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# Variation in Density Dependent Seedling Survival Across Forests of Different Successional Age and Hunting Protection Status

**By**

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# Variation in Density Dependent Seedling Survival across Forests of Different Successional Age and Hunting Protection Status

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Over 50% of the original extent of tropical forests has been cleared. Restoration of secondary forests is important for maintaining the ecosystem services that mature tropical forests provide. Density dependence (DD) is thought to be a major mechanism for shaping forest community structure and may cause reduced spatial aggregation among individuals of the same species, allowing for maintenance of diversity. While much research has focused on DD in mature tropical forests, few studies have examined how DD may influence community structure in secondary forests, many of which are also exposed to hunting. There are several important agents of negative and positive DD, including natural enemies and mutualists of trees. Mammals are important herbivores of seedlings. Hence, forest protection status is also likely to be a key factor influencing density-dependent seedling survival because it affects populations of mammals through trophic cascades. Here, we address the questions, (1) Is there an overall density dependent effect? (2) How the type, direction, and strength of DD differ between forests of different successional ages and protection status? We used neighborhood models fit to one-year survival of 8,042 seedlings of 114 species in early successional to old growth plots with different protection status in northeastern Costa Rica. We found that, averaging across forests, there was a negative significant conspecific density dependent effect (CND). Despite this overall effect, there was also significant variation among forests of different successional age and protection status. CND strength increased with successional age in protected forest and decreased in unprotected forests.

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## 1. Introduction

Globally, tropical regions are experiencing a deforestation crisis. Over half of the tropical forest area on Earth is now secondary forest, which is forest that has regrown after the mature, primary forest has been intensely disturbed or cleared for other land uses. Globally, conversion of primary into secondary forest continues at the rate of 7 million ha/year due to deforestation, and conversion to agriculture and subsequent abandonment (FAO 2016).

The process of regeneration of secondary forest from abandoned agricultural lands involves several interdependent processes (Figure 1). First, seeds must disperse from forested areas and, after arrival to a site, survive long enough to germinate. Next, the abiotic and biotic environment must match the regeneration niche of the new seedlings, which must grow fast enough to survive and become established, eventually becoming saplings. Saplings that survive must eventually grow to reproductive maturity and produce seeds, thereby contributing to continued forest development. This study focuses on the seedling regeneration processes which comprise a critical demographic filter (Harper *et al.* 1955), and are key to the restoration of secondary forests, which is important for conserving biodiversity and the ecosystem services that mature tropical forests provide.

Seedling regeneration depends on growth and survival, which have been shown in primary forests to be generally negatively density-dependent (Russo and Augspurger 2004). Negative density dependence is important because it contributes to tree species coexistence in tropical forests, (Chesson *et al.* 2000, Wright *et al.* 2002, Terborgh 2012, Comita *et al.* 2014). According to the Janzen-Connell Hypothesis (JCH; Janzen 1970, Connell 1971) host-specific natural enemies, such as seed predators, herbivores, and pathogens, reduce the survival of offspring recruitment when they are surrounded by a high density of conspecific neighbors. The reduction of the density of conspecific individuals will regulate population growth and promote species coexistence in diverse tree communities. Many studies of tropical and temperate forests have demonstrated that seed natural enemies such as seed predators and seedling herbivores are responsible for density- and distance-dependent seedling mortality (Russo & Augspurger 2004, Russo 2005, Bell *et al.* 2006, Swamy & Terborgh 2010). In addition, fungal and oomycete pathogens of tropical trees have also been implicated as agents of negative density dependence in experimental studies (Freckleton & Lewis 2006, Mangan *et al.* 2010). Dynamics have been found in temperate and tropical forest but while much research has focused on density dependence in primary tropical forests, its importance in tropical secondary forests remains poorly understood. Few studies have analyzed the processes influencing density-dependent seedling survival and how it changes during regeneration following deforestation after agricultural land use (Sansevero *et al.* 2011, Melo *et al.* 2009, Chazdon 2007).  Due to the complexity of interactions that influence seedling performance in nature, seedling survival is a result of multiple density-dependent factors that operate simultaneously and that may vary in strength (weak or strong) and direction (positive or negative) during forest succession. Negative interactions with neighboring trees might be caused by shared pathogens or herbivores and by competition for limiting resources. Rates of seed predation and seedling herbivory by mammals increase when seeds or seedlings are crowded at high density (Russo & Augspurger 2004, Wright & Duber 2001, Paine & Beck 2007). Fungal pathogens are also thought to be important agents of density dependent mortality in tropical forest (Augspurger & Kelly 1984, Dalling *et al.* 1998). In contrast, positive interactions with neighbors can be caused by shared beneficial mycorrhizae and shared responses to favorable abiotic conditions (Lovelock and Ewel 2005). Similarly, interactions among neighboring trees are asymmetric because adults are larger and have better established root systems and the capacity to shade smaller individuals (Weiner 1988, Lebrija *et al.* 2014, Record *et al.* 2016). Density dependence may also vary greatly by the alteration of some or many biotic factors (Getzin *et al.* 2006). One key biotic factor is the presence or absence of mammalian seed and seedling predators that have been shown to be important in forest regeneration (Russo 2005, Wright *et al.* 2007, Harrison *et al.* 2013). Because of trophic cascades, forest fragmentation and poaching of top predators can increase populations of mammalian herbivores, like peccaries and rodents, that prey upon or consume parts of seedlings (Wright & Duber, 2001). Because mammals often forage optimally (Shoener 1987), they can produce density dependent effects on seedling survival (Shipley *et al.* 1996). Thus, seedling survival in secondary forests depends upon the strength and direction of the net effects produced by the combined effect of all interactions underlying density dependence.

In the neighborhood modeling approach, density-dependence of tree growth and survival has been investigated using the neighborhood modeling approach, which allows observational data to be used to understand and separate possible mechanisms causing density dependence (Weiner 1984, Uriarte *et al.* 2005, Comita *et al.* 2014, Lebrija *et al.* 2014). Each focal seedling is quantify based on several characteristics. In this study, we categorized neighbors as conspecific versus heterospecific and adults versus seedlings which can be defined as different neighbor types and where the direction and strength of their effects implies the operation of different ecological mechanism affecting seedling survival. For example, asymmetric interactions can be detected when stronger effects are caused by adults than by seedlings. Similarly, conspecific effects are stronger than heterospecific, then intraspecific competition for shared species -species resources or natural enemies can be inferred (Table 1). Theory predicts that as succession proceeds, the relative importance of abiotic and biotic filtering processes will change (Chazdon 2008, Connell & Slatyer 1977, Leibold *et al.* 2004). Abiotic filtering is expected to dominate early successional stages whereas biotic filtering becomes more and more important as succession progress (Leibold *et al.* 2004), which will lead to stronger density dependent effects on forest of older successional age. For example, at early successional stages, most seeds arrive from nearby or distant mature forests but as succession proceeds, local seed shadow increases due to the increment of reproductive mature species into the forest resulting in a drop of the mean seed dispersal distance which will increase the potential for density dependence (Chazdon 2008). Competitive exclusion of species (Grime 2006) may be expected to play a stronger role in community assembly as forest becomes denser and resources, such as phosphorus, become limiting on the old growth forest (Wardle *et al.* 2004, Lambers *et al.* 2008).

Our overall goal was to investigate how density dependent seedling survival changes during forest succession and protection status. In this study, we used observational data on the survival of 8,042 seedlings of 114 species across six forest plots varying in successional age and hunting protection (Table 2) to parameterize neighborhood models incorporating the seedling and adult tree neighborhoods.

Specifically, we address the questions, (1) Is there an overall density dependent effect across all forests (2) How the type, direction, and strength of density dependence differ between forests of different successional ages and protection status? First, we predicted that adult trees will exert a stronger density dependent effect on seedling survival than will seedlings because larger adults have better established root systems and the capacity to shade smaller individuals. Second, type will change in relative importance, the direction will vary and the strength of density dependence should increase with increasing successional age. Also, higher populations of mammalian seedling herbivores in protected forests would cause stronger density-dependent seedling mortality.

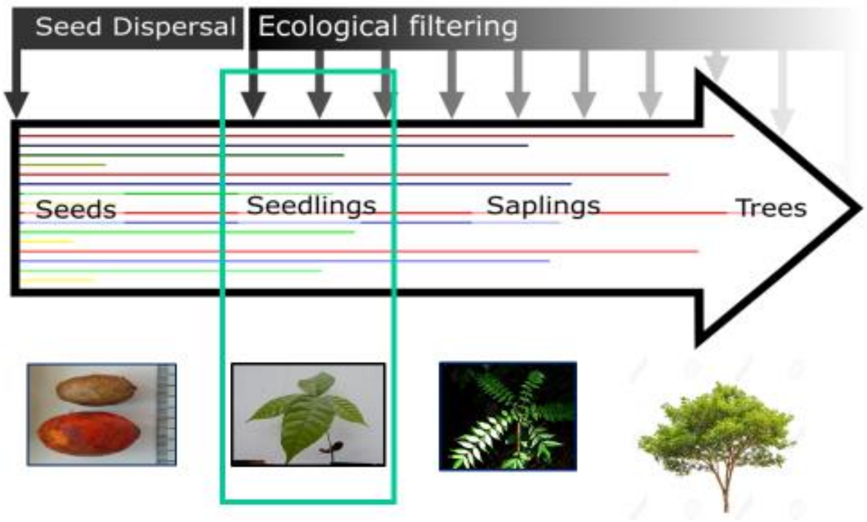

**Figure 1. Processes influencing tree regeneration from seed to adult tree establishment.** The process of seed to tree establishment is influenced by many factors including ecological filtering, which affects the community structure of the mature forest and is mediated in part by density-dependent processes. The lines inside the arrows represent individual trees, and the different colors represent different tree species. Depending on ecological filtering, individuals may only survive to different stages in the plant establishment process, and some of them may not reach maturity. In this study, we focused on the seedling stage of this process, which is a demographically important stage influencing forest regeneration.

**Table 1. Ecological mechanisms underlying neighborhood effect.** Relationship between the type of neighborhood, the direction of neighborhood effects, and the different possible ecological mechanisms underlying their effects on seedling survival.

| **Type of Neighborhood** | **Direction of Neighborhood Effect** | **Inferred Ecological Mechanism** |
|---|---|---|
| Conspecific | Positive | a) Habitat association<br>b) Shared mutualists |
| Conspecific | Negative | a) Shared natural enemies<br>b) Intraspecific resource competition |
| Heterospecific | Positive | a) Herd (or, dilution) effect<br>b) Habitat effect |
| Heterospecific | Negative | a) Interspecific resource competition |

## 2. Methods

### 2.1. Study system

The study was conducted in a tropical premontane wet forest (Holdridge *et al.* 1971) at La Selva Biological Station (hereafter, La Selva) and in surrounding areas of northeastern Costa Rica. Mean annual rainfall and temperature is about 4000 mm and 24C, respectively (Frankie *et al.* 1974, McDade & Hartshorn 1994). The study area is an alluvial flood plain with a mixed isohyperthermic soil (Haggar and Ewel 1995). All sites were within a matrix composed of secondary and mature forests patches and pastures. Three sites are located inside La Selva and three are about 6 km west of La Selva into privately owned farms in Chilamate. La Selva and surrounding areas comprises a diversity of more than 1,850 plant species, with 350 species of trees, and a large variety of epiphytes and many aroids. The dominant families in La Selva are Pteridophyta, Orchidaceae, Araceae, Rubiaceae, Melastomataceae, Fabaceae, and Piperace (Hartshorn and Himmel 1994), with *Welfia regia, Socratea exorrhiza,* and *Pentaclethra macroloba* being the most abundant. La Selva also protects more than 400 bird and 113 mammal species (McDade & Hartshorn 1994), including seed and seedling predators, such as collared peccaries *(Pecari tajacu)* and Central American agoutis *(Dasyprocta punctata).*

The relative importance of conspecific and heterospecific neighbors affecting seedling establishment was evaluated in a total of six 1-ha forest plots (Table 2) varying in successional age in which forest dynamics has been monitored annually over the past 17 years. Plot censuses have been conducted annually since 2000. The plots sample four secondary forests that were used as cattle pastures after initial cutting of the mature forest and that range in age (time since abandonment of pasturing) from 22 to 40 years old. The other two plots sample old-growth forest that has not been used for agriculture during modern times. Three plots located within La Selva, experienced protection from hunting over the past 50 years which has contributed to high abundance of the collared peccary (*Pecari tajacu*), a voracious seed predator, compared to unprotected forest areas in the region (Romero *et al.* 2013). The other three plots located outside of La Selva experienced hunting that reduces mammalian seed predator population. Within each plot all trees ≥ 5 cm in diameter at 1.3 m height (DBH) have been mapped, tagged, and identified to species, and subsequently censused for diameter growth and mortality annually. Seedlings (trees < 1 m height) have also been tagged and identified to species in modified Gentry transects (Phillips & Miller 2002), consisting of five parallel strips of 2 x 100 m, separated by 10 m totaling 0.2 ha in area in each plot (Figure 2).

**Table 2. Stand characteristics of six 1-ha forest plots near La Selva Biological Station, Costa Rica.** Logging is not allowed in any of these plots, so protection status is the restriction of people from hunting animals inside those areas.

| **Plot name** | **Protected Old growth** | **Protected Mid-successional** | **Protected Early successional** | **Unprotected Old growth** | **Unprotected Early successional 1** | **Unprotected Early successional 2** |
|---|---|---|---|---|---|---|
| **Stand age in 2017 (years)** | Old growth | 40 | 32 | Old growth | 22 | 22 |
| **Density of seedlings (no. stems/m$^2$)** | 0.5 | 0.6 | 0.4 | 2.0 | 2.1 | 2.4 |
| **Density of trees ≥ 5 cm DBH (no. stems / ha)** | 955 | 1293 | 950 | 1137 | 1004 | 888 |
| **Fisher's alpha diversity index** | 13.2 | 10.9 | 11.9 | 10.8 | 12.7 | 12.4 |
| **Location** | La Selva | La Selva | La Selva | Surrounding areas | Surrounding areas | Surrounding areas |
| **Protection status** | Protected | Protected | Protected | Unprotected | Unprotected | Unprotected |
| **Prior land use** | None | Pasture | Pasture | None | Pasture | Pasture |

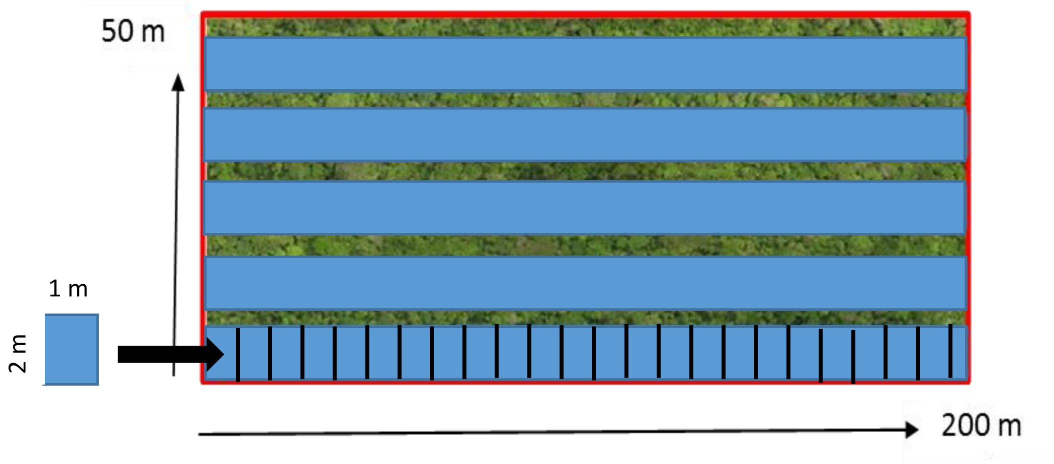

**Figure 2. Diagram of the seedling transects.** It is a 50 m x 200 m forest plot, showing subplots in which seedlings are censused. Adult trees are mapped using x, y coordinates within each plot. Seedlings were measured in subplots of 1 m x 2 m across five lines of 200 m separated by 10 m (blue bands) covering a total of 0.2 ha per plot.

### 2.2. Neighborhood metrics and predictors

We modelled one-year survival (2009-2010) of 8,045 seedlings of 114 tree species relative to the average type, direction and strength of the neighborhood predictors. We calculated widely used neighborhood predictors in which survival of a focal seedling is analyzed as a function of the sizes of and distances to neighboring trees and seedlings (e.g., Bella 1971, Vettenranta 1999, Uriarte *et al.* 2010, Lebrija et. al 2014, Comita *et al.* 2014). We considered four properties that are indicators of different ecological mechanisms underlying neighborhood effects (Table 2), in estimating neighborhood predictors: (1) whether individuals in the neighborhood were conspecific or heterospecific relative to the focal seedling, (2) the size class of the individuals in the neighborhood (adult or seedlings), (3) tree attributes used to calculate the neighborhood metric (abundance, basal area or DBH), and (4) the size of the neighborhood influencing the focal seedling (10 or 20 m radius). We estimated neighborhood metrics separately for seedlings versus adults due to asymmetric competition among plants of vastly different sizes (Wiener et al 1990). For seedlings in the neighborhood, we used the number of individual seedlings to calculate the neighborhood metric because there is little variation in diameter between seedlings < 1 m height. The density of seedling neighbors to a focal seedling was calculated as the number of individuals < 1 m height within the same 1 x 2 $m^2$ subplot as the focal seedling. For adult trees in the neighborhood (*i.e.*, trees ≥ 5 cm DBH within the specified neighborhood radius), we used model selection to test which of the following three metrics (calculated for a specified radius around a focal seedling) was most associated with seedling survival: (1) the sum of DBHs of all trees, (2) the sum of the basal areas of all trees, and (3) the number of number of trees. We also, used model selection to test which size of neighborhood best fit the data. We used the location of the subplot for seedling individuals and the x, y coordinates of each tree in the plot to find the trees within 10 and then 20 m of each focal seedling. We tested neighborhood radii of 10 m and 20 m because they have been found to be the best-supported distance for calculation of neighborhood metrics in previous studies of density dependence (Comita & Hubbell 2009, Metz et al 2010, Lebrija et al 2014).

### 2.3. Statistical analyses

All analyses were performed in R statistical software version R 3.3 (Team R 2016). We modelled seedling survival using generalized linear mixed-effects models (GLMM). GLMMs are appropriate for analysis of non-normal binary survival data and allow for the inclusion of both random and fixed effects (Bolker *et al.* 2009). We assumed survival was binomially distributed and used the logit link function to transform seedling fate (dead or alive) after one year (2009 to 2010) into a continuous annual survival probability. We subset the data to include all the individuals that have at least 10 individuals which are present in at least three different subplots and have a variation in the predictor effect bigger than zero. The subset process will avoid that slope and intercept estimations are based just in one subplot or include data that will generate rank deficient models.

We used fixed effects model selection to identify the most-supported neighborhood metric and size for conspecific and heterospecific adult neighborhood variables. For model selection, we used a base model that had the same random effects across all different fixed-effects models tested. The base model had random intercepts for each species and for each seedling subplot, nested within plot. Because the focus of model selection was to choose the best neighborhood metric for the adult trees in the neighborhood, the seedling neighborhood variables in the fixed effect model were the same across all models tested: Con_S, the number of conspecific seedlings, and Het_S, the number of heterospecific seedlings, in the same subplot as the focal seedling. For adults, the neighborhood metrics were calculated using either a 10 m or 20 m radius around the focal seedling for the following three possible neighborhood metrics, calculated for both heterospecific and conspecific neighborhoods: Het_A_DBH, (sum of the DBHs of heterospecific adults), Con_A_DBH (sum of the DBHs of conspecific adults), Het_A_BA (sum of the basal areas of heterospecific adults), Con_A_BA, (sum of the basal areas of conspecific adults), Het_A_Count (number of heterospecific adults), Con_A_Count (number of conspecific adults). The best-fit model was selected as the one with the lowest sample-size corrected Akaike information criterion (AICc), since all our models are equally parsimonious (Burnham & Anderson 2002). Model selection showed that for both conspecific and heterospecific trees the most-supported neighborhood metric was the sum of the basal areas of conspecific and heterospecific trees in the neighborhood with a 20-m radius (Table 3). Therefore, all models used this neighborhood metric for the effect of conspecific adults (CON_A), and heterospecific adults (HET_A). A neighborhood radius of 20 m has also been found to be the best-supported distance in previous studies of density dependence (Metz Sousa & Valencia 2010, Lebrija 2014). The final fixed effects model consisted of the following neighborhood metrics: Het_A, (sum of the basal areas of heterospecific adults), Con_A, (sum of the basal areas of conspecific adults), CON_S, (number of conspecific seedlings) and HET_S, (number of heterospecific seedlings). For both model selection and parameter estimation in the final model, we scaled these variables by subtracting the mean and dividing by the standard deviation based on data from all plots, so the magnitudes of the coefficients (odds ratios) are comparable across variables and plots. The fixed effect intercept in our model thus represents the survival at the mean value of these neighborhood predictors. Multicollinearity among fixed effect predictors was low (variance inflation factors $< 2$; Lindsey 1999), so, all four predictors could be included in the same model.

**Table 3. AICc model selection for neighborhood metric and size.** AICc model selection results testing which neighborhood metric and which neighborhood size (radius) was best supported by the data. Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight (relative likelihood of the model, which is exp ( -0.5 * ΔAIC score for that model)); K number of parameters in the model. Random factors in the base model were the same used across all different models tested during model selection. All models also included as fixed effects both seedling neighborhood metrics: Con_S, the number of conspecific seedlings, and Het_S, the number of heterospecific seedlings, in the same subplot as the focal seedling. For adults, the neighborhood metrics were calculated using either a 10 m or 20 m radius around the focal seedling for the following three possible neighborhood metrics: Het_A_BA, (sum of the basal areas of heterospecific adults), Con_A_BA, (sum of the basal areas of conspecific adults), Het_A_DBH, (sum of the DBHs of heterospecific adults), Con_A_DBH, (sum of the DBHs of conspecific adults), Het_A_Count, (number of heterospecific adults), Con_A_Count, (number of conspecific adults).

| **Models with 20m Neighborhood** | | **K** | **AICc** | **DeltaAICc** | **AICcWt** |
|---|---|---|---|---|---|
| Con_S + Het_S + Het_A_BA + Con_A_BA | | 7 | 7579.00 | 0.00 | 0.44 |
| Con_S + Het_S + Het_A_BA + Con_A_DBH | | 7 | 7580.98 | 1.99 | 0.39 |
| Con_S + Het_S + Het_A_DBH + Con_A_BA | | 7 | 7583.64 | 4.63 | 0.04 |
| Con_S + Het_S + Het_A_DBH + Con_A_DBH | | 7 | 7583.67 | 4.67 | 0.04 |
| Con_S + Het_S + Het_A_Count + Con_A_DBH | | 7 | 7584.26 | 5.26 | 0.03 |
| Con_S + Het_S + Het_A_Count + Con_A_BA | | 7 | 7584.32 | 5.32 | 0.03 |
| Con_S + Het_S + Het_A_BA + Con_A_Count | | 7 | 7586.03 | 7.02 | 0.01 |
| Con_S + Het_S + Het_A_DBH + Con_A_Count | | 7 | 7590.39 | 11.39 | 0.00 |
| Con_S + Het_S + Het_A_Count + Con_A_Count | | 7 | 7590.92 | 11.92 | 0.00 |
| **Models with 10m Neighborhood** | | **K** | **AICc** | **Delta_AICc** | **AICcWt** |
| Con_S + Het_S + Het_A_BA + Con_A_DBH | | 7 | 7583.22 | 0.00 | 0.50 |
| Con_S + Het_S + Het_A_DBH + Con_A_DBH + | | 7 | 7585.41 | 2.19 | 0.17 |
| Con_S + Het_S + Het_A_Count + Con_A_DBH | | 7 | 7585.41 | 2.19 | 0.17 |
| Con_S + Het_S + Het_A_BA + Con_A_BA | | 7 | 7587.41 | 4.19 | 0.06 |
| Con_S + Het_S + Het_A_BA + Con_A_Count | | 7 | 7588.39 | 5.16 | 0.04 |
| Con_S + Het_S + Het_A_DBH + Con_A_BA | | 7 | 7589.63 | 6.41 | 0.02 |
| Con_S + Het_S + Het_A_Count + Con_A_BA | | 7 | 7589.74 | 6.52 | 0.02 |
| Con_S + Het_S + Het_A_Count + Con_A_Count | | 7 | 7590.44 | 7.22 | 0.01 |
| Con_S + Het_S + Het_A_DBH + Con_A_Count | | 7 | 7590.46 | 7.24 | 0.01 |

We were interested in quantifying density dependent effects across all plots and separately in each plot. To address the former, we included data for all species and all plots in a single model (global model). To address the latter, all species present in each plot were included in the model for that plot (plot-specific models). However, species may respond differently to variation in neighborhood metrics and have different average ("background") mortality rates, so we tested the alternative random effects structures involving species, using a similar model selection approach as described above for the fixed effects. The fixed factors in the base model (as described above) were the same across all different models tested during random model selection.

We tested the following alternative random effects structures involving species identity, neighborhood predictors, plot, and subplot location in the global model and then in each forest plot. In the case of the global model, subplot was nested with in plot, whereas for the plot-specific models, only subplot was included in the random effect model. These models differ in the number of parameters, and so if multiple models were within two AICc units of lowest value, we selected the model with the fewest parameters.

1. Variation in average survival among species and subplot location.
2. Variation in average survival among species and variation among species in their response to neighborhood predictors, where *Neigh* represents all the possible combinations for the four neighborhood predictors: *i.e.* just adults, (Con_A + Het_A), just conspecifics (Con_A + Con_S), just heterospecific, (Het_A + Con_S), just seedlings (Con_S + Het_S), and all neighboors (Con_S + Het_S + Con_A + Het_A) and subplot location. In this formulation of the species effect, the intercept

and slope are correlated.

3. Variation in average survival among species and variation among species in their response to neighborhood variables, as in model 2, but in this formulation of the species effect, the intercept and slope are independent (uncorrelated).

For the global model the best-supported random effects model was model 3, in which variation among species in their response to the four neighborhood predictors is modelled Con_A, Het_A, Con_S, Het_S, with uncorrelated intercept and slope (Table 4.) For the plot-specific models, the best-supported random effects model was the one that included variation in average survival among species and subplot location for all successional plots except two plots, the protected, early successional plot and unprotected, early successional plot number two. The random effects model for the protected, early successional plot included variation in average survival among species and variation among species in their response to the adult heterospecific neighbors with independent intercept and slope. The random effects model for the unprotected, early successional plot number two included the variation in average survival among species and variation among species in their response to the heterospecific seedling neighbors with non-independent intercept and slope (Supplementary Tables A-F).

**Table 4: Global model AICc model selection for random effects.** Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A_BA, Heterospecific adult basal area, Con_A_BA, Conspecific adult basal area, species, plot and subplot variables.

| **Models** | **K** | **AICc** | **DeltaAICc** | **AICcWt** |
|---|---|---|---|---|
| Fixed + (1 \| Plot: subplot) + (0 + Con_A + Het_A + Con_S + Het_S \| species) + (1 \| species) | 17 | 7530.86 | 0.00 | 0.56 |
| Fixed + (1 \| Plot: subplot) + (Con_A + Het_A + Con_S + Het_S \| species) | 21 | 7533.53 | 2.67 | 0.41 |
| Fixed + (1 \| Plot: subplot) + (0 + Con_S + Het_S \| species) + (1 \| species) | 10 | 7534.37 | 3.51 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (Con_S + Het_S \| species) + (1 \| species) | 14 | 7542.37 | 11.51 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (Het_A_+ Het_S \| species) | 12 | 7544.59 | 13.73 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (0 + Het_A + Het_S \| species) + (1 \| species) | 10 | 7547.10 | 16.24 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (0 + Con_A + Con_S \| species) + (1 \| species) | 10 | 7559.95 | 29.09 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (Con_A + Con_S \| species) | 12 | 7560.28 | 29.42 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (0 + Con_A + Het_A \| species) + (1 \| species) | 10 | 7566.12 | 35.26 | 0.01 |
| Fixed + (1 \| Plot: subplot) + (Con_A+ Het_A \| species) | 12 | 7568.84 | 37.98 | 0.01 |
| Fixed + (1 \| species) + (1 \| Plot: subplot) | 7 | 7579.00 | 48.14 | 0.01 |
| Fixed + (1 \| Plot: subplot) | 6 | 8120.07 | 589.21 | 0.00 |

Thus, we used the following final models:

Global Model: To examine question 1 we used the global model in which seedlings for all plots were included in the same model with fixed and random effects indicated in table 3 and 4.

Model 1: To address question 2 we fitted the models separately for each plot using the same fixed effect as the global model but with the best random effect model (see supplementary materials)

The global model provides a general estimate of the type, strength, and direction of the effects of the neighborhood metrics on seedling survival across all plots when accounting for variation across plots in the random effect model. To determine the variation in the type, strength, and direction of density dependent effects on seedling survival in each forest plot, we used Model 1 fitted for each plot separately. Each plot represents a specific successional age: old growth, mid successional and young successional forests and two protection status: protected, unprotected. For our six models, we estimated the slope (odds ratio) of the neighborhood effect for each neighborhood metric, quantified its strength (magnitude of the slope and whether its confidence intervals included one), and direction (negative or positive) for each plot, and plotted these slope estimates per successional age and protection status.

In each model, the fixed effect slope parameters provide an estimate of the strength and direction of each of the four-neighborhood predictors, conspecific adult trees (CON_A), heterospecific adult trees (HET_A), conspecific seedlings (CON_S), and heterospecific seedlings (HET_S). Slope estimates for these factors are log odds ratios, which were back-transformed to odds ratios, along with their 95% confidence intervals. Odds ratios are calculated relative to one, so when the confidence interval overlaps the value of one, then there is no significant effect of this metric. Odds ratios significantly < 1 or > 1 indicate that the metric has negative or positive effects on survival, respectively, per one standard deviation unit change of that metric. The fixed-effect intercept of the model provides an estimate of survival when all the fix factors are set at their mean values.

## Results

### 3.1 Overall density dependent effect

Averaging all the forest plots, there was an overall significant negative density dependent effect of adult conspecific trees on seedling survival ($Z = -2.666$, $P < 0.01$); however, no other neighborhood variables significantly affected seedling survival in the global model (Figure 3).

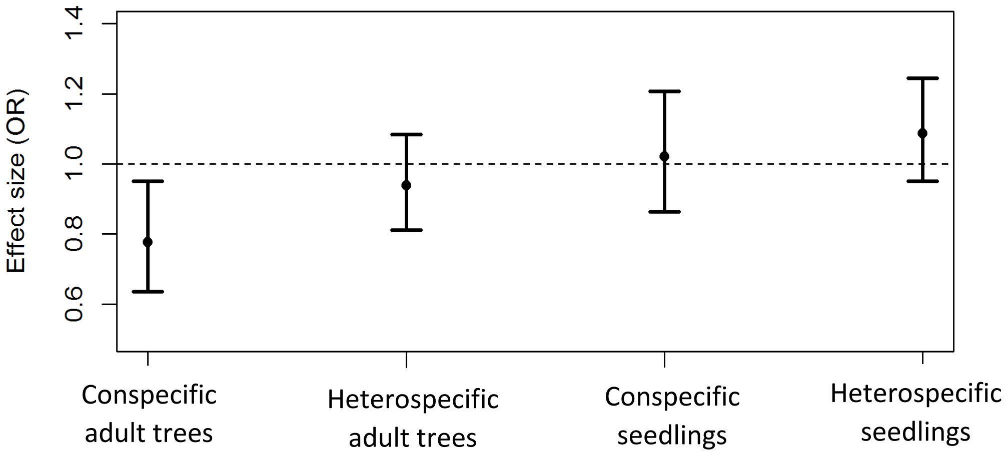

**Figure 3: Global model neighborhood predictors effect**. Effect sizes (odds ratio) and their 95% confidence intervals for the effects of four neighborhood predictors on seedling survival, averaging over six Costa Rican forests. The vertical dotted line indicates an odds ratio equal to one, which means that with a change in one standard deviation unit of that metric has no significant effect on seedling survival. Odds ratios significantly < 1 or > 1 indicate that the metric has negative or positive effects on survival, respectively.

### 3.2 Variation in density dependence due to successional age and protection from hunting

Despite the overall conspecific negative effect, there was significant variation in density dependence of seedling survival depending on forest successional age and protection status. While there were significant effects of the conspecific adult heterospecific adult, and conspecific seedling neighbors on seedling survival in some plot forests. There were no significant effects of seedling heterospecific neighborhood in any forest plot.

**Table 5. Summary table of neighborhood effects (fixed effects) by successional plot.** The abbreviation "n.s." indicates that the slope estimate was not different from zero. When odds ratios were significantly different from 1, then the estimate is provided, with confidence intervals in parentheses, along with the probability that the estimate is different from a value of one. Odds ratios < 1 and >1 indicate negative and positive effects on survival, respectively.

| **Neighborhood predictors/ Forest** | **Conspecific Adult** | **Heterospecific Adult** | **Conspecific Seedling** | **Heterospecific Seedling** |
|---|---|---|---|---|
| **Protected Early Successional** | n.s. | n.s. | n.s. | n.s. |
| **Protected Mid-Successional** | *0.57*<br>*(CI=0.38,0.86)*<br>$p < 0.01$ | n.s. | n.s. | n.s. |
| **Protected Old Growth** | *0.51*<br>*(CI=0.32,0.81)*<br>$p < 0.01$ | *0.58*<br>*(CI=0.36,0.94)*<br>$p < 0.05$ | 0.76<br>*(CI=0.58,0.99)*<br>$p < 0.05$ | n.s |
| **Unprotected Early Successional 1** | 0.76<br>*(CI=0.64,0.90)*<br>$p < 0.01$ | 1.39<br>*(CI=1.10,1.76)*<br>$p < 0.01$ | n.s. | n.s. |
| **Unprotected Early Successional 2** | n.s. | n.s. | 1.33<br>(CI=1.12,1.59)<br>$p < 0.01$ | n.s. |
| **Unprotected Old Growth** | n.s. | n.s. | 0.75<br>(CI=0.62,0.91)<br>$p < 0.05$ | n.s. |

In the protected old growth forest and the mid-successional forest the conspecific adult neighborhood exhibited significant negative effects on seedling survival ($Z = -2.808$, $p < 0.01$), and ($Z = -2.646$, $p < 0.01$) respectively; but have no significant effects in the protected early successional forest. Among the unprotected forests, the early successional forest 1 exhibited a significant negative effect ($Z = -3.235$, $p < 0.01$) but nor the old growth forest or the early successional 2 (Figures 4).

There was a significant negative effect of conspecific seedlings in the protected and unprotected old growth forest ($Z = -2.042$, $p < 0.05$) and ($Z = -2.869$, $p < 0.05$) respectively. However, the conspecific seedling neighborhood enhanced survival in one of the unprotected early successional forests ($Z = 3.211$, $p < 0.01$) (Figures 5).

Also, in the protected old growth forest, heterospecific adult trees showed a significant negative effect on seedling survival ($Z = -2.236$, $p < 0.05$), whereas in the unprotected early successional forest 1, the heterospecific adult neighbors showed a positive effect ($Z = 2.728$, $p < 0.05$) (Figures 6).

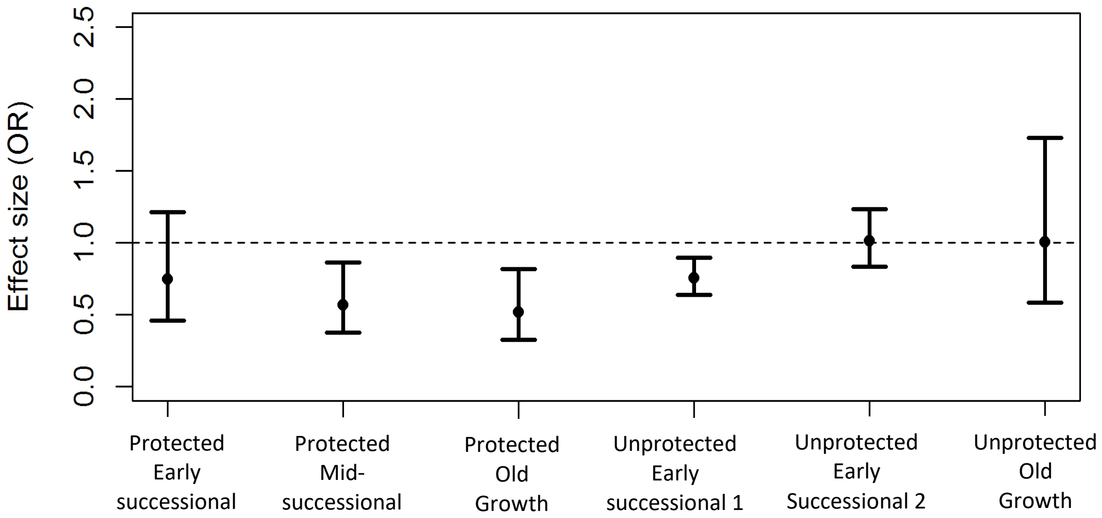

**Figure 4. Conspecific adult trees effect on seedling survival.** Effect sizes (odds ratio) and their 95% confidence intervals for the effect of conspecific adult trees on seedling survival across six forests of different successional ages in Costa Rican tropical forest. The horizontal dotted line indicates an odds ratio equal to one, which means that with a change in one standard deviation unit of that metric has no significant effect on seedling survival. Odds ratios significantly < 1 or > 1 indicate that the metric has negative or positive effects on survival, respectively in each plot. So, there's opposite effects of successional age for protected vs unprotected forest.

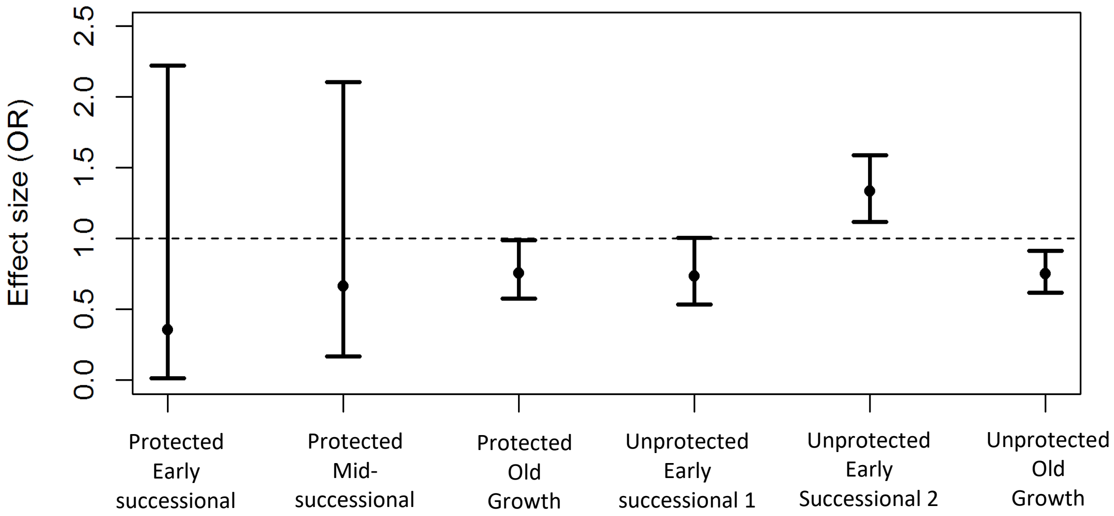

**Figure 5. Conspecific seedling trees effect on seedling survival**. Effect sizes (odds ratio) and their 95% confidence intervals for the effect of conspecific seedlings on seedling survival across six forests of different successional ages in Costa Rican tropical forest. The horizontal dotted line indicates an odds ratio equal to one, which means that with a change in one standard deviation unit of that metric has no significant effect on seedling survival. Odds ratios significantly < 1 or > 1 indicate that the metric has negative or positive effects on survival, respectively in each plot.

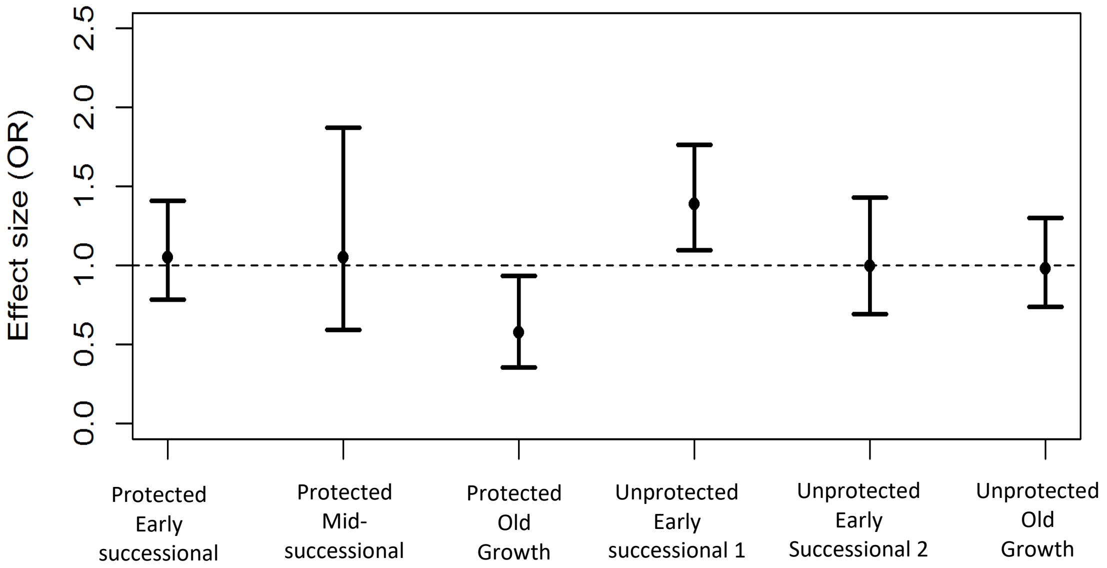

**Figure 5. Heterospecific adult trees effect on seedling survival**. Effect sizes (odds ratio) and their 95% confidence intervals for the effect of heterospecific adults on seedling survival across six forests of different successional ages in Costa Rican tropical forest. The horizontal dotted line indicates an odds ratio equal to one, which means that with a change in one standard deviation unit of that metric has no significant effect on seedling survival. Odds ratios significantly < 1 or > 1 indicate that the metric has negative or positive effects on survival, respectively in each plot.

# 4. Discussion

## 4.1 Overall density dependent effect

Seedling survival is a critical step in the regeneration of secondary forests, and yet much remains unknown about the dominant factors regulating it. Using neighborhood models, we quantified density dependent seedling survival across and in each secondary forest of varying successional age and protection status. Averaging across species, the most important factors were conspecific neighborhood predictors, implying that shared, species-specific natural enemies and intraspecific resource competition strongly influence seedling survival, consistent with findings from primary forests where conspecific density dependence is thought to be contributing to tree species coexistence in tropical forests (Comita *et al.* 2014).

We found that while the negative effect of the conspecific adult neighborhood on survival was pervasive across these forests, there was significant variation in the strength of this effect due to successional age of the forests and whether they were protected from hunting.

## 4.2 Variation in density dependence due to successional age and protection from hunting

In accordance with conceptual models (Chazdon 2008) in protected forests negative conspecific adult density effect were stronger compared to successional forests and negative conspecific seedling density effect were also stronger in old growth than successional forest. These findings agree with the results from studies using a similar methodology conducted in old growth forests (Wills and Condit 1999, Harms *et al.* 2000, Lebrija *et al* 2014). However, the conspecific adult effect in unprotected forests showed the opposite pattern with stronger negative conspecific adult effect in early successional forest suggesting that protection status may interact with successional age affecting density dependent processes. Nevertheless, this result is consistent with studies that have found that patterns of density and distance dependence can be altered when vertebrate seed disperser and seed predator populations are reduced due to poaching and other human disturbance (Harrison *et al.* 2013). Our results suggest that, once protected, secondary forests tend to recover the expected strength and direction of interactions related to density dependence that may lead to a recovering of diversity and allow the coexistence of tree species as succession proceeds.

Since conspecific and heterospecific adult and seedling neighborhood predictors had significant effect on seedling survival depending in the forest plot but not heterospecific seedlings neighborhood, interspecific resource competition and general natural enemies or intraspecific density dependence is a main determinant of variation in seedling survival depending in the stage of succession and protection status. Contrary to our expectation seedling intraspecific effect did have a significant effect for some forest plots neglecting that small seedlings do not have direct interactions this result disagree with result from primary tropical forests showing that seedlings may be too small to have strong, direct competitive interactions (Paine *et al.* 2012).

## Conclusions

There is a prevalence of conspecific negative density dependence across forest. However, density dependence of conspecific and heterospecific neighbors on seedling survival varies among the successional stages. Conspecific negative density dependent effect tends to increase with increasing successional age. However, unprotected forests do not follow this pattern, highlighting the importance of mammals in secondary forest regeneration dynamics.

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## Supplementary materials

**Table A: Model selection results for random factors at protected old growth forest**. Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A, Heterospecific adult basal area, Con_A, Conspecific adult basal area, species, plot and subplot variables.

| **Models Protected Old Growth Forest** | **K** | **AICc** | **DeltaAICc** | **AICcWt** |
|---|---|---|---|---|
| Fixed+ (1 \| species) + (1 \|subplot) | 7 | 484.60 | 0.00 | 1.00 |
| Fixed+ (1 \|subplot) + (0 + Het_S \| species) + (1 \| species) | 8 | 485.77 | 1.17 | 0.56 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (1 \| species) | 8 | 486.09 | 1.49 | 0.47 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (1 \| species) | 8 | 486.69 | 2.09 | 0.35 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (1 \| species) | 8 | 486.69 | 2.09 | 0.35 |
| Fixed+ (1 \|subplot) + (Het_A\| species) | 9 | 486.95 | 2.35 | 0.31 |
| Fixed+ (1 \|subplot) + (Het_S \| species) | 9 | 487.74 | 3.14 | 0.21 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (0 + Het_S \| species) + (1 \| species) | 9 | 487.87 | 3.27 | 0.19 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_S \| species) + (1 \| species) | 9 | 487.87 | 3.27 | 0.19 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Het_S \| species) + (1 \| species) | 9 | 487.88 | 3.28 | 0.19 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (1 \| species) | 9 | 488.19 | 3.59 | 0.17 |
| Fixed+ (1 \|subplot) | 6 | 488.26 | 3.66 | 0.16 |
| Fixed+ (1 \|subplot) + (Con_A\| species) | 9 | 488.33 | 3.74 | 0.15 |
| Fixed+ (1 \|subplot) + (Con_S\| species) | 9 | 488.78 | 4.18 | 0.12 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 488.78 | 4.19 | 0.12 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 488.78 | 4.19 | 0.12 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (0 + Het_S \| species) + (1 \| species) | 10 | 489.98 | 5.38 | 0.07 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S \| species) + (1 \| species) | 10 | 489.99 | 5.39 | 0.07 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S \| species) + (1 \| species) | 11 | 492.11 | 7.51 | 0.02 |

| | | | | |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) | 12 | 493.31 | 8.72 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) | 12 | 493.31 | 8.72 | 0.01 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Het_S \| species) | 12 | 493.31 | 8.72 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_S\| species) + (Het_S \| species) | 12 | 494.11 | 9.51 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_S \| species) | 12 | 494.11 | 9.51 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) | 12 | 494.70 | 10.10 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) + (Het_S \| species) | 15 | 500.58 | 15.98 | 0.00 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) + (Het_S \| species) | 15 | 501.02 | 16.42 | 0.00 |

**Table B: Model selection results for random factors at protected mid successional forest**. Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A, Heterospecific adult basal area, Con_A, Conspecific adult basal area, species, plot and subplot variables.

| Models protected mid successional | K | AICc | DeltaAICc | AICcWt |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (Con_S\|species) | 9 | 433.19 | 0.00 | 1.00 |
| Fixed+ (1 \|species) + (1 \|subplot) | 7 | 433.43 | 0.24 | 0.35 |
| Fixed+ (1 \|subplot) + (0 + Het_S\|species) + (1 \|species) | 8 | 435.51 | 2.32 | 0.19 |
| Fixed+ (1 \|subplot) + (0 + Het_A\|species) + (1 \|species) | 8 | 435.51 | 2.32 | 0.18 |
| Fixed+ (1 \|subplot) + (0 + Con_S\|species) + (1 \|species) | 8 | 435.51 | 2.32 | 0.12 |
| Fixed+ (1 \|subplot) + (0 + Con_A\|species) + (1 \|species) | 8 | 435.51 | 2.32 | 0.12 |
| Fixed+ (1 \|subplot) + (Het_S\|species) | 9 | 436.74 | 3.55 | 0.07 |
| Fixed+ (1 \|subplot) + (Het_A\|species) | 9 | 437.12 | 3.93 | 0.07 |
| Fixed+ (1 \|subplot) + (Con_A\|species) | 9 | 437.35 | 4.16 | 0.07 |
| Fixed+ (1 \|subplot) + (0 + Con_A\|species) + (0 + Het_A\|species) + (1 \|species) | 9 | 437.59 | 4.40 | 0.05 |
| Fixed+ (1 \|subplot) + (0 + Con_S\|species) + (0 + Het_S\|species) + (1 \|species) | 9 | 437.59 | 4.40 | 0.04 |
| Fixed+ (1 \|subplot) + (0 + Het_A\|species) + (0 + Con_S\|species) + (1 \|species) | 9 | 437.59 | 4.40 | 0.04 |
| Fixed+ (1 \|subplot) + (0 + Con_A\|species) + (0 + Het_S\|species) + (1 \|species) | 9 | 437.59 | 4.40 | 0.03 |
| Fixed+ (1 \|subplot) + (0 + Het_A\|species) + (0 + Het_S\|species) + (1 \|species) | 9 | 437.59 | 4.40 | 0.02 |
| Fixed+ (1 \|subplot) + (0 + Con_A\|species) + (0 + Con_S\|species) + (1 \|species) | 9 | 437.59 | 4.40 | 0.01 |
| Fixed+ (1 \|subplot) + (Het_A\|species) + (Con_S\|species) | 12 | 438.50 | 5.31 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_S\|species) + (Het_S\|species) | 12 | 439.50 | 6.31 | 0.01 |
| Fixed+ (1 \|subplot) + (0 + Con_A\|species) + (0 + Con_S\|species) + (0 + Het_S\|species) + (1 \|species) | 10 | 439.69 | 6.50 | 0.01 |
| Fixed+ (1 \|subplot) + (0 + Het_A\|species) + (0 + Con_S\|species) + (0 + Het_S\|species) + (1 \|species) | 10 | 439.69 | 6.50 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_A\|species) + (Con_S\|species | 12 | 440.04 | 6.85 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\|species) + (0 + Het_A\|species) + (0 + Con_S\|species) + (0 + Het_S\|species) + (1 \|species) | 11 | 441.79 | 8.60 | 0.00 |

| | | | | |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (Het_A\|species) + (Het_S\|species) | 12 | 442.95 | 9.76 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\|species) + (Het_S\|species) | 12 | 443.05 | 9.86 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\|species) + (Het_A\|species) | 12 | 443.42 | 10.23 | 0.00 |
| Fixed+ (1 \|subplot) + (Het_A\|species) + (Con_S\|species) + (Het_S\|species) | 15 | 444.90 | 11.71 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\|species) + (Con_S\|species) + (Het_S\|species) | 15 | 445.91 | 12.72 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\|species) + (Het_A\|species) + (Con_S\|species) + (Het_S\|species) | 18 | 451.40 | 18.21 | 0.00 |
| Fixed+ (1 \|subplot) | 6 | 492.96 | 59.77 | 0.00 |

**Table C: Model selection results for random factors at protected early successional forest.** Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A, Heterospecific adult basal area, Con_A, Conspecific adult basal area, species, plot and subplot variables.

| **Models protected early successional** | **K** | **AICc** | **DeltaAICc** | **AICcWt** |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (1 \| species) | 8 | 161.02 | 0.00 | 1.00 |
| Fixed+ (1 \|subplot) + (Het_A\| species) | 9 | 162.60 | 1.58 | 0.45 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 162.74 | 1.72 | 0.42 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) | 12 | 163.03 | 2.01 | 0.37 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 163.25 | 2.23 | 0.33 |
| Fixed+ (1 \|subplot) | 6 | 164.35 | 3.33 | 0.19 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 165.00 | 3.98 | 0.14 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Het_S\| species) | 12 | 169.37 | 8.35 | 0.02 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 15 | 170.17 | 9.15 | 0.01 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (1 \| species) | 8 | 188.99 | 27.97 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) | 9 | 191.02 | 30.00 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 191.23 | 30.20 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 191.23 | 30.20 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (1 \| species) | 9 | 191.23 | 30.20 | 0.00 |
| Fixed+ (1 \| species) + (1 \|subplot) | 7 | 192.02 | 31.00 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 193.49 | 32.46 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_S\| species) | 9 | 194.16 | 33.14 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Het_S\| species) + (1 \| species) | 8 | 194.23 | 33.21 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (1 \| species) | 8 | 194.23 | 33.21 | 0.00 |
| Fixed+ (1 \|subplot) + (Het_S\| species) | 9 | 195.51 | 34.49 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 11 | 195.78 | 34.75 | 0.00 |

| | | | | |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 196.46 | 35.44 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_S\| species) | 12 | 197.89 | 36.87 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) | 12 | 197.89 | 36.87 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) | 12 | 197.89 | 36.87 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_S\| species) + (Het_S\| species) | 12 | 200.86 | 39.84 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) + (Het_S\| species) | 15 | 205.03 | 44.01 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 18 | 212.45 | 51.43 | 0.00 |

**Table D: Model selection results for random factors at unprotected old successional forest.** Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A, Heterospecific adult basal area, Con_A, Conspecific adult basal area, species, plot and subplot variables.

| Models Unprotected old successional | K | AICc | DeltaAICc | AICcWt |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (Con_S\| species) | 9 | 1199.38 | 0.00 | 1.00 |
| Fixed+ (1 \| species) + (1 \|subplot) | 7 | 1200.35 | 0.97 | 0.62 |
| Fixed+ (1 \|subplot) + (0 + Het_S\| species) + (1 \| species) | 8 | 1202.38 | 2.99 | 0.22 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (1 \| species) | 8 | 1202.38 | 2.99 | 0.22 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (1 \| species) | 8 | 1202.38 | 2.99 | 0.22 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (1 \| species) | 8 | 1203.29 | 3.91 | 0.14 |
| Fixed+ (1 \|subplot) + (Het_S\| species) | 9 | 1204.24 | 4.86 | 0.09 |
| Fixed+ (1 \|subplot) + (Het_A\| species) | 9 | 1204.30 | 4.92 | 0.09 |
| Fixed+ (1 \|subplot) + (Con_A\| species) | 9 | 1204.39 | 5.01 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 1204.41 | 5.02 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 1204.41 | 5.02 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (1 \| species) | 9 | 1204.41 | 5.02 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 1205.32 | 5.94 | 0.05 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 1205.32 | 5.94 | 0.05 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 1205.32 | 5.94 | 0.05 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) | 12 | 1205.49 | 6.11 | 0.05 |
| Fixed+ (1 \|subplot) + (Con_S\| species) + (Het_S\| species) | 12 | 1205.49 | 6.11 | 0.05 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) | 12 | 1205.49 | 6.11 | 0.05 |
| Fixed+ (1 \|subplot) | 6 | 1205.79 | 6.41 | 0.04 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 1206.44 | 7.06 | 0.03 |

| | | | | |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 1207.35 | 7.97 | 0.02 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 11 | 1209.39 | 10.01 | 0.01 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Het_S\| species) | 12 | 1210.35 | 10.96 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_S\| species) | 12 | 1210.35 | 10.96 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) | 12 | 1210.41 | 11.03 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) + (Het_S\| species) | 15 | 1211.63 | 12.24 | 0.00 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 15 | 1211.63 | 12.24 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 18 | 1217.79 | 18.41 | 0.00 |

**Table E: Model selection results for random factors at unprotected Early successional forest 1.** Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A, Heterospecific adult basal area, Con_A Conspecific adult basal area, species, plot and subplot variables.

| **Models Unprotected Early Successional 1** | **K** | **AICc** | **DeltaAICc** | **AICcWt** |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (Con_A\| species) | 9 | 2071.46 | 0.00 | 1.00 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (1 \| species) | 8 | 2072.11 | 0.65 | 0.72 |
| Fixed+ (1 \| species) + (1 \|subplot) | 7 | 2073.13 | 1.67 | 0.43 |
| Fixed+ (1 \|subplot) + (Het_A\| species) | 9 | 2073.35 | 1.89 | 0.39 |
| Fixed+ (1 \|subplot) + (Con_S\| species) | 9 | 2073.38 | 1.92 | 0.38 |
| Fixed+ (1 \|subplot) + (0 + Het_S\| species) + (1 \| species) | 8 | 2073.56 | 2.10 | 0.35 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 2073.65 | 2.18 | 0.34 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 2074.12 | 2.66 | 0.26 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (1 \| species) | 9 | 2074.12 | 2.66 | 0.26 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) | 12 | 2074.60 | 3.14 | 0.21 |
| Fixed+ (1 \|subplot) + (Het_S\| species) | 9 | 2074.91 | 3.45 | 0.18 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (1 \| species) | 8 | 2075.05 | 3.59 | 0.17 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (1 \| species) | 8 | 2075.14 | 3.68 | 0.16 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 2075.57 | 4.11 | 0.13 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 2075.57 | 4.11 | 0.13 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 2075.66 | 4.20 | 0.12 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) | 12 | 2076.52 | 5.06 | 0.08 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_S\| species) | 12 | 2076.59 | 5.13 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 2077.06 | 5.60 | 0.06 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Het_S\| species) | 12 | 2077.53 | 6.07 | 0.05 |
| Fixed+ (1 \|subplot) + (Con_S\| species) + (Het_S\| species) | 12 | 2077.55 | 6.09 | 0.05 |

| | | | | |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 2077.59 | 6.13 | 0.05 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 11 | 2077.68 | 6.22 | 0.04 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) | 12 | 2079.36 | 7.90 | 0.02 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 15 | 2082.14 | 10.68 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) + (Het_S\| species) | 15 | 2083.63 | 12.17 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 18 | 2088.23 | 16.77 | 0.00 |
| Fixed+ (1 \|subplot) | 6 | 2225.28 | 153.82 | 0.00 |

**Table F: Model selection results for random factors at unprotected Early successional forest 2.** Abbreviations: AICc, corrected Akaike Information Criterion values; Delta AICc, differences between the model AICc and the lowest AICc; AICcWT, Akaike weight; K number of parameters in the model. Fixed factors in the base model were the same used across all different models tested during random model selection. The possible random factors included were: Con_S Conspecific count seedlings, Het_S, Heterospecific count seedlings and Het_A, Heterospecific adult basal area, Con_A, Conspecific adult basal area, species, plot and subplot variables.

| **Models Unprotected early successional 2** | **K** | **AICc** | **DeltaAICc** | **AICcWt** |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (Het_S\| species) | 9 | 1750.47 | 0.00 | 1.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) | 9 | 1753.10 | 2.63 | 0.27 |
| Fixed+ (1 \| species) + (1 \|subplot) | 7 | 1753.49 | 3.02 | 0.22 |
| Fixed+ (1 \|subplot) + (Het_A\| species) | 9 | 1755.06 | 4.59 | 0.10 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (1 \| species) | 8 | 1755.51 | 5.04 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (1 \| species) | 8 | 1755.51 | 5.04 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (1 \| species) | 8 | 1755.51 | 5.04 | 0.08 |
| Fixed+ (1 \|subplot) + (0 + Het_S\| species) + (1 \| species) | 8 | 1755.51 | 5.04 | 0.08 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Het_S\| species) | 12 | 1756.30 | 5.83 | 0.05 |
| Fixed+ (1 \|subplot) + (Con_S\| species) + (Het_S\| species) | 12 | 1756.54 | 6.07 | 0.05 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_S\| species) | 12 | 1756.54 | 6.07 | 0.05 |
| Fixed+ (1 \|subplot) + (Con_S\| species) | 9 | 1756.96 | 6.49 | 0.04 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 1757.53 | 7.06 | 0.03 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (1 \| species) | 9 | 1757.53 | 7.06 | 0.03 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (1 \| species) | 9 | 1757.53 | 7.06 | 0.03 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 1757.53 | 7.06 | 0.03 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 1757.53 | 7.06 | 0.03 |
| Fixed+ (1 \|subplot) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 9 | 1757.53 | 7.06 | 0.03 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) | 12 | 1759.17 | 8.69 | 0.01 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) | 12 | 1759.17 | 8.69 | 0.01 |
| Fixed+ (1 \|subplot) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 10 | 1759.55 | 9.08 | 0.01 |

| | | | | |
|---|---|---|---|---|
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 16 | 1844.67 | 9.49 | 0.01 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) | 16 | 1847.08 | 11.89 | 0.00 |
| Fixed+ (1 \|subplot) + (0 + Con_A\| species) + (0 + Het_A\| species) + (0 + Con_S\| species) + (0 + Het_S\| species) + (1 \| species) | 13 | 1849.88 | 14.69 | 0.00 |
| Fixed+ (1 \|subplot) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 13 | 1850.08 | 14.89 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Con_S\| species) + (Het_S\| species) | 21 | 1852.33 | 17.15 | 0.00 |
| Fixed+ (1 \|subplot) + (Con_A\| species) + (Het_A\| species) + (Con_S\| species) + (Het_S\| species) | 17 | 1858.17 | 22.98 | 0.00 |
| Fixed+ (1 \|subplot) | 6 | 2007.60 | 172.41 | 0.00 |