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Rewilding-inspired transhumance for the restoration of semiarid silvopastoral systems in Chile

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Abstract Nomadic pastoralism and transhumance are ancient human adaptations to the movements of large herbivores, which themselves migrate to follow favorable environmental conditions. Free-ranging livestock production has been criticized as less water efficient than factory farming and crop production. This fails to take into account both the additional ecosystem services made possible by rainfall over rangelands, and the ability of free-ranging animals to track water availability across environmental gradients. By analogy to transhumance, we propose a model of "transhumant rewilding," or species reintroduction with managed herding of wild ungulates for the ecological restoration and sustainability of food production in (silvo)pastoral systems. We consider preliminary evidence for the feasibility of this model with a case study from central Chile in which guanacos (*Lama guanicoe*) could be used to help restore a silvopastoral savanna ("espinal") via browsing and endozoochory. First, we present preliminary data on guanaco foraging in espinal. Second, we use a GIS analysis to identify least-cost paths between areas of high and low espinal condition in central Chile and assess the feasibility of using them as migratory pathways. Finally, we consider the relative ecosystem service advantages and costs of the transhumant rewilding scenario compared to other restoration and agricultural development scenarios for central Chile. We conclude that transhumant rewilding has the potential to be a useful model for rewilding-inspired land management in cultural landscapes and can contribute to food security and sustainable agricultural production.

Keywords Rewilding · Transhumance · *Lama guanicoe* · Ecosystem services · Food security · Silvopastoral

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Introduction

Traditional pastoralist systems, especially in drylands, are adapted to geographic and temporal variation in rainfall, and thus availability of resources. Nomadism and seasonal transhumance allow livestock to track environmental variability (FAO 2001; Kratli et al. 2013). Traditional pastoralist systems thus represent a solution to sustainable, extensive, biodiversity-friendly food production under variable, especially arid and drought-risk, conditions (FAO 2001). Pastoralism and various forms of extensive rangeland livestock production are gaining traction in some areas, e.g., novel silvopastoral systems funded by payment for ecosystem service (PES) schemes (Giraldo et al. 2011; Montagnini and Finney 2011), while losing ground elsewhere due to criticisms of inefficiency and poor

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management, particularly in drylands and rangelands (FAO 2001; Mekonnen and Hoekstra 2012). Here, we examine pastoral systems as a potential component in sustainable and biodiversity-friendly food production systems of the future (Oteros-Rozas et al. 2013).

Pastoralism encompasses a range of strategies, both over historical time and over space (FAO, 2001). Pastoralism broadly evolved from hunting large herbivore species as they track the environment on their own, to managing the take of these species, to domesticating them into a nomadic or transhumance system (Alvard and Kuznar 2001; Manzano Baena and Casas 2010; Bar-Oz et al. 2011; Niven et al. 2012), but arguably the greatest difference in the human–herbivore–environment relationship emerges with sedentarization of pastoralists. Sedentarization is often related to attempts to govern human populations rather than environmental imperatives, and often has negative effects on the socioecological system (Sayre et al. 2013). Transhumant and nomadic pastoralists often play an important role in the exchange of edible species, goods, and social relations within large and environmentally challenging regions (Scheele 2010; Manzano Baena and Casas 2010). If livestock cannot move significant distances, their raising becomes decoupled from environmental variability (not only climatic, but also related to any stochastic ecological processes). Livestock are thus both more exposed to local resource limitations and more coupled to external production systems that must be accessed to buffer local climatic variability (FAO 2001; Pedersen and Benjaminsen 2008; Kratli et al. 2013). Consequently, we must consider the design of an effective (silvo)pastoral system in the context of the challenges imposed by sedentary production, which decouples management from the local environment (Kratli et al. 2013). One kind of solution has been to disconnect livestock raising inputs from the local environment through intensive factory farming. Reacting against factory farming, traditional extensive pastoralism is now trying to make a case for its sustainability in terms of ecosystem service values (Hoffman and Boerma 2014; FAO 2001). Further along the continuum of human–large herbivore relations, is there another kind of solution in which pastoralism can move even more toward "wild" systems?

Rewilding is an emerging trend in conservation, primarily in developed countries (Svenning et al. 2016; Jepson 2016). Rewilding has been described, *inter alia*, as the reintroduction of one or more usually large animal species acting as a keystone species, ecosystem engineer or top–down trophic influence, to restore natural ecosystem functioning, resulting in ecological restoration usually via subsequent passive management, and potentially changing human relationships to the landscape (Sandom et al. 2012; Lorimer and Driessen 2014; Lindon and Root-Bernstein 2015; Svenning et al. 2016). One strand of rewilding

focuses on the use of large herbivores to transform habitats through herbivory (Olff et al. 1999; Vera 2000). This approach has roots in managed grazing to maintain certain types of grasslands and cultural landscapes (Gordon et al. 2004; Rook et al. 2004; Papanastasis 2009). Another important function is seed dispersal (Poschlod and Bonn 1998). Although the ecological principles are one and the same (Asner et al. 2004), rewilding is considered to be radically different from managed grazing due to its focus on the spontaneous activities of wild animals and, linked to this, by being process-oriented rather than end-state oriented (Hughes et al. 2011, 2012).

Proponents of rewilding often explicitly wish to create or preserve areas of "wilderness." Wilderness is a subjective cultural category (Cronon 1996) and herein lies the effect on human relationships to the environment. Rewilding as currently practiced takes advantage of the poor economy and rural land abandonment to create something that, in EU policy terms at least, is new (Navarro and Pereira 2012; Lorimer and Driessen 2014; Jepson 2016). There are, however, other possible models of rewilding that draw much less on classical European and North American visions of wilderness while addressing different challenges and policy gaps. Here, we focus on rewilding-inspired approaches to conservation and management of dryland silvopastoral systems.

Rewilding, (silvo)pastoralism, and food security

Food security refers to access to sufficient, safe, and nutritious food meeting dietary needs and food preferences (Declaration of the World Summit on Food Security, FAO 1996). A number of factors can threaten food security throughout the food chain, from crop failure, through to post-retailing waste (Eriksen et al. 2009; Parfitt et al. 2010; Ingram 2011). One aspect of maintaining food security involves diversifying food production and buffering it against environmental variability (Vermeulen et al. 2012). This can be particularly important in drylands with a history of soil degradation and variable rainfall (Budds 2004; Solh and van Ginkel 2014).

The production of animal products is less water and energy efficient than the production of nutritionally equivalent plant products, due to the inefficient conversion of plant material fed to animals (Pimentel et al. 1997; Capone et al. 2013; Mekonnen and Hoekstra 2012). Grazing systems are also many times less efficient in converting water to food than are industrial livestock production systems (Mekonnen and Hoekstra 2012; Gerbens-Leenes et al. 2013). A larger amount of rainwater goes into producing less-digestible forage and non-forage plants over wide areas in pastoral habitats, compared to the relatively small amount of rainwater used to produce nutritious feed

crops fed to fast-growing livestock in industrial systems (Mekonnen and Hoekstra 2012). According to these analyses, if the water footprint were the only variable in consideration, and assuming that food distribution problems were resolved, then global food production should shift away from animal production and toward industrially farmed plant products including vegetables and cereals in suitable environments (Vanham et al. 2013; Smith 2013; Stehfest et al. 2009), or at least switch to more efficient fodder crops (Bosire et al. 2015). These analyses are not without critique. Other approaches have claimed that low-input pastured cattle in non-irrigated systems have a water footprint similar to cereal crops (Ridoutt et al. 2012). Scholz et al. (2013) argue convincingly that water that soaks into the soil from rainfall in drylands has no other possible use than extensive grazing; the assumption underlying the analyses cited above, that it could be diverted to growing crops, is incorrect. Scholz et al. (2013) further argue that achieving increases in efficiency in extensive dryland pasture systems is feasible and makes this an attractive option for increasing food security in drylands.

An additional critique comes from a multifunctional perspective on extensive dryland livestock pasturing. Food security also considers access to traditional diets (including meat), provision of ecosystem services, and sustainability of the agricultural socioecological system (Vermeulen et al. 2012; Eriksen et al. 2009). Livestock production in semiarid rangelands can be compatible with wildlife conservation and associated ecosystem services (Tilman et al. 2002; Tscharntke et al. 2012; Bosire et al. 2015). If we take into account the contribution of rainwater over extensive (silvo)pastoral habitats to the production of provisioning, regulating, and cultural services, then extensive grazing systems have a much higher and more diverse "yield" than intensive farming (Hoffman and Boerma 2014).

Rewilding-inspired management approaches—i.e., with a focus on wild animals as the herded animals—can be applied to many aspects of silvopastoral systems, in particular those that respond to abiotic and biotic variability. Provocatively, we suggest that this might include restoring the human cultural practices or processes of coping with environmental variability that take the form of current and past (silvo)pastoral systems. We identify several elements of silvopastoral systems that could be rewilded to provide added adaptive dynamism and resilience, see Table 1.

Case study: restoration of the espinal with guanacos in central Chile

Central Chile is a semiarid region with a Mediterranean climate and high rainfall variability due to ENSO (van Leeuwen et al. 2013). Little is known about potential pastoralist practices of the now extinct indigenous people of central Chile, the Picunche. They had a domestic camelid called the chilihueque, which went extinct around the 1600s (Miller 1980). Like nomadic indigenous groups across the Andes, the Picunche might also have hunted or herded territorial or migratory guanacos (*Lama guanicoe*) (Medina and Rivero 2007). Guanacos were originally

Table 1 Elements of silvopastoralism that could be rewilded

Element	Potential rewilding example
Movement of large herbivores over the landscape	Keep some or all animals in a semi-wild state and allow to track environmental variability across large landscapes
Forage provision	Grazing and browsing with little supplementation from agriculture. Subject to natural rainfall and growing season patterns. Can include unpalatable as well as palatable plants, which can improve digestion and weight gain
Species identity and function	Non-domestic, semi-domestic or "dedomesticated" species and breeds that have needed ecological restoration functions as well as marketable products, e.g., camelids (wool), reindeer (fur). Mixed herds of compatible grazers and browsers, including guard animals such as llamas and donkeys
Tree and shrub cover mosaics	Allow to evolve through herbivory and disturbance. Overstocking should be regulated to prevent degradation where this is a potential outcome, but below the degradation threshold, temporal variation in cover should be expected
Habitat for biodiversity	Allow to evolve through herbivory and disturbance. Ground-nesting birds that are sensitive to trampling may decrease, as should rodents, but other species will move into newly created habitats
Human cultural adaptations to variability	Shepherding, transhumance. Foraging of, e.g., mushrooms, herbs, fruits, honey, game, reeds. Artesanal/ "paleotechnics" production from wild, semi-wild, and domestic herbivores, such as wool, fur, skins, milk, cheese, meat, horn, bone. Management that is responsive to (socio)environmental change via LEK and social learning, e.g., taking advantage of modern participative and adaptive management approaches and technologies

Rewilding is here used in the sense of allowing natural ecosystem processes to take effect through passive management of the system, allowing system components to react to environmental variability rather than meeting set targets, and allowing humans to also participate in carrying out ecosystem processes and to adapt their behavior flexibly along with other components of the system

native to a large part of the southern cone of South America (Baldi et al. 2008), including central Chile, until about 500 years ago when they were extirpated from this region by Spanish colonists (Miller 1980). Guanacos are generalists that can live in grasslands, savannas, woodlands, and forest (González et al. 2006). Guanacos are hypothesized to have brought *Acacia caven*, the dominant tree in modern central Chilean silvopastoral savannas ("espinal"), from the Argentinian chaco via endozoochory, between 10,000 and 2000 years ago (Ovalle et al. 1990). Despite this potentially late arrival date, this does not mean that savanna must also be relatively novel, as *A. caven* is proposed, on inductive grounds, to have replaced *Prosopis chilensis*, another Fabaceae, relatively recently in a savanna or open woodland habitat (Fuentes et al. 1989).

Historical trends in espinal conditions are largely unknown, but it appears that degradation pressures such as harvesting *A. caven* for firewood and charcoal production may have diminished somewhat since the 1990s (M. Root-Bernstein, pers. obs.). Despite estimates that *A. caven* espinal covers up to 2 million ha (Peri et al. 2016), espinal, as a silvopastoral system, or as an *Acacia*-dominated savanna, is not an official land cover type considered in maps created by the Chilean Forestry Service (in charge of conservation), and consequently data on its dynamics are incomplete. A recent pair of book chapters giving an overview of both traditional and novel silvopastoral systems in Chile spend exactly three sentences on espinal silvopastoralism, with more attention given to systems based on non-native plantation trees (Dube et al. 2016; Rojas et al. 2016). We believe that the espinal should be conserved because there is no evidence that it is an "unnatural" degradation (Root-Bernstein and Jaksic 2013). Rather, it appears to be part of the successional network linking matorral (scrub) habitat and sclerophyllous forest, and thus should be protected along with these other habitat types to ensure area for future forest regeneration and successional dynamics (Root-Bernstein and Jaksic 2015). All of these habitats, including espinal, are home to many central Chilean endemic plants and other species, and together they represent the only Mediterranean-climate habitats of South America (Simonetti 1999; Myers et al. 2000). We also believe (and examine, in this paper) that it is broadly preferable to the other land cover types into which it is most likely to be converted without conservation measures.

As in other drylands, water security is an important issue in central Chile (Budds 2004). As in other silvopastoral systems, a key factor in reducing water use and improving meat yield in espinal savanna is provision of shade (Olivares 2006; Ovalle et al. 2006; Campos Paciullo et al. 2011). Shade cover in espinals increases as *A. caven* canopies increase with tree age, and growth can be stimulated via pruning as a management intervention (Vita et al. 1995; Navarro Gutiérrez 1995). Specifically, like other acacias, *A. caven* shows compensatory growth, whereby pruning, simulating browsing, causes increased regrowth (Gadd et al. 2001; Fornara and du Toit 2007; Dangerfield and Modukanele 1996; Gowda 1997). Compensatory growth after pruning suggests that *A. caven* is adapted to browsing by missing herbivores (compare Bond et al. 2004; Doughty et al. 2016).

We hypothesize the guanaco (*L. guanicoe*) is likely to be one of the missing browsing herbivores to which *A. caven* is adapted, and the only one that is not extinct. Domestic species common in espinal (cattle, horses) are grazers, not browsers. After the Early Holocene megafaunal extinctions, guanacos spread and increased in abundance throughout South America (González et al. 2006). In addition to showing adaptations to browsing, *A. caven* seeds germinate at a higher rate after large herbivore endozoochory (Gutiérrez and Armesto 1981). Although there are reports of guanacos browsing on trees or shrubs when available during winter (Puig et al. 1996, 1997; Cavieres and Fajardo 2005; González et al. 2006), we have encountered uncertainty about guanacos as potential *A. caven* browsers under non-starvation conditions. One of our goals is thus to test whether guanacos voluntarily browse these spiny trees. We predict that guanacos can stimulate growth and help seed germination of *A. caven* in degraded espinals. We are currently running a multiyear experiment, called Proyecto REGenera (Restoration of Espinal with Guanacos) at the private nature reserve Altos de Cantillana in central Chile to test these predictions about browsing, growth, and germination. Proyecto REGenera, which uses penned guanacos, is a first approach to assess the feasibility of transhumance between espinals. Preliminary results are encouraging and allow us to address the challenges of extrapolating from the penning study to transhumance, including issues such as spatial scaling, temporal periodicity of browsing, and in a final step, social feasibility.

Here, we test the feasibility of a model for restoration in which shepherds herd guanacos across the landscape, along a network of suitable movement corridors in and out of fenced espinals, in a seasonal and cyclical manner in order to target areas that can be restored by guanaco browsing. To substantiate the feasibility of this model inspired by both transhumance and rewilding, we first present preliminary data from Proyecto REGenera, focusing on guanaco foraging behavior. Secondly, we use GIS analysis to ask whether guanacos could be used to deliver pulses of restoration browsing in the most degraded espinals (probably in winter), with shepherded movement along suitable corridors to more-productive espinals during the rest of the year (probably summer), following the logic of

either the seasonal movements of the wild guanacos, or the transhumance potentially practiced by the Picunche people with herded guanacos (hereafter "transhumant rewilding"). We see such a system as more feasible than re-establishing fully wild, freely migrating guanacos in central Chile due to the high density of fences, roads, and agricultural land, and feral dog packs. The likelihood of human–wildlife conflict and high guanaco mortality makes this scenario likely suboptimal, and we do not consider it further here. Guanacos will have to be owned (providing a monetary and regulatory stake in their welfare) and shepherded by shepherds for protection, along suitable corridors linking enclosed espinal habitats across the landscape. We assume that restoration of espinal by rewilding is a multidecade process and that transhumant rewilding will be cyclical. To address the feasibility of transhumant rewilding, we ask whether high- and low-quality espinals are near each other, compatible with a set of small-scale community-based networks of corridors linking high- and low-quality sites, or whether high- and low-quality espinals are dispersed at a regional scale, more compatible with a regionally organized, long-distance transhumant rewilding network. The least-cost paths forming the links in the networks we identify with this GIS analysis correspond to suitable movement corridors along which guanacos can be herded by shepherds between espinals. We also examine whether the networks show variation in length, connectivity, and position under fluctuations in climate associated with ENSO. Finally, we consider the potential ecosystem service benefits from guanaco restoration of the espinal silvopastoral system. We ask what the key benefits and costs are under four different scenarios of land-use change. Under the status quo, espinals are not restored and economic incentives continue to favor gradual conversion of espinal and other habitats to high-investment, high-yield fruit and wine production for export (Armesto et al. 2009; Schulz et al. 2010). We compare this to a scenario in which all espinal has already been rapidly converted either to factory farms or fruit and wine production, and a third scenario in which all espinal has been converted either to factory farms or protected sclerophyllous forest. Our fourth scenario is restoration of espinal with guanacos. Although we lack sufficient data to monetize or otherwise value these services and costs, we highlight key services and costs that distinguish between the cases.

Methods

Site and animals

The experimental site is a fenced 0.5 ha area of espinal at the entrance to the private reserve Altos de Cantillana

(Fig. 1). The size of the site was dictated by the availability and feasibility of fencing the site. A fence surrounded by an electrical circuit was necessary not only to keep the guanacos inside the site, but also to keep out feral dogs. The guanacos used in the experiment are five castrated adult males from the breeding facility of Fauna Australis, a research group of the Pontifical Catholic University of Chile. Approval for the conditions of the experiment was obtained from, and the ongoing welfare of the guanacos is monitored by, SAG (Agriculture and Livestock Service) and the veterinarians on our research team.

Experimental conditions and procedure

The site is divided into four sections of 0.125 ha each. In winter and spring (the wet season), the guanacos spend between 4 and 2 weeks in each section (the shorter time interval prevents over-grazing in late spring as aridity increases) and are rotated from one section to the next clockwise (the "pulse" treatment). In summer and fall (December–May), they are allowed to move freely throughout the enclosure, in order to reduce the intensity of grazing on the herbaceous understory. Although Oba et al. (2000) report that *Indigofera spinosa* shows the largest compensation effect when pruned in the dry season, we decided to implement the browsing pulse in the wet season due to the reverse phenology of *A. caven* compared to other deciduous plants in Chile (it has leaves during the dry season), which may also reverse its growth response relative to the season. In other words, we follow Oba et al. (2000) in implementing more-intense browsing when the trees have no leaves, in the expectation that this will stimulate increased growth during their next growth season. Cromsigt and Kuijper (2011) also report that early-growth-season pulses of herbivory are associated with trees adapted to herbivory. Whether or not the rotational plan replicates the natural migratory patterns of guanaco in central Chile is unknown as we are not aware of any historical data on their migration in that area. Guanacos may have avoided colder temperatures at higher altitude or further south by moving into the central valley of central Chile in winter (the rainy season), where they could have eaten the fresh herbaceous substrate and leafless *A. caven*. However, they may also have eaten *A. caven* leaves and shoots in early summer, before moving south or to higher elevations. Our rotational plan is based on the expectation that winter herbivory will give the largest compensatory growth response. The rotational phase of the experiment also allows us to track the temporal lag of growth following known periods of herbivory. These data will help us to assess how long guanacos should remain on a site to induce growth but not damage the trees.
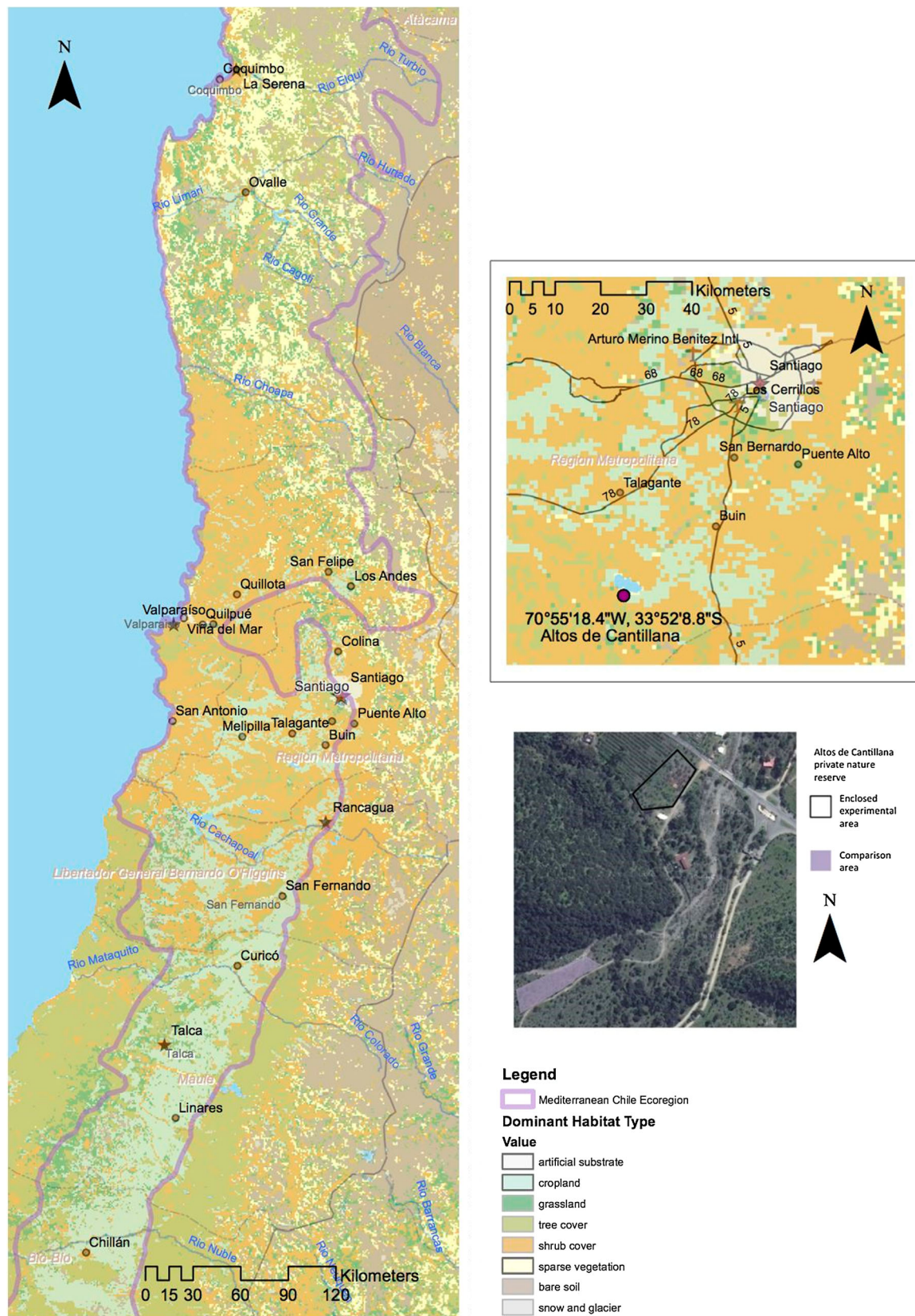
Fig. 1 Location of the experimental site for Proyecto REGenera

The rotational plan is not transhumance. However, it is intended to provide basic data on the guanaco–*A. caven* interaction, including information on the conditions under which guanaco browse *A. caven*, which parts of the tree are browsed, the size of the growth response of *A. caven* to guanaco browsing, and the effects of season and browsing intensity on that response, that could be applied to designing a transhumant rewilding system.

Characteristics of each experimental sector and the comparison site are shown in the Supplementary Data.

The guanacos were introduced to Section A on June 18, 2014. During the first month, we monitored their behavior in order to determine an appropriate supplementary feeding amount. We currently lack the necessary data to calculate the appropriate stocking rate for guanacos in espinal; these data will be obtained over the course of the experiment. The time required for the espinal to recover from intensive herbivory is also unknown, so, given the restricted space available for the experiment, attenuating the herbivory pressure with supplementary alfalfa is necessary. The amount of supplementary alfalfa is adjusted according to monitoring of the guanacos' body conditions.

To determine how guanacos forage and behave in *A. caven* savanna habitat, we record behaviors using a focal animal method. Each animal was observed by a single individual for four sessions of 10 min at a time, in a random order, over a period of 4 h during the day, 3 days per week. Here, we report on observations in September, October, and November of 2014. Behaviors were recorded in JWatcher.

In addition, we downloaded photographs from two camera traps that were originally set up to monitor the site rather than guanaco behavior *per se*, but which captured many images of the guanacos. These were in sections A (October 2014, January, and April 2015), and B (November 2014) of the enclosure.

GIS analysis

There is no regional map of espinal land cover, so we obtained a map of *A. caven* distribution derived from official land cover maps produced for Chile by CONAF, the Chilean Forestry Service (M. Bennett, unpublished data). The vast majority of the obtained areas with *A. caven* were classed as matoral which is defined as having <10 % tree cover and 10–75 % shrub cover, or as "matoral arborescente" or "tree matoral" which is defined as having between 10 and 25 % tree cover. While we do not focus on the contribution or role of shrubs in espinal in this paper, they are associated with increased ecosystem processes in espinal and thus contribute positively to espinal condition (Root-Bernstein and Jaksic 2015). We mapped an approximation of espinal condition using a multicriteria

analysis. We combined available measures of NDVI from AVHRR (http://noaasis.noaa.gov/NOAASIS/ml/avhrr.html), and NPP and evapotranspiration (ET) from MODIS. NDVI was split between summer (October–March) and winter (April–September). Due to the reverse phenology of *A. caven*, summer NDVI is dominated by the contribution of *A. caven* in espinal, while winter NDVI is dominated by the contribution of the understory in espinal (Gerstmann et al. 2010). This allows us to split the two vegetation components. Our measure of NPP and ET was available at 1 km resolution, while the NDVI data were only available at 8 km resolution. We therefore took the mean of NPP and ET data at 8 km resolution. The ET represents a combination of soil and plant evapotranspiration. We combined these factors to produce an equally weighted index from 0 to 4, with 4 being an espinal with the relatively highest carbon production, photosynthetic activity in both the tree and understory layers, and movement of water into the atmosphere from both the soil and vegetation. These represent interrelated factors that espinal restoration aims to increase: tree growth, shade provision, forage provision, and soil moisture. We refer to this index as "espinal condition." We do not explicitly consider biodiversity values in this index, as there are no available data, but we assume that biodiversity also benefits from less degraded and desertified conditions and greater shade, plant biomass, and available water (M. Root-Bernstein pers. obs.). Thus, 4 represents the best available espinal condition in a given year, and 0 the worst. We calculated the lowest cost paths from areas of high espinal condition (top two standard deviations) to lowest (bottom two standard deviations) and from lowest to highest (to ensure complete connectivity), to create a regional transhumance or transhumant rewilding network avoiding high elevation, urban areas, and roads. Lowest cost paths are representations of suitable movement corridors across the landscape, linking the identified espinal areas. We had complete data only between 1999 and 2006, and we focused on ENSO years, comparing El Niño (wet) years to La Niña (dry) years within this time period to assess the variability in paths across wet and dry years.

Ecosystem services

For each scenario (factory farms and orchards/vineyards; factory farms and sclerophyllous forests; Status quo; Restored espinals with guanacos), we followed and adapted the table of services in de Groot et al. (2010) to list the services provided via water input (rain, groundwater) in the landscape elements in question. We indicated those that are expected to increase relative to the status quo, and identified major costs and losses associated with establishing and maintaining the scenario. We further identified services that we expect to vary with or be independent of water

input (e.g., dry and wet ENSO years), since water efficiency has been proposed as a key variable in evaluating livestock production models.

Results

Preliminary experimental results

Guanaco behavior

We observed the guanacos eating herbs, leaves of *A. caven*, and branches of *A. caven*. The guanacos were observed eating branches with small thorns (approximately 1 cm in length) as well as those without. Leaves first emerged on *A. caven* in October; regrowth after browsing was observed in this period (Fig. 2). During the spring months of September, October, and November 2014, the guanacos spent between 1.2 and 10.6 % of observed time browsing on *A. caven* branches, and between 39.2 and 62.7 % of their total observed time foraging, including browsing (Supplementary Data Table 2). The proportion of *A. caven* in each sector of the enclosure is between 90 and 100 %, and guanacos were not observed to browse on other tree species present. The amount of time spent browsing on *A. caven* branches and leaves was not correlated with the total amount of time eating (branches, $r = 0.72$, $p = 0.17$; leaves, $r = -0.01$, $p = 0.05$, Pearson correlation). Based on the amount of time eating, the two most dominant guanacos (8 and 9902) preferred alfalfa > herbs > leaves > branches, while the two more subordinate guanacos preferred herbs > alfalfa > leaves > branches (Supplementary Data Table 2). Guanaco 9910, which was socially excluded by other guanacos, preferred alfalfa > herbs > branches and was not observed eating leaves (Supplementary Data Table 2). There was no relationship between

Fig. 2 Regrowth of an *A. caven* branch that had been eaten by a guanaco, observed October 2014. Photograph © Matías Guerrero

eating alfalfa and browsing on branches, such that increased time eating the favored food, comparing across guanacos, did not lead to a reduction in foraging on branches ($r = 0.66$, $p = 0.22$, Pearson correlation). Since the alfalfa was fed to the guanacos in bales, dominant individuals could exclude subordinates from eating it by defending access to it. Alfalfa and herbs have lower handling costs and times than *A. caven* leaves and branches; alfalfa was sometimes eaten lying down.

From the camera traps, we obtained 52 trap-days with images of guanaco. The data from 2014 correspond to pulse treatments, where all guanacos were in one section, so that the number of captured images was higher. We were able to observe the hours of greatest activity (hours with greatest percent photographs per day), group behavior, and foraging behavior (see Table 3, Supplementary Data). There were several peaks of activity during the morning, afternoon, and night. During the end of October–November 2014, the guanacos were photographically captured in a group, rather than alone, 59.6 % of the time (sections A and B combined), which fell to 32.2 % of the time in January (section A) and 5.8 % of the time in April (section A). At the end of October–November, grazing was observed 9/10 days with data in section A and 9/9 days in section B, while browsing was observed 7/10 days in A and 7/9 days in B. In January (section A), grazing was captured 7/20 days, while browsing was captured 5/20 days. In April (section A), grazing was captured only once and browsing only twice out of 13 days.

GIS analysis

Our map of potential espinal distribution included 43,189 polygons or individual espinals, covering 1,174,206 ha. The mean size of espinals was 27 ha $\pm$ 66 (SD). The area-to-perimeter ratio, providing a measure of fragmentation, was mean 0.07 ± 0.04 (SD).

The index of espinal condition shows a clear north–south and east–west gradient each year, with the lowest values in the north and along the Andes on the eastern side of the mapped espinal distribution. However, the highest values, although found in the south, were found exclusively along the western and eastern edges of the distribution. The flat low area between mountain ranges from north to south was dominated by values <2, showing that even in wet ENSO years, most espinal even in the southern end of its distribution does not approach its maximal potential condition .

Least-cost paths linking best condition and worst condition espinals split into regional subnetworks in 2 years, 2002 and 2005 (Fig. 3). In 2000, 2004, and 2006, a fully linked regional network was found. The total lengths of each network are shown in the Supplementary Data

(Table 4). The two shortest networks, 1982.4 km and 2795.9 km, are also found in the two dry ENSO years. Although networks differed between all years in both wet and dry years, a clear pattern of overlap is evident when all paths are compared (Fig. 4). The length of overlap is around 1700 km.

We further considered how the mean area, fragmentation, and espinal condition varied across years for the "high condition" and "low condition" selections used as the sources and targets for least-cost path construction, in order to understand the relative variation in espinal conditions and whether this was related to espinal characteristics (Table 2). Recall that high and low conditions were defined as the top two and bottom two standard deviations for each year. The number of espinal fragments in the low condition was higher in every year except 2002. The area of fragments in each selection varied significantly (ANOVA, $F = 79.5$, $df = 9$, $p < 0.001$), and this was explained by both the ENSO condition (dry or wet year) and espinal condition (high or low) (post test, $p < 0.01$, $t = 126.7$; $p < 0.01$, $t = 49.1$; mean square $= 102$, $df = 9$). Fragmentation also varied significantly among selections (ANOVA, $F = 334.6$, $df = 9$, $p < 0.001$), but not according to ENSO or espinal condition (post test, $p > 0.01$, $t = 1.6$; $p > 0.01$, $t = 1.5$; mean square $= 10.12$, $df = 9$). Finally, mean espinal condition also varied across selections (ANOVA, $F = 1029.6$, $df = 9$, $p < 0.001$), which was not affected by ENSO, but only by espinal condition (as expected, although not by definition because the mean and range of condition can vary between years, such that high and low conditions between years could overlap) (post test, $t = 0.081$, $p > 0.01$; $t = 3.79$, $p > 0.01$; mean square $= 55.5$, $df = 9$).

Ecosystem services

For the factory farms and fruit plantations/vineyards scenario, factory farms produce more meat (and associated animal products) per mm water/year than pastoral systems (Table 3; Mekonnen and Hoekstra 2012). However, most fruit production in central Chile requires irrigation. Economic incentives both favor investment in drip irrigation technologies and export of water-intensive fruits such as avocados during the Northern Hemisphere winter. Thus, we predict that although fruit production will clearly increase when espinal is converted to orchards or vineyards, regulating and supporting services of woody plants (fruit trees, vines) will be less water efficient than espinal. We assume that cultural and amenity services (aesthetic, recreational, inspirational, cultural, spiritual, and educational) are largely independent of yearly variations in water availability. We also predict that in this scenario, regional variation in water availability has little effect on meat and

fruit production due to legal and illegal exploitation of groundwater (Budds 2004). In the factory farms and sclerophyllous forest restoration scenario, the regulation, supporting, and cultural and amenity values of sclerophyllous forest are all assumed to be higher per mm water/year than espinal, since the services provided per unit area are expected to be higher, and loss of water via evaporation to be lower. The regulating and supporting services will, however, be dependent on water inputs. Finally, for the restoration with guanacos scenario, we predict that restoration of espinals via guanaco herbivory could directly and indirectly increase regulating and supporting services via increases in tree biomass and cover and associated herbaceous plant and animal diversity increases, along with reductions in water loss by evaporation. Although more efficient than the status quo, they will remain dependent on water input. Guanacos themselves can also contribute a high-value product to raw material provision, in the form of their high-quality fiber, and even meat. Finally, urban Chileans report that guanacos enhance a number of cultural and amenity values of espinal (Lindon and Root-Bernstein 2015). The costs associated with each of these scenarios are different and hard to compare, although the most diverse set of costs emerges for the restored sclerophyllous forest scenario.

Discussion

Guanacos browse *A. caven* leaves and branches, voluntarily including both structures in their diet despite the presence of thorns. A priori this demonstrates the feasibility of using guanacos as browsers for espinal restoration. While we do not yet have data related to how effects on individual trees will scale up to landscape patterns, such scaling-up is characteristic of herbivory by large mobile mammals (Shipley 2007; Olff et al. 1999). We are unable to predict whether the level of effect on individual trees will show a linear scaling-up to a landscape level due to factors such as the distribution of browsing by guanacos at larger scales, variation in soil water availability, historicity effects due to past disturbances, or competition between *A. caven* and other tree species for resources in mixed habitats. We emphasize that at this stage, we are only demonstrating the feasibility of the potential intervention, and we are not in a position to estimate its effectiveness or effect size at any scale.

The lowest quality espinals are found predominantly in the north of the central zone of Chile, although we also observe values below the mean throughout central Chile. These patterns did not change dramatically across wet and dry ENSO years. The least-cost paths between highest and lowest quality espinals are within a feasible length range,
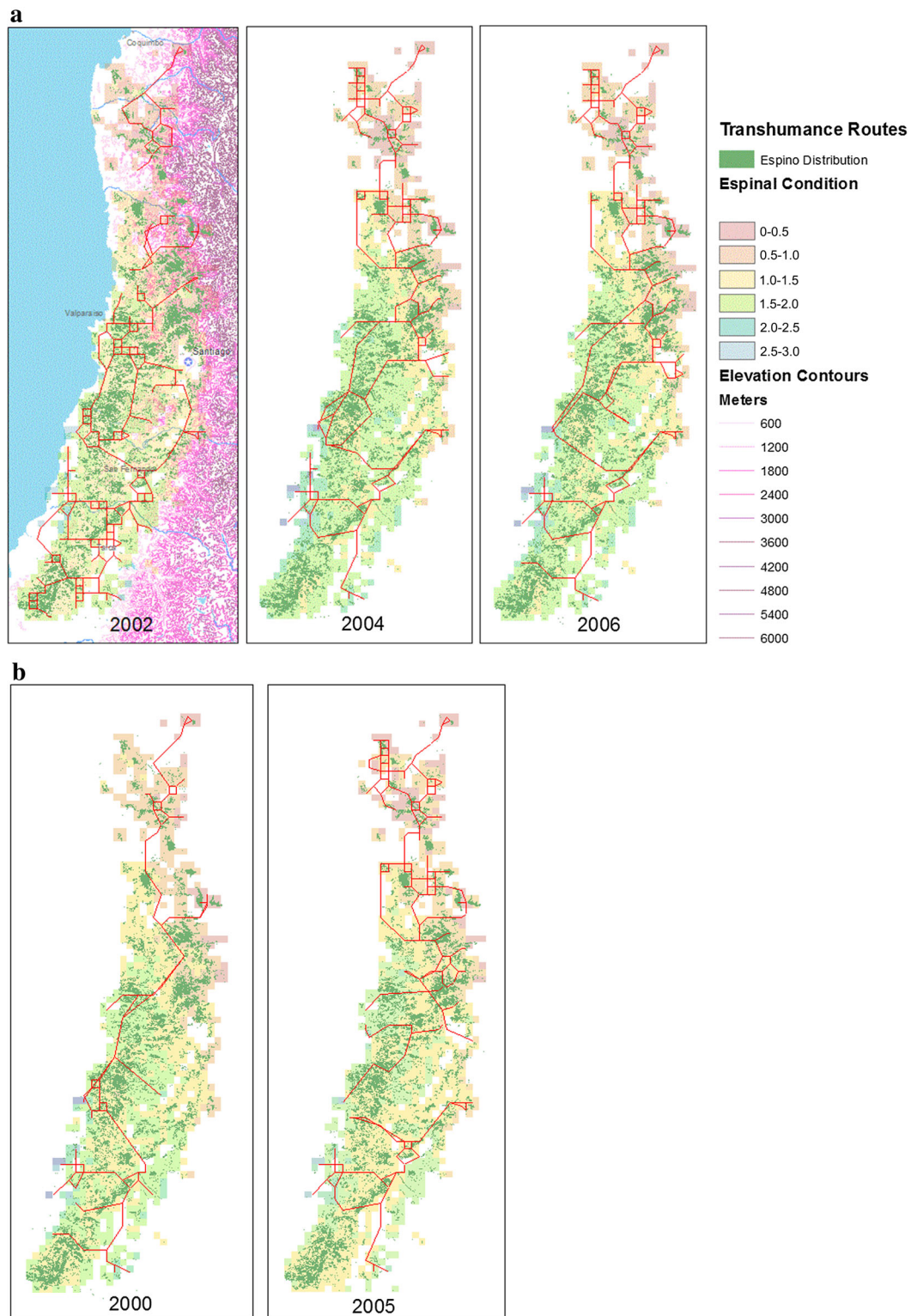
Fig. 3 a Wet ENSO years. **b** Dry ENSO years. Least-cost paths assessed between high- and low-quality espinal areas. In each year, least-cost paths connect high-quality espinal to low-quality espinal and low-quality espinal to high-quality espinal. The least-cost function in ArcGIS connects all sources to only the closest targets, so combining both high to low and low to high paths gives a fully connected network. All years are shown with a common scale to facilitate comparison, so the < 0.5 and 3–3.5 categories shown on maps do not correspond to the high and low restoration quality areas. Rather, these areas can be identified as the end points of the transhumance routes

Fig. 4 a Transhumant rewilding routes in wet ENSO years are shown in *blue*, in dry ENSO years in *red*. **b** Overlap of path densities and espinal densities with equal weighting (color figure online)
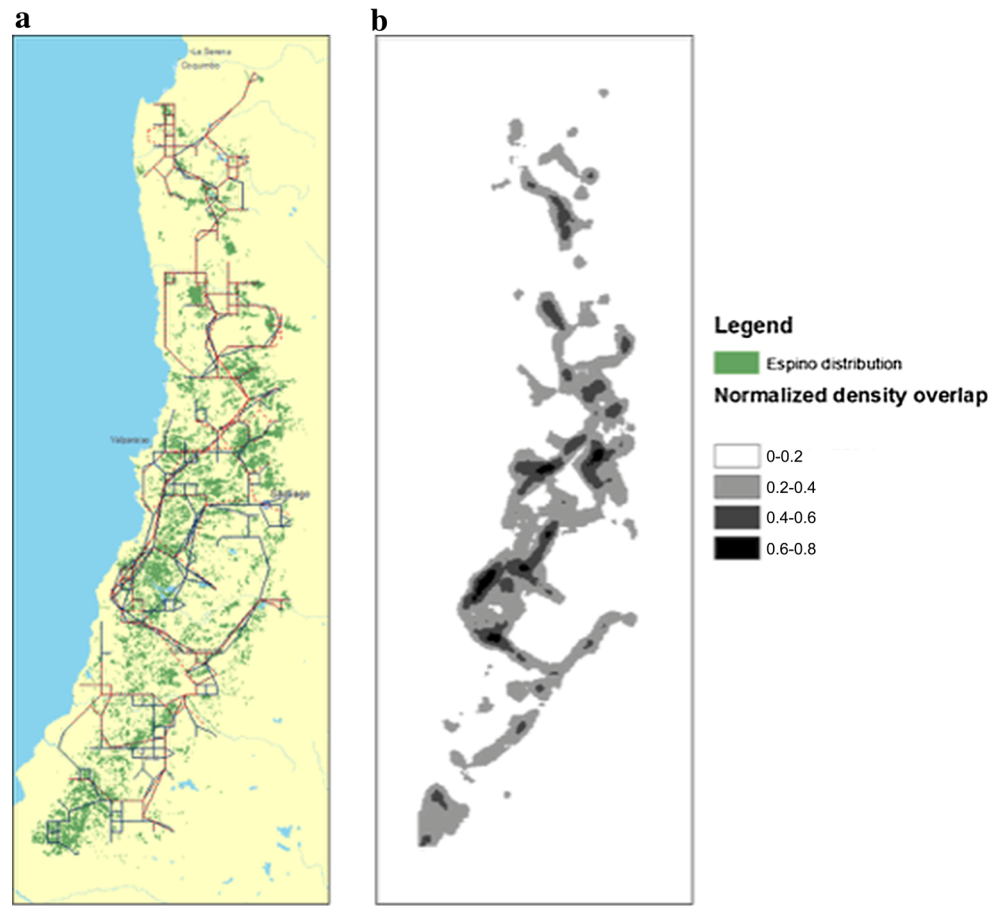
by comparison with guanacos' natural range sizes (see below) for a transhumant rewilding scenario using guanacos. Finally, the ecosystem service costs and benefits associated with guanaco transhumant rewilding are comparable to other scenarios, with potentially more institutionally achievable benefits and lower monetary costs.

Our observations of guanaco foraging on *A. caven* support the interpretation that leaves and branches are a normal element of their diet rather than a starvation food. Although our opportunistic camera trap data are probably biased due to the conflation of section, space availability (pulse treatments in 2014), and month, it suggests that group cohesion as well as browsing effort could be reduced in summer/fall. It remains to be seen whether the observed level of browsing during spring is adequate to stimulate a significant change in *A. caven* growth and with what lag time. Analysis of guanaco stocking density in espinal will allow us to determine a tree-to-guanaco density ratio where the amount of supplemental alfalfa provided could be reduced, which would substantially reduce guanaco maintenance costs as well as water input to the system.

The GIS analysis found very few putative espinals in the top range of condition for any year. This suggests that factors other than water availability are constraining espinal condition. The observed distribution of espinal condition values may be explained partially by the altitudinal gradient of the mountain ranges, the greater intensity of farming in the southern central valley, local socioeconomic factors affecting espinal exploitation history, or the interaction of these factors. The area of the selected espinals was larger in higher condition espinals and in wet years, which suggests that continuos espinals, regardless of the amount of edge, are in better condition and may capture available moisture more efficiently.

The obtained scale of transhumant rewilding also appears to be feasible. Guanacos can be either migratory, moving in family groups to winter ranges, or sedentary (Marino and Baldi 2014). The average range of three wild male guanacos, two of them solitary and one of them in a family group, tracked via GPS collar for a year in areas of savanna and shrub habitat, was 34 km^2, varying between 8 and 98.4 km^2 between seasons (Bonacic et al. unpublished data). This mean range size is close to the mean size of espinal fragments in our distribution map. The distances that guanacos migrate also appear to vary considerably, from 12 km (Ortega and Franklin 1995) to movements

Table 2 Fragment number, area, area-to-perimeter ratio, and mean espinal condition of high condition areas (top two SDs) and low condition areas (bottom two SDs)

Year espinal areas	Number of fragments	Mean area (km^2)	Mean area-to-perimeter ratio	Mean espinal condition index	ENSO
2000 H	39	3.50 ± 3.11	0.13 ± 0.04	2.28 ± 0.40	Dry
2000 L	72	7.50 ± 7.63	0.24 ± 0.21	0.47 ± 0.13	
2005 H	36	3.83 ± 3.01	0.12 ± 0.04	2.08 ± 0.23	Dry
2005 L	266	10.57 ± 11.22	0.25 ± 0.21	0.68 ± 0.21	
2002 H	348	10.98 ± 9.62	0.20 ± 0.09	1.62 ± 0.20	Wet
2002 L	90	7.77 ± 7.13	0.23 ± 0.16	0.50 ± 0.12	
2004 H	36	53.6 ± 0.39	1.82 ± 0.01	2.42 ± 0.38	Wet
2004 L	276	11.6 ± 11.70	0.25 ± 0.21	0.72 ± 0.24	
2006 H	38	4.19 ± 3.47	0.12 ± 0.04	2.48 ± 0.37	Wet
2006 L	279	11.43 ± 11.56	0.25 ± 0.21	0.74 ± 0.25	

from the east to west within a 1700 km^2 area [(actual distances moved are not reported) Puig et al. 2011]. This is comparable to the core overlap of paths in the identified transhumant rewilding network. The trade-offs in terms of body condition of guanacos for long-range movements should be studied further.

A finer-scale model informed by experimental results is necessary for the assessment of how a transhumant rewilding network can be implemented. Our analysis uses a coarse temporal scale (yearly) and a relatively coarse spatial scale (8 km resolution), and was only able to consider a small span of years for which all data were available. However, this is prudent given the clear limitations of our map of espinal distribution, which has not been ground-truthed, is outside the temporal range of our other data, and does not represent changes in espinal cover (estimates of which vary considerably, see Supplementary Data Table 5). The extent of espinal that we find, just over one million ha, is also only 25–50 % of published estimates (Serra 1997; Ovalle et al. 1990), i.e., less than can be accounted for by estimated land-cover change rates. In addition, the possibility of legacy effects from ENSO years was not examined here and should be considered (Monger et al.2015).

Our predictions for the relative water efficiency of potential ecosystem services under different land-use scenarios illustrate the complexity of trade-offs and valuation exercises that would be required in order to fully assess the water-use rationality of transhumant rewilding. The "factory farms and sclerophyllous forest restoration" scenario is the least realistic, since there is currently no governance mechanism by which a majority of espinal landowners would be induced to restore a protected forest type on their land (Root-Bernstein et al. 2013). The "factory farms and orchards/vineyards" scenario is similar to the current

condition of California, where despite increasing droughts affecting natural habitats and ecosystem services, industrial agriculture monopolizes water resources (Diffenbaugh et al. 2015). The "restored silvopastoral system with guanacos" is predicted to increase the water efficiency of ecosystem services, not only due to restored espinals losing less water to evaporation, but also due to the potential for a transhumant rewilding network that would adjust restoration and management to optimize production over dry and wet years. The costs of guanaco breeding, care, management, and protection within fenced espinals appear more complex than expensive. However, comparing costs and benefits across scenarios is beyond our capacity and points to important data shortfalls associated with nearly all services, and their valuation.

Finally, we believe that developing a transhumant rewilding system can be compatible with the local socioeconomic and cultural context, although this should be the focus of further studies. Livestock transhumance, called "veranada," is still practiced between the central valley of Chile and the Andes (Westreicher et al. 2007). Arrieros, or muleteers, also practice small-scale herding or pasturing throughout central Chile. Both smallholders and owners of large estates use espinal for extensive livestock, charcoal, and honey production, which we believe are compatible with guanaco browsing, either through rotation or coexistence. Reinforcement of fencing, adoption of guard animals, or active shepherding are possible strategies to reduce threats. However, uptake of guanaco management will clearly require regional or national programs for training and coordination, and a willingness among landholders to learn and adopt new skills.

In conclusion, our preliminary analysis and predictions associated with the Chilean case study suggest that traditions of transhumant or nomadic pastoralism can inspire

Table 3 Ecosystem services produced by water input in the form of rain or groundwater under four land-use scenarios, and associated land-use costs and losses

Services produced by water inputs (per mm/year)	Scenarios					
	Factory farms and orchards/vineyards		Factory farms and sclerophyllous forest restoration with strict protection		Status quo	Restored silvopastoral system with guanacos
	Farms	Orchard	Farms	Forest	Espinal	Espinal
Food	+ ~	+ ~	+ ~		=	+ ~
Raw materials	+ ~		+ ~		=	+ ~
Forest: air quality regulation		=		+	=	+ ~
Climate regulation		=		~	=	+ ~
Water regulation		=		~	=	+ ~
Erosion protection		=		~	=	+ ~
Soil formation				~	=	+ ~
Pollination				~	=	+ ~
Biological regulation				~	=	+ ~
Nursery habitat				~	=	+ ~
Genepool protection				~	=	+ ~
Aesthetic		=		+	=	+ ~
Recreational				+	=	+ ~
Inspiration for culture, art, design				+		
Cultural heritage and identity		~		+	=	+
Spiritual and religious inspiration				+		
Education and science	+	+	+	+	=	+
Notes	Wine and fruit production may come to acquire greater local specialty. Agronomical science opportunities		We assume that sclerophyllous forest has highest biodiversity and ecosystem services [1]. We assume no provisioning value of forest under strict protection [2]. Sclerophyllous forest is valued more highly than other landscapes/habitats [3]		Although there are no comprehensive estimates of espinal (or similar systems') ecosystem services, we assume that their provision is suboptimal both in the short term and in terms of sustainability [4]	High-quality guanaco wool can contribute to raw materials [5]. Urban Chileans positively rate areas with guanacos aesthetically and for tourism [6]. Opportunities for socioecological system research
Costs/Losses	Infrastructure; Polluted effluent water; Livestock diversity; Irrigation; Biodiversity; Traditional landscape and culture		Infrastructure; Polluted effluent water; Livestock diversity; Funding restoration of sclerophyllous forest; Opportunity cost to private landowners; Rural culture; *Arriero* land-use rights and forest protection conflicts		Soil erosion/degradation; Low biodiversity; Low efficiency of livestock production; Ongoing conversion to fruit plantations/vineyards	Guanaco breeding or relocation facility; Guanaco care and management; CITES certification of wool; Feral dog control and associated social conflicts

+ indicates an increase, ~ one that is dependent on water input. = indicates no change from the status quo. References: [1], e.g., Hernández et al. (2015), van Leeuwen et al. (2013), Schulz et al. 2010. [2] Root-Bernstein et al. (2013). [3] Root-Bernstein et al. (2013), Root-Bernstein unpublished data. [4] de Groot et al. (2010). [5] Montes et al. (2006). [6] Lindon and Root-Bernstein (2015)

feasible and flexible solutions to climate variation in drylands and silvopastoral systems. Notably, transhumant rewilding allows flexibility at regional and subregional scales of ecosystem processes and associated services in reacting to variance in water availability. (Silvo)pastoralism and transhumance here could serve as the human cultural interface, shepherding rewilded processes through complex anthropogenic landscapes.

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