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Predicting the impact of invasive trees from different measures of abundance

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Abstract:	Biological invasions produce negative impacts worldwide, causing massive economic costs and ecological impacts. Knowing the relationship between invasive species abundance and the magnitude of their impacts (abundance-impact curves) is critical to designing prevention and management strategies that effectively tackle these impacts. However, different measures of abundance may produce different abundance-impact curves. Woody plants are among the most transformative invaders, especially in grassland ecosystems because of the introduction of hitherto absent life forms. In this study, our first goal was to assess the impact of a woody invader, Pinus contorta (hereafter pine), on native grassland productivity and livestock grazing in Patagonia (Argentina), building abundance-impact curves. Our second goal, was to compare different measure of pine abundance (density, basal area and canopy cover) as predictors of pine´s impact on grassland productivity. Our third goal, was to compare abundance-impact curves among the mentioned measures of pine abundance and among different measures of impact: total grassland productivity, palatable productivity and sheep stocking rate (the number of sheep that the grassland can sustainably support). Pine canopy cover, closely followed by basal area, was the measure of abundance that best explained the impact on grassland productivity, but the shape of abundance impact curves differed between measures of abundance. While increases in pine density and basal area always reduced grassland productivity, pine canopy cover below 30% slightly increased grassland productivity and higher values caused an exponential decline. This increase in grassland productivity with low levels of pine canopy cover could be explained by the amelioration of stressful abiotic conditions for grassland species. Different measures of impact, namely total productivity, palatable productivity and sheep stocking rate, drew very similar results. Our abundance-impact curves are key to guide the management of invasive pines because a proper assessment of how many invasive individuals (per surface unit) are unacceptable, according to environmental or economic impact thresholds, is fundamental to define when to start management actions.
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Predicting the impact of invasive trees from different measures of abundance

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Highlights

- Invasive species abundance-impact curves are key to designing management strategies.
- We assessed how increasing abundance of invasive pines impacted grasslands.
- Pine canopy cover over 30% reduced grasslands productivity exponentially.
- Managers should start controlling invasive pines before this threshold is reached.

Abstract

Biological invasions produce negative impacts worldwide, causing massive economic costs and ecological impacts. Knowing the relationship between invasive species abundance and the magnitude of their impacts (abundance-impact curves) is critical to designing prevention and management strategies that effectively tackle these impacts. However, different measures of abundance may produce different abundance-impact curves. Woody plants are among the most transformative invaders, especially in grassland ecosystems because of the introduction of hitherto absent life forms. In this study, our first goal was to assess the impact of a woody invader, *Pinus contorta* (hereafter pine), on native grassland productivity and livestock grazing in Patagonia (Argentina), building abundance-impact curves. Our second goal, was to compare different measure of pine abundance (density, basal area and canopy cover) as predictors of pine´s impact on grassland productivity. Our third goal, was to compare abundance-impact curves among the mentioned measures of pine abundance and among different measures of impact: total grassland productivity, palatable productivity and sheep stocking rate (the number of sheep that the grassland can sustainably support). Pine canopy cover, closely followed by basal area, was the measure of abundance that best explained the impact on grassland productivity, but the shape of abundance impact curves differed between measures of abundance. While increases in pine density and basal area always reduced grassland productivity, pine canopy cover below 30% slightly increased grassland productivity and higher values caused an exponential decline. This increase in grassland productivity with low levels of pine canopy cover could be explained by the amelioration of stressful abiotic conditions for grassland species. Different measures of impact, namely total productivity, palatable productivity and sheep stocking rate, drew very similar results. Our abundance-impact curves are key to guide the management of invasive pines because a proper assessment of how many invasive individuals (per surface unit) are unacceptable, according to environmental or economic impact thresholds, is fundamental to define when to start management actions.

Keywords: Impact-based management, grasslands, livestock grazing, Pinus, primary productivity, woody invasions.

1. Introduction

Biological invasions are one of the major components of global change (Díaz et al., 2019), producing negative impacts globally (Cameron et al., 2016; Gallardo et al., 2016; Simberloff, 2011; Vilà et al., 2011) and incurring high economic costs (Diagne et al., 2021; Pimentel et al., 2005). All continents are affected by biological invasions (van Kleunen et al., 2015), even the remote Antarctica (Frenot et al., 2005; Hughes et al., 2015), as are all types of ecosystems (Vilà and Hulme, 2017), spanning tropical forests (Acurio et al., 2010) to deserts (Tellman, 2002). In addition to their severe ecological impacts, the negative impacts produced by these invasive species threaten the provision of essential ecosystem services and the economic activities that depend upon them (Vilà and Hulme, 2017). Knowing the relationship between invasive species abundance and the magnitude of their impacts (abundance-impact curves hereafter) is essential to forecasting and effectively managing damages (Cassey et al., 2006; Gilbert and Levine, 2013; Norbury et al., 2015; Thomsen et al., 2011). These relationships can inform economic analyses (costs vs. benefits) of management actions (Sofaer et al., 2018; Yokomizo et al., 2009) that are instrumental for designing management strategies that effectively mitigate these impacts (Bradley et al., 2019; Byers et al., 2002).

Woody plants are among the most transformative plant invaders, especially in grassland ecosystems because of the changes produced by the introduction of a new life form (Ehrenfeld, 2003; Rundel et al., 2014). This is a problem global in scope and growing, consequently requiring immediate action (Archer et al., 2017; Simberloff et al., 2010; Van Auken, 2000). While many impacts have been documented for invasive woody plants on natural grasslands (Davis et al., 2019; Ferraina et al., 2021; Pawson et al., 2010), no study has yet quantified the relationship between their abundance and the magnitude of their impacts on native grasslands productivity, or how these impacts progressively affect economic activities which depend on this ecosystem service, such as livestock grazing. For instance, a recent study has measured the impact of an invasive woody plant (*Gleditsia triacanthos*) on the productivity of native grasslands, but only comparing invaded vs uninvaded plots (i.e. with no gradient in invader abundance) (Ferraina et al., 2021). Another study, assessed the impact of increasing *P. contorta* cover on native grasslands species richness and relative cover (Taylor et al., 2016), which (although related) are different from grassland productivity (Catchpole and Wheeler, 1992; Chiarucci et al., 1999; Jiang et al., 2017). Further, none of the mentioned studies focused on the invader impact on the productivity of palatable grassland species (those foraged by livestock), which in turn would impact livestock grazing. Management of invasive woody plants to tackle their impacts on grasslands productivity and livestock grazing will benefit from detailed quantifications of their abundance-impact curves (Bradley et al., 2019; Yokomizo et al., 2009).

The *Pinus* genus is an ideal study system to assess the abundance-impact relationship that drives the impact of woody invasives on grassland productivity. Firstly, numerous species of this genus have become invasive in grassland ecosystems around the world (Nuñez et al., 2017; Richardson et al., 1994; Simberloff et al., 2010). Further, as most pine invasions start from plantations maintained for economical purposes (Nuñez et al., 2017), their spread away from these plantations, through wind dispersal, creates abundance gradients with the highest abundance near the source of propagules and lower abundance with increasing distance (Langdon et al., 2010; Taylor et al., 2016). These abundance gradients offer an exceptional opportunity to measure *Pinus* invasion impacts at varying levels of invader abundance. Finally, the invasion of *Pinus* species has notorious impacts in grasslands, and these impacts may affect grassland productivity, namely a strong reduction in plant species richness and cover (Davis et al., 2019; Franzese et al., 2017; Taylor et al., 2016), a steep increase in fuel load which affects the ecosystem fire regime (Paritsis et al., 2018; Taylor et al., 2017) and an increase in litter depth (Taylor et al., 2016) which may affect nutrients cycles (Araujo and Austin, 2015).

Abundance of invasive *Pinus* species can be measured in different ways, with a trade-off between simplicity and the detail in the information obtained. On one hand, density is the most easily obtained but it does not account for the difference in size between seedlings and adults, which is key when assessing the impact of invasive woody plants (Franzese et al., 2017). Basal area (the sum of the cross sections of all trees within a hectare) incorporates pine size through the additional measurement of individual diameters through a simple procedure that requires no specialized or expensive equipment. On the other hand, canopy cover is more resource and time-consuming, obtained through a more technical procedure which includes taking hemispheric pictures and analyzing the obtained images. This requires relatively expensive (photographic camera) and specialized (fisheye lens) equipment.

In this study, our first objective was to quantify the impact of *Pinus contorta* (hereafter pine) invasion on native grassland productivity in northwest Patagonia. For this purpose, we built abundance-impact curves, assessing the impact of pine invasion on grassland productivity along a gradient of increasing pine abundance. Our second objective was to compare different measures of pine abundance (density, basal area and canopy cover) as predictors of pine´s impact on grassland productivity. While pine density is quick and easy to measure, we expected that it would underestimate the individual impact of adults (which are considered equivalent to seedlings). We expected that basal area would be a better predictor of pine impact, since it incorporates individual size, while still being fairly straightforward to measure. Canopy cover moves a step further, since it integrates the distribution of pine sizes, according to the distance of each individual to the point of measurement, by recording the sky obstruction by pine canopies (Rich, 1990). Therefore, we expected that canopy cover would provide the best prediction of pine impacts. Last but not least, our third objective was to compare abundance-impact curves among different measures of pine abundance (previously mentioned) and among measures of impact, including total grassland productivity, productivity of palatable species (i.e. those that are foraged by sheep, the main livestock in the region (DNAP, 2018a, 2018b, 2018c)), and sheep stocking rate (i.e. the number of sheep that can be supported by this palatable productivity). Since these are semiarid grasslands, we expected that low pine abundance could facilitate grassland biomass growth (Belsky, 1994; Blaser et al., 2013; Dohn et al., 2013; Mazía et al., 2016) by ameliorating stressful abiotic conditions through the reduction of air temperature and soil water evaporation (Belsky et al., 1993) and via the pumping of water (by hydraulic lift) from deeper soil (Neumann and Cardon, 2012) (Figure S1). We also expected that low pine abundance would favor the proportion of palatable species in the grasslands (Bernardi et al., 2016; Peterson et al., 2007; Scholes and Archer, 1997), possibly by providing microsite conditions more favorable for these species, concomitantly increasing palatable productivity, even more than total productivity via positive effects on total productivity and the proportion of palatable productivity. Additionally, we also expected that high pine abundance would reduce both total and palatable productivity (Davis et al., 2019; Franzese et al., 2017; Taylor et al., 2016), mainly through the reduction in solar radiation (Rago et al., 2021).

2. Materials and Methods

2.1 Study area

We conducted our research on five sites (called A1, A2, A3, C1 and C2) in northwest Patagonia (Argentina; Figure 1a & 1b, Table 1) where plantations of *Pinus contorta* were established approximately 30 years ago, replacing areas of native grasslands. Each of these five plantations has invaded adjacent native grasslands producing a gradient of invasion abundance, with the highest abundance near the plantations and decreasing with distance. Mean annual precipitation is 900 mm and mean annual temperature is 8.3 °C (Bariloche Airport meteorological station, located within our study area). Vegetation cover in these native grasslands is on average 60%, and dominated by *Pappostipa speciosa* and *Festuca pallescens*, both perennial tussock grasses and palatable species to sheep, supplemented with other plant species present in lower abundances

(Anchorena and Cingolani, 2002; Bonvissuto et al., 2008). These grasslands cover a large proportion of the Patagonian region and are among the most susceptible ecosystems to pine invasions (Richardson et al., 1994; Simberloff et al., 2010). Pine plantations have replaced large areas of these grasslands (Schlichter and Laclau, 1998), becoming a source for invasions that, in turn, further replace areas of these native grasslands (Nuñez et al., 2017). The most important economic activity in these grasslands is extensive livestock grazing, mainly by sheep (DNAP, 2018b, 2018a, 2018c), which depends almost exclusively on native rangelands for forage (Golluscio et al., 1998; Soriano and Paruelo, 1990).

2.2 Experimental design

2.2.1 Assessing pine impacts on grassland productivity using abundance-impact curves

To quantify the impact of invasive pines on grassland productivity, we estimated grassland productivity along transects of increasing pine abundance, in the five sites described before (A1, A2, A3, C1 and C2). We defined grassland productivity as the dry aerial biomass produced annually per surface unit (kg /hectare/year). We used green biomass in the peak production as a metric for aboveground annual productivity, as proposed by Sala and Austin (2000) in sites where the growing season is brief and marked. In the region where our sites are located, the growing season spans from December to March (Heinemann and Kitzberger, 2006). In each of our five sites, we built transects (five transects per site) radiating from the edge of a pine plantation, following the main dispersal direction, until we reached a position beyond the invasion front, where invasive individuals were absent (Figure 1c and 1d). On each transect, we compared grassland productivity in the absence of pine invasion (control plot) with grassland productivity in paired plots with increasing levels of pine abundance (invaded plots). Since the distance between the plantation and invasion front varied across sites, we adjusted the length of our transects accordingly. Therefore, in sites A2 and C2 our transects were 200-m long, in site C1 transects were 350-m long, and in sites A1 and A3 transects were 500 m long. The distance between the five transects within the same site was 50 m. Along each independent transect, we set circular plots at the following distances from the pine plantation (propagule source): 0, 25, 50, 75, 100, 150, 200, 350 and 500 m (these two last distances only for sites with transects that reached 350 and 500 m) based on visible thresholds in pine density. Distance between plots was smaller closer to the pine plantation than near the invasion front because the greatest variation in invasion density occurs near the seed source and we wanted to capture this variability.

2.2.2 Comparing the performance of different measures of pine abundance as predictors of their impact on grassland productivity

We measured three different metrics of pine abundance, to find out which one best predicted their impact in grassland productivity:

a) Density (trees/ha): number of pines per hectare. Within each circular plot (10 m diameter), we counted the number of pine individuals and calculated the corresponding number of individuals for a hectare.

b) Basal area (m^2/ha): the sum of the cross sections of all pines per hectare. Within each plot, we recorded each individual diameter at ground level to calculate every cross section and add them up to obtain basal area (m^2/ha).

c) Canopy cover (%): the percentage of the sky that is blocked by the projection of the pine crowns. Within each circular plot, we randomly distributed six square subplots (0.25 m^2). In each of these subplots we took a hemispheric picture to estimate pine canopy cover using a Nikon Coolpix P80 camera with an Opteka fisheye lens 0.20x.

2.2.3 Comparing abundance-impact curves across metrics of pine abundance and among pine impacts

We compared abundance-impact curves across the metrics of pine abundance described above and across three measures of pine impacts on grasslands:

1) Total productivity: aerial green biomass per hectare, considering all grassland species. In the same subplots where we measured pine canopy cover (by taking hemispheric pictures), we estimated total grassland productivity by harvesting (using pruning scissors) all the green biomass of grasses, forbs and shrubs at the peak of the growing season (early summer) (Sala and Austin, 2000). We classified each species into palatable and non-palatable (foraged and not foraged by sheep, respectively) according to a handbook for natural grassland condition in Patagonia (Bonvissuto et al., 2008). We oven-dried the harvested biomass at 60°C for 48h and used a precision scale (0.001 grams) to measure the dry weight.

2) Palatable productivity: aerial green biomass per hectare, only considering species foraged by sheep. We followed the procedure described to estimate total productivity but here we only considered palatable grassland species, including grasses, forbs and shrubs.

3) Sheep stocking rate: number of sheep that can be sustained by the palatable productivity. To assess the impact of pine invasions on livestock grazing, mainly sheep, which relies almost exclusively on rangelands for forage, we calculated the sheep stocking rate that the grasslands of our study can sustainably support based on the feeding requirement of an Ovine Livestock Unit

(OLU). The OLU represents an individual Merino wether (castrated male sheep) with an average live weight of 40 kg that consumes 365 kg of dry forage in a year in Patagonia grasslands. We used this livestock equivalence as a reference that establishes a correspondence between different animal species. We also considered the vegetation Use Factor (UF) of each site, a value corresponding to a proportion of effectively consumable forage that can be grazed by sheep without compromising a sustainable forage production over time (Table 1) (Bonvissuto et al., 2008; Golluscio et al., 2009).

Because pines show rare events of long distance dispersal (Langdon et al., 2010), and even though our transects went beyond the invasion front (which is driven by the predominant short distance dispersal kernel), in some specific cases the plot that was most distant form the plantations ended up located in an area with small groups of invasive pine individuals. We did not consider for analyses the transects where pines were present in all plots along the transect because these transects lacked a control plot, making it impossible to assess their impact. The total number of transects (throughout the five sites) not considered for analyses was five: three in site A2, one in site A3 and one in site C2.

2.3 Statistical analyses

To evaluate the impact of increasing pine abundance on grassland productivity we used linear regression models (lm function in R) (Chambers and Hastie, 1992; Wilkinson and Rogers, 1973), with pine abundance as predictor variable and their impacts as response variables (abundance-impact curves). To compare different measures of pine abundance as predictors of their impact in grassland productivity we used the three different measures of pine abundance previously described (density, basal area and canopy cover) as predictor variables in our regression models. We only used one predictive variable for each regression model. We compared regression models with different prediction variables based on the Akaike Information Criterion (AIC).

To compare abundance-impact curves among different metrics of pine abundance, we used these regression models where the predictive variable was either pine density, pine basal area or pine canopy cover. To compare abundance-impact curves among measures of impact we used the three measures of impact described before (total grassland productivity, productivity of palatable species, and sheep stocking rate) as response variables in our regression models (one response variable for each regression model). In all cases, we built both a linear and a polynomial (order 2) regression, since both linear and nonlinear relationships between abundance and impact of invasive species have been documented (Bradley et al., 2019; Sofaer et al., 2018). For each predictive variable, we selected between the linear and nonlinear regressions based on AIC.

Since grassland productivity is variable across sites (Figure S2), we standardized our impact measures by calculating effect sizes. For each subplot we calculated three different effect sizes (ES), focusing on the three different impacts on grasslands mentioned before (Figure 2), using log-response ratios:

1) The effect size of pine invasion on grassland total productivity (EStp):
   EStp = ln (Bi/Bc).
2) The effect size of pine invasion on grassland palatable productivity (ESpp):
   ESpp = ln (Pi/Pc)
3) The effect size of pine invasion on the sheep stocking rate that the grassland can sustainably support (ESsr):
   ESsr = ln (Si/Sc)

where *Bi* is the total grassland dry aerial green biomass (including grasses, forbs and shrubs, both palatable and non-palatable) for subplots located in plots invaded by pines, *Pi* is the total dry aerial green biomass of palatable species for the same subplots, and *Si* is the sheep stocking rate that can be sustainably supported by the total dry aerial green biomass of palatable species for the same subplots. *Bc* is the total grassland dry aerial green biomass for subplots located in the paired control plot of the same transect, which is the most distant from the pine plantation and has not been invaded yet (Figure 1d), *Pc* is the total dry aerial green biomass of palatable species for subplots located in the control plot, and *Sc* is the sheep stocking rate that can be sustainably supported by the total dry aerial green biomass of palatable species for subplots located in the control plot.

For each plot, we calculated an average for each of the three effect sizes (EStp, ESpp and ESsr) using the data from the six subplots. A positive effect size would indicate that pine invasion increased grassland productivity, while a negative effect size would indicate that grassland productivity is negatively affected by the invasion of pines. The absolute value of the effect size indicates the magnitude of the response of grassland productivity to the invasion of pines, either positive or negative.

To understand how different measures of pine abundance relate to each other we built three regression models. In the first case, we built a generalized linear model, with pine density as predictive variable and pine basal area (rounded up to the nearest integer) as response variable, assuming a Poisson distribution. In the second model, we used pine density as predictive variable and pine canopy cover (converted from percentage to proportion data) as response variable, assuming a Beta distribution (“betareg” function from the “betareg” package) (Cribari-Neto and Zeileis, 2010). For the third model, we considered pine basal area as predictive variable and pine canopy cover (converted from percentage to proportion data) as response variable, assuming a Beta distribution.

Finally, for each subplot we assessed how pine density, basal area and canopy cover influenced the proportion of palatable (out of the total) productivity. For this purpose, we built a regression model assuming a Beta distribution ("betareg" function from the "betareg" package) (Cribari-Neto and Zeileis, 2010), with proportion of palatable productivity as response variable and pine density, basal area, or canopy cover as predictive variables. Each regression included only one pine abundance measure as predictive variable. We performed all statistical analyses using R v.4.1.1 (R Development Core Team, 2021).

3. Results

3.1 Assessing pine impacts on grassland productivity using abundance-impact curves

We found a predominantly negative effect of pine invasions on grassland total productivity, palatable productivity and sheep stocking rate, with increasing levels of pine abundance causing further declines on each of the measures of impact studied here (Figure 3). However, this pattern was affected by the measure of pine abundance with which abundance-impact curves were built. On one hand, pine density and pine basal area both produced only declines of grassland total productivity, palatable productivity and sheep stocking rate across the range of pine abundance explored here. On the other hand, low levels of pine canopy cover (below 30%) produced an increase of grassland total productivity, palatable productivity and sheep stocking rate, while higher levels of pine canopy cover caused a strong decline.

3.2 Comparing the performance of different measures of pine abundance as predictors of their impact on grassland productivity

We found variation among our measures of pine abundance in their adequacy as predictors of impact on grassland productivity (Table 3). The measure of pine abundance that best explained variability in the impact of pine invasion (across all three impact measures) was canopy cover, followed by basal area, and pine density came last, as we expected.

While all measures of pine abundance showed a positive relationship with each other, increases in one measure were not associated with proportional increases in other measures (Figure 4). While pine basal area increased exponentially with density, pine canopy cover at first increased exponentially with density and basal area, to then stabilize at high levels of pine density (approximately 3500 pines/ha) and basal area (approximately 60 m^2/ha), without reaching 100 % cover.

3.3 Comparing abundance-impact curves across metrics of pine abundance and among pine impacts

We found different relationships between abundance and impact for different pine abundance measures. When considering total productivity, the impact of pine density and basal area was best predicted by a linear function, while that of pine cover was best predicted by a nonlinear (polynomial order 2) function (Table 2a). In the case of palatable productivity and sheep stocking rate, the impact of pine density and cover were also best captured by a nonlinear function, while that of pine basal area was still best described by a linear relationship (Table 2b & 2c).

We found that pine density ($R^2 = 0.46$, $p < 0.0001$, Figure 3a) and basal area ($R^2 = 0.53$, $p < 0.0001$, Figure 3a) showed a strong negative linear relationship with grassland total productivity throughout the range of pine abundance surveyed. On the other hand, we found that the best model including pine cover as predictive variable had a negative linear component and a negative polynomial component, resulting in a nonlinear relationship where pine cover below ~30% slightly increased total productivity and higher values strongly reduced it ($R^2 = 0.53$, $p < 0.0001$, Figure 3a). In the case of palatable productivity, the best model including density as measure of abundance had a negative linear and a positive polynomial component, which resulted in a nonlinear relationship where the most rapid decline in palatable productivity occurred at low pine density ($R^2 = 0.42$, $p < 0.0001$, Figure 3b). On the other hand, pine basal area showed a strong negative linear relationship with palatable productivity ($R^2 = 0.43$, $p < 0.0001$, Figure 3b) and pine canopy cover showed a nonlinear relationship where cover values below ~30% slightly increased it and higher values strongly reduced it ($R^2 = 0.43$, $p < 0.0001$, Figure 3b).

When considering the sheep stocking rate that can sustainably be supported by these grasslands, pine density also showed a nonlinear relationship where the most rapid decline occurred at low density ($R^2 = 0.36$, $p < 0.0001$, Figure 3c), while pine basal area still showed a strong negative linear relationship ($R^2 = 0.40$, $p < 0.0001$, Figure 3c). Pine cover showed the same nonlinear relationship where values below ~30% slightly increased stocking rate and higher values strongly reduced it ($R^2 = 0.41$, $p < 0.0001$, Figure 3c). We found no significant effects of pine density ($p = 0.1727$), basal area ($p = 0.4236$) or canopy cover ($p = 0.7536$) on the proportion of palatable (out of the total) productivity.

4. Discussion

We have described the relationship between invasive pine abundance and the response of natural grassland productivity using abundance-impact curves. We found that pine canopy cover, closely followed by basal area, was the abundance measure that best explained the impact of pine invasion on grassland productivity. This is likely indicative of the effects of competition for light, as pine canopy cover quantifies the availability of light in the community (Rago et al., 2021; Trentini et al., 2017). We obtained different shapes (linear and nonlinear) for our abundance-impact curves depending on our different measures of pine abundance, highlighting the importance of defining how to measure invasive species abundance. Remarkably, our analyses revealed that while increases in pine density and basal area produced a negative response of grassland productivity throughout the range of pine abundance assessed, pine canopy cover below 30% produced a slight increase in productivity and higher values caused an exponential decline. Different measures of impact such as total productivity, palatable productivity and sustainable sheep stocking rate yielded very similar results.

Different measures of invasive pine abundance showed different relationships with grassland response to invasion (i.e., different abundance-impact curves). While pine density and basal area showed mostly negative impacts on grassland productivity, canopy cover showed positive and negative impacts at low and high pine abundances, respectively. Invasive species show multiple abundance-impact curves (Sofaer et al., 2018; Strayer, 2020; Yokomizo et al., 2009) due to variations in the invaded habitat (Thiele et al., 2010) and the impact measured (Kelemen et al., 2016; Robinson et al., 2005; Strayer, 2020). However, there is a glaring gap in our understanding of how abundance-impact curves for the same invasive species can be affected by the measure of abundance used. This novel result highlights the importance of defining an appropriate measure for invader abundance, an aspect intimately related to the impact studied (Strayer, 2020).

Different abundance-impact curves could be related to different mechanisms underpinning the impact of pine invasions in grasslands. There may be different species interactions behind each measure of abundance. Competition has been proposed as one of the key mechanisms affecting invaded grasslands (Levine et al., 2003; Simberloff, 2011; Strayer et al., 2006; Vilà et al., 2011) and pine invasions reduce grassland species richness and cover (Davis et al., 2019; Franzese et al., 2017; Taylor et al., 2016). However, facilitation may be the main interaction between trees and grasses under stressful abiotic conditions (Belsky, 1994; Blaser et al., 2013; Dohn et al., 2013; Mazía et al., 2016). In this sense, high pine canopy cover is an indicator of competition for light (Araujo and Austin 2015, Taylor et al. 2016, Rago et al. 2021) but low canopy cover may be associated with facilitation by reducing stressful abiotic conditions. On the other hand, density and basal area are indicators of competition for different resources (water, nutrients, light) (Álvarez Taboada et al., 2004; Biging and Dobbertin, 1995; Contreras et al., 2011; Tomé and Burkhart, 1989). Each new tree, and its concurrent increase in basal area, requires resources for growth, which if consumed by trees become unavailable for grassland species (Rago et al., 2021; Trentini et al., 2017).

Our results broadly concur with previous research focused on the impact of invasive pines in grasslands. For instance, the strong reduction in grassland productivity we found here parallels the sharp decrease in plant richness and cover caused by pine invasions (Davis et al., 2019; Franzese et al., 2017; Taylor et al., 2016). However, we also found positive impacts on grassland productivity when pine abundance was low, confirming the results from studies reporting the facilitation of grassland productivity by trees through the reduction of abiotic stress (Belsky, 1994; Blaser et al., 2013; Dohn et al., 2013; Mazía et al., 2016). Another possible mechanism by which pines are facilitating grassland species growth is by reducing soil erosion, which can be achieved at levels of plant cover below 30% (Eshghizadeh et al., 2018).

The abundance-impact curves described here may be useful to guide management of invasive pines. In particular, low pine canopy cover (below 30%) seems to slightly promote grassland productivity. Therefore, 30% cover is a good candidate threshold to trigger management actions (e.g. start control interventions) to prevent strong increases in negative impacts (Sofaer et al., 2018; Yokomizo et al., 2009). However, 30% cover is rapidly reached, at relatively low pine densities (such as 1000 pines/ha), which may help explain why grassland productivity shows a strong decrease with increasing pine density even for low values of density. In such cases, early detection and rapid response will be the most effective way to manage the impacts of pine invasions (Bradley et al., 2019).

For basal area, we found a linear relationship with impact, as reported by Bradley et al (2019) for cases where the invasive species and the impacted native populations are at the same trophic level, and competition is the prevalent interaction. In such cases, management of invasive populations may be beneficial at any level of basal area (Bradley et al., 2019). However, pine basal area increases exponentially with pine density, so there is a high risk of achieving high levels of basal area before being noticed, especially if abundance is monitored using density. Based on this, a key target for management should be to define a limit of grassland productivity loss or sheep stocking rate reduction beyond which further losses are not affordable, either from an economic (Barney, 2016; Higley and Pedigo, 1996; Sofaer et al., 2018; Yokomizo et al., 2009) or from an ecological point of view (i.e. “breakpoints”, Vilà et al. 2011). This limit could be context-specific, specified according to the impact measure (total grassland productivity, palatable productivity or sheep stocking rate), or according to the economic context and the trade-offs between cost of control and benefits of increases in grassland productivity (i.e. reduction of impacts) (Higley & Predigo 1996, Yokomizo et al. 2009, Soafer et al. 2018). Nevertheless, it is paramount that the pine abundance measure used to guide management matches those of the abundance-impact curves and is also used to monitor invasive pine abundance.

We have inferred possible mechanisms behind our results, but further research will be needed to test these ideas. For example, measuring and comparing abiotic conditions across gradients of pine abundance could help describe the growing conditions of grassland species. Our abundance-impact curves may be applicable to other invasive woody species, especially other members of the *Pinus* genus, and to grasslands in other temperate regions. However, some of our results may be specific to our study species and our study region. Therefore, replications of our study may be needed in new regions and with other invasive species to assess if our abundance-impact curves hold similar.

5. Conclusions

The abundance-impact curves we have built here may be useful to guide the management of invasive woody plants in grasslands with similar abiotic conditions. In temperate regions with lower summer abiotic stress, grassland productivity may be reduced by invasive woody plants throughout the whole range of woody canopy cover. Conversely, in regions with higher summer water deficit invasive woody canopy cover above 30% may still increase grassland productivity. While we show a predominant negative impact of invasive woody plants on native grassland productivity and their capacity to sustain livestock grazing, our abundance-impact curves differ among measures of invader abundance, and the timing of management actions could differ substantially according to the measure of abundance used to monitor the invader. Ideally, managers should consider using multiple measures of invader abundance to monitor invasions since they provide complementary information. However, in general, time and money are limiting and only one measure of abundance can be frequently assessed. In such cases, we suggest using invader canopy cover to monitor and guide the management of woody plant invasions in grasslands.

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.

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Data availability statement

The data are freely available from Environmental Information Data Centre (EIDC) (http://eidc.ceh.ac.uk/) for non-commercial use under Open Government Licence terms and conditions. https://doi.org/10.5285/54fe47f3-778e-4e0b-8cf5-b2fda2473b7f.

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Tables

Table 1: Location (latitude and longitude), mean individual tree diameter (and standard error; SE), surface covered (hectares) for each *Pinus contorta* plantation, as well as mean (and SE) grassland palatable productivity and its corresponding vegetation use factor (UF), for each study site.

Site	Latitude	Longitude	Diameter (cm)	Surface (ha)	Palatable productivity (kg/ha)	Vegetation use factor (%)
A1	41° 9' 48.13" S	71°15' 32.84" O	44.9 (2.4)	3.206	479 (96)	40
A2	41°12' 50.99" S	71°13' 10.64" O	29.9 (1.2)	2.171	281 (145)	30
A3	41°12' 25.95" S	71°13' 59.91" O	36.1 (1.2)	2.778	153 (73)	20
C1	41° 7' 33.55" S	71°12' 36.86" O	35.7 (2.2)	1.811	394 (119)	40
C2	41° 8' 53.55" S	71°13' 54.18" O	34.5 (1.7)	3.332	119 (25)	20

Table 2: Parameters of our models for different measures of *Pinus contorta* abundance as predictive variables and the following response variables:

a) Effect size on total productivity (EStp)

Model	Variable	Function	Estimate (linear)	Estimate (poly)	SE	t (linear)	p (linear)	t (poly)	p (poly)	R^2	AIC
1	density	linear	-0.002	-	0.0002	-10.873	**< 0.0001**	-	-	0.46	656
2		poly	-26.884	4.7271	2.4751	-10.862	**< 0.0001**	1.910	0.0583	0.48	654
3	basal area	linear	-0.145	-	0.0117	-12.392	**< 0.0001**	-	-	0.53	638
4		poly	-28.830	-2.1582	2.3277	-12.386	**< 0.0001**	-0.93	0.3550	0.53	639
5	cover	linear	-0.081	-	0.0091	-8.885	**< 0.0001**	-	-	0.37	670
6		poly	-24.030	-16.043	2.3370	-10.282	**< 0.0001**	-6.86	**< 0.0001**	0.53	631

b) Effect size on palatable productivity (Espp)

Model	Variable	Function	Estimate (linear)	Estimate (poly)	SE	t (linear)	p (linear)	t (poly)	p (poly)	R^2	AIC
7	density	linear	-0.002	-	0.0002	-9.666	**< 0.0001**	-	-	0.40	685
8		poly	-26.588	5.906	2.7143	-9.795	**< 0.0001**	2.176	**0.0313**	0.42	682
9	basal area	linear	-0.139	-	0.0135	-10.277	**< 0.0001**	-	-	0.43	677
10		poly	-27.554	0.3774	2.6906	-10.241	**< 0.0001**	0.14	0.8890	0.43	679
11	cover	linear	-0.082	-	0.0098	-8.376	**< 0.0001**	-	-	0.34	691
12		poly	-24.388	-12.268	2.7250	-8.950	**< 0.0001**	-4.5	**< 0.0001**	0.43	673

c) Effect size on the stocking rate that the grassland can sustainably support (Essr)

Model	Variable	Function	Estimate (linear)	Estimate (poly)	SE	t (linear)	p (linear)	t (poly)	p (poly)	R^2	AIC
13	density	linear	-0.001	-	0.0001	-8.399	**< 0.0001**	-	-	0.34	619
14		poly	-18.310	5.0612	2.1447	-8.537	**< 0.0001**	2.36	**0.0197**	0.36	616
15	basal area	linear	-0.100	-	0.0105	-9.592	**< 0.0001**	-	-	0.40	606
16		poly	-19.911	1.5593	2.0790	-9.577	**< 0.0001**	0.75	0.455	0.40	607
17	cover	linear	-0.062	-	0.0074	-8.373	**< 0.0001**	-	-	0.34	612
18		poly	-18.344	-8.5883	2.0711	-8.857	**< 0.0001**	-4.15	**< 0.0001**	0.41	598

Figure Legends

Figure 1: a) Map of Argentina showing the location of our study region (red square). b) Map of our study region showing the location of our study sites (yellow dots). c) Scheme of the experimental design, showing the five transects of 500 m included in one site and the location of sampling circular plots (10 m diameter) along each transect. d) Scheme showing one transect of 500 m as an example. Each circle represents a plot, including a representative picture. In both c) and d) the dotted line shows the location of the invasion front.

Figure 2: Conceptual model showing the different impacts measured here (orange bubbles) and which factors (green boxes) are considered in their calculation.

Figure 3: Estimate, 95% confidence and predictive intervals of the relationship between effect size of pine invasion on a) total grassland productivity, b) palatable productivity and c) sheep stocking rate, and pine density (left pane), basal area (center pane) and canopy cover (right pane). For each predictive variable we show the best regression model (based on AIC). While the confidence intervals show the likely range of values that contain each of the mentioned response variables (effect sizes), the prediction intervals predict in what range a future individual observation will fall. Prediction intervals are much wider than confidence intervals, since they show higher uncertainty.

Figure 4: Estimate and 95% confidence intervals of the relationship between pine basal area and density (left pane), between pine canopy cover and density (center pane) and between pine canopy cover and basal area (right pane).

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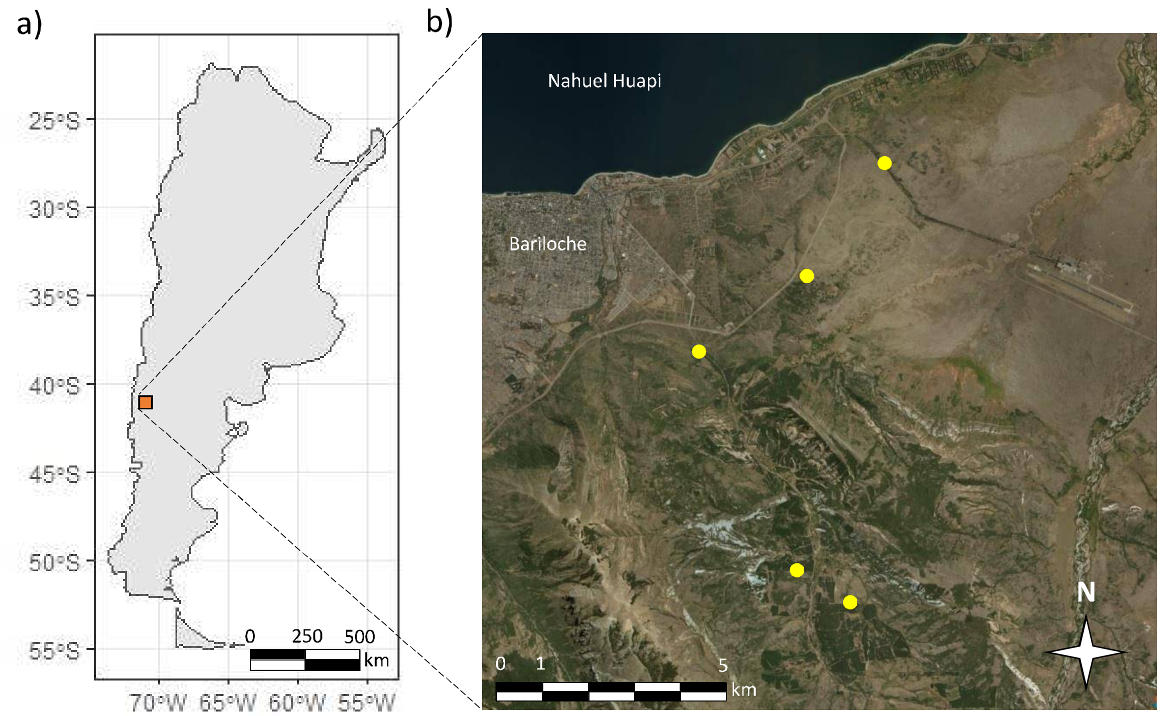
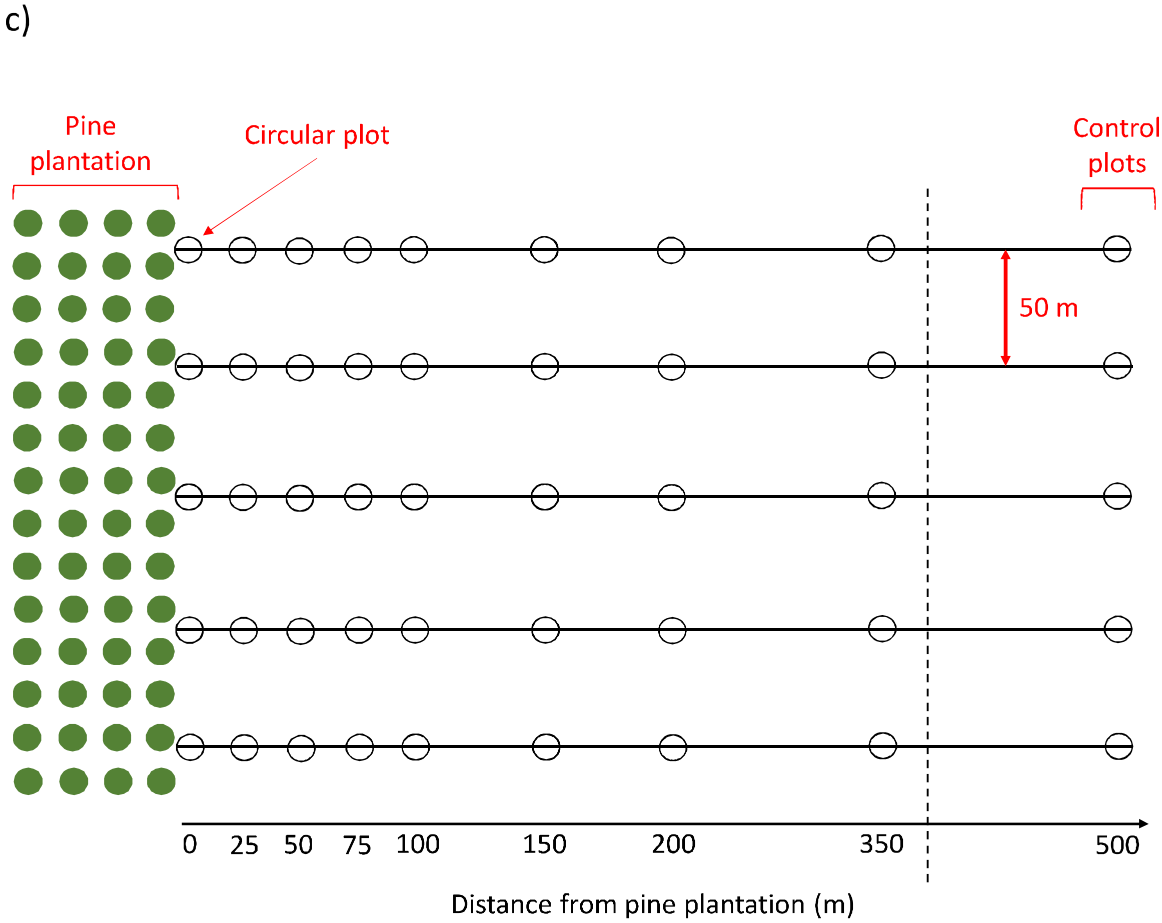

a)
25°S
30°S
35°S
40°S
45°S
50°S
55°S
70°W 65°W 60°W 55°W
0 250 500
km
b)
Nahuel Huapi
Bariloche
0 1 5
km
N


c)
Pine
plantation
Circular plot
Control
plots
50 m
0 25 50 75 100 150 200 350 500
Distance from pine plantation (m)

d)

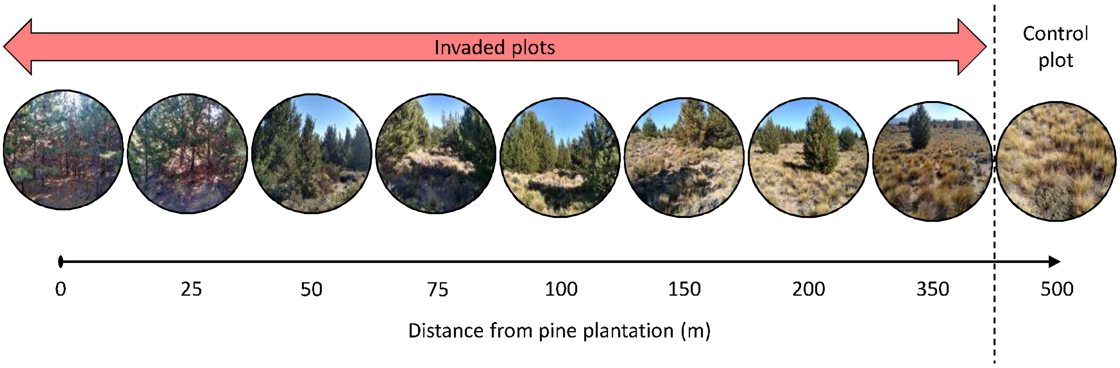


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Figure 2

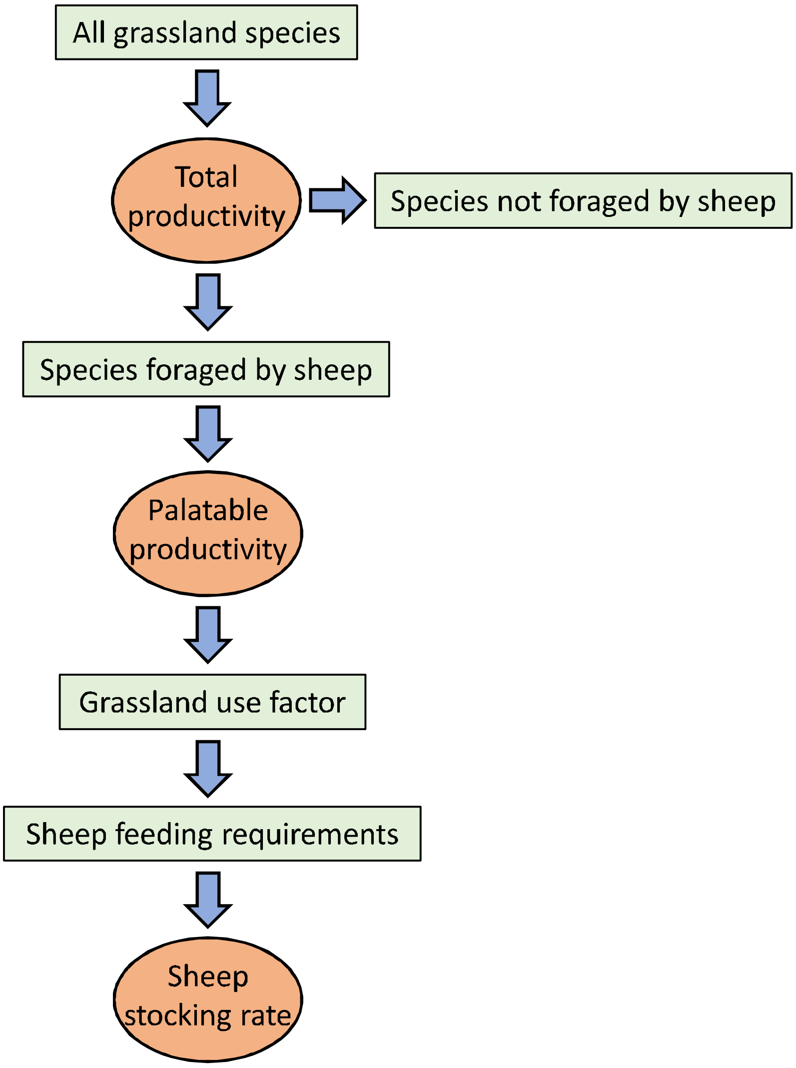

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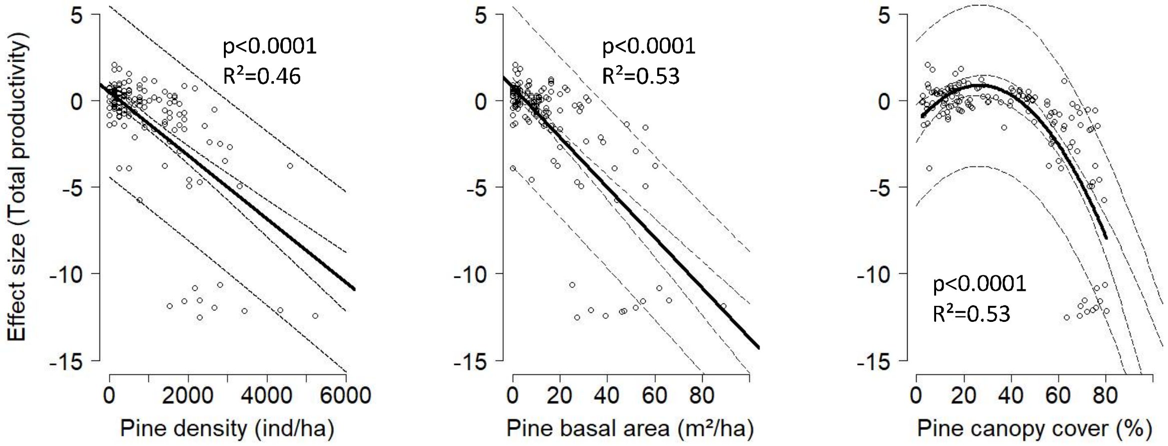
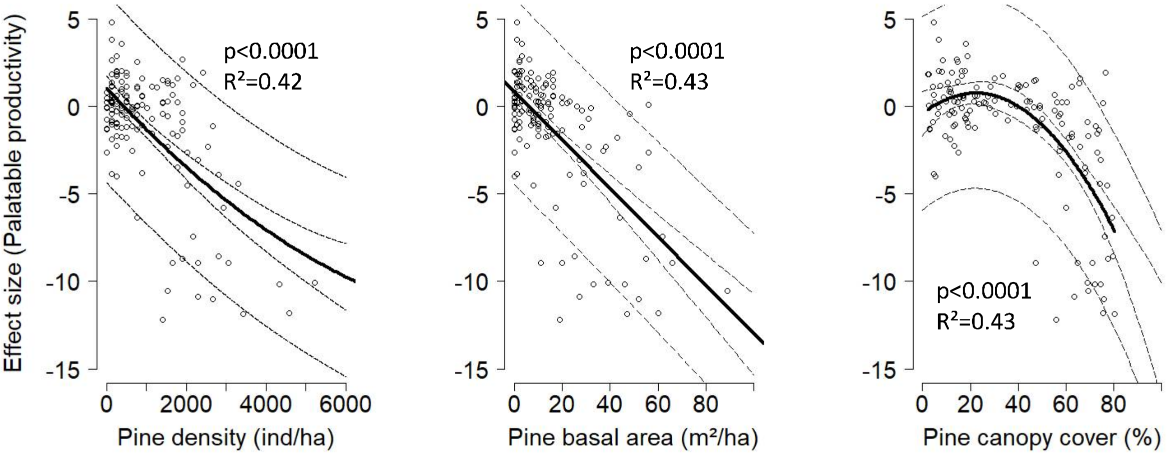
Figure 3

a)


Effect size (Total productivity)
5
0
-5
-10
-15
p<0.0001
R²=0.46
0
2000
4000
6000
Pine density (ind/ha)
p<0.0001
R²=0.53
0
20
40
60
80
Pine basal area (m²/ha)
p<0.0001
R²=0.53
0
20
40
60
80
Pine canopy cover (%)

b)


Effect size (Palatable productivity)
5
0
-5
-10
-15
p<0.0001
R²=0.42
0
2000
4000
6000
Pine density (ind/ha)
p<0.0001
R²=0.43
0
20
40
60
80
Pine basal area (m²/ha)
p<0.0001
R²=0.43
0
20
40
60
80
Pine canopy cover (%)

c)

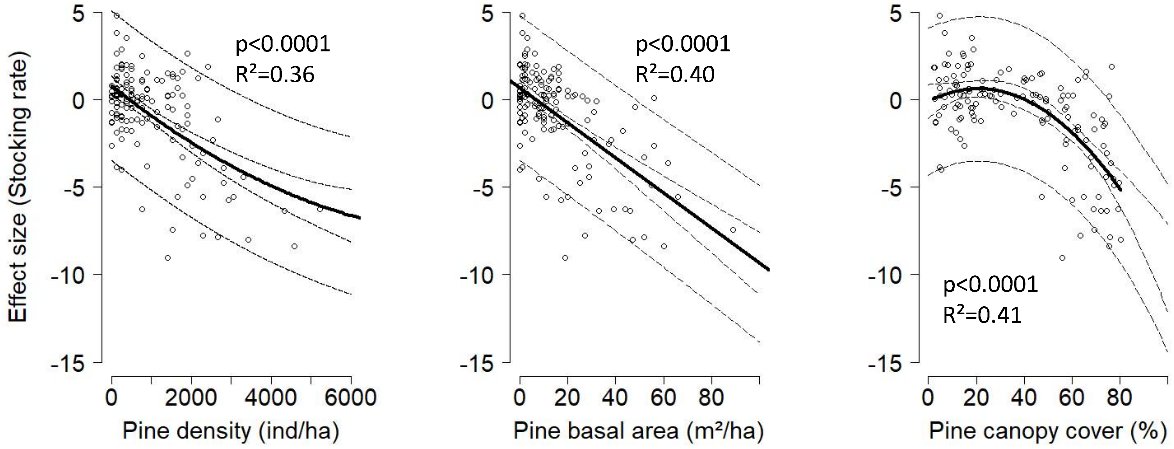


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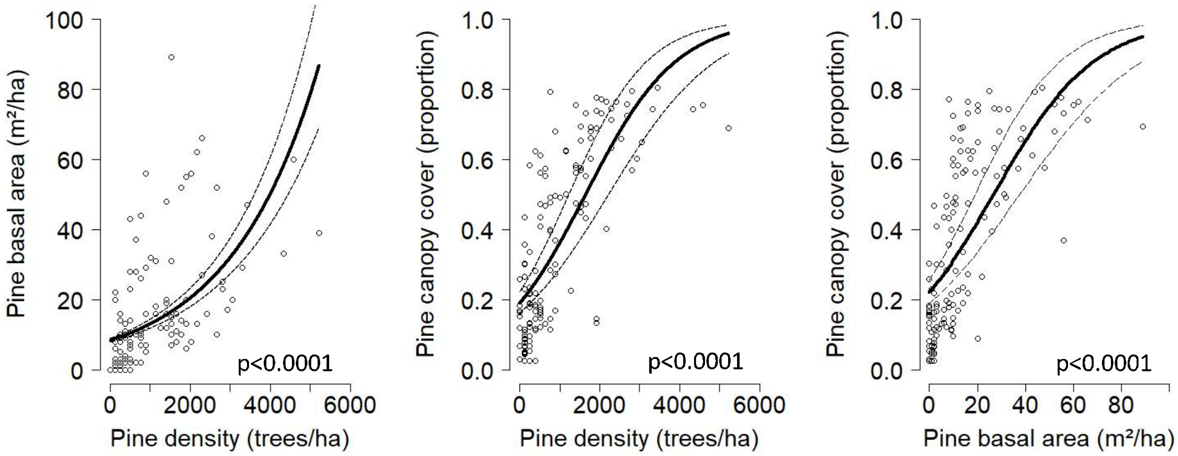
Figure 4



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