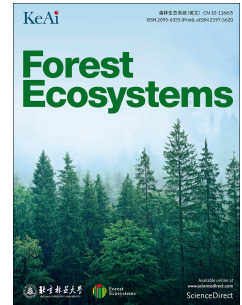


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Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance

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Abstract

Natural regeneration after disturbances is a key phase of forest development, which determines the trajectory of successional changes in tree species composition and diversity. Regenerating trees can originate from either seeds or sprouts produced by disturbed trees with sprouting ability. Although both regeneration strategies often develop and co-occur after a disturbance, they tend to affect forest development differently due to significant functional differences. However, the origin of tree regeneration is rarely distinguished in post-disturbance forest surveys and ecological studies, and the differential role of seed and sprout regeneration in forest productivity and diversity remain poorly understood. To address these research gaps, we explored the role of sprout and seed regeneration in the formation of woody species diversity and above-ground biomass (AGB) productivity in early-stage forest development. Data were collected in two experimental forest stands in the Czech Republic, where trees were cut with varying intensities with the density of residual (uncut) trees ranging from 0 to 275 trees per hectare. All trees were mapped and their sizes were measured before cutting and then, either as a stump with sprouts or a residual tree, remeasured 11 years later. In addition, all tree saplings were mapped and measured 11 years after logging, and their origin (sprout or seed) was identified. To assess abundances and productivity, we estimated AGB of all 2,685 sprouting stumps of 19 woody species and 504 generative (i.e., seed origin) individuals of 16 woody species, using allometric equations. Mixed-

effects models were used to analyze the effects of each regeneration strategy on woody species diversity and the total AGB under varying densities of residual trees. Nonmetric multidimensional scaling was used to evaluate the effect of regeneration strategies on species composition. AGB and diversity of sprouts were significantly higher than those of seed regeneration. Sprouts formed on average 97.1% of the total regeneration AGB in Hádý and 98.6% in Soběšice. The average species richness of sprouts was 4.7 in Hádý and 2.2 in Soběšice, while the species richness of seed regeneration averaged 2.1 and 1.1 in Hádý and Soběšice, respectively. Increasing density of residual trees reduced AGB and diversity of both sprouts and seed regeneration, but seed regeneration was affected to a greater extent. Residual trees had an especially strong inhibitory effect on the establishment of seed regeneration. Consequently, seed-originated saplings were nearly absent in plots with high residual tree density, and abundant sprouts accounted for most of the AGB and diversity. However, unlike sprouts whose species composition resembled that of the original stand, seed regeneration brought in new species, enriching the stand's overall species pool and beta diversity. Our results demonstrated differential roles of sprout and seed regeneration in the early stage of forest succession. Sprout regeneration was the main source of woody AGB productivity as well as species diversity, and its importance increased with the increasing density of standing mature trees. The results indicate the crucial yet previously underestimated role of sprout regeneration in post-disturbance forest dynamics. They suggest that the presence of residual mature trees, whether retained after partial cutting or undisturbed, can substantially suppress seed regeneration while the role of sprout regeneration in early succession becomes more distinctly evident.

Keywords

Resprouting, seeding, residual trees, tree diversity, above-ground biomass

1. INTRODUCTION

Post-disturbance natural regeneration is a critical initial stage of forest development (Frelich 2002). It plays a pivotal role in shaping the trajectory of forest recovery and determining the composition and structure of future stands (Chazdon and Guariguata, 2016). After disturbance, trees that are severely damaged either die and regenerate from seed (non-sprouters) or recover through resprouting (sprouters) (Bond and Midgley 2003). Sprouters can also produce seeds, but non-sprouters rely exclusively on seed production for

54 regeneration (Bond and Midgley, 2001; Fhemion and Steiner, 2008). The ability to resprout is common among
55 angiosperm tree species (Bond and Midgley 2003; Matula et al., 2012; Clarke et al., 2013), and has been
56 traditionally exploited in coppicing (Buckley, 2020).

57 Although sprouting and seeding are both important post-disturbance regeneration mechanisms, few studies
58 have explicitly examined their relative roles in the regrowth of disturbed forests. While some research has
59 looked at sprouting ability in certain tree species following disturbances, like fire or logging (Vesk and
60 Westoby 2004; Clarke et al., 2005; Matula et al., 2012), there has been little direct comparison of the
61 contribution of sprouts versus seeds to forest regeneration and development across different disturbance events
62 and forest types. The few studies that have attempted to study the relative contribution of generative and
63 vegetative regeneration to post-disturbance regrowth have often found strikingly different roles for these two
64 regeneration strategies in e.g., open woodlands in Africa (Ky-Dembele et al., 2007) and South America
65 (Svátek et al., 2018), Neotropical dry forests (Kennard et al., 2002), and Chinese temperate forests (Xue et al.,
66 2014; Li et al., 2022). However, such comparisons are largely lacking for European temperate forests, where
67 natural regeneration after logging remains a common forest practice.

68 Both regeneration strategies, sprouting and seeding, can be important for the persistence and continuity of
69 tree populations (Li et al., 2022). Because sprouters have the ability to regenerate from the existing root system
70 or stem of the damaged tree, they quickly reoccupy the growing space previously occupied by disturbed trees
71 and are less vulnerable to recruitment failure after severe disturbance compared to non-sprouters (Bond and
72 Midgley, 2001). However, some disturbed trees may fail to resprout after a disturbance event (Matula et al.,
73 2012). Also, sprouts are limited in their dispersal as they are spatially bound to the location of the original tree
74 (root collar and stem sprouts) and can spread only within the reach of the root system (Matula et al., 2019).
75 Therefore, the gaps between resprouting stumps can be colonized only by seed-origin regeneration (Howe and
76 Smallwood, 1982; Brokaw and Busing, 2000). Moreover, non-sprouters are better suited to colonize gaps
77 because their superior seed production, compared to sprouters, allow them to more efficiently disperse seeds
78 into gaps (Bond and Midgley 2003). Additionally, non-sprouters often form persistent seed banks, which can
79 store viable seeds over extended periods (Shiferaw et al., 2018, Tiebel et al., 2018).

80 The type of regeneration following disturbance has significant implications for tree species diversity in
81 recovering forests. Sprout regeneration produces new shoots of the same genetic individual, maintaining the
82 species composition of the preceding stand (Bond and Midgley, 2001; Del Tredici, 2001). In contrast, seed
83 regeneration enables both the persistence of species from the original stand as well as the introduction of new
84 species from external seed sources (Kammesheidt, 1998; Myers and Harms, 2009). As a result, seed
85 regeneration has the potential to both maintain and increase tree community diversity.

86 Both sprout and seed regeneration often co-exist after disturbances, each substantially contributes to newly
87 emerging tree regrowth (Matula et al., 2019). However, individuals originating from these two regeneration
88 strategies are likely to play differential roles in forest development, due to their distinct physiology
89 (Matoušková et al., 2022), resource storage capacities (Bellingham and Sparrow, 2000; Bond and Midgley,
90 2001), and growth dynamics (Matula et al., 2019). Trees of seed origin are typically single-stemmed and have
91 more stored carbon in their stems, allowing them to allocate more resources towards height growth (Midgley,
92 1996). Sprouters allocate considerable carbon belowground (Langley et al., 2002), and have much higher
93 starch levels than non-sprouters (Bond and Midgley, 2001), which allows them to persist through disturbances
94 and quickly resprout when above-ground tissues are destroyed (Bond and Midgley, 2003). In addition, after a
95 disturbance event, sprouters benefit from established large root systems, which provides better access to soil
96 resources (Clark and Hallgren, 2003; Atwood et al., 2011; Xue et al., 2014; Pietras et al., 2016; Stojanović et
97 al., 2017). Therefore, sprouters tend to dominate in less productive sites (Midgley, 1996; Ojeda, 1998;
98 Bellingham and Sparrow, 2000), while in productive environments, they are often overtopped by single-
99 stemmed seed regeneration (Midgley, 1996).

100 While sprouting and seeding represent two distinct regeneration strategies, many tree species exhibit a
101 mixed response, producing both sprouts and seeds following disturbance. The specific regeneration response
102 often depends on the severity, frequency and type of disturbance (Bellingham and Sparrow, 2000; Kennard et
103 al., 2002). For example, severe disturbances that destroy both the above- and below-ground tissues from which
104 a tree could sprout (e.g., high-intensity fire), may decrease the prevalence of sprouts (Kennard et al., 2002),
105 thus often leaving regeneration from seed as the only option. In contrast, intense disturbances that preserve

106 stumps, buds, and roots (e.g., coppicing and selective logging) may favor sprouting over seed regeneration
107 (Kvasnica et al., 2023) because many tree species have evolved vigorous sprouting abilities as an adaptation
108 to severe disturbances.

109 Silvicultural systems such as selective logging and coppicing, rely on the natural regeneration of a
110 disturbed stand. Both selective logging and coppice-with-standards systems can vary substantially in their
111 intensity, leaving certain parts of the stand uncut. After such anthropogenic disturbances, the emerging sprouts
112 and seedlings do not interact only with each other but also with the mature residual trees (standards). The
113 initial growth of sprouts is much faster than that of seedlings (Bond and Midgley, 2001; Dietze and Clark,
114 2008; Pietras et al., 2016). Therefore, sprouts are likely to be strong competitors for seed regeneration.
115 However, mature residual trees have been shown to limit the sprout development (Mejstřík et al., 2022),
116 primarily due to increased neighborhood competition for light (Matula et al., 2019). This interaction
117 potentially results in decreased competition between sprouts and seedlings, influencing the overall dynamics
118 of forest regeneration. In addition, the presence of residual trees provides a critical source of seed for natural
119 regeneration, contributing significantly to the composition and structure of the recovering stand (Norden et
120 al., 2009). In a long-term perspective, the influence of residual trees can shape the forest community, as they
121 can selectively favor species that are better adapted to local conditions and are more likely to withstand future
122 disturbances (Bergeron et al., 1999). Furthermore, their existence can also favor species richness and diversity
123 by creating a more heterogeneous environment, providing a range of microhabitats and resources necessary
124 for different species (Imai et al., 2012).

125 Tree seed ecology is a widely studied topic due to its significance in natural forest regeneration (Guariguata
126 and Pinard, 1998; Kitajima and Fenner, 2009; Yan et al., 2012; Kroschel et al., 2016). However, as a result of
127 climate change leading to more frequent and more severe droughts (IPCC, 2007), many tree species are
128 experiencing elevated mortality of seedlings (Engelbrecht et al., 2005, 2006; Browne et al., 2021). On the
129 other hand, the role of sprouting in early forest development, and its impact on biomass production, tree
130 species composition, and diversity of regrowing stands is not well understood. Moreover, the majority of prior
131 research on natural regeneration has predominantly focused on the initial few years after disturbance (Kennard

et al., 2002, Pang et al., 2011, Knapp et al., 2017, Zhang et al., 2018, Durr et al., 2019, Li et al., 2022), a phase that can be significantly impacted by high turnover rates, whereas studies considering established regeneration more than a decade after disturbance are rare (Swaim et al., 2016).

Quantifying woody biomass productivity of tree regrowth is critical for assessing both economic (e.g., the value of forest timber), and ecological characteristics (such as carbon storage) of newly emerging forests (Chave et al., 2005; Matula et al., 2015). Furthermore, studying the diversity of tree regeneration is essential for predicting forest development, since greater tree species diversity can positively impact forest growth (Chamagne et al., 2017) and ecosystem services, such as enhancing soil carbon storage and understory plant species richness (Gamfeldt et al., 2013). Given the differences in growth rates and diversity between sprouts and seedlings, exploring the relative post-disturbance roles of these two regeneration strategies could provide insight into mechanisms behind forest growth after disturbance.

In this study, we investigated woody biomass productivity and tree species diversity of both sprouts and seed regeneration in the two experimental temperate forests in the Czech Republic 11 years after logging disturbance. Specifically, we aimed to explore the early-stage above-ground biomass (AGB), tree species diversity, and composition of both regeneration strategies under a wide range of densities of residual trees. We asked the following questions: (1) How much do the seed regeneration and sprouts contribute to total AGB productivity and tree species diversity in the early development of temperate forests? (2) How are relative contributions of these two regeneration strategies to AGB productivity and regeneration diversity affected by increasing density of residual trees? (3) Do sprouts limit development of seed regeneration and vice versa? (4) Does the species composition of the regeneration from seed and sprout differ and how does the species composition of regrowth from sprout and seed origins compare to that of the original stand? We hypothesized that sprouts will contribute more to the early-stage stand biomass than seed-originated regeneration because of faster sprout growth in comparison with seedlings (Bond and Midgley, 2001). On the other hand, we expected seed regeneration to be the main source of woody plant diversity due to a potentially greater species pool, consisting of soil seed bank, residual trees as well as seed-source trees in the vicinity of the stand, while species pool for sprouting is limited to species present at the stand before disturbances. We

also predicted that the relative importance of seed regeneration in early-stage AGB productivity and tree species diversity would increase with higher densities of residual trees due to greater seed rain.

2. Materials and methods

2.1. Study site

The study was carried out in two experimental plots, Hády and Soběšice, located in the Training Forest Enterprise Křtiny of Mendel University in Brno, in the south-eastern Czech Republic (49°13'30" N, 16°40'55" E and 49°14'43" N, 16°35'59" E, respectively). Each plot was 4 ha (200 m × 200 m) and fenced due to high game pressure. The elevation is 401 m a.s.l. in Hády and 355 m a.s.l. in Soběšice. The average annual air temperature is 8.4 °C in both plots. The average temperature in January (the coldest month) is –2.1 °C and in July (the warmest month) is 18.4 °C, based on data from the nearest Brno weather station from 1960–2010 for both plots. The bedrock is formed by limestone in Hády and granodiorite in Soběšice. The soils are brown forest soils in Hády and cambisols in Soběšice, which are both highly productive for forestry. However, brown forest soils, characterized by their well-decomposed organic matter and rich nutrient content, often exhibit higher productivity compared to cambisols, which are younger, less developed soils with limited horizon differentiation (Weil and Brady, 2017).

Until the early 20th century, both plots were regularly managed coppices (Kadavý et al., 2011). However, coppicing was gradually abandoned and both forest stands were transformed into high forests. The dominant tree species in the Hády plot were sessile oak (*Quercus petraea* (Matt.) Liebl.), small-leaved lime (*Tilia cordata* Mill.), European hornbeam (*Carpinus betulus* L.), and field maple (*Acer campestre* L.), while the Soběšice plot was dominated by sessile oak (95% of all individuals). For detailed characteristics of both stands see Table S1.

2.2. Data collection

In the winter of 2008–2009 in Hády and 2009–2010 in Soběšice, most trees were cut down and removed (2,236 trees, i.e., 83% of the original stand density in Hády, and 2,453 (86%) in Soběšice). Before logging, all trees with a diameter at breast height (DBH) ≥ 7 cm were measured and identified to the species level, and

183 their spatial positions were recorded using the ground-based laser field-map technology (HLEK, Ltd., Jilové
184 u Prahy, Czech Republic). Each plot was divided into 16 subsquares (50 × 50 m each). To study the effect of
185 residual standing trees on tree regeneration, four subsquares in each plot were subjected to clearcutting while
186 in the remaining 12 subsquares, mature trees with varying densities were left uncut and served as residual
187 trees. The densities of residual trees used were 20 (1.1 m² in basal area, BA), 35 (1.8 m² BA), and 50 (2.5 m²
188 BA) trees per plot. Each density was replicated in four subsquares, which were distributed evenly throughout
189 plots to avoid adjacent subsquares with the same density. The residual trees averaged 25.6 cm in DBH and
190 18.0 m in height. In total 450 trees in Hády and 412 in Soběšice remained uncut as residual trees. The residual
191 trees in Hády were mostly sessile oak (394 trees), wild service tree (*Sorbus torminalis* (L.) Crantz; 94 trees),
192 and field maple (10 trees). The residual trees in Soběšice were all sessile oak.

193 In 2020–2021, 11 complete growing seasons after harvesting, all stumps of the cut trees were checked
194 for live sprouts. For stumps with sprouts, the DBH of three thickest sprouts on each resprouting stump was
195 measured. This method proved to be an accurate indicator for estimating the total sprout AGB of individual
196 sprouters as well as the populations of sprouters (Matula et al., 2015; Šrámek et al., 2020). Moreover, all
197 individuals of seed regeneration with DBH ≥ 5 cm and all new sprouting stumps (with pre-logging DBH < 7
198 cm) with at least one sprout with DBH ≥ 5 cm were also measured, identified to the species level, and their
199 positions were mapped using the Field-Map technology. For new trees, we set the DBH threshold at 5 cm
200 because it was the minimum size of individuals reaching the newly established, dense canopy typical of this
201 stage of forest development. Individuals with DBH less than 5 cm were much less abundant and suppressed
202 under the dense crowns and were not expected to significantly contribute to the newly formed canopy.

203 **2.3. Data analysis**

204 **2.3.1. AGB estimations**

205 To assess productivity and abundance of regrowth of sprout and seed origin, we estimated AGB for each
206 sapling and resprouting tree. Because resprouting trees (stumps) were multi-stemmed while saplings of seed
207 origin were mostly single-stemmed, we used different methods for the AGB estimation. AGB of sprouts from
208 each resprouting tree was estimated using allometric equations previously developed for this purpose at the

209 same study sites (Matula et al., 2015). As a predictor variable in allometric equations, we used mean DBH of
210 the three thickest sprouts per stump, which has previously proved to be an accurate predictor of total AGB of
211 sprouts per stump (Matula et al., 2015; Šrámek et al., 2020, 2023). To estimate AGB of individuals of seed
212 origin, we used species-specific allometric equations from Forrester et al., (2017), using DBH of each
213 individual as predictor variable. In total, AGB (stem and branches) was estimated for 1,496 resprouting trees
214 of 16 species in Hády and 1,188 resprouting trees of 9 species in Soběšice, and for 502 seed-originated
215 individuals of 14 species in Hády and 118 seed-originated individuals of 8 species in Soběšice (Table S2). To
216 account for spatial variability and irregularities in the distribution of residual trees, each of the 50×50 m
217 subsquares was uniformly divided into four smaller subplots (20×20 m) with a five-meter belt around each
218 subplot to ensure spatial separation. For each subplot, we determined several variables: the density of residual
219 trees, the density of sprouting stumps, and the density of seed regeneration. Additionally, we calculated the
220 total AGB of sprouts and the total AGB of seed regeneration. This was done by summing the AGBs of sprouts
221 and seed origin individuals, respectively.

222 To find out how residual trees affect sprout and seed regeneration, we modelled AGB and density of
223 sprouts and AGB and density of seed regeneration as a function of density of residual trees. To test the effect
224 of sprout regeneration on seed regeneration, we also created models with either AGB or density or occurrence
225 of seed regeneration as response variable and AGB of sprout regeneration as explanatory variable. We also
226 ran another set of models with either AGB or density or occurrence of sprouts used as a response variable and
227 AGB of seed regeneration as explanatory variable. We also used the density of stumps with live sprouts as a
228 predictor for sprout AGB, because it was previously shown to have a positive effect on total sprout AGB
229 (Mejstřík et al., 2022). Since plots have different environmental conditions, cutting history, structure and
230 species composition, we conducted all analyses separately for each plot. To account for autocorrelation among
231 subplots nested in subsquares, we used mixed-effects models in which the explanatory variables were defined
232 as fixed-effect variables and subsquare identity as random effect with varying intercepts. Linear mixed-effects
233 models were utilized for testing the effects on AGB of sprouts and AGB of seed origin individuals (i.e.
234 response variables). We used generalized mixed-effects models with Poisson error distribution for testing the
235 effects on density of regeneration of sprout and seed origin. To model the occurrence of sprout and seed

236 regeneration, we used generalized mixed-effect models with binomial error distribution, in which either sprout
237 or seed regeneration occurrence in subsquare (1 - present/0 - absent) was modelled as a function of the density
238 of residual trees and sprout AGB. Because of multicollinearity detected in the models including both density
239 of residual trees and AGB of sprouts and density of residual trees and AGB of seed regeneration, we did not
240 use these variables together in one model but created separate models with each of the explanatory and
241 response variables. The explanatory variables in the models with occurrence and density were standardized to
242 zero mean and unit variance to make their model estimates directly comparable. All analyses were performed
243 in R software (R Core Team, 2022) using the 'lme4' package (Bates et al., 2015) for linear mixed-effects
244 models.

245 2.3.2. Diversity

246 We calculated the number of species (richness) and Shannon H' index (diversity) for all woody
247 regeneration together (total richness) and separately for sprout regeneration and seed regeneration in each
248 subplot. Shannon H' index was calculated based on the number of individuals of each woody species using
249 the 'diversity' function of the 'vegan' package (Oksanen et al., 2016).

250 We also calculated beta diversity, which is a measure of the variability in species composition among
251 sampling units for a given area. Beta diversity was computed for each regeneration strategy as well as for the
252 original pre-logging stand by calculating the average distance from each individual subplot to the group
253 centroid defined in the principal coordinate space of the dissimilarity measure (Anderson, 2006; Anderson et
254 al., 2006). The calculation was performed with the Bray-Curtis index as the measure of dissimilarity using the
255 'betadisper' function of the 'vegan' package (Oksanen et al., 2016). To test for differences between different
256 strategies of regeneration, a pairwise permutation test provided by 'betadisper' was performed.

257 To explore how residual trees and regeneration abundance affect the diversity of each of the regeneration
258 strategies, we modelled richness and diversity as a function of the density of residual trees, sprout AGB (for
259 seed regeneration only), and seed regeneration AGB (for sprout regeneration only). For diversity as the
260 response variable, we used linear mixed-effect models. For richness, generalized mixed-effect models with
261 Poisson error distribution were performed. Subsquare identity was used as a random intercept effect in the

models. Because of multicollinearity, we ran models separately for each combination of explanatory and response variables (i.e. only models with one fixed-effect variable). We also calculated the ratio of seed-origin richness to total richness and sprout richness to total richness to explore the trend of relative contribution of each regeneration strategy to total regeneration with changing density of residual trees. To demonstrate this relationship, we used locally estimated scatterplot smoothing (LOESS).

2.3.3. Species composition and beta diversity

To test for differences between species composition of original stand and regrowth of sprout and seed origin, we used non-metric multidimensional scaling ordination (NMDS) with the Bray-Curtis index as the measure of dissimilarity using the ‘vegan’ package (Oksanen et al., 2016). To estimate difference in the species composition of different regeneration type as well as to compare it to original species composition before tree cutting, we fitted seed origin (as a categorical variable) into the results of NMDS using the function ‘ennvfit’, which also calculated statistical significance using permutation test. To compare species composition between regeneration categories, we used permutational multivariate analysis of variance using the Bray-Curtis index (function ‘adonis’). Multivariate homogeneity of group dispersions as a measure of beta diversity (Anderson et al., 2006; Anderson-Teixeira et al., 2013) was calculated for each of the regrowth strategy and original stand and the difference between the groups were tested using Tukey’s HSD post-hoc test.

3. RESULTS

3.1. Above-ground biomass

Sprouts represented the predominant proportion of the total above-ground biomass (AGB) in natural tree regrowth, with an average of 97.1% in Hádý and 98.6% in Sobešice. Seed-origin regeneration was much less abundant, contributing only 2.9% to the total AGB in Hádý and 1.4% in Sobešice (Table S3).

Sprout AGB on both plots decreased as the density of residual trees increased (Hádý: $t = -5.28$, $P < 0.001$; Sobešice: $t = -5.57$, $P < 0.001$; Fig. 1). The density of residual trees affected negatively AGB of seed regeneration in Hádý ($t = -4.68$, $P < 0.001$) but did not influence the AGB of seed regeneration in Sobešice significantly ($t = -1.39$, $P = 0.135$; Fig. 1).

287 sprouts were present in all subplots, while seed regeneration was absent in many subplots (41% and 47%
288 of all subplots in Hádý and Soběšice, respectively). The presence of seed regeneration was affected negatively
289 by the density of residual trees ($P < 0.001$; Fig. 2) but positively by increasing sprout AGB ($P < 0.010$, Fig.
290 2). The density of seed regeneration declined with increasing density of residual trees in Hádý ($P < 0.001$, Fig.
291 2), but not in Soběšice ($P = 0.080$; Fig. 2). Density of seed regeneration was positively affected by sprout
292 AGB, but the effect was significant only in Hádý ($P = 0.044$; Fig. 2).

293 Sprout AGB increased with increasing density of sprouting stumps (Hádý: regression coefficient = 0.039
294 ± 0.003 , $t = 11.48$, $P < 0.001$; Soběšice: regression coefficient = 0.064 ± 0.011 , $t = 5.84$, $P < 0.001$) but was
295 not affected by the AGB or density of seed regeneration ($P > 0.059$).

296 297 3.2. Diversity

298 In total, we recorded 19 and 11 species of natural tree regeneration in Hádý and in Soběšice, respectively.
299 Sprouts accounted for 16 and 10 species, while 14 and 8 species originated from seed, in Hádý and Soběšice,
300 respectively (Table S2). The diversity and richness of sprout regeneration were higher than the diversity and
301 richness of seed regeneration ($P < 0.001$; Table S4). The total diversity and richness of all regeneration were
302 higher than that of the original pre-logging stand ($P < 0.05$; Table S4).

303 The diversity of sprouts was not significantly affected by residual trees ($P > 0.060$), while the diversity
304 of seed regeneration declined steeply with increasing density of residual trees ($P < 0.001$; Fig. 3). Sprout AGB
305 had a positive effect on diversity of seed regeneration ($P < 0.001$; Fig. 3). Sprout regeneration accounted for
306 the majority of total richness, and its proportion even increased with a higher density of residual trees (Fig.
307 4). The proportion of seed regeneration in total richness was approximately 50% in clearcuts but decreased
308 significantly to near-zero values with increasing density of residual trees (Fig. 4). The diversity of seed
309 regeneration increased with increasing sprout AGB ($P < 0.006$; Fig. 3). The diversity of sprouts was not
310 affected by seed regeneration AGB ($P > 0.250$).

Both sprout and seed regeneration had higher beta diversity than the original stand ($P < 0.001$), but seed regeneration had significantly higher beta diversity than sprout regeneration ($P < 0.001$; Fig. 5).

3.3. Species composition

The species composition of sprout and seed regeneration differed significantly (Hády: $R^2 = 0.22$, $P < 0.001$; Soběšice: $R^2 = 0.38$, $P < 0.001$), and both differed from the species composition of original pre-logging stand ($P < 0.001$; Fig. 5). The difference between the composition of sprout regeneration and the original stand was smaller (Hády: $R^2 = 0.18$, $P < 0.001$; Soběšice: $R^2 = 0.20$, $P < 0.001$) than the difference between the composition of seed regeneration and the original stand (Hády: $R^2 = 0.28$, $P < 0.001$; Soběšice: $R^2 = 0.42$, $P < 0.001$; Fig. 6).

4. DISCUSSION

Our study examined both sprout and seed regeneration 11 years after disturbance, a sufficient duration for established natural regeneration to develop (Harvey et al., 2016; Stevens-Rumann et al., 2018; Kuehne et al., 2020; Demeter et al., 2021). By evaluating regeneration in relation to forest structure, our findings provide new insights into the complex post-disturbance interactions between sprouting, seeding, and residual stand. As we hypothesized, sprouts contributed more to the early-stage stand biomass than seed-originated regeneration. Moreover, contrary to our expectations, sprouts were also the primary source of woody plant diversity, as seed regeneration was suppressed by residual trees even more than sprouts. On the other hand, seed regeneration introduced new species which is not present in the original stand, thereby enhancing beta diversity and genetic diversity of the emerging forest. Overall, the results reveal the complementary yet distinct contributions of sprouting and seeding to early forest development following logging disturbance.

Density of residual trees negatively affected sprout AGB, which is consistent with previous studies (Joys et al., 2004; Mejstřík et al., 2022). However, contrary to our expectations, seed regeneration did not increase with residual tree density. We predicted higher seedling abundance in subplots with more residual trees due to lower competition from sprouts (Mejstřík et al., 2022) and greater seed input, since most seeds fall near parent trees (Clark et al., 1999; McEuen and Curran, 2004). Surprisingly, seed regeneration was suppressed by residual trees even more than sprouts, with most seed regeneration occurring in subplots lacking

338 residual trees. Moreover, fast-growing pioneer species like birch (*Betula pendula* Roth.), European aspen
339 (*Populus tremula* L.), willow (*Salix caprea* L.), and cherry (*Prunus avium* (L.) L.) dominated seed
340 regeneration, while seedlings of sessile oak (*Quercus petraea* (Matt.) Liebl.), the main residual tree species,
341 were rare. This likely reflects the shade intolerance of oak seedlings (Leuschner and Meier, 2018), and their
342 poor performance under closed canopies compared to sprouts and other faster-growing seedlings.
343 Additionally, residual oak trees may negatively affect the survival of conspecific seedlings due to increased
344 herbivory and pathogens (Janzen, 1970; Connell, 1971). Given that seedling growth is often limited by light
345 availability (Coomes and Allen, 2007; Wyckoff and Clark, 2005), residual tree density was probably too high
346 for oak seedling persistence in many subplots. Thus, for oak to regenerate after disturbance, sprouting was
347 crucial. More shade-tolerant species like European hornbeam (*Carpinus betulus* L.), small-leaved lime (*Tilia*
348 *cordata* Mill.) and field maple (*Acer campestre* L.) appeared in both sprout and seed regeneration but sprouting
349 dominated. In summary, counter to expectations, seedlings did not benefit from residual trees and instead
350 suffered from negative density-dependent effects, likely reflecting interactions between shade tolerance,
351 growth rates and stand density.

352 The negative effect of residual tree density on AGB of seed regeneration was significant only in Hádý.
353 This can be possibly attributed to differences in species composition and diversity of the forest stands
354 surrounding our study plots. In Soběšice, the surrounding stands are mostly monospecific sessile oak forests,
355 whereas the forest stands around the Hádý study plot are much more diverse. This greater diversity around
356 Hádý may have provided a richer seed source from various species not originally present, which could have
357 more effectively occupied available niches in areas with lower densities of residual trees. In contrast, Soběšice,
358 surrounded primarily by sessile oak stands, had a limited seed source from other species. This, together with
359 suppression of oak seedlings, resulted in much less seed regeneration across the entire plot (168 seed-origin
360 individuals in Soběšice, compared to 709 in Hádý), regardless of the density of standards. Additionally, the
361 differing microclimatic and soil conditions between Hádý and Soběšice could play a role. The brown forest
362 soils in Hádý have more nutrients and support higher productivity than the cambisols in Soběšice, which can
363 possibly lead to less competition for soil resources and greater potential for successful establishment of new
364 seed regeneration.

365 As expected, seed regeneration did not affect sprout growth. Surprisingly, however, sprouts did not
366 compete with seed regeneration either. In fact, sprouts had a positive effect on the occurrence of seed
367 regeneration on both plots, and also increased the density of seed regeneration in Hádý. This allowed both
368 regeneration strategies to co-exist without significant competition, resulting in an overall increase in AGB
369 production at the stand level. Seed regeneration could potentially benefit from the partial shading provided by
370 the initially faster-growing sprouts, which served as an early canopy cover, thereby moderating microclimate
371 temperatures and moisture levels after disturbance (Aussenac, 2003). Moreover, the initial rapid growth of
372 sprouts enables them to quickly exploit available spaces, and seed regeneration may thus be more likely to
373 occur in niches where sprouts have not yet established themselves or are unable to thrive. Another possible
374 reason for this lack of competition is that sprouts have already established extensive root systems inherited
375 from their parent trees, enabling access to deeper soil water and nutrients (Clark and Hallgren, 2003; Atwood
376 et al., 2011; Xue et al., 2014; Pietras et al., 2016; Stojanović et al., 2017). This deeper resource acquisition
377 potentially leaves the surface soil layers more available for the shallower, less-established root systems of
378 seed regeneration. In addition, sprouting stumps may release water from deeper soil layers into the upper soil
379 via hydraulic lift, providing access to this water source for shallow-rooted seedlings (Caldwell and Richards,
380 1989). While this mechanism has often been observed in arid or Mediterranean climates (Espeleta et al., 2004;
381 Peñuelas and Fillela, 2003), it is also documented for sessile oak in temperate forests (Zapater et al., 2011).
382 Furthermore, hydraulic lift facilitates favourable biogeochemical conditions near the surface by improving
383 microbial activity, nutrient availability, and root nutrient uptake (Caldwell et al., 1998). However, to fully
384 understand these dynamics, additional studies on belowground interactions of sprout and seed regeneration
385 with residual trees are needed.

386 The species diversity and richness of sprout regeneration were much higher than that of seed regeneration,
387 making sprouts the major source of tree diversity on both plots (Table S4). This is likely tied to the resilience
388 of mature trees, which can readily resprout after disturbance, thus maintaining the original stand's diversity
389 (Bond and Midgley, 2001). Therefore, the composition of sprout regeneration more closely resembled the
390 original stand compared to seed regeneration. Conversely, the composition of seed regeneration diverged more
391 from the original stand possibly due to changing seed dispersal trends after disturbance (Calviño-Cancela,

2002). Interestingly, while residual trees had no significant impact on sprout occurrence and diversity, increased density of residual trees corresponded sharply with declining diversity of seed regeneration. This aligns with a study showing that high residual tree density can potentially restrict light availability and hinder seed regeneration (Gray et al., 2002). Overall, sprouting played a major role in maintaining stand species composition and diversity.

In contrast to sprouting, seed regeneration did not significantly contribute to the regeneration of original species but rather introduced new species (birch, European aspen and willow in Hádý and European aspen in Soběšice, Table S2), increasing the overall species pool and beta diversity. The beta diversity of seed regeneration was much higher than that of sprout regeneration. However, the combined beta diversity of both regeneration strategies was higher than the original stand diversity, which is consistent with findings that disturbance often positively impacts beta diversity (Silva Pedro et al., 2016). Thus, while sprouting promotes high alpha diversity within communities, it limits opportunities for new species establishment, resulting in lower beta diversity between communities. In contrast, seed regeneration introduces genetically distinct individuals possibly representing species not present in the previous stand, thereby contributing to increased beta diversity (Török et al., 2018). This disturbance-diversity relationship is modulated by multiple factors such as disturbance severity, life-history traits, and the available species pool (Miller et al., 2012; Silva Pedro et al., 2016). The positive effect of disturbance on tree species diversity tends to be greater in stands with larger species pools and higher disturbance intensities (Silva Pedro et al., 2016). Moreover, in early succession, incorporating pioneer species into stands containing primarily intermediate or late-successional species (e.g., sessile oak) can strongly facilitate diversity-driven gains in stand productivity (Silva Pedro et al., 2016).

5. Management implications

Our study underlines the importance of employing strategic tree retention levels to optimize the balance between sprout and seed regeneration in post-logging forest recovery. To enhance biomass productivity and maintain biodiversity, forest managers should aim for tree retention patterns that avoid both extremes of too high or too low densities. Specifically, low to intermediate residual tree densities facilitate sprout regeneration effectively, while still permitting enough light for seed regeneration. Additionally, the findings of this study

suggest the value of promoting sprout-associated biomass as it positively impacts the diversity of seed-origin regrowth. However, although sprouts are a good source of woody biomass and help maintain woody plant diversity, in greater abundance, they suppress the development of the herbaceous layer, negatively affecting its diversity (Matula et al., 2020). Therefore, maintaining higher densities of residual trees may be a convenient way to limit sprout growth in areas with high conservation value.

6. Conclusions

This study provides novel insights into the relative roles of sprout and seed regeneration in early forest development following logging disturbance. Sprout regeneration, although often overlooked compared to seed regeneration, can serve as the primary driver of AGB and within-community diversity across sites, maintaining it even under higher densities of residual trees, which limit seedlings' establishment. In contrast, seed regeneration introduces new species to the stand despite being less abundant. Moreover, both regeneration strategies seem to use different resources and coexist without significant competition, increasing overall AGB production and carbon storage of the whole forest stand. These results demonstrate the differential but important roles of both seed and sprout regeneration in the early stages of forest diversity recovery and post-disturbance development. The study's implications extend to forest management strategies, emphasizing the need for a balanced approach. While residual trees provide habitat heterogeneity, nesting opportunities, and aesthetic values, our results indicate a trade-off between residual tree retention and seed regeneration abundance and diversity. Low retention that favors seedlings may boost compositional diversity, while high retention, which favors sprouts, may accelerate biomass recovery but limit diversity. Sprouting appears important for retaining existing diversity from the pre-disturbance community. Seeding enables new species to colonize, but these opportunities decline sharply with residual tree retention. A mix of both regeneration strategies may be ideal for balancing continuity and change in species composition. Given the importance of forest recovery for climate change mitigation, optimizing natural regeneration offers a cost-effective approach to enhance carbon sequestration while conserving biodiversity.

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Conflict of interest

The authors declare no conflict of interest.

Authors' contributions

Marek Mejstřík: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft.

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Data Availability

Data is available from the corresponding author upon reasonable request.

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Figures captions

Fig. 1. Total above-ground biomass (AGB) of sprouts and seed-origin regrowth 11 years after logging in Hádý and Soběšice in relation to the density of residual trees. Points represent observations, solid lines represent fitted models with $P < 0.05$ while dashed lines indicate fitted models with $P > 0.05$. 95% confidence intervals are shown for models with $P < 0.05$.

Fig. 2. Model estimates (points) and confidence intervals (lines) of the effects of density of residual trees and sprout biomass on presence and density of seed-origin regrowth 11 years after logging. Filled symbols indicate model estimates significantly different from zero.

Fig. 3. Mean Shannon H' diversity index of seed regeneration 11 years after logging in relation to the density of residual trees and sprout biomass. Points represent subplots, lines represent fitted linear mixed effect models ($P < 0.05$) with 95% confidence intervals.

Fig. 4. Proportion of species richness of sprouts and seed regrowth 11 years after logging in relation to the density of residual trees in Hádý and Soběšice. Blue line represents the fitted LOESS model, dots indicate means for a given number of residual trees and the vertical lines represent 95% confidence intervals (omitted for means based on ≤ 2 data points).

Fig. 5. Beta diversity of tree community expressed as multivariate dispersion based on Bray-Curtis dissimilarities within the original pre-logging stand, sprout, and seed-origin regrowth 11 years after logging in Hádý and Soběšice.

Fig. 6. Nonmetric multidimensional scaling of the species composition of the original pre-logging stand, sprout, and seed-origin regrowth 11 years after logging in Hádý and Soběšice. Points represent subplots for each type of regrowth and the points with which they connect represent their centroids. The lines denote the boundaries of clusters of plots belonging to the same treatment.

Fig. 1

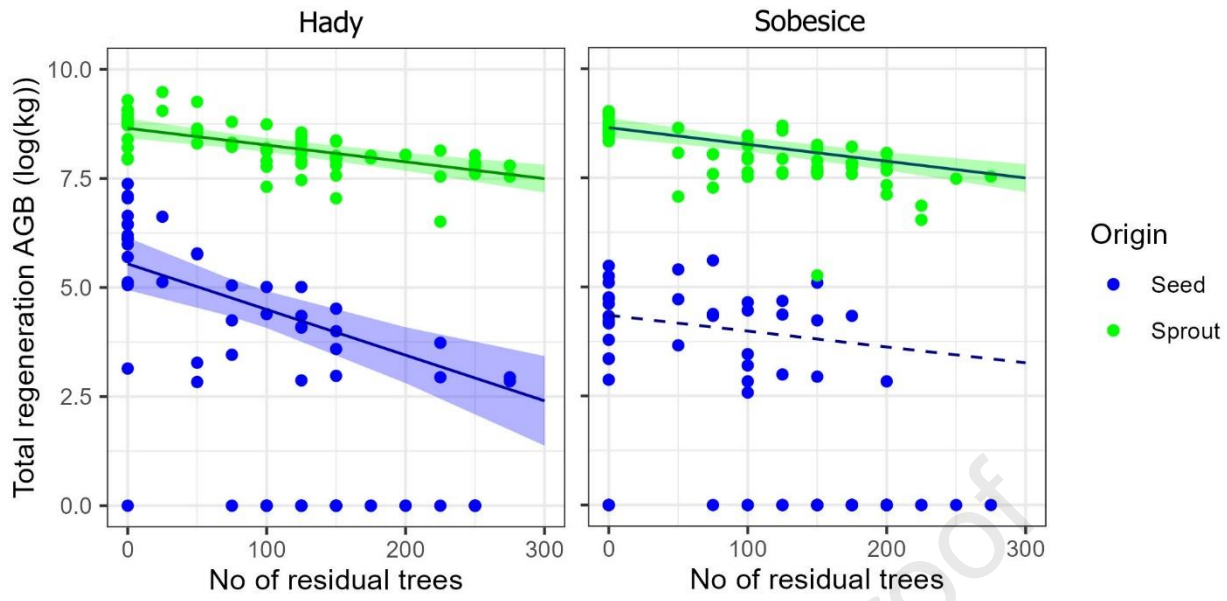


Fig. 2

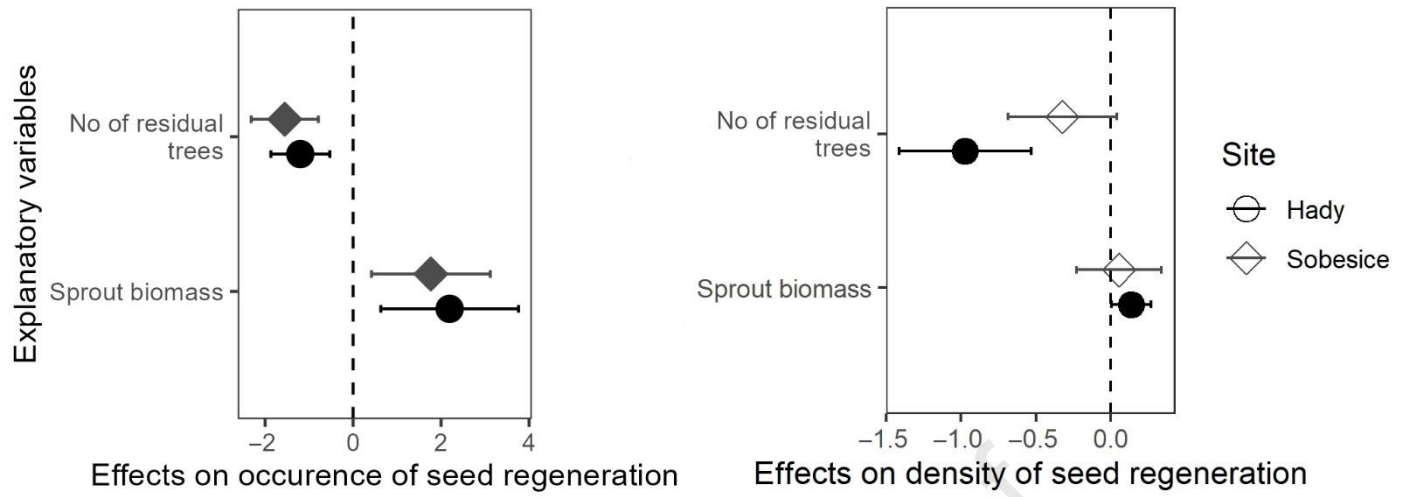
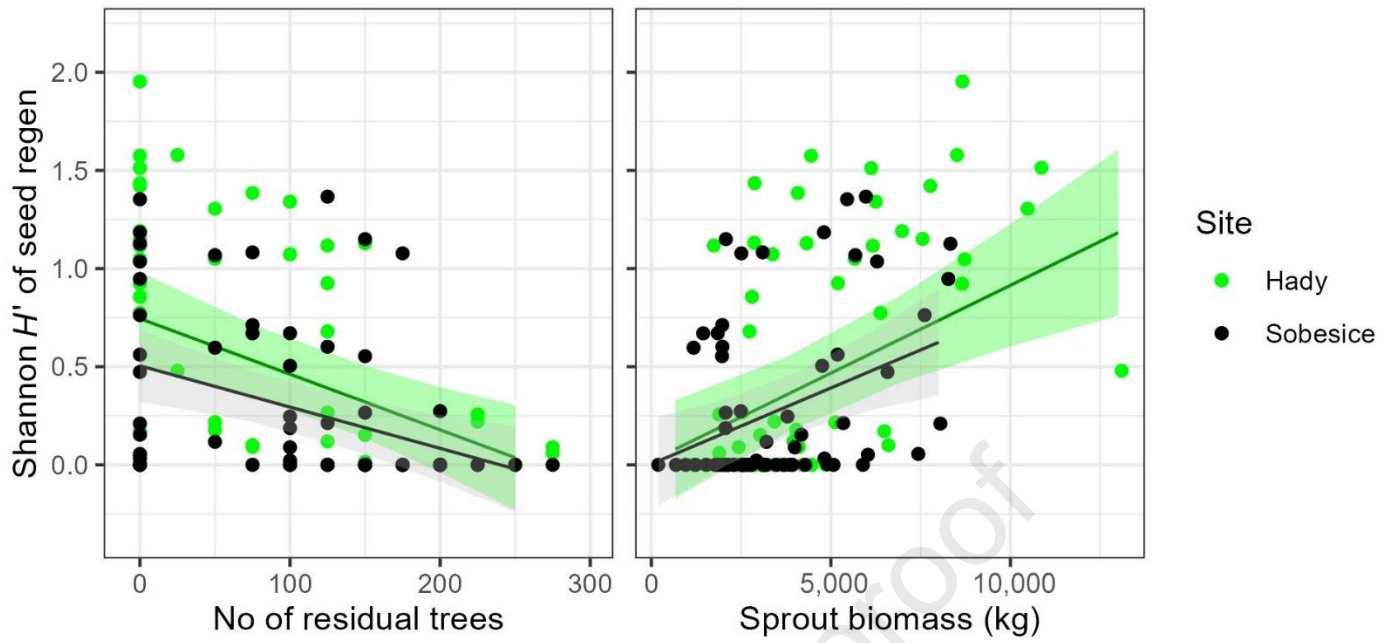


Fig. 5

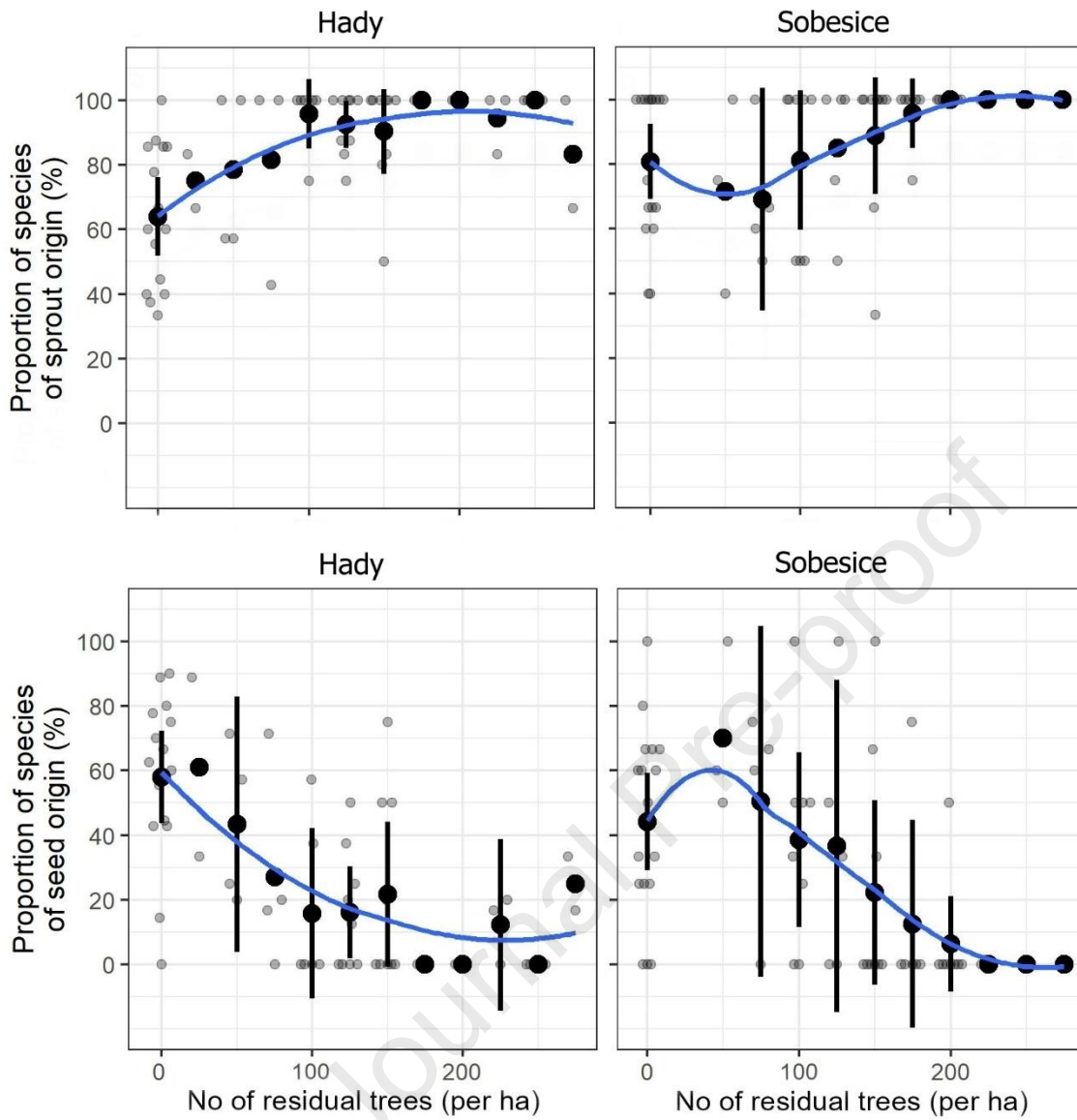


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Fig. 4

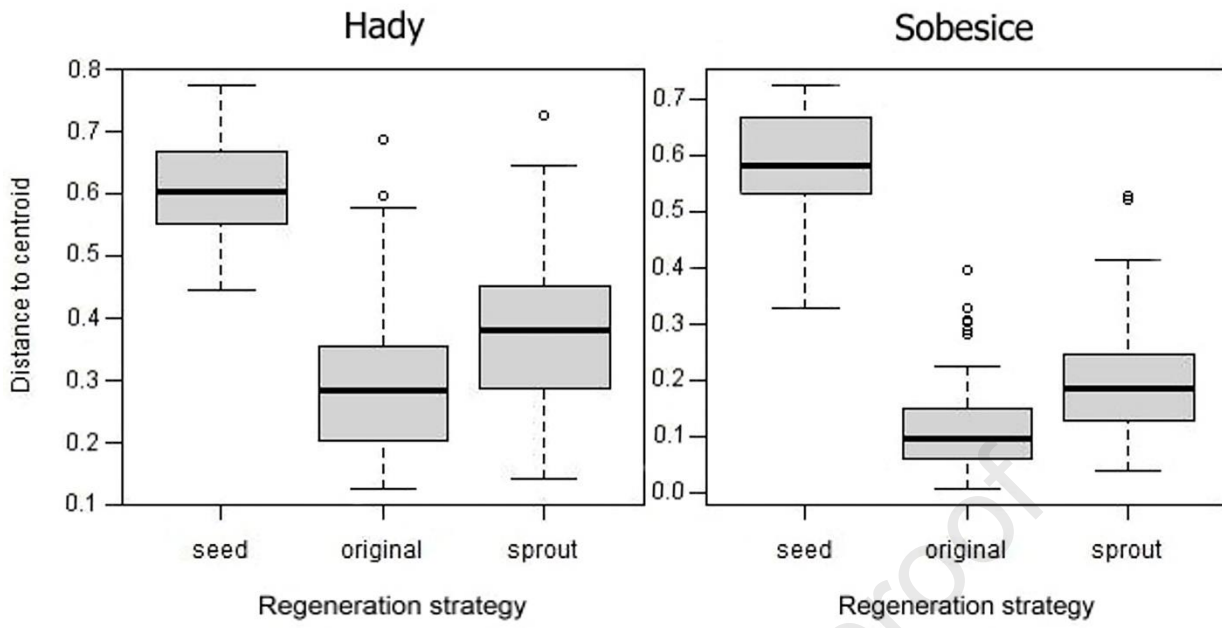


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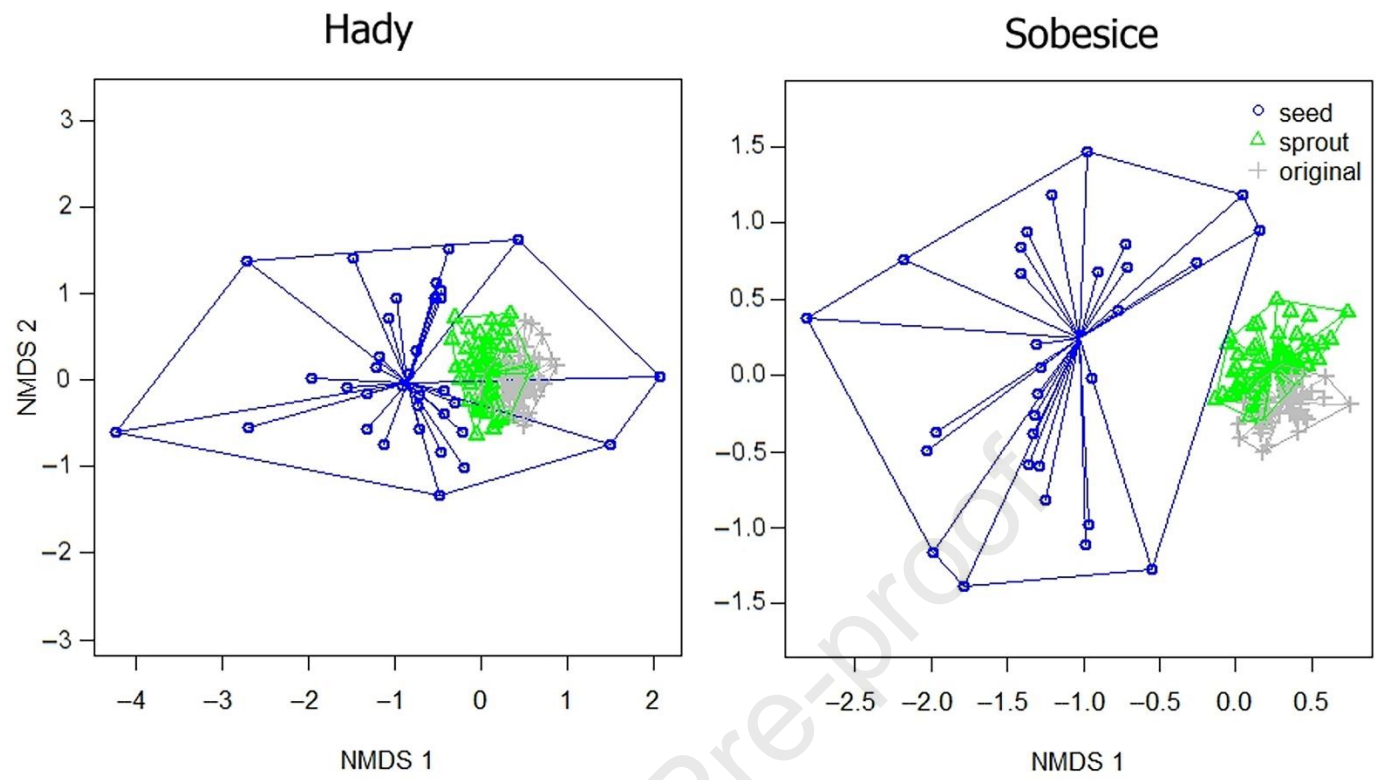


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Fig. 6



Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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