Understorey structural complexity mediated by plantation management as a driver of predation events on potential eucalypt pests

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A B S T R A C T

Current forest management aims to reduce the economic and environmental impact of pests on forest ecosystem productivity and to develop sustainable control approaches. The enemies hypothesis states that more diverse plant communities support a greater number and diversity of predators and parasitoids leading to a reduction in pest damage via top-down control. In forests, research on the enemies hypothesis typically focuses on tree species diversity. Here, we modify this hypothesis to determine how structural complexity of the forest understorey, as mediated by management, influences the abundance of predators and predation events on potential forest insect pests. To test this, we studied *Eucalyptus* sp. plantations managed under two approaches of tree establishment, hypothesising that those managed under the less disturbed system of regrowth (regeneration from clear cut stumps) will have greater vegetation structural complexity, predator abundance and predation events (as an indirect measure of predation rate) than the more disturbed seedling planting system. In six stands of each management type, we measured vegetation understorey layers (ground-, shrub- and sub-canopy cover), predator abundance (insectivorous birds, spider web counts) and predation events (artificial larvae attacks, spider web prey items).

Vegetation structural complexity, abundance of insectivorous birds and spider webs, and artificial larvae attacks and web prey items were all greater in the regrowth than in the seedling stands. Path analysis evidenced direct support for our modified enemies hypothesis for birds, the regrowth management with low disturbance levels after clearcutting promotes both predator abundance and predation events via increased vegetation structural complexity. However, for spiders the increase in web abundance and predation events was directly and positively associated with regrowth management, but there was no indirect link via vegetation structural complexity, suggesting other factors driven by forest management are important.

Manipulative experiments explicitly exploring the cause-and-effect relationship between predation rates and herbivory rates and consideration of the economic implications of the different approaches are required before changes to management are implemented. Our study agrees with the overarching paradigm in sustainable forest management that promotion of structural complexity will be beneficial to biodiversity, ecosystem function and resilience.

1. Introduction

Increasingly, pests are having profound impacts on forest plantation ecosystems due to the spread of invasive species by the movement of people or products (Liebhold et al., 1995), and, by more frequent outbreaks caused by changing ecosystem management and climates (Kirilenko and Sedjo, 2007). Globally, pests cause the forest industry significant economic losses (Wingfield et al., 2015). Consequently, the amount spent on pest control is significant, as is the environmental damage to key ecosystem components, such as biodiversity, soils and water, from the control approaches employed (Wingfield et al., 2008; Liebhold, 2012). For this reason, sustainable forest management seeks

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alternative approaches that reduce the economic and environmental impacts of pest control (Garnas et al., 2012; Wingfield et al., 2015).

In forest ecosystems, habitat structure is a key driver of biodiversity (Jactel et al., 2009, Košulič et al., 2021), altering light, soils and available food and space (Ceccon and Martínez-Ramos, 1999). Typically, plantation forests are highly modified environments that have reduced habitat complexity and support less biodiversity, including that of pest enemies (e.g., predators) (Garnas et al., 2012), in comparison with their more natural counterparts (Hartley, 2002; Brockerhoff et al., 2008). Further, this is exacerbated in those with a more intensive management approach (Košulič et al., 2021). Thus, a plantation supporting fewer enemies is expected to be more at risk from pest attack and outbreak, and ultimately less resilient to environmental change (Kirilenko and Sedjo, 2007). In the context of plantations and other highly managed forest ecosystems, vegetation structure can be directly influenced by the silvicultural approach employed for felling (e.g., clear-cutting, retention harvest, gap cutting) or tree establishment (e.g. seed or sapling planting, natural regeneration) which impacts the growth of understorey vegetation layers (Jactel et al., 2009).

The enemies hypothesis posed by Root (1973) states that more diverse plant communities support a greater number and diversity of predators and parasitoids through greater variety of habitat conditions and provision of more stable habitats. Consequently, changes in management that enhance structural complexity of vegetation should lead to an increase in enemies and predation rates, negatively influencing pest numbers. Biological control is a fundamental principle of integrated pest management (Garnas et al., 2012), aiming to enhance the abundance of enemies of pest species with the expectation of reduction in pest damage. The positive relationship between vegetation structural complexity and biodiversity in forest ecosystems is well known (Oxbrough et al., 2005; Zurita and Bellocq, 2012; Santoandré et al., 2019). However, there has been relatively little research on whether the structure of non-canopy vegetation layers leads to more abundant predators, by providing a greater range of resources, although the potential influence of non-canopy plants has been posed (Staab and Schuldt, 2020) and their role in moderating predator–prey food-webs and predator abundance has been explored by Michalko et al., (2021a) and Michalko et al., (2021b) respectively.

Eucalypts are native to Australia, New Guinea, and Indonesia, but are widely planted across South America, China, and India (Booth, 2013) for their fast-growing timber. Indeed, with typical rotations of just 10–14 years, eucalypt planting is now being trialled in more northerly regions (e.g., UK, France) with a view to establishing new plantation types as climates change (Leslie and Purse, 2016; Tomé et al., 2021). In current planting regions new eucalypt insect pests and pathogens are appearing at a faster rate and comprise both organisms invading from the native range and those typical of the introduced range (Wingfield et al., 2008; Paine et al., 2011). Research on the enemies hypothesis in eucalypt plantations has been scarce, correlative, and produced conflicting outcomes; Bragança et al. (1998) linked habitat heterogeneity to reduced pest diversity, whereas Dall'Oglio et al. (2016) found no relationship between increased understorey vegetation and hymenopteran parasitoid abundance. Further, though not framed around the enemies hypothesis, Michalko et al. (2021b) found web capture rates between mixed and monoculture eucalypt plantations varied depending on prey type, though web spider abundance was similar. Given that the extent of global eucalypt planting is likely to expand in the future there is a need to identify methods of insect pest prevention and control that meet the requirements of sustainable forest management, and which complement economical planting strategies.

There are two main management strategies for establishing the next rotation of eucalypts following clear-fell: natural regeneration from stumps (termed 'regrowth') and the planting of seedlings (Tomé et al., 2021).The seedling approach requires extensive ground preparation of burning and ploughing, which is costly, whereas the regrowth approach has less preparation and better preserves soils, as well as potentially quicker rotations (due to regeneration from existing stumps) but requires careful management of the multiple stems that grow from the stump. Both management approaches often require applications of pesticides to reduce insect pests. Typically, following seedling planting, there follows 2–3 rotations of regrowth management before yield decreases, and seedlings must be planted again (Tomé et al., 2021). However, when each approach is used, and how long for, varies widely depending on local conditions, site history and forest company expertise. Therefore, there remains debate over the economic and environmental advantages of each approach (Larocca et al., 2004) and the impacts of each on biodiversity and species interactions remains unknown.

Considering this, we hypothesise that eucalyptus plantations, managed under the less disturbed system of regrowth, have greater vegetation structure than those managed under the more disturbed system of seedling planting (Fig. 1). Further, we hypothesise that this increased vegetation structure will have a positive influence on the abundance of two different groups of predators - birds and spiders, resulting in increased predation in stands managed under regrowth. Birds and spiders are key forest-dwelling predatory groups which are strongly influenced by changes in habitat structure. For birds, understorey structural complexity is a key driver of richness and abundance, with more complex forests facilitating a greater range of niches (food and space provision) and protection from predation (Cody, 1985). For spiders, structural complexity provides a greater range of web attachment points, safe hunting spaces for active hunters and greater prey availability (Spears and MacMahon, 2012). Thus, we extend the classical enemies hypothesis posed by Root (1973); we determine how structural complexity of the forest understorey, as mediated by management, influences the abundance of predators and corresponding predation pressure on potential forest insect pests (Fig. 1).

2. Methods

2.1. Study area & experimental design

The study took place in the Pampas grasslands of the Entre Rios province, central eastern Argentina (32° 58′ S- 58° 13′ W) (Fig. 2). The climate is temperate with mean annual temperature of 18 °C. Precipitation is year-round, ranging from 1300 mm/yr. in the North to 1000 mm/yr. in the South. The region is in a grassland biome dominated by *Paspalum*, *Axonopus*, *Stipa*, *Bromus*, and *Piptochaetium* (Landi et al., 1987). Native trees are virtually absent in the region, but woodlots can be found in specialised edaphic conditions (Cabrera, 1971). Planted trees were initially associated with cattle-shelter, windbreaks, and citric production. In Argentina, eucalypts have been planted for around 50 years and are widely established, occupying about 25 % of the non-native forested surface (Sanchez-Acosta and Vera, 2005). Further, current forest policy is aiming for a 50 % increase in plantation cover by 2030 (AFOA, 2019).

The study area was typical of the region, consisting of a matrix of lowland (~20 m.a.s.l) agricultural pastoral land and commercial eucalyptus plantations. Within a 400 km² area twelve stands of 8–12-year-old *Eucalyptus* sp. were selected for study, six of regrowth management and six of seedling management, at least 1 km apart from each other. Regrowth stands consisted of naturally regenerated stems from stumps of *Eucalyptus globulus* with no other site intervention but pesticide application for leaf cutting ants control in the first year after clearcutting. Seedling stands consisted of planted seedlings of *Eucalyptus grandis* following clear-felling, ploughing, and then burning, fertilisation, pesticide application to reduce ground vegetation and leaf cutter ant abundance, pruning and thinning. Trees were originally planted at a density of ~ 1000 ind/ha and each stand was a minimum of 9 ha in size. All sampling took place between spring and summer (October 2021 to March 2022).
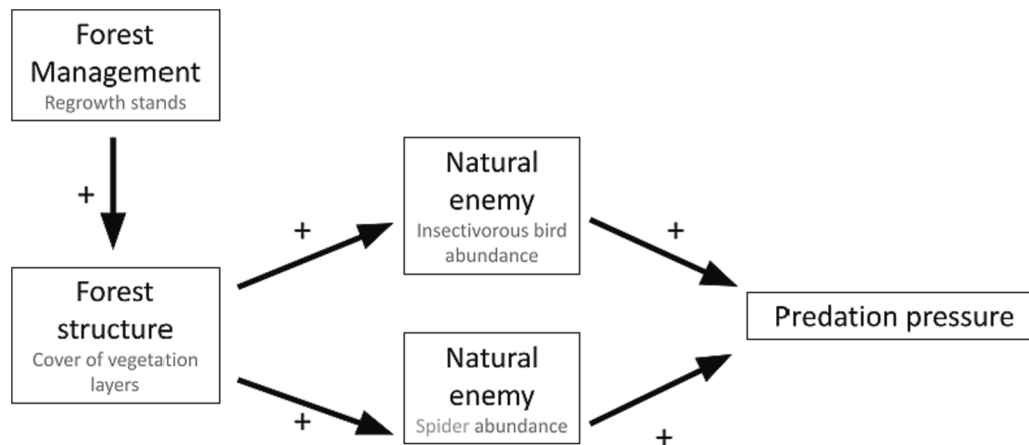
Fig. 1. Theoretical model of expected changes to predation pressure mediated by understorey structural complexity as a result of plantation management. Predation pressure is predicted to increase under regrowth management, in comparison with the seedling planting approach.
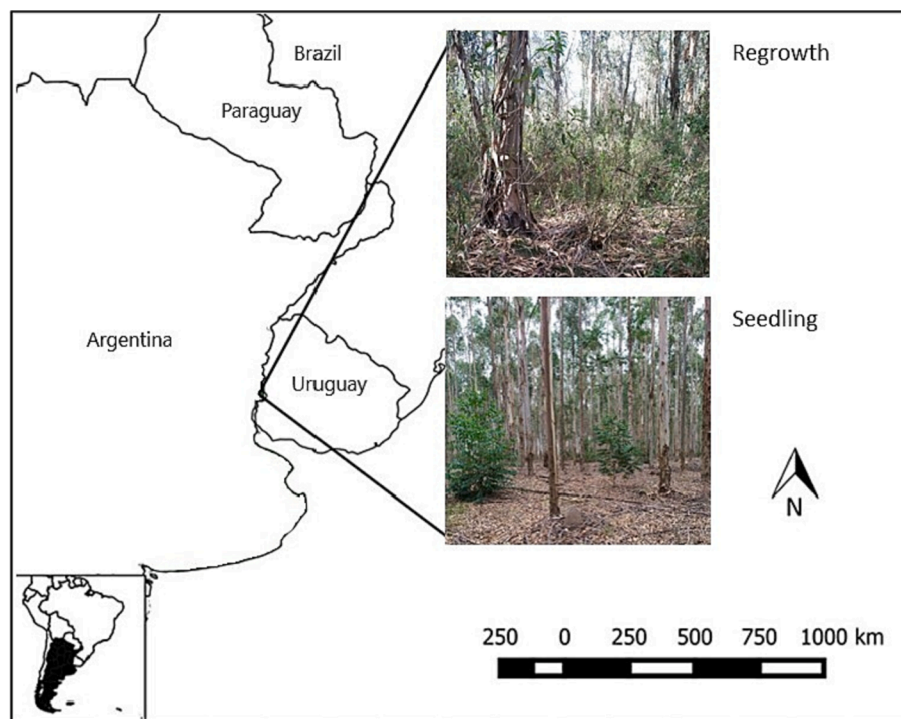

Fig. 2. Location of regrowth and seedling stands in the Entre Rios province, Argentina. Inset: overview of internal structure of typical regrowth and seedling stands.

2.2. Forest structure

To assess forest structure between regrowth and seedling management the following metrics were measured in five 10x10m plots in each stand: diameter at breast height (DBH) of five trees and the height of five trees, total number of stems counted, visual estimation of percentage cover of understorey layers (subcanopy, shrubs (woody species), and ground vegetation (percentage of non-woody species)). To estimate the percentage of canopy cover, a digital photograph of the sky was taken from a 1.5 m height within each plot and images were analysed using the ImageJ software (Schneider et al., 2012). Then, for each stand, we estimated understorey vegetation complexity by calculating the Shannon index based on the three understorey layers.

2.3. Natural enemies

Abundance of insectivorous birds was recorded using point counts (Ralph et al., 1996; Bibby et al., 1998) in the spring (October). In each stand five points were established at least 100 m apart to facilitate non-overlapped subsamples (Bibby et al., 1998), and located at least 100 m away from the plantation edge to minimise edge effect. Bird surveys took place between sunrise and 10:30am on sunny calm days. At each point a fixed 50 m radius was used. All heard and seen birds were recorded for a 5-min period and birds flying overhead were not considered. Bird surveys and identifications were conducted by two trained observers. Also, bird songs were recorded using a digital recorder (Zoom H4next Handy Recorder) during the surveys to aid in later identification. We analysed the recorded songs and identified bird species by comparing them with published recordings (Xeno-Canto Foundation, 2018). Bird species were classified as insectivorous following the foraging attributes (i.e., Elton traits) proposed in Wilman et al. (2014).

Abundance of spiders was measured by using web abundance as a proxy (Gollan et al., 2010). In each stand, five transects of 10 m length,

2 m width and 2 m height were established and all found webs were counted. A pressurised hand-held water mister was used to help locate spider webs. Web sampling took place six times during the summer (December-March), with the time of day altered for each visit (Ludwig et al., 2018).

2.4. Predation events

We used predation events by birds (attacks on artificial prey) and spiders (prey caught in spider webs) (Muiriri et al., 2016; Ludwig et al., 2018, respectively) as proxy measures of predation pressure and so interpret our findings as an indication of potential predation pressure rather than an absolute measure. Artificial prey, in the form of insect larvae, were made from odourless plasticine following (Muiriri et al., 2016) and resembling a lepidoptera larvae pest species of eucalypts in the region, *Phocides polybius* (https://www.sinavimo.gob.ar) (Supplementary information S.1). Larvae were mounted on pliable metal garden wire (0.2 mm diameter) affixed to lower branches at 1.5 m-2 m. Ten larvae were arranged in a 4 m × 4 m sampling plot and five plots were established per stand, each separated by 50 m and at least 50 m from the stand edge, in homogenous areas which are representative of that stand type. Larvae were left *in situ* for five days, at the end of which the number of pecks marks on each were recorded. This was carried out during the spring to coincide with high bird activity, and repeated four times (i.e., four visits) during this period, with at least one week between each experiment. Counts of prey items took place in the web transects described previously. A magnifier was used to scan webs and count the number of prey items or debris left from prey items. Where possible these were identified to Order. For small specimens the web portion and debris were collected and placed on a white sheet to aid identification. Where the taxonomic identity could not be determined the individual was recorded simply as invertebrate prey debris.

2.5. Data analyses

Mean DBH and tree height was calculated per plot within each stand. Bird abundance and web abundance (both total number and those with prey), were summed across the five point-counts and transects respectively, within a stand. All analyses were performed in the R programme, Version 4.2.0 (R Core Team, 2022). The mean number of stems per plot and the percentage of canopy cover within each stand were analysed for differences between management types using a *t* test. Mean DBH and mean tree height, as well as the percentage cover of the understorey layers (subcanopy, shrub and ground vegetation) and understorey vegetation complexity (Shannon index) per stand were tested for difference between the management types using Wilcoxon Rank Sum test as the data were not normally distributed.

To determine differences in the abundance of insectivorous birds a General Linear Model (GLM) was used, with management type as a fixed factor and a gaussian error distribution using the "glm" function in the base R programme. To determine differences in the abundance of spider webs, a Generalised Linear Mixed Model (GLMM) with a Poisson error distribution was used, with management type as a fixed factor and stand as a random factor (with a total of six observations per stand) using the "Lmer" function in the Lme4 package (Bates et al., 2015). To determine differences in the number of attacked artificial larvae, GLMMs were carried out using a binomial error distribution and with the response to management type weighted by the number of recovered larvae (i.e., included as "weights" in the model), stand was the random factor with 20 observations per stand. Lost larvae were not considered. To test for differences in the number of webs with identifiable prey or prey detritus between management types, a GLMM was conducted with a Poisson error distribution with the same factors and levels as described for the abundance of spider webs. For all models, assumptions were checked using the "simulateResiduals" function in the DHARMa package (Hartig, 2022).

Finally, we performed a path analysis through structural equation models (SEM) to test direct and indirect associations between explanatory and response variables. We ran two unique complete models, one per response variable, as we were focused on estimating the strengths of the direct and indirect pathways rather than alternative partial models (Grace, 2006). Following our theoretical model (Fig. 1) for the mean proportion of attacked larvae per stand we included a path reflecting the direct influence of management type and another path reflecting its indirect influence via the abundance of insectivorous birds and via subcanopy vegetation complexity (estimated through Shannon index). For the mean number of spider webs with identifiable prey or prey detritus per stand, we included a path reflecting the direct influence of management type and another path reflecting its indirect influence via the abundance of spider webs and via subcanopy vegetation complexity. All models were fitted with the piecewiseSEM package (Lefcheck, 2016).

3. Results

Across the season a total of 329 individual birds in 37 species were recorded, with 19 of them classified as Insectivores (Supplementary Information S.2). A total of 4048 individual webs from 30 different types were recorded. In total there were 83 larval attacks across the dataset. In total 338 of the webs (8 % of the total) had prey debris recorded in them (Supplementary Information S.3).

3.1. Forest structural characteristics

Some structural characteristics differed between management types (Table 1, Fig. 3). While the number of stems was similar between regrowth and seedling stands, the mean DBH of stems per plot within a stand and canopy cover was significantly higher in the seedling compared to the regrowth ones. Further, the mean height of trees per plot within a stand was marginally greater in the seedling management than in the regrowth stands. Cover of understorey layers differed between the management types. Subcanopy, shrub, ground vegetation cover and understorey vegetation complexity estimated through Shannon index were all significantly higher in the regrowth stands than the seedling stands (W = 35, N = 12, p-value = 0.008; W = 36, N = 12, p-value = 0.005; W = 36, N = 12, p-value = 0.005, W = 36, p-value = 0.002, respectively) (Fig. 3).

3.2. Natural enemies and predation events

According to the GLM and GLMM performed, there were significant differences in the abundance of potential pest predators between management types (Supplementary Information S.4). Bird insectivore abundance and spider web abundance were significantly greater in regrowth stands compared to seedling stands ($X^2 = 20.51$, p-value = <0.0001 and $X^2 = 7.35$, p-value = 0.0067 respectively) (Fig. 4a, b). We also found differences in predation events between management types. The GLMM showed that there were significantly more attacks on artificial larvae and more webs with identifiable prey or prey detritus in the

Table 1
Mean (±SD) or median (range) of structural variables between stand management type and associated test outcomes. **p < 0.01, p < 0.05, †p = 0.054.

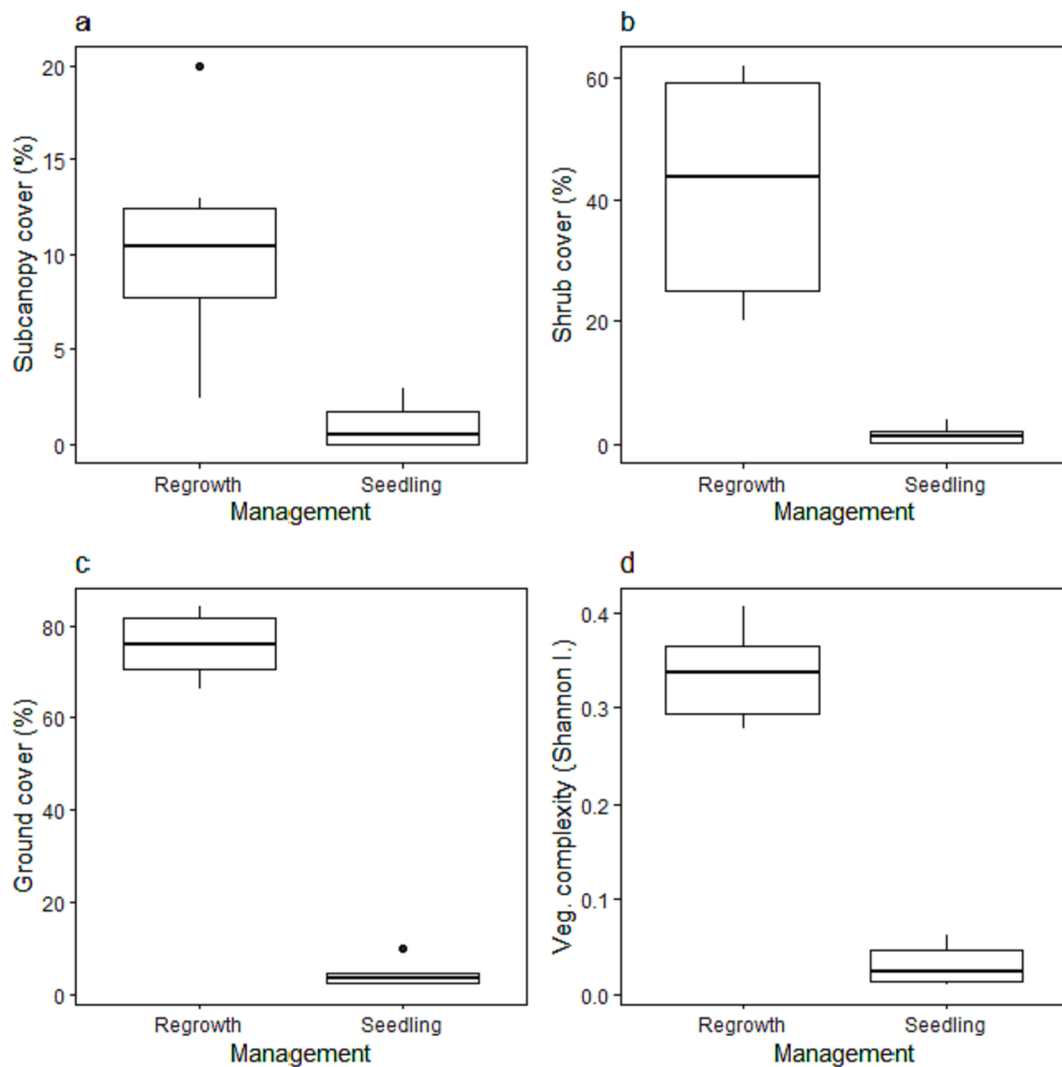| Structural variable	Regrowth	Seedling	Degrees of freedom / N	Test
Mean No. stems	8.37 ± 0.96	7.87 ± 1.19	10	t = 0.80
Median DBH (cm)	54.11, 4.60	66.75, 28.91	12	W = 0**
Median Height (m)	16.61, 3.49	18.61, 6.08	12	W = 5.5†
Mean % Canopy cover	56.80 ± 2.32	63.24 ± 1.51	10	t = -2.32*

Fig. 3. Percentage cover of structural layers below canopy: a) subcanopy, b) shrub, and c) ground vegetation; and d) understorey vegetation complexity between management types. All comparisons were significant at p-value < 0.05.

regrowth stands than in the seedling stands ($X^2 = 5.10$, p-value = 0.02 and $X^2 = 4.25$, p-value = 0.04 respectively) (Fig. 4c, d).

The evaluation of the SEMs indicated that there were no missing paths (Supplementary Information S.5). Analysis of the interactions in regrowth management and seedling management indicated a positive indirect association with the abundance of insectivorous birds via subcanopy vegetation complexity and an indirect association with the proportion of attacked larvae via the abundance of insectivorous birds (Fig. 5a). For the number of spider webs with prey, there was a positive indirect association with regrowth management via spider web abundance, however, the path via vegetation complexity was not significant (Fig. 5b).

4. Discussion

We found evidence that structural complexity of vegetation was a driver of predator abundance and the number of predation events under the framework of the enemies hypothesis. In forests, most research on the enemies hypothesis has focused on tree species diversity as the driver of predator-herbivore interactions; these studies have varying results, often suggesting that tree species identity is more important (Staab and Schuldt, 2020). However, our findings agree with recent evidence indicating that vegetation structure is also an important component of the enemies hypothesis (Schuldt et al., 2019), and that understorey

vegetation in forests is a key driver of predator abundance (Dall'Oglio et al., 2016, Michalko et al, 2021b) and therefore is a potentially important influencer of predator–prey food-webs (Michalko et al, 2021a). Our study found support for each element of our hypothetical model. This highlights the importance of selecting the appropriate forest management approach to promote understorey vegetation layers. Such management decisions fundamentally alter habitat structure and likely biodiversity and ecosystem functions.

As predicted, structural complexity of the understorey was higher under regrowth than seedling management in eucalyptus plantations. Vegetation cover was greater across all vertical layers, agreeing with Zhou et al. (2017); they attributed this to the lower disturbance under regrowth regimes. Indeed, seedling management typically involves more significant disturbance to the ground layer due to site preparation. Prescribed burning increases soil nutrients and enhances the growth rate of planted trees (Chungu et al., 2020), but it can also significantly reduce understorey vegetation layers (Lewis et al., 2012; Fuentes et al., 2018) and can negatively impact important soil microbial functions which benefit plant establishment and development (McMullan-Fisher et al., 2011). In contrast, under the less disturbed regrowth management, due to stump protection, some understorey vegetation, particularly in the ground layer, may remain in place following clearcut, allowing for quicker regrowth of vegetation. Disturbance via machinery can lead to direct physical damage of plants (Blair et al., 2016) and to soil
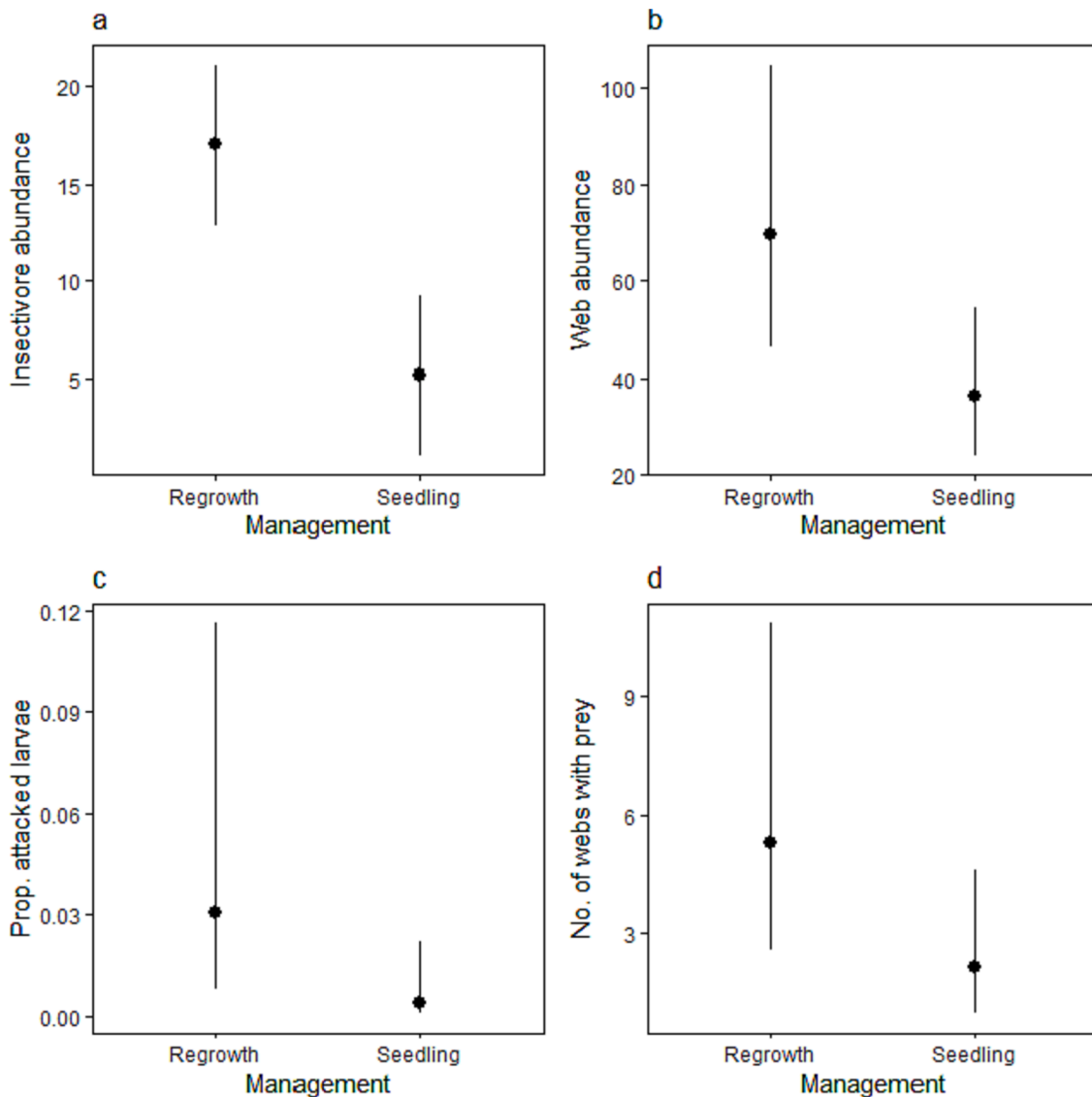
Fig. 4. Comparisons (mean ± 95 % CI) obtained from models between management types of a) bird insectivore abundance, b) spider web abundance, c) attacks on artificial larvae, d) number of webs with identifiable prey or prey detritus. Y-axes are expressed at the response variable scale; all comparisons were significant at p-value < 0.05.

compaction which negatively affects plant development (Unger and Kaspar, 1994). This disturbance is likely to be exacerbated under seedling management since they have more extensive ground preparation.

Insectivorous birds and likely spiders benefit from high coverage of vegetation layers under the forest canopy. Similarly, both Dall'Oglio et al. (2016) and Michalko et al. (2021b) have found that understorey vegetation has a positive effect on parasitoids of eucalypt pests and web spider abundance respectively. Diverse and dense understorey vegetation may lead to increased predator abundance through different mechanisms. First, directly through the variety of vegetation layers providing shelter resources e.g., protection from predation, web attachment points for spiders and nesting sites for birds (Cody, 1985; Spears and MacMahon, 2012). Further, the dense understorey may act as a physical barrier to prevent big mammals (e.g., deer, wild pigs, or cattle) from entering the stands (Jactel et al., 2009), and disturbing spider webs and bird nests. Second, indirectly through higher availability and diversity of prey because diverse plant communities usually provide more habitat for herbivorous species (Jactel and Brockerhoff, 2007). Moreover, although more complex vegetation may act as a reservoir for pests (Frew et al., 2013), a reduction in herbivory is still

expected (Jactel and Brockerhoff, 2007) because of the greater number of enemies, following the enemies hypothesis (Jactel and Brockerhoff, 2007; Root, 1973). Thus, it is expected that vegetation complexity affects predator abundance directly by providing shelter resources and indirectly via herbivore abundance and diversity.

Our study found that predation events by both birds and spiders are greater in stands managed under regrowth rather than seedling approach. However, our analysis suggests the mechanism driving potentially increased predation events by birds and spiders differ; for birds our hypothetical model is fully supported, with an indirect link between forest management and predation events driven by increased bird abundance via enhanced structural complexity. For spiders, analysis suggests a direct link between management and spider web abundance, circumventing the role of vegetation complexity. This is surprising given the well-known positive relationship between vegetation structure and web building (Rypstra et al 1999). In this case other factors related to forest management may be driving greater web abundance and prey captures in regrowth stands such as the reduced disturbance meaning a greater pool of spiders and prey are retained following clear-fell, which is unrelated to vegetation complexity *per se.*.
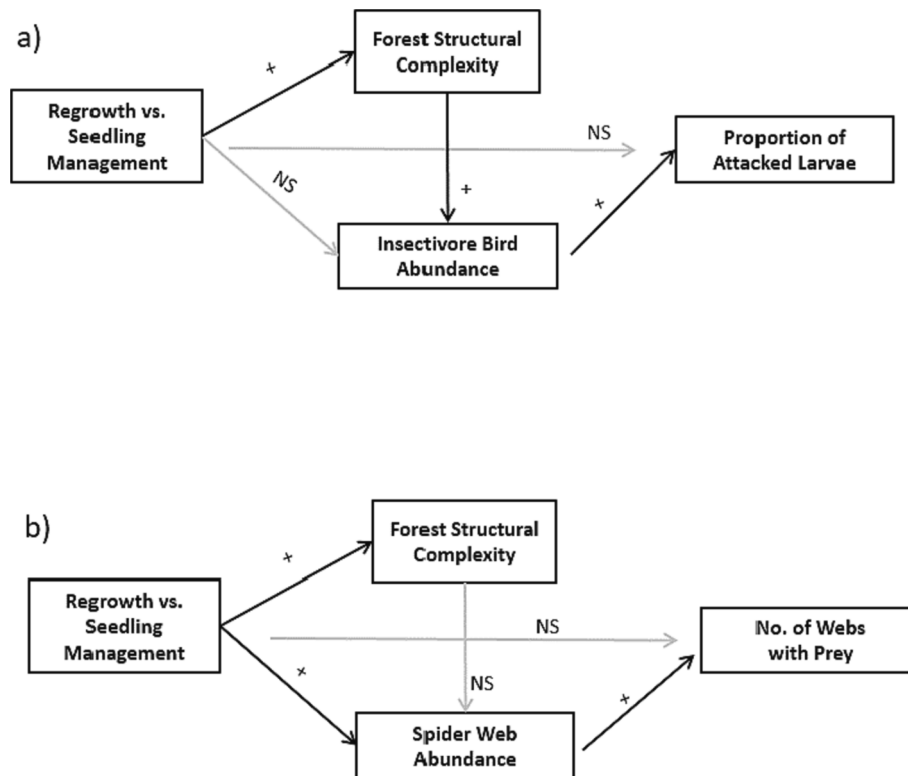
Fig. 5. Path analysis obtained from structural equation models reflecting our hypotheses of possible associations among variables for two potential predators of pests a) birds and b) spiders. We indicate the type of association for significant paths (+: positive, black arrows) and not significant paths (NS, grey arrows). Arrows on the left reflect the differential influence of regrowth management when compared to seedling management. Paths were significant at p-value < 0.05.

Alternatively, the lack of direct linkage between vegetation complexity and spider predation events may be due to more complex relationships between variables (i.e. nonlinear or interactions with alternate predictors). The interaction between birds and spiders, via intraguild predation, may also impact our findings; birds are well known predators of web spiders, though predation rate depends on spider size and behaviour (Gunnarsson, 2007). In this case the higher bird abundance in regrowth stands may limit spider abundance and suggest a reduced role in control of insect pests in comparison with birds. Further study exploring the relative importance of prey availability vs vegetation complexity, and consideration of more complex ecological interactions (e.g., predation) may help reveal the key drivers of spider abundance in these ecosystems.

For birds at least, the complexity of the understorey vegetation layers within regrowth stands appears to be a key driver of predation events. Higher predation rate by natural enemies was found in the understorey, compared to the canopy, in temperate forests in Canada (Aikens et al., 2013) showing the importance of below canopy strata for predation pressure on pests. Those authors also showed consistent and strong effects of bird exclusion on caterpillars implying that caterpillars are usually a favoured prey item of birds. We could also be underestimating potential predation pressure as it is usually higher on real prey than on artificial caterpillars (Lövei and Ferrante, 2017). Therefore, our results are consistent with the idea that plantation management leading to the preservation of understorey vegetation under the canopy will be more resistant to pest outbreaks.

4.1. Management implications

Regrowth management with low disturbance after clearcutting promotes both predator abundance and predation events via increased vegetation structural complexity. However, with the development of new genetically enhanced clones, and the fact that regrowth-yield dramatically decreases after a few cycles, replanting is eventually unavoidable. Therefore, as well as using the regrowth approach as a method to promote pest control within stands, temporal, and spatial rotation to ensure that regrowth stands are adjacent to seedling stands should encourage both landscape level heterogeneity and stand level spill over effects from more healthy and resilient neighbours. For instance, Roels et al. (2018) suggested that plantations interspersed with bird-friendly features could facilitate plantation use by birds and enhance the ecological function of herbivorous insect consumption. However, manipulative experiments explicitly exploring the cause-and-effect relationship between predation rates and herbivory rates and consideration of the economic implications of the different approaches are required before these recommendations are implemented. Our study agrees with the overarching paradigm in sustainable forest management that promotion of structural complexity will be beneficial to biodiversity, ecosystem function and resilience.

CRediT authorship contribution statement

Declaration of Competing Interest

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.foreco.2023.120799.

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