Title: Insights on global rangeland ecosystem services shaped by grazing and fertilization

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Abstract:

Rangelands are crucial to human wellbeing, but their ability to provide ecosystem services is threatened. We 1) quantified key ecosystem services provided by rangelands; 2) assessed short- and longer-term impacts of grazing exclusion and fertilization on services; and 3) identified synergies and trade-offs between services. We measured indicators of ecosystem services and plant diversity at 79 rangeland sites across six continents in the global Nutrient Network experiment. Short-term grazing exclusion increased forage quantity and soil fertility but longer-term exclusion decreased them along with plant richness and pollination. Fertilization improved forage provisioning, soil stability, climate regulation, and the control of soil erosion but reduced plant diversity and related services especially after prolonged application. We found synergies between plant diversity and pollination, and soil fertility, stability, and climate regulation. Trade-offs between forage stability and quality persisted after fertilization but disappeared with grazing exclusion. Alternative management actions may sustain livestock production while maintaining rangeland ecosystem services.

In a nutshell

-Rangelands provide essential ecosystem services demanded by human society, including forage provisioning, carbon sequestration, pollination, and biodiversity conservation.

-By using the multiple ecosystem services approach and standardized global data, we described the worldwide provision of rangeland ecosystem services and determine management strategies that ensure the sustainability of rangeland ecosystems.

-We showed that potential benefits of rangeland fertilization and grazing exclusion may entail trade-offs arising from lost plant diversity and long-term delivery of regulating ecosystem services.

-Our study generated important information for rangeland sustainability and illustrates how ecological experiments can inform natural resource management.

Keywords: Ecosystem services, Nutrients, Livestock production, Global change, Herbivores, Grasslands

Introduction

Rangelands comprising grasslands, savannas, shrublands, deserts, steppes, tundra, subalpine and alpine grasslands, and marshes (Carbutt et al., 2017; Yahdjian & Sala, 2008), span all continents, occupy more than 50 % of terrestrial land, and are biologically diverse (Rangeland Atlas, 2021). Rangelands provide a wide variety of critical regulating, cultural, provisioning, and supporting ecosystem services (Sala et al., 2017). Ecosystem services (i.e., nature's contribution to people sensu Díaz et al., 2015) are the different goods and benefits that society can obtain directly or indirectly from natural ecosystems (Daily, 1997). Biodiversity at different levels (e.g., genes, species, and ecosystems) can support ecosystem processes and functions and therefore may also elevate human well-being (Soliveres et al., 2016). Even though rangelands produce multiple, varied ecosystem services (Sala et al., 2017), their utility is undervalued by society, particularly when compared with tropical or temperate forests (Bardgett et al., 2021).

Increasing anthropogenic pressures for food production or urbanisation are rapidly transforming rangelands, reducing biodiversity, and increasing nutrient loads, with feedback to the climate system (Díaz et al., 2015). Indeed, contemporary intensive livestock production has transformed natural grasslands, reducing wild herbivore populations, plant diversity, and ecosystem functioning (Maestre et al., 2022). Replacement of native with domestic grazers can reduce native plant diversity, especially when exotic plant species are introduced accidentally or deliberately to increase livestock production (Paudel et al., 2023). The loss of native plant species can dramatically change plant community composition as well as having negative effects on ecosystem functioning (Tilman et al., 2014). Land management practices, which sometimes result in fertilization or exclusion of grazers, often alter ecosystem processes and drivers (Allan et al., 2015; Bardgett et al., 2021). Fertilization of rangelands used to increase forage quantity and quality for livestock is not a widespread practice in arid and semi-arid lands, but this form of intensification is happening more frequently in mesic rangelands (Paudel et al., 2023) as well as contamination with nutrients from nearby cropland. The increase in nutrient loads can further contribute to biodiversity loss, although big herbivores that reduce biomass, increase light and recover or maintain diversity that would otherwise be lost under fertilized conditions may compensate this negative effects (Borer et al., 2020). Reduction in plant diversity can lead to losses of forage temporal stability (Chen et al., 2023; Hautier et al., 2020) and reduces the diversity of higher trophic levels that depend on native plant biodiversity (Maestre et al. 2022).

Many rangelands are managed for forage production to support the production of domestic herbivores, mainly cattle, goats, horses, and sheep, and their associated marketable goods, such as milk, meat, leather, or wool (Bengtsson et al., 2019; Sala et al., 2017). However, management favouring livestock production can compromise other ecosystem services (Petz et al. 2014). While currently lacking, a framework including correlations among multiple ecosystem services will reveal the ecosystem services most likely to trade-off and those most likely to provide synergies. Synergies between ecosystem services can occur when land management that improves one type of ecosystem service is associated with or in some cases leads to improvements in others (Bennett et al., 2023). These co-varying ecosystem services often share underlying ecosystem processes and biophysical drivers. For example, reducing the number of animals or implementing temporary resting times can increase soil carbon sequestration as well as soil water holding capacity and fertility (Oñatibia et al., 2015).

Besides the exploitation of rangelands, it is also interesting to know whether short-term herbivory exclusion is a way to restore rangeland biodiversity and ecosystem services (Bradford, 2014). Biodiversity conservation can lead to indirect benefits such as reduced greenhouse gas emissions (Piñeiro-Guerra et al., 2019; Standish & Prober, 2020), increase pollination (Garibaldi et al., 2014), and control invasive species (Beaury et al., 2020; Kennedy et al., 2002). Restoring native biodiversity can also increase biomass production (Tilman et al., 2014) and biomass stability (Isbell et al., 2018), i.e. the consistency or invariability of plant biomass production over time which is particularly important for extensive livestock production that relies on native forage (Maestre et al. 2022). By understanding how livestock management such as short-term herbivory exclusion or fertilization affect the delivery of potentially related ecosystem services, it may be possible to identify alternative management strategies that minimise trade-offs (Maestre et al. 2022: Petz et al. 2024). Therefore, the conceptual framework developed under the science of ecosystem services can be adopted as a general approach to assess the consequences of human activities in rangelands (Allan et al., 2015; Tamburini et al., 2016).

The objectives of this study are to 1) quantify indicators of the different types of ecosystem services provided by global rangelands; 2) evaluate short and longer-term changes in these indicators in response to rangeland management practices (fertilization, herbivory exclusion, and their combination); and 3) identify synergies and trade-offs among indicators of rangeland ecosystem services and assess changes with management practices. To meet these objectives, we used data from a globally distributed experiment, the Nutrient Network, in which we measured indicators of provisioning, supporting, and regulating services, along with plant diversity at 79 rangeland sites across six continents (Borer et al., 2014; https://nutnet.org/). Therefore, the ecosystem services emerged from the variables commonly used as indicators to describe ecosystem services in ecological studies (i.e. Maestre et al., 2022) and that were measured at all sites in a standardized manner during the experiment. For most sites, this includes a standardised experimental and sampling design of nutrient addition and exclusion of large herbivores with fences in a complete factorial experiment (Borer et al., 2014; Appendix S1: Section S1). As such, the treatments simulate rangeland management practices: fertilizer application (Paudel et al., 2023), grazing management (herbivory exclusion; Oñatibia et al., 2015), and their combination (Briske et al., 2023). To tease apart the role of domestic vs. wild grazers in the delivery of multiple ecosystem services in rangelands, we categorised sites considering the presence of domestic livestock versus wild grazers (large mammals). The herbivory exclusion in these categories can be seen as different scenarios of change in rangelands where longer-term exclusion of wild herbivores may inform the consequences of defaunation (Dirzo et al., 2014; Risch et al., 2018).

Methods

Site selection and rangeland classification criteria

We used data from 79 grassland sites participating in the Nutrient Network (NutNet), including herbivory exclusion and/or nutrient addition factorial experiment (Borer et al., 2014; Appendix S1). Sites span six continents (Fig 1.a), representing a wide range of climate, elevation, and management practices (Fig. 1b). All sites have wild vertebrates but some of them have domestic large vertebrate grazers. We classified sites into three categories (Fig 1.a., Appendix S1: Table S1):

a. *Current livestock*: grazed by domestic livestock.

b. *Recent livestock*: grazed by domestic livestock until the start of the experiment.

c. *Wild grazers*: grazed by wild vertebrate herbivores only. Not grazed by domestic livestock for at least 10 years before the start of the experiment.

NutNet experimental design and site data collection

Most sites (n=70) established a replicated factorial of nutrient addition (nitrogen, phosphorus, potassium, and micronutrients), and large herbivores grazing exclusion (called herbivory exclusion from now on) experiment arranged in blocks. A few sites (n=8) only conducted the nutrient addition without herbivory exclusion, and one site conducted only the herbivory exclusion treatment (see Appendix S1: Table S1). Treatments commenced at most sites in 2008 and continued through 2022 (1 to 14 years of treatments when we compiled the data). Most ecosystem service indicators (see below) were measured every year, but those related to soil variables were recorded every three years. Consequently, we used 1-3 years for short and 6-8 years for longer-term responses of ecosystem services to these management practices.

Selection of ecosystem service indicators

We used ecosystem variables to quantify three provisioning ecosystem services (forage quantity, forage chemical quality, forage physical quality), three supporting services (forage stability, soil fertility, soil stability), and eight regulating services (erosion control, control of soil acidification, regulation of water quantity and quality, carbon storage, resistance to plant invasion, pest control, pollination; Appendix S1: Table S2). In addition, we identified three plant biodiversity variables closely related to the provisioning of ecosystem services (alpha richness, beta diversity, native diversity; Appendix S1: Section S2). These 17 variables are commonly used in ecological studies to describe ecosystem services (Bardgett et al., 2021; Hautier et al., 2018; Maestre et al., 2022).

Data analyses

We described the different categories of ecosystem services provided by global rangelands and examined the co-variation among the entire set of ecosystem services across sites by performing a probabilistic principal component analysis (pPCA) using data from pre-treatment and control plots of all year's data (Tipping & Bishop, 1999).

We used a log response ratio to evaluate how large herbivores grazing exclusion (as part of rotational grazing management) and/or fertilization can influence plot-level ecosystem service indicators and the provisioning of ecosystem services in short (1-3 years) and longer (6-8 years) time periods (Hedges et al., 2016). We performed t-tests ($\alpha = 0.05$) to evaluate if management practices modified ecosystem services in relation to the ambient condition.

We prepared radar plots according to rangeland classification for indicators measured in control plots (all years) and for the short (1-3 years) and longer-term (6-8 years) effects of excluding large herbivores with fences, fertilization, and their interaction (*fmsb* package in R library; Nakazawa M., 2022).

We calculated Spearman correlations between ecosystem services to identify synergies and trade-offs between ecosystem services across different management practices. All analyses were performed with R version 4.2.2 ('cor' function from corrr package, R Core Team, 2019). The database used for this study was the NutNet January 2022 complete set of variables.

Results

Ecosystem services provided by global rangelands

The first two axes of the probabilistic principal component analysis (pPCA) explained 30% and 22% of the total variance in ecosystem service indicators across rangelands, respectively (Fig. 2). The three rangeland categories (current livestock, recent livestock, and wild grazing, all unfertilized) offered similar delivery of ecosystem services under ambient conditions evidenced by substantial overlap in multivariate space, as represented by their 95% confidence ellipses. Axis 1 was primarily associated with supporting and regulating services, while Axis 2 was more related to provisioning services. Plant diversity metrics contributed to both axes. Forage quantity was orthogonal to alpha plant richness, native diversity, and pollination. In contrast, invasion resistance and forage stability were positively associated with plant diversity indicators. This ordination highlights that no strong gradients separate rangeland categories in terms of overall ecosystem service delivery, emphasizing the similarity of service bundles provided by these systems despite their different management histories.

Alterations in rangeland ecosystem services in response to experimental treatments

The three treatments fertilization, herbivory exclusion, and its combination affected ecosystem services both similarly and differently. For instance, the three had similar positive effects on forage quantity and negative effects on soil acidification, pollination, and alpha plant species richness, although they varied in magnitude with the combined treatments having the largest effect (Fig. 3). Soil fertility was the only supporting service that increased with herbivory exclusion, whereas fertilization alone, and combined with exclosures, significantly increased soil stability, climate regulation, water quality, and erosion control (Fig. 3b and 3c). Across these study sites, invasion resistance and plant beta diversity were unaffected by short-term fertilization or large herbivore exclusion (Fig. 3). Considering the multiple ecosystem services, In the short-term herbivory exclusion produced the smallest changes whereas fertilization produced the largest changes (Fig. 4). By contrast, fertilizing grazed rangelands significantly changed most ecosystem services, increasing seven and decreasing two (Fig. 4b). Fertilization also reduced plant richness and native diversity but had no significant effect on beta plant diversity (Fig. 4b). When fertilization was combined with large herbivore exclusion, the general effects on the delivery of multiple ecosystem services were like those for fertilization alone (Fig. 4c).

Changes in ecosystem services delivered in global rangelands in the longer-term (>6 years) were consistent although magnified from those observed in the short-term, particularly for fertilization (Table 1, Appendix S1: Fig. S2). For the herbivory exclusion, several short-term effects disappeared in the longer-term, such as forage provisioning, soil fertility, and the reduction in soil acidification and pollination. Radar plots also showed similarities between the short and longer-term effects, with exclosures producing smaller changes in ecosystem services than fertilization alone or combined with exclosures (Appendix S1: Fig. S3).

Alterations in synergies and trade-offs of ecosystem services in response to experimental treatments

Under ambient conditions (control), we identified synergies among plant-focussed services related to alpha plant species richness, native plant diversity, and pollination, and the supporting services of soil fertility, soil stability, and climate regulation (Fig. 5a). We also identified trade-offs between forage stability and the physical and chemical quality of the forage (Fig. 5a). The treatments did not significantly change this pattern, although herbivory exclusion reduced the trade-offs and even reversed the correlations among forage chemical quality, climate regulation, and supporting services (Fig. 5b). In contrast, with fertilization the positive relationship among pollination and native plant diversity disappeared (Fig. 5c). The combination of herbivory exclusion and fertilization reduced the trade-offs between forage quality and forage stability, maintaining the negative correlation with the physical but not chemical quality of forage (Fig. 5d).

Discussion

Rangelands provide a wide variety of ecosystem services (Appendix S1: Panel S1) and are thus important to human well-being. Here we used a standardized global experiment to quantify multiple ecosystem services in rangeland worldwide. We found that sites with the greatest forage provision differed from those with the highest stability of forage and services related to plant diversity, such as pollination and invasion resistance. We also show that rangelands grazed by wild as opposed to domestic livestock delivered similar assemblages of ecosystem services and were similarly affected by herbivory exclusion and fertilization, treatments that simulate rangeland management actions (Paudel et al., 2023). Fertilization modified more ecosystem services than herbivory exclusion and when combined, fertilization remained the dominant effect (Table 1). The effects of these treatments were mostly positive for provisioning services, negative for plant diversity, and variable for regulating services, with few effects on supporting services (Table 1). The longer-term application of treatments generally intensified effects, and when long-term exclusion of grazers produced a change, it only reduced ecosystem services (Table 1).

The patterns identified in our study expand on the known negative correlation between forage production and diversity in rangelands. Fertilization clearly shifts rangelands towards the productivity side of that trade-off. Management actions that promote biomass production not only reduce plant diversity, but also pollination, resistance to invasion, and to a lesser extent forage stability.

Therefore, this study describes trade-offs and synergies that can inform management practices designed to meet the priorities for ecosystem services for multiple stakeholders. The insight can be helpful to take informed actions to maintain and enhance landscape-scale multifunctionality and meet societal needs beyond food production.

Ecosystem services provided by global rangelands

Our standardized assessment of multiple variables in a wide range of physical and biogeographic gradients and rangeland categories provided a unique opportunity to generalize patterns at global scales (Borer et al., 2014). Contrary to our expectations, the three categories of rangelands provide similar ecosystem services under ambient conditions. The lack of differences among them may be explained by the fact that they had similar mean grazing scores and that each category showed significant variability in grazing intensity. Most natural and semi-natural grasslands are grazed at low densities by wild herbivores (Dirzo et al., 2014) and by livestock, probably because they have low primary productivity, and due to technological barriers hindering agricultural improvement of grasslands and land conversion (Bardgett et al., 2021). The desirable rangeland management should be the one that maximizes the provision of multiple ecosystem services as discuss below.

Impact of management on the delivery of ecosystem services

The multiple ecosystem services provided by rangelands changed only slightly with herbivory exclusion, particularly in the initial years, which might be because in some sites some natural grazers that were historically present in high density now have very reduced populations. So, these outcomes may be strongly influenced by grazing intensity. By contrast, the application of fertilizers significantly changed the multiple ecosystem services as it increased provisioning services although reduced plant diversity, both well-documented impacts (Hautier et al. 2018). Also, fertilizers seemed to benefit several regulating and supporting services at least in the short-term. Differences among sites in biomass responses to fertilization depend on the degree of nutrient limitation (Fay et al. 2015) and differences in plant species composition and phenology. Factors that improve productivity can also increase carbon storage (Swain et al., 2013) with implications for climate regulation and the control of soil erosion (Maestre et al., 2022). We identified both synergies and trade-offs among ecosystem services (Bennett et al., 2009), however the management practices analysed here did not change the trends of these correlations. Here, we expanded on the known negative correlation between forage production and diversity (Koerner et al. 2018) and the fertilization-induced diversity loss, as we included several soil ecosystem services and forage stability.

Short- vs longer-term management actions on ecosystem services

Our study shows small advantages of short-term herbivores exclusion but no additional (and sometimes negative) effects of longer-term exclosure. Considering wild and domestic animals, here we showed that ecosystem services that increased after short-term herbivore removal, such as forage quantity, reverted to baseline in the longer-term. Longer-term herbivory exclusion not only reduced plant species richness but also soil fertility and water quality. Removing domestic herbivores has been proposed as a conservation practice. However, previous studies showed contradictory effects of livestock exclusion on plant species diversity (Koerner et al., 2018; Price et al., 2022). Also, previous long-term herbivory exclusion in semiarid grasslands found reductions in vegetation cover, with older exclosures not always providing clear benefits to plants relative to newer exclosures (Sun et al., 2020; Velasco Ayuso et al., 2024).

Similarly, we found that the use of fertilizers, which is happening more frequently in mesic rangelands (Paudel et al., 2023), should be evaluated with caution. We found that some of the positive effects of fertilization on regulating services diminished with longer-term application, when negative effects on pollination and invasion resistance and stronger reductions in plant species richness became evident (Table 1). The increase in plant production resulting from fertilizer use might be considered an improvement by pastoralists but associated losses of plant species diversity may concern conservationists or other stakeholders (Bardgett et al., 2021). In addition to ecological concerns, limited water availability and low cost-effectiveness often constrain fertilizer use in native rangelands. Considering our analysis, we believe it is important to carefully analyse prior to use fertilizers due to the negative effects of longer-term application on ecosystem services.

Besides assisting researchers and stakeholders in identifying a robust set of indicators and methods to use for rangeland ecosystem service assessments, our study identified positive and negative relationships among the respective indicators and facilitate a synthesis of ecosystem service and multifunctionality studies. Although many studies calculate multifunctionality indices (Allan et al., 2015; Velasco Ayuso et al., 2024), we prefer to assess multiple individual ecosystem services so decisions can be made according to the services of interest to different stakeholders. Insights into the relationships between management practices and ecosystem services allow decision-makers to adapt grassland management to support desired ecosystem services at a given site. It is vital that all stakeholder groups are represented, and the full range of relevant ecosystem services considered, including cultural services (Yahdjian et al., 2015). Alternatively, prior planning on a regional scale may suggest which proportion of very productive land should be allocated for forage production and which proportion should be allocated for ecosystem services less dependent on production (Boesing et al. 2024). Although the approach applied in this study simplifies the processes of ecosystem service supply, our study provides a global overview of the consequences of excluding grazers and fertilizing for biodiversity and ecosystem services. We believe that our study represents a step forward in applied ecosystem service research, which is needed to assure human well-being in the future.

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Figure captions

Figure 1.a. NutNet experimental sites classified into the three rangeland categories defined in this study, current livestock (pink), recent livestock (green), and wild grazing (blue). The experimental sites are plotted using the biomes considered as rangelands as background. Source: Rangeland Atlas ILRI, IUCN, FAO, WWF, UNEP and ILC. (2021). 1.b. Distribution of NutNet rangeland sites in the mean annual temperature and annual precipitation space in Whittaker diagram behind that show biome distribution. Forms of dots in panel are according to the six continental masses covered by the experimental NutNet sites. See Table S1 for the list of sites and the main climate parameters.

Figure 2. Probabilistic principal component analysis of ecosystem services organized by categories (provisioning in yellow, supporting in purple, regulating in brown, and plant diversity in dark green) for the three categories of rangelands defined in this study, current livestock (pink), recent livestock (green), and wild grazers (blue). Ellipses indicate 95% confidence biplot space for each rangeland type. The data from initial conditions (pre-treatment) and control plots were averaged along all experimental years and normalized (uv or Z transformation) to perform the pPCA with the 'ppca' method (pca function from the PCA tools package in R version 4.2.2: Blighe and Lun, 2023).

Figure 3. Natural log response ratios (LRR) describing the general response across rangelands of short-term (1-3 years) exclusion of large herbivores (blue, Fence), fertilization of the grazed grassland (red, Fert), and the combination of both (purple, Fert + Fence). (a) provisioning (b) supporting (c) regulating ecosystem services, and (d) plant diversity. The LRR was calculated as: LRR = ln (treatment/control), in control is the ambient condition, (i.e., the unfertilized plot with grazers, located within the same experimental block). Dots are mean ± 95% confidence intervals; "*" shows that LRR was different from zero (t-test, $\alpha = 0.05$). Numbers in grey at the bottom refer to the number of sites included in the calculation of each LRR.

Figure 4. Radar plots describing the general response of short-term (1-3 years) effects of (a) herbivory exclusion with fences, (b) NPK fertilizing grazed rangelands, and (c) the combination of both (fertilization + fence) in the multiple ecosystem services assessed across rangelands. In each radar plot, the ambient condition (i.e., control unfertilized with grazers) is shown in grey. We standardized within sites, using the quotient transformation as st = xi/maxsite, in which xi is the value observed in each plot and maxsite is the maximum value observed for the variable across all treatments at each experimental site (Byrnes et al., 2014; Hautier et al., 2018), The average values were scaled from minimum (values close to the centre) to maximum (values close to the outside of the radar plot) to facilitate visualization of the different responses. Therefore, the minimum value

means that the provision of the ecosystem service is lower than in the other treatments. Asterisks indicate a significant effect of the treatment based on the LRR (t-test, $\alpha = 0.05$).

Figure 5. Synergies and trade-offs among ecosystem services across all rangelands in control (a), and short-term (1-3 years) changes with herbivory exclusion with fences (b), fertilization (c), and fertilized plots inside exclosures (d). Blue and red lines refer to significant positive (synergies) and negative (trade-offs) correlations respectively (Pearson correlation coefficient, P-values < 0.05).

Table 1. Comparison of short (1-3 years) and longer-term (6-8 years) effects in provisioning, supporting, and regulating ecosystem services of rangelands and plant community diversity with NPK fertilization, herbivory exclusion with fences, and the combination of both. For each ecosystem service, the significant increase (blue arrows) or decrease (red arrows) compared with the ambient condition is shown for the short and longer-term manipulations. The range of effect size are 0.01–0.30 for lightest colour, 0.31-0.60 medium colour, and 0.61-1.00 darkest colours. Horizontal lines indicate no significant changes. See Fig. 3, and Appendix S1: Fig. S2 for details of short- and long-term effects, respectively.

Type of ecosystem service		Fence		Fertilization		Fert + Fence	
		Short-term	Long-term	Short-term	Long-term	Short-term	Long-term
PROVISIONING	Forage quantity	↑ (light blue)	—	↑ (medium blue)	↑ (medium blue)	↑ (dark blue)	↑ (dark blue)
	Forage physical	—	—	↑ (light blue)	↑ (light blue)	—	—
	Forage chemical	—	—	↑ (light blue)	↑ (light blue)	↑ (light blue)	↑ (light blue)
SUPPORTING	Forage stability	—	—	—	—	—	—
	Soil fertility	↑ (light blue)	↓ (light orange)	—	—	—	—
	Soil stability	—	—	↑ (light blue)	↑ (light blue)	↑ (light blue)	—
REGULATING	Climate regulation	—	—	↑ (light blue)	↑ (light blue)	↑ (light blue)	—
	Soil acidification	↓ (light orange)	—	↓ (light orange)	↓ (light orange)	↓ (light orange)	—
	Erosion control	—	—	↑ (light blue)	—	↑ (light blue)	↑ (light blue)
	Water quality	—	↓ (light orange)	↑ (light blue)	↑ (light blue)	↑ (light blue)	
	Pollination	↓ (light orange)	—	—	↓ (medium orange)	—	↓ (medium orange)
	Invasion Resistance	—	—	—	↓ (medium orange)	—	↓ (medium orange)
DIVERSITY	Alpha richness	↓ (light orange)	↓ (light orange)	↓ (light orange)	↓ (medium orange)	↓ (light orange)	↓ (dark red)
	Beta diversity	—	—	—	—	—	—
	Native diversity	—	—	↓ (light orange)	↓ (light orange)	↓ (light orange)	↓ (medium orange)