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ORIGINAL ARTICLE

Land systems' asymmetries across transnational ecoregions in South America

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Abstract

The landscape configuration of socio-ecological land systems results from the interaction between the environmental conditions (relatively homogeneous within ecoregions) and country-level management and land-use decisions. However, social, land-use and sustainability research disciplines often study each independently. We used Euclidean distance analyses of five indicators of land systems functioning to explore the geographical patterns of across-border human-induced asymmetries in transnational ecoregions of South America. The most asymmetric transnational ecoregions occurred in the tropical rainforest biome which also showed the widest range of asymmetry values compared to other biomes. In contrast, transnational ecoregions in montane grasslands showed comparatively little asymmetries, and tropical dry forests showed intermediate asymmetry values. This pattern indicates that major asymmetries occur in land systems located in productive biomes with a comparatively recent history of development, whereas mature socio-ecosystems with a long history of human land use are more homogeneous across borders. In some cases, asymmetries may stabilize as a consequence of reinforcing feedbacks that promote contrasting land-use decisions across borders, including, for example, the establishment of protected areas, or the promotion of agro-industrial activities. Transnational socio-ecological land systems can be used to evaluate alternatives for sustainable development because they highlight the influence of institutions under different governance regimes in defining the spatial configuration and ecological properties of regions. We invite land-use and sustainability scientists to consider political border interactions as valuable "natural experiments" to better understand the interrelations between biophysical and political systems in defining planetary geographical-ecology in the Anthropocene.

Keywords Biomes · Border · Development · Historical land-use · Socio-ecological land systems

Introduction

Landscapes are shaped by the interplay of two different forces: (1) biophysical conditions that define natural systems (e.g., ecoregions and biomes) based on relatively homogeneous ecological characteristics, such as primary productivity, vegetation structure and composition; and, (2) human impacts (e.g., land uses and zoning) that modify the land cover (Bailey 2004; Chang 2010; Ellis and Ramankutty 2008; Olson et al. 2001). Human impacts can vary greatly among countries due to differences in legal and economic frameworks (Acemoglu and Robinson 2012). In contrast,

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common historical, administrative and cultural legacy can result in similar human impacts (Minghi 1963; Rumley and Minghi 1991). These differences and similarities can be studied by focusing on international borders, which are prominent administrative features that affect socio-ecological land systems at large scales. Socio-Ecological Land Systems are a set of human-natural elements that co-exist as units of land organization and use, where humans play an important role in the configuration of, or their dependency from, natural systems (Boillat et al. 2017; Sobal et al. 1998; Verburg et al. 2015). The existence of different socio-ecological land systems (further referred to as land systems; Verburg et al. 2015) at each side of a border has often generated conflicts and social tensions related with the access to natural resources, land rights and human migrations (Nolte and Wehner 2015; Parodi 2002; Van Houtum 2005; Wu 1998). Globally prominent examples of major across-border asymmetries in land use include the border between North and South Korea, between Israel and its neighboring Lebanon and the Palestinian authority, and between the Dominican Republic and Haiti; in all cases reflecting an interplay between distinctive colonial histories and mayor differences in recent socio-economic development. Systematizing the analysis of across-border land system differences should expand our understanding of the effect of borders on planetary functioning during the Anthropocene (Ellis 2019).

Ecoregions are climatically and biologically homogeneous geographical units (Smith et al. 2018) that are widely used for conservation planning (Dinerstein et al. 2017; Hoekstra et al. 2004; Olson et al. 2001). Ecoregions can be used for the integrated planning of socio-ecological land systems, because (1) they control, to some extent, their capacity to sustain different land uses (Bryce et al. 1999; Gallant et al. 2004), and (2) they potentially contribute to the resilience of systems under environmental change (Cumming 2011; Omernik 1995). Global, regional and national initiatives use ecoregions as units for nature assessment, report indicators and conservation goals setting (e.g., IPBES; Convention on Biological Diversity; Half Earth Initiative) but they often overlook the fact that many ecoregions are split in two or more countries, potentially including contrasting land use systems and socio-economic priorities across borders. Country-based decisions are likely reflected in transnational (eco) regions where cultural, economic and historical legacies may persist as contrasting patterns in the landscape (Foster et al. 2003; Munteanu et al. 2015; Ziter et al. 2017). Furthermore, recent global trends towards nationalist political movements may reinforce these patterns with the emergence of new borders or the reinforcing of preexisting ones (Allen et al. 2020; Sabanadze 2010).

Many studies (described below) have assessed transboundary differences, but in most cases focussed on a single border or even in a narrow section of it, not taking into account the initial biophysical potential of the system and often without integrating variables from different disciplines. Economists have looked into variables reflecting economic growth and demography in the vicinity of borders (Machado et al. 2009; Pinkovskiy 2013). Earth scientists have studied biophysical differences of borderlands, such as differences in terrain roughness in neighbour regions of Africa (Nunn and Puga 2012) or different soil erosion rates at the country scale as a consequence of differing national agricultural practices (Wuepper et al. 2019). Conservation scientists have developed initiatives for across-border cooperation (Liu et al. 2020, Prist et al. 2019, Taggart-Hodge and Schoon 2016), ecosystem services management (López-Hoffman et al. 2010, Rai et al. 2018), cross-border protected areas (Thornton et al. 2019), or across-border animal movement (Lennox et al. 2016). Land systems and sustainability scientists have analyzed forest use, management and disturbances under different human population growth and land ownership across borders (Kuemmerle et al. 2006; Röder et al. 2015; Wuepper et al. 2019; Wulder et al. 2007). Social scientists have studied borders as places of major socio-political conflicts associated with religion, identity, governance, trade or migration (Krichker 2019; Machado et al. 2009; Rumley and Minghi 1991; Van Houtum 2005). Political geographers have studied the uneven distribution of natural resources, such as water or energy, generating rent conflicts across national borders (Irarrazaval 2020; Mohammadpour et al. 2019). Yet, transboundary studies have overlooked, on the one hand, the biophysical potential of natural regions to determine their limitations or constraints for development (i.e., natural primary productivity of ecoregions) and, on the other hand, the possible influence of land management in multiple land systems (i.e., integrating variables from different disciplines, such as accessibility, land-use, land protection and wealth) at large scales. Moreover, the few multi-national studies that included economic development variables compared across borders, included either a narrow portion of the border territory in the analysis (i.e., buffer) (Crespo Cuaresma et al. 2017; Salisbury and Weinstein 2014) or looked at the effects of a single process of the land system (i.e., forest transition or deforestation) at the country level (Culas 2007; Perz et al. 2005; Redo et al. 2012; Southworth et al. 2011). Understanding transnational socio-ecological land systems at large scales that include a variety of ecosystems and land-management variability (i.e., multi-disciplinary and multi-variable studies) is still a challenge for the socio-environmental sciences.

Due to their similar biophysical conditions, transnational ecoregions can be used as comparative "natural experiments" to assess the effect of national policies on land systems outcomes and allow therefore for theory testing and development (Diamond and Robinson 2010). They also allow evaluating alternatives for sustainable development

and for nature conservation planning in relation to the influence of institutions on human wellbeing or natural capital under different governance regimes (Acemoglu and Robinson 2012; Rumley and Minghi 1991). To achieve this, it is important to incorporate in current research agendas questions about (1) the effects of national borders on the emergence of human-induced patterns in the landscape within the same ecoregion reflected in land use asymmetries, (2) the factors that promote the asymmetries in the land systems across borders and, (3) the potential implications for nature conservation and the socio-ecological land systems in the long term. These are the questions we investigate in our work for South America.

South America provides the opportunity to explore these questions in a setting of relative historical stability of national borders nearly over the past 200 years (Routley 2018), a wide range of biomes (#10), ecoregions (#106) and culturally diverse nations with different governance regimes (i.e., centralized/federal) (Parodi 2002); which results in a wide range of land system transformations due to human action and social idiosyncrasies. It includes areas where human land use has dominated the landscape for more than five centuries (i.e., from Pre-Columbian times), areas where early European colonization expanded new forms of agriculture, areas where early national colonization plants trigged a new wave of expansion (mostly of livestock-related activities) in the late 19th-early twentieth century, and areas which have been largely unmodified until the twentieth century and are currently the most active frontiers of agriculture expansion and land development in the world (Aide et al. 2013; Grau and Foguet 2021; Hansen et al. 2013; Lambin et al. 2013). For example, wealthy densely populated urban nucleus with good accessibility co-exists with other unconnected regions that lack socio-economic development despite its high population. From mid-1900s, there was a steep acceleration in cropland activities until the beginning of the twenty-first century when cropland boomed due to global market demands for grain commodities (Aide et al. 2013; Perz et al. 2005). This land-use intensification brought associated important losses of natural vegetation in lowland plains (Aide et al. 2013; Armenteras et al. 2017; Hansen et al. 2013). Yet, intense land uses co-exist with vast tracks of (grass) land managed in extensive ways using traditional fire techniques (Bowman et al 2011; Fernández et al. 2020), large areas of forest recovery, mostly in mountain sectors (Aide et al. 2019, 2013; Nanni et al. 2019) and the protection of land which differs importantly among countries and ecoregions (Baldi et al. 2018).

The aim of this work was to systematically assess transnational asymmetries in diverse socio-ecological land systems at the ecoregion level for the entire South America and to explore which factors potentially influence these asymmetries. We developed and applied a simple and descriptive approach at the continental scale to (1) quantify the level of Trans-National Ecoregion's (TNEs) asymmetries in land systems using multidisciplinary variables and how these vary among biomes; (2) explore what are the main factors associated with these asymmetries and, (3) assess if there are any continental patterns where international borders generate land systems' asymmetries between neighboring countries sharing ecoregions. We integrate in a coherent way and for the first time to our knowledge, (1) a biological variable accounting for the natural potential for development (i.e., the biome as a proxy for primary productivity), (2) variables from multiple disciplines which before have been used in isolated ways and that account for human land-use and management (e.g., cropland, protected areas or accessibility) and (3) large transboundary regions.

Materials and methods

Our units of analysis were all the Transnational Ecoregions of South America (**TNEs**, an ecoregion that lays in more than one contiguous country). Each TNE was formed of pairs of neighbour National Ecoregions (**NE**, i.e., the portion of an ecoregion that falls within the limits of one nation). For example, we compared the Llanos in Venezuela (i.e., NE: Llanos_VEN) against the Llanos in Colombia (i.e., NE: Llanos_COL) that formed the TNE "Llanos_VEN_COL". We selected ecoregions that covered more than one country and had more than 500,000 ha in each country as an arbitrary extension large enough to capture a country's land systems (Olson et al. 2001). Thus, a single ecoregion may be involved in more than one TNE when three or more countries are involved, such as the Chaco ecoregion between Argentina, Bolivia and Paraguay. Based on this principle, we excluded ecoregions that were largely located in only one country, such as all desert-biome ecoregions and the Cerrado ecoregion in Brazil. We also excluded ecoregions without spatial continuity (i.e., patches such as the coastal mangroves). These criteria resulted in 49 Transnational Ecoregions (TNEs), 30 ecoregions corresponding to seven of the ten biomes present in South America extending across national borders (Fig. 1, Table 1).

Land use variables (such as accessibility, population presence, land-use and zoning), constitute a good descriptor of land systems because, besides being spatially explicit, they summarize a historical process of interactions between people and the environment (Verburg et al. 2015). For example, the proportion of cropland in a landscape is not only an indicator of its aptitude for agriculture, but it is also the result of a social, economic and cultural context that favors its expansion or persistence. The transboundary comparisons of land systems and their patterns are likely to be explained by spatial determinants (e.g., the agricultural aptitude),

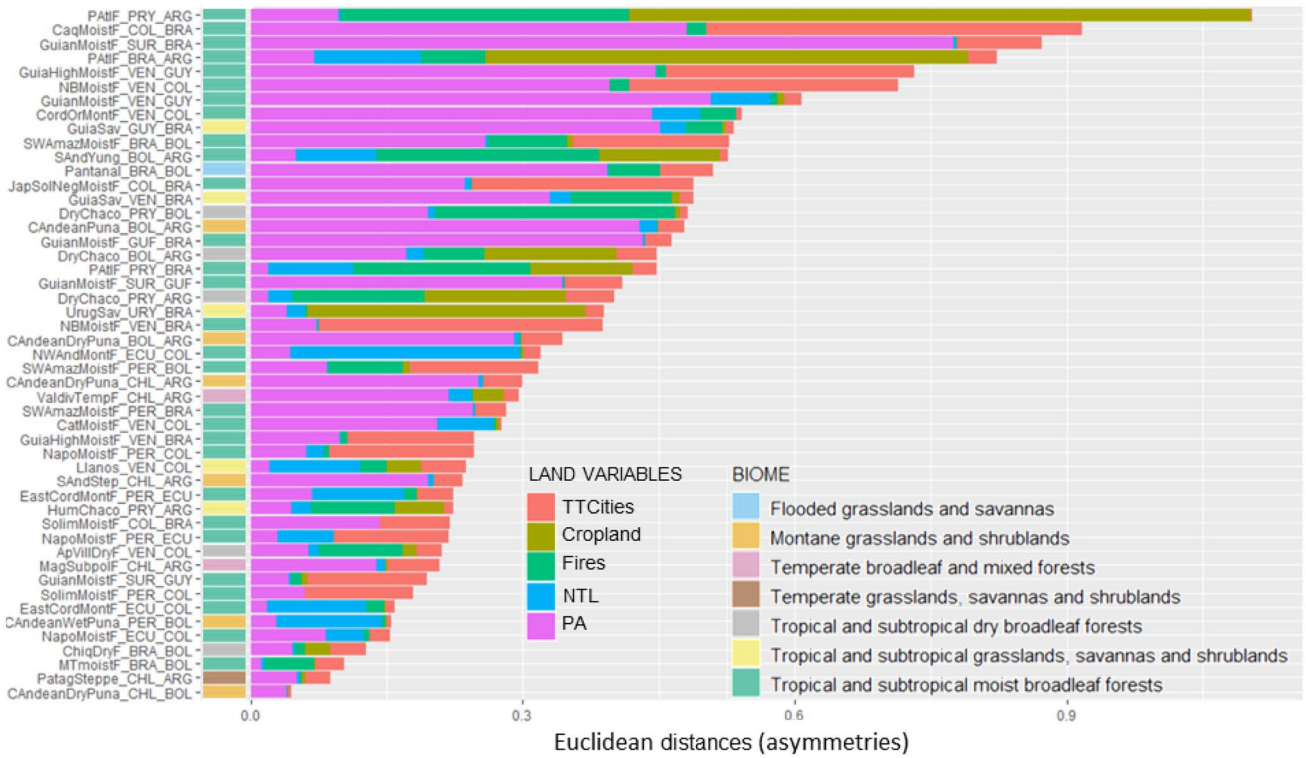

Fig. 1 Ranking of pairs of Transnational Ecoregions (TNE) according to their Euclidean distances (x axis) that characterize land-system asymmetries. Each bar is colored according to the relative contributions of the land variables used to characterize Euclidean distances of land systems

nation-level variables (e.g., GDP) as well as by the particular value and priority that a given country assigns to an ecoregion due to its singularity (Kenter et al. 2015; Lambin et al. 2013; Omernik 1995). To assess how different land systems in each side of the TNE border were, we first characterized each NE using a set of five land variables. These variables were chosen to represent different aspects of land use/management systems, acting as potential determinants of land-use changes (sensu Meyfroidt 2016): (1) the level of urban population and economic development was estimated using the density of Night Time Lights (NTL) in 2013 (DMPS-OLS v.4 average-stable visible lights, NOAA) as a proportion of NTL area per km^2 of the NE (Bruederle and Hodler 2018); (2) the level of infrastructure and territorial accessibility from populated centers of each NE was quantified using Travel Time to Cities per NE (TTCities, Nelson 2008), calculated as the average time of travel from every pixel in the NE to their nearest city with more than 50,000 inhabitants per km^2 of the NE (i.e., the lowest the value, the most accessible the region is); (3) the level of transformation and human appropriation of an ecoregion was calculated as the proportion of cropland area for each NE in 2014 (km^2 of cropland/km^2 of the NE) (Graesser et al 2015); (4) the level of low-technology and extensive land management (related to rural population presence) was measured using fire density based on the number of fires in 2013 per NE area unit (number of fires/km^2 of the NE) (NASA 2013); and (5) the level of government commitment to and societal valuation of nature conservation was measured as the proportion of the NE under protection (km^2 under protection/km^2 of the NE) of any of the categories of protected areas in the World database of Protected Planet (Protected Planet 2015) (Figs. 2, 3). All these variables were available as maps with different spatial resolutions, thus we resampled those with resolutions higher than 1 km^2 (i.e., cropland, NTL and fires) to a 1 km^2 pixel grid (using a majority algorithm) to facilitate a common overlay and spatial analysis. We then summarized each variable as density per NE by summing their values and dividing by the NE area (Figs. 4, 5). Some of these variables showed some association and for example, TTCities was positively correlated with protected areas ($r = 0.47$); indicating that protected areas tend to be located in less accessible areas and negatively correlated with NTL ($r = -0.35$); suggesting that cities tend to be well connected and thus travel time between them is low (Fig. 6). These correlations, although point at important functional associations, could potentially inflate some of the comparative results.

Once we characterized land use/management systems of each NE (i.e., each side of the border), we quantified land systems' asymmetries for a specific TNE (i.e., the differences in the land use/management variables between each pair of NE at both sides of the border). For this, we

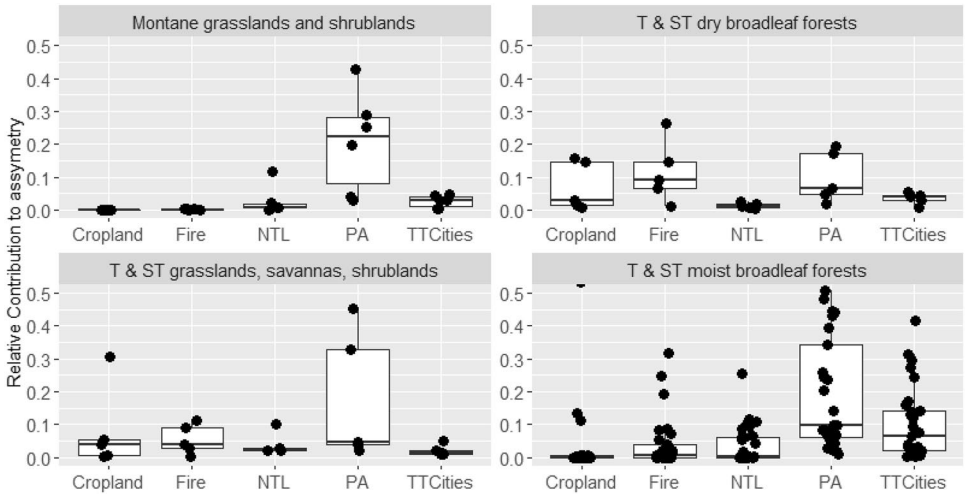

Fig. 2 Box plots showing the distribution of the relative contribution of each standardized land-system variable for the TNEs of the four major biomes in ranking of asymmetries. T and ST: tropical and Sub-Tropical biomes

calculated the pairwise Euclidean distances of the five land-system variables mentioned above. For country pair, *i* and *j*, which share the same ecoregion (*k*), the Euclidean distance metric (*D*) is the square root of the sum of the squared differences between the variables (*m*) used to characterize each TNE (Eq. 1).

$$D\left(k_{ij}\right) = \sqrt{\sum_{m=1}^{m=5}\left(x_{km_i} - x_{km_j}\right)^2} \quad (1)$$

Euclidean distance is a widely used metric to characterize dissimilarities because it is easy to calculate and interpret, with higher values pointing at more dissimilarities between the pairs under comparison. It combines quantitatively variables of different nature and is well suited to study geographic patterns (Pandit and Gupta 2011; Shirkhorshidi et al. 2015).

The variables used in the calculation of Euclidean Distances were previously standardized between 0–1, using a lineal transformation to fit the min–max values of all NEs entering the study, Table 2. This means that asymmetries of a TNE can range from 0 (exactly the same values for all variables in both sides of the border) to 2.23 (square root of five, when one side of the border would have the maximum values and the other side, the minimum values). We included the biome type of each TNE when ranking their asymmetries to describe broad-scale ecological patterns associated with the biophysical properties of each biome.

Besides, to better describe the relevance of the variables used to characterize land system asymmetries, we calculated the relative contribution of each of the five land-system variables per TNEs (i.e., each pair of NE). We analyzed the relative contribution of these five variables per biome to explore differences in the variable's influence in characterizing asymmetries.

In addition, to further explore factors that could explain asymmetries associated with human economic development, primary productivity, conservation preferences, and historical land use, acting at regional scales (i.e., country and ecoregion level), we used a common regression model (Generalized Linear Model - GLM with Gaussian family and identity link, see Appendix 2). The variables used in this model may influence asymmetries and function as predisposing (but not necessarily causal) factors which, together with other factors, may lead and shape land cover change (Meyfroidt 2016).These variables explained asymmetries of a TNE as a function of: (1) per capita Gross Domestic Product (GDPpc), (2) Gross Primary Productivity (GPP), (3) ecological singularity and (4) history of human use. The reasons behind choosing this set of variables were: first, GDPpc reflects the capacity of a country to invest in development, especially in marginal regions that are not remote. Richer countries would invest and develop further even remote regions. So, the asymmetry in TNE's land-use patterns is likely to be explained by the difference in GDPpc between both countries. To define this first variable, we used differences of the national per capita Gross Domestic Product (GDPpc) in 2013 of the two countries that define the TNE (i.e., absolute delta of per capita GDP, World Bank database). Second, GPP indicates eco-regional productivity. Ecoregions that are more productive would have a higher range of alternatives for developing productive or land systems and potentially activities at each side of a TNE can be very different. On the contrary, in less productive ecoregions, the ranges of development options are more restricted and land systems at each side of the TNE would potentially be more similar (Potosyan 2017; Ramankutty et al. 2008). To define this second variable, we used the median Gross Primary Productivity (GPP) (Zhang et al. 2017) of the remaining natural vegetation of the entire ecoregion in 2013 as in Graesser et al. 2015. Third, the ecological singularity

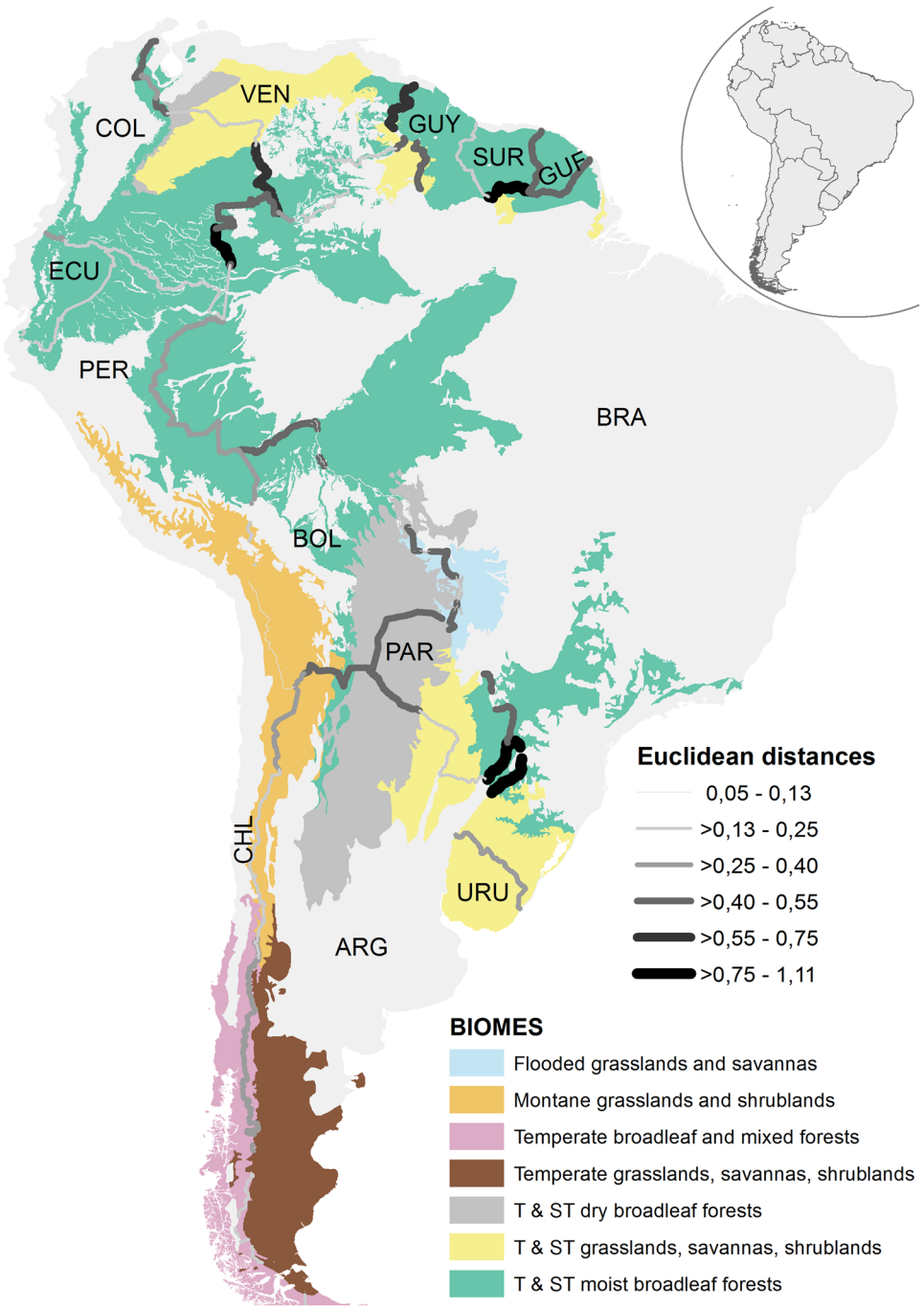

Fig. 3 Land systems' asymmetries in TNEs. Ecoregions entering the study are colored according to the biome they belong to and TNE borders are coloured by their Euclidean distances rank (i.e., land-use asymmetries). KMLs of these layers are available in Zenodo under DOI: https://doi.org/10.5281/zenodo.4813158, a Web Map Service (WMS) of these layers is available under reference link WMS (2021) and a Web Feature Service is available under reference link WFS3 (2021). Projection: South America Albers Equal Area Conic

of the ecoregion makes reference to a socio-economic perception of resource availability. We assumed that countries with a lower portion of an ecoregion within their territory may consider that ecoregion singular because it is a scarce resource for the country and thus may be more inclined to invest in its protection. In contrast, a country including a vast extension of a particular ecoregion may value its conservation comparatively less (Kenter et al. 2015; Omernik 1995). To quantify this third variable, we used the area percentage of ecoregion in relation to country area. Fourth, the "History of human use" of the ecoregion, would highlight regional patterns of human occupation. We assumed that neighbor regions under longer human occupation would be more similar than those regions with shorter or uneven human occupation. We defined this variable summing the area used by humans in 1700 and 1800 per ecoregion as in the "Anthromes 2" data base (Ellis et al. 2010).

Finally, we mapped at the continental-scale land systems' asymmetries per TNEs in a vector form and calculated descriptive statistic per biome and by country to highlight

country-level characteristics that can influence or explain border asymmetries.

Results

Land systems' asymmetries of transnational ecoregions across South American biomes

The eight most asymmetric TNEs occurred in the Tropical and subtropical moist broadleaf forests biome, which was also the biome with most of the TNEs (#28) and with the widest range of asymmetry values (Fig. 1). The ecoregion with highest asymmetries was the Atlantic forests between Argentina, Brazil and Paraguay, followed by the Caquetá moist forest between Colombia and Brazil and the Guiana moist forest between Venezuela, Brazil, Suriname and Guiana. Other TNEs with high asymmetries included the Tropical and subtropical grasslands, savannas and shrublands biomes located in the above-median section of the asymmetries ranking, with the Guiana savannas between Brazil, Venezuela and Guiana showing the highest asymmetries of this biome followed by the Uruguayan savanna between Uruguay and Brazil. Among the TNEs of dry forest biomes, the Dry Chaco between Paraguay and Bolivia and Paraguay and Argentina showed the highest values. In contrast, montane grasslands and shrublands showed lower levels of asymmetry, including, for example, two of the lowest asymmetric TNEs: The Andean Dry Puna between Chile and Bolivia and the Wet Andean Puna between Peru and Bolivia (Fig. 1).

Factors characterizing land systems' asymmetries of TNEs

Among the five land variables we used to characterize asymmetries, protected area was the most important variable defining land systems' asymmetries for moist and montane biomes in South America (Figs. 1, 2). Fire was the most important variable contributing to land asymmetries in dry forest biomes (Fig. 2). NTL tended to characterize land systems with overall low asymmetry levels (Fig. 2). Other important variables for the four biomes with highest to intermediate asymmetries were (in decreasing order of importance after protected areas): TTCities and then fire in moist forests; fire and cropland with the same importance in tropical grasslands; protected areas and TTCities in dry forest biomes; and TTCities and NTL in montane grasslands (Fig. 2).

The model we used to explore predisposing factors that could be associated to asymmetries did not result in statistically significant covariates and the deviance explained by the model was around 10% (Appendix 2). Although this is a relatively low explanatory level, the signs of the coefficients were in line with the reasoning behind using each model variable (all of them positive except for "history of human use" that was negative, Appendix 2) (Fig. 7). When relating Euclidean distances against *GPP* or *History of use,* we found a general pattern of higher asymmetries under conditions of higher primary productivity of an ecoregion, which generally occurs in the humid biomes (Fig. 8). Likewise, the longer a territory was used by humans (i.e., *History of use*), the least asymmetries with its neighbor NE, which was specially the case for the mountain regions of South America (Fig. 8). *GDP* difference and *Ecological singularity* did not show any distinguishable pattern in relation to asymmetries.

Continental patterns of land systems' asymmetries in national borders

High values of land systems' asymmetries in TNEs of forested lowlands often included: (1) countries with a border with Brazil (the country with more borders, Figs. 3, 7), such as Venezuela, the Guyana, Suriname, French Guyana, Argentina and Paraguay; or (2) new agricultural frontiers, such as the Gran Chaco (Paraguay, Bolivia, Argentina) (Fig. 3). In contrast, lowest asymmetries were observed particularly between Andean countries (Fig. 3, 7). Asymmetries tended to be intermediate to high where the area distribution of the ecoregion on each side of the border was uneven (e.g., the Atlantic forest in Argentina, with a small area of this ecoregion) (Table 2). TNE asymmetries also tended to be high when one of the two countries had its entire area under a single ecoregion, such as the case of the Uruguayan savanna in Uruguay, or the moist forest of Guyana, Suriname or French Guiana (Fig. 5).

Discussion

Our simple and intuitive approach is a first contribution towards developing a comparative, methodological and reproducible analysis of national borderland studies (Krichker 2019) including an ecological component. For the first time to our knowledge, we produced a large-scale border comparison, including multiple nations and multiple ecoregions, characterized according to the biome they belong to (i.e., a higher order of biophysical characterization and a proxy for primary productivity). Moreover, we integrated multiple land-use/management variables, which before have been used in isolated ways, and that relate economic growth with (1) current land use for agricultural production (i.e., cropland area), (2) a proxy of land management for small–medium-scale agriculture and rangeland management (i.e., fire), (3) governmental policies for the protection of land and natural resources (protected areas) and (4) human presence and economic development (Night

Time Lights and Travel Time to Cities). With our work, we complement the study of borders within several disciplines (1) econometrics, political or social sciences via giving it a more ecological and land system perspective, and within (2) conservation studies via including the land system perspective using across-border land-use/management variables and economic growth indicators. Our empirical analysis is mainly descriptive, consisting of an exploratory comparison of some relevant variables potentially influencing cross-border land system's asymmetries. Based on this, we hope to advance knowledge via opening a multi-disciplinary perspectival discussion to conceptualize land system asymmetries in transnational ecoregions at continental scales with application to other regions worldwide.

Our approach can be customized to different frameworks and can be used at different geographical scales. For example, other indicators of human activities can be included, such as mining activity, forest plantations, native forest exploitation, cattle ranching, or shifting cultivation (Jarvis et al. 2010). In this work, we explored asymmetries for adjacent transnational ecoregions; however, this could be used to measure asymmetries of subnational areas or not adjacent regions. Finally, our approach has the possibility to be used for monitoring and characterizing temporal patterns of land systems' asymmetries to explore the dynamics of convergence or divergence of land systems. Although our results cannot be interpreted as strictly causal, they can inform policy-makers about possible futures of land system's dynamics under different development scenarios.

Conditions that may favor land systems' asymmetries in TNEs

Our analysis of TNEs showed that they vary dramatically in their effects on land systems, and involve a wide range of asymmetry levels, resulting from varying biophysical and socio-ecological characteristics. Ecoregions located in humid or mesic biomes with high primary productivity and agriculture potential associated to flat topography showed higher average and broader range of TNE asymmetries since these geographic features allow wider options of land use and developmental opportunities (Potosyan 2017; Ramankutty et al. 2008) (Fig. 8). In consequence, both sides of the border can remain unchanged, evolve in parallel, or follow divergent land use trajectories. Because of the high agricultural potential of these regions, they would tend to be transformed unless they are protected or remain inaccessible (Baldi et al. 2017; Wu 1998). The Amazonian forests of Peru-Colombia and northern of Bolivia—west of Brazil (Solimoles and MT moist forests, respectively, Table 1) showed low asymmetries despite being a flat humid forest because of their low accessibility (Table 2), likely related to the low development of infrastructure in comparatively poorer countries. In contrast, the highly accessible Atlantic forest, between Argentina, Brazil and Paraguay is an iconic example of a humid forest ecoregion with extremely contrasting land systems' asymmetries: Brazil and Paraguay have largely transformed this ecoregion for agricultural activities; meanwhile, Argentina has maintained a high proportion of forest cover by both tree plantations and conservation areas (Grau 2016; Wilson et al. 2017).

The case of the Atlantic forest also exemplifies that asymmetries across TNEs could be especially accentuated under contrasting perceptions of the same ecoregion by different countries which could result in opposed priorities and valuation of nature protection vs socio-economic development (Kenter et al. 2015; Omernik 1995) (Fig. 5c). For Argentina, the Atlantic forest is the most important biodiversity hotspot (hosts 50% of the country biodiversity) and is highly valued as the singular example of a quasi-tropical moist forest; as well as an historical center of timber production and tourist activity based in iconic scenery landscapes (Grau 2016; Wilson et al. 2017). In contrast, the Atlantic forest in Paraguay absorbed main productive activities and human settlements to the point that deforestation was so high (c. 90%, Da Ponte et al. 2017) that Paraguay banned deforestation in the Atlantic forest in 2004 until today (Zero deforestation Law 2524/2004). A similar situation occurs in the triple frontier of the Dry Chaco ecoregion, the most endangered dry forest biome on Earth (Dinerstein et al. 2017; Kuemmerle et al. 2017), where each country (Argentina, Paraguay, Bolivia) uses the land differently (Fig. 5c). Meanwhile, Argentina uses the land for cropland and pasturelands, Paraguay does it mainly for cattle ranching and Bolivia protects the land under one of the largest National Parks of the Bolivian national territory (Baumann et al. 2017a). This suggests that national valuation of natural assets in combination with ecosystem singularity and the social perception of the ecoregion could be potential factors influencing transnational differences in land system that need more conceptual attention and empirical research (Beilin and Bohnet 2015; Costanza et al. 2014; Switalski and Grêt-Regamey 2020).

Our results also indicate that countries with a long common history and shared cultural background have low TNEs land systems' asymmetries (e.g., Chile, Ecuador, Bolivia, Peru), whereas countries with little Pre-Columbian development and diverse European colonialism (i.e., from Spanish, Portuguese, Dutch, French, English) tend to show higher asymmetries (e.g., Brazil, Argentina, Guianas, Paraguay) (Figs. 8, 7). In particular, the TNEs in the Andean region have been occupied for a longer time under intensive agricultural land use, from Pre-European and early colonial times, and the imprint of historical land-use co-exists with traditional ancestral practices still in place in ecoregions with biophysical conditions that restricted the spectrum of land use options (i.e., highlands with high slope, steep

topography and overall ecosystems with lower primary productivity, Fig. A5- mountain biomes) (Mann 2005; Williamson 1993). Land systems' asymmetries between tropical Andean countries (i.e., Peru, Bolivia) were minor when compared to subtropical Andean TNEs, where asymmetries seemed to reflect different types of regional economies focused in mountains or lowland areas dependent on the national development priorities. For example, asymmetries in the Andean Puna between Bolivia and Argentina reflected that while the former is a typical Andean country with a long history of socio-economic development and political power in the highlands, Argentina is a "lowland-based" economy in which the Puna region has been marginal to the economic development for the last two centuries and now includes a high proportion of area under conservation (Grau and Gasparri 2018). Chile is also a "lowland-based "economy, and the low asymmetries between the Chilean and Argentine Patagonian steppe reflect that this ecoregion is marginal for agriculture production in both countries, which also similarly use(d) these territories for extensive grazing, mining and tourism (Matossian and Vejsbjerg 2018).

These examples suggest a relationship between the level of asymmetries and the development stage of the region: while cross-border differences have the potential to be maximized under contrasting levels of development (e.g., Atlantic forest between Paraguay and Argentina), both in "underdeveloped" remote regions and in "mature" systems, the two sides would tend to be similar. In the first case, because no one had experienced significant transformation; in the second, because development strategies that work in one side of the border tend to be replicated in neighbor regions due to spillover effects, such as those identified in the agricultural systems in South-East Asia and South America (Friis and Nielsen 2016; le Polain de Waroux 2019). This could be the case of the old agricultural frontiers of the moist forests between Colombia and Peru (i.e., Napo and Solimoes forests) that also share similar patterns of cultural values and society-nature relationships due to their long history of use or the Chiquitanian border between Brazil and Bolivia under agricultural development (le Polain de Waroux et al. 2016).

Comparing complex land systems at large scales is challenging. We believe that the different development stages of the multiple and diverse cases of land systems' asymmetries influenced (1) the low deviance explained by the model that tried to characterized asymmetries using predisposing factors and (2) the lack of statistically significant covariates of these models. This complexity makes it difficult to obtain statistically significant estimations of the disruptions of natural experiments because often the disturbing variable may be part of a nested package of changes of fuzzy or even single processes (i.e., forest transition) as already pointed out in the literature (Crespo Cuaresma et al. 2017; Diamond and Robinson 2010; Redo et al. 2012).

Other factors, such as technological adoption and national development policies, have the power to influence border asymmetries via differential speed of transformation (Wu 1998). This could be the situation of "young" agriculture frontiers currently experiencing early transformation like those in the Gran Chaco, where modern agricultural expansion, aided by technology and at the expense of forests, occurs since the 1990s (Baumann et al. 2017a; Gasparri et al. 2015; Piquer-Rodríguez et al. 2018). This pattern emphasizes the role of governments investments in improving the accessibility of regions or via colonization programs (e.g., in Roraima, Mato Grosso, Acre and Rhondonia); or non-governmental actor-groups' investments (e.g., Menonites in Paraguay) (le Polain de Waroux et al. 2018). The different speed in land system transformation across borders can also activate a switch effect due to feedbacks emerging from different activities at each side of the border that could end up with stable and contrasting land system developments (Keys et al. 2019; Wu 1998). For example, because one country modifies a large proportion of an NE (due to, for instance, the specialization of economies, such as mining, logging, cattle ranching, etc.), the same ecoregion that is less modified in the neighbor country, may (1) increase its value for conservation due to its enhanced singularity or (2) claim land sovereignty via the establishment of protected areas against the neighboring development "threat" (Marinaro et al. 2012). And this situation may act as a limitation to the transition towards a highly transformed landscape in the second country (Grau 2016). Probably this was the situation that influenced nature protection in the Atlantic forest of Argentina in contrast to Paraguay and Brazil, or the conservation of the Bolivian Dry Chaco in contrast to Argentina and Paraguay.

Land variables contribution to TNEs asymmetries

The role of governments is also emphasized by the fact that, protected area was the most important variable contributing to TNEs asymmetries in moist and montane biomes. Protected areas are not easily detectable when looking at land cover from space, but they have the power of "stabilizing" natural cover persistence; and of the studied variables is the one that reflects most directly a governmental decision (Baldi et al. 2017). For example, the moist forest bordering Suriname and Brazil looks similar in satellite images but differ greatly in terms of protected areas (Brazil has a protected area on its side, Table 2 and Fig. 5a). Protected areas do not require the specific biophysical conditions as agricultural or fire activities do, but tend to be located in regions that are peripheral to economic activities, which in South America often includes borders (e.g., Bolivian vs Argentinean Puna, Argentinean vs Paraguayan Atlantic forest) (Baldi et al. 2017; Thornton et al. 2019). Protected areas

have been used in South America as a low-cost way to claim land sovereignty and stabilize borders (e.g., peace parks) (Baldi et al. 2017; Guo 2012; Marinaro et al. 2012; Matossian and Vejsbjerg 2018; Rumley and Minghi 1991). Therefore, the conservation priorities of a country and the uneven distribution of protected and transformed area, as part of a land system, are very relevant issues when considering the feasibility of achieving a specific conservation target for an entire ecoregion that is transnational (Dinerstein et al. 2017).

Fires were the most important variable characterizing land-use systems' asymmetries in biomes dominated by extensive ranching activities, such as dry forests, and tropical grasslands and savannas. Fire is used as a management tool associated to deforestation (for shifting or permanent cultivation), to promote grassland regrowth and palatability, to control shrubland encroachment in pastureland, and to prevent big fires by reducing fuel accumulation (Bowman et al. 2011; Fernández et al. 2020). Examples of regions where fire's density is reflecting land system asymmetries are the Dry Chaco forest between Bolivia and Paraguay or the Yungas between Bolivia and Argentina, where Bolivia has lower fire density in both cases (Table 2). In addition, fire occurrences are commonly related with rural population density and related land use; a pattern reflected in different fire activity between the Atlantic forest of Paraguay and Argentina, with more fires in the Paraguayan side, and the Dry Chaco between Bolivia and Paraguay (Table 2) with a more active deforestation frontier and large extensions of pasturelands that explained a major fire density in the Paraguayan side (Baumann et al. 2017b).

TTCities (as a proxy for accessibility) was an important factor characterizing TNE asymmetries in lowland forested biomes and also in montane grassland, and it was positively correlated with protected areas (i.e., TNEs with higher proportion of protected areas tend to have low accessibility, (Fig. 6). One example of a TNE with an important contribution of TTCities to its asymmetry was the moist forests between Venezuela–Colombia and Venezuela–Brazil, with Venezuela having lower accessibility than its neighbors (Table 1 and Fig. 5b). The construction of roads is usually a state decision that triggers land use transformations and activate positive feedbacks with croplands and urban expansion (Gasparri et al. 2015; O'Kelly and Bryan 1996; Piquer-Rodríguez et al. 2018). As such, road construction could represent an early signal of the intensification of a land system asymmetry.

Night-time lights (as a proxy for economic development and urban population) was the variable contributing the most to explain TNEs asymmetries when the overall Euclidean distances are low, independently from its biome. This was the case, for example, of the East Cordillera Montane moist forest between Colombia, Ecuador and Peru, where Ecuador hosts very important urban centers (including its capital city, Quito) and the neighboring countries have a lower human population density and therefore lower accessibility. The same is observed in the Andean Wet Puna between Bolivia and Peru, with La Paz capital city and El Alto associated massive urbanization with important commercial activity in the former country.

Cropland was an important variable associated to asymmetries in grasslands and savannah biomes which can both hold grazing (reflected in fire frequency) or cropland activities, which are more profitable in this biome due to lower investments in soil preparation than in forest areas (Piquer-Rodríguez et al. 2018). Cropland characterized some of the most asymmetric borders of our study, such as the Atlantic forest between Paraguay or Brazil (with cropland) and Argentina (with forest cover) or the Dry Chaco between Bolivia or Paraguay (with Protected areas and cattle ranching, respectively) and Argentina (with cropland). The example of the Atlantic forest between Brazil and Paraguay supported again the spillover effect (i.e., development strategies that work in one side of the border tend to be repeated in neighbor regions) because both sides experienced a similar expansion of cropland area. The Uruguayan savanna between Brazil (with more cropland) and Uruguay was also characterized by this variable.

Conclusion

Our study represents a first step towards understanding the spatial manifestation of border differences in ecoregions, a neglected topic within the sciences of the Anthropocene that pertains to many places of the world.

International borders have the potential to become a major feature of landscape and ecoregional configuration and our discussion can serve as a guide for future research directions in the land-use and sustainability science communities (Box 1). Our analysis showed that the impact of national borders varies across South America, depending on the biome type. Subtropical lowland humid and dry forest TNEs frequently have dramatic asymmetries in land systems across borders, especially when there has been different colonization history. In contrast, less productive Andean regions, with a common legacy of Pre-Columbian and early

colonial agricultural societies, showed low land systems' asymmetries. We suggest that asymmetries are mediated by the primary production of the ecosystems, agriculture aptitude and by contrasting perceptions and valuation of the same ecoregion across national borders. In addition, the land-use history, legacies and cultural heritage could promote land systems' asymmetries depending on complex interactions and feedbacks of socio-ecological systems that need to be better understood.

Land systems' asymmetries of TNEs may be transient conditions reflecting different stages of economic land development and national valuations of ecoregions (e.g., singularity). However, some asymmetries may stabilize as a consequence of reinforcing feedbacks. For example, protected areas and sustainable forestry industries can promote the persistence of a highly forested region, whereas policies promoting access and infrastructure, which increase the agricultural value of land, may reinforce a transformed landscape persistence hampering nature conservation and favouring agricultural development. The interplay of national conservation and development policies of neighbour nations have the power of promoting or minimizing dramatic and long-lasting uneven distributions of socio-ecological impacts or benefits. Thus, eco-regional wide conservation and development strategies should include national perspectives to foster feasibility and sustainability of these integrated agendas. Further efforts, conceptually and empirically, are needed to understand what promotes human perturbation in border ecosystems and its consequences for sustainability and nature conservation. We invite land-use and sustainability scientists to consider national border interactions in their studies to achieve a holistic understanding of land systems.

BOX 1 Future research directions for the land-use and sustainability science communities:

(1) Understanding the social and ecological consequences of land asymmetries at different scales,
(2) Exploring ways to optimize transnational ecoregional management to improve biodiversity, ecosystem services and social wellbeing and,
(3) Assessing the mechanisms by which different transnational land uses may result in alternative stable land system states.

Appendix 1 Complementary figures and tables to manuscript

See Figs. 4, 5, 6, 7, 8 and Tables 1 and 2.

Appendix 2 Exploration of other factors influencing asymmetries using a common multiple regression model (GLM)

We used a Generalized Linear Model (GLM) to explore other variables that could be influencing the asymmetries we calculated. We used variables at a different scale than that used for calculating Euclidean distances. In our case we used variables at the country or ecoregion scale to include

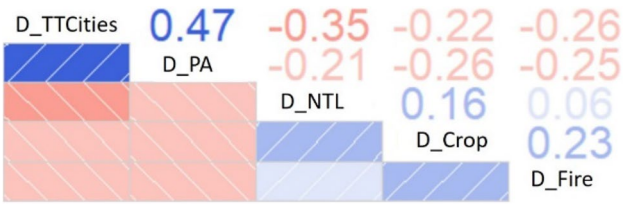

Fig. 5 Correlations of the variables (standardized densities) used in the calculations of Euclidean distances (*D* densities, *PA* protected areas, *TTCities* travel time to cities, *NTL* night time lights)

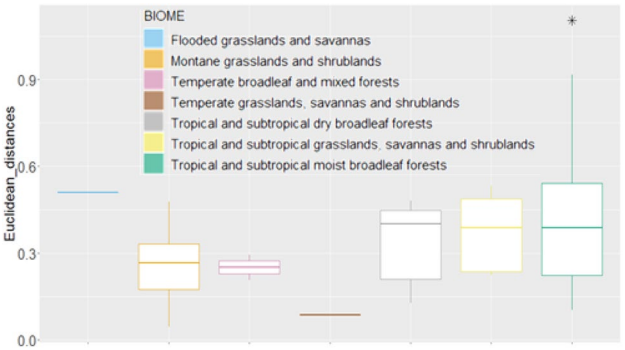

Fig. 4 Boxplots of Euclidean distances of TNEs grouped by their biomes

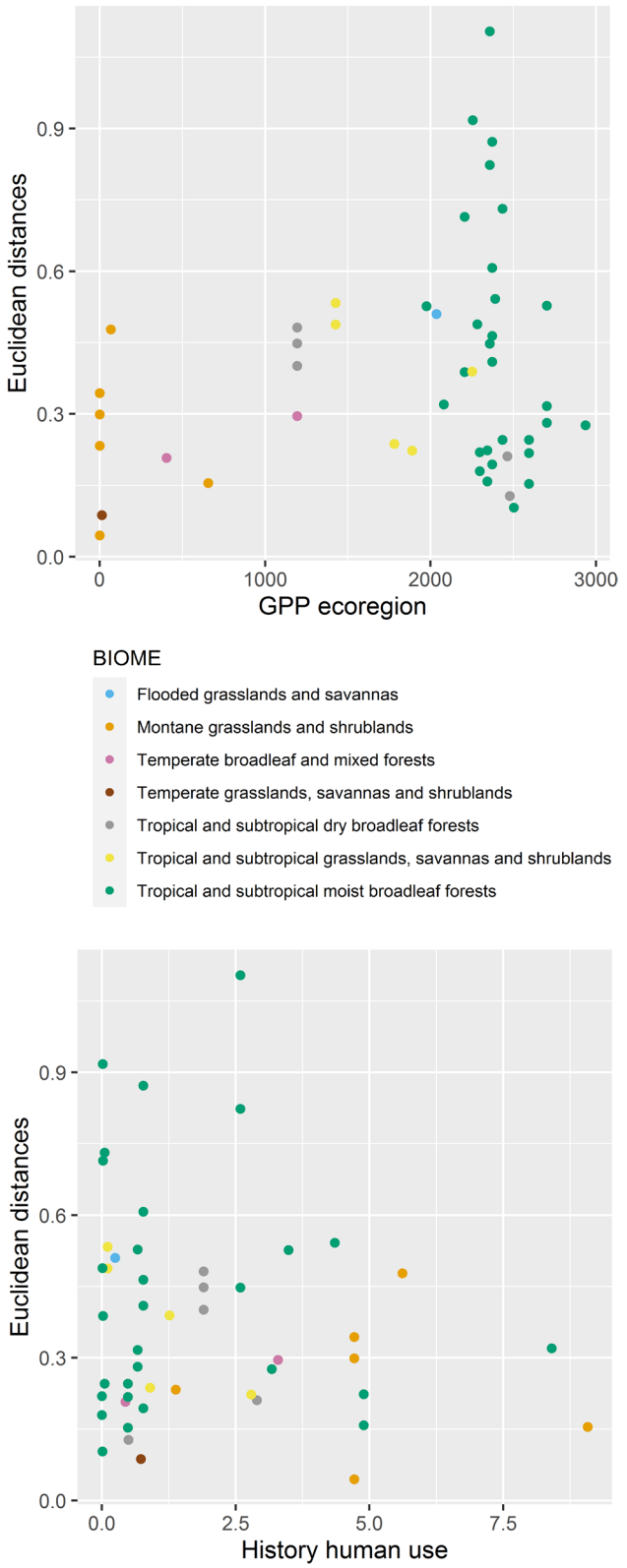

Fig. 6 Scatterplot of Euclidean distances between TNE and their relationship with median Gross Primary Productivity (GPP) for the natural vegetation left in 2013 in each entire ecoregion (above) and History of human use (area percent) of each ecoregion used by humans for the centuries 1700 and 1800 (below)

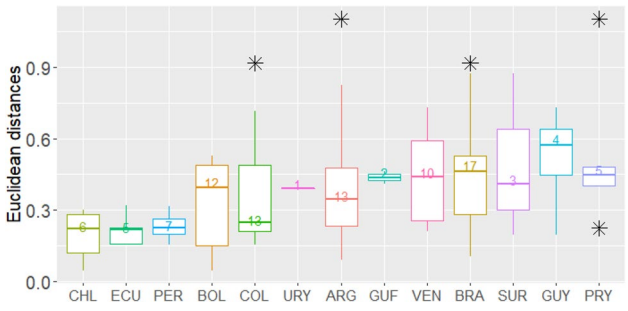

Fig. 7 Basic statistics of the asymmetries values (Euclidean distances) of all TNEs per country. Numbers in the boxes show the value count of NE per country

potential regional patterns occurring at bigger scales. We explored the following variables, explained also in the main body of the manuscript:

GLM variables: delGDP: delta of GDP of each neighbour country sharing a border = abs(GDP1-GDP2). This is a variable at the country level. Source: World Bank database

GPPmed: median Gross Primary Productivity (Zhang et al. 2017) for the entire ecoregion. This is a variable at the ecoregion level

Singular: singularity of the ecoregion calculated as the % of the ecoregion in the country

perc_anthrom: percentage of ecoregion under human use in 1700 and 1800 (accumulated sum of pixels in 1700 and 1800) (Ellis et al. 2010). This is a variable at the ecoregion level

Despite minor violations to model assumptions (the residuals of the model were not normally distributed, Fig. 9), we chose GDP, GPP and anthromes (variables entering model 2 below) as those variables with influence in land system asymmetries

GLM formula: Euclidean_distances ~ delGDP + GPPmed + singular + perc_anthrom, family = Gaussian, link = identity

Test of GLM assumptions: we checked model assumptions using regressions diagnostic plots (residuals vs. fitted plot, Normal Q-Q plot, scale-location plot, residuals vs. leverage plot). Although the residuals of the GLM model were not normally distributed (Fig. 9), we consider that this minor violation to model assumptions does not affect the overall simplification of the results

GLM results (model 1):

Deviance Residuals:

Min	1Q	Median	3Q	Max
−0.34983	−0.16039	−0.03662	0.10442	0.65730

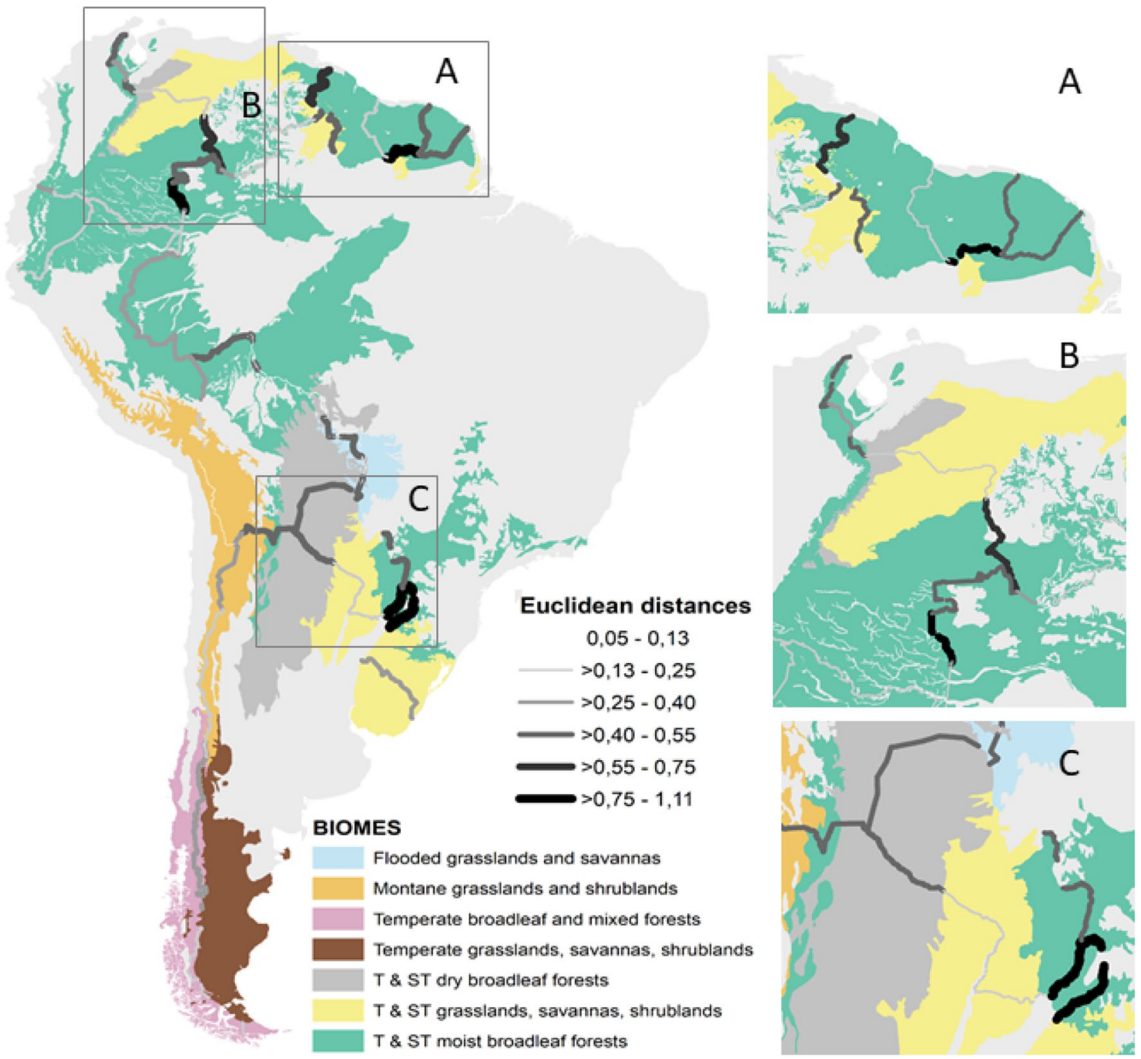

Fig. 8 Detail inlets of continental patterns of land system asymmetries in South America. Projection: South America Albers Equal Area Conic

Table 1 Abbreviations of Ecoregions names used in the figures of this study

Ecoregion name	Abbreviations
Alto Paraná Atlantic forests	PAtlF
Apure-Villavicencio dry forests	ApVillDryF
Caqueta moist forests	CaqMoistF
Catatumbo moist forests	CatMoistF
Central Andean dry puna	CAndeanDryPuna
Central Andean puna	CAndeanPuna
Central Andean wet puna	CAndeanWetPuna
Chiquitano dry forests	ChiqDryF
Cordillera Oriental montane forests	CordOrMontF
Dry Chaco	DryChaco
Eastern Cordillera real montane forests	EastCordMontF
Guianan Highlands moist forests	GuiaHighMoistF
Guianan moist forests	GuianMoistF
Guianan savanna	GuiaSav
Humid Chaco	HumChaco
Japurá-Solimões-Negro moist forests	JapSolNegMoistF
Llanos	Llanos
Madeira-Tapajós moist forests	MTmoistF
Magellanic subpolar forests	MagSubpolF
Napo moist forests	NapoMoistF
Negro-Branco moist forests	NBMoistF
Northwestern Andean montane forests	NWAndMontF
Pantanal	Pantanal
Patagonian steppe	PatagSteppe
Solimões-Japurá moist forests	SolimMoistF
Southern Andean steppe	SAndStep
Southern Andean Yungas	SAndYung
Southwest Amazon moist forests	SWAmazMoistF
Uruguayan savanna	UrugSav
Valdivian temperate forests	ValdivTempF

Coefficients:

	Estimate	Std. error	*t* value	Pr(>|t|)
(Intercept)	2.249e-01	1.159e-01	1.941	0.0587
delGDP	1.079e-05	9.603e-06	1.124	0.2672
GPPmed	4.988e-05	4.126e-05	1.209	0.2331
singular	1.595e-03	1.414e-03	1.128	0.2654
perc_anthrom	− 7.713e-03	1.624e-02	− 0.475	0.6372

Model tests:

Model 1:

formula = Euclidean_distances ~ delGDP + GPPmed + singular + perc_anthrom

AIC: 0.8493, R^2: 0.1048, RSME: 0.2159

Shapiro–Wilk normality test for GLM residuals:

$W = 0.93675$, p value = 0.01106

Model 2:

formula = Euclidean_distances ~ delGDP + GPPmed + perc_anthrom

AIC: 0.2466, R^2: 0.0789, RSME: 0.2190

Shapiro–Wilk normality test for GLM residuals:

$W = 0.93792$, p value = 0.01227

Model 3:

Euclidean_distances ~ delGDP + perc_anthrom

AIC: 0.2176, R^2: 0.0411, RSME: 0.2235

Shapiro–Wilk normality test for GLM residuals:

$W = 0.92824$, p value = 0.005278

Note: $R^2 = 1$—(Residual Deviance/Null Deviance)

Shapiro–Wilk normality test for all single GLM variables ($n = 49$):

Euclidean distances: $W = 0.91644$, p value = 0.001981

delGDP: $W = 0.92848$, p value = 0.005386

Singular: $W = 0.63369$, p value = 8.225e-10

GPPmed: $W = 0.79129$, p value = 6.786e-07

perc_anthrom: $W = 0.81009$, p value = 1.828e-06

Table 2 Standardized densities of the spatial land variables used to characterize TNEs asymmetries of South America

TNE1	TTCities1	Fire1	NTL1	PA1	Crop1	PixelEco1	TNE2	TTCities2	Fire2	NTL2	PA2	Crop2	PixelEco2
ApVillDryF_COL	0.0746	0.0848	0.1382	0.0341	0.0108	43,762	ApVillDryF_VEN	0.0243	0.251	0.1174	0.1493	0.0393	24,456
CAndeanDryPuna_ARG	0.1172	0	1,00E-04	0.4046	0	141,219	CAndeanDryPuna_BOL	0.0634	0.0022	0.0067	0.0648	0	29,884
CAndeanDryPuna_ARG	0.1172	0	1,00E-04	0.4046	0	82,709	CAndeanDryPuna_CHL	0.0676	0	0.007	0.1097	0	29,884
CAndeanDryPuna_BOL	0.0634	0.0022	0.0067	0.0648	0	82,709	CAndeanDryPuna_CHL	0.0676	0	0.007	0.1097	0	141,219
CAndeanPuna_ARG	0.087	0.0023	0.0013	0.5771	0	56,132	CAndeanPuna_BOL	0.0553	0.0031	0.0235	0.1007	0	87,033
CAndeanWetPuna_BOL	0.0634	0.0068	0.1845	0.1774	0	98,834	CAndeanWetPuna_PER	0.0693	0.0125	0.0342	0.1409	0.001	17,917
CaqMoistF_BRA	1	0	0	0.986	0	170,831	CaqMoistF_COL	0.401	0.0313	3,00E-04	0.2917	0	12,542
CatMoistF_COL	0.0224	0.0045	0.234	0.0966	0	16,048	CatMoistF_VEN	0.0253	0.0069	0.1535	0.3611	0.0057	6694
ChiqDryF_BOL	0.1191	0.1139	0.028	0.2381	0.0776	65,532	ChiqDryF_BRA	0.0453	0.1354	0.0228	0.1516	0.024	164,073
CordOrMontF_COL	0.0813	0.0191	0.0603	0.188	2,00E-04	8739	CordOrMontF_VEN	0.0888	0.0671	0.1244	0.7238	6,00E-04	58,752
DryChaco_ARG	0.0312	0.2098	0.0497	0.043	0.2815	123,188	DryChaco_BOL	0.116	0.0854	0.0131	0.3634	0.0088	489,088
DryChaco_ARG	0.0312	0.2098	0.0497	0.043	0.2815	174,385	DryChaco_PRY	0.128	0.473	0.0013	0.0775	5,00E-04	489,088
DryChaco_BOL	0.116	0.0854	0.0131	0.3634	0.0088	174,385	DryChaco_PRY	0.128	0.473	0.0013	0.0775	5,00E-04	123,188
EastCordMontF_COL	0.0975	0	0.0295	0.2324	7,00E-04	65,509	EastCordMontF_ECU	0.0842	0.0278	0.183	0.2073	0.0027	10,655
EastCordMontF_ECU	0.0842	0.0278	0.183	0.2073	0.0027	25,445	EastCordMontF_PER	0.1527	0.0048	0.0073	0.089	1,00E-04	65,509
GuiaHighMoistF_BRA	0.4382	0.0047	8,00E-04	0.9295	0	88,975	GuiaHighMoistF_VEN	0.6384	0.0167	0.0016	0.787	0	28,036
GuiaHighMoistF_GUY	0.2572	0.0019	0	0.163	0	88,975	GuiaHighMoistF_VEN	0.6384	0.0167	0.0016	0.787	0	26,520
GuianMoistF_BRA	0.31	7,00E-04	3,00E-04	1	0	80,545	GuianMoistF_GUF	0.3408	1,00E-04	0.0028	0.5368	0	68,267
GuianMoistF_BRA	0.31	7,00E-04	3,00E-04	1	0	130,855	GuianMoistF_SUR	0.4151	5,00E-04	0.0039	0.134	0	68,267
GuianMoistF_GUF	0.3408	1,00E-04	0.0028	0.5368	0	130,855	GuianMoistF_SUR	0.4151	5,00E-04	0.0039	0.134	0	80,545
GuianMoistF_GUY	0.231	0.0162	0.0077	0.0756	0.0096	130,855	GuianMoistF_SUR	0.4151	5,00E-04	0.0039	0.134	0	163,438
GuianMoistF_GUY	0.231	0.0162	0.0077	0.0756	0.0096	32,356	GuianMoistF_VEN	0.209	0.0241	0.0857	0.6772	0	163,438
GuiaSav_BRA	0.0781	0.287	0.0338	0.53	0.0108	13,507	GuiaSav_GUY	0.0675	0.334	7,00E-04	0	0.0061	77,505
GuiaSav_BRA	0.0781	0.287	0.0338	0.53	0.0108	12,857	GuiaSav_VEN	0.0995	0.1298	0.0023	0.9904	0	77,505
HumChaco_ARG	0.0364	0.6037	0.0373	0.0922	0.1366	128,760	HumChaco_PRY	0.0547	0.7766	0.0776	0.0073	0.0326	161,668
JapSolNegMoistF_BRA	0.5457	3,00E-04	0.0099	0.6024	0	34,608	JapSolNegMoistF_COL	0.8977	6,00E-04	0	0.2635	0	232,455
Llanos_COL	0.1364	1	0.0161	0.0341	0.0085	223,063	Llanos_VEN	0.0425	0.9454	0.2099	0.0731	0.083	152,736
MagSubpolF_ARG	0.0918	0.0011	0.0154	0.3187	0.0052	115,962	MagSubpolF_CHL	0.17	6,00E-04	0.003	0.5107	0.0018	27,258
MTmoistF_BOL	0.1304	0.11	4,00E-04	0.4107	0	59,005	MTmoistF_BRA	0.1815	0.0221	0.0069	0.4289	0.002	657,245
NapoMoistF_COL	0.1643	0.0095	0.0274	0.1002	0	70,827	NapoMoistF_ECU	0.2006	0	0.0948	0.2327	0	39,560
NapoMoistF_COL	0.1643	0.0095	0.0274	0.1002	0	140,194	NapoMoistF_PER	0.3923	0	6,00E-04	0.1878	0	39,560
NapoMoistF_ECU	0.2006	0	0.0948	0.2327	0	140,194	NapoMoistF_PER	0.3923	0	6,00E-04	0.1878	0	70,827

Table 2 (continued)

TNE1	TTCities1	Fire1	NTL1	PA1	Crop1	PixelEco1	TNE2	TTCities2	Fire2	NTL2	PA2	Crop2	PixelEco2
NBMoistF_BRA	0.5542	4,00E-04	7,00E-04	0.5041	0	55,365	NBMoistF_VEN	0.9319	0.0018	1,00E-04	0.5926	0	48,370
NBMoistF_COL	0.5035	0.0315	9,00E-04	0.0217	0	55,365	NBMoistF_VEN	0.9319	0.0018	1,00E-04	0.5926	0	97,056
NWAndMontF_COL	0.0758	4,00E-04	0.0591	0.1542	0.008	31,842	NWAndMontF_ECU	0.0518	0.0013	0.3738	0.0996	0.0111	48,814
Pantanal_BOL	0.1113	0.3161	4,00E-04	0.5575	0	136,231	Pantanal_BRA	0.0374	0.3887	0.0018	0.0581	4,00E-04	32,065
PatagSteppe_ARG	0.0513	0.0035	0.0117	0.056	0.002	27,591	PatagSteppe_CHL	0.0931	0.0018	0.0042	0.1326	0.0071	533,488
PAtlF_ARG	0.0475	0.0144	0.0729	0.1635	0.0058	374,367	PAtlF_BRA	0	0.1199	0.2469	0.0588	0.7951	22,520
PAtlF_ARG	0.0475	0.0144	0.0729	0.1635	0.0058	85,950	PAtlF_PRY	0.0496	0.4747	0.0763	0.0231	1	22,520
PAtlF_BRA	0	0.1199	0.2469	0.0588	0.7951	85,950	PAtlF_PRY	0.0496	0.4747	0.0763	0.0231	1	374,367
SAndStep_ARG	0.1047	0.0039	0.0065	0.2859	0	30,329	SAndStep_CHL	0.0688	0.0037	0.014	0.0557	0	94,441
SAndYung_ARG	0.0618	0.4973	0.1735	0.2793	0.2567	27,743	SAndYung_BOL	0.0783	0.0612	0.0185	0.1899	0.0216	47,410
SolimMoistF_BRA	0.7417	0	6,00E-04	0.4007	0	72,596	SolimMoistF_COL	0.637	0	6,00E-04	0.2075	0	35,857
SolimMoistF_COL	0.637	0	6,00E-04	0.2075	0	58,472	SolimMoistF_PER	0.4767	0	3,00E-04	0.2888	0	72,596
SWAmazMoistF_BOL	0.0982	0.1449	0.0034	0.1556	0.0116	316,610	SWAmazMoistF_BRA	0.3791	0.0023	0.0074	0.5789	0	169,600
SWAmazMoistF_BOL	0.0982	0.1449	0.0034	0.1556	0.0116	260,301	SWAmazMoistF_PER	0.3413	0.0024	0.0042	0.3002	0	169,600
SWAmazMoistF_BRA	0.3791	0.0023	0.0074	0.5789	0	260,301	SWAmazMoistF_PER	0.3413	0.0024	0.0042	0.3002	0	316,610
UrugSav_BRA	0.001	0.0131	0.0982	0.0261	0.6266	177,733	UrugSav_URY	0.0265	0.0089	0.0732	0.0758	0.2422	174,285
ValdivTempF_ARG	0.0644	0.0057	0.0274	0.5165	0.0657	196,945	ValdivTempF_CHL	0.0866	0.0071	0.0619	0.2272	0.021	44,380

Each NE matches its pair of TNE evaluated (#49). Country names are abbreviated in their standard initials

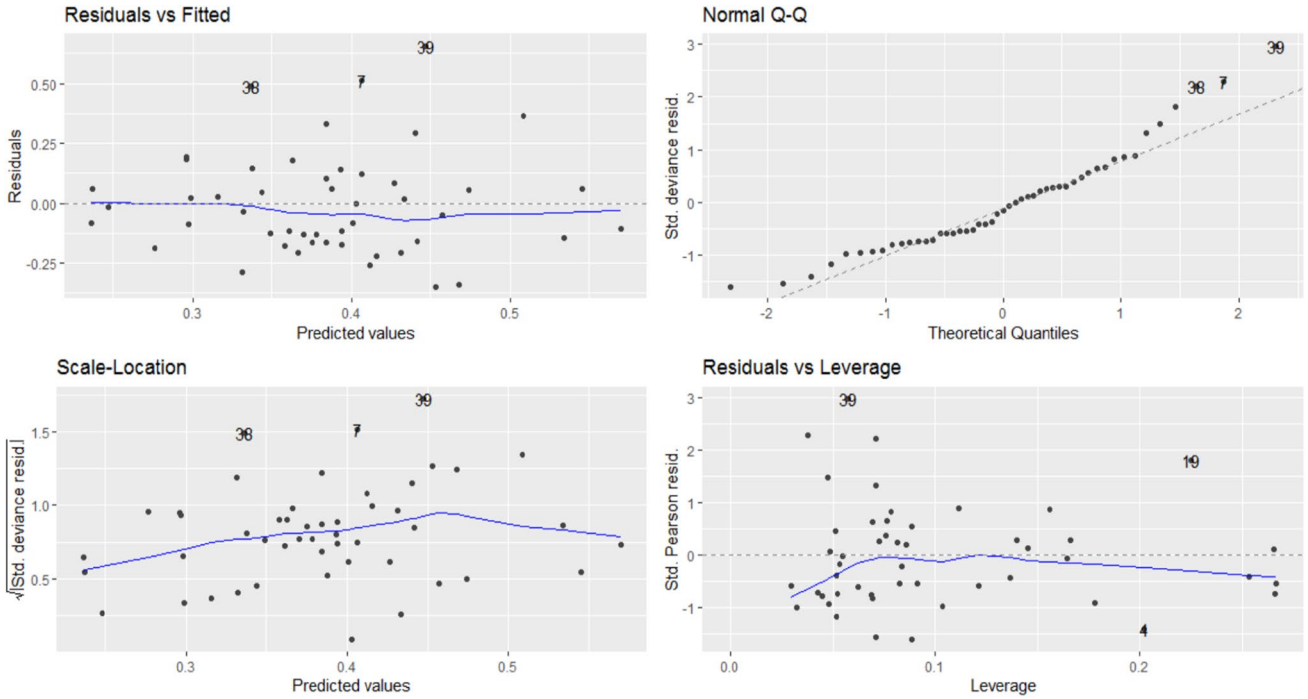

Fig. 9 Regressions diagnostic plots used to check model assumptions

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References

Acemoglu D, Robinson JA (2012) Why Nations fail. The origins of power, prosperity and poverty. New York.

Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M (2013) Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45:262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x

Aide TM, Grau HR, Graesser J, Andrade-Nuñez MJ, Aráoz E, Barros AP, Campos-Cerqueira M, Chacon-Moreno E, Cuesta F, Espinoza R, Peralvo M, Polk MH, Rueda X, Sanchez A, Young KR, Zarbá L, Zimmerer KS (2019) Woody vegetation dynamics in the tropical and subtropical Andes from 2001 to 2014: satellite image interpretation and expert validation. Glob Change Biol 25:2112–2126. https://doi.org/10.1111/gcb.14618

Allen, J.F., Burns, N., Garrett, L., Haass, R., Ikenberry, J., Mahbubani, K., Shivshankar, M., Niblett, R., Nye Jr, J.S., O'Neil, S.K., Schake, K., Walt, S.M., 2020. How the World will look after the coronavirus pandemic. Foreign Policy. URL https://foreignpolicy.com/2020/03/20/world-order-after-coroanvirus-pandemic/ (accessed 6.9.20).

Armenteras D, Espelta JM, Rodríguez N, Retana J (2017) Deforestation dynamics and drivers in different forest types in Latin America: three decades of studies (1980–2010). Glob Environ Change 46:139–147. https://doi.org/10.1016/j.gloenvcha.2017.09.002

Bailey RG (2004) Identifying ecoregion boundaries. Environ Manage 34:S14–S26. https://doi.org/10.1007/s00267-003-0163-6

Baldi G, Texeira M, Martin OA, Grau HR, Jobbágy EG (2017) Opportunities drive the global distribution of protected areas. PeerJ 5:e2989. https://doi.org/10.7717/peerj.2989

Baldi G, Schauman SA, Texeira M, Marinaro S, Martin OA, Gandini P, Jobbágy EG (2018) Nature representativeness in South American protected areas: Country contrasts and conservation priorities (preprint). Ecology. https://doi.org/10.1101/456558

Baumann M, Gasparri I, Piquer-Rodríguez M, Gavier Pizarro G, Griffiths P, Hostert P, Kuemmerle T (2017a) Carbon emissions from agricultural expansion and intensification in the Chaco. Glob Change Biol 23:1902–1916. https://doi.org/10.1111/gcb.13521

Baumann M, Israel C, Piquer-Rodríguez M, Gavier-Pizarro G, Volante JN, Kuemmerle T (2017b) Deforestation and cattle expansion in the Paraguayan Chaco 1987–2012. Reg Environ Change 17:1179–1191. https://doi.org/10.1007/s10113-017-1109-5

Beilin R, Bohnet IC (2015) Culture-production-place and nature: the landscapes of somewhere. Sustain Sci 10:195–205. https://doi.org/10.1007/s11625-015-0289-5

Boillat S, Scarpa FM, Robson JP, Gasparri I, Aide TM, Aguiar APD, Anderson LO, Batistella M, Fonseca MG, Futemma C, Grau HR, Mathez-Stiefel S-L, Metzger JP, Ometto JPHB, Pedlowski MA, Perz SG, Robiglio V, Soler L, Vieira I, Brondizio ES (2017) Land system science in Latin America: challenges and perspectives. Curr Opin Environ Sustain 26–27:37–46. https://doi.org/10.1016/j.cosust.2017.01.015

Bowman DMJS, Balch J, Artaxo P, Bond WJ, Cochrane MA, D'Antonio CM, DeFries R, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Mack M, Moritz MA, Pyne S, Roos CI, Scott AC, Sodhi NS, Swetnam TW (2011) The human dimension of fire regimes on Earth: the human dimension of fire regimes on Earth. J Biogeogr 38:2223–2236. https://doi.org/10.1111/j.1365-2699.2011.02595.x

Bruederle A, Hodler R (2018) Nighttime lights as a proxy for human development at the local level. PLoS ONE 13:e0202231. https://doi.org/10.1371/journal.pone.0202231

Bryce SA, Omernik JM, Larsen DP (1999) Environmental review: ecoregions: a geographic framework to guide risk characterization and ecosystem management. Environ Pract 1:141–155. https://doi.org/10.1017/S1466046600000582

Chang B (2010) The power of geographical boundaries: Cultural, political, and economic border effects in a unitary nation (Master of Arts). Iowa State University, Digital Repository, Ames. https://doi.org/10.31274/etd-180810-4515

Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. Glob Environ Change 26:152–158. https://doi.org/10.1016/j.gloenvcha.2014.04.002

Crespo Cuaresma J, Danylo O, Fritz S, McCallum I, Obersteiner M, See L, Walsh B (2017) Economic development and forest cover: evidence from satellite data. Sci Rep 7:40678. https://doi.org/10.1038/srep40678

Culas RJ (2007) Deforestation and the environmental Kuznets curve: an institutional perspective. Ecol Econ 61:429–437. https://doi.org/10.1016/j.ecolecon.2006.03.014

Cumming GS (2011) Spatial resilience: integrating landscape ecology, resilience, and sustainability. Landsc Ecol 26:899–909. https://doi.org/10.1007/s10980-011-9623-1

Da Ponte E, Mack B, Wohlfart C, Rodas O, Fleckenstein M, Oppelt N, Dech S, Kuenzer C (2017) Assessing forest cover dynamics and forest perception in the Atlantic forest of Paraguay, combining remote sensing and household level data. Forests 8:389. https://doi.org/10.3390/f8100389

Diamond, J., Robinson, J.A., 2010. Natural Experiments of History.

Dinerstein OD, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, Locke H, Ellis EC, Jones B, Barber CV, Hayes R, Kormos C, Martin V, Crist E, Sechrest W, Price L, Baillie JEM, Weeden D, Suckling K, Davis C, Sizer N, Moore R, Thau D, Birch T, Potapov P, Turubanova S, Tyukavina A, de Souza N, Pintea L, Brito JC, Llewellyn OA, Miller AG, Patzelt A, Ghazanfar SA, Timberlake J, Klöser H, Shennan-Farpón Y, Kindt R, Lillesø JPB, van Breugel P, Graudal L, Voge M, Al-Shammari KF, Saleem M (2017) An ecoregion-based approach to protecting half the terrestrial realm. Bioscience 67:534–545. https://doi.org/10.1093/biosci/bix014

Ellis EC (2019) To conserve nature in the Anthropocene, half Earth is not nearly enough. One Earth 1:163–167. https://doi.org/10.1016/j.oneear.2019.10.009

Ellis EC, Ramankutty N (2008) Putting people in the map: anthropogenic biomes of the world. Front Ecol Environ 6:439–447. https://doi.org/10.1890/070062

Ellis EC, Goldewijk KK, Siebert S, Lightman D, Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. Glob Ecol Biogeogr 19:589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x

Fernández PD, Matthias B, Germán B, Natalia BR, Sandra B, Ignacio GN, Mauro L, Sofia M, Sofia NA, Nasca JA, Torcuato T, Ricardo GH (2020) Grasslands and open savannas of the dry chaco. In: Goldstein MI, DellaSala DA (eds) Encyclopedia of the World's biomes. Elsevier, Oxford, pp 562–576. https://doi.org/10.1016/B978-0-12-409548-9.12094-9

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. Bioscience 53:77

Friis C, Nielsen JØ (2016) Small-scale land acquisitions, large-scale implications: exploring the case of Chinese banana investments in Northern Laos. Land Use Policy 57:117–129. https://doi.org/10.1016/j.landusepol.2016.05.028

Gallant AL, Loveland TR, Sohl TL, Napton DE (2004) Using an ecoregion framework to analyze land-cover and land-use dynamics. Environ Manage 34:S89. https://doi.org/10.1007/s00267-003-0145-3

Gasparri NI, Grau HR, Sacchi LV (2015) Determinants of the spatial distribution of cultivated land in the North Argentine Dry Chaco in a multi-decadal study. J Arid Environ 123:31–39. https://doi.org/10.1016/j.jaridenv.2015.05.005

Graesser J, Aide TM, Grau HR, Ramankutty N (2015) Cropland/pastureland dynamics and the slowdown of deforestation in Latin America. Environ Res Lett 10:034017. https://doi.org/10.1088/1748-9326/10/3/034017

Grau, 2016. Equilibrios alternativos mediados por decisiones humanas y retro-alimentación entre patrones y procesos. Bases para el manejo del territorio en América Latina, in: Naturaleza y Sociedad: perspectivas socio-ecológicas Sobre Cambios Climáticos Globales En América Latina. p. 444.

Grau and Gasparri (2018) Los socioecosistemas de la Puna en contexto nacional y global, In: La Puna Argentina: Naturaleza y Cultura. Fundación Miguel Lillo, Tucumán, Argentina., pp. 484–497.

Grau, H.R., Foguet, J., 2021. El legado de la urbanización europea en el cono sur sudamericano: una aproximación a la historia de las teleconexiones sobre la ecología del territorio 31, 114–128.

Guo R (2012) 8-Options for cross-border conflict management, In: Guo R (Eds) Developments in environmental science, cross-border resource management. Elsevier, pp. 233–254. https://doi.org/10.1016/B978-0-08-098319-6.00008-X

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853. https://doi.org/10.1126/science.1244693

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2004) Confronting a biome crisis: global disparities of habitat loss and protection: confronting a biome crisis. Ecol Lett 8:23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x

Irarrazaval F (2020) Contesting uneven development: the political geography of natural gas rents in Peru and Bolivia. Polit Geogr 79:102161. https://doi.org/10.1016/j.polgeo.2020.102161

Jarvis A, Touval JL, Schmitz MC, Sotomayor L, Hyman GG (2010) Assessment of threats to ecosystems in South America. J Nat Conserv 18:180–188. https://doi.org/10.1016/j.jnc.2009.08.003

Kenter JO, O'Brien L, Hockley N, Ravenscroft N, Fazey I, Irvine KN, Reed MS, Christie M, Brady E, Bryce R, Church A, Cooper N, Davies A, Evely A, Everard M, Fish R, Fisher JA, Jobstvogt N, Molloy C, Orchard-Webb J, Ranger S, Ryan M, Watson V, Williams S (2015) What are shared and social values of ecosystems? Ecol Econ 111:86–99. https://doi.org/10.1016/j.ecolecon.2015.01.006

Keys PW, Galaz V, Dyer M, Matthews N, Folke C, Nyström M, Cornell SE (2019) Anthropocene risk. Nat Sustain 2:667–673. https://doi.org/10.1038/s41893-019-0327-x

Krichker D (2019) Making sense of borderscapes: space, imagination and experience. Geopolitics. https://doi.org/10.1080/14650045.2019.1683542

Kuemmerle T, Radeloff VC, Perzanowski K, Hostert P (2006) Cross-border comparison of land cover and landscape pattern in Eastern Europe using a hybrid classification technique. Remote Sens Environ 103:449–464. https://doi.org/10.1016/j.rse.2006.04.015

Kuemmerle T, Altrichter M, Baldi G, Cabido M, Camino M, Cuellar E, Cuellar RL, Decarre J, Díaz S, Gasparri I, Gavier-Pizarro G, Ginzburg R, Giordano AJ, Grau HR, Jobbágy E, Leynaud G, Macchi L, Mastrangelo M, Matteucci SD, Noss A, Paruelo J, Piquer-Rodríguez M, Romero-Muñoz A, Semper-Pascual A, Thompson J, Torrella S, Torres R, Volante JN, Yanosky A, Zak M (2017) Forest conservation: remember Gran Chaco. Science 355(465):1–465. https://doi.org/10.1126/science.aal3020

Lambin EF, Gibbs HK, Ferreira L, Grau R, Mayaux P, Meyfroidt P, Morton DC, Rudel TK, Gasparri I, Munger J (2013) Estimating the world's potentially available cropland using a bottom-up approach. Glob Environ Change 23:892–901. https://doi.org/10.1016/j.gloenvcha.2013.05.005

le Polain de Waroux Y (2019) Capital has no homeland: the formation of transnational producer cohorts in South America's commodity frontiers. Geoforum 105:131–144. https://doi.org/10.1016/j.geoforum.2019.05.016

le Polain de Waroux Y , Garrett RD, Heilmayr R, Lambin EF (2016) Land-use policies and corporate investments in agriculture in the Gran Chaco and Chiquitano. Proc Natl Acad Sci 113:4021–4026. https://doi.org/10.1073/pnas.1602646113

le Polain de Waroux Y, Baumann M, Gasparri NI, Gavier-Pizarro G, Godar J, Kuemmerle T, Müller R, Vázquez F, Volante JN, Meyfroidt P (2018) Rents, Actors, and the Expansion of Commodity Frontiers in the Gran Chaco. Ann. Am. Assoc. Geogr. 108:204–225. https://doi.org/10.1080/24694452.2017.1360761

Lennox RJ, Chapman JM, Souliere CM, Tudorache C, Wikelski M, Metcalfe JD, Cooke SJ (2016) Conservation physiology of animal migration. Conserv Physiol 4:Cov702. https://doi.org/10.1093/conphys/cov072

Liu J, Yong DL, Choi C-Y, Gibson L (2020) Transboundary frontiers: an emerging priority for biodiversity conservation. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2020.03.004

López-Hoffman L, Varady RG, Flessa KW, Balvanera P (2010) Ecosystem services across borders: a framework for transboundary conservation policy. Front Ecol Environ 8(2):84–91. https://doi.org/10.1890/070216

Machado LO, Novaes AR, Monteiro L, do R., (2009) Building walls, breaking barriers: Territory, integration and the rule of law in frontier zones. J Borderl Stud 24:97–114. https://doi.org/10.1080/08865655.2009.9695742

Mann, C., 2005. 1491: New revelations of the Americas before Columbus. New York, NY.

Marinaro, S., Grau, H.R., Aráoz, E., 2012. Extensión y originalidad en la creación de parques nacionales en relación a cambios gubernamentales y económicos de la Argentina. Ecol. Austral 10.

Matossian B, Vejsbjerg L (2018) Mountains and borders, geographical approaches from the South. An Araucanía-North Patagonia case study. J Borderl Stud 33:157–177. https://doi.org/10.1080/08865655.2016.1257363

Meyfroidt P (2016) Approaches and terminology for causal analysis in land systems science. J Land Use Sci 11:501–522. https://doi.org/10.1080/1747423X.2015.1117530

Minghi JV (1963) Boundary studies in political geography. Ann Assoc Am Geogr 53:407–428. https://doi.org/10.1111/j.1467-8306.1963.tb00457.x

Mohammadpour P, Mahjabin T, Fernandez J, Grady C (2019) From national indices to regional action—an analysis of food, energy, water security in Ecuador, Bolivia, and Peru. Environ Sci Policy 101:291–301. https://doi.org/10.1016/j.envsci.2019.08.014

Munteanu C, Kuemmerle T, Keuler NS, Müller D, Balázs P, Dobosz M, Griffiths P, Halada L, Kaim D, Király G, Konkoly-Gyuró É, Kozak J, Lieskovsky J, Ostafin K, Ostapowicz K, Shandra O, Radeloff VC (2015) Legacies of 19th century land use shape contemporary forest cover. Glob Environ Change 34:83–94. https://doi.org/10.1016/j.gloenvcha.2015.06.015

Nanni AS, Sloan S, Aide TM, Graesser J, Edwards D, Grau HR (2019) The neotropical reforestation hotspots: a biophysical and socioeconomic typology of contemporary forest expansion. Glob Environ Change 54:148–159. https://doi.org/10.1016/j.gloenvcha.2018.12.001

NASA, 2013. Active Fire Data | Earthdata [WWW Document]. Real-Time MCD14DL MODIS Act. Fire Detect. URL https://earthdata.nasa.gov/earth-observation-data/near-real-time/firms/active-fire-data (accessed 3.19.18).

Nelson, A., 2008. Estimated travel time to the nearest city of 50,000 or more people in year 2000.

Nolte, D., Wehner, L., 2015. Geopolitics in Latin America, Old and New, in: Routledge Handbook of Latin American Security. Mares,D and Kacowicz,A.

Nunn, N., Puga, D., 2012. Ruggedness: the blessing of bad geography in Africa. Rev. Econ. Stat. 17.

O'Kelly M, Bryan D (1996) Agricultural location theory: von Thunen's contribution to economic geography. Prog Hum Geogr 20:457–475. https://doi.org/10.1177/030913259602000402

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico ItouaStrandMorrisonLoucksAllnuttRickettsKuraLamoreuxWettengelHedaoKassem JAHEJCCJTFTHYJFWWP (2001) Terrestrial ecoregions of the World: a new map of life on earth. Bioscience 51:933. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Omernik, J., 1995. Ecoregions: A Spatial Framework for Environmental Management, in: Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. Davis, W. and Simon, T., p. 432.

Pandit S, Gupta S (2011) A comparative study on distance measuring approaches for clustering. Int J Res Comput Sci 2:29–31. https://doi.org/10.7815/ijorcs.21.2011.011

Parodi C (2002) The politics of South American boundaries. Praeger, USA

Perz SG, Aramburú C, Bremner J (2005) Population, land use and deforestation in the pan Amazon Basin: a comparison of Brazil, Bolivia, Colombia, Ecuador, Perú and Venezuela. Environ Dev Sustain 7:23–49. https://doi.org/10.1007/s10668-003-6977-9

Pinkovskiy, M.L., 2013. Economic discontinuities at borders: evidence from satellite data on lights at night 77.

Piquer-Rodríguez M, Butsic V, Gärtner P, Macchi L, Baumann M, Gavier Pizarro G, Volante JN, Gasparri IN, Kuemmerle T (2018) Drivers of agricultural land-use change in the Argentine Pampas and Chaco regions. Appl Geogr 91:111–122. https://doi.org/10.1016/j.apgeog.2018.01.004

Prist PR, Levin N, Metzger JP, de Mello K, de Paula Costa MD, Castagnino R, Cortes-Ramirez J, Lin D-L, Butt N, Lloyd TJ, López-Cubillos S, Mayfield HJ, Negret PJ, Oliveira-Bevan I,

Reside AE, Rhodes JR, Simmons BA, Suárez-Castro AF, Kark S (2019) Collaboration across boundaries in the Amazon. Science 366(6466):699–700. https://doi.org/10.1126/science.aaz7489

Protected Planet, 2015. WDPA [WWW Document]. World Database Prot. Areas. URL https://www.protectedplanet.net/c/world-database-on-protected-areas (accessed 3.19.18).

Potosyan, A.H., 2017. Geographical features and development regularities of rural areas and settlements distribution in mountain countries. Ann. Agrar. Sci. S1512188717300246. https://doi.org/10.1016/j.aasci.2017.02.012

Rai R, Zhang Y, Paudel B, Acharya BK, Basnet L (2018) Land use and land cover dynamics and assessing the ecosystem service values in the Trans-Boundary Gandaki River Basin, Central Himalayas. Sustainability 10(9):3052. https://doi.org/10.3390/su10093052

Ramankutty, N., Evan, A.T., Monfreda, C., Foley, J.A., 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000: GLOBAL AGRICULTURAL LANDS IN 2000. Glob. Biogeochem. Cycles 22, n/a-n/a. https://doi.org/10.1029/2007GB002952

Redo DJ, Grau HR, Aide TM, Clark ML (2012) Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America. Proc Natl Acad Sci 109:8839–8844. https://doi.org/10.1073/pnas.1201664109

Röder A, Pröpper M, Stellmes M, Schneibel A, Hill J (2015) Assessing urban growth and rural land use transformations in a cross-border situation in Northern Namibia and Southern Angola. Land Use Policy 42:340–354. https://doi.org/10.1016/j.landusepol.2014.08.008

Routley, N., 2018. All of the World's Borders by Age.

Rumley D, Minghi JV (1991) Introduction: the border landscape concept. The geography of border landscapes. Routledge, New York, pp 1–14

Sabanadze N (2010) Globalization and Nationalism: the relationship revisited, in: Globalization and Nationalism: the cases of Georgia and the Basque Country. Central European University Press, Budapest, p. 218.

Salisbury DS, Weinstein BG (2014) Cultural diversity in the Amazon borderlands: implications for conservation and development. J Borderl Stud 29:217–241. https://doi.org/10.1080/08865655.2014.916462

Shirkhorshidi AS, Aghabozorgi S, Wah TY (2015) A comparison study on similarity and dissimilarity measures in clustering continuous data. PLoS ONE 10:e0144059. https://doi.org/10.1371/journal.pone.0144059

Smith JR, Letten AD, Ke P-J, Anderson CB, Hendershot JN, Dhami MK, Dlott GA, Grainger TN, Howard ME, Morrison BML, Routh D, San Juan PA, Mooney HA, Mordecai EA, Crowther TW, Daily GC (2018) A global test of ecoregions. Nat Ecol Evol 2:1889–1896. https://doi.org/10.1038/s41559-018-0709-x

Sobal J, Kettel Khan L, Bisogni C (1998) A conceptual model of the food and nutrition system. Soc Sci Med 47:853–863. https://doi.org/10.1016/S0277-9536(98)00104-X

Southworth J, Marsik M, Qiu Y, Perz S, Cumming G, Stevens F, Rocha K, Duchelle A, Barnes G (2011) Roads as drivers of change: trajectories across the Tri-National Frontier in MAP, the Southwestern Amazon. Remote Sens 3:1047–1066. https://doi.org/10.3390/rs3051047

Switalski, M., Grêt-Regamey, A., 2020. Operationalising place for land system science. Sustain. Sci. https://doi.org/10.1007/s11625-020-00827-5

Taggart-Hodge TD, Schoon M (2016) The challenges and opportunities of transboundary cooperation through the lens of the East Carpathians Biosphere Reserve. Ecol Soc 21(4). JSTOR. https://www.jstor.org/stable/26270039

Thornton, D., Branch, L., Murray, D., 2019. Distribution and connectivity of protected areas in the Americas facilitates transboundary conservation. Ecol. Appl. https://doi.org/10.1002/eap.2027

Van Houtum H (2005) The geopolitics of borders and boundaries. Geopolitics 10:672–679. https://doi.org/10.1080/14650040500318522

Verburg PH, Crossman N, Ellis EC, Heinimann A, Hostert P, Mertz O, Nagendra H, Sikor T, Erb K-H, Golubiewski N, Grau R, Grove M, Konaté S, Meyfroidt P, Parker DC, Chowdhury RR, Shibata H, Thomson A, Zhen L (2015) Land system science and sustainable development of the earth system: a global land project perspective. Anthropocene 12:29–41. https://doi.org/10.1016/j.ancene.2015.09.004

WFS3 (2021) Euclidean distances of Transnational Ecoregions with biomes, Authors, v1, WFS3

WMS link (2021) Euclidean distances of Transnational Ecoregions with biomes, Authors, v1, WMS

Williamson, E., 1993. The Penguin History of Latin America. Penguin Books Ltd.

Wilson, S.J., Schelhas, J., Grau, R., Nanni, A.S., Sloan, S., 2017. Forest ecosystem-service transitions: the ecological dimensions of the forest transition. Ecol. Soc. 22, art38. https://doi.org/10.5751/ES-09615-220438

Wu C-T (1998) Cross-border development in Europe and Asia. GeoJournal 44:189–201

Wuepper, D., Borrelli, P., Finger, R., 2019. Countries and the global rate of soil erosion. Nat. Sustain. https://doi.org/10.1038/s41893-019-0438-4

Wulder MA, Campbell C, White JC, Flannigan M, Campbell ID (2007) National circumstances in the international circumboreal community. For Chron 83:539–556. https://doi.org/10.5558/tfc83539-4

Zhang Y, Xiao X, Wu X, Zhou S, Zhang G, Qin Y, Dong J (2017) A global moderate resolution dataset of gross primary production of vegetation for 2000–2016. Sci Data 4:170165. https://doi.org/10.1038/sdata.2017.165

Ziter C, Graves RA, Turner MG (2017) How do land-use legacies affect ecosystem services in United States cultural landscapes? Landsc Ecol 32:2205–2218. https://doi.org/10.1007/s10980-017-0545-4