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How human-induced transitions from forest to treeless ecosystems affect litter decomposition

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Abstract. The transformation of forests to treeless landscapes as a result of disturbances (deforestation transitions) is an ongoing process in many regions of the world. Here we first revise the historical context of these transformations and then, we focus on its consequences for litter decomposition. We also present a case study, based on four ecosystems of central Argentina (Sub-Andean, Mountain Chaco, Espinal and Arid Chaco), evaluating how deforestation transitions can modify ecosystem decomposition by altering its main controls. Although there is evidence of consequences of deforestation transitions on the local environment for decomposition and on leaf litter quality it is not clear how those changes would impact the decomposition of natural mixed litter in the field. In our study case, we show that the deforestation transitions evaluated across four ecosystems resulted in no consistent changes in standard substrate decomposition but a consistent increase in the litter mixtures' decomposability and quality. Likely as a consequence of this pattern, the loss of trees resulted in a consistent increase in the *in situ* mixtures decomposition across the ecosystems studied. Beyond our particular findings, our analysis highlights how the accurate prediction of the consequences of deforestation transition on changes in carbon and nutrient cycling needs to understand the behaviour of its controls. Only through this understanding, we will be able to interpret the patterns of *in situ* mixtures decomposition and predict the consequences of deforestation transitions adequately on carbon (C) and nutrient cycling. Additionally, the recent literature, in coincidence with our results, gives evidence that the presence of non-leafy plant debris and local-scale variation in the local environment may play a stronger role than previously thought in C and nutrient cycling.

[Keywords: deforestation, litter mass loss, standard materials, decomposability, litter quality, woody debris, Sub-Andean, Mountain Chaco, Espinal, Arid Chaco]

Resumen. Efecto de la transición antropogénica desde ecosistemas forestales a ecosistemas sin árboles sobre la descomposición de broza. La transformación de los bosques en paisajes sin árboles como resultado del disturbio (transiciones de deforestación) es un proceso en desarrollo en muchos lugares del mundo. En este trabajo revisamos el contexto histórico de estas transformaciones y luego nos enfocamos en sus consecuencias sobre la descomposición. También presentamos un estudio de caso basado en cuatro sistemas del centro de la Argentina (Sub-Andino, Bosque Montano, Espinal y Chaco Árido) en los que evaluamos cómo las transiciones de deforestación pueden modificar la descomposición de mezclas naturales de broza incubadas *in situ* al modificar sus controles. Mostramos que aunque existen evidencias de las consecuencias de las transiciones de deforestación en las condiciones climáticas locales y en la calidad de la broza, no está claro cómo esos cambios impactarán en la descomposición de las mezclas naturales de broza a campo. En nuestro estudio de caso mostramos que las transiciones de deforestación no generan un cambio en la descomposición de sustratos estándar, pero sí aumentan consistentemente la descomponibilidad de las mezclas naturales de broza. Posiblemente, como consecuencia de este patrón, la descomposición de mezclas de broza *in situ* aumenta cuando los bosques se transformaron en fisonomías sin árboles a lo largo de todos los sistemas analizados. Más allá de nuestros hallazgos, nuestro análisis destaca la necesidad de entender el comportamiento de los controles de la descomposición para interpretar adecuadamente su integración en la descomposición de mezclas *in situ* y las consecuencias de la deforestación en el reciclado de carbono y nutrientes. En concordancia con nuestros resultados, la literatura reciente muestra que la presencia de broza no-foliar y las variaciones del ambiente local tendrían un rol importante en el reciclado de C y nutrientes, incluso a escalas regionales.

[Palabras clave: deforestación, pérdida de masa de broza, materiales estándar, descomponibilidad, calidad de broza, broza leñosa, Sub-Andino, Chaco Serrano, Espinal, Chaco Árido]

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INTRODUCTION

The interest in disturbance as a driver of ecosystem displacement from a reference state has grown with the realisation of the extensive and deep influence of human activities on ecosystems (Rykiel 1985; Thompson et al. 2009; Hanna et al. 2019). This has led to prolific research on whether and how ecosystems would be able to absorb the impact of human activities and continue providing the benefits societies depend on (Holling 1973; Donohue et al. 2013; Thom and Seidl 2016; Kefi et al. 2019). Although the concept of disturbance itself has evolved from being focused on catastrophic exogenous events to be considered an intrinsic process in many ecosystems (Supplementary Material 1-Box S1), there has been always agreement on its key role in triggering plant communities transitions at a wide range of spatial and temporal scales (White and Jentsch 2001; Newman 2019; Johnson and Miyanishi 2021). To what extent, and by which mechanisms, those transitions affect ecosystem processes —in particular soil processes— have been less evaluated and it is not always easy to predict (Thom and Seidl 2016; Thom et al. 2017; Newman 2019; Kozák et al. 2021).

Excluding land-use changes such as urbanization and conversion to annual-crop agriculture, one of the deepest human ecosystems' modifications is the transformation of forests to treeless landscapes as a result of acute and chronic disturbances, such as logging, fire, domestic ungulate grazing and, especially, their combination (Conant et al. 2001; Cingolani et al. 2008; Ellis et al. 2021). This type of land cover transition —hereafter 'deforestation transition'— has shaped terrestrial ecosystems across all continents throughout the Holocene, as forests were exploited to sustain growing human populations (Miehe et al. 2006; Marchant et al. 2018; Roberts et al. 2018; Malhi 2018). While in many places in the Northern Hemisphere forests have bounced back over treeless landscapes in the last two centuries (Marchant et al. 2009), in most regions of the world the loss of forest ecosystems is an ongoing process (Sodhi et al. 2010; Ordway et al. 2017; Daneyrolles et al. 2020).

Here we analyse how deforestation transitions affect soil processes. To this end, we first revise the historical context of these transformations, and then, focus on how the loss of trees affects ecosystem processes and, in particular, litter decomposition. Finally, we present a case study where we evaluate the effect of the deforestation transitions on decomposition and its main controls under different climatic conditions in seasonally dry temperate and subtropical ecosystems of central Argentina.

DEFORESTATION TRANSITIONS AND THEIR CONSEQUENCES ON SOIL PROCESSES

Although deforestation transitions have expanded and intensified in the last centuries as a consequence of globalization and industrialisation, early human societies initiated this land cover change thousands of years ago associated with subsistence practices (Marchant et al. 2009; Armesto et al. 2010; Ellis et al. 2021). Traditionally, the negative impacts of deforestation transitions have been linked to habitat and species loss resulting from a decrease in structural complexity (Ochoa-Quintero et al. 2015; Giam 2017; Aguilar et al. 2018). However, the loss of a whole plant growth form can also impact ecosystem functioning because the dominant plant attributes, which are one of the main drivers of ecosystem processes, are largely modified (Díaz and Cabido 2001; Lavorel and Garnier 2002; Brose and Hillebrand 2016). With the loss of trees and the dominance of grasses, forbs and/or shrubs, there is not only a simplification of vegetation structure and a reduction in total live biomass, which usually increases the amount of light reaching the soil, but also a reduction in the total litterfall. As a consequence, not only soil temperature and moisture can be modified but also the amount of carbon (C) and nutrients that enter the soil (Morecroft et al. 1998; Smith and Johnson 2004; D´Odorico et al. 2013; De Frenne et al. 2021). At the same time, the loss of trees modifies litter quality because of the reduction in the proportion of woody debris, the elimination of tree leaf litter and the replacement of herbaceous shade-tolerant species by shade-intolerant ones (Veldkamp 1994; Thuille et al. 2000; Eviner and Chapin 2003; Elmore and Asner 2006; Carvahlo and Uidea 2010).

Many classic examples of anthropogenic deforestation transitions are related to the long-term use of fire. One of them is the conversion of temperate and coniferous forests into heathlands across northern Europe by clear-cutting and fire, and its maintenance by grazing and small-scale controlled fire (Mallik 1995, 2003; Newton et al. 2009; Roberts et al. 2018; St Martin and Mallik 2021). The communities arising from this vegetation change, dominated by slow-growing dwarf ericaceous shrubs with tough leaves, have slower carbon and nutrient cycling rates, compared to the original forests (Mallik 1995, 2003; Newton et al. 2009; St Martin and Mallik 2021). Another long-date example of change in biogeochemical dynamics by a deforestation transition is the case of *Nothofagus* southern temperate forests in Patagonia and New Zealand. In those forests, the increase in fire frequency, associated with human populations' arrival and expansion from the mid-Holocene until the present led to landscapes in which pyrophobic *Nothofagu*s forests and pyrophytic treeless plant communities coexist side by side (Kitzberger et al. 2016; Mundo et al. 2017). The transition from pyrophobic to pyrophytic communities is triggered when a first *Nothofagus* forest burning initiates a positive feedback towards more frequent fires in this otherwise fire-resistant ecosystem (Paritsis et al. 2015). This feedback maintains alternative states of treeless plant assemblages with unfavourable local conditions for tree establishment (i.e., warmer and drier than in the *Nothofagus* forest). The loss of trees combined with more frequent fires also reduces soil C and nitrogen (N) content and microbial activity of several microbial groups (Alauzis et al. 2004; Longo et al. 2011; Fajardo and Gundale 2015).

Even in seasonally dry forests, where fire is fundamental for maintaining vegetation structure over long time scales, human alteration of fire regimes can result in transitions to treeless landscapes (Driscoll et al. 2010; Pausas and Bond 2020; Pilon et al. 2021; Giorgis et al. 2021). For instance, the increase in fire frequency in Mediterranean chaparral (California) favours the dominance of highly competitive non-native grasses over native woody species recruiting from the seed bank, which promotes a further increase in fire frequency that redirects the system towards a trajectory of higher dominance of grasses (Keeley 2012; Keeley and Pausas 2019). This physiognomic change can cause a reduction in soil C storage associated with a decrease in net primary production and an increase in soil respiratory losses (Koteen et al. 2011). In central Argentina Mountain Chaco, Kowaljow et al. (2018) showed that a *Lithraea molleoides*-dominated forest was associated with a low fire frequency (no evidence of a widespread fire in 85 years), while nearby shrublands —with 75% fewer tree cover and 80% more grasses and forbs— were associated with a high fire frequency (at least six widespread fires in 80 years). The (almost) treeless site —dominated by shrubs, grasses and forbs— had shallower soils as a consequence of increased erosion rates and lower input of woody debris and leaf litter from woody species, compared to the forest with low fire frequency.

In Arid Chaco forests and woodlands of central Argentina, removal of trees followed by recurrent roller chopping of resprouting vegetation interrupts the successional trajectory towards a tree-dominated landscape and maintains a matrix of grasses and shrubs, in which livestock grazing makes tree recruitment is unlikely because of direct consumption of saplings and soil compaction (Steinaker et al. 2016). The maintenance of treeless physiognomies in this region implies a decrease in soil C storage associated with a decrease in litter input and an increase in soil respiration losses (Conti et al. 2014, 2016). Nosetto et al. (2020) also found that the transformation of forests to grasslands in this region is associated with a decrease in gross primary productivity and ecosystem respiration, which is explained by a lower tolerance of the pasture to climatic variability, in particular, to cool and dry winters. A similar decrease in productivity within the Arid Chaco was reported by Somovilla Lumbreras et al. (2019), as a consequence of the conversion of forest to grasslands and shrublands by roller-chopping. The authors suggest that the pattern could be caused by the loss of key species, like *Prosopis flexuosa*, or by the loss of whole functional groups with key attributes, like trees with deep roots and nitrogen-fixing capacity. Despite this change in productivity, the soils of the resulting shrublands and grasslands presented high soil organic C content, which the authors attribute to the decomposition of the dead plant material generated by the effect of the roller-chopper. Also in central Argentina, but in Sub-Andean forests dominated by *Polylepis australis*, historic use of fire combined with cattle grazing on seedlings and saplings has promoted a replacement of forests by grasslands communities (Renison et al. 2006; Cingolani et al. 2008; Giorgis et al. 2020). As an outcome of *P. australis* deforestation transition, the simplification in vegetation structure and the decrease in standing and litter biomass resulted in soils with lower infiltration capacity, probably as a consequence of lower soil organic matter content (Renison et al. 2010, 2018; Poca et al. 2018).

Deforestation transitions and the controls of litter decomposition

Decomposition of dead biomass determines C and N fluxes and it is strongly linked to the provision of two fundamental societal benefits: soil fertility and soil C sequestration (Anderson et al. 2019). Decomposition rates are controlled by climate, litter quality and the communities of soil detritivores and decomposers (Aerts 1997; Zhang et al. 2008). Disturbance can alter decomposition through different pathways. One of the most important is the above-mentioned alteration of the structural and functional characteristics of the vegetation which, in turn, can modify local climate and litter quality (Quested et al. 2007; Fortunel et al. 2009; Poca et al. 2015).

When forests are converted to treeless communities, either grasslands or shrublands, the most immediate change is in the local climate, one of the main controls of decomposition. There is an increase in the amount of solar radiation reaching the lower vegetation strata and the soil, which could increase soil temperature and decrease soil moisture (Reiners et al. 1994; De Frenne et al. 2021). However, the decrease in biomass and vegetation structural complexity may also lead to lower transpiration and higher albedo, which can be associated with an increase in soil surface humidity (Niemann and Edgell 1993; Gaertner et al. 2001; Houspanossian et al. 2013, 2017). When a deforestation transition occurs, the temporal climatic amplitude (i.e., daily and seasonal differences between maximum and minimum temperatures) can increase because the canopy is no longer acting as a climatic buffer (Yates et al. 2000; De Frenne et al. 2019, 2021). In temperate forests, both maximum and minimum temperatures are buffered below trees while in boreal forests a stronger buffering is found at minimum temperatures. In tropical rainforests, where water is non-limiting, maximum temperatures seem to be more buffered than minimum temperatures (De Frenne et al. 2019, 2021). In seasonally dry forests, with a higher water limitation and less dense canopies, forest litter cover can be an even stronger regulator of soil direct evaporation than canopy cover itself and, through this, litter can reduce the rate at which soils lose their moisture (Magliano et al. 2017). All these changes in local climate can affect decomposer abundance and activity and thus decomposition rates (Smith and Johnson 2004; Mayer 2008; Vaieretti et al. 2018). For example, the increase of temperature and the decrease of soil moisture as a consequence of deforestation transitions in temperate ecosystems were associated with a decrease in decomposers abundance and diversity, simplifying soil food webs (Tsiafouli et al. 2015). In a subtropical humid forest of Southwest China, the conversion from forests to grasslands also decreased humidity, pH, C and nutrients, and —probably as a consequence of those changes— the abundance of several microbial and fungi groups (Zhao et al. 2019). In a seasonal tropical mountain rainforest from southwestern China, Paudel et al. (2015) reported that the decomposition of two common substrates decreased when the system is transformed from mature forest to grasslands (dominated by *Imperata cylindrica* (L.) Raeusch.). This effect was explained by a decrease in soil moisture resulting from canopy opening. Lorenzo et al. (2014) reported similar findings for the central Amazonia rainforest, where the conversion of primary forest to pasture led to a slower decomposition of a high-quality common substrate (leaves of *Acalypha communis* Müll. Arg.). In temperate ecosystems, because of changes in microclimate, decomposition rates, carbon sequestration and microbial activity has been shown to either decrease (Riutta et al. 2012; Chen et al. 2018) or increase (Köchy and Wilson 1997) in treeless habitats compared to adjacent forests.

Litter quality, another main control of decomposition, can be modified when plant composition changes, altering the activity of decomposers (Díaz and Cabido 1997; Garnier et al. 2007; Fortunel et al. 2009; Poca et al. 2015). When forests are transformed to treeless physiognomies, leaf litter quality can decrease if deciduous trees are replaced by perennial grasses, but can increase if coniferous, evergreen or sclerophyllous trees are replaced by annual grasses and forbs (Pérez-Harguindeguy et al. 1997; Cornelissen et al. 1999; Cornwell et al. 2008). Quested et al. (2007) found that forb- and grass-dominated herbaceous communities, under current use or recently abandoned, had higher decomposability and litter quality than *Pinus sylvestris-Betula* spp.-dominated forest (after 60 years of land-use abandonment). In contrast, Vaieretti et al.

(2021) reported that the removal of trees was associated with communities dominated by more conservative leaf attributes (e.g., higher leaf toughness and lower decomposability) in cold-temperate and sub-humid ecosystems of central Argentina, mainly associated with the increase of perennial grasses. The changes in litter quality and decomposability resulting from deforestation transitions can change the abundance and activity of decomposers as both microbial decomposers and detritivores prefer high-quality substrates (Gessner et al. 2010). For example, the conversion of mountain forests to grasslands in northern Iran caused a decrease in the abundance of all groups of soil fauna, which the authors attributed to a reduction in litter quality (Kooch et al. 2021).

The patterns described above regarding changes in litter quality, however, only consider leaf litter. Natural mixed litter from forest floor can have a significant proportion of woody debris (Dearden et al. 2006; Harmon 2009), which have inherently slower decomposition rates than the leaf litter of the same species (Weedon et al. 2009; Freschet et al. 2013; Araujo and Austin 2020). Forest litter may include between 10 and 30% of woody materials compared to none or negligible amounts in treeless ecosystems (Vogt et al. 1986; Scott et al. 1992; Boddy and Watkinson 1995; Poorter et al. 2012; Freschet et al. 2013). The loss of the woody debris input after a deforestation transition may increase the quality and decomposability of the natural litter mixtures reaching the soils. Despite the long-dated recognition of the importance of woody debris in forests (Vogt et al. 1986; Scott et al. 1992; Boddy and Watkinson 1995; Frangi et al. 1997), the vast majority of studies on decomposition in those ecosystems has focused on leaf litter decomposition (Lousier and Parkinson 1976; Martín et al. 1997; Portillo-Estrada et al. 2016; Wang et al. 2021; Zhou et al. 2020), and only recently wood begun to be considered more frequently in local and global studies (Zhou et al. 2007; Gonzalez-Polo et al. 2013; Harmon et al. 2020; Seibold et al. 2021).

As described up to here there is ample information on the consequences of deforestation transitions on the controls of the decomposition process, in particular in the local environment and in leaf litter quality and decomposability. However, the consequences of those changes for the decomposition of naturally mixed litter in the field has been far less explored and seems to be not easy to predict. This is because the effects of tree loss on the controls of decomposition can act in opposite directions and, thus, it is difficult to predict its net outcome in a natural context.

Does the loss of trees affect decomposition in ecosystems of central Argentina?

In South American forests, the expansion of anthropogenic treeless ecosystems started with the growing human populations more than 6000 years ago, as a consequence of changes in fire regimes, clearing for logging and later conversion into agriculture and open rangelands (Marchant et al. 2009; Armesto et al. 2010; Mundo et al. 2017). However, it is not until the last two centuries that unprecedented high rates of forest disruption were documented (Grau et al. 2008; Hoyos et al. 2013,2018; Armenteras et al. 2017; Cabido et al. 2018; Rojido et al. 2021). According to Graesser et al. (2015) from 2001 to 2013, 57% of new pastureland replaced forests throughout Latin America. In a recent analysis of land cover changes related to fire, Armenteras et al. (2021) reported that between 2001 and 2018 almost 48% of South American evergreen forests were transformed into other land covers, mainly grasslands, to intensify forage production for cattle.

Central Argentina forest ecosystems are an example of the historical deforestation transitions described above as a consequence of past and present anthropogenic disturbances. Most forests, from sub-humid Sub-Andean *Polylepis australis* forests at high elevations (Renison et al. 2006; Cingolani et al. 2008; Giorgis et al. 2020) to the driest Chaco plains (Hoyos et al. 2013, 2018; Steinaker et al. 2016; Somovilla Lumbreras et al. 2019) have been partially transformed and maintained as treeless ecosystems as a consequence of logging, fire and its combination with grazing. Previous work in the region showed that in Sub-Andean, Mountain Chaco and Espinal ecosystems, the removal of trees with high-quality leaves leads to communities with low SLA, high leaf toughness and lower leaf decomposability (i.e., it leads to more conservative communities in their use of resources). In Arid Chaco ecosystems, however, the average leaf functional characteristics do not change with the loss of trees, as removal of trees leads to shrubby vegetation with a high presence of Fabacea and high-quality annual grasses (Vaieretti et al. 2021).

Here, we aimed at understanding how the forest transitions in central Argentina impact decomposition and whether this process is controlled by changes in the local environmental conditions for decomposers or by changes in the decomposability of litter mixtures. To achieve this goal, we studied four systems under different climates in central Argentina, whose forests have been partially transformed into treeless ecosystems by a combination of deforestation, fire and/or domestic grazing: Sub-Andean *Polylepis australis* forests, Mountain Chaco *Lithraea molleoides* forests, Espinal *Prosopis caldenia* forests and Arid Chaco *Aspidosperma quebracho-blanco* forests (Figure 1, Supplementary Material 2-Table S1 and Supplementary Material 3-Table S2).

In each of the four systems, we selected three stands of forests and three stands of treeless physiognomies. At each stand, we evaluated the controls of decomposition as well as the actual decomposition of litter natural mixtures (Figure 2). On the one hand, we estimated local environmental conditions for decomposers

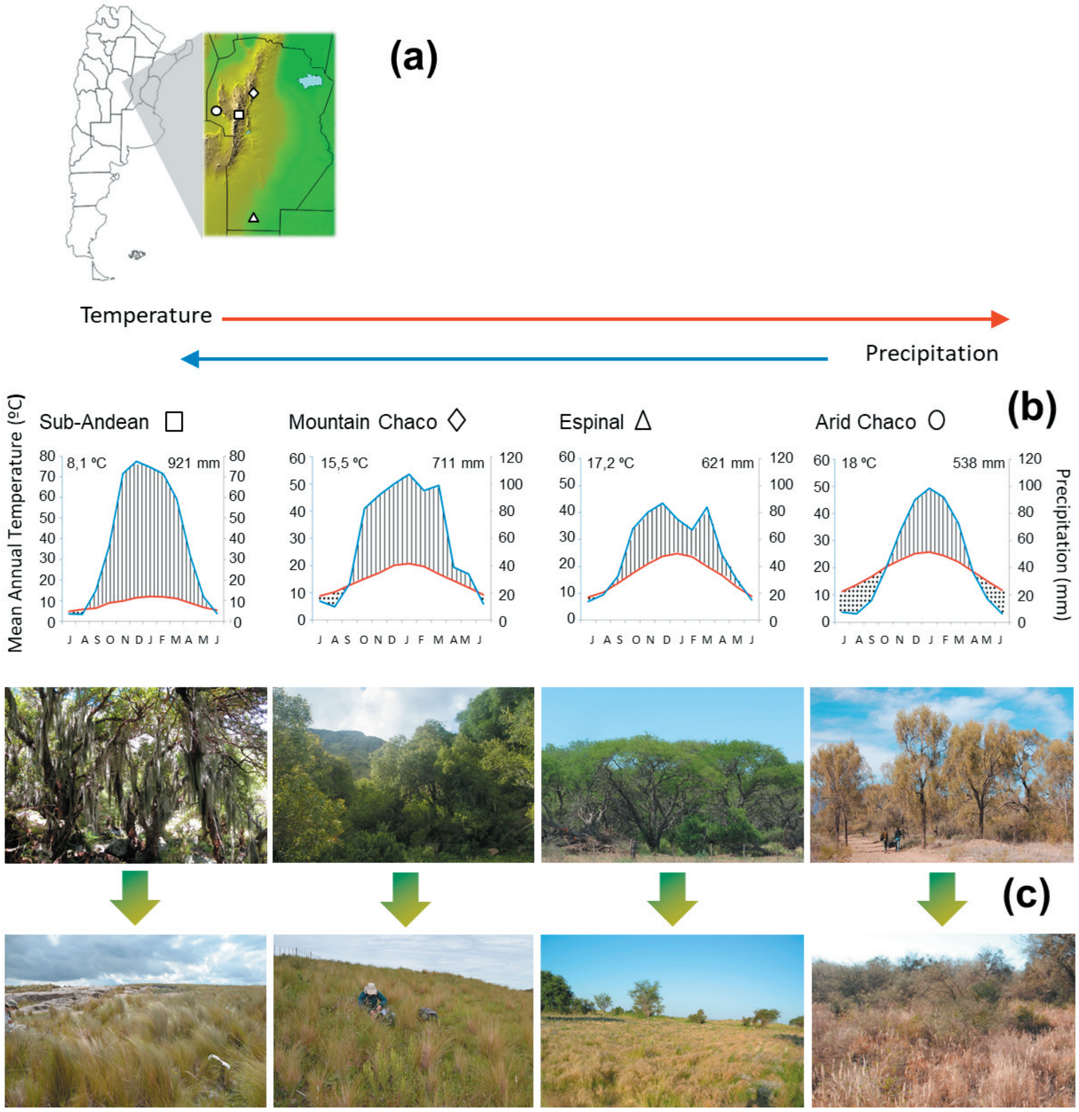

Figure 1. (a) Location of the four systems selected within the map of Córdoba province (Argentina) with its corresponding (b) climatic diagrams arranged in a gradient of increasing temperature and decreasing precipitation, and c) photographs of the transitions from forests to treeless physiognomies as a result of logging, fire and grazing.

Figura 1. (a) Ubicación en el mapa de la provincia de Córdoba (Argentina) de los cuatro sistemas seleccionados y sus correspondientes (b) diagramas climáticos ordenados a lo largo de un gradiente de aumento de temperatura y disminución de precipitaciones, y c) imágenes de las transiciones de fisonomías de bosque a sistemas sin árboles como resultado de la tala, el fuego y el pastoreo.

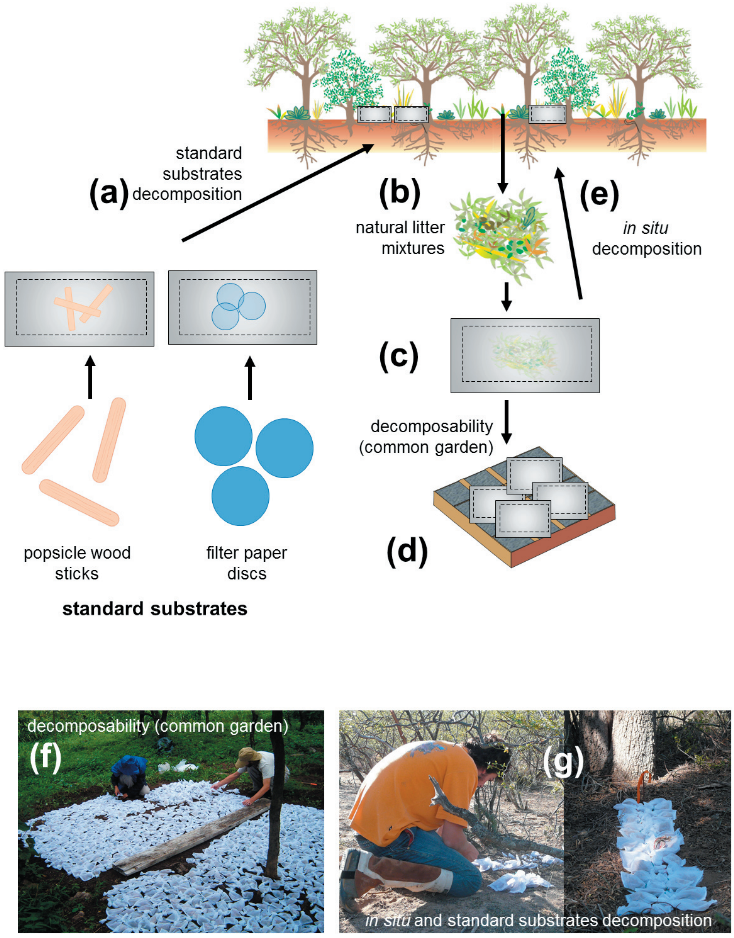

Figure 2. Decomposition experiments. In each stand (of forest and treeless physiognomies of the four systems selected) we incubated two substrates (popsicle wood sticks and filter paper) to estimate local conditions for decomposers (a, g). In each stand we also collected natural litter mixtures on top of soils (b) with which we build litterbags to determine decomposability of those mixtures (c) by incubating them in a common garden experiment (d, f). With the same litter mixtures, we build additional litterbags that we placed in the same stand from which litter mixtures were collected to determine *in situ* mixtures decomposition (e, g).

Figura 2. Experimentos de descomposición. En cada sitio (bosques y sitios sin árboles de los cuatro ecosistemas elegidos) incubamos dos sustratos comunes (palitos de madera para helados y papel de filtro) para estimar las condiciones microambientales para los descomponedores (a, g). En cada sitio también recolectamos, de la superficie del suelo, mezclas naturales de broza (b) con la cual rellenamos bolsas de descomposición para determinar la descomponibilidad de esas mezclas (c) por medio de su incubación en un jardín común (d, f). Con las mismas mezclas de broza, elaboramos bolsas adicionales que se colocaron en los mismos sitios de los cuales estas mezclas se recolectaron, a los fines de determinar la descomposición de

by measuring the decomposition of standard substrates, filter paper and wood sticks, incubated in each stand (hereafter 'standard substrates decomposition'). On the other hand, we determined the decomposability of natural litter mixtures, which have been collected from the ground in the same stand, by incubating those mixtures in a common garden experiment (hereafter 'mixtures decomposability'). We also incubated the same natural litter mixtures in the same stand from where they have been collected (Figure 2, Supplementary Material 4-Materials and Methods) to estimate the ecosystem decomposition rates (hereafter '*in situ* mixtures decomposition').

In deforestation transitions, both the local environment and the decomposability of the litter naturally mixed on top of the soil can change, and those changes can affect decomposition. On the one hand, we expect that —in the system where metabolic activity is most limited by temperature (Sub-Andean)— the loss of trees will lead to a higher decomposition because an increase in soil temperature may improve the environmental conditions for decomposers (estimated as standard substrates decomposition). At the same time, in the system in which metabolic activity is most limited by moisture (Arid Chaco), the loss of trees will decrease decomposition because forest clearing may decrease soil moisture and, thus, standard substrates decomposition would decrease. In the other two systems, less limited by water and/or temperature, we expect little change in the decomposition of standard substrates. On the other hand, we expect that the decomposability (and litter quality) of the natural mixtures across the deforestation transitions will not differ because the decrease in litter quality (caused by the increase in grasses abundance that has been detected in previous works) (Vaieretti et al. 2021) would be counterbalanced by the increase in quality caused by the loss of woody debris. Finally, we expect that if the litter quality of the mixtures, and hence its decomposability, does not change, the local environment for decomposers will be the main driver of ecosystem decomposition (i.e., the *in situ* mixture decomposition).

We found that the deforestation transitions evaluated did not produce a change in standard substrate decomposition (Figure 3a, Table 1). However, these transitions produced a consistent increase in the litter mixtures' decomposability (Figure 3b, Table 1) as well as a consistent increase in *in situ* mixtures decomposition (Figure 3c, Table 1). Across the four ecosystems studied standard substrates decomposition was higher in the Espinal and the Mountain Chaco and lower in the Sub-Andean and the Arid Chaco while mixtures´ decomposability was higher in the Espinal and the Arid Chaco, followed by the Subandean, and lower in the Mountain Chaco (Figure 3, Supplementary Material 5-Table S3). *In situ* mixtures followed a similar pattern to that of standard materials decomposition (Figure 3, Supplementary Material 5-Table S3); it was highest in the Espinal (k=0.0025 days^{-1}), followed by Mountain Chaco (k= 0.0015 days^{-1}), intermediate in the Sub-Andean (k=0.0013 days^{-1}) and lowest in the Arid Chaco (k=0.0010 days^{-1}). The multiple regression model across sites indicated that the combination of standard materials decomposition and litter decomposability explained 82% of the variability in *in situ* litter mixtures decomposition (P=0.0001). Specifically, and in line with the patterns reported for the variables isolated, the effect of litter decomposability on *in situ* mixtures decomposition (53% of variance explained, P<0.0001) almost doubled the effect of environment (29% of variance explained, P<0.0001). In other words, the deforestation transitions had their main effect on ecosystem decomposition through an increase of litter decomposability, while the environment had also a significant effect but associated with regional environmental changes across systems.

The lack of differences in the decomposition of standard substrates across the deforestation transitions may relate to the opposite effects caused on soil moisture and temperature. The loss of trees in systems with a marked dry season can trigger an increase in soil temperature, which may enhance decomposers activity, and a decrease in soil moisture, which may reduce it (Reiners et al. 1994; Mesquita et al. 1999; Yanai et al. 2003; De Frenne et al. 2021). Other works that detected significant microclimatic changes, in temperate secondary forests in the eastern US (Bradford et al. 2014) or tropical forests (Both et al. 2017), involved changes of only one major microclimatic factor, either temperature or moisture, but not both of them changing simultaneously. Our results are partially consistent with a previous study within the Sub-Andean system which showed that when grazing lawns released from grazing are transformed into tall tussock grasslands, temperature and light at the soil level are reduced, while soil moisture tends to increase (Vaieretti et al. 2013). Although the impact of the local environment has been extensively studied for

Table 1. Results of general linear models examining the effects of the ecosystem (Sub-Andean, Mountain Chaco, Espinal and Arid Chaco) and physiognomies (forests, treeless) on decomposability, standard substrates decomposition, and *in situ* mixtures decomposition (% dry mass loss). Response variables and P-values in bold indicate significant differences.

Tabla 1. Resultados de modelos lineares generalizados examinando los efectos de los ecosistemas (Sub-Andino, Chaco Serrano, Espinal y Chaco Árido) y las fisonomías (bosques y sistemas sin árboles) en la descomponibilidad, descomposición de sustratos estándar, y descomposición de mezclas *in situ* (% de materia seca perdida). Las variables de respuesta y los valores de P en negritas indican diferencias significativas.

	Response variables	DF	F	P
Standard substrates decomposition average (dry mass loss %)	**System**	**3**	**19.63**	**<0.0001**
	Physiognomy	3	0.003	0.95
Decomposability (dry mass loss %)	**System**	**3**	**8.96**	**0.0001**
	Physiognomy	**1**	**58.36**	**<0.0001**
In situ mixtures decomposition (dry mass loss %)	**System**	**3**	**24.29**	**<0.001**
	Physiognomy	**1**	**51.98**	**<0.001**

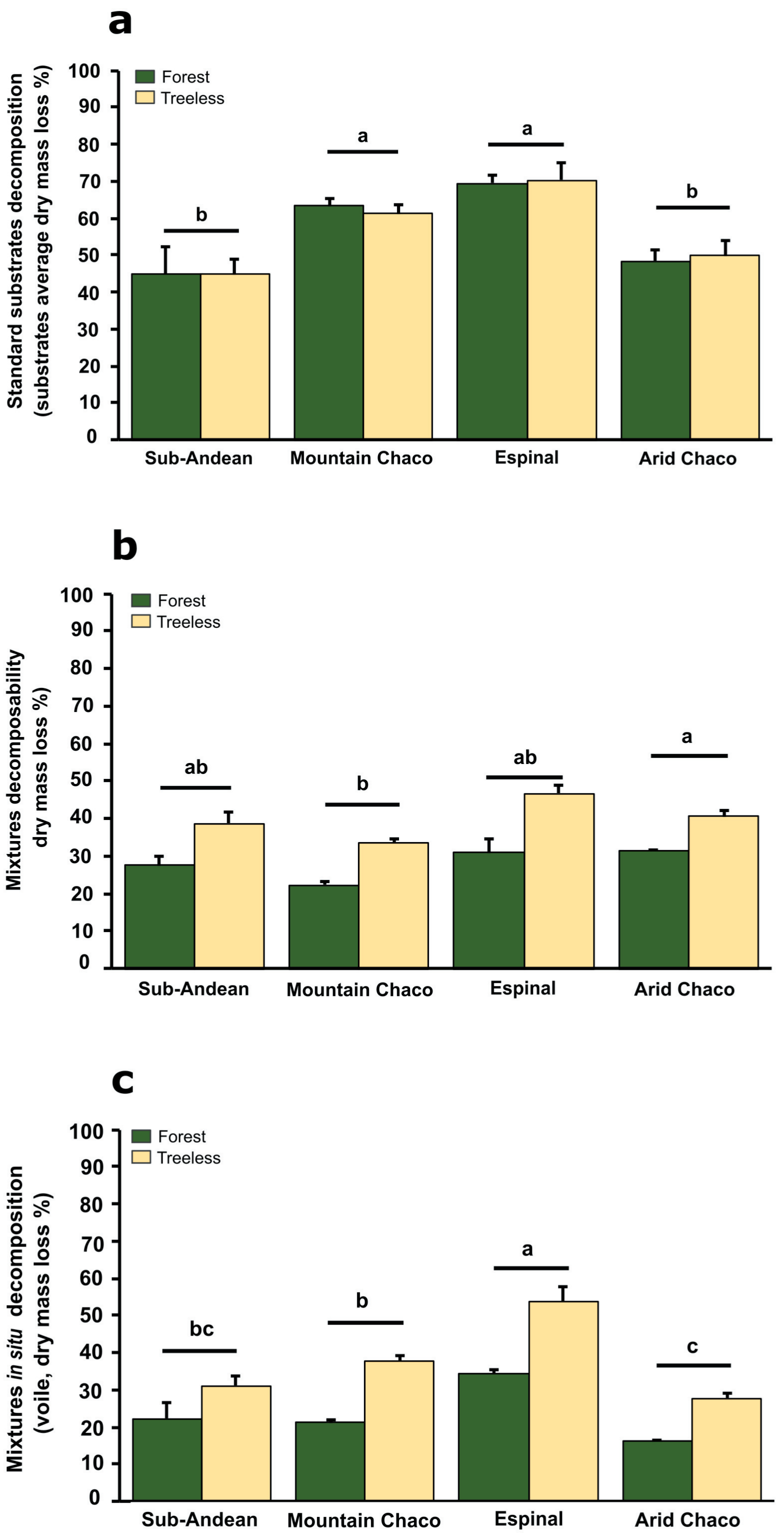

Figure 3. Decomposition patterns of : a) standard substrates (average of filter paper and popsicle wood sticks incubated in all systems and physiognomies to estimate microenvironment for decomposers) after 8 months of incubation, b) natural litter mixtures collected from all stands (systems and physiognomies) incubated in a common garden experiment (decomposability *sensu* Cornelissen et al. [1999]; Pérez-Harguindeguy et al. [2013]), and c) natural mixtures incubated in the same sites from which they have been collected after 8 months of incubation. Different letters indicate significant differences between systems and asterisks indicate differences between physiognomies, according to Table 1 and Supplementary Material 5-Table S3.

Figura 3. Patrones de descomposición de: (a) sustratos estándar (promedio de la descomposición de papel de filtro y palitos de helado de madera incubados en todos los sitios durante 8 meses para estimar microambiente para los descomponedores), (b) mezclas naturales de broza recolectadas en todos los sitios (sistemas y fisonomías) incubados en jardín común (descomponibilidad *sensu* Cornelissen et al. [1999]; Pérez-Harguindeguy et al. [2013]), y (c) mezclas naturales incubadas, durante 8 meses) en los mismos sitios (sistemas y fisonomías) en los que fueron recolectadas. Letras diferentes indican diferencias significativas entre sistemas y asteriscos indican diferencias significativas entre fisonomías, de acuerdo a Tabla 1 y Material Suplementario 5-Tabla S3.

its effect on many ecosystem processes (Chen et al. 1999; Vanwalleghem and Meentemeyer 2009; Zellweguer et al. 2019; De Frenne et al. 2021) it has been far less considered in the context of decomposition. This can be particularly relevant when microclimatic conditions interact with the composition and activity of decomposers communities, further affecting decomposition patterns (Kooch et al. 2021). The fact that in our study the effect temperature and humidity may have acted in opposite directions on decomposition, and this may have resulted in no detectable changes on standard materials decomposition, does not necessarily mean this will be the case under other circumstances, but that the outcome would depend on the absolute and relative magnitude of the change in different microenvironmental variables (Bradford et al. 2014; Both et al. 2017; De Frenne et al. 2021).

Across systems, the higher decomposition of standard substrates in Mountain Chaco and Espinal is not surprising as those are the less limited systems when considering simultaneously temperature and precipitation (Figure 2, Supplementary Material 2-Table S1) and, thus, may have fewer restrictions for decomposers activity. In general, the pattern across systems is also in line with a previous study in which Mountain Chaco woodlands had the highest decomposition of standard substrates (Pérez-Harguindeguy et al. 2007) while Sub-Andean grasslands and Arid Chaco forests had the lowest. We attributed this consistent pattern to a possible limitation of decomposition by temperature in the Sub-Andean system, similar to the one reported for other mountain systems (Salinas et al. 2011) and to a limitation of decomposition by moisture in the Arid Chaco (Mesquita et al. 1999; Yanai et al. 2003).

The increase in mixtures' decomposability with the deforestation transition was contradictory to our prediction of no change in decomposability. A previous study in the same systems showed that when forests were transformed to treeless physiognomies there was a reduction in the community weighted mean of leaf decomposability, caused mainly by the increase in the proportion of grasses in the community (Vaieretti et al. 2021). In our study, we included woody debris in the litter mixtures, which, according to literature from other systems can represent at least 11% and as much as 30% of the litter production (Vogt et al. 1986; Boddy and Watkinson 1995; Harmon 2009; Freschet et al. 2013; Harmon et al. 2020). As woody debris usually causes a reduction in litter-mixtures quality, we had expected a null outcome of the increase in grass litter and a decrease in woody debris as forests are transformed to treeless physiognomies. However, in the natural mixtures collected from the soils of our systems, the impact in decomposability of the decrease in woody debris in the treeless physiognomies may have surpassed the effect of the increase in grass litter reverting the pattern found by Vaieretti et al. (2021). This pattern would have been caused by the intrinsically lower decomposability of woody debris related to its higher lignin content. This interpretation is in line with the consistent decrease in lignin in the litter mixtures of all the deforestation transitions evaluated (Supplementary Material 6-Figure S2 and Table S4). These results are also in agreement with the idea that the consistently lower decomposability of woody debris can have a relevant role on mixtures decomposability and, thus, in in situ mixtures decomposition that will be more or less important depending on the relative inputs of different plant organs (Harmon 2009; Freschet et al. 2012, 2013; Harmon et al. 2020). Although leaves have been traditionally indicated as the main drivers of carbon and nutrient cycling in the short term (Laiho and Prescott 2004; Schlesinger and Bernhardt 2013), woody debris can play a significant role in the carbon cycling and soil organic matter build-up of forested ecosystems (Harmon 2009; Cornelissen et al. 2012; Harmon et al. 2020). The relative importance of woody debris in decomposability becomes particularly relevant in forest transitions where the physiognomic transformation may already imply a major decrease in the amount of C reaching the soil through litter (Koteen et al. 2011; Conti et al. 2014, 2016; Kowaljow et al. 2018). If in addition to the decrease in the amount of C reaching the soil, there is an increase in its decomposability, this may lead to further C losses through decomposition.

The pattern of mixtures' decomposability across systems, lower in Mountain Chaco and high in Arid Chaco, is also in partial agreement with the patterns found in our previous studies at a larger regional scale, where the potential leaf decomposition of dominant species (weighted means of decomposability of dominant species) from Mountain Chaco woodlands was lower than the decomposition of dominant species from Arid Chaco woodlands (Pérez-Harguindeguy et al. 2007). This pattern also coincides with the one found, for the same systems studied here, but for leaf litter decomposability (estimated through the weighted means of decomposability of the leaves of dominant species) by Vaieretti et al. (2021) as discussed above. The consistency of the patterns between leaf litter (Vaieretti et al. 2021) and the present study, despite the difference in absolute values, could be related to the coordination in strategies across plant organs (Freschet et al. 2012, 2013). This coordination implies that systems dominated by species with more decomposable leaves may also produce more decomposable woody debris. We cannot discard that the consistency of the rankings could also be related to the importance of leaf litter in the mixed litter even in forests (Laiho and Prescott 2004; Schlesinger and Bernhardt 2013; Freschet et al. 2013).

Contrary to our expectations, we found that the main effect of the loss of trees in *in situ* mixtures´ decomposition was driven by the decomposability (and litter quality) of the natural mixtures, while the environment for decomposition (evaluated through standard substrates) was only important at the regional level, associated with climatic differences. As discussed above, this may relate to the markedly lower decomposability of treeless physiognomies, probably caused by the loss of woody debris in the litter of those physiognomies. It is interesting that this result is partially contradictory with some of our studies in similar systems, while partially coincident with others. In contradiction with the patterns found here, Vaieretti et al. (2013), comparing different grasslands types within the Sub-Andean system, found that in situ mixtures decomposition was mainly explained by environment (evaluated through common substrates decomposition) and in second place by litter mixtures decomposability. In a study with a similar design but comparing different woody physiognomies with the Arid Chaco, Cuchietti (2016) found the opposite pattern, the *in situ* mixtures decomposition was mainly explained by litter mixtures decomposability. Another similar pattern was found by Fernández et al. (2021) when comparing native Yunga secondary forest and *Ligustrum lucidum* invaded forests, mixtures decomposability was the main driver of *in situ* mixtures decomposition at local scales. The discrepancy in the results across studies, some of them in similar systems to the ones analysed here, suggest that a wider study across regions would be needed to investigate how the effect of the different drivers of decomposition on the control of in situ mixtures patterns relate to the magnitude of change in those drivers.

Across ecosystems, the pattern found in the present study is in partial agreement with the results of Pérez-Harguindeguy et al. (2007) who found that decomposability of the dominant species and the decomposition of standard substrates in the dominant physiognomies across a wide climatic gradient showed different trends. As here, in that study, standard substrates decomposition was higher in Mountain woodlands, while leaf litter decomposability was higher in xerophytic woodlands (Arid Chaco). This type of inverse relationship between rates decomposition of standard substrates, a proxy of environmental conditions, and decomposability (or litter quality) has been reported even at the species level in other ecosystems. For instance, in a precipitation gradient within native forests on Hawai´i. Austin and Vitousek (2000) found that decomposability of *Metrosideros polymorpha* leaves collected from driest sites decomposed faster than leaves collected from wetter sites, but in situ mixtures decomposition was faster in the wettest sites. This inverse relationship, that contradicts the idea that the climate and the litter quality act in the same direction in decomposition (Aerts 1997), may be caused by the relatively high quality of species from dry ecosystems (Killingbeck and Whitford 1996; Cornelissen et al. 1999) in which standard materials decomposition is strongly limited by moisture.

CONCLUDING REMARKS

We found consistent evidence that deforestation transitions across a wide range of ecosystems in central Argentina lead to an increase in decomposition driven by an increase in litter decomposability. What is more interesting, our findings —which reflect the actual decomposition of natural litter mixtures— show opposite patterns in the consequences of forest transitions, to the ones found when considering only leaf litter (Vaieretti et al. 2021). At the same time, the lack of changes in standard materials decomposition across deforestation transitions may evidence the complexity of the changes in microclimate in these transitions and the difficulty to predict its outcomes for ecosystem processes (De Frenne et al. 2021). Our results are in line with classical models indicating the importance of litter quality as a driver of decomposition at regional or local scales (Lavelle et al. 1993; Aerts 1997; Cornwell et al. 2008), models that have been recently challenged (Bradford et al. 2016, 2017).

Beyond our particular findings, our analysis highlights some knowledge gaps in our understanding of how deforestation transitions may affect carbon and nutrient cycling. Even though community structure changes caused by disturbance have been proposed to be linked to changes in ecosystem processes since the first studies on disturbance ecology (Supplementary Material 1-Box S1) empirical evidence on those links, particularly for below-ground processes is still relatively scarce. It is rather surprising that although the multiple controls of decomposition and carbon and nutrient cycling have been identified long ago, until recently most studies have focused either in the climate or microclimate, either on decomposability, and those last ones have strongly focused on leaves even when other organs can also be important drivers of carbon and nutrient cycling. Both the literature and our findings suggest that the accurate prediction of the consequences of deforestation transition on carbon and nutrient cycling through decomposition requires the understanding of the different controls of this process that may be operating in different directions, for instance, depending on the relevance of different microclimatic variables as well as the importance of woody debris within litter mixtures.

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