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RESEARCH ARTICLE

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Land-use intensity indirectly affects ecosystem services mainly through plant functional identity in a temperate forest

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Abstract

1. Land-use change is known to affect biodiversity, and there is increasing concern regarding how these changes may impact the provision of ecosystem services. Although functional composition (diversity and identity) could influence ecosystem properties and services at the community level, there is little quantitative understanding of these relationships in the field. Here, we evaluate the direct and indirect effects (through ecosystem properties) of biodiversity on the provision of multiple ecosystem services in native mixed forest in north-west Patagonia, and how land-use intensity influences these relationships.
2. We used structural equation modelling to test hypotheses regarding the relationship between understorey plant functional composition, two ecosystem properties, four ecosystem services and silvopastoral use intensity (SUI). We also evaluated two alternative models to assess the mechanism behind biodiversity and ecosystem properties relationships (biomass ratio and niche complementarity). Finally, we performed pairwise correlations to identify synergies and trade-offs between ecosystem services.
3. SUI affected functional composition, and the provision of three out of four ecosystem services was indirectly affected by land-use intensity through changes in ecosystem properties. We found that this indirect effect of biodiversity on ecosystem services happens mainly through changes in functional identity rather than functional diversity. Under increasing land-use intensity, functional composition changed towards a community characterized by a resource acquisition strategy. Trade-offs between ecosystem services (provisioning vs. regulating) were enhanced under high SUI, while synergies where enhanced under low SUI (provisioning vs. cultural). Thus, although the strength of these relationships varied between SUI, its nature (trade-off or synergy) stayed the same.
4. Our results expand on previous studies by simultaneously considering the effect of land-use intensification directly on functional composition and on the ecosystem processes underpinning ecosystem services, as well as on the relationship

among them. We provide evidence of an indirect effect of land-use intensification on multiple ecosystem services through biodiversity. Moreover, we found that functional identity is more important than diversity for ecosystem functionality. Land-use intensification affects biodiversity, and thus, ecosystem properties, but does not change the relationship among ecosystem services.

KEYWORDS

biodiversity–ecosystem functioning, biomass ratio hypothesis, ecosystem services trade-offs, functional diversity, functional traits, litter decomposition, Patagonia, silvopastoral use intensity

1 | INTRODUCTION

A key issue in the study of biodiversity is its role in maintaining ecosystem functioning and in the provision of ecosystem services (Cardinale et al., 2012), and the extent to which human activities alter this relationship through biodiversity loss (Bennett et al., 2015). Land-use change has been recognized as a major driver of biodiversity loss (Hooper et al., 2012), which can affect the provisioning of ecosystem services directly or indirectly (Isbell et al., 2017). For example, there is evidence that higher diversity systems support higher production of cattle in grasslands and wood in forests, as well as higher cultural and aesthetic value (Cardinale et al., 2012). There is also increasing evidence that land-use intensification can modify biodiversity and species composition in ways that can alter the ecosystem functions that underlie ecosystem services (Allan et al., 2015). Decomposing the effect of land-use intensification on ecosystem services is crucial for sustainable management (Isbell et al., 2017), as it may allow to identify if the main effect would be given directly by land-use change or indirectly through biodiversity.

Species diversity influences ecosystem functioning through the type, range and relative abundance of functional traits, defined as the characteristics of an organism that have an impact on ecosystem functioning (Tilman et al., 2001). For example, leaf economic spectrum (Wright et al., 2004) is a set of plant traits that determines strategies in leaf resource use and investment. Changes in these traits can lead to trade-offs between a rapid acquisition of carbon and nutrients and the long-term persistence of the leaf (Westoby & Wright, 2006). Plants with a resource acquisition strategy of rapid growth have higher leaf nitrogen content and lower carbon inputs than plants with a resource conservation strategy. Consequently, leaves of rapidly growing species are less resistant to decomposition processes (Cornelissen et al., 1999). Recently, Lavorel and Grigulis (2012) proposed that these trade-offs in plant traits can be scaled up to understand how environmental change modulates ecosystem functioning and services.

Indirect effects of biodiversity on ecosystem services can be mediated by two main mechanisms that determine the way in which increasing diversity increases ecosystem functioning (Cardinale et al., 2012): “biomass ratio” and “niche complementarity.” Biomass ratio (also known as an identity effect) implies that the contribution of species to ecosystem functioning is proportional to their biomass (Grime, 1998). Thus, ecosystem functioning is determined mainly by the trait values of the most abundant species (Grime, 1998), so functional composition is more important than functional diversity in determining ecosystem functioning (Díaz & Cabido, 2001). For example, the most abundant values of plant functional traits such as leaf size and leaf dry matter content may determine key ecosystem processes like primary productivity (Mokany, Ash, & Roxburgh, 2008), while the most abundant values of stem traits such as plant height may determine carbon storage in woodlands (Conti & Díaz, 2013). Alternatively, niche complementarity (also known as a diversity effect) means that the diversity of functional traits influences ecosystem processes mainly through complementary resource use (Tilman et al., 2001). Thus, greater functional diversity (rather than functional composition) leads to greater effects on ecosystem properties (Díaz & Cabido, 2001). For example, the coexistence of different functional trait values such as species with different life cycles or a combination of sun and shade-adapted species in the understorey should lead to a fuller resource exploitation in time and space, leading to higher primary productivity and decomposition rate (Lavorel & Grigulis, 2012).

In addition to understanding the mechanisms that might mediate the effect of biodiversity on services, we should also aim to consider the trade-offs among ecosystem services (Bennett, Peterson, & Gordon, 2009). Trade-offs between provisioning and other ecosystem services have been reported in many studies (Cardinale et al., 2012; Mitchell, Bennett, & Gonzalez, 2014). For example, in Andean-Patagonian forests, Lara et al. (2009) found that increases in timber production is attained at the expense of regulating ecosystem services (i.e. runoff control). These trade-offs may be complex, with multiple and nonlinear relationships among ecosystem services (Bennett et al., 2009), and may emerge from biophysical properties of the ecosystem. Moreover, Cavender-Bares, Balvanera, King, and Polasky (2015) demonstrated that, at several case studies, management practices could be improved to diminish trade-offs and enhance both provisioning and regulating services.

Here, we evaluate direct and indirect effects (through ecosystem properties) of biodiversity changes due to land-use intensification on the provision of ecosystem services, and examine how management practices influence these relationships in Andean-Patagonian temperate forests (Argentina) under different silvopastoral use intensities (SUI). In particular, we assessed the relationships between

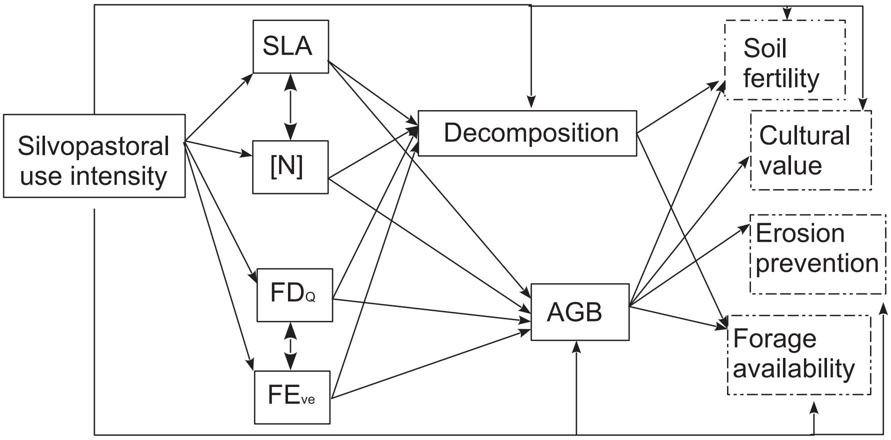

FIGURE 1 Path diagram describing the hypothesized causal relationships linking silvopastoral use intensity to biodiversity, ecosystem processes and ecosystem services (see definition of all ecological variables in Table 1). SLA, community weighted mean index of specific leaf area; [N], community weighted mean index of leaf nitrogen content; FD_Q, functional diversity index; FE_{ve}, functional evenness index; AGB, above-ground green biomass. Ecosystem services are farmed within dashed boxes. Justifications of the relationships between the ecological variables shown in this complete model are presented in detail in Table S1

functional diversity, ecosystem properties and ecosystem services in these forests. Silvopastoral practices (extensive cattle grazing and localized canopy opening) are a common activity in the region (Gowda, Kitzberger, & Premoli, 2011) that generate contrasting effects on understorey vegetation. Canopy opening due to wood extraction usually leads to increased light availability, in turn leading to increased plant richness (Lencinas, Martínez Pastur, Gallo, & Cellini, 2011), while cattle usually leads to decreased species richness (Relva, Núñez, & Simberloff, 2010; Vázquez, 2002) and increased herb cover (Piazza, Garibaldi, Kitzberger, & Chaneton, 2016). Increased net primary productivity due to increased light availability, increased decomposition rate and decreased litter input has also been recorded (Arias-Sepúlveda & Chillo, 2017; Peri et al., 2016).

Our first hypothesis is a causal model (Figure 1 and Table S1 for detailed hypothesized links) which follows the hierarchy of mechanisms proposed by Díaz et al. (2007). We propose that livestock grazing and canopy opening (silvopastoral use) generate changes in understorey plant functional diversity and composition, which will modify decomposition rate and above-ground green biomass (indicators of ecosystem properties) (Lavorel & Grigulis, 2012). As the provision of different ecosystem services depends on ecosystem properties (Cardinale et al., 2012), changes in ecosystem properties will modify the provision of ecosystem services such as forage availability, cultural uses of plant species, soil fertility and erosion prevention. Our second hypothesis is about the mechanisms underlying the biodiversity–ecosystem functioning relationship. We propose biomass ratio as the main mechanism in our study system, as it has been found in other forest ecosystems (Conti & Díaz, 2013). To assess this, we evaluate two alternative, mutually non-exclusive models which are reduced versions of the general causal model (Figure 1). The first and second hypotheses are evaluated using structural equation modelling (SEM). Finally, we assess trade-offs and synergies between ecosystem services, and potential changes under different SUI. Our third hypothesis is that, due to biophysical relationships between ecosystem properties and ecosystem services in the study region (Table S1), increasing the provisioning service will exacerbate trade-offs with other services (Cavender-Bares et al., 2015). To evaluate this hypothesis, we do a pairwise correlation between ecosystem services (Mitchell et al., 2014) under different SUI.

2 | MATERIALS AND METHODS

2.1 | Study site and sampling design

We measured functional diversity, ecosystem properties and proxies of ecosystem services in native mixed forest of ciprés de la cordillera (*Austrocedrus chilensis*) and coihue (*Nothofagus dombeyi*) of northwest Patagonia in 2013–2014. We worked in private lands under silvopastoral management at El Manso, El Foyel and El Bolsón locations, Río Negro Province, Argentina. The climate is characterized by cold wet winters and mild dry summers. The mean annual temperature is 9.3°C and the mean annual precipitation is approximately 900 mm. Soils are Andisols with deep profiles containing volcanic ash.

In this region, the traditional cattle production system consists of moving cattle seasonally through different elevations and forest types. During summer migrations, cattle spend most of the time in highlands dominated by deciduous lenga forests (*Nothofagus pumilio*), while in winter migrations cattle graze in lowlands dominated by evergreen forests. The latter are characterized by a mixed canopy composition of ciprés and coihue, the forest type studied here. Cattle graze in open canopy areas (<50% cover) generated by past wood extraction, followed by continuous but erratic timber extraction. These areas represent intense cattle grazing under partly open canopy, hereafter "high" SUI treatment. The canopy of the surrounding forest (beyond 100 m) is partly closed (90%–50% cover), as less timber extraction occurs here. These areas have fewer cattle and are hereafter called the "low" SUI treatment. We chose 10 sites inter spread across the landscape and within different land properties, but keeping the slope (low), orientation (S to SE) and stage of forest stand development similar between sites. Within each site we developed a pairwise sampling design, where we chose one sampling site in high SUI and one sampling site in low SUI (sites location are available from Chillo, Vázquez, Amoroso, & Bennett, 2018). In other words, the sampling design consisted of two pairwise treatments (high and low SUI) with 10 sampling sites for each treatment. These paired sampling sites were not far away from each other (up to 500 m), thus belonging to the same type of forest and with similar past natural disturbances and current environmental factors. Each sampling site (20) consisted of a 40 × 40 m forest stand, an area big enough to include at least 10 trees of the two dominant species and capture the heterogeneity of canopy cover. Within each sampling site, we established three parallel 4 × 10 m transects, separated by 20 m. SUI, functional traits, ecosystem properties and proxies of ecosystem services were measured within each transect.

2.1.1 | Silvopastoral use intensity indicator

In order to obtain a continuous variable of SUI out of the high and low SUI treatment, we built a multivariable indicator. Silvopastoral use represents a complex modification of habitat due to an increase in herbivory pressure but also in light availability due to canopy openness, thus we selected key variables of these habitat changes to build the indicator. The variables selected represent the effect of the disturbance on microenvironmental and biotic factors, which may directly modify the plant community. The chosen variables were browsing index and total basal area of *A. chilensis* and *N. dombeyi*. These were estimated by splitting each transect into ten 2 × 2 m segments and measuring: (1) the number and intensity of browsed juvenile trees (browsing index as proposed by Relva & Veblen, 1998); and (2) the diameter at breast height of all *A. chilensis* and *N. dombeyi* trees higher than 3 m tall. Then, for each variable, we summed the values of the 10 segments to obtain one value per transect. Finally, we performed a principal components analysis (PCA) which clearly segregates sites with different SUI along PCA axis 1 (Figure S1). Higher values of PCA axis 1 correspond to sites with low SUI, while lower values of PCA axis 1 correspond to sites with high SUI. As this could be counter intuitive, we decided to express SUI indicator as -(PCA axis 1 scores) (Table 1). Thus, higher values of SUI indicator represent sites with higher browsing values and lower values of canopy tree's basal area (higher SUI).

2.1.2 | Functional diversity indices

We selected functional effect traits related to the ecosystem properties of interest (Table S2). Different methodological approaches were used for traits with low and high intraspecific variation: (1) traits with low intraspecific variation were estimated from information obtained from the literature and species abundance obtained in the field (percent cover). These traits were leaf texture, life cycle, life form and plant architecture. (2) Traits with high intraspecific variation were estimated in the field, on six individuals of each of the most abundant species of each transect (those which together represent 80% of total cover) (Carmona, Rota, Azcárate, & Peco, 2015; Garnier et al., 2007). Depending on each transect diversity, measurements were taken on a minimum of 5 and a maximum of 25 species. These traits were: specific leaf area (SLA hereafter) and leaf nitrogen concentration ([N] hereafter). Traits were measured following the protocols proposed by Pérez-Harguindeguy et al. (2013).

To assess species abundance, we split each transect into ten 2 × 2 m segments, in which we visually estimated the percent cover of each species using the summed cover of the 10 segments. To estimate community functional diversity, we calculated three indices at each transect: Rao's entropy (FD_Q) and functional evenness (FE_{ve}), considering all functional effect traits. FD_Q depends on the range of functional space occupied and on the similarity between species with the highest abundances. A community with high FD_Q will tend to have high functional divergence, and high levels of functional divergence can be associated to a high degree of niche differentiation among species within communities (Mouchet, Villéger, Mason, & Mouillot, 2010). FE_{ve} is independent of functional richness and abundance, and measures the regularity of the distribution of abundance in functional space. FE_{ve} values are higher when there is an even distribution of both species and abundances in the functional space, and lower when some parts of the functional space are empty while others are densely populated (Mouchet et al., 2010). Both functional diversity indices can be related to the niche complementarity mechanism, as largest values mean that functionally different species reach similar abundances. We also calculated the community-weighted mean (CWM) value of SLA and [N]. We chose those traits because they tend to be closely related to both ecosystem properties under study (Cornwell et al., 2008; Garnier et al., 2007; Jewell et al., 2017) (Table 1). This index allows for a better approach on the biomass-ratio mechanism, as it assesses dominant trait values (Allan et al., 2015). Analyses were done in R software with the FD package (Laliberté, Legendre, & Shipley, 2015; R Core Team, 2013).

2.1.3 | Ecosystem properties

We measured two ecosystem properties: litter decomposition rate and maximum above-ground green biomass (AGB) (Table 1). These ecosystem properties are considered good proxies of ecosystem functions because they are indicators of processes (fluxes of matter and energy) measured as rates. Litter decomposition rate is related to soil fertility (Laliberté & Tylianakis, 2012; Lavorel & Grigulis, 2012), a key supporting ecosystem service. AGB is a performance trait modulated by morphophysiological traits, and at the community level, it is directly related to above-ground net primary productivity (Violle et al., 2007). Litter decomposition rate was estimated using the litter-bag technique. We manually collected fresh senescent leaves of the dominant understorey species of each transect and prepared each bag (2 mm mesh 10 × 10 cm nylon) with 3 g of air-dried litter. Due to the importance of tree species identity in

TABLE 1 Ecological variables used in the models and their description

Ecological variable	Description of the variable	Reference
Land-use change		
Silvopastoral use intensity	Relative between sites. Estimated as the first axis of a principal components analysis (74% of the variance) considering soil compaction, browsing index, and total basal area of canopy tree species.	
Functional effect traits related to ecosystem properties		
Functional diversity (FD_Q)	Rao's entropy index, unit-less. The distribution of species and their abundances in the functional space[a] of a community. It represents the variety of trait values in the community, weighted by their abundance	Mouchet et al. (2010)
Functional eveness (FE_{ve})	Unit-less index. It measures the regularity of the distribution of abundance in a functional space. It will be maximized by an even distribution of both species and abundances in the functional space.	Mouchet et al. (2010)
Specific leaf area (SLA)	Community weighted mean of the one-sided area of a fresh leaf, divided by its oven-dry mass (cm^2/g)	Pérez-Harguindeguy et al. (2013)
Leaf nitrogen content (LNC)	Community-weighted mean of percentage of leaf nitrogen content.	Pérez-Harguindeguy et al. (2013)
Ecosystem properties		
Above-ground green biomass (AGB)	Harvested green biomass (g/m^2) of understorey in the peak of production.	Garnier et al. (2007); Quijas et al. (2010)
Decomposition rate	Loss weight in time (g/time). Community litter was decomposed in situ, to integrate the combined role of the environment, soil organisms and litter quality	Garnier et al. (2007)
Ecosystem services		
Soil fertility	Percentage of soil organic matter. Considered as an intermediate or support ecosystem service, which can affect ecosystem properties as well as other ecosystem services	Quijas et al. (2010)
Forage availability	Absolute cover of palatable species	Quijas et al. (2010)
Stability of soil cover, as a proxy of Erosion prevention	Proportion of woody/herbaceous soil cover. The availability of biomass and its stability over time (type of cover) are the main factors of soil protection against erosion	Quijas et al. (2010); Carreño, Frank, and Viglizzo (2010)
Occurrence of plants with cultural value	Absolute cover plants with known uses' cover (for food, medicine and ornamental)	Ladio (2005); Quijas et al. (2010)

[a] Functional space: a multidimensional space where the axes are functional traits along which species are placed according to their functional trait values (Mouchet et al., 2010).

litter decomposition, all bags were placed under a mixed canopy of ciprés and coihue. At each transect, four bags were left to incubate above-ground during 12 months. Ash-free dry mass was determined for all samples to correct for soil contamination from the field. Decomposition rate was estimated as the percent weight lost per day. At each transect, AGB was estimated using the dry weight of all AGB (up to 1.5 m tall) harvested in three plots of 50 × 50 cm at the end of the growing season (late summer). Plots were placed regularly along a transect, separated by 5 m.

2.1.4 | Proxies of ecosystem services

We used proxies to estimate one cultural (plant with cultural value), one provisioning (forage availability) and two regulating (erosion prevention and soil fertility) ecosystem services (following definitions used by the Millennium Ecosystem Assessment 2006) (Table 1). These proxies were chosen because they are expected to vary spatially and are relevant to local landowners (pers. comm.).

For the occurrence of *plants with cultural value*, we classified species based on their ornamental, medicinal and edible usage by native and local people based on well-documented published information for the region (Estomba, Ladio, & Lozada, 2006; Morales & Ladio, 2012). We then calculated the total abundance of species with known cultural uses within each transect, considering species abundance data obtained from vegetation sampling (see Functional diversity indices). *Forage availability indicator*—a key provisioning service in this silvopastoral system—reflects the total abundance of palatable species within each transect. All species were classified in palatable/not palatable based on their natural history and published information on nitrogen, lignin and/or secondary compounds content. The proxy for *erosion prevention* was estimated based on the stability of soil cover, considering percent plant cover of herbaceous and understorey woody species (up to 1.5 m tall). Finally, *soil fertility* was estimated as percent organic matter content in soil. It is considered as an ecosystem service and not an ecosystem process because it is a stock measured as an amount, and a stock that is obtained from a process. We took a soil sample of the first 15 cm of soil at the beginning and at the end of each transect, and determined percent organic matter using the Davies method (Davies, 1974). These values were averaged to obtain one value per transect.

2.2 | Data analysis

We used SEM (Shipley, 2009) to assess the relationship between biodiversity, ecosystem functioning, ecosystem services and SUI. This analytical approach is appropriate for the analysis of complex networks in ecosystem relationships, as it allows evaluating causal hypotheses representing alternative pathways of ecosystem functioning (Shipley, 2009).

We built a general SEM model based on current knowledge of biodiversity-ecosystem functioning and biodiversity-ecosystem services relationships (Cardinale et al., 2012; Díaz et al., 2007; Lavorel & Grigulis, 2012) and on specific knowledge of the study site natural history and response to disturbances (see Table S1 for specific details of each causal relationship proposed) (Figure 1). The model aims at understanding the effect of silvopastoral disturbance on trait diversity, and the relationship of trait diversity influencing ecosystem properties and ecosystem properties influencing ecosystem services. Furthermore, the model allows us to evaluate whether changes in functional identity of the dominant trait values (biomass-ratio mechanism) provided a better explanation of indirect effects than changes in functional diversity did (niche complementarity mechanism). To do so, we compared the fit of a SEM containing CWM of SLA and [N] with another SEM containing FD_Q and FE_{ve} (Figure S2), using Akaike information criterion modified for d-sep test (AIC_c) (Shipley, 2013) and selecting the model with the lowest AIC_c value.

We constructed a generalized multilevel path model based on the directional separation (d-sep) test (Shipley, 2009). This type of model is appropriate because of the nested nature of the data (i.e. traits measured on individuals, individuals nested in species, transects nested in SUI) and because different variables were measured at different hierarchical levels (i.e. from individual traits to ecosystem services). Due to the nested nature of the sampling design (Schielzeth & Nakagawa, 2013), and in order to consider within-site variability in species composition, we used sampling sites (20 sites, three transects within each one) as a random effect and SUI (2) as a fixed effect. Pathway coefficients for the SEM were estimated with the LME function of the NLME library in R software (R scripts are available from Chillo et al., 2018). From the generalized model, we generated a reduced model by removing path coefficients smaller than 0.15, which simultaneously improved path coefficient and the model fit. The goodness-of-fit of each causal model was estimated by comparing Fisher's *C* value of each model to a chi-squared distribution (χ^2) with 2*k* degrees of freedom (*k* being the total number of free parameters in each model). A significant χ^2 statistic indicates that the model does not fit the data well. Once a model cannot be rejected and is thus considered plausible, parameter estimates can be used to study direct and indirect effects (Shipley, 2009). As several causal models were supported by the data, we used AIC_c to choose among the competing models.

To evaluate the relationships between pairs of ecosystem service indicators, we performed Pearson correlation analysis on each pair of services for the overall dataset (all sites), for sites with low SUI and for sites with high SUI, using R software. We aim at identifying positive (synergy) and negative (trade-off) correlations between pairs of ecosystem services, and if that relationship changed under different SUI.

3 | RESULTS

Our SEM approach resulted in four models: (1) the generalized hierarchical model (Figure 1); (2) a generalized hierarchical model without path coefficients <.15 and two models nested within the generalized hierarchical model without path coefficients <.15, both proposed to answer our second hypothesis; (3) the biomass-ratio model; and (4) the niche complementarity model. Field data did not support the generalized hierarchical model (Tables 2 and S3), but the removal of links with weak path coefficients greatly improved model fit (Figure 2 and Table 2). SUI positively affected functional identity (SLA and [N]) and functional diversity (FD_Q) indices (Figures 2 and S3). Notably, there was no direct effect of SUI on ecosystem properties or on most ecosystem services; instead, these were driven by indirect effects through functional identity (both CWM indices) and functional diversity (only FD_Q) metrics (Figure 2). Above-ground green biomass had a significant effect on most ecosystem services, while decomposition rate only affected soil fertility (Figure 2). All bivariate relationships of the significant path coefficients can be seen in Figure S3.

We constructed the causal models proposed to evaluate the biomass ratio (Figure S2) and the niche complementarity mechanisms (Figure S2) based on the reduced generalized hierarchical model (Figure 2). Both models were supported by the data (Table 2), but the biomass ratio model had the best fit (lowest AIC_c, Table 2). The niche complementarity model had a relatively small ΔAIC_c (<10; Table 2), suggesting that it may be a complementarity explanation. Path coefficients varied between models at the lower part of the hierarchy, as in the niche

TABLE 2 Statistical parameters to evaluate the models derived from Figure 1

Model	*C*	*k*	*p*	AIC_c	ΔAIC_c
Biomass ratio	45.8	12	.52	107.3	0.0
Niche complementarity	79.5	6	.51	113.4	6.07
Reduced	83.6	14	.39	184.8	77.51
Complete	197.9	26	.00	313.9	206.56

Reduced model is the complete model after eliminating path coefficients >.15. Biomass ratio and niche complementarity are reduced models with only functional identity and functional diversity indices respectively. *C* is the Fisher's *C* statistic used for the d-sep test, *k* is the number of parameters needed to fit the model, *p* is the null probability of comparing *C* to a χ^2 distribution with 2*k* degrees of freedom, AIC_c is Akaike's information criterion and ΔAIC_c is each model's difference in AIC_c relative to the best fit model (Biomass-ratio model).

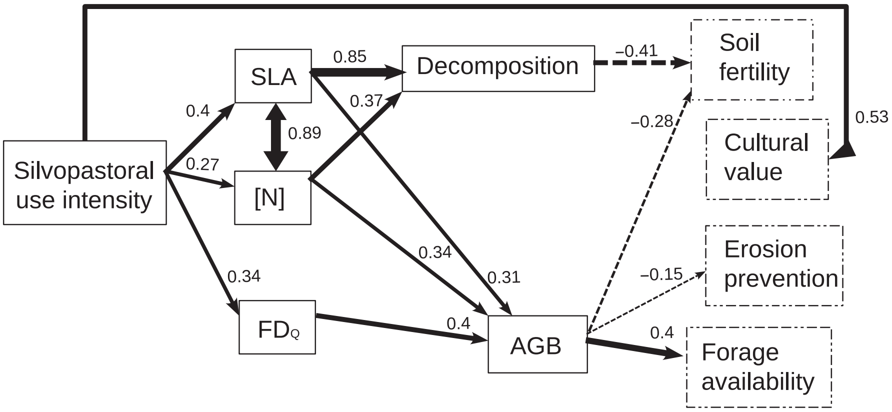

FIGURE 2 Best-fitting structural equation model examining direct and indirect relationships among land-use intensification, biodiversity, ecosystem processes and ecosystem services. SLA, community-weighted mean index of specific leaf area; [N], community-weighted mean index of leaf nitrogen content; FD_Q, functional diversity index; AGB, above-ground green biomass. The width of the arrows reflects the strength of dependency between two variables, dashed arrows reflects negative relationship, solid arrows reflects positive relationships and standardized path coefficients are shown on the path. Only significant ($p < .05$) paths values higher than .15 are presented. Table 2 shows the parameters of all models in a comparative way

complementarity model FD_Q had a moderate-to-small positive effect on AGB (Figure S2); in the biomass ratio model, both functional composition indices (CWM of SLA and of [N]) had a strong-to-moderate positive effect on both ecosystem processes (Figure S2).

We found positive (synergy) and negative (trade-off) correlations between pairs of ecosystem services indicators (Table 3). Of the 18 pairwise correlations, only six were significant, out of which three were synergies and three were trade-offs. In an overall approach, where all sites were pooled together, we found a synergy between cultural and provisioning services and a trade-off between regulating and provisioning services. The strength of the synergies was enhanced under low SUI and reduced under high SUI, while the strength of the trade-offs was reduced under low SUI and enhanced under high SUI. One non-significant relationship of the overall approach between regulating and cultural services turned out significant when data were separated into high and low SUI, and showed the same pattern as the latter: a trade-off that was enhanced under high SUI. Pairwise relationships were non-significant when the erosion prevention proxy was considered, showing that it may not be an appropriate indicator of the process. For all the significant correlations, a similar trend can be found, where the strength of the pairwise relationship varied between SUI, while the basic nature of the relationship—either trade-off or synergy—stayed the same (Table 3).

4 | DISCUSSION

Biodiversity is expected to have a positive effect on the provision of ecosystem services (Quijas, Schmid, & Balvanera, 2010), but current knowledge of the links between measures of diversity and ecosystem services is still limited, in part because ecosystem services are regulated by multiple processes that may not all respond to biodiversity changes in the same way (Cardinale et al., 2012). Our results showed that increasing light availability and livestock grazing disturbance modifies the provision of several ecosystem services indirectly through changes in biodiversity – mainly in functional identity – and in key ecosystem properties. Some of these effects have been reported for the biodiversity–ecosystem functioning relationship at a local scale (Garnier et al., 2007; Laliberté & Tylianakis, 2012) and for the biodiversity–ecosystem services relationship at a landscape scale (Lavorel et al., 2011). Our results expand on these studies by simultaneously considering the effect of real land-use intensification directly on biodiversity and ecosystem properties underpinning ecosystem services, and the relationship among ecosystem services at a local scale, a recognized research need (Isbell et al., 2017; Mulder et al., 2015). Our results support our first hypothesis of a significant effect of biodiversity on ecosystem properties. These results can be explained by the fact that SLA is an important component of plant growth (Lambers, Raven, Shaver, & Smith, 2008), and by leaves with high SLA have low carbon and lignin content, as well as high nitrogen content, which produces easily decomposable litter (Cornelissen et al., 1999; Jewell et al., 2017). The best-fitting model presented a positive and strong relationship between SUI and both SLA and leaf nitrogen content, showing that increasing land-use intensity moves the community towards a more resource acquisition type community (Shipley, Lechowicz, Wright, & Reich, 2006). When resources are allocated to acquisition rather than to resource conservation, this implies potentially higher net primary productivity (Sterck, Poorter, & Schieving, 2006) and faster litter decomposition rates (Cornwell et al., 2008).

Notably, and opposite to findings in other type of ecosystems (Allan et al., 2015; Newbold et al., 2015), our results show that functional diversity was positively associated with land-use intensity. This might be due to increasing light availability with canopy opening releases resources which favours the establishment and growth of new species, as has been found in other Patagonian forests (Lencinas et al., 2011). This increase in functional diversity, together with a change in functional identity towards a resource acquisition strategy could imply

TABLE 3 Pairwise correlations between ecosystem services

	Overall	Low SUI	High SUI
Soil fertility ↔ cultural values	−0.18	−0.09 (↓)	**−0.38 (↑)****
Soil fertility ↔ forage availability	**−0.25***	−0.14 (↓)	**−0.57 (↑)****
Soil fertility ↔ erosion prevention	0.07	−0.21 (↑)	−0.22 (↑)
Cultural values ↔ forage availability	**0.6****	**0.68 (↑)****	**0.5 (↓)****
Cultural values ↔ erosion prevention	−0.02	−0.12 (↑)	−0.23 (↑)
Forage availability ↔ erosion prevention	0.04	0.08 (↑)	−0.17 (↑)

The analysis was done for all sites pooled together (overall), and for two contrasting silvopastoral use intensities (low SUI and high SUI). Positive correlations represent synergies and negative correlations represent trade-offs between ecosystem services. Significant correlations are highlighted in bold. Arrows indicate increases (↑) or decreases (↓) in correlation strength given by SUI, compared to the overall correlation.

SUI, silvopastoral use intensity.

*$p < .05$; **$p < .01$.

that, as in resource-rich environments, plants may cope with herbivory through tolerance and re-sprouting after defoliation, rather than local extinction (Cingolani, Noy Meir, & Díaz, 2005; Lind et al., 2013).

Our study goes beyond analysing land-use intensity effect on biodiversity and ecosystem functioning to identify the main mechanisms behind this relationship. First, we found that indirect effects are more important than direct effects of land-use intensity on ecosystem functioning. As theory predicted, we found that both functional identity and diversity determines biodiversity effect on ecosystem functioning, reinforcing their complementarity role (rather than mutuality exclusive) (Cardinale et al., 2012). Similar results were found by Allan et al. (2015) in agricultural lands, were land-use intensification was associated with a strong shift in functional richness and composition (with regional differences in the relative importance of the main mechanism), indirectly increasing ecosystem multi-functionality. But, in agreement with our hypothesis, we found that the functional identity of the plant community is more important than functional diversity in determining the relationship.

Our results also show that changes in SUI affected the occurrence and strength of trade-offs and synergies between ecosystem services. Ecosystem service trade-offs and synergies have been quantified in several ecosystems, primarily at the landscape scale, and typically showing that increasing provisioning services negatively affects regulating and cultural services (Laterra, Orúe, & Booman, 2012; Raudsepp-Hearne, Peterson, & Bennett, 2010). But such scale of analysis gives little information relevant to manage multiple ecosystem services at the local scale (i.e. for a single landowner) (Isbell et al., 2017).

Moreover, when a trade-off was identified, the strength of this negative relationship increased with increasing SUI. The opposite was true for synergies, which appear to become stronger with decreasing SUI. This result partially supports our hypothesis that efforts to increase provisioning services would negatively affect other ecosystem services, because trade-offs were also found between cultural and regulating services. For example, increasing forage availability (high SUI) changes community towards plants with higher leaf nitrogen content and higher decomposition rate, thus, soils with lower organic matter proportion (our indicator of soil fertility) than those of low SUI. But we also found that the occurrence of plants with cultural value was positively related to forage availability, and this positive relationship was stronger under low SUI. This could occur because plants with ornamental, medicinal and editable uses are more common in forests gaps (i.e. *Alstroemeria aurea*, *Aristotelia chilensis*, *Chamomilla suaveolens*) (Morales & Ladio, 2012), but may be affected by cattle grazing (i.e. *A. aurea* is strongly selected by cattle).

Interestingly, land-use intensification modified the strength but not the direction of the pairwise relationship between ecosystem services (i.e. trade-off relationships in the overall analysis remained as trade-offs under different silvopastoral use intensities). Similar results were found by Mitchell et al. (2014), where differences in forest fragment size and isolation changed the strength but not the direction of the relationship between ecosystem services in agricultural landscapes. The biophysical properties related to ecosystem services trade-offs did not change with SUI, rather the magnitude of the property. Thus, an improvement in this type of management practice, referring to a gradient of SUI, may not help enhance both provisioning and regulating services (sensu Cavender-Bares et al., 2015). Instead, these results imply that the provisioning of multiple ecosystem services across landscapes might be achieved by managing for varying levels of land-use intensity at the landscape scale.

5 | CONCLUSION

We found that indirect effects of land-use intensity are related to changes in ecosystem functioning. Moreover, our results support the biomass-ratio hypothesis as the main mechanism behind the biodiversity–ecosystem functioning relationship; that is, the identity of dominant species was more important than the diversity of functional traits in determining the effect of vegetation on ecosystem processes. In other words, decomposition and above-ground green biomass are mainly determined by the dominance of plants with higher SLA and leaf nitrogen content, instead of by changes in the diversity of those traits. We also found that the provision of key ecosystem services is indirectly affected by land-use intensity through changes in ecosystem processes, meaning that management strategies should focus on keeping a desirable community characterized by key traits related to ecosystem processes of interest. Finally, our finding that the magnitude, but not the direction, of the pairwise relationship between ecosystem services is modified by changes in land-use intensity, stands out as an important tool for sustainable management, as planning different land-use intensities through the landscape may allow for the provisioning of multiple ecosystem services.

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AUTHORS' CONTRIBUTIONS

V.C., D.P.V. and E.M.B. conceived the idea; V.C., D.P.V. and M.M.A. decided the sampling design; V.C. and M.M.A. collected field data; V.C. and D.P.V. carried out data analysis; V.C. and D.P.V. wrote the manuscript with contributions from all authors. All authors gave final approval for publication.

DATA ACCESSIBILITY

All database is available at Dryad Digital Repository https://doi.org/10.5061/dryad.n9882 (Chillo et al., 2018).

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