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Research Article

Keywords:

Posted Date: October 23rd, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11236441/v1>

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Additional Declarations: No competing interests reported.

Raptor distributions reveal the conservation consequences of forestry-driven landscape transformation in a grassland biome

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ABSTRACT

Context

Land-use change is the main driver of South American grassland loss, and commercial tree plantations promoted by national incentive policies are expanding over agro-pastoral landscapes. The landscape-scale effects of this transformation on the taxonomic, functional and phylogenetic facets of biodiversity remain poorly understood.

Objectives

We evaluated how forestry cover and landscape heterogeneity influence the alpha and beta diversity of diurnal raptors. We also asked whether the three diversity facets respond in a coupled way.

Methods

We sampled diurnal raptor species along roadside transects in 17 landscape cells of 100 km² in the Mesopotamian Pampas, Argentina. Land cover was classified from satellite imagery, and we estimated taxonomic, functional and phylogenetic diversity (TAD, FAD and PAD) per cell.

Results

We recorded 153 individuals of 12 species. Forestry cover did not affect alpha diversity in any facet. Greater landscape heterogeneity drove a significant and coupled decline in TAD and FAD, while PAD remained unaffected. Taxonomic and functional beta diversity were structured by forestry cover, whereas phylogenetic beta diversity was not. Assemblages shifted from large, long-winged grassland specialists that soar to smaller, perching habitat generalists as forestry cover increased.

Conclusions

Declines in TAD and FAD reflected the re-arrangement of open habitats, whereas forestry cover drove turnover in taxonomic and functional composition. These findings underscore the importance of multi-facet, landscape-scale approaches for biodiversity assessment and highlight the need for preserving extensive areas of native open habitats to maintain taxonomically and functionally diverse raptor assemblages in South American grasslands.

Keywords land-use change; afforestation; alpha diversity; beta diversity; habitat heterogeneity; South American Grasslands

Introduction

South American grasslands are one of the most threatened ecosystems in the world, with only about 1% formally protected (Henwood 2010), and forestry emerging as a growing productive practice in this biome (Phifer et al. 2017). Nowadays, the expansion of commercial forestry occurs over already modified, open agro-pastoral lands rather than native grasslands (Phifer et al. 2017). This transition drives a radical shift in landscape physiognomy, replacing open

agricultural matrices with novel vertical complexity and microclimatic conditions that affect native species occurrence (Veldman et al. 2015; Cardoso et al. 2023). Although most studies rely on the local-scale impacts of forestry activity on forest biome biodiversity (Brockerhoff et al. 2008; Castaño-Villa et al. 2019), the implications of these plantations at the landscape level for contrasting open biomes have become a growing concern in recent years (e.g., Santoandré et al. 2019; Pezda et al. 2021; Vaccaro and Filloy 2022; Ribero and Filloy 2023; Oddi et al. 2025). Under this scenario, agro-pastoral replacement by commercial forest plantations serves as an ideal framework to evaluate how land-use change reshapes grassland biodiversity.

Typically, heterogeneous landscapes with high internal structural complexity support greater species richness than landscapes mostly composed of anthropogenically simplified habitats (Tews et al. 2004; Tschardt et al. 2012; Stein et al. 2014). During the initial stages of expanding commercial tree plantations into agro-pastoral landscapes, the introduction of a novel land cover increases overall landscape heterogeneity. This initial increase in heterogeneity can temporarily maintain or even increase taxonomic richness by allowing generalist and disturbance-tolerant species to colonize newly created forest edges (Marcacci et al. 2021). However, the late stages of anthropogenic land-use expansion may negatively affect species richness through homogenization and habitat simplification because increasingly homogeneous landscapes provide lower variability in resources to biodiversity and reduce natural habitat connectivity (Ekroos et al. 2010; Scott et al. 2024). For example, previous studies suggest a hump-shaped response of species richness or taxonomic diversity to increasing environmental heterogeneity driven by the expansion of new land uses (area-heterogeneity trade-off) at local scales (Allouche et al. 2012). However, it remains unknown whether such a hump-shaped pattern of biodiversity also occurs with increasing forestry cover in landscapes where the new land-use is structurally and functionally distinct from the original matrix.

75 Taxonomic diversity, namely species richness, is often insufficient to capture biodiversity
76 responses to environmental disturbance (Fletcher et al. 2025). Because taxonomic, functional,
77 and phylogenetic diversity capture distinct dimensions of assemblage organization driven by
78 different ecological (Corbelli et al. 2015; Tinoco et al. 2018; Mastrogianni et al. 2024) and
79 evolutionary processes (Devictor et al. 2010; Tucker et al. 2017), these three facets frequently
80 respond differently to land-use change (Monnet et al. 2014; Perronne et al. 2014). For instance,
81 the conversion of open grasslands into structurally novel systems such as commercial
82 plantations can modify the historical environmental filters (Bremer and Farley 2010; Veldman et
83 al. 2015), promoting the replacement of specialized grassland taxa by disturbance-tolerant
84 generalists and thus affecting functional diversity (Flynn et al. 2009; Clavel et al. 2011). In
85 transformed landscapes where species may be replaced without apparent changes in species
86 richness or even in certain functional traits, there can still be changes in the evolutionary history
87 contained in such assemblages that can only be revealed by evaluating their phylogenetic
88 diversity (Swan et al. 2022). The relationship between functional and phylogenetic diversity
89 depends heavily on the phylogenetic conservatism of the considered functional traits.
90 Specifically, if functional traits are phylogenetically conserved, environmental filtering can drive
91 a simultaneous and coupled decline in both functional and phylogenetic diversity as entire
92 lineages are excluded (Emerson and Gillespie 2008). In contrast, if functional traits are not
93 phylogenetically conserved or have evolved convergently across unrelated lineages,
94 assemblages may experience substantial functional reorganization while maintaining
95 unchanged phylogenetic diversity (Losos 2008; Tucker et al. 2017). Assessing how beta diversity
96 changes between undegraded and degraded sites can disentangle these patterns observed in
97 alpha diversity (Philippi et al. 1998; Baselga 2010). Consequently, relying on a single biodiversity
98 facet may either overestimate or underestimate the consequences of habitat degradation,
99 leading to incomplete assessments of biodiversity change and its implications for ecosystem
100 functioning and conservation planning (Devictor et al. 2010; Cadotte et al. 2011).

So far, most knowledge regarding the effects of land-use change on biodiversity at the landscape scale has been primarily based on the aggregation of local responses (Fahrig et al. 2011; Steckel et al. 2014; Santana et al. 2017). While certain species may tolerate local habitat changes, their responses at broader spatial scales can vary depending on the extent of land-use change (Levins 1968; Rolstad 1991; Andrén 1994). Raptors are particularly well suited to assess the effects of human activities over extensive land areas on biodiversity, because they require large territories and are highly sensitive to anthropogenic disturbances (Tinajero et al. 2017). Raptors form a polyphyletic group in which species from different evolutionary lineages share similar functional roles (Hertel et al. 2015; Montaña-Centellas et al. 2023). For example, both *Falco femoralis* (Falconidae) and *Elanus leucurus* (Accipitridae) act as important active predators in open habitats despite being phylogenetically unrelated. This ecological similarity between these two raptor species arises through convergent evolution rather than phylogenetic conservatism (Mindell et al. 2018). As top predators, these birds play key roles in regulating prey populations and maintaining ecosystem stability, and their occurrence is often associated with high levels of biodiversity (Ellis and Smith 1986; Sergio et al. 2008; O'Bryan et al. 2018). Consequently, raptors have been recognized as effective umbrella species and bioindicators for monitoring ecosystem health, habitat loss and environmental degradation (Sergio et al. 2008; Burgas et al. 2014; Cruz et al. 2021). Despite these critical ecological functions, raptors are among the most globally threatened vertebrate groups, primarily driven by ongoing land-use changes (McClure et al. 2018; O'Bryan et al. 2025).

In this study, we evaluated how the conversion of native grasslands and agro-pastoral matrix into landscapes progressively dominated by commercial forestry influences raptor alpha and beta diversity. Specifically, we aimed to (i) quantify the influence of increasing forestry cover and landscape heterogeneity on taxonomic, functional and phylogenetic alpha diversity (TAD, FAD and PAD); (ii) assess whether the three biodiversity facets show coupled responses to landscape-scale afforestation; and (iii) determine how taxonomic, functional and phylogenetic

beta diversity (TBD, FBD and PBD) change along the forestry gradient. Based on these goals, we proposed two contrasting predictions depending on how raptors respond to landscape transformation (or landscape afforestation): (i) if raptors perceive changes at the landscape scale regardless of patch configuration, their response should be driven primarily by the cumulative loss of original open habitats due to forestry cover expansion. Thus, we predict a coupled, monotonic decline across all three alpha diversity facets. Under this scenario, increasing forestry cover acts as a severe environmental filter that progressively excludes open-habitat specialists without a replacement by novel species, leading to simultaneous decreases in raptor TAD, FAD, and PAD (Emerson and Gillespie 2008). Conversely, (ii) if raptors are highly sensitive to local patches and spatial configuration, they should perceive the forestry expansion as an overall gain in habitat heterogeneity at least at early expansion stages (Tscharntke et al. 2012). In such a case, we predict that TAD, FAD, and PAD will show uncoupled, distinct tendencies along the forestry cover. In this scenario, raptor TAD is expected to exhibit a hump-shaped response to increasing forestry cover, with an initial increase driven by the incorporation of species associated within newly established habitats, followed by a decline as forestry becomes dominant and open-habitat specialists are excluded. Consequently, FAD would exhibit an asymptotic decline with increasing forestry cover, initially remaining stable due to functional redundancy among incoming generalists and disturbance-tolerant species, but decreasing once environmental filtering excludes specialized ecological functions. Finally, under this heterogeneous scenario, raptor PAD will exhibit a non-linear response similar to TAD, with initial increases at low to intermediate levels of forestry cover due to the incorporation of phylogenetically distant generalist species, followed by a decline at higher levels of forestry cover as strong environmental filtering promotes phylogenetic clustering.

Methods

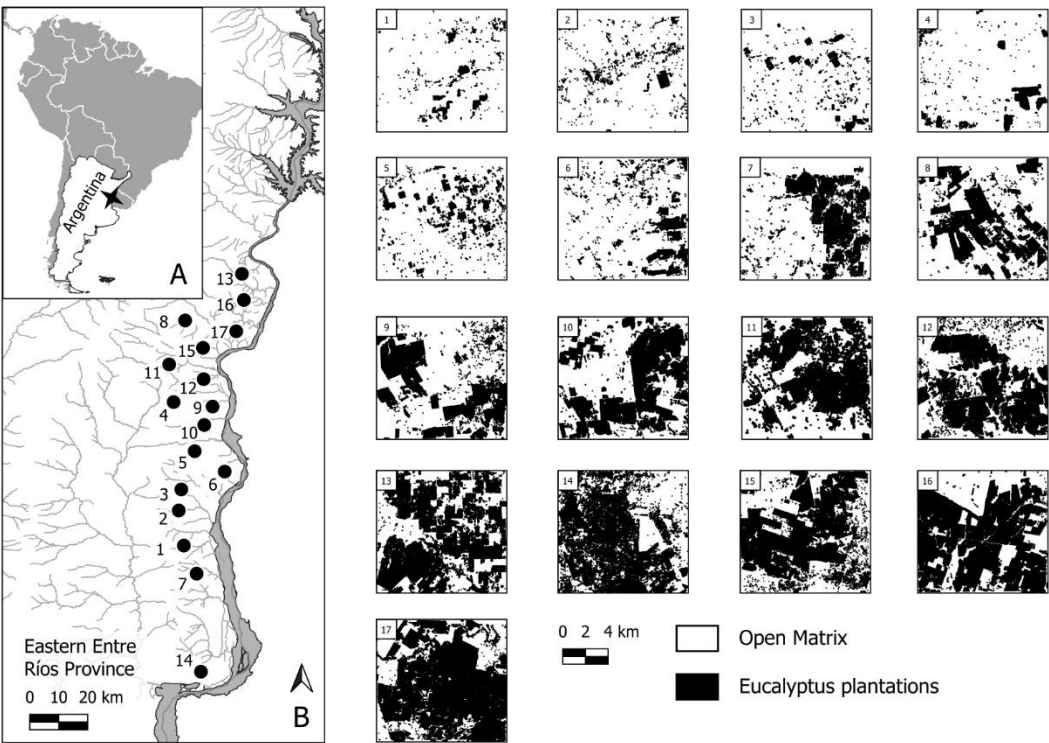
Study site

We conducted the study in the northeastern portion of the Mesopotamian Pampas (Cabrera 1971) located in Entre Ríos province, Argentina (32°06'S 59°18'W) (Fig. 1), which is characterized by a temperate climate. Annual precipitation is approximately 600 mm (Morrone 2001; Morello et al. 2012). Natural vegetation consists of grasslands, woodlands of scattered trees and riparian forests (Cabrera 1971; Morello et al. 2012). Nowadays, the landscape is dominated by a mosaic of agroecosystems, commercial forests, seminatural grasslands, and urban areas (Morello et al. 2012). The principal land uses are cattle and cropping (Morello et al. 2012), and to a lesser extent commercial forestry (Baldi et al. 2006). Commercial forestry in Argentina began in the 1950s; by 1980 the forested area was 51,931 hectares, reaching 231,200 hectares by 2012 (de la Peña 2016), and it is expected to continue growing due to government incentives (e.g., AFOA 2019). These commercial plantations are primarily established on the terraces of the Uruguay River and consist mostly of *Eucalyptus grandis* monocultures, along with a smaller proportion of other species such as *E. dunni*, *E. globulus*, *Pinus elliottii*, and *P. taeda* (Díaz and Tesón 2001).

General design and raptor survey

We delimited a total of 17 landscape cells (sites) of 100 km² each, with percentages of *Eucalyptus* plantations coverage ranging from 3.24 to 62.20% (Fig. 1). Within each cell, we first estimated the relative coverage of the different land-use types and then laid out five transects with a minimum linear distance of 1 km among them proportionally covering all environments within the cells. We sampled diurnal raptor species belonging to the avian orders Accipitriformes, Cathartiformes, Falconiformes, and Strigiformes using roadside surveys (Ellis et al. 1990). To minimize the influence of traffic on raptor detectability, we conducted surveys along unpaved secondary roads in a vehicle at a moderate speed (<40 km/h). All surveys were conducted by two trained observers, who recorded the identity and number of every raptor species detected within a range of 100 m. To maximize the detection of soaring raptors during peak thermal activity, each transect was surveyed once between 10:00 and 14:00 during the austral spring-

177 summer season (October to November 2023), restricting the sampling to days with clear skies
 178 and calm winds (Bunn et al. 1995; Vergara 2010).



179
 180 **Fig. 1** Map of study places in the eastern Entre Ríos province of Argentina. Panel A shows the
 181 location of Entre Ríos province within South America. Panel B displays the eastern region of
 182 Entre Ríos province and the location of the 17 surveyed cells (numbers 1–17), showing in light
 183 grey the Uruguay river basin. Panels 1-17 provide a detailed view of the surveyed cells indicating
 184 an increase in the proportion of forest cover. White areas primarily correspond to agricultural,
 185 livestock, urban, natural and other non-commercial forest land uses.

186 *Land use classification*

187 We quantified the proportion of each cell covered with different land-use types through a
 188 supervised random forest algorithm (Breiman 2001) in Google Earth Engine (Gorelick et al.
 189 2017), combining radar and optical imagery acquired in 2023, the same year as the raptor
 190 surveys. Land cover was classified into five categories based on the dominant vegetation type:

total *Eucalyptus* forest cover (%), cattle ranching cover (%), cropland cover (%), native vegetation cover (%), and urbanized cover (%) (Online Resource 1, Table S1). Classification accuracy was assessed with an error matrix (Congalton 1991), overall accuracy was 77.20% and Cohen's Kappa was 0.70 (Online Resource 2). Finally, land-use percentages within each cell were quantified through the package *landscapemetrics* (Hesselbarth et al. 2019) in R (R Core Team 2024).

Alpha diversity indices

We quantified three different alpha diversity indices using Hill numbers to allow comparisons between them. This family of indices expresses diversity as an “effective number of species” and differs in the weight given to species according to their relative abundance, as determined by the diversity order q (Chao et al. 2014). At $q = 0$ all species are weighted equally regardless of abundance (equivalent to species richness); as q increases, common species receive progressively more weight; at $q = 1$ each species contributes exactly in proportion to its own relative abundance, whereas at $q = 2$ common species are weighted disproportionately more than their actual frequency (Chao et al. 2014). We used $q = 1$ for all three facets because it provides a balanced measure that neither ignores rare species ($q = 0$) nor is dominated by the most abundant ones ($q = 2$). To estimate TAD of raptors within the cells, we used the *hill_taxa* function from the *hillR* package with the diversity order set to $q = 1$ (Li 2018; Chao et al. 2019). Regarding FAD, we selected a set of six functional traits (Table 1) related to raptor species life history and ecology, commonly used in studies analyzing the effects of land-use change on birds (López-Lanús et al. 2008; Wilman et al. 2014; Tinajero et al. 2017; Tobias et al. 2022). We computed pairwise functional dissimilarities between species by applying the *gawdis* function (de Bello et al. 2021) to our species-by-site and species-by-trait incidence matrices. We quantified FAD through the *alpha.fd.hill* function from the mFD package, with $q = 1$ and tau = mean (Magneville et al. 2022). To estimate PAD of raptors in the cells, we obtained a set of phylogenetic trees comprising our recorded species from the BirdTree database

(<http://birdtree.org/>; Jetz et al. 2012). We computed a consensus tree using the *consensus.edges* function in the phytools package (Revell 2012), which summarizes the phylogenetic relationships across the sampled trees. Finally, we quantified PAD through the *hill_phylo* function from the package hillR using $q=1$. Because FAD and PAD are not independent of TAD (Chao et al. 2014), we analyzed their relationship by comparing each facet through Spearman correlation with species richness at $q = 0$ versus $q = 1$, using Steiger's Z-test for dependent correlations (Steiger 1980), to test the influence of relative abundance on their species-richness dependence.

Table 1. Functional traits included for raptor species.

Trait	Trait measurement	Trait type
Primary lifestyle	Aerial, terrestrial, insessorial, or generalist	Qualitative
Diet specialization	Generalist or specialist	Qualitative
Habitat	Open areas or closed areas	Qualitative
Wing length	Length from carpal joint to tip of longest primary feather (mm)	Quantitative
Tail length	Length from base to tip of longest rectrix (mm)	Quantitative
Average weight	Average weight combining males and females (g)	Quantitative

Data analysis

To evaluate the effect of forestry expansion on the three facets of raptor alpha diversity, we fitted generalized linear models (GLMs) using TAD, FAD, and PAD as separate response variables. As explanatory variables, we included the percentage of forestry cover and compositional

landscape heterogeneity. The compositional landscape heterogeneity was calculated for each cell using the Shannon Diversity Index (SHDI) based on the proportions of the five land-use categories. These analyses were conducted using the *stats* package (R Core Team 2024). Because Hill numbers yield continuous positive values, all GLMs were built with a Gaussian family error distribution and *glm* function via the base R *stats* package. To validate our models, we evaluated residual normality and homoscedasticity using a simulation-based approach with the *DHARMA* package (Hartig 2022). Furthermore, we evaluated spatial autocorrelation in the model residuals by performing Mantel tests between the matrix of geographic distances among sites and the matrix of distances based on GLM residuals using the *mantel* function from the *vegan* package (Oksanen et al. 2024). Finally, we verified the absence of multicollinearity among our predictors using Spearman rank correlations with the *cor.test* function of the *stats* package.

To evaluate whether the three facets of raptor alpha diversity were coupled across sampling sites, we calculated Spearman correlations between all pairwise combinations of TAD, FAD, and PAD (Hill numbers, $q = 1$) using the *cor.test* function of the *stats* package. The correlation between TAD and FAD was computed using all 17 sites. Correlations involving PAD were restricted to the 15 sites (sites C1 and C17 excluded because Hill-number-based phylogenetic diversity is mathematically undefined for single-species assemblages). All analyses were conducted with a significance threshold of $\alpha = 0.05$. To evaluate phylogenetic trait conservatism, we tested phylogenetic signal in the six functional traits used to compute FAD. For the three quantitative traits, we calculated Blomberg's K and Pagel's λ using the *phylosig* function of the *phytools* package, and for the three qualitative traits, we calculated the D statistic of Fritz and Purvis (2010) using the *phylo.d* function of the *caper* package.

To assess how beta diversity was affected by land-use change, we performed nonmetric multidimensional scaling (NMDS) for each diversity facet using the *metaMDS* function of the *vegan* package (Oksanen et al. 2024). For TBD, the NMDS was performed directly on the species

abundance matrix, using Bray-Curtis dissimilarity as the default distance measure. For FBD and PBD, the NMDS was performed on the normalized Hill-number pairwise dissimilarity matrices previously computed for each biodiversity facet. The relationship between the NMDS ordination space and the forestry cover gradient was visualized by fitting a smooth surface using the *ordisurf* function of *vegan*. For the taxonomic NMDS, species were projected onto the ordination space as passive weighted-average scores using the default biplot scores from *metaMDS*. For functional and phylogenetic NMDS, functional traits (as community-weighted means, CWM) and species abundances were projected onto the ordination space using the *envfit* function of *vegan* (999 permutations). Since the functional space was built using CWMs, quantitative traits were included directly as continuous CWM values, computed as the abundance-weighted average of each trait across species present at each site. Qualitative traits were included as the abundance-weighted proportion of species at each site belonging to each trait state (Lavorel et al. 2008). All statistical analyses were conducted in the R environment, version 4.4.0 (R Core Team 2024).

Results

We recorded a total of 153 individuals representing 12 diurnal raptor species across the sampled sites. Species recorded were *Athene cunicularia* (7), *Buteo magnirostris* (31), *Buteogallus meridionalis* (1), *Caracara plancus* (68), *Cathartes aura* (2), *Coragyps atratus* (7), *Falco femoralis* (2), *Falco sparverius* (25), *Geranospiza caerulescens* (1), *Milvago chimachima* (2), *Parabuteo unicinctus* (3), and *Rostrhamus sociabilis* (4). *Eucalyptus* plantation cover ranged from 3.24% to 62.20%.

Spearman test correlations revealed no significant association between forestry cover and landscape heterogeneity ($r_{\text{Spearman}}=0.468$, $P = 0.058$). The correlation between PAD and TAD was significantly lower at $q = 1$ ($r_{\text{Spearman}} = 0.550$, $P = 0.034$) than at $q = 0$ ($r_{\text{Spearman}} = 0.805$, $P < 0.001$; Steiger's $Z = 2.57$, $P = 0.010$), indicating that the abundance-weighted PAD metric captures ecological information beyond species richness. For FAD, the correlation with TAD did not differ

significantly between $q = 0$ ($r_{\text{Spearman}} = 0.888$, $P < 0.001$) and $q = 1$ ($r_{\text{Spearman}} = 0.856$, $P < 0.001$; Steiger's $Z = 0.62$, $P = 0.533$), indicating that FAD dependence on species richness remained similar. When evaluating the influence of landscape transformation on raptor alpha diversity, GLM analyses revealed that forestry cover did not affect any of the biodiversity facets (Table 2; Fig. 2a-c). In contrast, TAD and FAD exhibited a significant and coupled negative response to increasing landscape heterogeneity, whereas phylogenetic diversity was unrelated to either forestry cover or landscape heterogeneity (Table 2 and Fig. 2d-f).

Table 2. Results from GLMs with Gaussian link function and analysis of deviance (Type II LR tests) for predicting TAD, FAD and PAD (Hill numbers, $q = 1$) of raptor species in 100 km² cells in eastern Entre Ríos province.

Variable	Standardized Coefficient	Standardized SE	P-value	Deviance explained (%)
<i>Taxonomic Alpha Diversity</i>				
<i>Forestry cover (%)</i>	0.08	0.26	0.748	0.68
<i>Heterogeneity (SHDI)</i>	-0.55	0.26	0.036*	29.05
<i>Functional Alpha Diversity</i>				
<i>Forestry cover (%)</i>	-0.13	0.14	0.339	15.63
<i>Heterogeneity (SHDI)</i>	-0.31	0.14	0.026*	84.23
<i>Phylogenetic Alpha Diversity</i>				
<i>Forestry cover (%)</i>	5.05	0.16	0.760	0.02
<i>Heterogeneity (SHDI)</i>	-15.86	0.16	0.338	0.24

Significance codes: * $P < 0.05$. Standardized coefficients and SE from GLM summary (scaled predictors). P-value from type II test ANOVA. Deviance explained (%) = $LR \chi^2 / \text{Null deviance} \times 100$ (Type II tests). Forestry cover = total *Eucalyptus* forestry cover (%); Heterogeneity (SHDI) = landscape heterogeneity index.

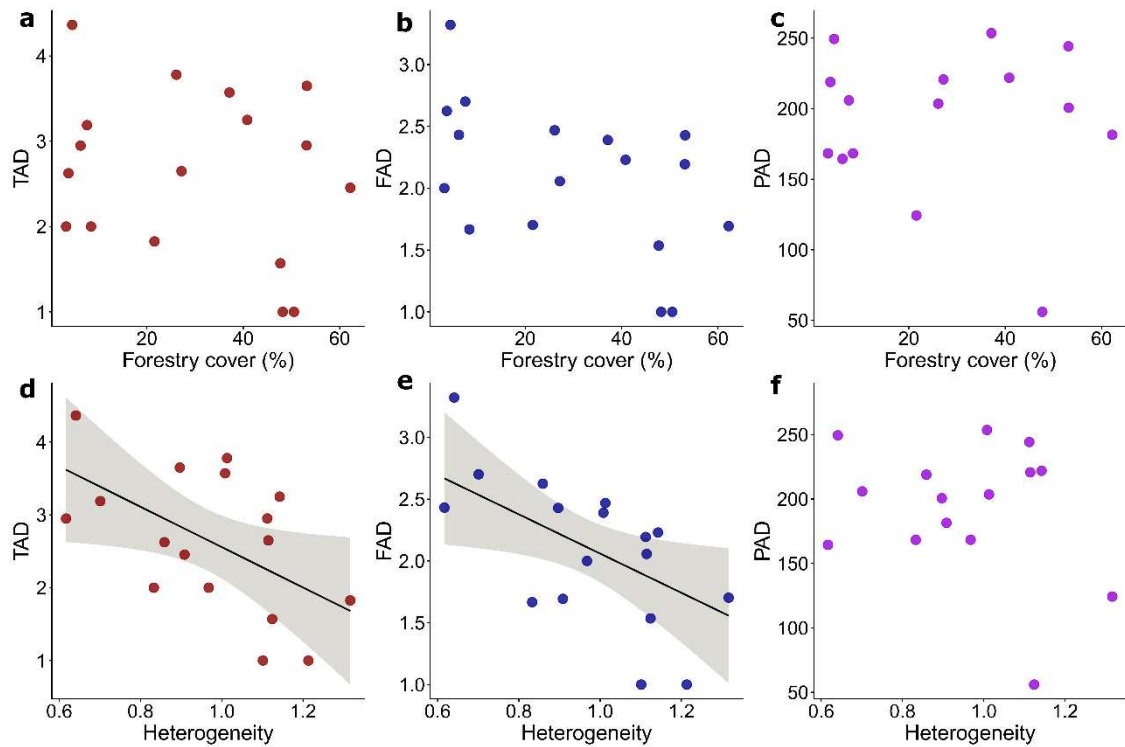


Fig. 2 Relationship between raptor taxonomic (TAD), functional (FAD), and phylogenetic (PAD) alpha diversity and the two landscape predictors. (a-c) TAD, FAD, and PAD in relation to forestry cover. (d-f) TAD, FAD, and PAD in relation to landscape heterogeneity. Lines represent fitted values from the GLMs, visualized using the *ggplot2* and *visreg* packages. A solid line indicates a statistically significant relationship ($P < 0.05$). The shaded area around each line indicates the 95% confidence interval of the prediction.

Spearman test correlations revealed significant positive associations among all three facets of raptor alpha diversity, indicating that the three biodiversity facets were coupled across sampling sites. TAD and FAD showed a positive association ($r_{\text{Spearman}} = 0.850$, $P < 0.001$). TAD and PAD were also positively and significantly correlated ($r_{\text{Spearman}} = 0.714$, $P = 0.003$). The correlation between FAD and PAD was positive and significant ($r_{\text{Spearman}} = 0.542$, $P = 0.037$). Phylogenetic signal in the functional traits revealed that the insessorial and terrestrial primary-lifestyle categories departed significantly from a random distribution across the phylogeny ($D = -0.67$; $P = 0.015$ and $D = -1.39$; $P = 0.002$, respectively) but did not differ significantly from a Brownian motion model

of evolution ($P = 0.736$ and $P = 0.897$, respectively), indicating significant phylogenetic signal.

The remaining qualitative traits (generalist and aerial lifestyle, diet specialization, and habitat; $D = -1.18$ to 1.30 , $P = 0.105$ – 0.585) showed no significant phylogenetic signal. The three quantitative traits (average weight, wing length, and tail length; Blomberg's $K = 0.54$ – 0.67 , $P = 0.057$ – 0.090) showed no significant phylogenetic signal.

The two-dimensional NMDS ordinations represented raptor assemblages, with stress values of 0.108 for taxonomic, 0.097 for functional, and 0.117 for phylogenetic facets. The ordisurf revealed that forestry cover significantly structured the taxonomic ordination space ($R^2_{\text{adj}} = 0.271$, $P = 0.041$), separating high-cover afforested sites from open agro-pastoral sites (Fig. 3a).

Sites with high forestry cover were characterized by an association with *Buteo magnirostris*, whereas *Buteogallus meridionalis* and *Coragyps atratus* were associated with intermediate-to-high forestry cover. Conversely, *Athene cunicularia* was positively associated with open habitats characterized by low forestry cover. A similar pattern was observed for FBD (Fig. 3b), where forestry cover significantly structured the ordination ($R^2_{\text{adj}} = 0.306$, $P = 0.030$). Grassland habitat affinity, dietary specialization, wing length, and tail length were associated with low forestry cover, whereas an insessorial perching lifestyle characterized sites with high forestry cover. In contrast, forestry cover did not significantly structure the phylogenetic ordination ($R^2_{\text{adj}} = 0.035$, $P = 0.315$), indicating no phylogenetic association across the forestry gradient (Fig. 3c).

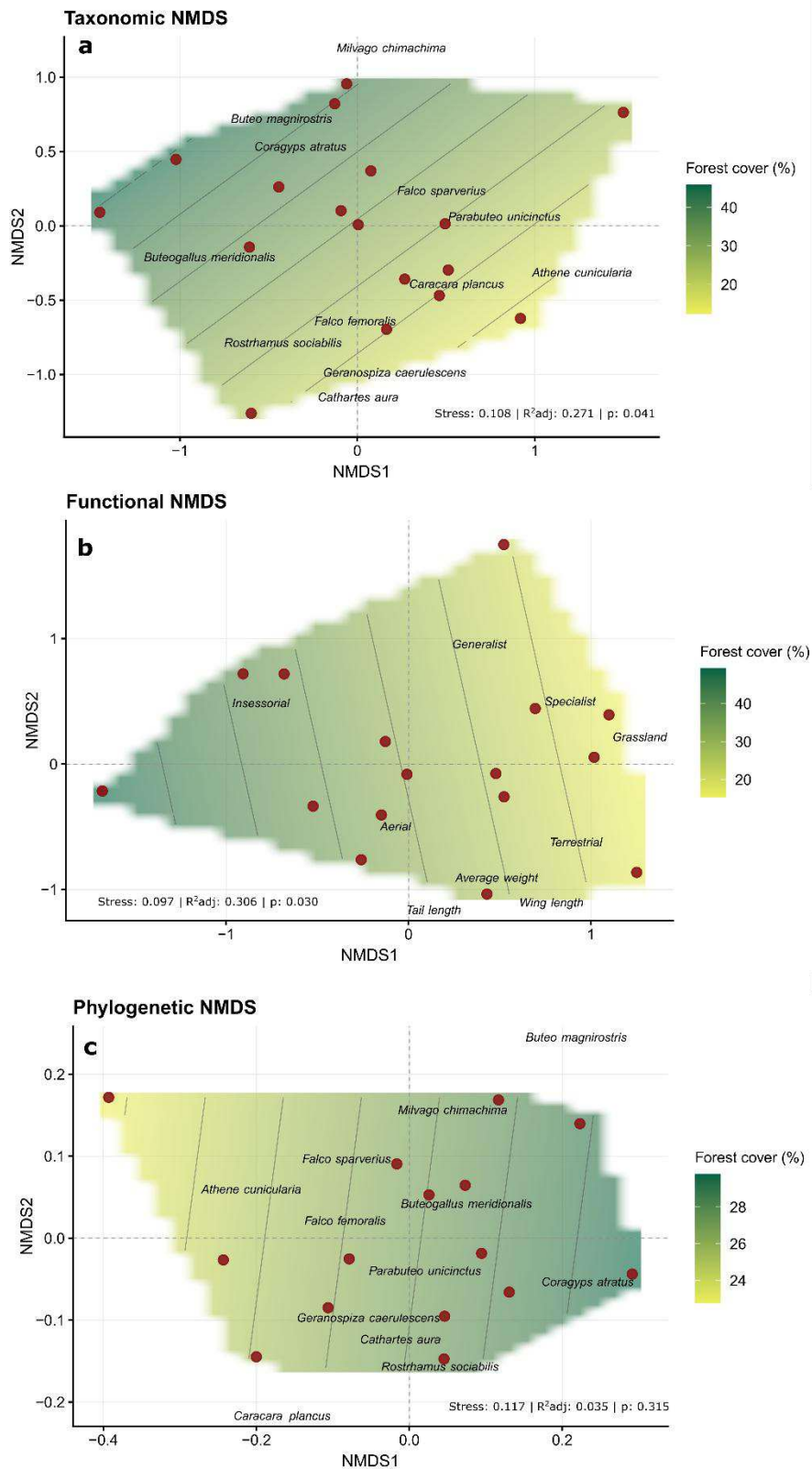


Fig.3 Non-metric multidimensional scaling of raptor beta diversity across sampling cells in the Pampean ecoregion. The background surface represents the *Eucalyptus* forestry cover gradient (%) fitted using a generalized additive model, colored from yellow (low forestry cover) to dark

green (high forestry cover); the statistical significance of the fitted surface is indicated for each panel. (a) Species were projected onto the ordination space as passive abundance-weighted centroid scores. (b) Functional traits were projected as CWMs using the *envfit* function (999 permutations). (c) Species were projected onto the ordination space using *envfit* (999 permutations).

Discussion

We found that the expansion of *Eucalyptus* commercial plantations into the Mesopotamian Pampas of Argentina influenced raptor alpha diversity facets in different ways, diverging from the traditional assumption of simultaneous biodiversity loss (Mayfield et al. 2010; Romero-Muñoz et al. 2021). Although TAD, FAD and PAD were positively coupled across sampling sites, which may reflect shared responses to common environmental gradients (Devictor et al. 2010; Meynard et al. 2011), their responses to landscape transformation were not similar. In turn, raptor TBD and FBD shifted significantly across the forestry gradient, whereas PBD did not. Taken together, our findings suggest that raptors perceived landscape-level afforestation primarily as a loss of their natural open habitat rather than a gain in novel resources (Fahrig 2003; Phifer et al. 2017). These results underscore how the loss of grasslands and other open areas driven by extensive land-use change might affect native raptor assemblages, with effects varying depending on the biodiversity facet considered.

Contrary to what we expected, the expansion of *Eucalyptus* plantations *per se* did not influence raptor TAD, FAD, or PAD. These results reject both our first prediction of a coupled, monotonic decline of the three biodiversity facets along the forestry cover, and our second prediction of uncoupled, non-linear trajectories driven by the integration of novel resources. This lack of response may suggest that forestry neither provides substantial new resources for raptors nor necessarily eliminates those available in the pre-existing agro-pastoral landscape. Because the Mesopotamian Pampas had already been extensively transformed before the establishment of

commercial forestry (Morello et al. 2012), the regional raptor species pool may be dominated by phylogenetic lineages already capable of tolerating human-modified landscapes (Vaccaro and Filloy 2022). This result suggests that the historical conversion of the Pampas grasslands may have filtered out the most sensitive species before afforestation began. Accounting for such land-use histories is particularly relevant in South America, where successive waves of agricultural and forestry expansion have overlapped within a few decades. However, we found that increasing landscape heterogeneity drove a coupled decline in TAD and FAD, while leaving PAD completely unaffected. This result supported our first hypothesis, that raptors perceive landscape-level changes primarily as a loss of suitable native open habitats rather than as a gain in resource diversity. Nevertheless, our results also revealed that these responses were triggered by the spatial composition of the matrix rather than forestry cover per se, indicating that highly mixed mosaics with no dominant open habitat act as a harsh environmental filter for raptors. This landscape transformation reduces the availability of large, continuous hunting territories required by most raptor species (Newton 2010; Tinajero et al. 2017), as increasing landscape heterogeneity decreases the contiguous area of open habitats, triggering an area–heterogeneity trade-off (Allouche et al. 2012) that ultimately excludes open-habitat specialists (Flynn et al. 2009). Crucially, the fact that PAD remained stable despite the significant loss of species and trait diversity implies that the species excluded by heterogeneity are phylogenetically redundant; that is, their evolutionary lineages remain represented by the disturbance-tolerant species that persist in the community (Montaño-Centellas et al. 2023). Integrating the three biodiversity facets revealed that raptor ecological functions and species richness are highly vulnerable to the landscape transformation driven by heterogeneous productive mosaics, whereas the evolutionary history of raptors contained in our study region was resilient to current landscape homogenization.

Although raptor alpha diversity did not respond to forestry cover, beta diversity did, indicating that forestry cover reshaped species identity rather than overall richness. This result supported

the principal mechanism proposed in our first hypothesis, that afforestation acts as an environmental filter replacing specialized grassland species with forest-associated generalists. Specifically, the association between high forestry cover and *Buteo magnirostris* is explained by its ecology as a forest-edge generalist that relies heavily on perching structures for both hunting and nesting, allowing it to benefit from tree cover expansion in modified Neotropical landscapes (Bierregaard et al. 2024). *Eucalyptus* plantations provide abundant perching and nesting substrates that this species can use. In contrast, *Coragyps atratus* was associated with open, intermediate forest-cover sites, reflecting its biology as an obligate scavenger that requires open terrain to detect carcasses through wide-ranging soaring flight (Buckley et al. 2022). Furthermore, *Athene cunicularia* exhibited a strong affinity for open areas, reflecting its specialized diet and dependence on open grassland habitats for hunting (Bellocq 1997). In the case of *Caracara plancus*, its association with open and intermediate areas aligns with its highly opportunistic, omnivorous nature; while it effectively exploits open terrain for foraging, its broad niche breadth allows it to navigate heterogeneous, human-modified landscape configurations with relative tolerance (Tinajero et al. 2017).

At the functional level, the conversion of open habitats into tree plantations restructured the morphological and behavioral traits of raptor assemblages. Our analysis of functional beta diversity analysis indicated that forestry cover drove a functional shift from assemblages dominated by large-bodied, long-winged, grassland-specialist soaring raptors towards assemblages characterized by smaller, perching generalists capable of exploiting structurally complex and closed habitats (Flynn et al. 2009; Vaccaro et al. 2019). In contrast, our phylogenetic analysis revealed no consistent structuring of PBD across the forestry cover gradient. This decoupled response between TBD, FBD and PBD can be explained through raptor evolutionary history. The species that responded most positively to the *Eucalyptus* gradient belong to deeply divergent lineages; specifically, *Buteo magnirostris* and *Rostrhamus sociabilis* (Accipitriformes), *Cathartes aura* (Cathartiformes) and *Caracara plancus* (Falconiformes), which represent three

phylogenetically independent lineages (Prum et al. 2015; Montaña-Centellas et al. 2023). As raptors constitute a polyphyletic group characterized by evolutionary convergence, several of the ecological traits differentiating these species along the gradient have evolved independently across multiple lineages (Hertel et al. 2015; Mindell et al. 2018). Consistent with this, phylogenetic signal was largely absent for diet specialization, habitat association, and body size, indicating low phylogenetic niche conservatism for the trait combination that differentiates species along the forestry gradient (Losos 2008; Wiens et al. 2010). However, foraging-stratum traits (insectivorous and terrestrial primary lifestyle) did show significant, Brownian motion-consistent phylogenetic signal, indicating that phylogenetic conservatism is not uniformly absent across all functional traits, but rather concentrated in a specific trait dimension. This suggests that the forestry matrix acted as a convergent ecological filter operating on a particular subset of traits (diet, habitat association, body size) rather than as a phylogenetic filter that would systematically exclude or retain entire clades (Vaccaro and Filloy 2022). However, this apparent phylogenetic resilience might reflect a temporal lag, given that commercial afforestation in the region began only approximately 70 years ago. Persistent habitat conversion could eventually breach the historical niche conservatism of open-habitat lineages, eroding the phylogenetic diversity of Pampean raptor communities over longer temporal scales (Mastrogianni et al. 2024).

Our NMDS analyses showed that the taxonomic and functional turnover along the gradient was not random but structured by forestry cover. Sites with similar forestry cover supported similar taxonomic and functional assemblages, indicating that commercial forestry imposed an environmental filter on assemblage composition across the Pampean grasslands (Corbelli et al. 2015; Santoandré et al. 2019). These results also support our prediction that forestry cover acts as a strong environmental filter. Interestingly, landscape heterogeneity explained additional variation exclusively for functional beta diversity. This suggests that, although forestry cover acts as the primary driver of taxonomic turnover, landscape heterogeneity further modifies the

distribution of ecological strategies independently of the amount of forestry itself (Perović et al. 2015). Heterogeneous landscapes alter habitat resources and prey availability, forcing an additional functional restructuring of raptor assemblages (Martínez-Ruiz et al. 2020). In contrast, PBD remained insensitive to all landscape predictors, reinforcing the idea that forestry cover did not selectively reaccommodate evolutionary lineages. Instead, assemblage turnover occurred within the same raptor clades, producing substantial ecological reorganization while maintaining a remarkably stable phylogenetic structure across the landscape. Our analysis provided complementary evidence that forestry cover reorganized raptor communities primarily through taxonomic and functional sorting rather than phylogenetic filtering (Corbelli et al. 2015; Vaccaro and Filloy 2022). Taken together, these results suggest that increasing *Eucalyptus* forestry cover drove a TBD and FBD shift among raptor assemblages across the forestry gradient, whereas phylogenetic structure remained unresponsive to landscape change. Afforestation is being promoted worldwide as a climate mitigation strategy, often without considering the biodiversity of native grasslands (Veldman et al. 2015). Our results suggest that the effects of such policies depend less on plantation extent than on how plantations reconfigure the composition of the landscape mosaic, a pattern that may also apply to other grassland regions undergoing tree planting.

Conclusion

Our findings revealed that the conversion of native grasslands into commercial *Eucalyptus* plantations in the Mesopotamian Pampas of Argentina drove a decoupled, facet-dependent reorganization of raptor biodiversity that cannot be fully captured by any single diversity metric alone (Devictor et al. 2010). Raptor alpha diversity was insensitive to the amount of forestry cover per se, but landscape heterogeneity drove a significant and coupled decline in TAD and FAD while leaving PAD unaffected. This pattern indicated that afforestation acted primarily as an indirect driver of local biodiversity loss through the diversification of land uses and the

associated reduction in open habitat, rather than through the direct displacement of species by novel forest structures (Fahrig 2003; Phifer et al. 2017). In contrast, afforestation selectively filtered species according to their ecological strategies, without corresponding changes in the evolutionary history contained in the regional species pool. Consequently, assessments based solely on one facet of biodiversity would substantially underestimate the ecological consequences of afforestation. From a landscape planning perspective, maintaining extensive areas of native grasslands and open habitats, and minimizing their transformation by forestry mosaics, should be prioritized over simply limiting plantation extent. Incorporating landscape composition into the design of forestry policies would help reconcile productive expansion with biodiversity conservation in South American grasslands. Future studies should evaluate whether the apparent resilience of the phylogenetic facets represents a transient legacy of recent land-use change or whether prolonged afforestation will ultimately erode the evolutionary history of Pampean raptor assemblages via local extinction.

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Statements and Declarations

Funding: This work was funded by UBACyT grant 2026 and CONICET PIP grant 2026. K.T. was supported by a doctoral scholarship from CONICET and the UBA.

Competing interests: The authors have no relevant financial or non-financial interests to disclose.

Author contributions: Kevin Tkach, José Oddi, Fabricio Villalobos, and Julieta Filloy contributed to the study conception and design. Data collection and analyses were performed by Kevin Tkach and José Oddi. Fabricio Villalobos and Julieta Filloy supervised the work and critically revised the manuscript. Julieta Filloy acquired funding for the study. The first draft of the manuscript was written by Kevin Tkach, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

748 The datasets generated and analysed during the current study are available in OSF repository,
749 https://osf.io/csm5a/overview?view_only=cbf627683d89479884f5659a613d844f

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