Land systems’ asymmetries across transnational ecoregions in South America

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Received: 25 June 2020 / Accepted: 27 April 2021 / Published online: 9 June 2021
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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,
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 major 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 trans-boundary 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; Walder 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 triggered 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),
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
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).

\[
D(k_{ij}) = \sqrt{\sum_{m=1}^{5} (x_{km_i} - x_{km_j})^2}
\]

(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
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 Guyana. 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 Uruguay 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; Raman-kutty 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 (Solimóes 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; Kueffer 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 “undeveloped” 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 Rondonia); 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. 4 Boxplots of Euclidean distances of TNEs grouped by their biomes](image1)

![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)](image2)
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 = \(\text{abs}(\text{GDP}_1 - \text{GDP}_2)\). 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:**
\[
\text{Euclidean}\_\text{distances} \sim \text{delGDP} + \text{GPPmed} + \text{Singular} + \text{perc_anthrom}, \text{family} = \text{Gaussian}, \text{link} = \text{identity}
\]

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 | IQR | Median | 3Q | Max |
| 0.34983 | 0.16039 | 0.03662 | 0.10442 | 0.65730 |

---

**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
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                             | GuianSav                 |
| 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     | 1.0E-04| 0.4046| 0     | 141,219   | CAndeanDryPuna_BOL| 0.0634     | 0.0022| 0.0067| 0.0648| 0     | 29,884    |
| CAndeanDryPuna_ARG| 0.1172 | 0     | 1.0E-04| 0.4046| 0     | 82,709    | CAndeanDryPuna_CHL| 0.0676     | 0     | 0.007 | 0.1097| 0     | 29,884    |
| CaqMoistF_BRA  | 0.401     | 0.0313| 3.00E-04| 0.2917| 0     | 12,542    | CaqMoistF_COL| 0.2224     | 0.0045| 0.234 | 0.0966| 0     | 16,048    |
| CordOrMontF_BOL| 0.116     | 0.0854| 0.0131| 0.3634| 0.0088| 174,385   | CordOrMontF_PER| 0.0693     | 0.0125| 0.0342| 0.1409| 0.001 | 17,917    |
| DryChaco_BOL   | 0.116     | 0.0854| 0.0131| 0.3634| 0.0088| 98,834    | DryChaco_BOL| 0.0634     | 0.0068| 0.1845| 0.1774| 0     | 98,834    |
| 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    |
| GuiaSav_BRA    | 0.231     | 0.0162| 0.0077| 0.0756| 0.0096| 130,855   | GuiaSav_BRA| 0.0781     | 0.287 | 0.0338| 0.53   | 0.0108| 130,855   |
| GuianMoistF_BRA| 0.31      | 7.00E-04| 3.00E-04| 1   | 0   | 80,545    | GuianMoistF_BRA| 0.3408     | 1.0E-04| 0.0028| 0.5368| 0     | 80,545    |
| GuianMoistF_BRA| 0.31      | 7.00E-04| 3.00E-04| 1   | 0   | 130,855   | GuianMoistF_BRA| 0.3162     | 0.162 | 0.0077| 0.0756| 0.0096| 130,855   |
| HumChaco_ARG   | 0.0364    | 0.6037| 0.0373| 0.0922| 0.1366| 128,760   | HumChaco_ARG| 0.0547     | 0.7766| 0.0776| 0.0073| 0.0032| 161,668   |
| JapSolNegMoistF_BRA| 0.5457 | 3.00E-04| 0.0099| 0.6024| 0     | 34,608    | JapSolNegMoistF_BRA| 0.5457     | 3.00E-04| 0.0099| 0.6024| 0     | 34,608    |
| Llanos_COL    | 0.1364    | 0.0161| 0.0341| 0.0085| 0     | 223,063   | Llanos_COL| 0.0425     | 0.9454| 0.2099| 0.0731| 0.083 | 232,455   |
| MagSubpolF_ARG| 0.0918    | 0.0011| 0.0154| 0.3187| 0.0052| 115,962   | MagSubpolF_VEN| 0.2788     | 0.0011| 0.0154| 0.3187| 0.0052| 115,962   |
| 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_BRA| 0.2637    | 0.0095| 0.0274| 0.1002| 0     | 70,827    | NapoMoistF_BRA| 0.0163     | 0.0095| 0.0274| 0.1002| 0     | 140,194   |
| NapoMoistF_BRA| 0.2637    | 0.0095| 0.0274| 0.1002| 0     | 140,194   | NapoMoistF_BRA| 0.0163     | 0.0095| 0.0274| 0.1002| 0     | 140,194   |
| NapoMoistF_BRA| 0.2637    | 0.0095| 0.0274| 0.1002| 0     | 140,194   | NapoMoistF_BRA| 0.0163     | 0.0095| 0.0274| 0.1002| 0     | 140,194   |
| 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_BRA          | 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   |
| ValdivTemp_Arg       | 0.0644    | 0.0057 | 0.0274 | 0.5165 | 0.0657 | 196,945   | ValdivTemp_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.
Acknowledgements  We are grateful for the positive and constructive revisions from three anonymous reviewers. We would like to acknowledge support from the GLP South American Nodal office and funding from the projects PICT 2015-0521 and PUE 2017-IER. MPR thanks ESRI and the GLP for a travel grant to the OSM GLP Bern 2019 and funding from the Geo.X Research Network (Grant number: SO_087_ GeoX). We are thanked to J. Graesser for sharing his South American land-use dataset. M. Aide provided very helpful comments and editions on early versions of this manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

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Fig. 9  Regressions diagnostic plots used to check model assumptions
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