

Research paper

## Variations in habitat metrics along plantation chronosequences: contrasting tree plantations in subtropical forest and grassland

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**Abstract.** The increasing demand for raw materials favours habitat conversion into tree plantations in different biomes over the world. In Argentina, fast-growing plantations occur in physiognomically contrasting biomes, such as the subtropical forest and grassland. Our objectives were to analyze variations in basic habitat metrics and their similarity to the natural habitat along pine plantation cycles, and to compare those patterns between plantations developing in a subtropical forest and a grassland biome. In each biome we selected pine stands of eight ages to represent the environmental gradient of the forest cycle, and natural areas. At each site we estimated the temperature, thermal variability, relative humidity, and percentage coverage of herbaceous plants, shrubs and canopy. We explored environmental similarity between plantations and the natural habitat. In general, patterns of the environmental variables along plantation chronosequences were similar between plantations developing in different biomes. As expected, opposite patterns of similarity in most environmental variables between plantations and the natural habitat were observed along chronosequences developing in contrasting biomes. The time period of high environmental similarity between plantations and the natural environment was longer in the subtropical forest than in the grassland. Our results have implications for land use planning and biodiversity conservation.

**Key words:** environmental variables, monoculture, land use planning, pine, regional context, silviculture.

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### Introduction

The increasing demand for raw materials favours the conversion of natural habitats into tree plantations in different biomes over the world. Furthermore, the econom-

ic market drives habitat conversion from one land use to others. In Argentina, government incentives to the forest industry resulted in the conversion of both natural and human-modified (especially livestock) habitats into monoculture plantations of

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exotic trees over the last three decades (Matteucci, 2012; AFOA, 2021); currently, tree plantations occur in both subtropical forests and grassland biomes. Although both biomes are physiognomically contrasting, they hold fast-growing exotic tree plantation (such as pines and eucalyptus) in short cycles.

Direct and indirect effects of silvicultural practices on abiotic conditions and biodiversity may depend on the characteristics of the biome where tree plantations developed. In general, when anthropogenic habitats preserve features and conditions of the original environment, they have more chances to preserve native species (Petit & Petit, 2003). For example, Filloy *et al.* (2010) found that eucalypt plantations preserved more native bird species than croplands in a subtropical forest biome, but the opposite pattern was observed in a grassland biome where croplands held more native species than plantations. Studying environmental changes caused by forestry practices in different biomes is relevant to land use planning at the interregional spatial scale.

Environmental changes occur during tree plantation growth and throughout forest secondary successions (Tilman, 1985). For example, the increase in canopy cover along plantation cycles reduces the entrance of light quality and quantity resulting in a decline in temperature and an increase in shade and humidity of the forest surface, influencing vegetation diversity and abundance. Plant species from open habitats such as grasslands, clearcuts or recent plantations are adapted to relatively high solar radiation (Gibson, 2009); in contrast, understory vegetation in forests is typically shade-tolerant (Montti *et al.*, 2014). Changes in environmental conditions along tree plantation chronosequences, relative to the native habitat, are expected to be the opposite in structurally contrasting biomes, such as the subtropical forest and grassland. Surprisingly, however, we found no study in the literature contrasting habitat variables between tree

plantation cycles developing in different biomes.

Our aims are to analyze variations in basic habitat metrics and their similarity to the natural habitat along pine plantation cycles, and to compare those patterns between plantations developing in a subtropical forest and a grassland biome. In the subtropical forest, we expect the natural habitat to be environmentally more similar to mature than to recent plantations; in contrast, in the grassland biome, we expect the natural habitat to be more similar to recent than to mature plantations. Thus, patterns of variation in the similarity of environmental variables between tree plantations and the natural habitat along the plantation cycle will be the opposite. Specifically, we describe the pattern of temperature, humidity, and vegetation coverage (herbaceous plants and canopy) and their similarity to the native habitat along a pine plantation chronosequence, and compare those patterns between plantations growing in a subtropical forest and a grassland biome in Argentina. We expect similar patterns of habitat variables but opposite patterns of similarity along a plantation cycle between the subtropical forest and the grassland biome.

## Material and Methods

### Study area

The study was conducted in pine (*Pinus taeda* L.) plantations and protected areas located in two biomes in South America (Figure 1): the subtropical forest in the south of the Atlantic Forest ecoregion (between 25° 41' 20" S, 54° 20' 13" W and 25° 51' 8" S, 54° 35' 31" W) (from here on referred to as the subtropical forest biome) and the grassland in the Campos ecoregion (between 28° 57' 45" S, 56° 42' 54" W and 29° 35' 53" S, 57° 11' 33" W) (from here on referred to as the grassland biome). The south of the Atlantic Forest has subtropical climate, with the mean annual temperature and precip-

itation of 20 °C, and 2000 mm, respectively (Oliveira-Filho *et al.*, 2000). The native vegetation is a subtropical semideciduous forest with five vegetation strata (Plací & Di Bitetti, 2006). The main land use is tree plantations (exotic pines and eucalypts) (Zurita & Bellocq, 2010). The Campos has temperate climate; the average annual temperature and precipitation are 19 °C and 1200 mm, respectively. The native grassland is used for extensive ranching, and in the last decades pine plantations have been scattered replacing grasslands (Matteucci, 2012). Plantation management is conducted mainly for pulp production in the subtropical forest and for timber in grasslands (AFOA, 2021). Silvicultural practices showed some differences between the biomes, mainly due to a higher tree density (20% higher at the beginning of the cycle) and the absence of pruning and thinning in plantations developed in the subtropical forest (Santoandré *et al.*, 2019).

### Study design and environmental variables estimation

To analyze environmental changes along the pine plantation chronosequence and compare them between the biomes, we estimated environmental variables in pine plantations of different ages and in the natural habitat located in a grassland and a subtropical forest biome from end of November (late spring) to mid-January (early summer). In each biome, we selected pine stands of eight ages. We selected the following ages: 1, 2, 3, 4, 5, 6, 9 and 12 years; three stands per age. We also used three sites with natural vegetation within the landscape as a reference habitat to analyze environmental similarities between plantations of different ages and the natural habitat.

We consider the following basic environmental metrics that are expected to change along plantation cycles: temperature, thermal variability, relative humidity, and percentage coverage of herbaceous plants, shrubs and canopy. At each site, we placed an automatic sensor of temperature and relative humidity at 10 cm above the ground, which recorded data every five minutes during two weeks. Because we handled fewer sensors than sites, the devices were rotated between replicates during the study period. Thus, in each biome, the average temperature and relative humidity were calculated for each plantation age. Thermal variability was estimated as the standard deviation of temperature during those two weeks (Santoandré *et al.*, 2019). At each site, we established two 5 x 5 m plots (subsamples), 40 m apart, to visually estimate the percentage cover of herbs and shrubs. Within each plot, a photograph was taken in digital format pointing to the sky from a height of 1.5 m (Vespa *et al.*, 2014; Santoandré *et al.*, 2019); images were then analyzed to estimate the percentage canopy cover using the ImageJ software (Schneider *et al.*, 2012; Santoandré *et al.*, 2019).



Figure 1. The circles indicate the location of study sites (plantations and the natural habitat) in the subtropical forest biome of the Atlantic Forest ecoregion (colour green) and the grassland biome of the Campos ecoregion (colour orange).

## Data analysis

For each environmental variable and plantation age, we estimated the average value of three replicates. To estimate environmental similarity between the natural environment and plantations of different ages, we used the 1 - Gower index considering all environmental variables together and then each variable separately (Legendre & Legendre, 2012). To analyze the influence of the biome on the pattern of variation of environmental variables along the plantation cycle and on the similarity to the natural habitat, we performed a model selection process based on Akaike information criterion (AIC) of each environmental variable as well as their similarity to the natural environment in relation with the plantation age (NLS, LM, AIC, NPLR functions of R project (R Core Team, 2021) and Infostat Software (Di Rienzo *et al.*, 2011)). The proposed models were: 1) a null model suggesting no pattern of environmental change throughout the chronosequence; 2) a simple linear model that proposes either increasing or decreasing monotonic variation in environmental variables throughout the forest cycle; and 3) a logistic model describing threshold and asymptotic responses. We ranked all models and retained those with the lowest AIC value (Burnham & Anderson, 2002).

## Results

Along plantation chronosequences, the mean temperature declined throughout one to four years of age and then remained stable in both biomes; although the model selected was logistic in both biomes (Table 1; Figure 2 a), the drop in temperature was more abrupt in the subtropical forest. Thermal variability showed similar patterns to temperature in both biomes; however, it was greater throughout the entire forest cycle in plantations developing in the grassland (Table 1; Figure 2 b). Patterns of relative humidity along plantation cy-

cles differed between biomes, increasing during the first four years to then remaining constant in the subtropical forest and showing no change in the grassland (Table 1; Figure 2 c). In the subtropical forest, canopy cover increased suddenly from two to three years of plantation age and then remained stable along the plantation cycle (Table 1; Figure 2 d). In the grassland, canopy cover increased more smoothly from one to six years after plantation and then remained stable (Table 1; Figure 2 d). The herbaceous cover declined suddenly between two and four years after plantation and then remained constant at low values in the grassland (Table 1; Figure 2 e); the herbaceous cover showed no trend along plantation chronosequences in the subtropical forest.

Table 1. Model selection for environmental variables in relation with the age of pine plantations, and for the similarity in environmental variables between plantations and the natural environment (Sim) with plantation age.

	Grassland	Subtropical forest
Environmental variable	Model	Model
Temperature	Logistic	Logistic
Thermal variability	Logistic	Logistic
Relative humidity	Null	Logistic
Canopy cover	Logistic	Logistic
Herbaceous cover	Logistic	Null
Sim temperature	Logistic	Logistic
Sim thermal variability	Logistic	Line
Sim relative humidity	Null	Logistic
Sim canopy cover	Logistic	Logistic
Sim herbaceous cover	Logistic	Null
Sim total	Logistic	Logistic

As expected, the total environmental similarity between plantations of different ages and the natural habitat showed opposite trends between biomes, decreasing in the grassland and increasing in the subtropical forest throughout chronosequences (Table

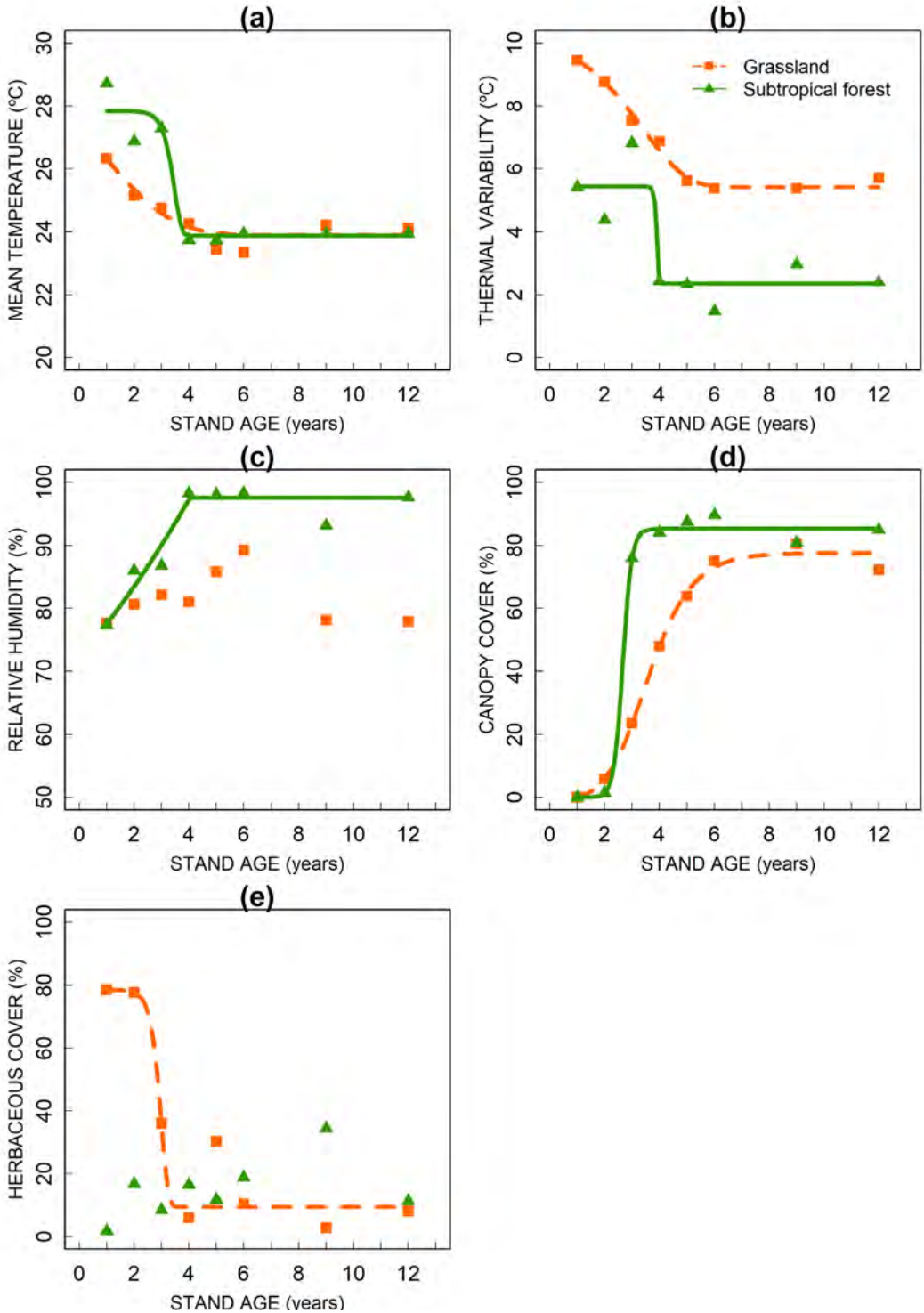


Figure 2. Environmental variables along different ages of pine plantations in both biomes. Lines indicate the selected model.

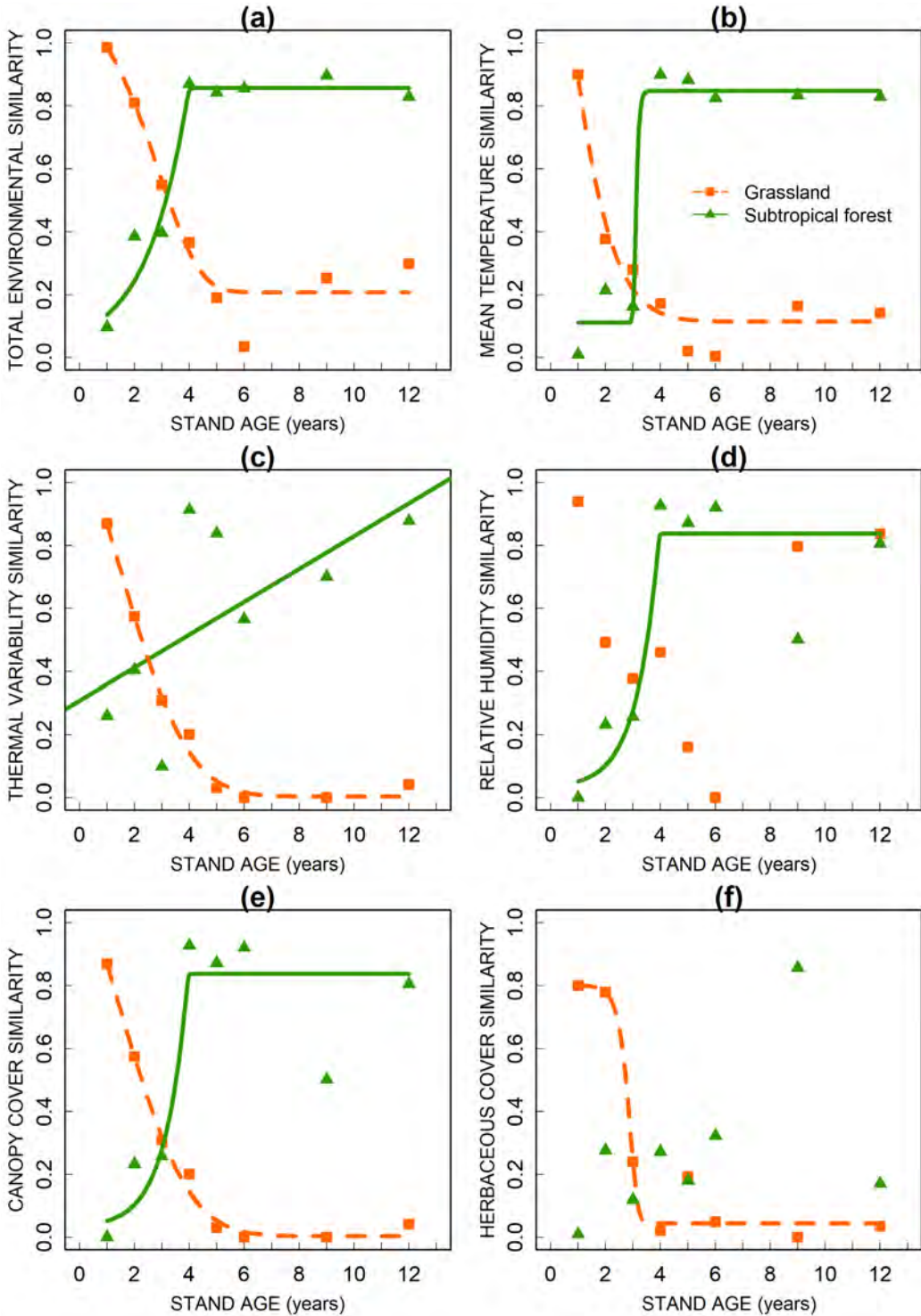


Figure 3. Environmental similarity between plantations and the natural environment along the ages of pine plantations in both biomes. Lines indicate the selected model.

1; Figure 3 a). Also, the similarity of most individual variables between plantations and the natural habitat showed opposite trends, decreasing in the grassland and increasing in the subtropical forest. The mean temperature declined in similarity during the first three years after plantation in the grassland, and increased suddenly in the third year in the subtropical forest, after which it remained stable (Table 1; Figure 3 b). Similarity in thermal variability decreased from one to five years after plantation and then remained at low values in the grassland (Table 1; Figure 3 c), whereas it increased linearly along the chronosequence in the subtropical forest. Relative humidity similarity varied along the forest cycle showing no clear pattern in the grassland, and increased rapidly until it stabilized after the fourth year in the subtropical forest (Table 1; Figure 3 d). Similarity in canopy cover declined smoothly during the first six years of plantation cycles and then remained at low values in the grassland, whereas it increased after the second year and then remained stable up to the fourth year in the subtropical forest (Table 1; Figure 3 e). Herbaceous cover similarity decreased rapidly between two and four years after plantation and then remained stable at very low values in the grassland; in the subtropical forest, similarity in herbaceous cover was always relatively low (except at age nine), and no trend was observed throughout the forest cycle (Table 1; Figure 3 f).

## Discussion

In general, patterns of the selected basic environmental variables along plantation chronosequences were similar between plantations developing in different biomes, although changes were more abrupt in the subtropical forest than in the grassland. As expected, opposite patterns of similarity in most environmental variables between plantations and the natural habitat were

observed along chronosequences developing in contrasting biomes. Furthermore, the time period of high environmental similarity between plantations and the natural habitat was longer in the subtropical forest than in the grassland.

Canopy cover is a key variable explaining changes in temperature and humidity. The increase in canopy cover during plantation development was associated with decreasing temperature and increasing humidity (in the subtropical forest) due to the reduction in light reaching the forest floor. Because temperature and humidity were measured independently of canopy cover, they provide additional evidence of environmental patterns consistent with canopy cover.

In plantations from the grassland biome, the decline in herbaceous cover is also consistent with the increase in canopy cover along plantation cycles. Most of the herbaceous vegetation in the grassland is composed of shade-intolerant grasses (Ratnam *et al.*, 2011); the reduction in light intensity with plantation growth inhibit germination of many grass species (Gibson, 2009) and change the natural temperature and humidity conditions resulting in a reduction in grass species richness (Kleidon *et al.*, 2009). In contrast, most herbaceous vegetation in the subtropical forest is composed of shade-tolerant dicots (Di Bitetti *et al.*, 2003); thus, reduction in light availability due to canopy closures had little effects on the understory (Di Bitetti *et al.*, 2003).

Our results showed that the increase in canopy cover with plantation age was more abrupt in the subtropical forest than in the grassland biome. That is most likely due to differences primary in silvicultural practices affecting tree density during the plantation cycle, and secondarily in the speed of plantation growth. In the subtropical forest, trees are planted at a density of 1200 trees ha<sup>-1</sup> and the canopy close suddenly (80% closure) in the third year after plantation. In the grassland, however, trees are planted at 1000 trees ha<sup>-1</sup> and

in the third year after plantation canopy cover was approximately 25%. The faster and more sudden increase in canopy cover at the beginning of the forest cycle in the subtropical forest than in the grassland is most likely due to faster plantation growth in subtropical than in temperate climates. Furthermore, plantations developing in the grassland biome are subjected to pruning and thinning after the fourth year and harvested at a final density of 400 trees ha<sup>-1</sup> (Santoandré *et al.*, 2019), which is consistent with a smoother increase in canopy cover and a lower value of the final cover in the grassland than in the subtropical forest biome.

As expected, similarity in environmental variables between plantations and the natural habitat showed opposite patterns in the subtropical forest and the grassland. As the plantations grew, they became more similar to the native forest and more different from the grassland.

The period of high environmental contrast between tree plantations and the natural habitat along plantation cycles was longer in the grassland than in the forest biome. Changes in similarity occurred early in the forest cycle in plantations from both biomes. In the subtropical forest, environmental similarity increased rapidly at the beginning of the forest cycle until the fourth year after plantation, indicating that the period of the greatest environmental contrast between plantations and the natural habitat lasted only three years. In contrast, similarity between grasslands and plantations declined during the first tree year of the cycle and then remained at very low values, indicating that the period of the greatest environmental contrast lasted eight years. Thus, the time period of high environmental similarity between plantations and the native habitat was longer in our subtropical forest than in our grasslands, and presumably similar patterns will be observed in other forests and open biomes.

Our results have implications for land use planning and management. Given that exotic conifer plantations retained the characteristics of the native habitat for a longer time period when developed in forests than in grasslands, sustainable silviculture will be easier to reach in the forest than in open biomes. The greater environmental similarity between plantations and the native habitat allows that more native species will be able to support tree plantations (Gómez-Cifuentes *et al.*, 2017). When tree plantations are located in grasslands, it is especially recommended to have stands of different ages and retain unplanted areas and corridors in the landscape. Our study demonstrated that the biome where commercial tree plantations developed drive the environmental similarity between plantations and the natural habitat along the forest cycle. Future studies should include alternative biomes and assess biodiversity responses along plantation cycles developing in different biomes.

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