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Global Spatial–Temporal Variability in Terrestrial Productivity and Phenology Regimes between 2000 and 2012

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The productivity and phenology of vegetation are spatially and temporally variable ecosystem functions. Monitoring spatial–temporal patterns in these functions can improve our understanding of global change and natural ecosystem variability and inform management actions. Researchers typically focus on temporal changes within or among static regions and omit dynamics of spatial configuration. Our goal was to assess global spatial–temporal variability in productivity and phenology regimes between 2000 and 2012 using a temporally dynamic functional type classification. Fourteen functional types were defined for each year by clustering the annual sum and annual variability (seasonality) of the fraction of photosynthetically active radiation (fPAR)—a biophysical proxy for vegetation greenness or productivity—from the Moderate Resolution Imaging Spectrometer (MODIS). The fourteen functional types ranged from tundra (low cumulative fPAR and highly seasonal) to tropical forests (high cumulative fPAR and low seasonality). Variability in the mean of the fPAR metrics and in two spatial pattern metrics was assessed for each functional type. Many pixels changed from one cluster to another then back again, suggesting considerable short-term variability. Temporal variability in the mean of the fPAR metrics was relatively low, with changes instead primarily manifested in spatial pattern. Spatial pattern was most variable within tundra, grasslands, shrublands, and savannas. A dynamic classification demonstrated the variability in spatial patterns of primary productivity and can be used for future monitoring. *Key Words:* ecosystem function, fPAR, MODIS, monitoring, regionalization.

植栽的生产力与生物气候,在时间与空间上是多变的生态系统功能。监测这些功能中的时空模式,能够改进我们对于全球变迁和自然生态系统变化的理解,并告知管理的行动。研究者一般聚焦静态区域中或区域间的时间变迁,并忽略空间组成的动态。我们的目标便是利用时间上动态的功能类别,评估2000年至2012年间,生产力与生物气候体制中的全球时空变异。我们透过聚集中级分辨率成像光谱仪(MODIS)上光合作用仍然活跃的部分辐射(fPAR)——一种植栽绿化或生产力的生物近似值——之年度总和与年度变异(季节性),定义每年的十四种功能类别。这十四种功能类别包括苔园(低度累积的fPAR与高度季节性)和热带森林(高度累积的fPAR与低季节性)。本文分别评估每种功能类别在fPAR矩阵平均中和两大空间模式矩阵中的变异。诸多像素从一集群转变至另一集群,并再度返回,显示出大量的短期变异。fPAR矩阵平均的时间变异相对而言较低,而改变主要展现在空间形态之中。空间脉络在苔园、草原、灌木地与热带稀疏草原中最为多变。动态的形态分类,证实主要生产力的空间模式之变异性,并且能够为未来的监测所用。 *关键词:* 生态系统功能, fPAR, MODIS, 监测, 区域化。

La productividad y la fenología de la vegetación son funciones ecosistémicas variables espacial y temporalmente. El monitoreo de los patrones espacio–temporales de estas funciones puede mejorar nuestra comprensión del cambio global y de la variabilidad ecosistémica natural, e informar las acciones de manejo. Típicamente, los investigadores se enfocan sobre los cambios temporales dentro o entre regiones estáticas y omiten la dinámica de la configuración espacial. Nuestro propósito fue evaluar la variabilidad espacio–temporal en perspectiva global, en términos de regímenes de productividad y fenología entre el 2000 y el 2012 usando un tipo de clasificación funcional temporalmente dinámica. Catorce tipos funcionales se definieron para cada año aglomerando el monto total y la variabilidad anual (estacionalidad) de la fracción de radiación fotosintéticamente activa (fPAR)—un proxy biofísico para el verdor o productividad de la vegetación—del Espectrómetro de Imágenes de Resolución Moderada (MODIS). Los catorce tipos funcionales estuvieron dentro del ámbito de la tundra (baja fPAR acumulativa y altamente estacional), hasta los bosques tropicales (alta fPAR acumulativa y

baja estacionalidad). Se evaluó la variabilidad en la media de las medidas de la fPAR y en las medidas de dos patrones espaciales para cada tipo funcional. Muchos píxeles cambiaron de un agrupamiento a otro, una y otra vez, lo cual sugiere considerable variabilidad de corto término. La variabilidad temporal en la media de la medida de la fPAR fue relativamente baja, sustituida con cambios manifiestos primariamente en el patrón espacial. El patrón espacial tuvo su máxima variabilidad dentro de la tundra, los pastizales, zonas arbustivas y sabanas. Una clasificación dinámica demostró la variabilidad en los patrones espaciales de productividad primaria y puede usarse para monitoreo futuro. *Palabras clave:* función ecosistémica, fPAR, MODIS, monitoreo, regionalización.

Human well-being depends on ecosystem services such as the provision of natural resources, climate regulation, water purification, and cultural and spiritual benefits (Millennium Ecosystem Assessment 2005). Net primary productivity (NPP), the rate of photosynthetic production per unit area, is a basic ecosystem function that supports all other ecosystem services (Kremen 2005; Carpenter et al. 2009; Andrew et al. 2015). For instance, the extraction of timber resources and the production of oxygen through photosynthesis are both tied to primary productivity. Although the exact nature of the relationship is contested, primary productivity is also one of the most widely recognized drivers of global patterns in biodiversity (Wright 1983; Pianka 1966; Field et al. 2008; Whittaker 2010). Vegetation phenology, the timing of developmental stages of plant life such as green-up, flowering, senescence, and length of growing season, is also a key functional trait of ecosystems that influences ecosystem processes such as pollination, carbon, water, and nutrient cycling (Morissette et al. 2009; Richardson et al. 2013). Planning conservation and sustainable development to ensure the continued provision of ecosystem services requires that these basic functions and services are spatially quantified and monitored (Braat and de Groot 2012; Cabello et al. 2012).

Both primary productivity and phenology exhibit considerable variability across space and time. Continental and global gradients in productivity and phenology reflect spatial variation in climate, especially temperature and precipitation (Polis 1999; Kimball 2014; Richardson et al. 2013). Landscape and regional variability in these processes might also reflect finer scale abiotic processes and the response of species or functional groups to these patterns (Hansen et al. 2000; Schöngart et al. 2002; Baeza et al. 2010; Diez et al. 2012). The productivity and phenology of a given region or ecosystem could fluctuate as a result of inter-annual climatic variability (Mohamed et al. 2004; Piao et al. 2006; Zeng et al. 2013). As the global climate warms (Intergovernmental Panel on Climate Change 2014), persistent changes in primary productivity and

vegetation phenology have also been identified. Specifically, in many areas, an increase in NPP and growing season length have been observed over the long term, concomitant with increasing global mean temperature over the same time period (Boisvenue and Running 2006; Xu et al. 2013; Keenan et al. 2014; Buitenwerf, Rose, and Higgins 2015; Sitch et al. 2015).

Monitoring spatial and temporal variability of ecosystem functions, such as productivity and phenology, with remote sensing can be used to assess changes in the delivery of ecosystem services (Volante et al. 2012; Andrew, Wulder, and Nelson 2014) and biodiversity (Coops et al. 2008). Spatial-temporal trends in productivity and phenology can also inform management and conservation (Crabtree et al. 2009; Cabello et al. 2012) and climate change science (Botta et al. 2000; Bonan et al. 2002; Nelson et al. 2014; Holmes et al. 2015). At global scales, quantitative, highly repeatable, and spatially comprehensive information regarding above-ground NPP and phenology can only be derived from remotely sensed data that are spatially and temporally aggregated and are representative of whole ecosystems or biomes (Boisvenue and Running 2006; White and Nemani 2006; Morissette et al. 2009; Ustin and Gamon 2010; Alcaraz-Segura et al. 2013). Such data have been used in numerous studies to assess recent global changes in productivity (e.g., Zhao and Running 2010; De Jong et al. 2012; De Jong et al. 2013; Mao et al. 2013) and phenology (e.g., Jeong et al. 2011; Eastman et al. 2013).

These types of global studies typically report changes over time in the magnitude of productivity (e.g., mean annual greenness) or the timing of phenological events (e.g., mean growing season length). Although some have used explicit spatial-temporal methods to detect extreme events in remotely sensed indicators of primary productivity (e.g., Zscheischler et al. 2013), most focus on the temporal aspect, with spatial variation in these changes simply assessed along latitudinal gradients or among static regions such as biomes, countries, or continents. Monitoring more nuanced variability can be equally as important as detecting extreme events, and

the use of static regions to assess this variability is limiting because ecological boundaries are dynamic and respond to intra- and interannual changes in climate. The spatial configuration of vegetation can also influence ecosystem services related to the flow of water, soil, nutrients, and organisms such as pollination and carbon storage (Mitchell et al. 2013). For instance, flowering and fruiting in fragmented landscapes might be earlier and more productive at edges due to altered abiotic conditions (Herrerías-Diego et al. 2006). Such changes in phenology can affect plant reproduction and pollination (Burgess et al. 2006). As such, analyses that integrate the dynamic nature of ecosystems could highlight important spatial–temporal variation and change. As an example, as ecosystem conditions change, neighboring units will become more or less similar, but this variability is not reflected under a system of static boundaries (Handcock and Csillag 2002). A regionalization methodology that is dynamic allows the possibility of detecting spatial shifts in environmental conditions (Reygondeau et al. 2013). The goal of this research was to assess spatial–temporal variability in vegetation productivity and phenology across the globe between 2000 and 2012, at three-year intervals, using a classification based on dynamic ecosystem functional types. Ecosystem functional types provide a meaningful framework for understanding, monitoring, assessing, and predicting changes to ecosystems and ecosystem services (Paruelo, Jobbágy, and Sala 2001; Ivits et al. 2013). To meet our goal, we used cluster analysis to classify and map remotely sensed proxies for productivity and phenology into functional types for five years from 2000 and 2012. Previous researchers have used remotely sensed proxies of primary productivity and phenology to delineate ecosystem functional types at regional (Paruelo, Jobbágy, and Sala 2001; Alcaraz-Segura et al. 2013) and global scales (Ivits et al. 2013). Our analysis is unique in that we allow mapped boundaries of the functional types to change through time, rather than using a static classification, and then focus our analysis on the change in spatial pattern.

Methods

Data

Classification of ecosystem functional types in this study was based on remotely sensed estimates of the fraction of photosynthetically active radiation (fPAR) absorbed by vegetation. Whereas vegetation indexes

such as the Normalized Difference Vegetation Index (NDVI) are composite measures of leaf chlorophyll content, leaf area, canopy cover, and structure, fPAR is an intrinsic biophysical variable that directly influences primary productivity (Myneni et al. 2002; Glenn et al. 2008; Huete et al. 2011). fPAR depends on vegetation type and structure and is commonly used in the estimation of ecosystem productivity and other biogeochemical cycles (Myneni et al. 2002). Values of fPAR range from zero to one; larger values indicate high vegetation greenness and productivity, whereas values approaching zero are indicative of more sparsely vegetated areas with low productivity (Myneni et al. 2002). For this study, fPAR data were obtained from the earth observing satellite Moderate Resolution Imaging Spectrometer (MODIS). Specifically, we used MODIS eight-day composites with a spatial resolution of 0.05° , or approximately 5.5 km at the equator (MOD15A2, V5, Climate Modeling Grid). MODIS terra data are collected daily with an equatorial crossing time of approximately 10:30 a.m.; the eight-day composite products available for download represent the best (least cloud contaminated) value over that eight-day period for each pixel. The forty-six composite images available in any given year were compiled for the years 2000, 2003, 2006, 2009, and 2012 to capture the range of fPAR variability within this time period.

To classify ecosystem functional types, two fPAR metrics were calculated for each of the five years of interest: total annual sum (fPAR_{sum}) and the annual coefficient of variation (fPAR_{cv}). The total annual sum is representative of annual net primary productivity (Goward, Tucker, and Dye 1985). Higher values are indicative of areas that are productive throughout the year or that are highly productive for the growing season. As the maximum fPAR value for any pixel is one and the number of images used per year was forty-six, fPAR_{sum} in theory ranges from zero to forty-six. Excluding nonvegetated areas for which MODIS fPAR data are absent, our calculated values of fPAR_{sum} ranged from 0.1 to 42 for the years assessed. The annual coefficient of variation of fPAR (fPAR_{cv}) quantifies the seasonality of primary productivity and represents phenological variation. High variability in fPAR (or NDVI) occurs where the climate exhibits extremes within a year and where vegetation is highly temperature or precipitation limited, such as in annual and desert grasslands or arctic and subarctic environments, or where there are cyclical agricultural practices in

place (Reed et al. 1994; Coops et al. 2008; Coops, Wulder, and Iwanicka 2009). Values of $fPAR_{cv}$ in our data set ranged from 0 to 6.7.

Classification and Mapping of Functional Types

A quantitative regionalization approach was used to classify and map functional types. The two $fPAR$ metrics, $fPAR_{sum}$ and $fPAR_{cv}$, from each of the five target years were used in a cluster analysis to generate a map of global ecosystem functional types. Cluster analysis is an unsupervised classification technique that partitions data into natural groups based on (dis)similarity (Jain, Murty, and Flynn 1999; Jain 2010). We applied a nonspatial clustering to the $fPAR$ data that did not enforce spatial contiguity in the classification. Specifically, we used the two-step clustering method in the statistical software SPSS (Version 22, IBM Corp., Armonk, NY, USA) because it can accommodate very large data sets. This method combines both partitional and hierarchical clustering approaches. First, raw data points are partitioned into a set of preclusters using an approach called a cluster feature (CF) tree (Zhang, Ramakrishnan, and Livny 1996) that is in some ways similar to the well-known k -means algorithm. Once the preclusters are defined, a hierarchical agglomerative (bottom-up) clustering method consecutively joins the preclusters into a smaller number of clusters based on their distance in feature space (Mooi and Sarstedt 2011). All five years of the $fPAR$ measures were incorporated into one data frame, standardized to z scores, and then clustered with the two-step algorithm and applying a log-likelihood distance measure. Clustering data from all years together, rather than each year separately, reduces the chance of detecting spurious change that might result from the clustering procedure itself (e.g., due to randomness associated with cluster initiation; Rinsurongkawong and Eick 2010; Mills et al. 2013).

In partitional clustering methods such as k -means, the analyst must select the number of clusters prior to clustering. In hierarchical clustering, the analyst selects the number of clusters after the fact based on the resultant level of (dis)similarity among clusters at each successive stage of the hierarchy (Jain, Murty, and Flynn 1999; Jain 2010). In SPSS's two-step algorithm, either option can be used. Previous studies have mapped ten to fifteen global ecosystem functional

types (Bonan et al. 2002; Friedl et al. 2010; Poulter et al. 2011; Ivits et al. 2013). To maximize thematic resolution yet enable general comparisons with these and other global mapping products (e.g., Olson et al. 2001), we specified that fourteen clusters should be delineated. Nonvegetated pixels ($fPAR = 0$) were excluded from the classification.

The output data frame contained cluster membership values for each pixel, corresponding to each year. This data frame was then imported into ArcGIS (Version 10.3, Esri, Redlands, CA, USA). Cluster membership values for each of the five years were displayed one by one, producing five separate maps. An overall map representing all years was also produced by calculating the majority (modal) cluster value of each pixel using the Cell Statistics tool in ArcGIS. The maps were smoothed using a 3×3 majority filter.

Clusters were interpreted by assessing the statistical distribution (e.g., mean, median, range) of each cluster with respect to $fPAR_{sum}$ and $fPAR_{cv}$ (i.e., the input variables). To provide additional context to the clusters, we then determined the dominant (International Geosphere–Biosphere Programme) land cover type (Friedl et al. 2010) and biome type (Olson et al. 2001) within each of the resultant clusters.

Spatial–Temporal Variability and Change

We assessed the direction and magnitude of change, as well as the frequency of change in ecosystem functional types over time. We also assessed the change in spatial pattern (composition and configuration) of ecosystem functional types.

Direction, Magnitude, and Frequency of Change over Time

For each of the five years of data, mean annual greenness ($fPAR_{sum}$) and mean annual seasonality ($fPAR_{cv}$) were calculated for each cluster. Each cluster was then described in terms of its long-term variability (coefficient of variation and standard deviation, respectively) in each of these two metrics. To further characterize temporal variation in the clustering, change matrices were built for each of four change periods: 2000 to 2003, 2003 to 2006, 2006 to 2009, and 2009 to 2012. Each matrix contained the number of pixels classified as each cluster type for each date, thus providing information on the type and magnitude of change. We mapped the results for each of the four change

periods and summed the results of the four individual matrices to generate one table representing total change over all years. To determine whether changes were sustained and directional or short-term and variable, we also assessed the frequency of change for each individual pixel (zero to four times). For those pixels that changed more than two times, we then assessed the number of unique values. Pixels with four unique cluster classifications represent a very different type of change than pixels that changed four times but had only two unique values during that time.

Spatial Pattern Changes in Ecosystem Functional Types

The novelty of our approach is a dynamic regionalization based on global fPAR measures and an assessment of changes in spatial pattern over time. Two components of spatial pattern in the clusters were assessed: composition and configuration. *Composition* refers to the area of a cluster, indicating what and how much is present (Gustafson 1998; Fahrig 2005). We calculated the area of each cluster at each time step by summing the total number of pixels in each. Note that the sum of pixels in each cluster is also contained in the change matrices previously described; the key difference is that to measure *variability* in spatial pattern, we then also computed the coefficient of variation of cluster area over time.

Configuration refers to explicit spatial arrangements such as aggregation, fragmentation, and adjacency (Gustafson 1998; Fahrig 2005). To assess spatial configuration, we calculated a measure of aggregation using FRAGSTATS (McGarigal and Ene 2013), a tool designed to calculate landscape metrics from categorical maps. We chose a single measure of spatial configuration, *clumpiness*, because it is bounded (ranges from -1 to $+1$), thus facilitating interpretability (Crews-Meyer 2004), and responds linearly to changes in aggregation regardless of class area (Neel, McGarigal, and Cushman 2004). Values of clumpiness approaching -1 occur in maximally disaggregated situations, whereas values approaching $+1$ occur in maximally clumped situations. We emphasize that the spatial resolution and total landscape extent remained constant at each time step, thus avoiding challenges with metric comparison (e.g., Wu et al. 2002; Wu 2004). Clumpiness was calculated for each cluster for each

of the five years (2000, 2003, 2006, 2009, 2012) and the coefficient of variation was computed.

Results

Classification and Mapping of Functional Types

The fourteen derived clusters (functional types) corresponded reasonably well to existing global biome and land cover classifications (Table 1), and each functional type had a unique distribution with regard to cumulative annual greenness and annual seasonality of greenness. Clusters 1 through 4 were generally found at high elevations, high latitudes, or both, with relatively low annual greenness and relatively high seasonality (Figures 1 and 2). Clusters 1 and 2 were labeled as tundra functional types and were the least green (mean $fPAR_{sum}$ values of 6.3 and 7.9, respectively) and most seasonal (mean $fPAR_{cv}$ values of 1.4 and 1.2, respectively) of all clusters (Figure 1, Table 1). Cluster 3 was similar to Clusters 1 and 2 in terms of annual greenness (mean $fPAR_{sum} = 7.8$) but was less seasonal (mean $fPAR_{cv} = 0.75$). Cluster 3 was grass-dominated and lay primarily within the Eurasian steppe and the Great Plains region of North America. Cluster 4 was an open, shrubby functional type with a slightly higher annual greenness than the first three (mean $fPAR_{sum} = 11.4$) and its degree of seasonality was intermediate between Clusters 2 and 3 (mean $fPAR_{cv} = 0.98$). It was found in Scandinavia, Siberia, Alaska, and northern Canada, as well as the Aspen Parkland region in central Canada.

Cluster 5 was grass or shrub dominated and had low annual greenness (mean $fPAR_{sum} = 6.2$) similar to Clusters 1 through 3 but was much less seasonal than those clusters (mean $fPAR_{cv} = 0.45$). It occurred at lower latitudes, primarily in arid regions of Eurasia, central Australia, northern Africa, the southwestern United States, and southern Chile. Clusters 6 and 7 were also grass and shrub dominated but with a slightly higher annual greenness than Cluster 5 (mean $fPAR_{sum} = 9.4$ and 12.1 , respectively). They occurred in semiarid regions such as southern Africa, Australia, India, and the western United States. Clusters 8 and 9 were dominated by forests, with moderately high annual greenness (mean $fPAR_{sum} = 18.5$ and 15.1 , respectively) and moderately high annual seasonality (mean $fPAR_{cv} = 0.58$ and 0.80 , respectively). They

Table 1. Relationship of clusters with existing land cover and biome types and our functional interpretation

Cluster	Dominant biome ^a (% of cluster)	Second dominant biome ^a (% of cluster)	Dominant land cover type ^b (% of cluster)	Second dominant land cover type ^b (% of cluster)	Interpreted functional type
1	Tundra (67)	Boreal forests/taiga (32)	Open shrublands (80)	Grasslands (15)	Tundra (low productivity)
2	Boreal forests/taiga (51)	Tundra (42)	Open shrublands (72)	Grasslands (14)	Tundra (low productivity)
3	Temperate grasslands, savannas, and shrublands (44)	Deserts and xeric shrublands (21)	Grasslands (77)	Croplands (10)	Grasslands (low productivity)
4	Boreal forests/taiga (56)	Temperate grasslands, savannas, and shrublands (17), tundra (17)	Open shrublands (31)	Woody savannas (17)	Forests and shrublands (low productivity), and grasslands (moderate productivity)
5	Deserts and xeric shrublands (59)	Tropical and subtropical grasslands, savannas, and shrublands (13)	Open shrublands (65)	Grasslands (19)	Grasslands (low productivity)
6	Deserts and xeric shrublands (26)	Tropical and subtropical grasslands, savannas, and shrublands (23)	Grasslands (59)	Open shrublands (17)	Grasslands and shrublands (moderate productivity)
7	Deserts and xeric shrublands (34)	Tropical and subtropical grasslands, savannas, and shrublands (22)	Open shrublands (55)	Grasslands (23)	Grasslands and shrublands (moderate productivity)
8	Boreal forests/taiga (42)	Temperate broadleaf and mixed forests (29)	Mixed forest (34)	Croplands (20)	Forests (moderate productivity)
9	Boreal forests/taiga (58)	Temperate broadleaf and mixed forests (18)	Woody savannas (19)	Croplands (18)	Forests (moderate productivity)
10	Tropical and subtropical grasslands, savannas, and shrublands (37)	Temperate broadleaf and mixed forests (23)	Woody savannas (30)	Savannas (17)	Forests and savannas (high productivity)
11	Temperate broadleaf and mixed forests (36)	Boreal forests/taiga (24)	Mixed forest (40)	Savannas (15)	Forests (high productivity)
12	Tropical and subtropical grasslands, savannas, and shrublands (38)	Mediterranean forests, woodlands, and scrub (15)	Savannas (29)	Croplands (22)	Grasslands and savannas (high productivity)
13	Tropical and subtropical moist broadleaf forests (85)	Temperate broadleaf and mixed forests (4)	Evergreen broadleaf forest (86)	Cropland/natural vegetation mosaic (5)	Forests (high productivity)
14	Tropical and subtropical moist broadleaf forests (18)	Temperate broadleaf and mixed forests (19), tropical and subtropical grasslands, savannas, and shrublands (19)	Woody savannas (22)	Evergreen broadleaf forest (18) and mixed forest (18)	Forests and shrublands (high productivity)

^aFrom Olson et al. (2001).^bFrom Friedl et al. (2010).

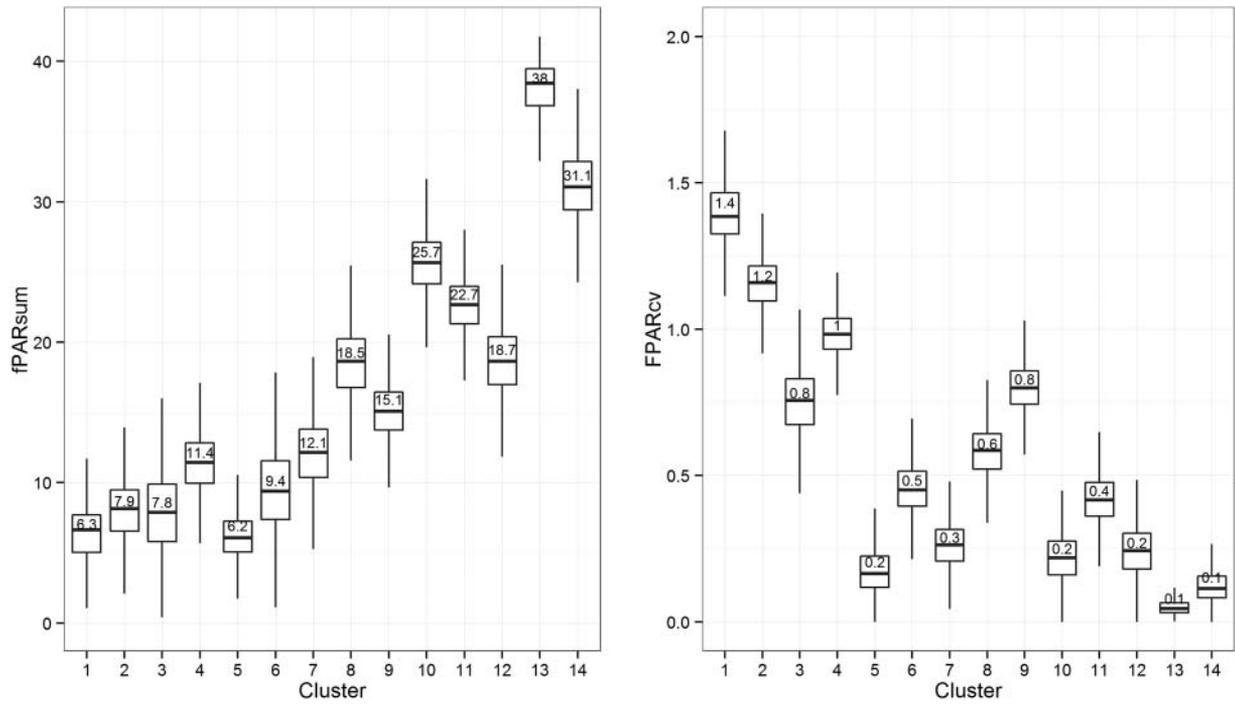


Figure 1. Distribution of total annual productivity (fPAR_{sum}) and seasonality in productivity (fPAR_{cv}) for the fourteen clusters, with mean values labeled. Boxplots were produced with values for all years combined.

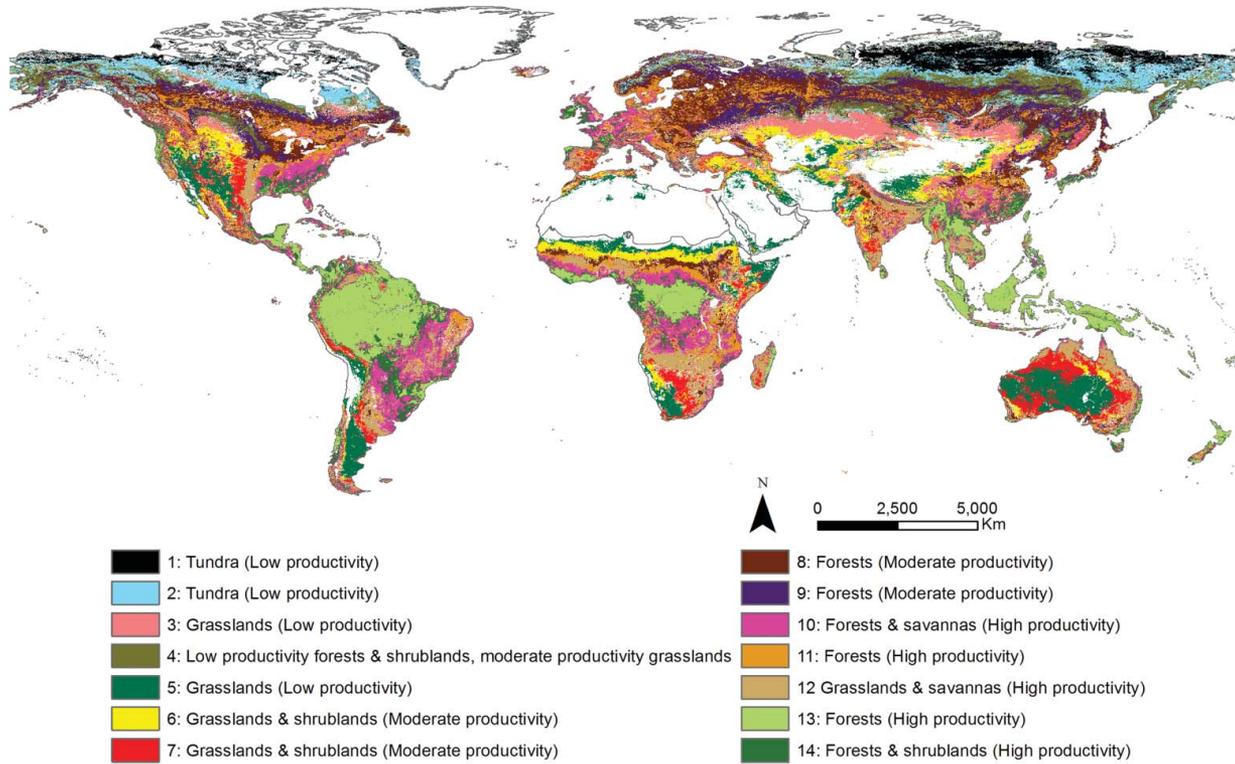


Figure 2. Fourteen global ecosystem functional types were delineated that represent unique combinations of annual greenness (fPAR_{sum}) and annual seasonality (fPAR_{cv}). Depicted is the majority (modal) value between 2000 and 2012. (Color figure available online.)

occurred primarily at moderately high latitudes across large areas of Europe, Eurasia, and North America within the boreal forests and taiga biome.

Clusters 10 through 14 were characterized by high annual greenness and low seasonality. Cluster 10 was dominated by savannas and scattered across temperate, subtropical, and especially tropical regions of the globe (Table 1, Figure 2). It had a mean annual greenness of 25.7 and a mean annual seasonality of 0.22. Cluster 11 was slightly less productive (mean $fPAR_{sum} = 22.6$) and slightly more seasonal than Cluster 10 (mean $fPAR_{cv} = 0.42$). It occurred primarily within temperate broadleaf and mixed forests in central Europe and North America. Cluster 12 was dominated by savannas with a mean annual greenness value of 18.8 and a mean $fPAR_{cv}$ of 0.24. It occurred in regions such as northeastern Australia, parts of southern and central Africa, and the Indian subcontinent. Clusters 13 and 14 occurred in the tropical Amazon and Congo River basins and had very low seasonality (mean $fPAR_{cv} = 0.05$ and 0.12 , respectively) and very high annual greenness (mean $fPAR_{sum} = 38.0$ and 31.1 , respectively). Cluster 13 was predominately tropical forest, and Cluster 14 (substantiated by a visual assessment of higher spatial resolution satellite imagery on GoogleEarth) was more open, representing pastures, croplands, or regenerating forests.

Spatial–Temporal Variability and Change

Direction, Magnitude, and Frequency of Change over Time

The mean values of $fPAR_{sum}$ and $fPAR_{cv}$ for each cluster were somewhat variable over time (Figure 3). Annual greenness ($fPAR_{sum}$) was highly variable in Cluster 1 ($CV = 0.043$), moderately high in Cluster 5 (grasslands; $CV = 0.018$), and less variable in the other clusters ($CV < 0.010$). Annual seasonality ($fPAR_{cv}$) was most variable in Cluster 1 (tundra) but was quite stable in all other clusters.

An assessment of change frequency and uniqueness indicated that the majority (50 percent) of pixels with a high frequency of change had only two unique values through time, and 44 percent had three unique values over time. The cumulative change matrix (Table 2) indicates that most changes represented pixels changing from one functional type to another functional type that was relatively similar (e.g., Figure 1). For instance, pixels that changed from Cluster 1 (low

productivity tundra) were primarily reclassified as Cluster 2 (also tundra but with slightly higher annual greenness and slightly lower seasonality), whereas change in Cluster 2 was primarily toward Cluster 1 (Table 2). As another example, pixels that changed in Cluster 8 (moderately productive forests) were mostly reclassified as Cluster 11 (highly productive forests), and the dominant change for pixels in Cluster 9 (moderately productive forests) was to Cluster 8 (also moderately productive forests).

Spatial Pattern Changes in Ecosystem Functional Types

Change matrices were generated for each of the four change periods and used to calculate the net difference in cluster extent (i.e., total magnitude of change) for each cluster at each time step. From 2000 to 2003, Cluster 1 (tundra) changed the most of all clusters, decreasing ~ 19 percent in area (Figures 4 and 5, Table 3). Cluster 4 (forests, shrublands, and grasslands with low to moderate productivity), Cluster 7 (grasslands and scrublands with moderate productivity), Cluster 8 (moderately productive forests), and Cluster 12 (grasslands and savannas) also changed by at least ± 10 percent. Conversely, the change in area from 2000 to 2003 in Cluster 10 (highly productive forest and savanna) and Cluster 13 represented less than 1 percent of their area in 2000. In the next time step

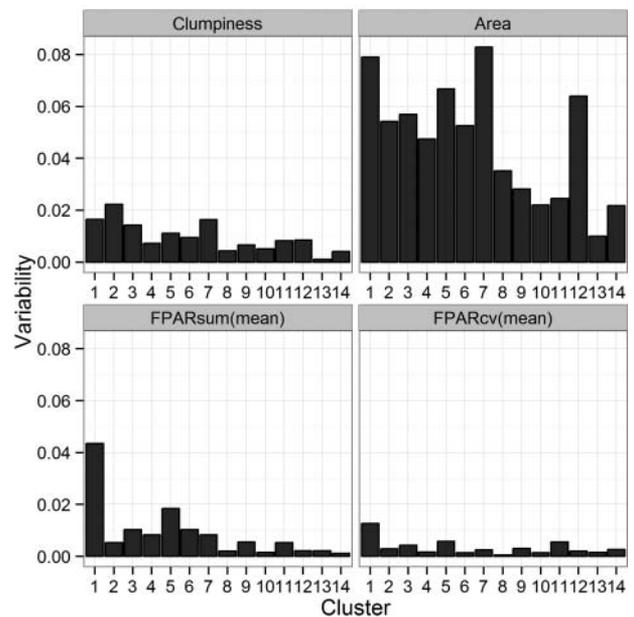


Figure 3. Spatial–temporal variability in global ecosystem functional types.

Table 2. Change in cluster area over time, calculated from change matrices (e.g., Table 3) for each year (not shown) by differencing row sums and column sums for each cluster

Cluster	Percentage change			
	2000–2003 ^a	2003–2006 ^b	2006–2009 ^c	2009–2012 ^d
1	–18.76	23.12	–11.38	0.76
2	–5.78	2.24	13.95	–10.77
3	1.52	1.85	–3.45	15.84
4	12.05	–12.56	4.53	–7.67
5	5.59	–11.95	20.70	–13.85
6	1.18	12.81	–6.81	–6.31
7	–14.97	8.34	–14.36	20.86
8	10.92	–6.97	2.52	1.42
9	5.47	–4.42	1.74	5.04
10	0.50	2.09	–5.09	–0.84
11	5.99	–6.25	2.88	–2.48
12	–13.31	12.40	–4.85	12.86
13	0.98	–1.23	–0.34	–1.47
14	1.80	0.06	–5.71	2.96

Note: Change greater than |10%| is shown in bold.

^aRelative to cluster area in year 2000.

^bRelative to cluster area in year 2003.

^cRelative to cluster area in year 2006.

^dRelative to cluster area in year 2009.

(from 2003 to 2006), Cluster 1 again changed the most, this time gaining area equivalent to ~23 percent of its area in 2003. Clusters 4, 5, and 6 (all low to moderately productive forests, grasslands, or shrublands) and Cluster 12 changed by ~12 to 13 percent. Cluster 14 (highly productive forests and shrublands) changed the least, increasing in area by only 0.06 percent. From 2006 to 2009, Cluster 5 (grasslands) changed the most, increasing in area by ~21 percent; Cluster 13 (high productivity forests) changed the least, losing approximately 0.3 percent of its area. Finally, in the last time step (from 2009 to 2012), Cluster 7 changed the most, increasing in area by ~21 percent, whereas the area of Cluster 1 (tundra) changed by only ~0.8 percent.

The spatial pattern and, in particular, composition (area) of the fourteen clusters was more variable through time than was the change in magnitude of the fPAR values (Figure 5). For all clusters, variation in composition (area) was greater than variation in configuration (clumpiness). Variability in area was particularly high in Cluster 1 (tundra), Cluster 5 (low productivity grasslands), Cluster 7 (moderate productivity grasslands and shrublands), and Cluster 12 (highly productive grasslands, savannas, and shrublands; $CV > 0.06$). Variability in cluster area was much lower in the highly productive forests represented by Cluster 13 ($CV = 0.01$). The

most variable ($CV \geq 0.014$) clusters in terms of spatial configuration (clumpiness) were Clusters 1 and 2 (tundra), Cluster 3 (low productivity grasslands), and Cluster 7, whereas Cluster 13 (highly productive forests) had the lowest variation in this indicator ($CV = 0.001$).

Discussion

Classification and Mapping of Functional Types

Our functional type classification captures an informative proportion of existing global biome and land cover maps but conveys specific information regarding functional variability that is unique and complementary to biome and land use mapping. Regionalizations aggregate information and allow for environmental assessment, management, and planning (Loveland and Merchant 2004). Depending on scale, perceived importance, and objectives, regions can be constructed using any number or type of environmental variables, including productivity, land cover, topography, geology, climate, and phytogeographic and zoogeographic information. Functional types represent collections of species that respond to or affect one or more ecosystem processes or conditions in a similar manner (Hooper et al. 2005), and regionalizations representing functional types could also be used to assess, monitor, manage, and predict changes to ecosystems. Remote sensing can capture many functional properties of vegetation, including structure and productivity (Ustin and Gamon 2010). Yet, in the global change literature, regions used to summarize temporal variability in remotely sensed proxies of functions like primary productivity (e.g., fPAR, NDVI) are normally defined by other data sets such as land cover (e.g., De Jong et al. 2012; Eastman et al. 2013). As boundaries of land cover classes do not necessarily translate to boundaries of function types, spatial heterogeneity in functional attributes is generalized when using land cover boundaries for assessment. We used two remotely sensed indicators of primary productivity and phenology in a data-driven methodology to classify and map ecosystem functional types (Figure 2). Primary productivity can vary independent of changes in land cover or vegetation structure because the latter changes more slowly in response to climatic or anthropogenic perturbations (Parelo, Jobbágy, and Sala 2001) and does not capture seasonal variability. Our clusters capture a combined measure representative of annual greenness and seasonality and we note that the two measures

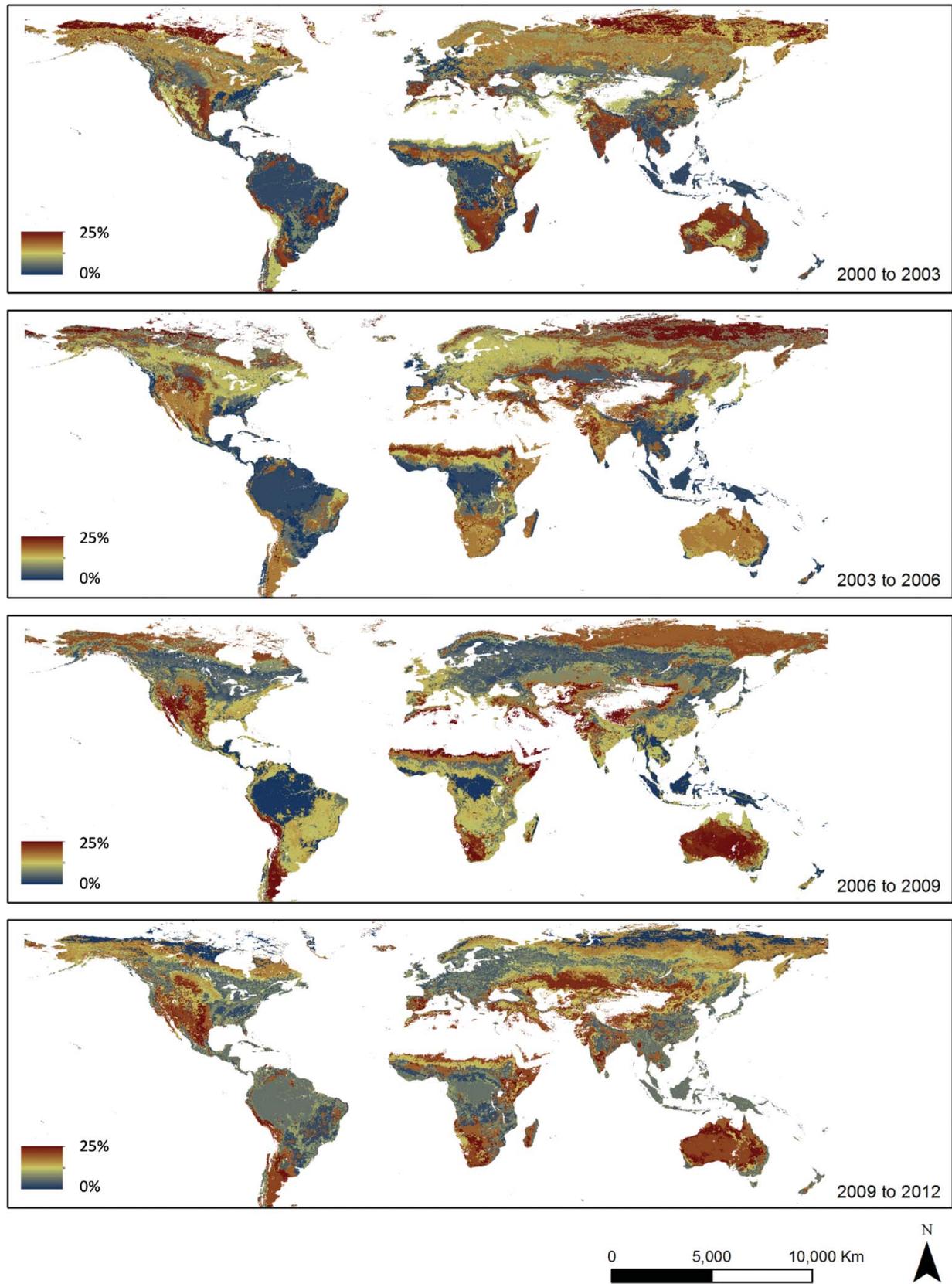


Figure 4. Change per ecosystem functional type (cluster) at each step in time, corresponding to Table 2. (Color figure available online.)

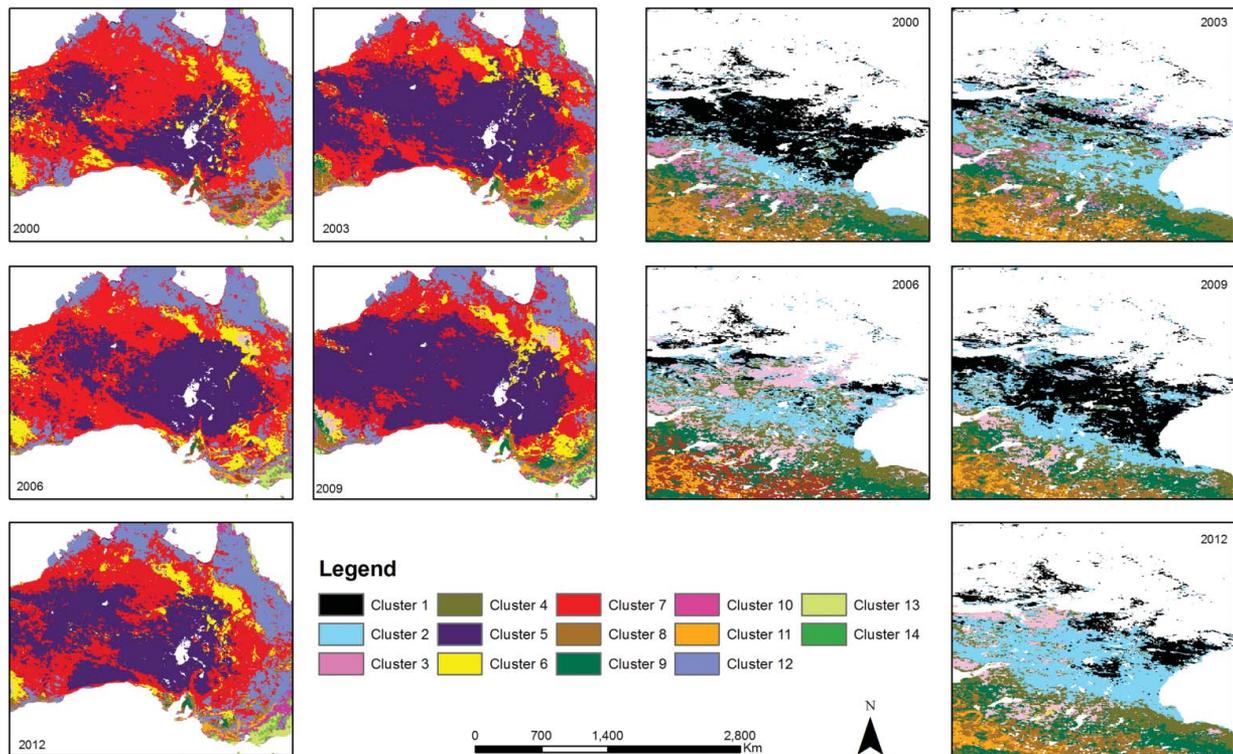


Figure 5. Changes occurring in particularly dynamic clusters and regions from 2000 to 2012. The left panel shows the back-and-forth nature of Clusters 5 and 7 in Australia, whereas the right panel shows similar dynamics between Clusters 1 and 2 in Arctic Canada. (Color figure available online.)

($fPAR_{sum}$ and $fPAR_{cv}$) are inversely related. Pixels that shift from one cluster to the next could be interpreted as areas where climatic change or disturbance, over the time period assessed, led to changes in the cumulative sum and intra-annual variability of $fPAR$. Such a transition represents a change in ecosystem function, and not necessarily a structural change. We note that this indirect or nonperfect relationship between $fPAR$ and land cover also makes it difficult to verify the changes we have identified.

Spatial–Temporal Variability and Change

Many of the changes observed at one time step in this study were not sustained through time, suggesting that our analysis is largely capturing short-term vegetation responses to climatic variability or land use and disturbance dynamics. Pixels generally changed from one cluster to another with relatively similar distributions of $fPAR_{sum}$ and $fPAR_{cv}$ values and then back again at a later date (Figure 4, Tables 2 and 3). For instance, in Australia in the year 2000, Cluster 7 (moderately productive

grasslands and shrublands) was more abundant than Cluster 5 (low productive grasslands; Figure 4). Three years later, the opposite was true. In 2006, the amount of Cluster 7 increased again, corresponding to a decrease in the area of Cluster 5. This back-and-forth nature continued through 2009 and 2012. In Arctic Canada, Clusters 1 and 2 (both tundra functional types) had a similar dynamic over time (Figure 4). Changes in primary productivity might follow long-term global climate change (Boisvenue and Running 2006; Xu et al. 2013; Keenan et al. 2014; Buitenwerf, Rose, and Higgins 2015; Sitch et al. 2015). Primary productivity can also vary as a result of climatic patterns and anomalies such as the El Niño Southern Oscillation (ENSO; Nemani et al. 2003; Peng et al. 2012) and droughts (Zhao and Running 2010), as well as natural disturbances such as volcanic eruptions (Lucht et al. 2002), fire (Hicke et al. 2003; Goetz, Fiske, and Bunn 2006), and land use/land cover change (Mao et al. 2013). A stable regionalization where boundaries remained fixed over time would not capture this spatial variability in ecosystem function.

Table 3. Change matrix representing pixel counts changing from one cluster to another, summed over all four time periods (2000–2003, 2003–2006, 2006–2009, and 2009–2012)

From	To														
	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7	Cluster 8	Cluster 9	Cluster 10	Cluster 11	Cluster 12	Cluster 13	Cluster 14	Sum
Cluster 1	576,128	384,910	36,237	110,572	203	384	3	85	7,347	2		7			1,115,878
Cluster 2	344,929	675,032	84,772	310,306	304	1,442	12	406	24,984	0	1	7			1,442,195
Cluster 3	37,700	76,980	574,140	98,448	16,128	145,867	2,227	7,697	40,365	4	48	268		1	999,873
Cluster 4	116,963	273,033	117,627	837,668	26	4,861	32	8,259	250,060	3	101	78		0	1,608,711
Cluster 5	295	252	16,961	139	1,134,045	177,082	129,552	447	142	4	30	916		1	1,459,866
Cluster 6	407	995	161,926	5,373	148,699	702,726	118,482	49,948	20,816	54	693	16,692		2	1,226,813
Cluster 7	4	5	3,497	93	146,383	118,970	598,824	23,952	903	799	3,212	130,539	1	43	1,027,225
Cluster 8	118	470	8,012	9,396	746	42,062	22,223	1,179,932	223,332	4,340	245,845	67,927		40	1,804,443
Cluster 9	7,126	23,123	34,579	215,288	253	16,369	801	244,040	885,368	24	6,854	943			1,434,768
Cluster 10		2	3	0	11	112	1,676	5,853	69	1,235,891	187,485	124,781	1,511	147,159	1,704,553
Cluster 11		7	215	165	23	1,262	6,207	249,155	7,104	173,033	876,252	88,649	27	4,706	1,406,805
Cluster 12	4	8	547	52	1,203	14,678	133,718	65,969	1,386	114,863	80,367	1,044,009	76	3,263	1,460,143
Cluster 13							8			2,011	34	149	1,739,863	93,233	1,835,298
Cluster 14			1		4	7	60	66	3	158,934	4,818	3,118	84,368	802,738	1,054,117
Sum	1,083,674	1,434,817	1,038,517	1,587,500	1,448,028	1,225,822	1,013,825	1,835,809	1,461,879	1,689,962	1,405,740	1,478,083	1,825,846	1,051,186	19,580,688

Note: Values along the diagonal represent pixels that did not change.

Because the boundaries between our regions varied through time, processes leading to variability in annual greenness or annual seasonality were overwhelmingly manifested as changes in spatial composition (area) of the functional types (Figures 4 and 5). Clusters exhibited variability over time with respect to area (Figure 4), often increasing in area at one time step and decreasing at the next (Table 3). Clusters at high latitudes representing tundra and taiga ecosystems (e.g., Clusters 1, 2, 4) and those in temperate or subtropical regions representing arid or semiarid ecosystems (e.g., Clusters 5, 7, 12) had the highest magnitude of change in spatial area, whereas tropical forests (Clusters 13 and 14) changed the least.

High spatial–temporal variability in the area of arid and semiarid areas is most likely due to the effect of climatic variability on primary productivity. Other processes such as shrub encroachment and agriculture interact with climate to influence vegetation dynamics and spatial configuration in arid and semiarid ecosystems (Asner et al. 2004; Knauer et al. 2014) but, at the spatial extent and resolution of this analysis (5-km pixels, global extent), are likely less obvious than broader climatic processes. In arid and semiarid regions, water is the dominant limiting factor to vegetation productivity, although temperature and solar radiation also interact with water availability to impose constraints on growth (Nemani et al. 2003; Fensholt et al. 2012). Vegetation productivity and phenology in these ecosystems can be particularly sensitive to variability in rainfall; a rain event can produce a sudden flush, or pulse, of growth in vegetation (Noy-Meir 1973). In a study in west-central North America, annual grasses such as cheatgrass (*Bromus tectorum*) were found to be exceptionally reactive to variation in rainfall, and extensive areas of these green areas were easily detectable from space (Bradley and Mustard 2005). Across multiple biomes in North America, Knapp and Smith (2001) found interannual variability in above-ground NPP to be considerably greater in grasslands than in forests in North America and highlighted that the magnitude of production pulses following precipitation pulses was likewise much greater for grasslands. Globally, De Jong et al.'s (2012) study identified sequential periods of abrupt greening followed by gradual browning for semiarid ecosystems such as shrublands and grasslands. Savannas, which consist of both woody and herbaceous vegetation and are found in tropical and subtropical regions, are also known to be a very highly dynamic ecosystem strongly limited by rainfall (Sankaran et al. 2005). Variability

is especially high at the drier end of the savanna spectrum, where Ma et al. (2013) found savannas dominated by annual grasses in northern Australia to be the most responsive to variation in precipitation. Woody species and, to a lesser extent, perennial grasses, with their deeper roots that can access water stored below ground, are slower to grow and show less variable responses to precipitation patterns (Bradley and Mustard 2005; Rich, Breshears, and White 2008; Ma et al. 2013). Our results demonstrate that on a global scale, vegetation greenness in tropical forests is stable throughout the year here relative to drier, nonforested ecosystems and corroborate the greater variability of tropical pastures (e.g., Cluster 14) compared to tropical forests (e.g., Cluster 13; Huete et al. 2006). Some tropical forests exhibit high variability in leaf area and photosynthesis due to seasonality of rainfall and cloud cover (Huete et al. 2006; Myneni et al. 2007; Bi et al. 2015; Xu et al. 2015). In other tropical systems, the ability of trees' roots to access and redistribute soil water helps buffer these systems against seasonal droughts, and trees can remain green and actively photosynthesize for most of the year (Davidson et al. 2012; Ma et al. 2013). Variability in productivity in the Amazon could also be due to large-scale forest clear-cutting, grazing, and subsequent agricultural abandonment (Vieira et al. 2003; Foley et al. 2007). The results of our research regarding the high degree of variability in Arctic tundra align with studies that have identified increasing trends in remotely sensed indexes of productivity in these regions (e.g., Beck and Goetz 2012; Mao et al. 2013; Buitenwerf, Rose, and Higgins 2015). At high latitudes and high elevations, primary productivity is strongly limited by temperature, although moisture and solar radiation are also limiting (Bliss and Matveyeva 1992; Nemani et al. 2003). Warmer temperatures in Arctic and alpine regions can lead to earlier flowering and greening and a longer growing season (Oberbauer et al. 2013), and there is substantial evidence of shrub proliferation and increased above-ground biomass (e.g., Hill and Henry 2011; Myers-Smith et al. 2011; Elmendorf et al. 2012; Lantz, Marsh, and Kokelj 2012; Fraser et al. 2014). Primary productivity is also variable over space and time due to variations in snow and ice cover and melt (Stow et al. 2004; Grippa et al. 2005; Choler 2015), which in turn are affected by temperature variability (Rumpf et al. 2014). Thus, cumulative annual greenness and variability of greenness will vary considerably if snow cover lasts a month longer or a month less from one year to the next. We also note that remotely

sensed estimates of primary productivity in snow-covered areas will increase following snowmelt even if unrelated to increased vegetation growth (Beck et al. 2006). In the subarctic and northern Boreal regions (e.g., as represented by portions of Cluster 4), both in situ and remote-sensing studies have found periods of greening and browning, the latter of which has been attributed to drought and temperature stress (Lloyd and Bunn 2007; Goetz et al. 2011; De Jong et al. 2012). Large forest fires are also a natural disturbance that can occur over very large, contiguous areas, with millions of hectares typically burning annually in the northern Boreal (Stocks et al. 2002; Kasischke and Turetsky 2006), and might explain some of the variability in Cluster 4 (as well as Clusters 8 and 9).

Clusters with high temporal variability in spatial pattern also tend to be spatially heterogeneous on the landscape (i.e., occurring within a mosaic of multiple classes for any given time period). For instance, Clusters 1 and 2 occur in Arctic regions where the extreme environment can lead to landscapes with highly patchy (i.e., spatially discontinuous) vegetation (Billings and Mooney 1968; Bliss and Matveyeva 1992) and the spatial configuration of trees at their northern limit is highly variable and dynamic (Harper et al. 2011). Clusters 3, 5, 6, 7, 10, and 12, which represent grasslands, savannas, and shrublands, are often heterogeneous in that woody vegetation is interspersed in various degrees with herbaceous vegetation, or patches of bare ground might be present. Cluster 7, for example, includes linear swaths of green vegetation within the valleys of arid canyon lands of the western United States (e.g., Nevada and Utah). We expect greenness within some of these ecosystems to be more spatially expansive during the wet season, whereas greater spatial heterogeneity in greenness would arise in dry periods because of the aforementioned differences in the response of woody and herbaceous species to drought.

Scientists have called for research to address variability in ecosystem functional types caused by climatic and anthropogenic impacts (Ivits et al. 2013), and spatial information has been suggested as a useful addition to a time-based collection of ecosystem change indicators (Kéfi et al. 2014). At local and regional scales, studies have shown that the spatial configuration of productivity and phenological responses affects and is affected by other ecological processes such as seed dispersal, hydrology, pollination, and carbon storage (e.g., Asner et al. 2004). In this study, we have demonstrated that a dynamic regionalization approach is an effective framework to capture

temporal variability in the spatial heterogeneity of ecosystem function at global scales.

Conclusion

We used remotely sensed fPAR data to delineate fourteen global ecosystem functional types, each representing a unique productivity and phenology regime. Such classifications, or regionalizations, can be a vital component of global biodiversity and ecosystem service assessment and conservation efforts, as demonstrated by the popularity and widespread use of the World Wildlife Fund's global ecoregion map (Olson et al. 2001). As well, a discrete functional type classification is complementary to monitoring continuous, pixel-based values of productivity or phenology because the classification captures and presents a simplified representation of spatial heterogeneity in ecosystem function. Specifically, a regionalization provides context to changing fPAR values by providing a multivariate or joint-measure assessment of changes in ecosystem function. Our dynamic framework is novel in that it allows an assessment of spatial-temporal variability in ecosystem functional units that would not be possible using a static regionalization.

We have demonstrated that the spatial patterns of primarily productivity in arid and semiarid ecosystems, including polar regions, are considerably more variable than in tropical forests. Climatic change and land use are major pressures in these ecosystems. Future work should examine the explicit relationship between the spatial pattern of global ecosystem functions and hypothesized drivers of such change, such as climatic variability and anthropogenic disturbance. Understanding these linkages will facilitate management and projections of future change. As more data become available and computational power increases, our methodology could be repeated using longer temporal sequences at a higher temporal resolution, enabling the creation of a long-term baseline. Deviations from this baseline spatial-temporal variability can then be detected, signaling areas where more fine-scale monitoring and management efforts might need to be prioritized. Earth observation data are systematic, repeatable, and globally comprehensive data at a variety of spatial and temporal resolutions that can be used in a quantitative, data-driven, and dynamic framework for monitoring changes to essential ecosystem processes in these and other ecosystems.

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