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REVIEW

Pathways of megaherbivore rewilding transitions: typologies from an Andean gradient

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In most of the planet, large herbivore communities have been replaced by livestock, but this process is reversing in many places. Here, we outline and review the pathways of "megaherbivore rewilding transitions" in three social-ecological-systems of subtropical Argentina. In the extensive arid high-elevation Puna plateau we observed a "rapid rewilding pathway" where the reduction of livestock was accompanied by the recovery of native camelid populations from near extinction in a few decades. In the forest-grassland ecotone, decreasing livestock favored higher fire frequency, probably limiting the speed of native herbivore recovery in an "increasing fire pathway". In lowland montane forests, the recovery of native herbivore communities appears to be lagged by fragmentation, local extinctions and human pressure, representing a case of "connectivity-limited rewilding". These typologies exemplify the complexity of outcomes resulting from livestock diminishing density, and provide a framework to understand and optimize processes of large herbivore rewilding according to different social-ecological contexts.

Keywords: Land use change; Land abandonment; Elevational gradient; Herbivory transitions

Introduction

Human land use is a major component of global environmental dynamics. By analyzing spatial patterns of vegetation, land science has largely focused on research questions in which land use is mostly reflected in land cover. Research initially focused on deforestation as the main land change process (eg, Geist and Lambin, 2002); and later looked at "forest transition" processes of forest recovery in originally forest-dominated regions or countries (eg, Rudel et al., 2005). Forest and non-forest cover dynamics are easily described by remote sensing and reported in government statistics, and the relevance of these studies derives from the fact that forests' ecological properties are very different from those of non-forested ecosystems (e.g., higher biomass, better watershed and soil protection, higher habitat quality for wildlife) (Crossman et al., 2013).

Other important components of ecosystem functioning, however, are not captured by land cover studies, of which the composition of herbivores is a particularly important one. In areas unsuitable for cropland, the main human land use is extensive livestock grazing. While agriculture today occupies approximately 40% of the global land area, the current livestock population (cattle, sheep, equines, goats) represents more than 90% of the global megafauna biomass (excluding humans), leaving less than 10% to large wild herbivores (Bar-On et al., 2018). Changes in the composition of large herbivores generate land changes that are comparatively subtler than deforestation or forest recovery, but they still structure ecological systems in important ways (Augustine and Mc Naughton, 1998). For example, large herbivores regulate vegetation structure and species composition (and therefore biomass stocks) by selective consumption and trampling, produce greenhouse gas emissions (mainly methane through their metabolism), affect large carnivore populations (due to replacement of preys and hunting aimed to protect livestock), and change fire regimes by controlling both fuel availability and ignition sources (Fleischner, 1994).

Several regions of the world and of South America in particular, are experiencing a decrease in land use intensity (Grau and Aide, 2008; Meyfroidt et al., 2018; Nanni et al., 2019) in association with socioeconomic modernization changes such as rural-urban migration, agriculture concentration in the most productive lands, and active conservation and restoration. A similar redistribution process is occurring with livestock production as intensive systems expand and extensive production is gradually abandoned (Ilea, 2009). These processes are also likely to produce changes in large herbivore communities. However, the decrease in livestock intensity and its ecological consequences have received relatively little research attention (Svening et al., 2016).

The replacement of extensive livestock by native herbivores can be considered a particular case of "rewilding"

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(Speed et al., 2019). The effects of livestock reduction and potential "rewilding" of the herbivore community is expected to vary depending on its replacement or not by native herbivores, in turn depending on landscape connectivity, vegetation flammability, hunting pressure, and other interactions with anthropic systems. All these variables are likely to depend on social and biophysical factors that co-vary along environmental gradients. Here, we take advantage of studies in subtropical South America to conduct a comparative analysis covering a wide range of such conditions. Understanding the drivers and consequences of livestock decrease is a major research goal in the context of global environmental change; and comparisons in different social-ecological contexts could provide key guidelines towards that end. By analogy with the well-studied "forest transition" process, we call the reversal trend towards a native-dominated large herbivore community, "megaherbivore rewilding transition".

We use examples along an extensive environmental range (from 500 to c. 5000 meters above sea level; from less than 150 mm to more than 1500 mm of annual rainfall, and from sparsely populated to high density peri-urban areas), to 1- identify different pathways of this transition, 2-explore its driving and limiting factors as well as its trajectories, and 3- propose hypotheses on how these factors may drive, or limit, its trajectories and ecological consequences. While our identified pathways are likely a subset of a much richer set of possibilities, we believe they include a valuable diversity of processes that may serve as a reference for more refined studies in different social-ecological systems. Ultimately, we expect our identified pathways to highlight the importance of addressing the drivers and consequences of megaherbivore transitions, still an understudied issue.

Study system and pathways of megaherbivore rewilding transitions

Humans arrived in northwestern Argentina earlier than 10,000 years before present, predating a major extinction of several components of the megafauna, which included native horses, the largest camelids, giant sloths, mastodons, and elephant-like gomphothers (Barnosky and Lindsey, 2010; Martinez 2018). As a result, the current list of native mid to large herbivores within the region includes, in the highlands, two species of camelids (*Vicugna vicugna* and *Lama guanicoe*) and one of Taruca deer (*Hippocamelus antisensis*); and in the middle and low elevation mountains, two species of small *Mazama* deer (*M. gouazoubira* and *M. Americana*); two species of peccaries (*Pecari tayacu* and *Tayassu pecari*), and a Tapir (*Tapirus terrestris*) (Mares et al., 1990). In pre-European times, megaherbivore domestication was limited to one species (llama, derived from guanacos, used for wool, meat and transport), and occurred in the highlands in association with the development of tropical Andean societies between 5000 and 4000 BP (Olivera, 2018). After the arrival of Europeans in the early 16th century, sheep largely replaced llamas, becoming the main high elevation livestock for meat and wool; cattle throve in the most productive areas as the most valuable meat and leather producer; goats become the dominant livestock in drier areas below 3500 meters above sea level; horses were bred for local transportation, while donkeys and mules developed into a local export industry to supply the large demand for transport from Bolivian mines during the 17th and 18th centuries (Langer and Conti 1991). Since the mid-20th century, many areas unsuitable for modern agriculture because of steep slopes, low rainfall and poor soils, are additionally experiencing livestock reduction (Izquierdo and Grau, 2009). This occurred mostly because these marginal lands cannot compete with modern meat and wool production systems with better market access, infrastructure or land productivity; and because equines were replaced by motor vehicles as means of transportation. In northwestern Argentina, this has been the case of the dry highlands of the Puna, and the steep slopes of the yungas forests and foggy grasslands (Izquierdo and Grau, 2009). By revising case studies in these three ecosystems (**Figure 1**), we propose hypothetical pathways of the megaherbivore rewilding transition.

Rapid herbivore rewilding pathway: Camelid recovery in Puna highlands

The Puna region is a high elevation desert (>3300 meters above sea level, <300 mm of annual rainfall, and some areas with less than 150 mm yr^{-1}). Human population density is very low (c. 2 persons per square kilometer), even lower than in other parts of the ecoregion such as Bolivia), and further decreasing in the rural areas (Izquierdo et al., 2018). European colonization resulted in a replacement of the native herbivore community, largely dominated by camelids (wild vicuñas and guanacos, domestic llamas), by a comparatively diverse community of Eurasian ungulates: sheep, goats, donkeys, horses, and cattle. Vicuña populations were decimated due to fur hunting, while llamas were largely replaced by equines in the role of transport and by sheep in the role of meat and wool producers. Since the last decades of the 19th century, sheep dominated the herbivore community for more than a century, representing more than 70% of livestock biomass (Gil Montero, 2018; Quiroga-Mendiola and Cladera, 2018).

This pattern has been gradually reversing during the last 30 years following rural outmigration and changes in the economy, including a larger impact of mining and tourism (Izquierdo et al., 2018). The region is mostly unsuitable for croplands due to arid conditions (Grau, 2018), for which historical human impacts did not imply major habitat fragmentation, and wildlife populations were able to persist in the extensive and well connected remote places far from human settlements (Wursten et al., 2014). This pattern facilitated recolonization: from the verge of extinction, the population of vicuñas went from a few thousands in the 1960s to more than 120,000 in the onset of the 21st century (Izquierdo et al., 2018), due to a combination of decreasing incentives for conventional livestock (as local production cannot compete with modern production systems in the lowlands, and access to "imported" food and fibers has increased through commerce), replacement of equines by vehicles as a mean of transportation, rural population decline, protective laws prohibiting hunting, and incentives to produce high quality wool from vicuñas in semi-captivity (Vila et al., 2018) probably the only case here analyzed where the rewilding process has a direct economic benefit.

There is evidence that grazing intensity changes plant species composition, with non-palatable and toxic species being more abundant in heavily grazed places (Adler and Morales 1999), but these patterns are likely to be significant only near populated sites. At the regional scale, the replacement of livestock by native wild herbivores has been so steady and fast, that the total biomass of large herbivores has remained relatively constant during the past five decades (less than 15% fluctuation; Navarro, 2020; **Figure 2a**). Although it has been often hypothesized that camelids and Eurasian ungulates differ in their effects on plant communities, there is little solid empirical evidence of this, and in peatlands (the most productive and herbivore rich ecosystems) the dominant plant species are similar, irrespective of being grazed by vicuñas or by exotic livestock (Carilla et al., 2018). While distance to population centers is a strong predictor of herbivore community composition (**Figure 2b**), at the regional scale this variable appears to be little related to plant productivity and phenology: there is almost no correlation between distance to human settlements (a surrogate of wild herbivore relative importance) and NDVI (Normalized Difference of Vegetation Index, a surrogate of primary productivity) (Navarro, 2020). Further, in the last 15 years, vegetation productivity in peatlands far from populated centers (where rewilding is likely more advanced) decreased more than in the rest of the area, suggesting that hypothesized benefits from rewilding (e.g. less overgrazing) are not being realized.

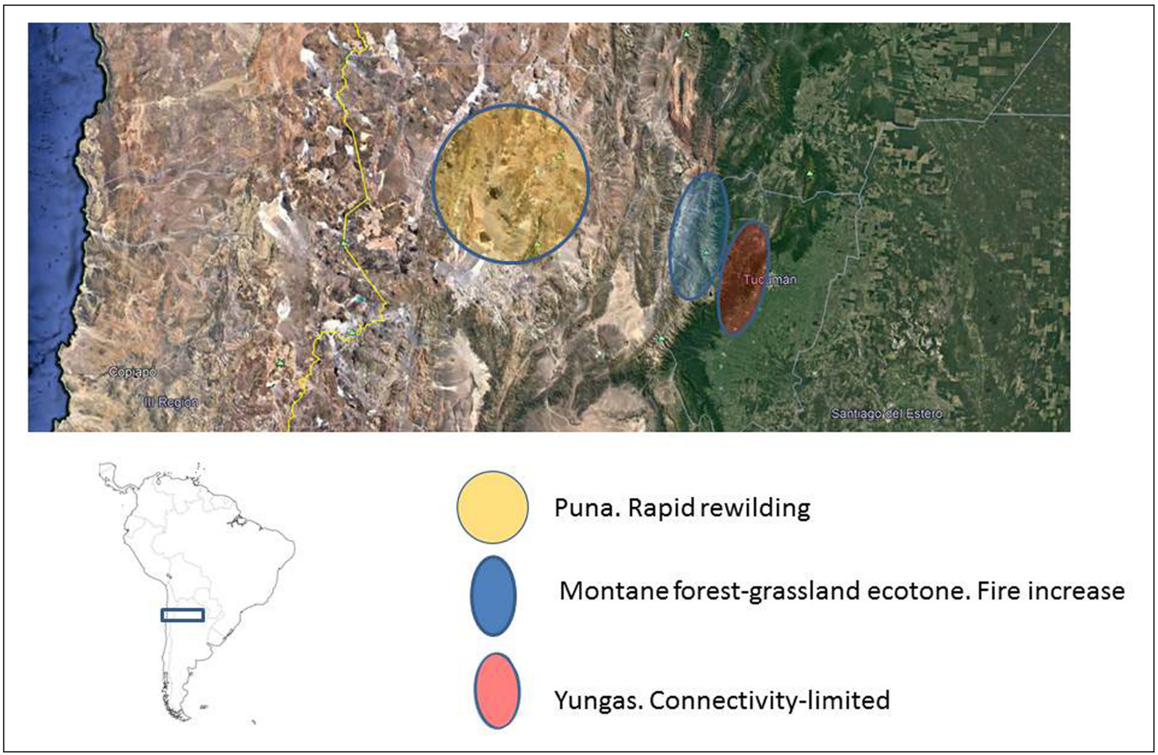

Figure 1: Location of the different studies along the elevational gradient of the eastern slope of the subtropical Andes. DOI: https://doi.org/10.1525/elementa.415.f1

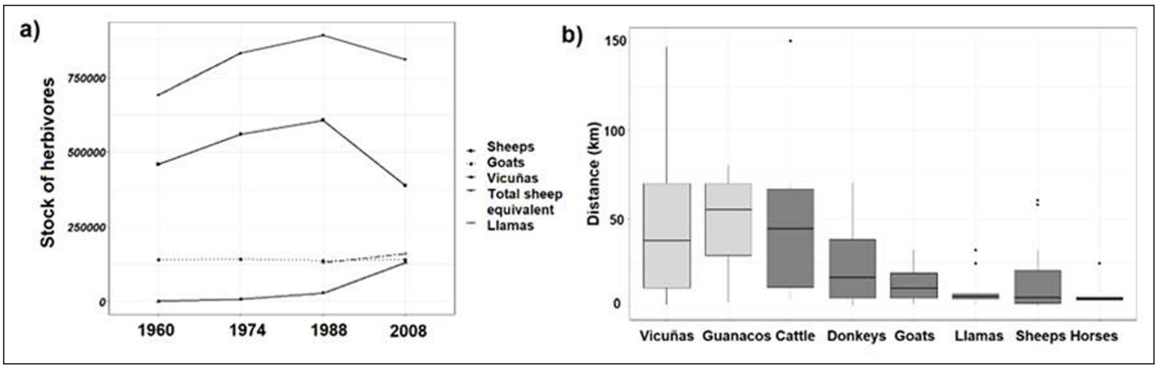

Figure 2: a) Sheep, vicuñas, goats, llamas in the Puna since 1960, and overall herbivory load (based on Izquierdo et al. 2018). **b)** Distance to human settlements of observations of different herbivores (based on Navarro, 2020). DOI: https://doi.org/10.1525/elementa.415.f2

Herbivore rewilding in the Puna also contributes to restoring an important trophic interaction in the region: the puma-vicuña predator-prey interaction, whose effects cascade to lower trophic levels (Donadio and Buskirk, 2016). Studies in the Puna show that, when camelids populations are abundant, pumas prey heavily on them, shifting to smaller native species (e.g. rodents) and domestic species only when camelid abundance is low (Donadio et al., 2009). It could thus be expected that increasing camelid abundance reduces puma predation on livestock. This would lead to the mitigation of human-puma conflicts, and of the negative attitudes and behaviors of the people towards the species (Lucherini and Merino, 2008).

Interestingly, certain areas of the Puna have experienced the expansion of feral and semi feral populations of donkeys, originating in recent socioeconomic changes. Until the 1980s, donkeys and mules were used as pack and transport animals. However, mainly due to expanding roads, this transportation system was largely replaced by trucks and cars (García et al., 2002), and in many places free ranging donkeys populations became feral (Grau 2018). This can be interpreted as a case of exotic species invasion, or as a case of "Pleistocene rewilding" (Donlan et al., 2006) given that *Equus* and *Hippidion* likely existed in the region for millions of years, until the onset of the Holocene when they became extinct almost simultaneously with the arrival of the first humans (Alberdi and Prado, 2004; Martínez et al., 2004).

In summary, in the more remote sites of the Puna, livestock abandonment resulted in a rapid rewilding of the megafauna community. The relative continuity of a large herbivore's density has resulted in relatively small changes in plant communities (Carilla et al., 2018), despite a clear geographic segregation of areas grazed by native (more remote) and domestic herbivores (nearby towns) (Wurstten et al., 2014). Overall, low plant primary productivity, biomass and fuel accumulation in this ecosystem implies that fire is not a main ecological factor (unlike the grassland ecosystem discussed later). Important trophic interactions, such as the puma-camelid predator-prey interaction could be re-established due to camelid increases, opening a window of opportunity for the reduction of livestock-carnivore conflicts as vicuñas and guanacos replace livestock as their main prey, hence reducing the incentives for carnivores' protective or retaliatory hunting.

Increasing fire pathway: montane grassland-forest ecotone

Humid slopes on northwestern Argentina mountains between 1800 and 3000 meters above sea level are characterized by a mosaic of grasslands and monodominant *Alnus acuminata* forests. Mesic precipitation levels, a monsoonal rainfall regime (dry winters, rainy summers), and strong thermal seasonality make the area prone to relatively frequent and low intensity fires (Grau and Veblen, 2000; Grau, 2001). The dominant herbivores are sheep and cattle introduced with the arrival of the Europeans, as reflected in large increases in erosion rates and phosphorus fluxes in lake sediment records (Lupo et al., 2006). As in the Puna region, livestock has been decreasing for the last five decades to approximately 30% of the 1960s level (Aráoz and Grau, 2010), in association to rural outmigration (Nanni and Grau, 2014). Such decreasing grazing intensity has been more marked in Argentina than in similar ecosystems of neighboring Bolivia, and simultaneously, forest has expanded over grasslands (Aráoz et al., 2014; Nanni and Grau, 2014). However, there is no evidence of a significant native herbivore recovery. Native herbivores include guanacos and tarucas towards higher elevations; and the red brocket deer at lower elevation. Despite having historically coexisted with domestic livestock, it has been documented that tarucas are negatively affected by competition for forage with livestock grazing, opportunistic hunting, and predation by domestic dogs (Barrio, 2013). Guanacos may experience the same type of pressures, as observed in other ecosystems (Moraga et al., 2014).

There are no detailed studies on the direct effect of decreasing herbivory on vegetation in this ecosystem, where the complex interaction among climate variability, vegetation productivity, grazing and fire results in a less predictable system behavior. It is clear, however, that simultaneously with the decrease in sheep density (the most abundant livestock) and with a regional increase in rainfall (which favors fuel production), fire frequency has significantly increased (**Figure 3**; Aráoz and Grau, 2010). Since all the winters and early springs are dry enough to desiccate fuels (Grau and Veblen, 2000) the probability of fire occurrence during the dry season (June to October) is mostly regulated by fuel availability, which depends on the rainfall of the previous growing season (November to April) and on its removal by grazing. This implies that to some extent grazing intensity controls fire regime, which in turn may shape the forest-grassland dynamics but in very unpredictable ways. In particular cases, fire appears to favor the expansion of *Alnus* trees into grasslands, but this is likely to work the opposite way at higher fire frequencies or intensities (Grau and Veblen, 2000; Aráoz and Grau, 2010). In a comparatively humid valley where the dominant tree species in secondary forests is *Podocarpus parlatorei*, decreases in grazing also resulted in more frequent fires, but in this case, it clearly limited forest expansion into grasslands (Carilla and Grau, 2010).

In summary, extended continuous grasslands, low human population density and decreasing livestock could allow a relatively rapid recovery of native herbivores in principle, as camelids and cervids would have better chances to avoid overlapping with domestic herbivores (Wurstten et al., 2014). However, these landscape characteristics also facilitate fire spread, which makes this pathway less predictable, with nonlinear responses, potential tipping points, and feedbacks to attain alternative states (Bond, 2010). To the present, research indicates that the increase in fire frequency (favored by livestock reduction and based in human ignition sources) seems to prevent the rapid rewilding of the system by cervids and camelids, and allows extensive low-density livestock management in a dynamically stable situation.

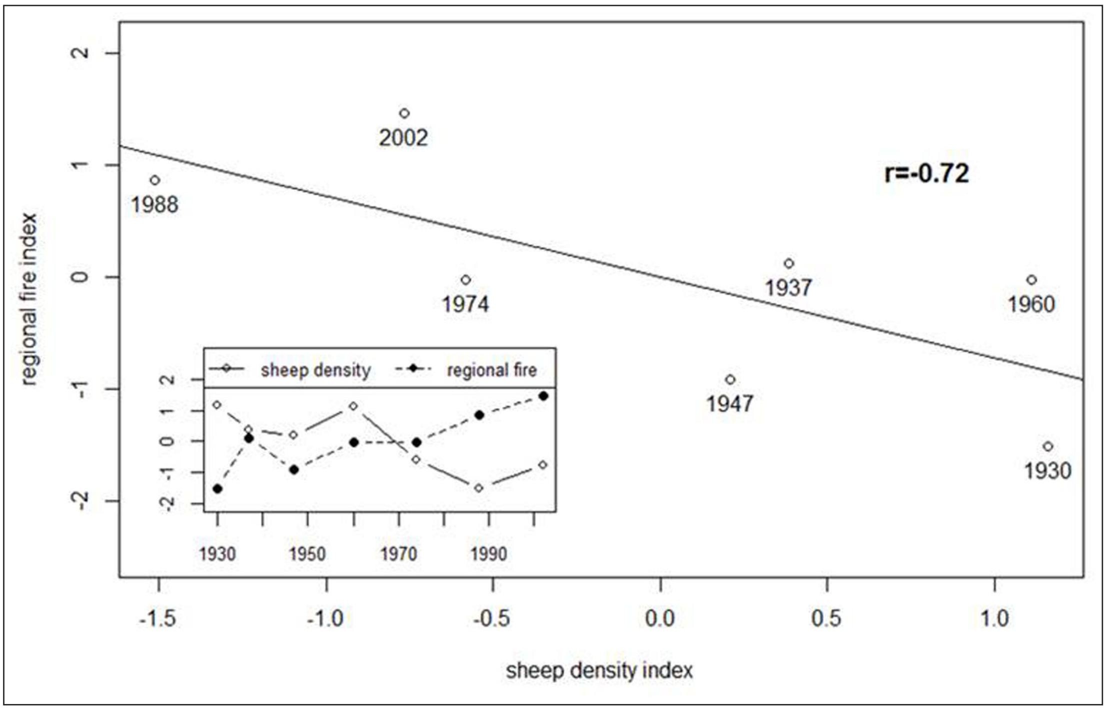

Figure 3: Fire-sheep density relationships (based on Aráoz and Grau 2010). Inset shows the same data ordered in the time sequence. DOI: https://doi.org/10.1525/elementa.415.f3

Connectivity – limited rewilding pathway: post defaunation subtropical montane forests

Lower montane "yungas" are subtropical forests growing above 1000 mm of annual rainfall and between 400 and 1500 meters above sea level. Due to their high productivity and greater accessibility to human population, they have been heavily used for extensive cattle ranching, selective logging, and shifting agriculture for the past two or three centuries (Brown et al., 2001). In relatively flat areas of this ecosystem type (foothills, valley bottoms), agriculture has continued intensifying in recent decades, while urban and peri-urban settlements have expanded (Gutierrez-Angoneze and Grau, 2014), following a similarly observed pattern in other low elevation sectors of the Andes (Aide et al., 2019) and the Atlantic forests (da Silva et al., 2016). During the last decades, however, important areas of this ecosystem in rough terrain (and more intensively near peri-urban areas) are experiencing a decrease in land use intensity also consistent with patterns in other humid Neotropical mountains (Grau and Aide, 2008), following rural-urban migration, livestock reduction, cropland abandonment, and forest expansion (Gutierrez Angonese and Grau, 2014; Nanni and Grau, 2014). Certain native herbivore species were able to persist (e.g. collared peccary, *Mazama* deer), although presumably at low densities, while others, such as the tapir, went locally extinct in large sectors of the ecoregion (Nuñez Montellano et al., 2010). No study has addressed the occurrence of native megafauna changes in these areas, but a study (Nanni, 2015) found a negative correlation between density of livestock and density of the most frequent wild herbivore, the grey-brocket deer (*M. goazoubira*) (**Figure 4b**). Daily activity patterns of the native deer at sites with high extensive livestock density showed a clear temporal segregation, reflecting either direct competition between native and domestic species, or indirect responses to human presence and associated dogs.

After cattle abandonment, vegetation changes in lower montane forests reflect slow recovery of native fauna, a resulting decrease in herbivory, and an increase in plant biomass particularly in the understory accessible to ungulates. Malizia et al. (2013) assessed tree species morpho-physiological features to identify possible drivers and found that vegetation changes were inconsistent with predictions derived from past canopy disturbance or climatic change (mainly rainfall or temperature increase). Instead, the increase in nutrient-rich soft leaved species suggested an effect of reduced herbivory (**Figure 4a**). For example, *Piper tucumanum*, a palatable understory species, experienced a two-fold increase in density over a 15-year period, becoming the dominant understory species (Malizia et al., 2013). Consistently, in an upper montane forest where livestock had been excluded, a disproportionate increase in understory species was found (Carilla and Grau, 2011). These examples suggest that livestock has not been fully replaced by native herbivores, hence providing a window of opportunity for plant biomass accumulation.

In areas where livestock decreasing density occurs over deforested patches previously used for intensive grazing, ecological changes followed a different pattern: secondary forest succession is typically dominated by plant species favored both by decreasing grazing which no longer conceal tree regrowth but whose low density remaining presence allows seed dispersal and gives advantages for some species through selective herbivory. A clear example of this is the invasion by the exotic species *Gleditzia*

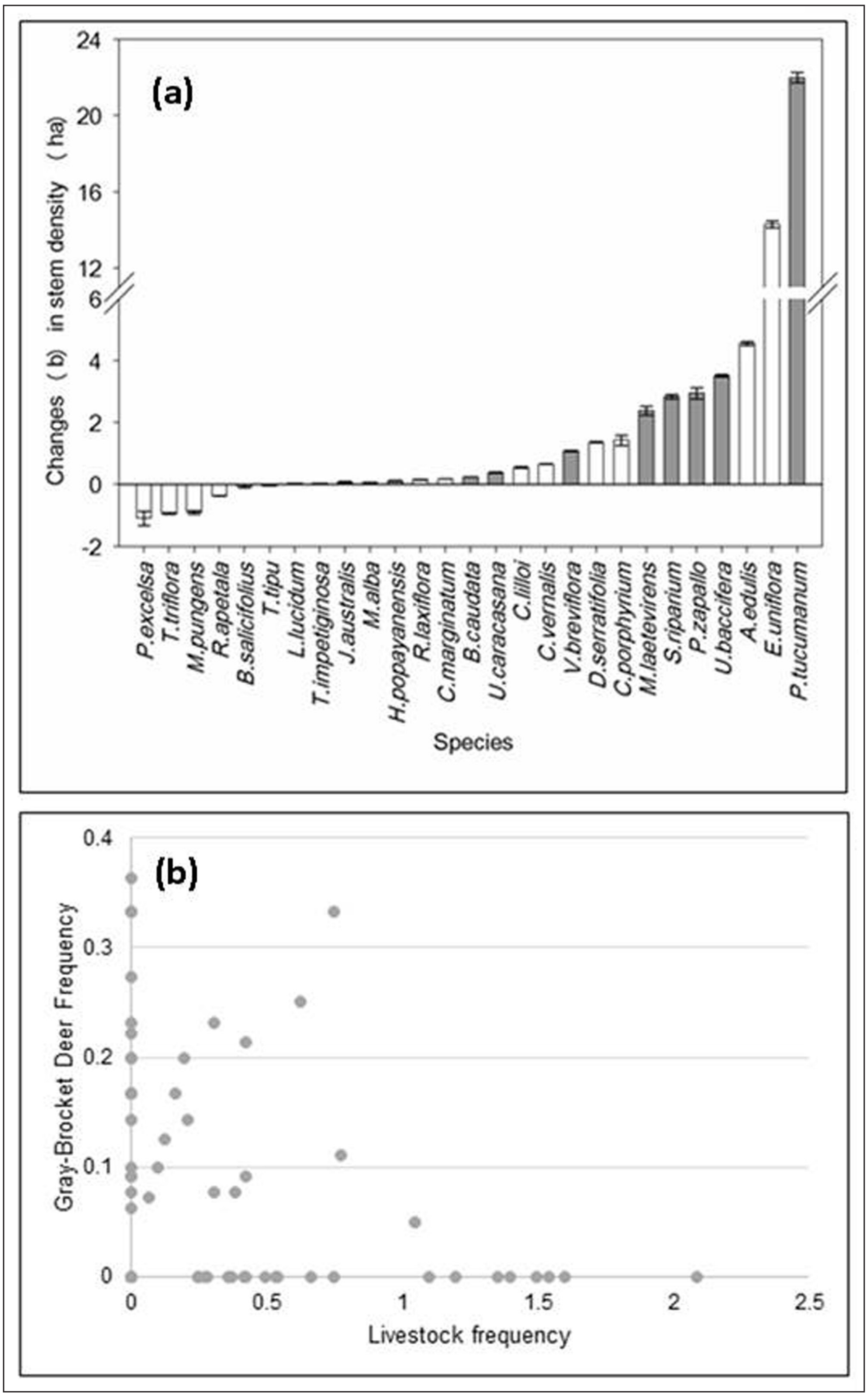

Figure 4: (a) Changes (b = slope of the regression) calculated for stem density per hectare across species in 15 years. Grey bars indicate nutrient-rich soft-leaved species. Error bars correspond to standard error (based on Malizia et al., 2013). **(b)** Scatterplot of livestock and Gray-Brocket Deer frequencies (n°records/n°days), in a subtropical area of NW Argentina. Modified from Nanni (2014). DOI: https://doi.org/10.1525/elementa.415.f4

triacanthos, a spiny non-palatable tree which is well dispersed by cattle (Fernandez et al., 2017).

In summary, wildlife recovery in ecosystems that are fragmented by agriculture, or nearby populated peri-urban settings might be substantially slower due to habitat discontinuity, persistent hunting and other anthropic pressures such as negative interactions with domestic fauna (e.g., dogs). Different native and nonnative plant species may take advantage of the window of opportunity to increase plant biomass provided by reduced herbivory pressure.

Discussion

The comparison of three pathways described here (**Figure 5**, **Table 1**) shows that megaherbivore rewilding transitions may follow different trajectories and result in different ecological responses according to (1) the availability and demographic capacity of native herbivores species to recover, (2) the potential of the ecosystem to develop frequent fires; and (3) the landscape configuration and level of habitat connectivity as a conditioner of (1) and (2); and of the interactions between humans

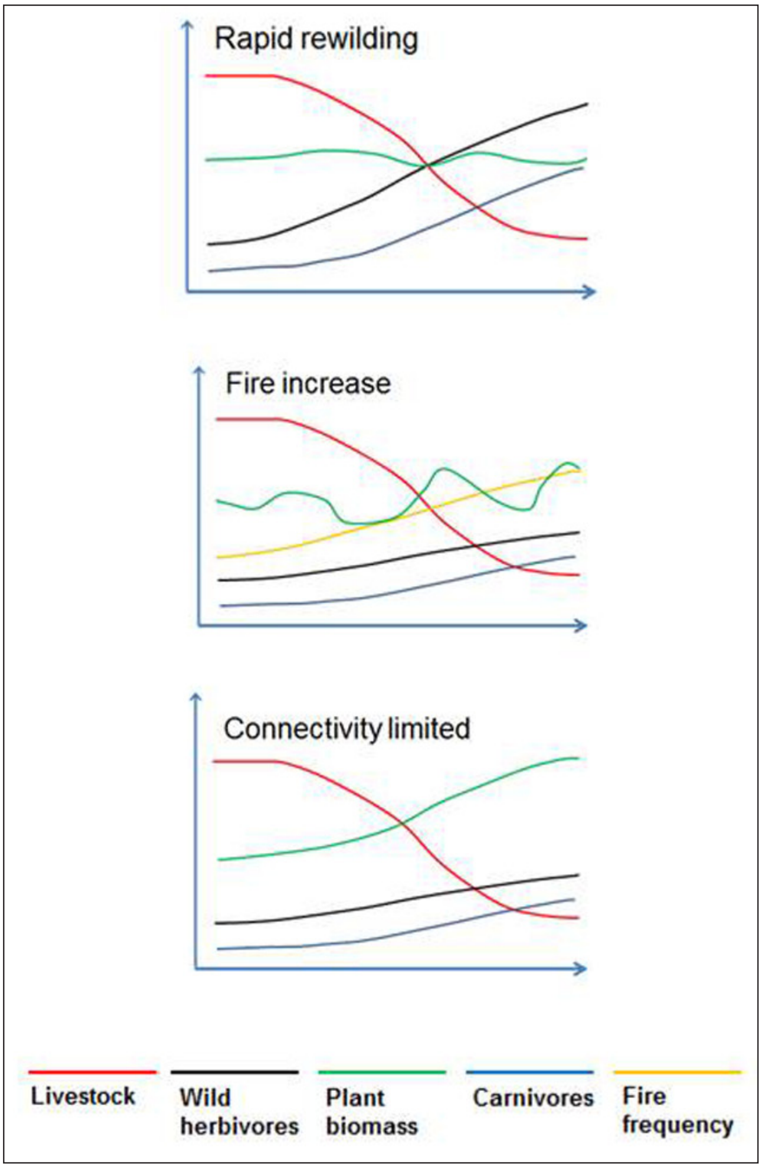

Figure 5: Pathways of Megaherbivore rewilding transitions here described. Hypothetical trajectories of livestock, native ungulates, carnivores, fire and vegetation biomass. DOI: https://doi.org/10.1525/elementa.415.f5

Table 1: Characteristics of the three pathways, their favoring conditions, ecological effects and emerging conflicts. DOI: https://doi.org/10.1525/elementa.415.t1

Pathway	Favoring condition	Ecological effects	Emerging conflicts
Rapid rewilding	High landscape connectivity Remaining wildlife populations	Native herbivore and carnivores increase.	Carnivores vs remaining pastoral communities
Fire increase	Vegetation flammability High landscape connectivity	Fire frequency increase	Fire vs non-pastoral Communities (e.g. urban and suburban)
Connectivity-limited	Fragmented landscape Locally extinct wildlife High human population density	Plant biomass increase	Native herbivores vs agriculture Wildlife vs urban and agriculture population

and wildlife, including different potential conflicts and opportunities.

The "rapid rewilding" pathway occurs when populations of native herbivores are available, rural human population is comparatively low, allowing the persistence of wildlife in less accessible places, and habitat continuity allows the recovery of remaining wildlife populations. This pattern facilitates "passive rewilding" (Gillson et al., 2011), and has been observed in the western USA (Lorimer et al., 2015), the former Soviet Union (Sieber et al., 2015), and Patagonia (Baldi et al., 2010), where native ungulates and carnivores have expanded as livestock has receded over extensive rangelands. Laws prohibiting hunting, even with moderate or low levels of enforcement as in the Puna appear to suffice to allow the native herbivore recovery under these conditions. In this case, effects on vegetation appear to be comparatively smaller, and predator recovery might follow restoring trophic cascades, as livestock predation may imply an additional cost for already underperforming pastoral economies (Loveridge et al., 2010). This pathway appears highly promising for biodiversity conservation, as it provides good conditions for the recovery of herbivores and predators alike at a relatively low cost. However, predator recovery may lag behind herbivore recovery, potentially resulting in overgrazing and, as our examples show, at least in the relatively short time this pathway does not necessarily lead to improvements of functioning factors or ecosystem services such as plant productivity or soil erosion.

The "fire increase" pathway is likely found in other grasslands and savannas of the world (Johnson et al., 2018), and appears as the least predictable, and probably more fluctuating in terms of plant biomass. Its unpredictability is further enhanced by the fact that, in addition to land use, fire is strongly associated to climate variability (Grau and Veblen, 2000; Aráoz and Grau, 2010). Although studies analyzing the interactions between fire occurrence and grazing are scarce (Bond, 2010), it has been observed that fire occurrence may reshape spatial grazing patterns (Archibald et al., 2005), and generate landscapes with alternative states resulting from the interactions between grazing/fuel/vegetation composition. While this dynamics can be directed to rewilding vegetation – herbivore interactions (Fuhlendorf et al., 2009), in our case study, the gradual livestock disintensification favored more frequent fires that appear to prevent the fast recovery of native herbivore populations.

Fire maintenance can regenerate favorable habitats for native herbivores and carnivores when hunting is low and livestock ranching is abandoned (as is typical of developed economies with no subsides for marginal agriculture). Instead in marginal areas of middle or low income countries (as in our example in subtropical Argentina) fire may allow the persistence of very extensive livestock management, where a rural marginal population continues using fire as a management tool to deal with labor scarcity. Increases in fire frequency and intensity might lead to important conflicts with human settlements, infrastructure and productive systems. The reintroduction of native herbivores, which consume aboveground biomass, could take the system back to previous equilibrium states of moderate intensity and intermediate frequency fire events (Johnson et al., 2018). However, and despite the apparent existence of adjacent populations of native herbivores, this does not occur in our example, likely because such native herbivore population density in these areas is low, or because conflicts between livestock and wildlife persist, generating a stable dynamic state of frequent fires, low livestock and delayed occurrence of megaherbivore rewilding. Fire prescription appears as a potential management tool to move the system towards an alternative state. However, to implement fire prescription certain conditions are necessary such as advance knowledge of the local fire ecology (i.e., fuel behavior and productivity, weather-fire relationships) and resources to conduct sophisticated management practices (e.g., Reinhardt et al., 1989; Block and Conner, 2016). Unfortunately, this is far from reached in the current social-ecological conditions of the Andes.

The "connectivity limited" rewilding pattern occurs when landscape fragmentation is high, and previous defaunation has led to local extinctions of native megafauna; a typical pattern in regions of relatively high agriculture development, and high human population density. While in the "fire increase" pathway one major ecological effect is the emergence of a new form of vegetation consumption (i.e., by an abiotic factor, fire), here a major outcome would be the increase in biomass, due to lack of herbivores and lack of fire (either limited by landscape fragmentation or nonflammable vegetation). This typology might be relatively common in areas of land abandonment within a matrix of urban or intensive agriculture (e.g., Brazilian Atlantic forests, densely populated areas of the Andes, rapidly developing areas of southeast Asia); and areas of suburban expansion associated to high intensity of recreational activities (e.g., Alps, Pirineans, Rocky mountains, Appalachia). Slow herbivory recovery, as reported here, may also result in different plant species taking advantage of a window of opportunity, thus leading to major changes in vegetation composition (Derham et al., 2018). Additionally, high human density may result in new types of conflicts involving wildlife (e.g., disease transmission or direct conflicts between wild and domestic carnivores). For example, fear of attacks by large carnivores in peri urban areas is frequent in North America (Timm et al., 2004) where urban and suburban expansion occurred decades ago, as socio economic changes favored urbanization land uses over livestock production. Emerging interactions, however, may include positive ones as wildlife adapts or even benefits from such new contexts (De Stefano and De Graaf, 2003). Despite potential conflicts, however, a sound strategy to allow rewilding overcoming connectivity limitations would be reintroduction (Castellanos and Gómez, 2015; Zamboni et al., 2017).

The wide environmental gradient analyzed in this article suggests there are key variables affecting the potential for megaherbivore rewilding, even when livestock abandonment occurs: habitat continuity, habitat productivity, and human population density. The relevance of habitat continuity is made clear by comparing the rapid rewilding in the Puna with the connectivity limited (hence slower rewilding) pathway in the Yungas. Low productivity of the Puna implies that agriculture cannot develop, and therefore habitat connectivity remains high; however, moderate plant productivity allows the use of fire as an extensive management tool, limiting rewilding in the grassland/forest ecotone. While these two systems are characterized by low human population density in the case of the Yungas, high population density favors habitat fragmentation, discourages fire, and might lead to the emergence of novel interactions and conflicts between humans and wildlife.

The different examples show how feedbacks and "tipping points" (Milkoreit et al., 2018) in the social-ecological systems may affect the trajectories of the different pathways. The rapid rewilding pathway might be reinforced by both increasing carnivore recovery that discourage marginal livestock, and by the growing value of native wildlife for tourism, which provides alternative economic activities (Izquierdo et al., 2018). The fire increase pathway suggests that current management activities may limit native wildlife recovery due to a positive feedback between growing fuel availability and decreasing livestock, but this may rapidly change when native herbivores recover to a level which limits fuel availability (e.g. Hempson et al., 2017). The existence of increased plant biomass due to reduced herbivory in the connectivity-limited pathway may imply a large potential for of native herbivore rapid expansion if connectivity limitations are overcome (e.g., by means of reintroduction) and if other emerging uses (e.g., recreational) reinforce the valuation of native fauna by the society (Murray, 2017).

Conclusions

Decreasing livestock intensity offers opportunities for transitions towards native herbivore megafauna rewilding and for increasing provision of ecosystem services (e.g., by reducing emissions and soil/vegetation degradation; Erb et al., 2016; Swaine et al., 2018). The processes that drive these transitions are still poorly understood, but they will probably be more widespread in the future, particularly in areas unsuitable for cropland and pasture intensification, such as the mountainous regions in our study cases. Nonetheless, ways of achieving these environmental benefits are hard to define (Svenning et al., 2016): the different pathways depicted here imply that dramatically different ecological outcomes might follow according to biophysical, social-ecological and landscape contexts: rapid rewilding is more likely to occur when native herbivore populations have persisted in well-connected habitats; but such rewilding may not necessarily result in increases in biodiversity or environmental services (Omeja et al., 2014); in fire-prone ecosystems, livestock reduction might result in increased fire frequency, with less predictable results, including maintenance of low-density livestock management whose compatibility with rewilding is unclear; in less connected habitats due to intensive agriculture or urbanization, recovery of native herbivores might be slower, likely resulting in major vegetation changes associated to gains in biomass. To understand and direct these transitions towards positive ecological outcomes, key factors to be addressed are the decision processes driving livestock decreasing intensity and the novel conflicts between and synergistic interactions between humans, livestock and wildlife (**Table 1**).

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The authors have no competing interests to declare.

Author contributions

- Contributed to conception and design: HRG
- Contributed to acquisition of data: HRG, EA, CJN; ASN, AM
- Contributed to analysis and interpretation of data: HRG, EA, CJN; ASN, AM
- Drafted and/or revised the article: HRG, EA, CJN; ASN, AM
- Approved the submitted version for publication: HRG, EA, CJN; ASN, AM

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