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Understorey removal effects on tree regeneration in temperate forests: a meta-analysis

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Abstract

1. The unwanted development of dense understorey vegetation composed of resource-acquisitive, tall plant species competing strongly with tree regeneration can pose formidable problems for

managers attempting to regenerate temperate forests. Despite many studies on the effects of understorey removal, no comprehensive review has summarised and quantified its effects on subsequent life stages of tree regeneration in temperate forests.

2. We synthesised data from 32 experimental studies from temperate forest regions. We used meta-analytic techniques to find general patterns in terms of the characteristics of the understorey, overstorey, and characteristics of the regenerating tree species, which are most responsible for possible positive understorey removal effects on early life stages of tree regeneration, i.e. emergence, survival and growth.
3. Both seedling survival and growth increased in response to understorey removal; emergence did not show a clear pattern. Seedlings growing free from competition mainly increased their biomass growth (total and aboveground), whereas diameter and height growth responded less. These positive effects were largest when removing denser understorey vegetation and under more open overstorey conditions. Multiple management options influenced the regeneration responses to understorey removal. For instance, growth of older, planted seedlings responded less to removal, whereas protection against large browsers increased growth responses.
4. Tree species with differing strategies responded differently to understorey removal. Growth and survival responses of early-successional species responded more strongly to understorey removal than mid- or late-successional tree species.
5. *Synthesis and applications.* Our study showed that understorey removal can have strong positive effects on tree regeneration across temperate forest contexts. The magnitude of these effects depended on overstorey and understorey conditions, but also on the type of tree species that is regenerated. Our results can support forest managers in their decision-making and help assess under what conditions understorey removal will be most justified.

Keywords: competition release, gap creation, herb layer, temperate forest, tree seedling, vegetation management, overstorey, successional status

1. Introduction

Tree regeneration is of key importance in forest ecosystems, as it provides the next generation of overstorey (canopy) trees. Each tree in the overstorey has recruited in and passed through the forest understorey as a seedling. Through its initial competitive interactions with the regeneration of overstorey tree species, the understorey community can act as a filter (George & Bazzaz, 1999a), reducing performance of the early life stages of tree seedlings (Royo & Carson, 2006). This filter effect may severely decrease forest growth rates, impact forest overstorey structure and composition, and delay or even arrest forest succession (Royo & Carson, 2006; Thrippleton, Bugmann, & Snell, 2018). That is why forest managers may choose to remove competing understorey vegetation (hereafter referred to as 'understorey removal'). Such management interventions can, however, be expensive and labour intensive, e.g. mowing of understorey vegetation, or can have detrimental effects, e.g. the use of chemical treatment with herbicides is under debate (Ammer, Balandier, Bentsen, Coll, & Löf, 2010). Furthermore, from a forest biodiversity conservation point of view, removal of the species rich understorey vegetation, which may also contribute to other forest functions (Landuyt, De Lombaerde, et al., 2019), may not be desired. Therefore, we need a better understanding of the effectiveness of understorey removal, and more specifically, given potential detrimental side effects, under what conditions such a treatment is most beneficial to regeneration.

Tree species with differing ecological strategies are expected to respond differently to competition from understorey vegetation (George & Bazzaz, 1999b; Pagès, Pache, Joud, Magnan, & Michalet, 2003). Plant traits and trait syndromes can provide a valuable way to generalise across a large set of species (McGill, Enquist, Weiher, & Westoby, 2006) and to make inferences of how species (types) are likely to respond to competition or changes in environmental conditions (Kunstler et al., 2015; Laughlin, 2014; Suding et al., 2008). More specifically, tree species can be classified into trait syndromes according to their successional status. This classification is proposed by and useful for forest managers (Bugmann, 1996; Leuschner & Meier, 2018). As competition for light is one of the main factors, if not the main one, determining interactions between tree regeneration and understorey vegetation, this classification can give further insights in how different tree species respond to understorey removal or competition. Such knowledge is important because depending on the species one wants to regenerate, managers need to know whether vegetation management is likely to be necessary.

The most common practice to stimulate natural regeneration of trees is by opening up the forest canopy to increase light availability, which may simultaneously increase temperature, moisture and nutrient availability (Wagner, Fischer, & Huth, 2011). This may not only lead to increased seedling performance (e.g. Busing 1994; Pacala 1994), but may also result in the development of dense understorey vegetation composed of resource acquisitive, tall plant species competing strongly with tree seedlings for available resources (Balandier, Collet, Miller, Reynolds, & Zedaker, 2006; De Lombaerde, Verheyen, Van Calster, & Baeten, 2019). In temperate forests, overstoreys are opened up to different degrees, ranging from small increases in light by creating single-tree gaps (e.g. Walters et al. 2016), to gradually removing the canopy in shelterwood systems (e.g. Horsley 1993) or to full removal of the overstorey in clearcuts (e.g. Nilsson and Örlander 1999). Understorey species or species groups may respond in various manners to overstorey opening, but can also influence consecutive life stages of seedling s differently (Balandier et al., 2006). For instance, strongly reducing overstorey cover could stimulate regeneration of early-successional, shade intolerant species; but at the same time, these species will suffer more from competition with the understorey that may become denser and more competitive (De Lombaerde et al., 2019; Pagès et al., 2003). The effects and potential of understorey removal will thus vary depending, not only on tree species, but also on the local understorey and overstorey conditions, and changes therein.

Multiple case studies have reported on the effects of understorey vegetation and its removal on tree regeneration (reviewed in Balandier et al., 2006; Royo & Carson, 2006). Individual experiments generally focus on a restricted set of tree species, making it difficult to generalise findings to different species and groups of species with similar ecological characteristics. Furthermore, experiments generally cover small gradients in overstorey conditions, understorey vegetation type, and seedling life stages that are monitored. Here, we synthesised the current knowledge by performing a systematic literature search to identify studies that report the effect of understorey vegetation removal. We used meta-analytic methods to quantify overall removal effects on critical early life stage responses of tree regeneration, i.e. emergence, survival and growth (in height, diameter and biomass). Furthermore, we perform multilevel meta-regression to determine the effects of moderators related to overstorey and understorey characteristics, management options and tree species characteristics.

We address the following research questions:

(1) What is the overall effect of understorey removal on subsequent life stages of tree regeneration: emergence, growth and survival? We expected that seedlings will emerge and perform better without surrounding vegetation as release from competition for light, nutrients and moisture is likely to benefit regeneration.
(2) Can variation in the responses of different species be explained using characteristics of tree species? We predicted decreasing removal effects from early-, to mid-, to late-successional species, which is at least partly explained by the increasing shade tolerance of the species that occur in these subsequent successional stages.
(3) Under what overstorey and understorey conditions is the removal of vegetation most opportune for forest managers? Removal of denser understorey vegetation and under open overstorey conditions is expected to result in stronger benefits for tree seedlings.

(4) What other management related interventions or choices have been studied and could increase efficacy of understorey removal? For instance, different regeneration methods (e.g. planting vs. seeding) or seedling age when planting, as younger trees might be more affected by competition, could result in more beneficial seedling responses to understorey removal.

2. Materials & Methods

2.1 Literature search

We conducted a systematic search using the Web of Science and Scopus, for peer-reviewed studies that compared tree regeneration performance with or without surrounding understorey vegetation (published up to December 31, 2019; detailed search string in Appendix S1 in Supporting Information). After removal of duplicate records, this search yielded 689 articles (Appendix S1 Fig. S1). We selected relevant studies according to title and abstract, and after reviewing the full text, we selected experimental studies from the temperate broadleaved and mixed forest region (Olson et al., 2001). Experiments were allowed from both natural as well as strongly controlled conditions, such as greenhouse or pot experiments, to cover a large range of species and environmental conditions. Controlled experiments were allowed as they are valuable in isolating the effects of understoreys on tree regeneration, and are most relevant in the context of understoreys dominated by one or a few species (e.g. Bloor, Leadley, & Barthes, 2008), on tree regeneration. Natural conditions could range from closed overstorey forest vegetation, to early successional, open conditions (e.g. open forest or old-field vegetation). The main requirement for studies was that they had to test the effect of the presence of neighbouring vegetation (plants added or no removal treatment) vs. no surrounding vegetation (removal treatment or no plants added). Throughout this study, we will refer to regenerating trees as seedlings, but this comprises both seedlings (< 1 year old and < 0.5 m height) and saplings (> 1 year, > 0.5 m but diameter < 10 cm) (Gibert, Gray, Westoby, Wright, & Falster, 2016). The understoreys that were removed, or added could be comprised of herbaceous as well as woody, small shrub vegetation (e.g. *Rubus* spp.; but height < 2m) or a mix of both; no removal or addition of other vegetation strata were allowed (e.g. Beckage et al. 2008; Abe et al. 2002). Different understorey removal treatments were allowed (mowing, manual weeding, clipping, herbicide or combinations); but the removal treatment had to be thorough: the present vegetation had to be fully removed and treatments had to be maintained for the duration of the study. Studies were not included that reported on seedling responses to mechanical site preparation (e.g. ploughing, harrowing), one-time treatments or studies that only reported on treatment effects after a certain time, thus allowing regrowth of the understorey vegetation. The studies had to report effects on one or more of the following responses: seedling emergence, survival, height, diameter or biomass growth. Even though biomass (total and aboveground), height and diameter growth are closely linked, they can respond differently to environmental changes, depending on where a plant allocates its carbon (e.g. Mašková & Herben, 2018). No observational studies were selected as these studies primarily report the effects of understorey cover on seedling occurrence or density (e.g. Kuijper et al., 2010), and not on emergence, survival or growth over time.

To retrieve as many relevant data as possible, we further searched through the reference lists of these selected papers, relevant reviews (i.e. Balandier et al., 2006; Royo & Carson, 2006) and modelling studies (Thrippleton, Bugmann, Kramer-Priewasser, & Snell, 2016; Thrippleton et al., 2018). In total, we identified 32 original research articles that met the inclusion criteria. Of these studies, published between 1983 and 2017, we extracted data from 3 studies on emergence, 18 on survival and 28 on growth (Appendix S1 Table S1.1). We found 14 studies from Europe, 17 from North America and 1 study from the temperate forest zone in Argentina, South America (Fig. 1).

2.2 Data extraction and effect size calculation

We extracted the mean and if available, standard error, standard deviation and/or sample size for the different tree seedling responses grown surrounded by understorey vegetation or without. We retrieved data directly from tables or the main text, and we used the application WebPlotDigitizer (Rogathi, 2019) to extract data only available from graphs. In addition, we extracted the name of each tree species analysed. Where possible, we extracted data for each independent observation from different sites, i.e. different coordinate locations, within the same study; these were considered as independent studies and were given separate Study IDs. Otherwise, we used pooled treatment means from different sites within studies. For studies that compared effects of different seedling species provenances (e.g. Putnam and Reich 2017), only the provenance closest to the study area was included. Growth was expressed as a variety of thirteen different outcomes on height, diameter and biomass growth, which will be referred to as Response groups. These different growth outcomes were expressed as means at one time point, absolute increments, or proportional to the initial values (for more details see Appendix S2 Table S2.1). Survival was expressed as proportion surviving or survival probability at the end of the experiments. Emergence was expressed as mean density emerged seedlings or as emergence percentage. In total, we extracted data on 9, 31 and 41 species for emergence, survival and growth, respectively.

Additionally, we collected a set of moderator variables from each paper. The moderators were selected because we hypothesised that they might explain heterogeneity in effect sizes, if observed. The overstorey strongly determines light, but also water and nutrient availability for understorey vegetation, including tree seedlings (Wagner et al., 2011). To characterise the overstorey conditions, we extracted percentage of full light transmitted by the canopy (measured as photosynthetic active radiation [PAR]) or gap size. Light conditions in our data covered a large range, from open (100% light transmittance) to closed forest conditions (3% of above overstorey light; Appendix S2 Table S2.3). Next, we collected data from the selected papers on multiple understorey characteristics expressing competitive stature such as biomass, light reduction by understorey vegetation at seedling (apex) height, understorey height and cover. When available, these measures of competitive stature were extracted for different plant species groups: graminoid, forb (including ferns), small shrub or mixed. In addition, we also extracted data on management related variables of interest such as fencing against herbivores (only under natural conditions), regeneration method (natural, seeded or planted) and seedling age at the start of the experiment and method of understorey removal. The removal methods were divided into mechanical (clipping, manual weeding or mowing), herbicide or combined mechanical/herbicide removal. Furthermore, duration of the experiment (expressed in growing seasons) and experimental environment where the experiment was carried out (forest, open/old field, controlled greenhouse conditions) were extracted to test effects of differences in experimental design. The mean values and ranges for the continuous variables used in our analyses are given in Appendix S2 Table 2.3.

We divided tree species into early-, mid- and late-successional species as a way to classify species into groups with similar characteristics and to generalise results across taxa (Appendix S4). We opted to use this classification because of its relevance for forest ecologists, modellers and forest managers (Bugmann, 1996; Leuschner & Meier, 2018). Additionally, we gathered values for the shade tolerance ranking for juvenile trees presented by Niinemets and Valladares (2006) and values for three commonly measured functional traits for adult individuals representing broad variation in plant growth strategies that are expected to relate to plant strategies, including the ability to compete with understorey vegetation: specific leaf area (SLA), wood density and seed mass (see Appendix S5 for more details).

2.3 Data analysis

We calculated log response ratios (RR) as a measure of effect size (Hedges, Gurevitch, & Curtis, 1999)**:**

$$RR = ln\left(\frac{Response_{without\ US}}{Response_{with\ US}}\right)$$

Response ratios were calculated between the mean response of a tree seedling species without understorey vegetation present (removal treatment or no vegetation addition) and the mean response of that species with understorey vegetation (vegetation addition or no removal). In a few cases no individuals survived, the ratios were calculated adding one to the number of individuals in each category for all observations (e.g. Maestre et al. 2005; Albert et al. 2015). Furthermore, we defined growth as conditional on survival, meaning that observations were not included where no seedlings in control or treatment plots survived, and growth was thus not measured. A positive response ratio (RR > 0) means that removal of understorey vegetation positively influences tree seedling performance, a negative response ratio (RR < 0) means a negative influence of understorey removal on tree seedling performance, and effect sizes close to zero (RR ≈ 0) indicate little or no effect. For the majority of the selected studies, no estimates of uncertainty (standard error, standard deviation, coefficient of variation or confidence intervals) were reported. Applying a conventional meta-analysis with weighting of the different observations by their variances was thus not possible on the full dataset here (Gurevitch, Koricheva, Nakagawa, & Stewart, 2018). We therefore applied unweighted Bayesian multilevel regression analysis on the full data, and performed conventional weighted meta-analysis on the subset for which variability was available as a sensitivity analysis.

2.3.1 Random-effects models

To test the overall effect of understorey removal and to obtain a mean pooled effect size for each response (research question 1), we fitted random-effects models in a Bayesian framework with crossed random effects (Fernández-Castilla et al., 2019) for Study ID and Species. For the growth response, multiple outcomes were included per Study ID, so we included a random effect for Outcomes. In this way, we accounted for the non-independencies of measurements within the same species, studies or outcomes. These models allowed us to estimate the variance between the different studies $\boldsymbol{\tau^2_{Study\ ID}}$, between different species $\boldsymbol{\tau^2_{Species}}$, as well as between outcomes $\boldsymbol{\tau^2_{Outcome}}$ (for the growth models). We report 95% credible (i.e. Bayesian confidence) intervals (CI); given the observed data, there is a 95% probability that the parameter is contained within a 95% CI. For mathematical details on the applied models using a Bayesian framework as well as specification of priors see Appendix S3. To increase interpretability, in the results (text), we back-transformed RR to percentage increase of responses to understorey removal.

2.3.2 Moderator and species analyses

To explain the heterogeneity between studies, we test the influence of potential moderators using mixed-effects models, with the same random-effects structure as described earlier (Nakagawa & Santos, 2012). The effects of moderator variables describing overstorey and understorey conditions (research question

3), and management related interventions (research question 4) were tested. We only did this for survival and growth; emergence had too few observations to allow further analyses explaining heterogeneity in response. We fitted a separate model for each moderator variable, as fitting one model with all moderators would restrict the data set to the relatively few studies that have values for all the moderators. Next, for both responses, we tried to explain heterogeneity between different species' responses by applying mixed-effects models using the successional grouping as fixed effects (research question 2). Growth was expressed as height, diameter, or biomass responses (Response groups). To account for the potentially different effect of the traits on these different aspects of growth, the models allowed the effects of the traits to differ between the three response groups. This means the models had two-way interactions for the successional grouping, and response group. Similarly, separate models were fitted for the three functional traits (SLA, seed mass and wood density) and the shade tolerance (see Appendix S5). All models were fitted with the probabilistic programming language Stan through the *brms* package in R (Bürkner, 2017; R Core Team, 2020). We found no strong evidence for publication bias based on both visual estimation of funnel plots and Egger's test (see Appendix S6).

3. Results

3.1 Random-effects models

The removal of understorey vegetation increased survival responses of seedlings by 70% (95% CI = [22, 135%]) and growth responses by 135% on average (95% credible interval = [43, 278%]) (Fig. 2A). Understorey vegetation removal increased seedling emergence on average by 23%, but credible intervals included zero (95% CI = [-56, 245%]) (Fig. 2A). Heterogeneity between Study IDs, Species and Outcomes was moderate to substantial for all responses; all τ values were on a similar scale of the data (RR) (Appendix S2 Table S2.2).

Seedling growth response varied between Outcomes (Fig. 2B). We found that biomass growth increased the most in response to understorey removal (Fig. 2B; Fig. 4). Diameter and height Outcomes increased on average but could also decrease or show no effect in response to understorey removal (Fig. 2B; Fig. 4). For both survival and growth responses, we found similar effects using the conventional weighted meta-analysis models on the subset of data for which sampling variances could be calculated (see Appendix S2 Fig. S2.1).

3.2 Moderator analyses

3.2.1 Species analyses

We found that species with different strategies responded differently to understorey removal. Early-successional tree species' survival and growth responded more strongly to removal than mid- and late-successional species (Fig. 3). For more details on the functional traits and shade tolerance results see Appendix S5.

3.2.2 Overstorey and understorey characteristics

The positive effect of understorey removal was stronger for both survival (log-linear relation) and growth responses with increasing overstorey light transmittance, i.e. more open overstoreys. Removing the understorey at low light conditions (10% transmittance), growth would increase by 59% (95% CI = [8, 133%]), whereas under full sun (100% transmittance), it would increase by 135% (95% CI = [59, 243%]). We found removing understoreys with a higher competitive stature, expressed in terms of understorey light reduction, biomass, cover or height, mainly resulted in increased seedling survival and growth responses (Fig. 4); except for survival, there were no effects of understorey biomass or cover. For instance, we found that removing an understoreys with biomass 200 g/m² or 400 g/m², representing a well-developed and a very dense understoreys in temperate forests respectively (Landuyt, Maes, et al., 2019), would result in a mean increase in growth of 110% (95% CI = [25, 248%]) and 151% (95% CI = [50, 319%]). For growth, no differences in responses were found to removal of different dominant understorey plant species groups, i.e. the amount of biomass removed had an effect, but the identity of what was removed did not. However, the understorey cover and/or biomass data was mainly provided by graminoids, which may confound these effects. Our results (Fig. 4) show no clear response of survival to removal of dominant graminoid vegetation, as the effect varied around zero. Only for forb-dominated vegetation we found a clear positive effect of removal on survival.

3.2.3 Management related moderators

Different understorey removal techniques yielded similar benefits for growth responses (Fig. 4). For survival, however, we found that combined mechanical and herbicide treatments could results in decreases in survival. We believe this is because the combined treatment was primarily applied in plots dominated by graminoids, thus confounding this effect (see previous section). Survival increases in planted seedlings in response to understorey removal were less marked (even slightly overlapping zero), and had less variation, compared to seeded or naturally established individuals (Fig. 4). Similar growth responses were found for seedlings using different regeneration methods, with marginally larger (yet more varied) responses of regeneration grown from seeds (Fig. 4). Older seedlings' growth benefitted less from removal, but survival was similar across seedlings with different ages at planting (Fig. 4). Fencing resulted in stronger growth responses, whereas survival responses to understorey removal were similar in fenced and unfenced plots (Fig. 4). Furthermore, we found no strong variation in growth or survival responses to understorey removal for the experimental design moderators, i.e. duration of the experiments and the experimental environment (Appendix S2 Fig. S2.2).

4. Discussion

Quantifying the effects of understorey removal on early life stages of tree regeneration and knowing under which conditions this is most opportune, is an important step in the development of management practices to successfully regenerate temperate forests. Our analysis synthesised current knowledge and quantified the effects of understorey removal on subsequent life stages of tree regeneration, i.e. emergence, survival and growth. Our results largely confirmed our expectations: (1) understorey vegetation removal positively influenced tree seedling survival and growth; (2) we found that early-successional tree species benefitted most from understorey removal; (3) removal effects were largest when removing more dense understorey vegetation and under more open canopy conditions; and, (4) we found that management options, e.g. choice of seedling age when planting or protection against browsers, influenced the response to understorey removal. Based on these findings, we discussed implications for forest managers.

4.1 Understorey removal predominantly results in increased seedling performance

Overall, seedling survival and growth benefitted from the removal of understorey vegetation. Our results show that even across different contexts and across temperate forest regions, the direction and even magnitude of survival and growth responses to understorey removal were quite similar. Positive responses for survival and growth were expected, as in temperate forests competition for resources will largely outweigh possible facilitative effects by understorey vegetation (Royo & Carson, 2006; Wright, Schnitzer, & Reich, 2014). In general, when resource availability to an individual seedling increases, e.g. when competition is reduced, it will likely fix more carbon and thus increase its growth. This is clearly shown in the highest response for biomass growth, and might also apply for height and diameter growth. Yet, for height and diameter growth, we found weaker and more variable responses to understorey removal. First of all, this weaker response may be because height and diameter growth trade off against each other under varying conditions and life stages in seedlings (e.g. Gaudio et al., 2011). Second, when removing vegetation, this might induce drought stress resulting in increased allocation of carbon into belowground organs to enhance belowground resource capture (Vandenberghe, Freléchoux, Gandallah, & Buttler, 2006). Third, plant size differences between individuals in communities can also be driven by asymmetric competition for light, resulting in increasing seedling height with increasing vegetation cover (e.g. Blondeel et al., 2020)¶. These mechanisms may explain the weaker and more variable responses of both height and diameter, compared to biomass growth.

Understorey removal showed no unidirectional effects on emergence of seedlings; emergence responses could increase or decrease in response to understorey removal. However, these findings are from a limited set of three studies that met our inclusion criteria. Studies that investigate effects of vegetation on tree seedling emergence are mostly focused on forest management. They study the effects of interventions to remove vegetation and prepare the seedbed, e.g. herbicide treatments or different degrees of mechanicals soil scarification from light harrowing to deep ploughing (e.g. Dassot & Collet, 2015; Löf et al., 1998). These studies, however, after applying their preparation treatment, allowed competing vegetation to invade the seedlings' surrounding again. They were thus not suited to sufficiently isolate the effect of vegetation on seedling emergence and not included in this study. More ecologically focused studies would be needed in the future to really determine the effects of surrounding understorey vegetation on tree seedling emergence.

4.2 Species respond differently to understorey removal

Species selection can be an important tool for forest managers, as choosing the right species for a certain context may preclude the need for vegetation management or may result in the largest benefits from understorey removal. Our results show that tree species that are linked to later stages in succession benefit less strongly from understorey removal than their mid- and early-successional counterparts. This was mainly consistent for both survival and biomass growth responses. We found that this effect is at least partly driven by the increase in shade tolerance of species appearing at later successional stages. These relations confirm that light, and competition for it, is a strong driver for the interactions between tree seedlings and understorey vegetation in temperate forests (Walters, Kruger, & Reich, 1993). The functional traits, i.e. SLA, wood density, seed mass, showed effects on seedling responses to understorey removal, but these effects were inconsistent between growth and survival responses (see Appendix S5). This suggests that these functional traits, which were gathered from literature and are generally measured for adult individuals (SLA and wood density), may not fully capture how juvenile trees will respond to environmental stresses (Gibert et al., 2016; Paine et al., 2015). Furthermore, the effects of single traits such as SLA might be mediated via other traits, such as wood density (e.g. Gibert et al., 2016).

The clearer effects of successional status and linked with it shade tolerance, compared to those of SLA, seed mass and wood density, are likely because these syndromes are more closely linked to how species can respond to disturbances or tolerate stresses, than single functional traits (Leuschner & Meier, 2018; Violle et al., 2007).

4.3 Understorey characteristics and management effects

The positive effect of understorey removal on regeneration increased when removing vegetation that reduced more light for seedlings, with higher biomass, cover and height, especially for growth. Denser understorey vegetation is expected to compete more strongly with seedlings, thus removal of more dense vegetation will result in more beneficial seedling responses (e.g. Gaudio et al. 2011). Removal of understoreys dominated by different plant species groups generally resulted in similar positive effects on seedling growth, whereas for survival, only removal of forb dominated vegetation (including ferns) showed a clear positive effect. However, when removing graminoid-dominated vegetation, survival could increase or even decrease. This could be due to the fact that graminoid mostly compete with seedlings for belowground resources (Bloor et al., 2008); so even if aboveground organs have been fully removed, belowground root competition could still be present. Alternatively, this might be because graminoid-dominated understoreys were mostly limited to open overstorey conditions (result not given). Under the presence of an understorey, growth might be reduced but survival may increase, as herbaceous vegetation can reduce frost damage, heat or desiccation stresses on tree seedlings (e.g. Berkowitz, Canham, & Kelly, 1995).

Furthermore, we found that survival and growth responses to understorey removal increased with overstorey openness. Under more open conditions, understorey vegetation will in general be more dense and competitive (De Lombaerde et al., 2019; Wagner et al., 2011). Seedlings will thus not only survive and grow better when the competition is removed, but due to higher light availability, they will be able to increase their performance. Under more closed canopy conditions, understorey vegetation may be less dense, or even when dense competing vegetation is present and removed, light availability may be lacking, thus precluding strong benefits (e.g. Pagès et al. 2003). Possibly, these mechanisms might also lead to differences in growth responses within the studied successional groups. Despite the large range in overstorey and understorey conditions present in our data, many studies have not reported in detail on these context variables, which precluded us a robust test for this. The fact that the total number of experimental studies on this topic with wide relevance to forest management is lower than expected, is an important outcome of our literature search as well. This then calls for new experimental work focusing on these aspects and reporting both overstorey and understorey density and composition in a more detailed manner.

We found that different methods for understorey removal, i.e. herbicides, mechanical/manual or combined application, as well as addition of understorey plants, yielded no differences in seedling responses. This shows that when different treatments are applied thoroughly, i.e. full removal with maintenance over the duration of the experiment, the effects are similar. Costs and time investments, but also changes in composition of regrown vegetation will differ between different removal treatments (Balandier et al., 2006). When fenced against large herbivores, seedling growth responses to understorey removal were larger. Understorey vegetation can act as a shelter or provide an alternate food source for herbivores (Perea & Gil, 2014; Walters et al., 2016); removal may thus lead to more damage and lower growth in unfenced areas. Alternatively, this can be because browsers reduce cover of competing understorey vegetation, reducing growth responses in unfenced conditions. This, however, is less likely as heavy browsing leads to depauperate understoreys with species that are unpalatable (due to mechanical or chemical defences) or tolerant (species able to quickly regrow) against browsing (Royo & Carson, 2006).

Our results showed that understorey removal benefitted seeded, planted or naturally established seedlings' survival and growth. The strength of this response was, however, smaller for survival response and varied less for growth response when applying artificial regeneration by planting. Responses of seeded or naturally regenerated individuals were more varied and when seeding, growth responses were larger. Furthermore, in general, planted seedlings' growth increased in response to understorey removal, but this response diminished with age at time of planting. This shows the vulnerability of seedlings in very early development stages to understorey competition. Once seedlings have a more developed root system and increase in height and start to escape competition for light, they are less susceptible to competition, primarily for light (Balandier et al., 2006; Kozlowski, 2002).

4.4 Management implications and research perspectives

Opening up forest canopies is a key tool for forest managers to initiate or stimulate natural regeneration of trees. This may lead to unwanted development of dense understorey vegetation composed of resource-acquisitive, tall plant species competing with regeneration (Wagner et al., 2011). The increase in understorey vegetation may become aggravated in the future, as at present closed canopies are buffering rising temperatures due to global warming (De Frenne et al., 2019) and understorey vegetation in high N deposition regions is gaining acquisitive species that possibly cause stronger negative effects on regenerating trees (Staude et al., 2020). This may increase the need for understorey removal to safeguard regeneration in the future. We showed that across temperate forest contexts understorey removal leads to overall positive survival and growth responses. Thrippleton et al. (2018) showed using vegetation modelling and simulation that understoreys with biomass of 200 g/m² are unlikely to halt regeneration, however, above a biomass of 400 g/m² inhibition for tree regeneration increases disproportionately; other empirical studies have found similar results (e.g. Standish et al. 2001). Our results showed that even removing an understorey with biomass 200 g/m² would result in a clear increase in growth of 110% on average and for 400 g/m² this will result on average in a growth increase of 151%. Furthermore, we showed that even under dense overstoreys at low light levels, removing understorey vegetation might result in worthwhile growth increases of 59% on average, and these growth effects increase with overstorey openness up to 135% at full light. When planting trees, our results on growth will be most important for managers, as survival responses are less affected by understorey removal. On the other hand, for natural regeneration or by seeding, results on survival as well as growth are important. Our results also show that removal of understorey vegetation will differently affect tree species with contrasting strategies. The grouping in successional types, i.e. early-, mid- and late-successional species, as well as ranking by shade tolerance, provided clear results for survival and biomass growth responses and an applied perspective for forest managers. For height and diameter growth responses, we only found weak relations with the different traits and syndromes, potentially due to the coarse nature of the used data. To investigate and detect relations for these responses, more controlled experiments, across standardised gradients in overstorey and understorey conditions are necessary. This would allow the study of potential interactive effects between different variables and, in this way, future research should attempt to pinpoint possible optimal light conditions for removal or determine under which conditions removal is unnecessary, and for which type of species this is possible.

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Authors' contributions

EDL, DL, LB, KV and MPP conceived the idea of this study. EDL, MPP and SM collected the data. EDL performed statistical analyses, with significant inputs from DL and LB. EDL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data available via the figshare https://doi.org/10.6084/m9.figshare.13042595.v1 (De Lombaerde et al., 2020).

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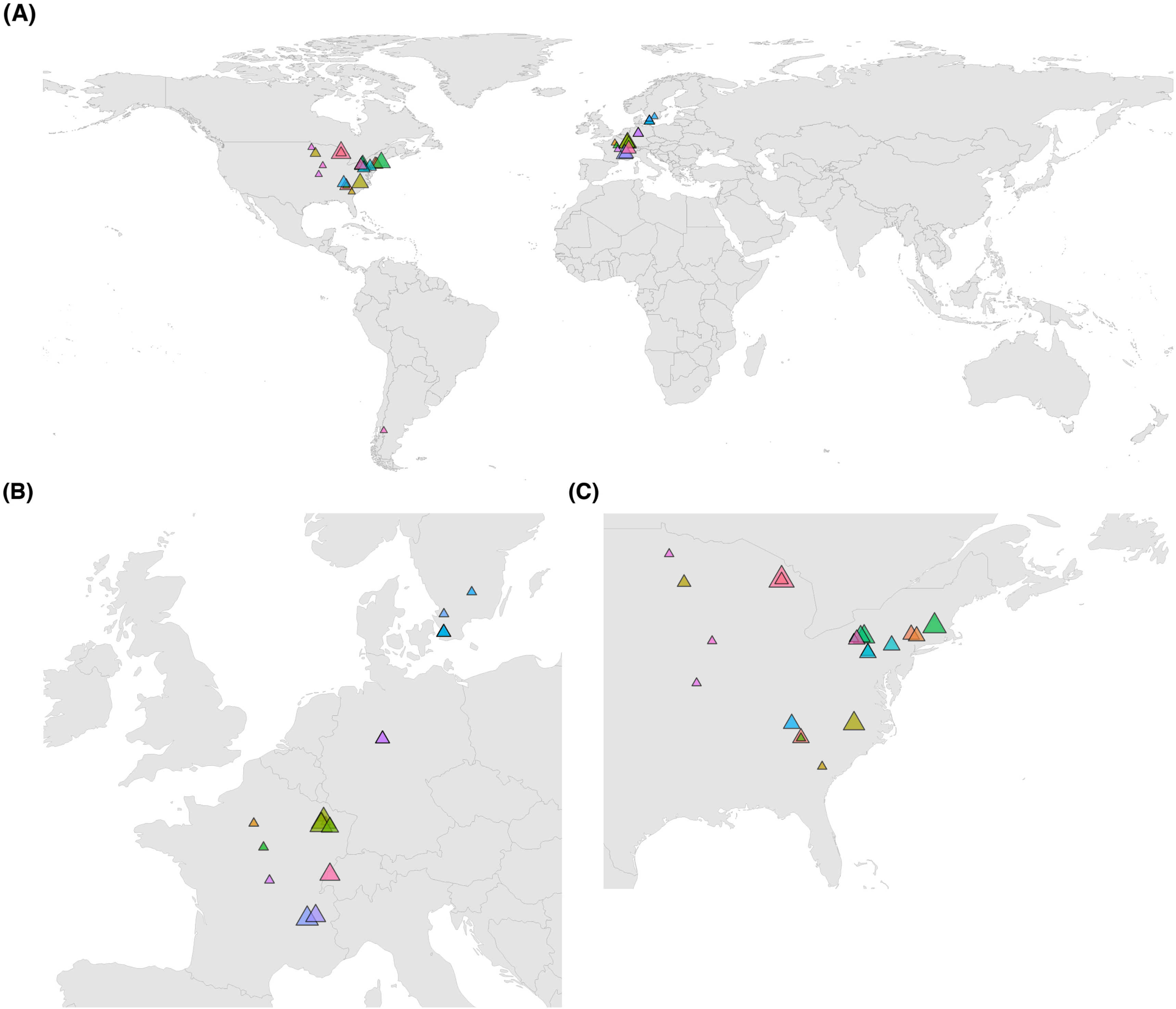
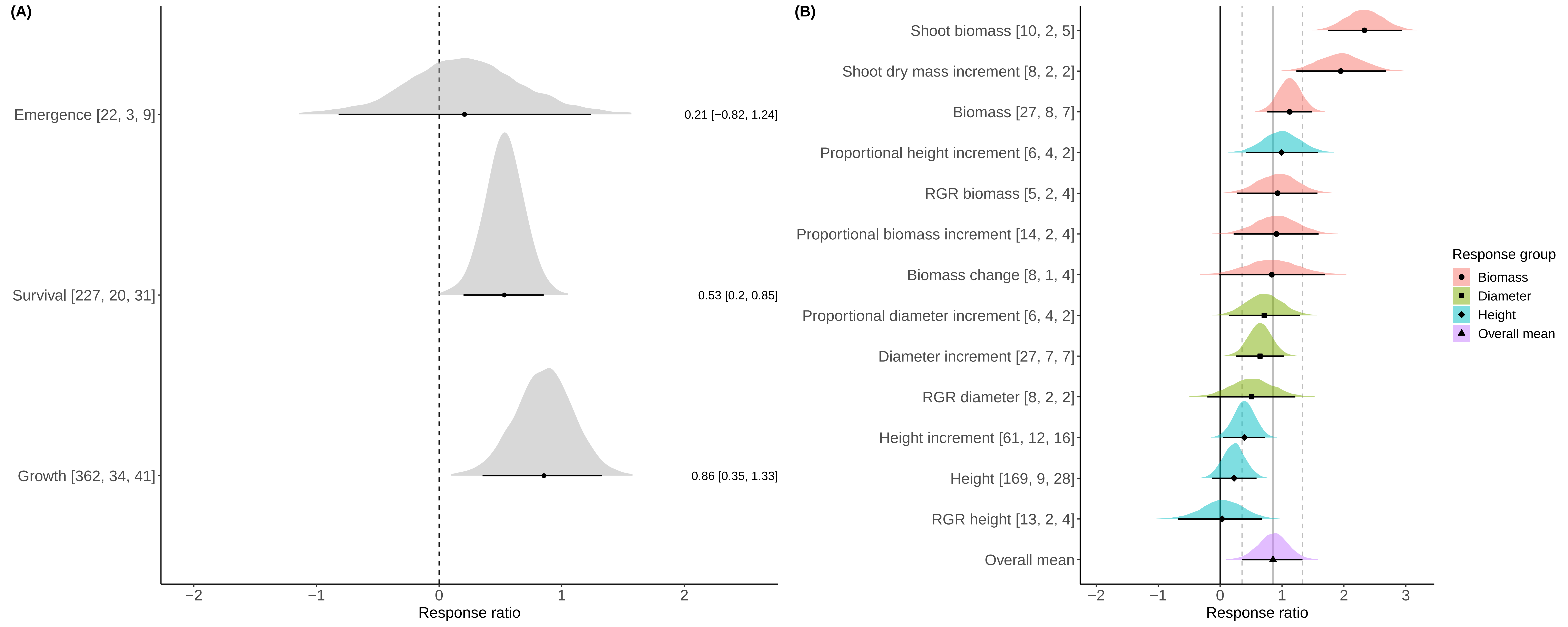
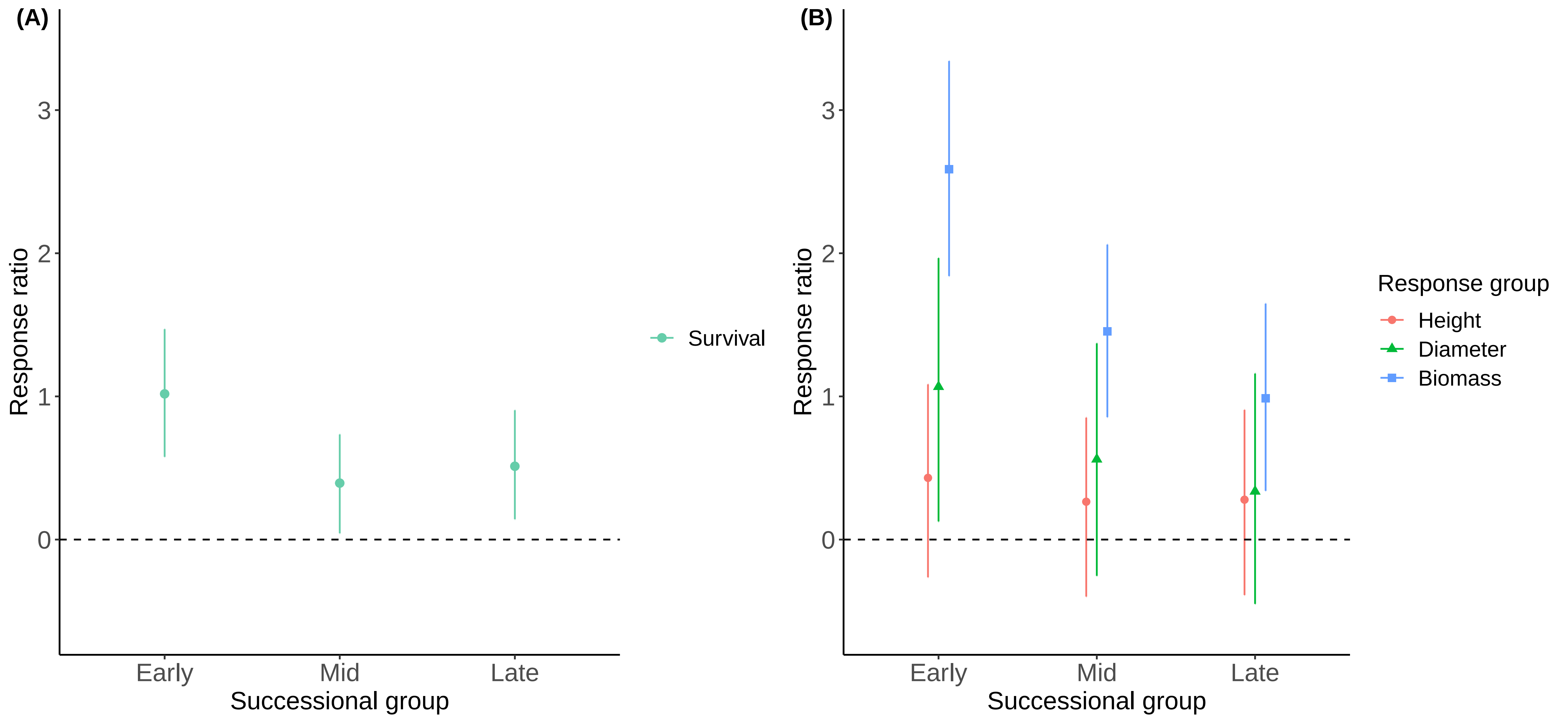
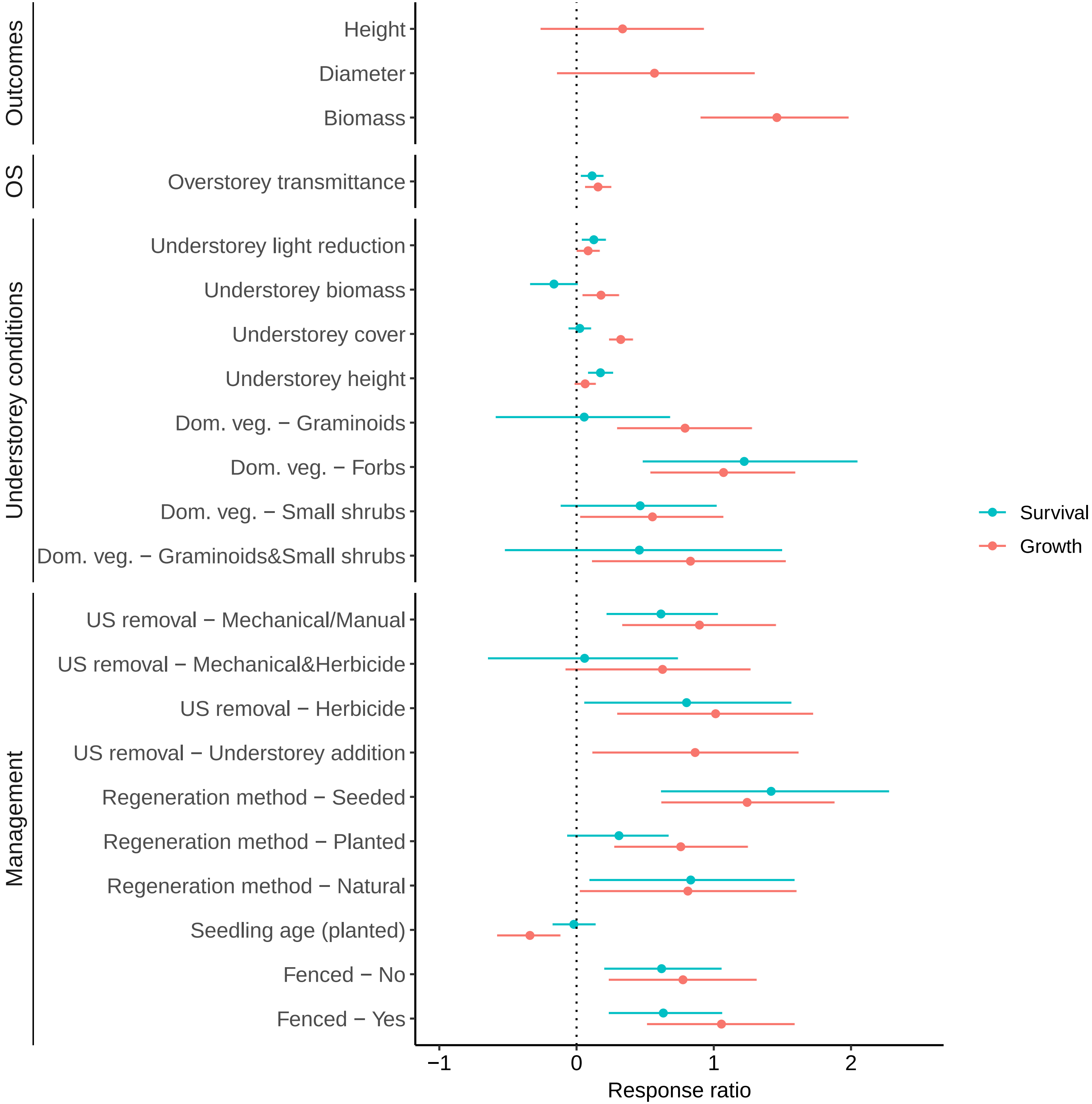

(A)
(B)
(C)


(A)
Emergence [22, 3, 9]
Survival [227, 20, 31]
Growth [362, 34, 41]
0.21 [−0.82, 1.24]
0.53 [0.2, 0.85]
0.86 [0.35, 1.33]
−2
−1
0
1
2
Response ratio
(B)
Shoot biomass [10, 2, 5]
Shoot dry mass increment [8, 2, 2]
Biomass [27, 8, 7]
Proportional height increment [6, 4, 2]
RGR biomass [5, 2, 4]
Proportional biomass increment [14, 2, 4]
Biomass change [8, 1, 4]
Proportional diameter increment [6, 4, 2]
Diameter increment [27, 7, 7]
RGR diameter [8, 2, 2]
Height increment [61, 12, 16]
Height [169, 9, 28]
RGR height [13, 2, 4]
Overall mean
−2
−1
0
1
2
3
Response ratio
Response group
Biomass
Diameter
Height
Overall mean


(A)
3
2
1
0
Response ratio
Early
Mid
Late
Successional group
Survival
(B)
3
2
1
0
Response ratio
Early
Mid
Late
Successional group
Response group
Height
Diameter
Biomass



Outcomes
Height
Diameter
Biomass
OS
Overstorey transmittance
Understorey conditions
Understorey light reduction
Understorey biomass
Understorey cover
Understorey height
Dom. veg. − Graminoids
Dom. veg. − Forbs
Dom. veg. − Small shrubs
Dom. veg. − Graminoids&Small shrubs
Management
US removal − Mechanical/Manual
US removal − Mechanical&Herbicide
US removal − Herbicide
US removal − Understorey addition
Regeneration method − Seeded
Regeneration method − Planted
Regeneration method − Natural
Seedling age (planted)
Fenced − No
Fenced − Yes
−1
0
1
2
Response ratio
Survival
Growth