The ecohydrology of ecosystem transitions: a meta-analysis

Ernesto F. Viglizzo,[1,2,3]* Marcelo D. Nosetto,[4] Esteban G. Jobbágy,[4] M. Florencia Ricard[2]
and Federico C. Frank[1,3]

[1] *INTA, EEA Anguil, Grupo de Investigaciones en Gestión Ambiental (GIGA), Av. Spinetto 785, 6300 Santa Rosa, La Pampa, Argentina*
[2] *CONICET, INCITAP, Ruta 35, km 335, 6300 Santa Rosa, La Pampa, Argentina*
[3] *Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Av. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina*
[4] *IMASL-CONICET, Grupo de Estudios Ambientales (GEA), Ejército de los Andes 950, 5700 San Luis, San Luis, Argentina*

ABSTRACT

A vast body of literature demonstrated that anthropogenic disturbances such as overgrazing and fire are key drivers of abrupt transition between vegetation types in ecosystems. In this study, we propose that the hydrological context (described in terms of rainfall, evapotranspiration and water yield) is a first-order, primordial determinant of the propensity of ecosystems to undergo transition. This implies that the anthropogenic disturbance is a second-order determinant that is strongly conditioned by the first one. Through the meta-analysis of existing studies, a collection of 685 geo-referenced study cases was organized to study the hydrological characteristics of three climatic regions and three ecosystems that vary in their relation between woody and grassy plants. Thus, humid, sub-humid and dry climatic regions, respectively, receiving >1000, 500–1000 and <500 mm year^{-1}, were studied, and possible transition mechanisms among grasslands/savannas, shrublands and forests were analysed. The results showed that the ecohydrological context determines the probabilities of ecosystems transitions in different climatic regions and the prevalence of alternative transition mechanisms. We showed that transition of forests into other ecosystems is highly improbable in high-precipitation regions, more probable and likely subject to a bi-stable and reversible regime in sub-humid regions, and highly probable and irreversible in dry regions. Factors such as runoff, deep-water drainage, fire, flammable/ nonflammable biomass and overgrazing were considered as hypothetical transition mechanisms. As a novel finding, we demonstrate that ecohydrology, as a determinant of transition, is a factor that operates at a hierarchical level higher than that of the human-driven disturbance. A synthetic graphical model was proposed to characterize resilience (the capacity of ecosystems to withstand transition) in the three study climatic regions. Copyright © 2014 John Wiley & Sons, Ltd.

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INTRODUCTION

The growing concern about global change has brought attention to the abrupt conversion of one ecosystem into another different one (transition), with the consequence of major alterations in basic ecological functions and the provision of essential ecosystem services. Various anthropogenic (grazing and fire use) and biophysical (rainfall, temperature and extreme events) factors have been considered as predominant causes of transitions (Westoby *et al.*, 1989), but the anthropogenic versus biophysical debate is still open, with no definite consensus among scientists (D'odorico *et al.*, 2012). Shrub encroachment (the increase in cover and biomass density of shrubby plants at the expense of other nonshrubby species) of arid and semiarid grasslands and savannas has been the most-reported transition case (Eldridge *et al.*, 2011). However, cases of sudden transitions have also been reported in the sub-humid and humid tropics, which may lead forests and savannas to show a striking bimodal behaviour (Rietkerk *et al.*, 2011). This double-way bi-stable transition suggests that the savanna may be a distinct and possible alternative stable state to the forest and vice versa. According to Mayer and Khalyani (2011), three main feedback mechanisms may be involved in the bimodal expression: a strong feedback between vegetation density and annual precipitation (PP), a strong feedback between rainfall seasonality and grass cover, and a very strong feedback between grass cover and fire frequency.

The influence of hydrology on ecosystem transitions has been less studied. Few authors (Archer *et al.*, 1995; Snyder and Tartowski, 2006) have ventured preliminary ideas and hypothesis with no definite conclusions. However, recent results from global satellite-based studies in tropical regions (Hirota *et al.*, 2011; Staver *et al.*, 2011a, b; Hoffmann *et al.*, 2012) suggest that PP and its seasonality

*Correspondence to: Ernesto F. Viglizzo, Area of Environmental Management, INTA. Centro Regional La Pampa-San Luis, Av. Spinetto 785, 6300, Santa Rosa, La Pampa, Argentina.
E-mail: evigliz@cpenet.com.ar

have an important influence on the sensitivity of ecosystems to experience transitions in response to human-induced disturbances. Likewise, Archer (2010) demonstrated that grasslands in dry areas with markedly seasonal rainfalls are exposed to suffer shrub encroachment in sites where the pastoral use of the land (characterized by overgrazing and fire suppression) is common. A functional peculiarity regarding transition propensity or transition resistance should be noted: in quantitative terms, the evapotranspiration (ET) flows of forests, savannas/grasslands and shrublands tend to resemble in dry areas, but the magnitude of those flows tends to differ markedly in areas of middle and high PP (Zhang *et al.*, 2001). The small ET gap differences observed in dry areas suggest (i) that the coexistence of contrasting vegetation types would be more common in low than in high rainfall areas and (ii) that the probability of transition after a human-driven disturbance would be also higher in low than in high PP areas. Confirming this, frequent cases of mixture of different vegetation types were reported below 500 mm year^{-1} of PP (Van Auken, 2000; Goslee *et al.*, 2003; Wiegand *et al.*, 2006; Knapp *et al.*, 2008).

These sparse pieces of evidence suggest that hydrology defines a background scenario for ecosystem transitions and that it may play a determinant role in changes of vegetation type. As a contribution to elucidate the hydrological–anthropological debate, in this study, we propose that the hydrological context [characterized in terms of rainfall, ET and water yield (WY)] is a first-order, primordial determinant of the propensity of ecosystems to undergo transitions among dominant vegetation types. This implies that the anthropogenic disturbance (e.g. grazing pressure and fire use) may be a second-order cause of transition that is strongly conditioned by the first one. Given that various ecosystem functions including energy fluxes and nutrient and water cycles are linked to aboveground biomass (AGB) as Webb *et al.* (1983), Sala *et al.* (1988) and Carreño *et al.* (2012) have demonstrated, here we propose the *biomass gap* notion in ecosystems, which represents the AGB difference between two vegetation types as a measure of the probability of ecosystems to trigger or withstand transitions. In our view, the closer the biomass gap, the higher the probability of transition between vegetation types. Possible transition mechanisms (like deep-water drainage, fire, flammable–nonflammable biomass relations and overgrazing) are discussed, and a synthetic hypothetical model is later proposed to set the functional basis of resilience of ecosystems in three contrasting climatic regions.

MATERIALS AND METHODS

The logic of this investigation aimed at finding a link between the hydrological context of three well-known ecosystems (forests, shrublands and grasslands/savannas)

and their likelihood to undergo transitions. On the other hand, three contrasting climatic regions (humid, sub-humid/semiarid and dry) were considered in the analysis. Three variables were used to characterize the hydrological context: PP, actual ET and WY, all of them expressed in millimetres per year. Real figures on PP and ET were obtained from independent, geo-referenced site-specific data sources (New *et al.*, 2002; Mitchell and Jones, 2005; Sterling *et al.*, 2012). WY is the result of the simple arithmetic difference between PP and ET (Jobbágy *et al.*, 2012). On the other hand, a theoretical estimation of AGB, expressed in tons of dry matter per hectare (Mg DM ha^{-1}) was undertook for the three aforementioned ecosystems in the three climatic regions. AGB values were used to estimate the biomass gap between vegetation types in each study region.

Data meta-analysis was applied to test our hypothesis. One database was built on the basis of actual ET data compiled by Sterling *et al.* (2012), who gathered over 1500 available actual ET observations that were related to a single discrete land-cover type. The study sites were distributed as follows: North America (45%), Europe (16%), Asia (13%) and South America (10%). We selected 685 sites from the original database and discarded the rest. The criteria to discard sites were the following: (i) the original source could not be found in refereed published journals; (ii) some values were not the result of case studies but the opinion of experts; (iii) the relation between PP and actual ET showed extreme cases of imbalance (potential anomaly in measuring data); and (iv) the spatial location of the geo-referenced site was uncertain. The worldwide distribution of all geo-referenced sites that we considered in the analysis is displayed in Figure 1. The dataset was then organized into humid, sub-humid and dry climatic regions, respectively, receiving >1000, 500–1000 and <500 mm year^{-1}.

Sites were geo-referenced on the basis of reported coordinates. Then, we used the Climate Research Unit (CRU) dataset to retrieve annual site-specific information on historical rainfall between 1901 and 2012. The CRU system (New *et al.*, 2002; Mitchell and Jones, 2005) provided average rainfall figures on all study sites across the world. The CRU climate datasets were constructed for nine climate variables, and values were interpolated onto a 0.5° grid covering the global land surface and combined with published data. WY values were estimated by calculating the difference between the average annual figures of PP provided by CRU and the actual ET figures provided by Sterling *et al.* (2012).

On the basis of AGB data from IPCC (2006) and ET data (Sterling *et al.*, 2012), a set of algorithms were developed to calculate AGB in the studied ecosystems and climatic regions. Relying on theoretical and empirical evidence (Bradford and Hsiao, 1982; Steduto *et al.*, 2007;
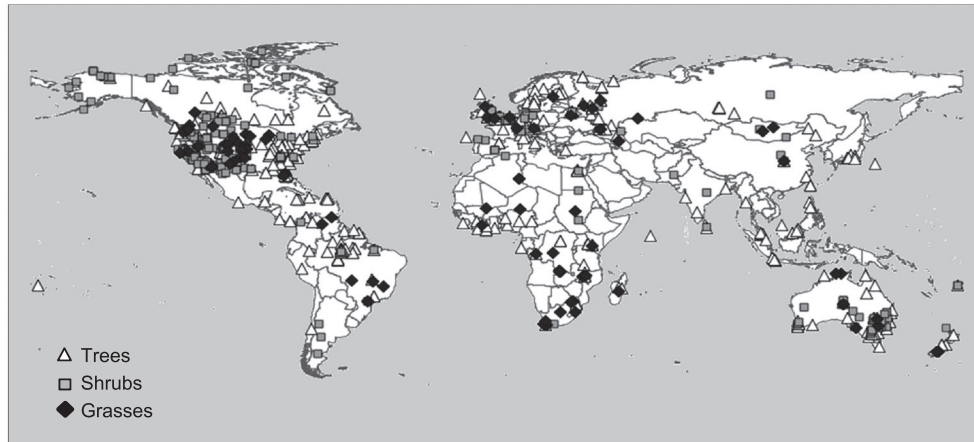
Figure 1. Worldwide distribution of the 685 study sites discriminated by three dominant ecosystems.

Hsiao *et al.*, 2009), we assumed that AGB and ET maintain a significant positive correlation. In order to avoid a spurious circular analysis, and considering that the estimated AGB values are not independent from ET, AGB was only associated with figures obtained from the independent PP and WY data sources. The mean value and standard deviation of ET and AGB from the aforementioned independent datasets supplied us the ranges of covariation to estimate the values of AGB. Nine different algorithms were developed to represent the three ecosystems in the three climatic regions. Given that the theoretical algorithms allowed us the calculation of AGB from ET data, we tested consistency of our procedure by applying a semi-quantitative method based on IPCC (2006) guidance to uncertainty. Based on a probability distribution scheme, the uncertainty of our estimations was tested by measuring the percentage of figures overlapping between our calculated AGB values and the AGB field records provided by IPCC (2006). We assumed that high overlapping indicates low uncertainty and vice versa. Uncertainty was expressed as the percentage estimated data that fall outside the variability range of IPCC (2006). The uncertainty levels were arbitrarily ranged as follows: low (0–33%), moderate (34–66%) and high (67–100%). The test showed that a high degree of uncertainty was only detected in the case of grasslands and savannas in cold regions. An opposite result (low uncertainty) was found for planted forests in cold regions. The rest of ecosystems and regions showed a moderate uncertainty, suggesting that we were operating under reliable conditions and a safe meta-analysis could be undertook.

To assess the functional closeness between vegetation types, we proposed the notion of the *biomass gap*, which represents the AGB difference between vegetation types that potentially can suffer a transition. Because essential functions of the ecosystem (such as energy, nutrients and water flows) are directly associated with AGB (Webb *et al.*, 1983; Sala *et al.*, 1988; Carreño *et al.*, 2012), a small

biomass gap suggests a high functional closeness between two different vegetation types. In general, the biomass gap tends to be large, and the functional proximity small, in regions of high rainfall, occurring the opposite in regions of low PP.

To test the consistency of the 'biomass gap' notion, we focused our analysis on WY as a key functional hydrological variable; so we analysed the coefficients of variability (CV) of WY in the three study ecosystems and the three climatic regions. The CV of ecosystems was analysed considering regions and ecosystems independently and jointly. We interpreted that high CV in WY is indicative of high functional instability and therefore indicative of a high propensity of ecosystems to undergo transition. If our assumptions were correct, we expected to find the higher CV values (greater instability) in dry than in humid regions and, within those dry regions, in grassy and shrubby than in forest ecosystems. In other words, we expect to find a higher probability of transition in dry than in humid regions and between those ecosystems that have a smaller biomass gap.

The statistical analysis was based on linear and nonlinear (polynomial or logarithmic) regression models. The detection of negative values of WY in low PP areas deserved special attention. To explain some contrasting attributes of ecosystems, an analysis was performed to evaluate actual ET values per unit of AGB ($mm\,Mg\,DM^{-1}$). Potential mechanisms to explain ecosystem transitions were proposed and discussed, and finally, a hypothetical interpretative model was proposed to synthesize main findings in our investigation.

RESULTS

The biomass gap of vegetation types across climatic regions

At the global scale, PP appears to be a first-order factor explaining differences of AGB between contrasting

ecosystems and climatic regions. Built from the global database described in the methodological section, Figure 2a provides a picture on the behaviour of AGB of the study ecosystems under different PP regimes. These results offer a first view about the impact of one hydrological factor on AGB and some ecological functions related to AGB. A second major issue, not clarified in Figure 2a, is whether the distribution of ecosystems responds smoothly or abruptly to biophysical or anthropogenic disturbing factors. In line with results from Scheffer *et al.* (2001), Sankaran *et al.* (2005) and Staver *et al.* (2011b), forest and savanna/grassland may represent a bimodal transition that connotes nonlinear dynamics.

To show evidence on transition propensity, in Figure 2b, we displayed data on a semi-logarithmic graphic that enhances the AGB difference among forests, shrublands and grasslands/savannas. The forest seems to be the unique

vegetation type that dominates over 2500 mm year^{-1} without the existence of other alternative vegetation types. Another relevant aspect is that while AGB in forests tends to respond markedly to increasing PP in the full range of data, this does not occur in the case of shrublands and grasslands/savannas, which stop responding at relatively low levels of rainfall (Figure 2a). These patterns of Scheffer *et al.* (2001), Sankaran *et al.* (2005) and Staver *et al.* (2011b) would indicate that rainforests in the tropics are ecologically distant (and show a large biomass gap) from shrublands and grasslands/savannas. Then, the probability of transition appears to be extremely low. On the other hand, AGB values suggest that shrublands and grasslands/savannas are ecologically close (small biomass gap) and are mixed throughout the rainfall range of 0–500 mm year^{-1}. Therefore, the probability of transition seems to be very low on the humid tropics over
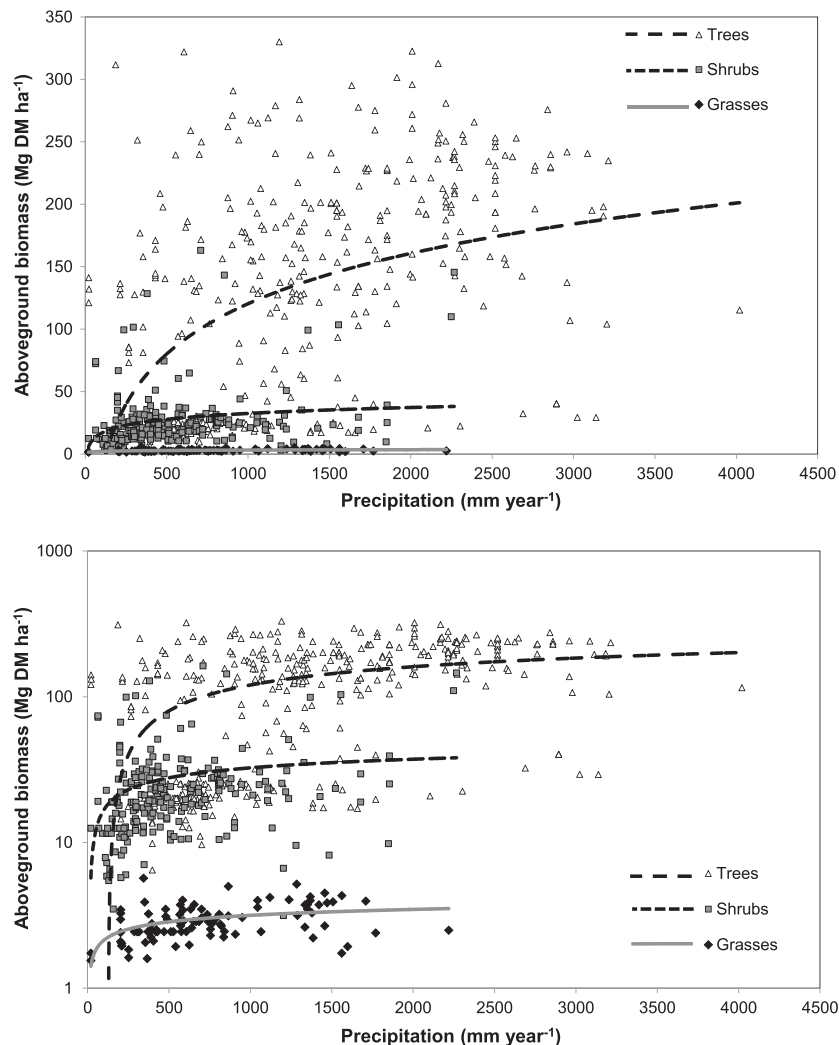

Figure 2. (a) Worldwide relationship between precipitation and aboveground biomass in all climatic zones discriminated by dominant ecosystems. The relationships were highly significant ($P < 0.01$). (b) Worldwide relationship between precipitation and aboveground biomass in all climatic zones discriminated by dominant ecosystems. A logarithmic data conversion was used to better appreciate difference among trees, shrubs and grasses. The relationships were highly significant ($P < 0.01$).

2500 mm year^{-1} but dramatically increases on dry climatic regions where PPs are below 500 mm year^{-1}.

A direct perception of the biomass gap between ecosystems under different hydrological contexts is showed in Figure 3. Confirming trends shown in Figure 2b, the biomass gap is narrow, and the likelihood of transition is high, in dry and sub-humid regions. On the contrary, the biomass gap is large, and the probability of transition is low, in humid regions. The smallest gap in this study occurs between shrublands and grasslands/savannas, followed by forests and shrublands. Then, we can presume that grasses and shrubs in dry areas are more exposed to suffer transition than grasses and trees, or shrubs and trees, in humid areas.

Water yield and ecosystem transitions

An additional confirmation test was based on the analysis of CV of WY on the studied ecosystems and climatic regions. CV of WY values were considered indicative of both hydrological instability and transition propensity. Results in Table I provide what we have considered a sound confirmation of Figure 3 outcomes. As expected, CV values in dry regions exceeded in several orders of magnitude the corresponding values of sub-humid and humid regions. Because of their high CV (and low stability), dry regions show different combinations of shrubs and grasses, confirming that dry regions are less resilient and are more prone to suffer transitions than the humid ones. This contributes to explain why WY in shrublands and grasslands/savannas is much more unstable in dry than in sub-humid and humid lands. Forests in dry regions seem to be four times more resilient than shrublands and shrublands two times more resilient than

Table I. The water yield sensitivity of all vegetation types, trees, shrubs and grasses in dry, sub-humid and humid regions.

	Climatic regions		
	Dry	Sub-humid	Humid
All vegetation types	5.74	1.21	0.74
Trees	2.09	1.52	0.77
Shrubs	8.93	0.78	0.41
Grasses	14.19	1.11	0.75

Sensitivity was measured by means of the coefficient of variability (CV). Note that variability decreases from dry to sub-humid and humid regions.

grasslands/savannas. In practical terms, this would indicate that grasslands and savannas in dry regions are the most unstable and exposed ecosystems to suffer transition.

The analysis of WY in the three study ecosystems allowed us to introduce a novel perspective based on the peculiarities of this ecohydrological variable. The whole dataset analysis reveals a positive and highly significant ($P < 0.01$) relation between PP and WY (Figure 4). Given that WY is the result of discounting actual ET from PP, positive values of WY reveal a soil-surface outflow because of the PP surplus. The case of negative values of WY is particularly interesting. It may indicate that vegetation has to capture water from sources other than rainfall (generally underground water and surface and subsurface runoff from other areas) to sustain the ET demand of vegetation. This is common in the case of forests in riparian zones of dry regions, where the ET demand of woody vegetation can only be sustained if a high water inflow, out of rainfall, is supplied (Bosch and Hewlett, 1982).
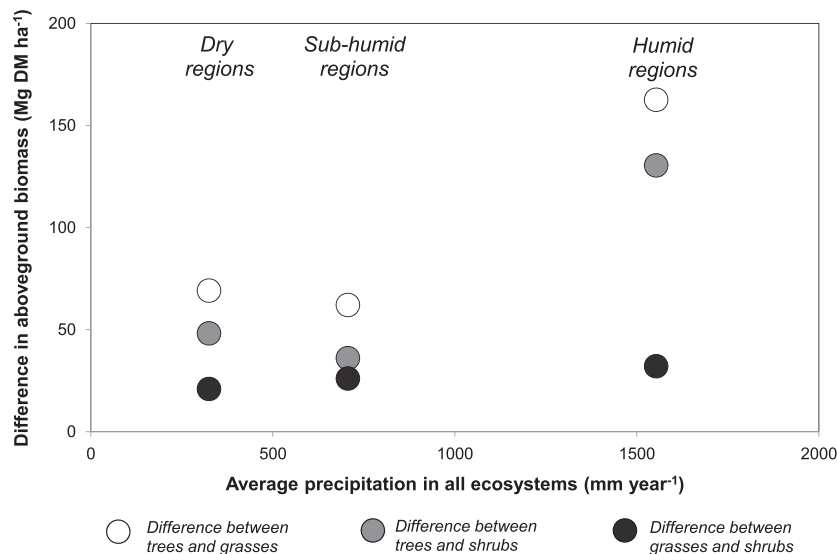

Figure 3. Distance among trees, shrubs and grasses expressed as the difference in their respective average amount of aboveground biomass (ton DM ha^{-1} year^{-1}) in three climatic regions.
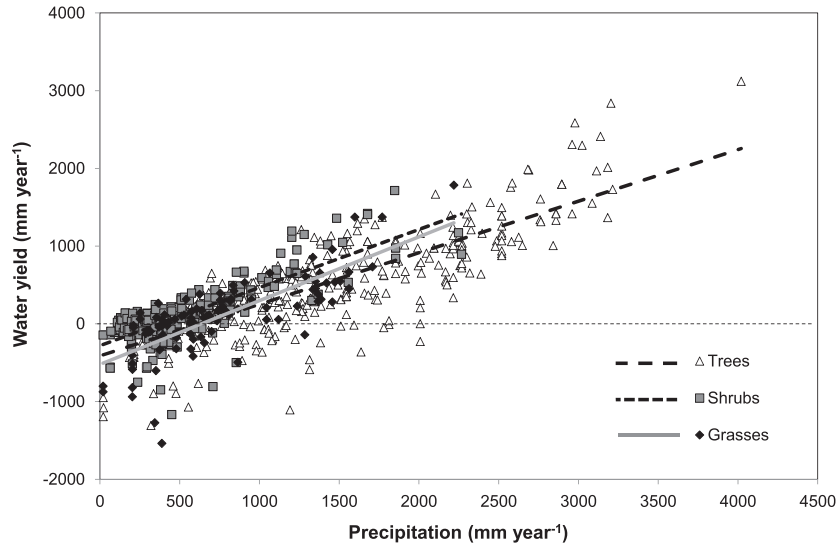
Figure 4. Worldwide relationships between precipitation and water yield in all study climatic zones discriminated by ecosystems. All regression models are highly significant ($P < 0.01$). Positive water yield values express the soil-surface outflow after discounting evapotranspiration from precipitation. Negative values indicate that plants are capturing water from sources other than rainfall, normally soil moisture, to sustain evapotranspiration demand of aboveground biomass.

Another striking ecological aspect deserves attention. Table II shows results from a regression analysis that aimed at assessing the relationships between AGB and WY in all regions and ecosystems. The value of slope (b) was negative in all climatic regions and all ecosystems, indicating that WY weakens as AGB increases. The more water is lost to the atmosphere, the less water reaches the soil surface. Regressions were significant ($P < 0.01$) in all cases because of the large sample size regardless of the value of the determination coefficient (R^2). It should be noted that the negative value of the slope was very high in the case of grasslands/savannas, intermediate in shrublands and low in forests. In the case of grasslands/savannas, it can be appreciated that the strong fall in the WY in all climatic regions occurred in response to small increments of AGB, suggesting that grasses have a high actual ET per unit of AGB. Such response was smooth in the case of shrubs and trees, both having greater AGB. This contrasting behaviour suggests that trees and shrubs can maintain more biomass (woody material in particular) than grasses per unit of ET water.

A detailed analysis of some attributes of AGB and actual ET provides additional information (Table III). Because ecosystems differ in their absolute ET values, the actual ET is not strictly related to the absolute amount of AGB. Despite showing consistently lower AGB values, the average figures indicate that grasses transpire, in relative terms (per unit of dry matter), more water than shrubs and trees. When those ET values were expressed per unit of standing biomass ($mm \, Mg \, DM^{-1}$), grasslands and savannas seem to use much more water than shrubs and forests. In ecological terms, we can infer that such functional attribute may become especially critical in dry regions where water normally is the most important constraining resource to sustain an active ET.

The ecohydrology of transition: a hypothetical model

The notion of biomass gap between ecosystems showed in Figure 3 can help interpreting the resilience of ecosystems to undergo transition. Two aspects deserve attention: (i) the narrow biomass gap between grasses and shrubs would indicate that its probability of transition is larger than between shrubs and trees, and even larger than between grasses and trees, and (ii) given that the gap widens as PP increases, we assume that the probability of transition decreases as the water availability increases. In other

Table II. Statistics of the regression analyses assessing the relationship between aboveground biomass and water yield in the study vegetation types and climatic regions.

Climatic regions	Vegetation types	N	a	b	R^2	P-value
Dry	Trees	58	74.7	−2.29	0.71	<0.01
	Shrubs	85	118.40	−5.91	0.24	<0.01
	Grasses	65	485.67	−214.64	0.62	<0.01
Sub-humid	Trees	116	234.53	−1.20	0.18	<0.01
	Shrubs	55	456.84	−8.97	0.28	<0.01
	Grasses	33	1102.30	−340.25	0.57	<0.01
Humid	Trees	227	1119.90	−2.07	0.07	<0.01
	Shrubs	24	1146.30	−10.53	0.28	<0.01
	Grasses	25	1765.10	−347.28	0.50	<0.01

Table III. Hydrological behaviour of forests, shrublands and grasslands/savannas in dry, sub-humid and humid areas through mean value and standard deviation (in italics between brackets).

	Vegetation types	Climatic regions		
		Dry	Sub-humid	Humid
Aboveground biomass (AGB) (Mg DM ha^{-1} year^{-1})	Trees	65.53 (*68.42*)	63.56 (*76.02*)	165.30 (*75.72*)
	Shrubs	17.62 (*10.69*)	24.57 (*10.77*)	25.46 (*18.73*)
	Grasses	2.30 (*0.39*)	2.77 (*0.39*)	3.44 (*0.87*)
Evapotranspiration (ET) (mm ha^{-1} year^{-1})	Trees	509.33 (*235.33*)	559.73 (*249.48*)	1061.97 (*406.40*)
	Shrubs	254.08 (*148.58*)	476.07 (*164.51*)	455.76 (*287.79*)
	Grasses	360.71 (*14.67*)	535.53 (*146.67*)	840.46 (*284.41*)
ET/AGB (mm Mg DM^{-1})	Trees	15.01 (*8.31*)	16.84 (*7.97*)	8.31 (*5.75*)
	Shrubs	14.84 (*4.34*)	20.50 (*7.31*)	17.96 (*6.67*)
	Grasses	150.68 (*39.29*)	189.67 (*27.41*)	245.88 (*83.39*)

words, the resistance to transition tends to be low in dry regions and high in humid ones. This can explain why humid regions contain more resilient ecosystems than the arid counterparts. As reviewed literature demonstrated, it is unlikely that rainforests in regions over 2500 mm year-1 can naturally change into another ecosystem in absence of strong disturbing forces (e.g. extensive and deep deforestation). A hypothetical model to explain such dynamics is proposed in Figure 5. In graphical terms, each ball movement represents one transition way, and the deep of the attraction domain (valley) represents the propensity of ecosystems to resist transitions. The deeper the valley the more resilient is the ecosystem. The model shows that attraction domains are deeper in humid than in dry regions, explaining why the displacement of the ball from one attraction domain to another in humid regions is unlikely and why humid regions tend to show a more resilient behaviour than the drier ones. On the contrary, because their domains of attraction are shallow, the ball can be displaced easily (and generally irreversibly) from grasses to shrubs in dry regions in response to disturbances such as fire use or grazing.

DISCUSSION

Confirming our hypothesis, one of the most outstanding finding of this research is that ecohydrology, as a determinant cause of transition, is a first-order factor that operates at a hierarchical level higher than that of the human-driven disturbance. Furthermore, our results show that the ecohydrological context tends to strongly modulate the expression of anthropogenic disturbances that may cause ecosystem transitions, such as overgrazing, devegetation or fire use. However, beyond our findings, this work also confirms various outcomes from previous investigations: (i) no transition is expected in high rainfall regions unless a large-scale disturbance appears; (ii) a bimodal dynamics (from grasses to woody plants and vice versa) in response to disturbing factors such as fire and seasonal rainfall is expected in mid-rainfall regions; (iii) a uni-modal, irreversible dynamics from grasses to shrubs in response to stressors such as overgrazing is likely to occur in low-rainfall regions. However, transitions from tree to shrub ecosystems are uncertain because of lack of evidence.
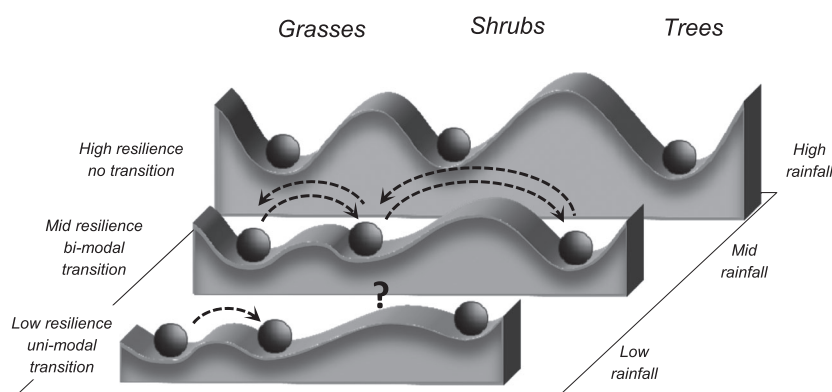

Figure 5. Synthetic graphical model showing the functional distance among grasses, shrubs and trees and the sensitivity of ecosystems to suffer abrupt transition in humid, sub-humid and dry climatic regions.

Our results are confirmatory of research results from Hirota *et al.* (2011), Staver *et al.* (2011a, b) and Hoffmann *et al.* (2012) for tropical regions (see Figure 2a and 2b in this work). Those authors found that sites with more than 60% tree cover predominated in regions receiving over 2500 mm year⁻¹ rainfall where rainfall was, besides, temporally uniform. They also found that sites receiving rainfall between 1000 and 2500 mm year⁻¹ were either forests or savannas, showing a bimodal (bi-stable) behaviour. Pure savannas, on the other hand, tend to dominate where rainfall was highly seasonal and fire favours the maintenance of a savanna cover. Those authors demonstrated that the states of forest and grasslands/ savannas in tropical regions are distributed discontinuously at the global scale. In synthesis, in agreement to our results in Figure 2a and 2b, dense forests over 60% cover were found mainly in regions receiving more than 2500 mm year⁻¹ rainfall, savannas (5% to 50% tree cover) were most commonly found between 750 and 2000 mm year⁻¹ and grasslands below 750 mm year⁻¹. The authors suggested that the scarcity of areas with intermediate tree cover indicates that transitions between forests and savannas are sharp and may occur rapidly. Staver *et al.* (2011a) found that tree cover across sub-Saharan Africa and South America was typically bimodal, with low tree cover (<50%) in savannas and high tree cover in forests (>55–60%). Despite those authors who did not differentiate forests from shrublands, the mixed distribution of shrubs and grasses within the rainfall range of 500–2000 mm year⁻¹ in our results confirms that a bi-stable woody-grassy state is likely to occur at intermediate rainfall regimes.

It should be noted that the high resilience showed by tropical rainforests over 2500 mm year⁻¹ rainfall could be substantially altered by a large-scale disturbance caused by deforestation and fire. Davidson *et al.* (2012) and Silvério *et al.* (2013), for example, stated that the resilience of the Amazon forest has already been altered. They demonstrated that a trend from continuously wet conditions in the northwest to long and pronounced dry conditions in the southeast is occurring nowadays. If this trend to dryness reinforces during the coming years, it is likely that the high resilience of the Amazon rainforest can change, and ecosystems can move to a bi-stable condition, falling in a transitional process that ranges between forests and savannas.

The encroachment of shrublands into grasslands and savannas has been widely reported in review articles such as those of Eldridge *et al.* (2011) and D'Odorico *et al.* (2012). Encroachment is usually confined to dry regions of the world where a pastoral land use has been common (Archer, 2010). One mainstream scientific view attributes shrubland encroachment to two disturbing factors: overgrazing and fire suppression. Van Auken (2009), for

example, considered that high and constant levels of grazing by domestic animals reduce fine fuels with a concomitant reduction or elimination of fire, creating the conditions for the expansion of woody plants over grasses. According to Gibbens *et al.* (2005) and Viglizzo (2011), overgrazing may trigger a positive feedback that accelerates the loss of grasses and the growth of shrubs, causing a parallel and progressive decline of the livestock carrying capacity of the ecosystem. Furthermore, the loss of grassland biota due to encroachment may reinforce the shrub-dominant state (Eldridge *et al.*, 2009).

The arid ecosystem may be favouring an ecological succession based on those plant structures that minimize the loss of water to the atmosphere (evaporation and transpiration) prioritizing on the contrary those water pathways that occur close to the soil surface. Because dense woody tissues predominate in shrubs but not in grasses (IPCC, 2006) and given that shrubs have a greater capacity than grasses to cover the soil (Eldridge *et al.*, 2013), shrub encroachment may be a successful emergent property that allows minimizing direct evaporation and transpiration per unit of standing biomass. Transitions from grass to shrub can plausibly be a defensive mechanism of ecosystems to preserve essential ecological functions in arid regions. It also offers a sound evolutionary argument to explain the predominance of shrubs in the dry domain. However, it should be noted that this 'water-preservation' attribute would have no biological meaning in regions where rainfall is not a limiting factor.

Our results let us conclude that PP and the related ecohydrological conditions play a primordial role in ecosystem transitions. The hypothesis supporting that the probability of transition is low under humid and high under dry conditions is sound. Some authors (Snyder and Tartowski, 2006; Sankaran and Anderson, 2009; Kulmatiski and Beard, 2013) have suggested that the hydrological context may, or may not, allow the expression of disturbing anthropogenic factors that can cause transition. In turn, those factors can feedback to the ecosystem and even cause deep alteration in the hydrological balance of ecosystems, reinforcing the transition from one vegetation type to another.

What about mechanisms behind the ecosystem transitions? The relationship between runoff and deep drainage appears to be at the core of transition mechanisms in dry regions. Ecosystems that allow deep drainage tend to favour the dominance of plant species that have deep-root systems, generally woody plants. Regarding mechanisms in dry regions, various investigations have put attention on the competition for soil moisture between grassy and woody plants (Walker and Noy-Meir, 1982; Kambatuku *et al.*, 2013). An early contribution from Walter (1939) settled the basis for the so-called 'two-layer hypothesis', which postulated a niche separation between shrubs and

grasses to capture soil moisture. Given that both functional types may require more water than that provided by rainfall, they inevitably have to rely on water stored in the soil to survive. Under rain-fed conditions, grasses capture water in the upper soil layer, whereas woody plants can get water from deeper soil layers. Woody species in arid and semiarid environments generally extend their rooting structures deeper than herbaceous vegetation (Sala *et al.*, 1989; Scholes and Archer, 1997), which results in a distinct partitioning of soil moisture between shrubs and grasses. Grasses growth is constrained when fire use or overgrazing remove standing biomass and favour water evaporation, thus reducing the possibility of grasses to absorb water from upper layers. On the contrary, woody plants tend to proliferate and replace grasses because their root systems are able to capture water from deeper layers in the soil (D'odorico *et al.*, 2012). The deep drainage hypothesis supports the cases of irreversibility of shrub encroachment. The competitive elimination of grasses and their replacement by woody species would trigger a positive feedback where the increasing soil cover with shrubs favours deep drainage and amplifies the proliferation of woody species. This positive feedback would impede the restoration of surface-water pathways that favours grasses proliferation.

In sub-humid and humid savannas where woody and grassy plants may keep a bimodal coexistence, strong surface-water and deep-water mechanisms may operate at the same time impeding the irreversible suppression of grasses by woody plants. As Hirota *et al.* (2011) and Staver *et al.* (2011*b*) have demonstrated, fire may trigger bi-stable states below 60% tree cover in areas where grasses produce large amounts of flammable fuel. However, if tree cover becomes dense in high PP regions, both grass growth and the resulting fires are inhibited, favouring conditions for dense, nonflammable forests. Hoffmann *et al.* (2012) indicated that forest preservation from fire is governed by two critical thresholds: (i) a *fire-resistant threshold* that is reached when individual trees have accumulated enough bark to avoid stem death and (ii) a *fire suppression threshold* that is reached when the forest has accumulated sufficient plant canopy to exclude grasses and suppress fire. As a result, nonflammable thresholds are found in high rainfall sites, dramatically reducing the opportunity of transition from forests to savannas in regions receiving more than 2500 mm year^{-1}.

CONCLUSIONS

As a vast body of literature has shown, several disturbing anthropogenic and biophysical factors (overgrazing, fire, de-vegetation and droughts) are dominant drivers of ecosystem transitions. However, the results in this research tend to confirm our hypothesis that the dominant ecohydrological context plays a primordial, first-order role in ecosystem transitions. If the same disturbing factors could similarly affect the ecosystem under different hydrological conditions, we could presume that our hypothesis was trivial or irrelevant. But this does not occur. Recent scientific evidence and our own results prove that transitions and transition mechanisms differ under different ecohydrological conditions.

A first sound proof of ecohydrological determinism can be found in tropical rainforests that receive more than 2500 mm year^{-1} rainfall. The tropical rainforest seems to be extremely resilient and insensitive to disturbing factors such as fire use. A fire suppression mechanism based on a dense green-vegetation barrier against fire expansion is strong enough to neutralize the effect of such disturbance.

A second proof that confirms our hypothesis is found in regions of intermediate rainfall (more than 500 mm year^{-1} and less than 2500 mm year^{-1}). A bi-stable transition mechanism allows the coexistence of reversible woody and grassy states. Two tipping points arise: on the one hand, mediated by fire and seasonal rainfall, the ecosystem can indistinctly move towards a woody state or a grassy state that, respectively, depend on increasing or decreasing PP. On the other hand, while the higher PP regime seems to favour the woody-plant dominance, the lower one seems to favour the grass proliferation. It has been demonstrated that fire strongly contributes to maintain a grass-dominated phase at mid-rainfall regimes.

A third proof can be found in dry regions. It is not easy to find sound cases of bi-stability and mutual reversibility between grasses and shrubs. The lack of evidence led us to think that it prevails a unique, irreversible transition from grasses to shrubs under low-rainfall conditions. In these regions, water-conservation mechanisms are essential to maintain ecosystems in operation. A tipping point triggered by overgrazing and vegetation uncover has probably been transgressed once grasses have been replaced by shrubs. It is very unlikely that the encroached ecosystem can return to the previous grassy condition unless a strong human intervention interferes the shrubby phase. This grass-to-shrub shift may be a successful emergent property to maintain water pathways close to the soil surface in arid and semiarid regions.

Finally, a highly relevant argument that supports our findings is that the hydrological context operates on an upper hierarchical level than that of the anthropogenic disturbance. While the hydrological context extends over large spatial scales, the anthropogenic effect tends to be site-specific, reduced to local actions that can only become relevant when they extend over large geographical areas. In terms of natural hierarchies, it is clear that local actions are always embedded into a broad-scale hydrological context.

The implications of a dominant hydrological context may potentially be very relevant in a planet that is exposed to increasing hydrological shifts caused by global climate change.

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