mott, J.J. & Andrew, M.H. (1997) Building grass castles: integrating ecology and management of Australia's tropical tallgrass rangelands. *Rangeland Journal*, **19**, 123–144.

Bailey, R.G. (1996) *Ecosystem geography*. Springer, New York.

Baldwin, K.A. & Meades, W.J. (2008) Canadian National Vegetation Classification. *Proceedings of the Fourth International Conservation of Arctic Flora and Fauna (CAFF) Flora Group Workshop, 15–18 May 2007, Torshavn, Faroe Islands* (ed. by S.S. Talbot), pp. 66–69. CAFF Technical Report No. 15. Akureyri, Iceland.

Bontemps, S., Defourny, P., Van Bogaert, E., Arino, O., Kalogirou, V. & Perez, E.V. (2011) *Globcover 2009 products description and validation report*. European Space Agency & Université catholique de Louvain. Available at: http://due.esrin.esa.int/globcover/LandCover2009/GLOBCOVER2009_Validation_Report_2.2.pdf.

Box, E.O. (1981) *Macroclimate and plant forms: an introduction to predictive modeling in phytogeography*. Dr. W. Junk, The Hague, Belgium.

Breymeyer, A.I. (1987–1990) *Managed grasslands: regional studies*. Elsevier, Amsterdam.

Brown, D.E. (1982) *The biotic communities of the American southwest – United States and Mexico.* General Technical Report RM-78. U.S. Forest Service, Fort Collins, CO. Reprinted with revisions in 1994 by University of Utah Press, Salt Lake City, UT.

Bucini, G. & Hanan, N. (2007) A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography*, **16**, 593–605.

Coupland, R.T. (1979) *Grassland ecosystems of the world*. Cambridge University Press, Cambridge, UK.

Coupland, R.T. (1992) *Ecosystems of the world: natural grasslands: introduction and western hemisphere*, Vol. 8A. Elsevier, Amsterdam.

Davies, C.E., Moss, D. & Moss, M.O. (2004) *EUNIS habitat classification revised 2004*. Report to the European Topic Centre on Nature Protection and Biodiversity, European Environment Agency, Paris.

Defries, R., Hansen, M. & Townshend, J. (1995) Global discrimination of land cover types from metrics derived from AVHRR Pathfinder data. *Remote Sensing of the Environment*, **54**, 209–222.

DiGregario, A. & Janssen, L.J.M. (1998) *Land Cover Classification System (LCCS): classification concepts and user manual*. Environment and Natural Resources Service, GCP/RAF/287/ITA Africover – East Africa Project and Soil Resources, Management and Conservation Service. Food and Agriculture Organization of the United Nations (FAO), Rome.

Edwards, E.J., Osborne, C.P., Strömburg, C.A.E. & Smith, S.A. (2010) The origins of C_4 grasslands: integrating evolutionary and ecosystem science. *Science*, **328**, 587–591.

Ellenberg, H. (1988) *Vegetation ecology of central Europe*, 4th edn, English translation (translated by Gordon K. Strutt). Cambridge University Press, Cambridge, UK.

European Commission (2009) Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009 on the promotion of the use of energy from renewable sources and amending and subsequently repealing Directives 2001/77/EC and 2003/30/EC. *Official Journal of the European Union,* **L 140**, 16–62.

Faber-Langendoen, D. & Josse, C. (2010) *World grasslands and biodiversity patterns*. NatureServe, Arlington, VA.

Faber-Langendoen, D., Tart, D.L. & Crawford, R.H. (2009) Contours of the revised U.S. National Vegetation Classification standard. *Bulletin of the Ecological Society of America*, **90**, 87–93.

Faber-Langendoen, D., Keeler-Wolf, T., Meidinger, D., Josse, C., Weakley, A., Tart, D., Navarro, G., Hoagland, B., Ponomarenko, S., Saucier, J., Fults, G. & Helmer, E. (2012) *Classification and description of world formation types. Part I (Introduction) and Part II (Description of formation types, v2.0)*. Hierarchy Revisions Working Group, Federal Geographic Data Committee, FGDC Secretariat, U.S. Geological Survey, Reston, VA, and NatureServe, Arlington, VA.

Faber-Langendoen, D., Keeler-Wolf, T., Meidinger, D., Tart, D., Hoagland, B., Josse, C., Navarro, G., Ponomarenko, J.P.S., Weakley, A. & Comer, P. (2014) EcoVeg: a new approach to vegetation description and classification. *Ecological Monographs*, in press.

FAO (2010) *Global forest resources assessment*. Food and Agriculture Organization of the United Nations (FAO), Rome.

Federal Geographic Data Committee (2008) *National Vegetation classification standard, version 2*. Federal Geographic Data Committee (FGDC), FGDC-STD-005-2008. Vegetation Subcommittee, U.S. Geological Survey, Reston, VA.

Foley, J.A., Ramankutty, N., Brauman, K.A. *et al.* (2011) Solutions for a cultivated planet. *Nature*, **478**, 337–342.

Gavier-Pizarro, G.I., Calamari, N.C., Thompson, J.J., Canavelli, S.B., Solari, L.M., Decarre, J., Goijman, A.P., Suarez, R.P., Bernardos, J.N. & Zaccagnini, M.E. (2012) Expansion and intensification of row crop agriculture in the Pampas and Espinal of Argentina can reduce ecosystem service provision by changing avian density. *Agriculture, Ecosystems and Environment*, **154**, 44–55.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N. & Foley, J.A. (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences USA*, **107**, 16732–16737.

Gibson, D.J. (2009) *Grasses and grassland ecology*. Oxford University Press, New York.

Guinin (2005) *Ecosystems of Mongolia (map)*. WWF-Mongolia; WWF-Russia, Moscow.

Hoesktra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.

Holdridge, L.R. (1967) *Life zone ecology*. Tropical Science Center, San José, Costa Rica.

House, J.I., Archer, S., Breshears, D.D. & Scholes, R.J. (2003) Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography*, **30**, 1763–1777.

IUCN and UNEP (2010) *The World Database on Protected Areas*. UNEP-WCMC, Cambridge, UK. http://www.protectedplanet.net/ (accessed 5 June 2013).

Jacobs, B.F., Kingston, J.D. & Jacobs, L.L. (1999) The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden*, **86**, 590–643.

Joffre, R. & Rambal, S. (2006) Tree–grass interactions in the south-western Iberian Peninsula *dehesas* and *montados*. *Sécheresse*, **17**, 340–342.

Josse, C., Navarro, G., Comer, P., Evans, R., Faber-Langendoen, D., Fellows, M., Kittel, G., Menard, S., Pyne, M., Reid, M., Schulz, K., Snow, K. & Teague, J. (2003) *Ecological systems of Latin America and the Caribbean: a working classification of terrestrial systems*. NatureServe, Arlington, VA.

Keith, D.A., Rodríguez, J.P., Rodríguez-Clark, K.M. *et al.* (2013) Scientific foundations for an IUCN Red List of ecosystems. *PLoS ONE*, **8**, 5.

Kucera, C.L. (1981) Grasslands and fire. *Fire regimes and ecosystem properties* (ed. by H.A. Mooney, T. M Bonnicksen, N.L. Christensen, J.E. Lotan and W.A. Reiners), pp. 90–111. USDA Forest Service Technical Report WO-26, Washington, DC.

Küchler, A.W. (1969) Natural and cultural vegetation. *The Professional Geographer*, **21**, 383–385.

LANDFIRE (2013) *LANDFIRE: LANDFIRE existing vegetation type layer*. Department of Interior, Geological Survey, United States. Available at: http://www.landfire.gov/(accessed 23 October 2013).

Landis, D.A. & Weling, B.P. (2010) Arthropods and biofuel production systems in North America. *Insect Science*, **17**, 220–236.

Li, W.J., Ali, S.H. & Zhang, Q. (2006) Property rights and grassland degradataion: a study of the Xilingol Pasture, Inner Mongolia, China. *Journal of Environmental Management*, **85**, 461–470.

Lincoln, R., Boxshall, G. & Clark, P. (1998) *A dictionary of ecology, evolution and systematics*. Cambridge University Press, Cambridge, UK.

Lock, J.M. (2006) The seasonally dry vegetation of Africa: parallels and comparisons with the neotropics. *The neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation* (ed. by R.T. Pennington and J.A. Ratter), pp. 449–468. CRC Press, Boca Raton, FL.

Lonsdale, W.M. (1994) Inviting trouble: introduced pasture species in northern Australia. *Australian Journal of Ecology*, **19**, 345–354.

Loveland, T.R. & Belward, A.S. (1997) The IGBP-DIS global 1 km land cover data set, DISCover: first results. *International Journal of Remote Sensing*, **18**, 3289–3295.

Maeda, E.E., Pellikka, P.K.E., Siljander, M. & Clark, B.J.F. (2010) Potential impacts of agricultural expansion and climate change on soil erosion in the Eastern Arc Mountains of Kenya. *Geomorphology*, **123**, 279–289.

Marañón, T. (1988) Agro-sylvo-pastoral systems in the Iberian Peninsula: Dehesas and Montados. *Rangelands*, **10**, 255–258.

Matthews, G.V.T. (1993) *The Ramsar Convention on wetlands: its history and development* (Ramsar, 1993). PDF version, re-issued 2013. Ramsar, Gland, Switzerland (in English only).

Miles, L., Newton, A., DeFries, R., Ravilious, C., May, I., Blyth, S., Kapos, V. & Gordon, J.E. (2006) A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, **33**, 491–505.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: current state and trends*, Vol. 1. Island Press, Washington, DC.

Mucina, L. & Rutherford, M.C. (eds) (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. John Wiley and Sons, New York.

NatureServe (2009) *International ecological classification standard: terrestrial ecological classifications*. NatureServe Central Databases, Arlington, VA.

Navarro, G. (2011) *Clasificación de la vegetación de Bolivia*. Centro de Ecología Difusión Simón I Patiño, Santa Cruz, Bolivia.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.

Noss, R.F. (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. *Forest Ecology and Management*, **115**, 135–146.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, **51**, 933–938.

Pereladova, O. (2002) *Development of the Econet for long-term conservation in the Central Asia Ecoregions*. WWF-Russia, Moscow. Available at: http://www.wwf.ru/about/where_we_work/asia/closed/econet/eng (accessed 22 April 2013).

Pignatti, S., Oberdorfer, E., Schaminée, J.H.J. & Westhoff, V. (1994) On the concept of vegetation class in phytosociology. *Journal of Vegetation Science*, **6**, 143–152.

Qiu, H., Huang, J., Yang, J., Rozelle, S., Zhang, Y., Zhang, Y. & Zhang, Y. (2010) Bioethanol development in China and the potential impacts on its agricultural economy. *Applied Energy*, **87**, 76–83.

Ramankutty, N., Evan, A.T., Monfreda, C. & Foley, J.A. (2008) Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles*, **22**, 1–19.

Raunkiær, C. (1934) *The life forms of plants and statistical plant geography*. Clarendon Press, Oxford, UK.

Rodríguez, J.P., Rodríguez-Clark, K.M., Baillie, J.E.M. *et al.* (2010) Establishing IUCN Red List criteria for threatened ecosystems. *Conservation Biology*, **25**, 21–29.

Rodríguez, J.P., Rodríguez-Clark, K.M., Keith, D.A., Barrow, E.G., Benson, J., Nicholson, E. & Wit, P. (2012) *IUCN Red List of Ecosystems*. S.A.P.I.E.N.S. [Online], 5. Available at: http://sapiens.revues.org/1286 (accessed 12 February 2013).

Rodwell, J.S., Schamineé, J.H.J., Mucina, L., Pignatti, S., Dring, J. & Moss, D. (2002) *The diversity of European vegetation. An overview of phytosociological alliances and their relationships to EUNIS habitats*. Report EC-LNV nr. 2002/054. Wageningen, The Netherlands.

Sayre, R., Comer, P., Hak, J. *et al.* (2013) *A new map of standardized terrestrial ecosystems of Africa*. Association of American Geographers, Washington, DC.

Scholes, R.J. & Archer, S.R. (1997) Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.

Scholes, R.J. & Hall, D.O. (1996) The carbon budget of tropical savannas, woodlands, and grasslands. *Global change: effects on coniferous forests and grasslands* (ed. by A.K. Breymeyer, D.O. Hall, J.M. Melillo and G.I. Agren) pp. 69–100. SCOPE, Vol. 56. Wiley, Chichester, UK.

Schultz, J. (1995) *The ecozones of the world*. Springer-Verlag, New York.

Sun, S-z. (1989) The vegetation of Qaidam Basin and its surrounding mountains. *Acta Phytoecologica et Geotanica Sinica*, **13**, 3 (English abstract).

Suttie, J.M., Reynolds, S.G. & Batello, C. (2005) *Grasslands of the world*. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.

UNESCO (1973) *International classification and mapping of vegetation, Series 6, Ecology and Conservation*. United Nations, Paris, France.

Uvardy, M.D.F. (1975) *A classification of the biogeographical provinces of the world*. IUCN Occasional Paper no. 18. IUCN, Morges, Switzerland.

Walter, H. & Box, E. (1976) Global classification of natural terrestrial ecosystems. *Vegetatio*, **32**, 75–81.

Westhoff, V. & van der Maarel, E. (1973) The Braun-Blanquet approach. *Handbook of vegetation science, Part V. Ordination and classification of communities* (ed. by R.H. Whittaker), 617–726. W. Junk, The Hague, The Netherlands.

White, F. (1983) *The vegetation of Africa*. UNESCO, Paris.

White, R., Murray, S. & Rohweder, M. (2001) *Grassland ecosystems: pilot analysis of global ecosystems*. World Resources Institute, Washington, DC.

Whittaker, R.H. (1975) *Communities and ecosystems*, 2nd edn. Macmillan, London.

Wikramanayake, E., Dinerstein, E., Loucks, C.J., Olson, D.M., Morrison, J., Lamoreux, J., McKnight, M. & Hedao, P. (2002) *Terrestrial ecoregions of the Indo-Pacific: a conservation assessment*. Island Press, Washington, DC.

Wovcha, D.S., Delaney, B.C. & Nordquist, G.E. (1995) *Minnesota's St. Croix River Valley and Anoka Sandplain: a guide to native habitats*. University of Minnesota Press, Minneapolis, MN.

Zhao, Y. & Herzschuh, U. (2009) Modern pollen representation of source vegetation in the Qaidam Basin and surrounding mountains, north-eastern Tibetan Plateau. *Vegetation History and Archaeobotany*, **18**. 245–260.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Types of ecosystem classification and mapping approaches.

Appendix S2 Grassland ecosystem characterization review: (a) African and Malagasy grasslands; (b) Australian and oceanic grasslands; (c) Eurasian grasslands; (d) North American grasslands; (e) South American grasslands.

DATA ACCESSIBILITY

GIS data produced by this report may be obtained from: http://www.worldwildlife.org/pages/conservation-science-data-and-tools.

BIOSKETCH

Adam Dixon is a Conservation Geographer, interested in observing biodiversity at the landscape to global scale, based at World Wildlife Fund – United States. His work includes applications in land use planning and ecosystem service analysis.

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