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Forest management affects ecosystem functioning (predation and herbivory) but not ecosystem constancy: A comparative study across four forest ecosystems around the world

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ABSTRACT

Forest management can affect both the functioning and stability of ecosystems. Constancy and persistence are key factors that contribute to the overall stability of an ecosystem. These factors can be highly variable and change across forest ecosystems. We studied the effects of forest management on the strength of resource-consumer interactions (bird predation and insect herbivory) as important measures of ecosystem functioning, as well as on their constancy in time in four different forested regions globally. Within each region, we selected (i) three heavily managed or plantation forests, and (ii) three urban/peri-urban forests or urban plantings, and paired each of them with pristine/semi-natural forests. Bird predation was estimated using plasticine caterpillars of different colors. Chewer, galler, and miner herbivory on leaves were estimated for 15 plants (shrubs and trees) per study site. Constancy was quantified as the invariability of both predation and herbivory during a period of three (exceptionally two) years. We found no consistent responses of either predation or herbivory to forest management practices across study regions. Bird predation was higher in urban/peri-urban forests than in pristine/semi-natural forests in Patagonian and boreal forest, with intermediate levels of predation in managed or plantation forests. These differences might be explained by the increase of resource availability during the winters and by the higher abundances of generalist predators due to increase of temperatures (i.e., urban heat effect), for those regions where winter temperatures could be a limiting factor. Chewing insect herbivory was lower in urban/peri-urban forests, probably due to the exclusion of certain herbivores in response to warming and the higher predation pressure

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relative to pristine forests. No differences were found in other types of herbivory, indicating that effects of urbanization are guild-specific. In addition, we consistently found no effects of forest management practices on predation invariability and herbivory, thereby demonstrating the high constancy of ecosystem functioning to different forest management practices across regions. These findings advance our knowledge of the generalized effects of forest management on ecosystem functions and stability by establishing a connection between the ecology and management and conservation of plantations and natural forests.

1. Introduction

Ecosystem functions are defined by the biotic and abiotic processes that occur within an ecosystem and may contribute to ecosystem services either directly or indirectly (Garland et al., 2021). Trophic relationships, including those occurring between plants, plant-eating insects, and insectivorous predators, are key ecosystem functions because they affect productivity, modify nutrient cycling, and support biodiversity (Lamarre et al., 2012; Metcalfe et al., 2014; Eötvös et al., 2020). Ecosystem functions, in turn, respond to land use intensification (Felipe-Lucia et al., 2020), and vary spatially (Pringle et al., 2010). These fluctuations, through time, collectively influence the stability of ecosystems (Arnoldi et al., 2016).

Stability is defined as the capability of natural systems to return to a steady state after a disturbance. This capability is typically measured as resistance or resilience against perturbations, predictability, or the inverse of temporal variability (Arnoldi et al., 2016). According to current theory, ecosystem functioning stability tends to increase with higher levels of biodiversity (Loreau and de Mazancourt, 2013), and this is inversely related to the intensity of management and modification of the natural environment (Newbold et al., 2015). Some examples of the effects of biodiversity on ecosystem stability include research on coral reefs (Nyström et al., 2000), agricultural systems (Cabell and Oelofse, 2012), urban areas (Alberti and Marzluff, 2004), and forests (DeClerck et al., 2006; Lloret et al., 2007).

Forests provide a wide range of ecosystem services to humans. For example, carbon capture by trees is one of the most effective strategies for limiting the rise in global CO_2 concentrations (IPCC, 2018). Forests have proved resilient to climatic changes during the past 400 million years (Tidwell, 1998). However, variations in biodiversity and ecosystem functions due to increases in the intensity of forest management regimes, forest destruction, fragmentation, and degradation have made them more vulnerable to climate change (Noss, 2001). These transformations are especially obvious in urban and peri-urban environments, where they have simplified and homogenized species compositions (Führer, 2000).

The use of forests affects ecosystem functions, such as resource–consumer interactions, but the direction and strength of these differ among forest ecosystems. For example, management of urban forests has been shown to either decrease (Gering and Blair, 1999; Eötvös et al., 2018; Ferrante et al., 2014) or increase predation (Posa et al., 2007; Kozlov et al., 2017) compared with pristine forests, and to either decrease (Kozlov et al., 2017; Moreira et al., 2019) or increase herbivory (Cuevas-Reyes et al., 2013; Rivkin & de Andrade, 2023). Indeed, the effects of forest management on ecosystem stability have been investigated widely in recent years, especially since the loss of diversity due to persistent human disturbance has been shown to increase the vulnerability of ecosystems to collapse (MacDougall et al., 2013; Hautier et al., 2015). Ecosystem stability is greatly affected by resilience, along with persistence, and constancy (Grimm and Wissel, 1997). Constancy, or "temporal stability", is defined as the unchanging state of a system compared to its reference condition; it may be a consequence of stability but not a definitive indicator of it (Van Meerbeek et al., 2021).

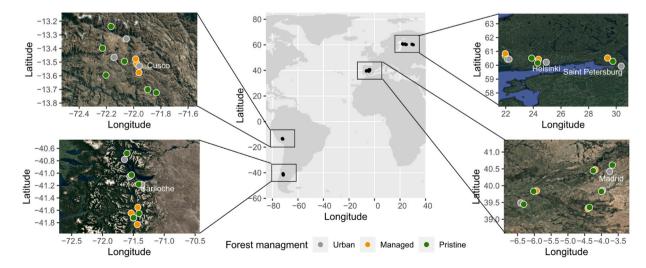


Fig. 1. Locations of study sites: Andean forests in Peru (top left), boreal forests in Finland and Russia (top right), Mediterranean forests in Spain (bottom right), and Patagonian forests in Argentina (bottom left).

The previous studies that investigated the effects of forest management on resource–consumer interactions (Cuevas-Reyes et al., 2013; Ferrante et al., 2014; Kozlov et al., 2017) or ecosystem constancy (Christie and Hochuli, 2009; Karp et al., 2011) were generally conducted at small spatial scales or within a particular forest ecosystem. However, identifying general patterns and exploring the sources of variation in these relationships requires comparisons across forest ecosystems. Therefore, in the present study, we aimed to compare the effects of forest management on the intensity of resource–consumer interactions (predation and herbivory) and on their constancy in forest ecosystems across different regions throughout the world.

2. Methodology

2.1. Study sites

Four regions were selected for this study, with two in South America (Peru and Argentina) and two in Europe (Finland/Russia and Spain). Each study region was representative of a particular forest ecosystem (Andean forest, boreal forest, Mediterranean forest, Patagonian forest; Fig. 1). In each region, 12 study sites were established, with six in areas under some type of management (three in heavily managed or plantation forests, and three inside or nearby cities) and six in natural or semi-natural areas with low management (i.e. with low agronomic, forestry or recreational human use; Appendix Fig. S1). Within each region, study sites were selected using a paired design. In this design, each natural or semi-natural area with minimal human management (referred to hereafter as "pristine") was located in proximity to a managed or peri-urban area. In every region, each pair of sites was separated by at least 10 km from the nearest pair, except from Peru, where the orography prevented such spatial separation.

The climate and environmental characteristics differed greatly among the four study regions. In Peru, the study was conducted in Andean forests with a latitudinal gradient of 0.48° and mean altitude of 3672 m.a.s.l. (standard deviation of study sites (SD): 299 m). The climate at all sites exhibited little seasonal variation in terms of temperature but substantial seasonal variations in rainfall, with seasonal precipitation during the autumn and winter, a mean temperature of 9.38° C (SD: 1.62° C), and annual precipitation of 720 mm (SD: 39 mm). In Finland and Russia, the study was conducted in boreal forests with a latitudinal range of 0.75° and mean altitude of 51 m.a.s.l. (SD: 27 m). The climate at all sites was characterized by a mean temperature of 4.68° C (SD: 0.35° C) and annual precipitation of 653 mm (SD: 22 mm). In Spain, the study was conducted in Mediterranean forests with a latitudinal range of 1.4° and mean altitude of 593 m.a.s.l. (SD: 190 m). The climate at all sites was characterized by mild and rainy winters, and hot and dry summers, with high variability in temperature and rainfall between years, a mean temperature of 14.49° C (SD: 1.44° C), and annual precipitation of 442 mm (SD: 41.19 mm). In Argentina, the study was conducted in the North Patagonian high-density forest and woodlands located within a latitude range of 1.11° and mean altitude of 821 m.a.s.l. (SD: 53 m). The climate at all sites was characterized by cold-temperate winters (seasonal precipitation during autumn and winter) and dry summers, with high variability in temperature and rainfall between years, a mean temperature of 7.86° C (SD: 0.74° C), and annual precipitation of 1134 mm (SD: 145 mm).

2.2. Field sampling

2.2.1. Predation

We used model caterpillars to estimate the intensity of predation by birds on herbivorous insects (Eötvös et al., 2018; Fricke et al., 2022; Ferrante et al., 2022). These models (30 mm long and 4 mm in diameter) were fabricated from odorless plasticine (Luch Chemical Plant, Yaroslavl, Russia). Fifteen caterpillars of three different colors (brown, green, and yellow) were attached by wire to thin branches (3–10 mm) at a height of 1.5–2 m. We placed them in five haphazardly selected trees at each study site, and distributing them evenly with one caterpillar of each color on each tree. The average distance between caterpillars was approximately 30 cm. The order of placement (brown, green, and yellow) was consistently followed. We chose these specific colors based on the findings of a prior experiment (Zvereva et al., 2019) to capture a broader range of predation variability across different regions. Within each site, models were attached to trees of the same species, although the tree species sometimes varied among sites, even within the same region (Appendix Table S1). Tree species were selected among the most abundant species within each region. Based on the results of a previous experiment (Zvereva et al., 2019), every study site was revisited three times each year at monthly intervals (mean = 27.03 days, SD = 6.52) during the bird breeding period (mean = 73.43 days from beginning to end of the sampling season, SD = 23.9). Every time a study site was revisited, the presence of damage marks was checked on each model. When damage was detected, the models were repaired and molded into their initial shape or replaced if the damage was excessive or they were lost. Following Low et al. (2014), the identifications and intensity of damage were consistently recorded in the field or by examining photographs. The predation experiment was conducted in only three of the study regions (boreal forest, Mediterranean forest, and Patagonian forest) and repeated during three consecutive years (2017-2019 in boreal and Patagonian forests, and 2018-2020 in Mediterranean forest). Out of the total 1674 models deployed, 60 models (3.6 %) were lost during the experiment.

2.2.2. Herbivory

Insect herbivory was measured in five individuals of three native tree or shrub species, with a total of 15 individual plants per study site. The tree or shrub species were chosen based on their abundance, prioritizing the dominant species and ensuring the inclusion of the same species in each pair of sites, always including the tree species used in the predation experiment (Appendix Table S2). The plants sampled within each study site were haphazardly selected at least 15 m apart. To avoid the impact of unconscious bias on the herbivory values, targeted branches (one per plant) were selected while standing 5–10 m away, which prevented visual evaluations of

leaf damage by insects. The branches selected for measurements of herbivory were reachable from the ground (at a height of 0.1–2 m) and had a minimum of 50 leaves. The branches were placed inside a mesh bag and transported to the laboratory, where each leaf was assigned to one of seven damage classes according to the percentage of leaf area consumed by chewing insects (0, 0.1–1 %, 1.1–5 %, 5.1–25 %, 25.1–50 %, 50.1–75 %, and 75.1–100 %) (Alliende, 1989; Kozlov et al., 2015). This process was repeated for gallers and miners. The proportion of herbivory per individual plant was estimated by multiplying the median values of every damage class by the number of leaves in this class divided by the total number of leaves. This assessment was conducted in all study regions and repeated during two to three consecutive years (2018–2019 in Andean forests, 2017–2019 in boreal forests, 2018–2020 in Mediterranean forests, and 2017–2018 in Patagonian forests). In all study sites intensity of herbivory was measured at the beginning of the growing season, but at least four weeks after the leaves emergence (for deciduous species), except for boreal forests, where it was measured twice each year: once at the middle and once at the end of the growing season.

2.3. Data analyses

For each study site and study period, we estimated the predation intensity as the probability of larvae of a certain color being attacked during one day (the probability of bird predation) as:

$$P(X = 1) = 1 - P(X = 0) = 1 - \left[1 - \left(\frac{N}{T}\right)\right]^{\left(\frac{1}{T}\right)}$$

where P(X = 1) is the probability of one or more larvae being attacked by birds, N is the number of caterpillars attacked, T is the total number of caterpillars used per period, and t is the period length in days. Exposed model caterpillars positioned 30–50 cm apart were considered statistically independent in previous studies (Tvardikova and Novotny, 2012; Bereczki et al., 2014; Dattilo et al., 2016). The herbivory intensity was estimated as the proportion of leaf area consumed (or otherwise damaged) by chewing, galling, and mining insects at tree level.

To quantify the ecosystem constancy, we estimated the invariability of both insect herbivory and bird predation as the inverse of the coefficient of variation (1/CV) (see Karp et al., 2011) across years for each study site, which was calculated as the mean of either the proportion of herbivory or the probability of predation per year divided by the SD. By doing so, we extracted a value related to the constancy of ecosystem functioning through years. Zero SD values (indicating no inter-annual variability) were replaced by 0.00001 to avoid indeterminate values when estimating 1/CV. For predation, we estimated the invariability per study site and color of the model, and for insect herbivory, we estimated the invariability per type of damage (chewer, galler, miner) nested with tree/shrub species in each study site.

We used generalized linear mixed models (GLMMs) with a beta error distribution and a logit link function to investigate the effects of forest management on bird predation and insect herbivory across forest regions. We used GLMMs with a Gaussian error distribution and a log link function to investigate the effects of forest management on the invariability of bird predation and herbivory across regions. We explored the influence of different random effects on the model intercept, i.e., the paired design (i.e., each pair of pristine vs managed/peri-urban forest sites close to each other), and also the tree species in the case of herbivory. Forest management, region, color of the model, and all their interactions were used as fixed effect predictors of the probability of bird predation and invariability of predation. Forest management, region, and their interactions were used as fixed effect predictors of the proportion of insect herbivory (separately for each feeding guild) and the invariability of herbivory.

Alternative models in terms of random and fixed effects were compared using Akaike's information criterion corrected for small sample sizes (AICc). This criterion summarizes how well each model fits the data (maximum likelihood) by penalizing for the number of parameters in the model according to the parsimony principle (Schwarz, 1978; Burnham and Anderson, 2004). A difference in AICc > 2 indicated that the worst model could be omitted. First, we compared GLMMs with different random error structures (Appendix Tables S3 and S4), including a null model with no random effects (i.e., a GLM). After selecting the best fit random structure, we compared models with different fixed effects (Zuur et al., 2009). Following Nakagawa and Schielzeth (2013), we estimated the R² values for all plausible models, where two components of R² were calculated: (1) the marginal R² (R²m) by only considering the variability explained by fixed effects; and (2) the conditional R² (R²c) by considering the variability supported by both fixed and random effects. If forest management affected either predation or herbivory, multiple Tukey post-hoc comparisons were conducted to identify the forest management type with the lowest herbivory or predation within each region and the region with the least intense resource-consumer interactions. These tests were conducted using the "Ismeans" and "cld" functions in the "Ismeans" package (Lenth, 2016). Model residuals were explored using a simulation-based approach to obtain readily interpretable scaled (quantile) residuals for the fitted GLMMs (Hartig, 2019). Beta GLMMs were fitted with the "glmmTMB" function in the R package "glmmTMB" (Brooks et al., 2017), whereas Gaussian GLMMs were fitted with the "glmer" function in the "lme4" package (Bates et al., 2015). Beta GLMs used for models with no random effects were fitted with the "betareg" function in the "betareg" package (Zeileis et al., 2016), whereas Gaussian GLM were fitted with the "glm" function in the "stats" package (R Core Team, 2020). Predicted variables in beta GLM models were transformed according to the suggestions provided with the package, as follows:

$$y_2 = (y_1 * (n-1) + 0.5)/n,$$

where y_1 is the original variable value, n is the total number of replicates, and y_2 is the transformed value. All analyses were conducted with R software version 4.0.5 (R Core Team, 2020).

3. Results

3.1. General results

We estimated bird predation based on 4383 records (i.e every time checked) from 1614 model caterpillars. We estimated area losses for 283,236 leaves on 2283 different branches from 35 woody plant species (Table 1).

3.2. Effects of forest management on ecosystem functions (predation and herbivory)

Comparison of alternative models with AICc values for variables related to ecosystem functions yielded one single best model in all cases (Table 2). Forest management practices had effects on the probability of predation and proportion of chewer herbivory, but these effects differed across regions, as indicated by the presence of the interaction between forest management practices and region in the best-fit models (see Appendix Table S3 for the AICc results). Forest management practices had no effects on the galler and miner herbivory (Table 2; Appendix Table S4).

Table 1
Mean values, standard deviations (SDs), and ranges of response variables used in this study comprising the probability of bird predation, proportions of chewer, galler, and miner herbivory, invariability of predation, and invariability of chewer, galler, and miner herbivory to illustrate the types of resource–consumer interactions. Images represent the type of resource–consumer interaction.

		Response variable	Range	Mean	SD
	1	Probability of daily attack of a model	0-0.5167	0.0817	0.1325
Predation		Bird predation invariability	0.5774–18.1679	2.2366	2.1704
		Chewer herbivory	0-0.5516	0.0549	0.0689
		Chewer herbivory invariability	0-162.786	6.1080	19.64
		Galler herbivory	0-0.8750	0.0077	0.0434
Herbivory		Galler herbivory invariability	0–577.698	4.9531	48.767
		Miner herbivory	0-0.8750	0.0050	0.2317
		Miner herbivory invariability	0–27.135	1.0923	2.547

Table 2

Best fit models for all response variables. Fixed factors included in each model are shown for variables related to bird predation and insect herbivory. Asterisk indicates terms included in the best fit models. R^2 values are shown for the best fit models when the best model did not include random effects. In addition, marginal R^2 values (R^2 m) that only consider the variability explained by fixed effects and conditional R^2 values (R^2 c) that consider the variability supported by both fixed and random effects are shown when generalized linear mixed models were applied. Images illustrate the type of resource–consumer interaction.

Response variable	Region	Forest management	Color	Region: Forest management	Forest management: Color	Region: Color	Triple Interaction	R ²
Predation	*	*	*	*	*	*	*	R ² m: 0.163 / R ² c: 0.226
1/CV Predation	*		*			*		R ² : 0.234

	Response variable	Region	Forest management	Region: Forest management	R^2
	Chewer herbivory	*	*	*	R ² m: 0.423 /R ² c: 0.550
	1/CV Chewer herbivory	*			R ² : 0.213
•	Galler herbivory				R ² : 0.000
9	1/CV Galler herbivory				R ² : 0.000
	Miner herbivory			,	R ² : 0.000
	1/CV Miner herbivory	*			R ² : 0.093

Model predictions and Tukey post-hoc tests showed that predation in boreal forest was higher in urban forests compared to pristine sites (Fig. 2a–c). In Mediterranean forests, there were no differences in predation between forest management practices regardless of the caterpillar color (Fig. 2a–c). Finally, in Patagonian forests, we detected higher predation in urban forests compared with pristine or managed forests only for green caterpillars, but lower predation for yellow caterpillars (Fig. 2a–c). Post-hoc tests showed that bird predation was lower in boreal forests than in Mediterranean forests, and bird predation in Patagonian forests differed from the others depending on the caterpillar color.

In terms of herbivory, we found that forest management practices only affected chewer herbivory (Fig. 2d), with lower proportions in urban forests in all regions, except for Patagonian forests. No differences were found in the effects of forest management practices or regions on the proportions of herbivory by gall feeders or miners (Fig. 2e–d; Table 2). Post-hoc tests showed that the percentage of chewer herbivory was lower in Patagonian forests than the other regions, but no differences were detected in galler and miner herbivory among regions.

3.3. Effects of forest management on ecosystem constancy

Comparisons of alternative models with AICc values for variables related to invariability of predation yielded one best model, which included the interaction between model color and region, but not the effect of forest management. For invariability of herbivory, the best model for chewers and miners only included the region, and no differences from null models were detected for gallers (Table 2;

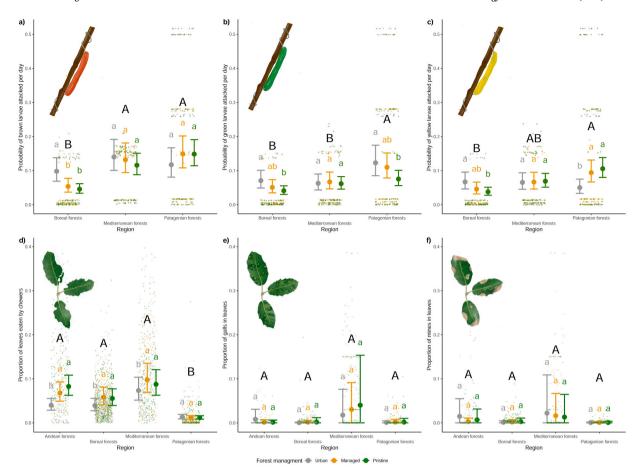


Fig. 2. Model predictions for generalized linear mixed models. The 95 % confidence intervals are represented as error bars around mean model predictions (a–d) or standard deviations based on the observed data (e, f). Forest management practices are plotted in different colors. (a–c) Model predictions explaining the probability of predation during one day as a function of forest management and region for each caterpillar color: brown (a), green (b), and yellow (c). Mean values of the probability of caterpillar predation at every study site are represented by dots. (d–f) Model predictions explaining the proportions of different types of herbivory as functions of forest management and region: chewer (d), galler I, and miner (f). Mean proportions of leaf areas eaten at every study site are represented by dots. Lowercase letters on top of bars represent Tukey post-hoc test results obtained by comparing forest management practices within regions for each color of caterpillar or type of herbivory, where a, b, and c indicate management practices related to significantly higher and lower attack and herbivory rates, respectively, and uppercase letters denote significant differences between regions regardless of the effects of forest management practice. Insets illustrate the response variables shown in each plot.

Fig. 3). Post hoc test showed that invariability of predation in boreal forests was smaller than in other regions for brown caterpillars, smaller only than in Patagonian forests for green caterpillars, and for yellow caterpillars the invariability was higher for boreal and Mediterranean forests than in Patagonian forests. Post hoc test showed that invariability of chewer herbivory was smaller for Patagonian forests than the others, and the invariability was lower in Mediterranean forests than boreal and Andean forests. Finally, invariability of miner herbivory was lower in boreal forests than Mediterranean forests, with no differences in the other regions. All of the best fit models included no random effects (Appendix Table S4).

4. Discussion

Different effects were found in response to forest management for every region and type of resource-consumer relationship. Differences were found in bird predation between some forest management practices in particular regions, but the effects of forest management on herbivory were less obvious. These differences were mostly found between urban and non-urban (i.e., managed and pristine) forests, where urban/peri-urban forests had a higher probability of predation and lower herbivory compared with pristine/ semi-natural and managed or plantation forests. Overall, we found no effects of forest management practices on variables reflecting ecosystem constancy.

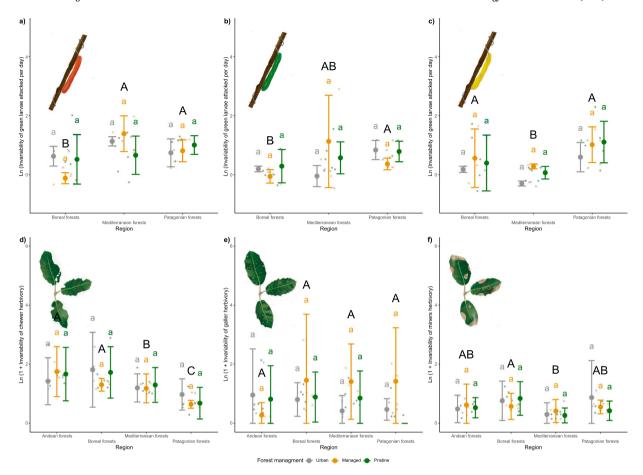


Fig. 3. Model predictions for generalized linear models of invariability (1/coefficient of variation on log scale) of predation and herbivory. The 95 % confidence intervals are represented as error bars around mean model predictions. Forest management practices are plotted in different colors. (a–c) Model predictions explaining the invariability of predation during one day as a function of forest management and region for each caterpillar color: brown (a), green (b), and yellow (c). (d–f) Model predictions explaining the invariability of herbivory as functions of forest management and region: chewer (d), galler (e), and miner (f). Observed values for each response variable are represented by dots. Lowercase letters on top of bars represent Tukey post-hoc test results obtained by comparing forest management practices within regions for each color of caterpillar or type of herbivory, where a, b, and c indicate management practices related to significantly higher and lower invariability of bird predation and insect herbivory respectively, and uppercase letters denote significant differences between regions regardless of the effects of forest management practice. Insets illustrate the type of response variable represented in each plot.

4.1. Ecosystem functions

In this study, we found effects of forest management on resource–consumer interactions, particularly for predation, although these effects were highly variable across regions.

4.1.1. Predation

The observed increase in predation in urban/peri-urban forests, at least in some regions, could have been a consequence of the higher abundances of generalist predators usually found in these forests (Posa et al., 2007). Moreover, the higher temperatures of cities compared with non-urban environments could have increased the fitness and abundance of species by affecting their metabolism, development, and fecundity (Bale, 2002). Indeed, the urban heat island effect produced in cities due to the presence of impervious surfaces (Kim, 1992) can increase the ambient temperature by up to 10 °C compared with surrounding rural areas. Increased temperatures can promote the survival of insects during the cold winter months (Dawadi and Sadof, 2022), thereby leading to increases in the abundance of birds by increasing their food availability (Seress et al., 2018), resulting in higher levels of bird predation. In Mediterranean regions, the heat island effect could be less pronounced than under temperate and cold regimes (Wienert and Kuttler, 2005). This is primarily due to the reduced demand for heat production in milder environments, like the Mediterranean, which is known as the latitudinal variation of anthropogenic heat production.

The behavior of birds has been shown to change in different ways in response to the presence of humans between latitudes (Díaz et al., 2021), where the tolerance of humans by birds increases from low to high latitudes (Poddubnaya et al., 2019). This could also help to explain why we found a higher probability of predation in urban/peri-urban forests, where birds might exhibit less neophobic behavior (i.e., where novel stimuli often fail to elicit an attack response from avian predators) in response to model caterpillars. Our results also showed that birds did not select prey according to color in the same manner in all regions, possibly because the color preferences for bird predation change latitudinally (Zvereva et al., 2019), or due to differences in detectability caused by variations in illumination affecting the color depending on the light that passes through the tree canopy. In Patagonian and boreal forests, we found color-dependent responses of bird predation to forest management. Some antipredation strategies could have reduced the probability of predation and masked the effects of forest management on predation. In particular, brown (Mariath, 1982) or green (Hernández-Agüero et al., 2020) colors are considered to be cryptic, whereas yellow color is aposematic (Hernández-Agüero et al., 2020).

4.1.2. Herbivory

In every region except for Patagonian forests, chewer herbivory differed across forest management practices, with urban forests displaying lower levels of insect herbivory compared to pristine and managed forests. The high host specificity of herbivore (Hernández-Agüero et al., 2022) could explain these differences, because specialist species survive worse in urban areas than generalist ones (Herrmann et al., 2012). Our results agree with similar previous demonstrations of the negative effect of urban management on herbivory (Miles et al., 2019; Kozlov et al., 2017; Moreira et al., 2019; Meineke et al., 2019). Moreira et al. (2019) also found that the effects of urbanization differed among guilds of herbivorous insects, with chewer herbivory decreased in response to urbanization but miner herbivory was not affected. This was explained by the effects of urbanization, which can alter species composition, consequently influencing both the quantity and type of herbivory. In previous studies, the decrease in herbivory in response to urban management was explained also by the local exclusion of certain herbivores in response to warming (Meineke et al., 2019) due to the urban heat island effect (Kim, 1992). Finally, the higher mortality of herbivorous insects due to predation (top-down forces) has also been used to explain the lower herbivory recorded in cities (Kozlov et al., 2017). This higher mortality could explain the lower chewer herbivory we found in boreal urban forests where predation was higher, but not in Mediterranean forests. These decreases in chewer herbivory agree with Gray's increasing disturbance hypothesis (Gray, 1989), which predicts that urban management negatively affects the intensity of resource-consumer interactions. Considering that urban greening has been proposed as a planning strategy to meet the needs of people worldwide (Xie and Bulkeley, 2020), it is critical to enhance our understanding of the impacts of urbanization on ecosystem functions. This is especially pertinent given that 54 % of the world's population currently resides in cities (with > 300,000 inhabitants), and this percentage is projected to rise to 70 % by 2050 (United Nations, 2018).

4.2. Ecosystem constancy

Overall, we found no effect of forest management practices on ecosystem constancy in terms of any of the variables analyzed in this study (predation and herbivory).

4.2.1. Predation

In the case of predation, we detected differences in terms of ecosystem constancy between caterpillar colors and regions, but not between forest management practices. Color affects predation by birds either via visual signaling or detectability (Edmunds and Grayson, 1991). The preferences of predators can be greater for some colors (i.e. brown), or lower for others (i.e. yellow), while the variance of others (i.e. green) depends on detectability (Zvereva et al., 2019). This detectability is explained by foliage and spatial configuration, and thus the variability will be higher between years (Loreau and de Mazancourt, 2013), whereas preference or avoidance signals are maintained temporary (Hernández-Agüero et al., 2020), resulting in higher constancy. Latitudinal variation can help explain the differences in ecosystem constancy between forest regions, because biodiversity generally decreases as the latitude increases (Fischer, 1960; Gaston, 1996; Hillebrand, 2004; Novotny et al., 2006). In tropical areas, higher productivity and less seasonality allow greater diversity (MacArthur, 1969). The stability, and with it constancy, of ecosystem functions is predicted to increase with biodiversity (Loreau and de Mazancourt, 2013), and considering that biodiversity is expected to change with latitude, it is logical to detect higher stability in forest ecosystems with higher biodiversity, such as Mediterranean forests.

4.2.2. Herbivory

Similar to predation, the higher biodiversity observed at lower latitudes (MacArthur, 1969) could help to explain the variations in ecosystem constancy for chewer and miner herbivory observed in our study. In addition, climate can affect ecosystem stability and constancy, where wetter sites have a greater potential for long-term recovery after disturbance than drier climates (e.g., Speed et al., 2010). Moreover, galler herbivores belong to highly specialized families (Hernández-Agüero et al., 2022) and their low diversity could reduce the resilience of this trophic group, which could help explain the lack of differences detected in this study.

5. Conclusions

We did not find a consistent response to different management practices in either the intensity of ecosystem functions related to resource–consumer interactions or ecosystem constancy, which contributes to the overall stability of forests across different regions. Further cross-regional studies are required to enhance our knowledge regarding the generalized effects of forest management on

ecosystem functions and stability in order to establish a connection between ecology and the management and conservation of plantations and natural forests.

CRediT authorship contribution statement

Zverev Vitali: Conceptualization, Data curation, Investigation, Methodology, Validation. **Salinas Norma:** Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – original draft. **Nacif Marcos:** Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Kozlov Mikhail:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Hernández-Agüero Juan Antonio:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Cayuela Luis:** Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Caribaldi Lucas:** Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision. **Cosio Eric:** Data curation, Investigation, Methodology. **Ruiz-Tapiador Ildefonso:** Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

I have shared the data in the manuscript Hernández-Agüero et al., 2023: https://doi.org/10.6084/m9.figshare.24463879.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02780.

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