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Forested riparian buffer environmental variables are more important than size for species functional diversity in production forests

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ABSTRACT

Retention of forested buffers around streams following forest cutting operations is a common management technique used to protect aquatic resources and conserve the surrounding ecosystem services. Species richness, or α-diversity, is commonly used as an indicator of the effects of forestry management although it provides very little information about those effects on ecosystem processes and function. Functional diversity links species traits and ecosystem function incorporating species diversity, community composition, and functional guild and is more suitable to investigate the direct and indirect effects of forestry on ecosystem function. We sampled spiders and vascular plants in buffered and unbuffered stream-forest systems in southern Sweden and used a trait-based approach to assess the effects of buffer size and environmental variables on functional diversity. We used structural equation modeling (SEM) to explore the effects of buffer size and condition on spider and vascular plant diversity. We found no effect of buffer size on the functional richness or functional redundancy for spiders or vascular plants. Buffer size had a slight effect on the α-diversity of spiders within small buffers and fully forested sites but the effect was small. Other buffer variables including canopy closure, buffer density, bare ground coverage, and soil fertility had direct effects on spider and vascular plant functional diversity. The main driver of functional richness was α-diversity, but our SEM analysis illustrated other environmental variables working jointly to drive functional diversity. Using a trait-based approach, we showed that forested buffers have a minimal overall impact on spider and vascular plant functional diversity. However, it is important to maintain high levels of α-diversity to preserve and promote both spider and plant functional richness in production forests and we suggest that forest management conserves and encourages high levels of α-diversity to increase overall functional diversity.

1. Introduction

Stand management in production forests varies between forest types, landowners, countries, and conservation goals. Most forest management-techniques result in distinct changes in biodiversity and structure at both local and landscape levels (Chaudhary et al., 2016; Shakeri et al., 2021; Triviño et al., 2017; Díaz-Yáñez et al., 2019). Identifying and measuring ecosystem functions is critical to determine the effects of forestry practices on natural systems (Capon et al., 2013). Ecosystem functions specific to riparian systems include energy exchange, structural function, refuge, and biological control (Capon et al., 2013). Forestry operations around riparian systems pressure these functions (Hoppenreijs et al., 2022), complicate conservation initiatives, and have immediate and long lasting effects on the terrestrial and aquatic environments (Broadmeadow and Nisbet, 2004; Jyväsjärvi et al., 2020; Kuglerová et al., 2014b; Lazdinis and Angelstam, 2005).

A common management technique is the establishment of forested buffers (Broadmeadow and Nisbet, 2004; Cole et al., 2020; Lee et al., 2004). Buffers around streams and rivers provide protection for aquatic ecosystems through shading and temperature regulation, control of upland nutrient and sediment runoff, and bank stabilization (Broadmeadow and Nisbet, 2004; Burdon et al., 2020; Wenger, 1999). Buffers also provide terrestrial ecosystem services including increased habitat complexity, connectivity, and shade and humidity regulation (Marczak et al., 2010; Wenger, 1999). Buffer usage and regulation is highly variable around the world but they are generally deployed around most streams and rivers (Lee et al., 2004; Kuglerová et al., 2020). Recently, researchers have shown that the effectiveness of riparian buffers to

preserve aquatic and terrestrial ecosystem services, provide complex habitats, and increase biodiversity, is dependent on variables such as geographic location, stream slope, and the surrounding forest composition (Chellaiah and Kuglerová, 2021; Hasselquist et al., 2021). Further, aquatic, terrestrial, and riparian flora and fauna each respond differently to riparian buffer size, adding to the complexity of determining optimum effectiveness (Lind et al., 2019; Marczak et al., 2010). A growing body of evidence has shown that riparian buffers>30 m are adequate to provide protection for both riparian and aquatic systems when managers account for site-specific conservation goals (Chellaiah and Kuglerová, 2021; Marczak et al., 2010; Oldén et al., 2019a,b). However, we argue that these studies often rely on simple measures of observed diversity while overlooking the effects of diversity on the function of riparian and upland systems.

Buffer size, forestry disturbances, tree species, canopy coverage, and other biotic and abiotic conditions are some of the drivers of riparian buffer diversity (Biswas and Mallik, 2010; Chellaiah and Kuglerová, 2021; Elliott and Vose, 2016). Riparian invertebrate diversity plays a key role in riparian function through aquatic-terrestrial energy exchange as predators, prey items, and decomposers (Muehlbauer et al., 2014; Lafage et al., 2019b). Similarly, species diverse riparian plant communities support riparian function through enhanced aquatic protection and by providing a complex habitat to local fauna (Tabacchi et al., 1998). However, a deeper understanding of the cascading and causal effects of environmental variables on riparian communities and subsequently ecosystem function requires a more thorough description of the species diversity in those systems. Species richness, or α-diversity, is often used but is not always a relevant indicator of the effects of forest management as it provides little information about the overall effects that different species assemblages have on ecosystem processes and services at the local level (Biswas & Mallik, 2011). Instead, functional diversity measurements link species traits and ecosystem function, like functional richness or functional redundancy, may provide a more robust assessment of species community roles and may uncover the acute effects of local disturbances on those communities (Díaz and Cabido, 2001; Laureto et al., 2015). Functional diversity is an especially robust measure as it incorporates species diversity, community composition, and functional guild (Chapin et al., 1997; Petchey & Gaston, 2002).

Riparian buffer effectiveness is rarely measured through exploration of species functional diversity and organism responses to changes in α-diversity and functional diversity due to forestry management practices is complex (Lelli et al., 2019). In addition, spatial variables such as distances from streams may shape these riparian communities (Muehlbauer et al. 2014; Kuglerová et al, 2014a). To explore that complexity, we performed an intensive survey of ground dwelling and low shrub spider communities and vascular plant communities in and around riparian systems in Swedish production forests. The habitat selectivity as well as substrate preferences, and varying hunting guilds between spider species make the Araneae group an ideal community to use functional traits to investigate the habitat and microclimatic conditions in varying sized riparian buffers, vegetation structure, and forestry practice (Foelix, 2011; Lambeets et al., 2008; Larrivée et al., 2008). Likewise, the range of vascular plants that populate riparian systems in production forests provide structure and substrate to spider communities while directly regulating the microclimatic conditions necessary for spider assemblages.

Using species level functional traits, we calculated spider and vascular plant functional richness (FR) and functional redundancy (RED) and compared those values to riparian buffer size, distance from stream, and other abiotic variables along 15 forested and clear-cut streams. We also explored the effects of buffer width and abiotic variables on spider and plant α-diversity. We hypothesize that larger forested buffers (>40 m) will be more functionally complex and species rich compared to smaller buffers and clear-cuts. In addition, we believe there exists a strong correlation between spider and plant α-diversity

and their respective measures of FR. Finally, we hypothesize that the abiotic environmental variables within the buffers and clear-cuts have a direct effect on the α-diversity and functional diversity response of spiders and vascular plants. For example, in increase in canopy openness will have a positive effect on vascular plant α-diversity or higher average shrub heights will increase the functional richness of spider communities.

2. Materials and methods

2.1. Sampling design

As buffer efficiency is known to depend on site location, we chose to sample several areas within a region with homogeneous climatic conditions. In Sweden, landowners are only provided guidelines regarding buffer characteristics and not size standards, resulting in very heterogeneous buffer sizes. Consequently, we selected sites to cover the all size gradient observed in the area. Finally, even though selecting sites with same buffer widths on both sides would have facilitated our analysis, these types of sites are very uncommon in Sweden as streams are often used as borders between property owners using differing forestry techniques. Consequently, sites with different management on each side of the streams were included in the study.

2.2. Study sites

We completed sampling in four areas in the Värmland and Örebro counties of central Sweden within the Göta Älv catchment (Fig. 1). Sampling sites in each area were located in riparian zones along streams in Norway spruce (*Picea abies*) production forests with the exception of the Storfors location sites (STO) that were composed primarily of Scots pine (*Pinus sylvestris*). Birch (*Betula* spp.) and alder (*Alnus* spp.) were also scattered throughout most sites often within proximity of the streams. All streams were comparable in size (mean width ± SD: 2.2 ± 0.94 m; mean depth: 0.41 ± 0.20 m) but were surrounded by different sizes of forested riparian buffers. We categorized the buffers on each side of the stream as either None, Small (1–40 m), Large (41–120 m), or Forested (>120 m). Our decision to classify a buffer as "Small" when it is<40 m wide is based on the work of Marczak et al. (2010) and Lind et al. (2019). Responses of different taxa to buffer treatments vary significantly in buffers<50 m wide, suggesting that even buffers this size may not be sufficient to conserve terrestrial species diversity (Marczak et al., 2010). Furthermore, to maintain an ecologically functional riparian zone with high plant and animal diversity, a buffer of>30 m is needed in most cases (Lind et al., 2019).

Both spiders and vegetation were sampled at each of the fifteen sites. At each site, six 3 × 3 m quadrats were centered at 1.5, 15, and 30 m along a transect perpendicular to the edge of the streams on each side, giving us totally 90 sampling units across all areas. Quadrats placed outside of the buffer into a clearcut were categorized in the *None* buffer group. In June and July of 2020, a full vegetation inventory was completed by estimating vascular plant species cover as the percentage of canopy coverage in each quadrat based on a modified Braun-Blanquet scale (Pfadenhauer et al. 1986). Each plant species was assigned a classification between 1 and 8 based on the following coverage percentages: <1, 1–3, 3–5, 5–15, 15–25, 25–50, 50–75, 75–100. We recorded maximum herb and shrub height and percent coverage of bare ground, litter, mosses, herbs, and shrubs.

In July and August of 2020, spiders were sampled using a suction sampler running at maximum power by pulling the trigger 100 times for 2 s per pull and covering the entire ground and vegetative area within each quadrat up to ~ 1 m high (~9 m³). We choose suction sampling as it is a highly efficient method for quantitative measurement of spider diversity (Brook et al., 2008). Each quadrat suction sample was sifted through a litter separator to remove large pieces of litter, moss, and other debris before being placed in a sample pan. Living spiders were
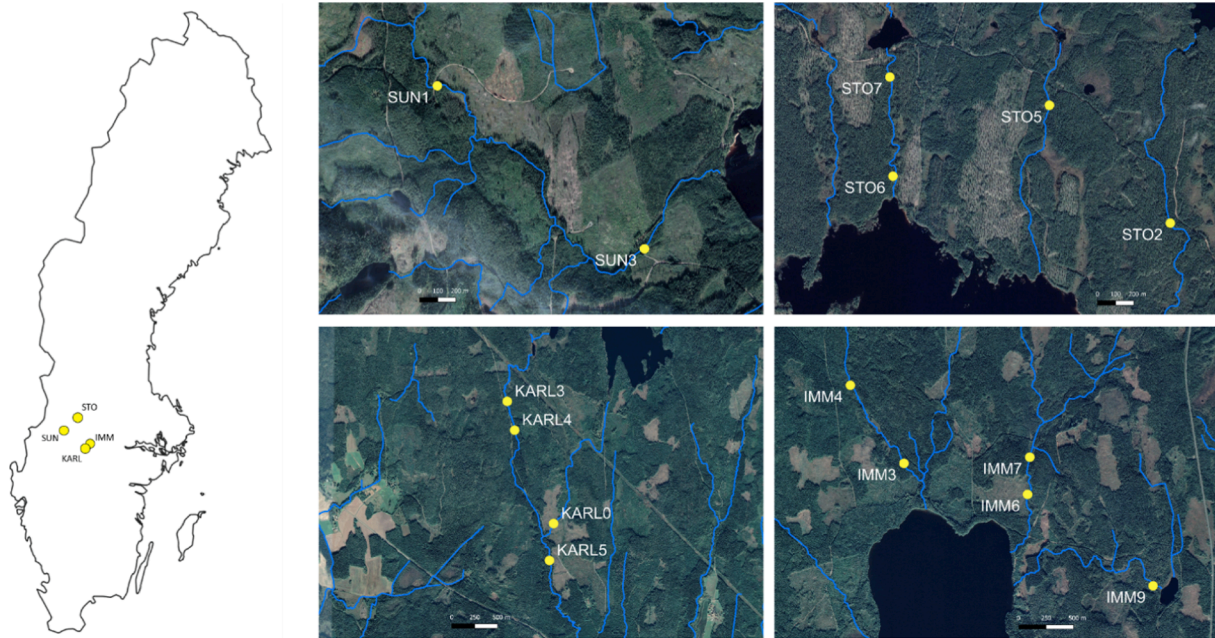
Fig. 1. Site locations in southern Sweden.

collected with an aspirator by searching until no spider could be found in the remaining litter for sixty seconds. All spiders were stored in 70 % ethanol and returned to the lab for identification.

At each site, we also recoded biotic and abiotic predictor variables related to the forested buffer and vegetation (Table 1 & 2; see Supplementary Material for variables by sampling unit). Forest age in years was recorded using Skogsstyrelsen's basic forest data (Skogsstyrelsen, 2022). Average buffer density in trees/hectare around each sampling quadrat was measured using a point quarter method and calculated according to Mitchell (2007). Percent canopy closure was measured above each sampling quadrat by taking a digital picture with a 170 degree fish eye lens and processing the images using the R program Heimphot.R (ter Steege, 2018). Within each sampling quadrat, we estimated the percent cover of bare ground (soil and rocks), litter (leaves, woody debris, and dead plants), moss, herbs, and shrubs. We recorded the maximum height in cm for herbs and shrubs. Finally, Ellenberg values for light (L), moisture (M), fertility (N), and pH were derived and averaged for each sampling quadrat using the moss and vascular plant species trait values as complied by Bernhardt-Römermann et al. (2018) and Tyler et al. (2021). The sampling distance from the stream was also added as a factored predictor variable.

Table 2

Mean $\pm$ SD Ellenberg index values by site. L = light, M = moisture, N = soil fertility.

Site	L	M	pH	N
IMM3	4.77 ± 0.2	4.90 ± 0.4	3.21 ± 0.4	2.83 ± 0.4
IMM4	4.80 ± 0.5	5.17 ± 0.5	2.80 ± 0.3	2.38 ± 0.5
IMM6	4.76 ± 0.4	5.19 ± 1.1	2.51 ± 0.4	2.36 ± 0.7
IMM7	4.80 ± 0.3	5.34 ± 1.3	3.06 ± 0.7	2.66 ± 0.5
IMM9	4.78 ± 0.4	5.10 ± 0.7	2.94 ± 0.4	2.38 ± 0.8
KARL0	5.11 ± 0.2	4.24 ± 0.4	2.90 ± 0.4	3.42 ± 0.8
KARL3	4.88 ± 0.2	5.04 ± 0.6	2.86 ± 0.5	2.80 ± 0.9
KARL4	4.67 ± 0.2	4.64 ± 0.3	2.98 ± 0.1	2.97 ± 0.6
KARL5	4.68 ± 0.3	5.02 ± 0.5	2.79 ± 0.3	2.45 ± 0.6
STO2	5.12 ± 0.2	4.69 ± 0.4	2.77 ± 0.4	2.23 ± 0.6
STO5	5.12 ± 0.4	5.21 ± 1.1	2.88 ± 0.5	2.39 ± 0.7
STO6	4.95 ± 0.2	5.03 ± 0.8	2.62 ± 0.4	2.27 ± 0.6
STO7	5.04 ± 0.3	5.10 ± 1.1	2.61 ± 0.6	2.32 ± 0.7
SUN1	4.71 ± 0.4	5.52 ± 0.6	2.10 ± 0.4	2.57 ± 1.0
SUN3	4.64 ± 0.3	5.09 ± 1.0	2.71 ± 0.8	2.88 ± 0.7

Table 1

Biotic and abiotic variables of all quadrats averaged by site. Buffer density = tree/hectare. Canopy closure = % coverage. Bare, litter, moss, herb, and shrub = % coverage. Herb max and shrub max = cm. Canopy closure for site IMM9 was not recorded and was excluded from the analysis.

Site	Buffer Density	Canopy Closure	Bare	Litter	Moss	Herb	Shrub	Herb Max	Shrub Max
IMM3	1565.5	0.5	1.0	4.5	80.2	6.3	13.8	91.0	44.8
IMM4	1165.5	0.5	1.7	11.8	80.5	9.7	35.8	51.0	38.7
IMM6	673.0	0.2	2.5	7.5	63.3	41.2	29.2	94.7	35.2
IMM7	1752.5	0.4	0.7	3.8	85.5	16.2	11.5	60.2	37.3
IMM9	1400.5	–	1.3	7.7	72.5	16.0	46.0	58.7	44.2
KARL0	0.0	0.0	21.8	19.2	9.2	51.7	21.3	93.0	75.7
KARL3	2140.0	0.4	0.7	25.0	70.0	27.5	23.3	56.5	68.2
KARL4	1576.0	0.4	0.3	9.2	89.2	27.5	14.7	64.8	18.0
KARL5	679.7	0.6	0.8	14.2	84.2	13.3	29.2	71.8	47.3
STO2	1308.0	0.3	1.2	6.8	70.0	16.7	45.5	34.3	54.3
STO5	1308.0	0.4	0.5	12.5	57.5	32.7	57.5	57.5	107.2
STO6	1812.0	0.3	2.0	10.8	73.3	26.3	35.0	70.7	61.8
STO7	1008.0	0.5	7.0	14.2	55.8	30.0	50.0	31.3	85.2
SUN1	1682.0	0.3	14.2	7.5	59.2	15.2	30.2	36.5	42.3
SUN3	1661.0	0.4	7.5	15.0	69.2	13.5	8.2	54.2	19.8

2.3. Trait selection

For spiders, six trait categories were selected and recorded from the literature (Table 3): feeding guild, maximum female body size, dispersal by ballooning, humidity preference, substrate preference, and light preference. These traits affect spider community assemblage and signal different functional and ecological strategies (Cardoso et al., 2011; Baldissera et al., 2020). We specifically selected these traits because they are driven by environmental variables or forestry practices. Riparian plant diversity, vegetation height, and types of forested riparian buffer all influence spider assemblages of certain feeding guilds (Lafage et al., 2019a; Ramberg et al., 2020). Spider body size is often an indicator of the size and types of prey spiders consume but is also limited by landscape structure and agricultural practices (Drapela et al., 2011; Lafage and Pétillon, 2014; Lafage et al., 2015; Zuev et al., 2020). In addition, assemblages of ballooning spiders are strongly influenced by landscape factors such as non-crop habitats around forests and watercourses (Schmidt and Tscharntke, 2005). Finally, humidity, substrate, and light availability are all regulated in riparian buffers through forestry practices such as selective thinning and clearcutting (Dignan and Bren, 2003; Oldén et al., 2019b; Sonesson et al., 2021).

To ensure a more robust description of the functional space occupied by spiders, we relied on a finer trait resolution for humidity, substrate, and light preferences. Rather than assigning each spider species a single preference in these categories, we used an ordered factor within each category to highlight the range of abiotic preferences. Humidity, substrate, and light preferences were determined for each species as either marginal, basic, or preferred. Using finer trait levels or assigning species a range of traits that better reflects their ecological space is critical to estimate the functional patterns in a community accurately (Kohli & Jarzyna, 2020).

For vascular plants, six traits were selected and recorded from the literature (Table 4): nectar production, seed dispersal mode, dependence on soil disturbance, specific leaf area (SLA), leaf dry matter content (LDMC), and mean canopy height. First, we chose structure related vascular plant traits (SLA, LDMC, and height) that influence spider and insect diversity (Scheidler 1990; Horváth et al., 2009; Moretti et al., 2013). We included nectar production in flowers as higher levels may attract more pollinators thus increasing prey availability to spiders and some spiders will supplement their diets by feeding on flower nectar (Jiménez-Salinas & Corcuera-Martínez, 2007; Nyffeler, 2016). Finally, forestry and riparian management has a direct influence on riparian soil disturbance thus affecting plant establishment and seed dispersal (Goodson et al., 2001; Nagamatsu and Miura, 1997; Taylor et al., 1999).

2.4. Statistical analysis

2.4.1. Response variables

For each 3×3 m plot, we calculated the α-diversity, FR, and RED for spiders and vascular plants. For spiders, calculations were based on the abundance and richness of adults identifiable to species level. For vascular plants, calculations were based on the coverage and richness of plants identifiable to species level. The α-diversity was calculated as the species richness of spiders or vascular plants in each sampling quadrat. Because functional traits each provide an unbalanced contribution when calculating dissimilarities, we used the 'gawdis' package in R to determine an optimal solution for spider and vascular plant trait weights using an iterative genetic algorithm (Bello et al., 2021). Using those trait weights, we calculated FR according to Villéger et al. (2008) with a Gower dissimilarity matrix using the 'FD' package (Laliberté & Legendre, 2010; Laliberté et al., 2014). RED was calculated according to Ricotta et al. (2016) and represents an abundance based functional redundancy measure that accounts for interspecies dissimilarity within each community (Ricotta et al., 2016). Similar to FR, RED was calculated using weighted species traits.

2.4.2. Structural equation modeling

We used mixed model Structural Equation Modeling (SEM) to analyze the effects of forested buffer size and environmental variables on spider and vascular plant FR, RED, and α-diversity. SEM is a multivariate modeling technique used to investigate causal relationships between variables (see: Fan et al., 2016). As opposed to other modeling methods, SEM tests for direct *and* indirect effects on the assumed relationships between responses and predictor variables and estimates regression (path) coefficients between variables. All predictor variables were checked for correlation with a Spearman's test and we kept those with non-significant or poorly correlated values ($R < 0.5$) that were deemed most important to spider or vascular plant assemblages. For example, Ellenberg moisture values and pH values were correlated but we retained moisture as it is a more important factor for spider assemblage. Remaining predictor variables (Table 5) were scaled to a mean of zero and variance of one. Before loading our SEM, we created separate sub-models (Table 6) to estimate the relationships for each response variable to the predictor variables. We then built linear mixed-effects sub-models with FR, RED, and α-diversity as response variables, selected environmental and categorical variables as predictors, and set the *Site* as a random factor. All sub-models were created using the R package 'nlme' (Pinheiro et al. 2021) and the *dredge* function in the R package 'MuMIn' (Barton, 2020) to generate a set of models with all possible predictor variable combinations weighted based on the Akaike information criteria for small samples (AICc). We selected all final predictor variables from the dredged models with a ΔAICc < 0.5. We used all selected predictor variables to fit selected sub-models into a piecewise SEM using the R package 'piecewiseSEM' (Lefcheck, 2016). To confirm significance in categorical variables, we performed post hoc analyses using pairwise comparisons of estimated marginal means between each buffer category or distance from stream using the R package 'emmeans' (Lenth, 2021).

Table 3
Trait categories, variables, type, and reference sources for all spiders. The number in parenthesis for each trait variable shows the number of levels in each variable. Multiple trait variables may have been selected for ordered factor trait types. Humidity, light, and substrate preference.

Trait category	Trait variables	Trait type	Reference
Body size	Maximum female body size in mm	Continuous	Roberts, 1987; Almquist, 2005, 2006
Feeding guild	Ground hunter, ambush hunter, other hunter, orb web weaver, space web weaver, sheet web weaver, sensing web weaver, specialist (8)	Categorical	Cardoso et al., 2011
Dispersal	Ballooning, non-ballooning (2)	Binary	Bell et al., 2005; Blandenier, 2009; Simonneau et al., 2016; Birkhofer et al., 2017
Humidity preference	very dry, dry, semi humid, humid, very humid (5)	Ordered factor	Ashmole and Merrett, 1981; Roberts, 1987; Buchar et al., 2002; Almquist, 2005, 2006; Hajdamowicz et al., 2014
Light preference	open, semi open, partial shade, shade, dark (5)	Ordered factor	
Substrate preference	Underground, ground, herb, shrub, tree trunk, canopy (6)	Ordered factor	

Table 4

Trait categories, variables, type, and reference sources for all vascular plants. The number in parenthesis for each trait variable shows the number of levels in each variable.

Trait category	Trait variables	Trait type	Reference
Specific leaf area	The ratio of leaf area to leaf dry mass in mm^2/mg	Continuous	TRY Plant Trait Database (Kattge et al., 2011); LEDA Trait Database (Kleyer et al., 2008)
Leaf dry matter content	ratio of leaf dry mass to fresh mass	Continuous	TRY Plant Trait Database (Kattge et al., 2011); LEDA Trait Database (Kleyer et al., 2008)
Mean canopy height	Maximum mature height in cm	Continuous	LEDA Trait Database (Kleyer et al., 2008)
Nectar production	No nectar production (0 g sugar/m^2/year), nectar production insignificant (<0.2), nectar production small (<0.2–5), nectar production modest (5–20), rather large (20–50), large (50–200), very large (>200) (7)	Categorical	Tyler et al., 2021
Seed dispersal mode	Hooked/sticky fruits, wind by weight, wind by hairs, wind by winged fruit, bird, ballistic, ant, passive, vegetative, water (10)	Categorical	
Soil disturbance	1–9 scale reflecting increasing levels of soil disturbance required for the occurrence/survival of a plant species (9)	Categorical	

Table 5

Environmental and qualitative variables used in SEM sub-models.

Variable	Description	Units (variable type)
Bare ground coverage (bare)	Measurement in each plot of soil and bare rock coverage	% (continuous)
Litter coverage (litter)	Measurement in each plot of leaf, woody debris, and log coverage	% (continuous)
Shrub height (SH)	Height of tallest shrub within each plot	cm (continuous)
Canopy closure (CC)	Average canopy coverage along the stream reach to 30 m into upland zone	% (continuous)
Buffer density (density)	Average tree stand density around each sampling plot	trees/ha (continuous)
Forest age (age)	Average stand age within 30 m of stream	years (continuous)
Moisture (M)	Ellenberg derived values based on plant community weighted trait means (CWM) in each sampling plot	no unit (continuous)
Light (L)	Ellenberg derived values based on plant CWM in each sampling plot	no unit (continuous)
Fertility (N)	Ellenberg derived values based on plant CWM in each sampling plot	no unit (continuous)
Opposite cut (OC)	Is the opposite side of the stream buffered or clear-cut?	no unit (binary)
Buffer category (cat)	Buffer category: clear-cut, small (1–40 m), large (40–120), forested (>120)	no unit (categorical)
Stream distance (dist)	Distance in meters sampling plot is from edge of stream (0, 15, 30)	m (categorical)

Table 6

Initial and selected sub-models used for spiders and vascular plant piecewise SEM. Selected sub-models were used to build the SEMs for each group. Each sub model also used Site as a random factor. All models were run as linear mixed effects models using the *nlme* package in R. FR: functional richness; RED: functional redundancy; SH: shrub height; density: buffer density; CC: canopy closure; bare: bare ground cover; litter: litter cover; OC: opposite cut; cat: buffer category; dist: distance from stream; M: moisture; age: buffer forest age; L: light; N: nitrogen;

Group	Initial sub-model	Selected sub-model
Spiders	Spider FR ~ bare + litter + SH + density + CC + OC + M + cat + dist + α-diversity + plant α-diversity	Spider FR ~ litter + CC + α-diversity
	Spider RED ~ bare + litter + SH + density + CC + OC + M + cat + dist + α-diversity + plant α-diversity	Spider RED ~ bare + density
	Spider α-diversity ~ bare + litter + SH + density + CC + OC + M + cat + dist + plant α-diversity	Spider α-diversity ~ bare + cat + density
Vascular plants	Plant FR ~ age + density + CC + litter + bare + L + N + plant α-diversity + OC + cat + dist	Plant FR ~ density + CC + plant α-diversity + dist
	Plant RED ~ age + density + CC + litter + L + N + plant FR + OC + cat + dist	Plant RED ~ L + N + plant FR
	Plant α-diversity ~ age + density + CC + litter + L + N + OC + cat + dist	Plant α-diversity ~ CC + dist

2.4.3. Null models

To explore FR further, we used null models to determine whether the observed FR was lower or higher than expected based on the α-diversity in each sampling unit. Using null models controls for the effect of α-diversity and shuffles the traits using artificial communities. If the average null value of FR is different from the observed, then we can assume there is another variable affecting FR. We created artificial communities by holding species richness and abundance constant for each sampling unit and randomly reassigning species from the overall study species pool (see: Gerisch, 2014; Rader et al., 2014). We repeated this 999 times to calculate a mean null value for each sampling unit and then tested whether the observed FR was significantly lower or higher than the mean null. All statistical analyses were performed using R 4.1.1 (R Core Team 2021).

3. Results

We collected 16,037 individual spiders belonging to 20 families. Our sampling effort contained a high number of juvenile spiders (~76 %)

and we identified 3919 adult spiders belonging to 154 species (Supplementary Material). In each 3 × 3 m sampling unit, species richness varied between 1 and 31, with a mean richness of 14.0 (SD ± 4.9). The Linyphiidae family dominated the collection representing 92 species and 68.2 % of all spiders collected. Other families with high abundance included Lycosidae, Salticidae, and Theridiidae at 8.3 %, 5.8 %, and 4.5 % of the total number of individuals, respectively. The three most commonly collected species were *Minyriolus pusillus*, *Neon reticulatus*, and *Centromerus arcanus* representing 15 %, 10 %, and 9.8 % of the total number of individuals, respectively.

We identified 85 species of vascular plants representing 30 families (Supplementary Material). In each 3 × 3 m sampling unit, species richness varied between 1 and 23, with a mean of 7.1 (SD ± 4.8). We removed unidentifiable singleton species of *Carex* and the aquatic plant *Potamogeton gramineus* from the analysis, as it would not be utilized by spiders collected in this study. *Vaccinum myrtillus* and *V. vitis-idaea* were the most dominant vascular plants in both coverage and occurrence

across all plots. Along streams not dominated by mosses, grasses of *Calamagrostis* spp. were very common.

The weighted sub-models for spider FR retained litter cover, canopy coverage, and spider α-diversity as significant model predictor variables. Spider RED sub-models retained bare ground coverage and buffer density. Spider α-diversity sub-models retained bare ground coverage, buffer density, and buffer category. Vascular plant FR sub-models retained buffer density, canopy closure, plant α-diversity, and distance from stream. Vascular plant RED sub-models retained Ellenberg derived light and fertility values, and plant FR. Vascular plant α-diversity sub-models retained canopy closure and distance from stream.

The SEM for spider responses indicated a good fit with the selected data (Fisher's $C = 12.477$, $p = 0.899$). The SEM (Fig. 2) showed that an increase in α-diversity had a positive effect on FR ($p < 0.001$). In turn, α-diversity was affected by buffer size with post-hoc testing revealing small buffers (1–40 m) have a significantly higher average α-diversity compared to forested buffers (mean ± SD: 4.76 ± 1.48) (Fig. 3). Distance from stream showed no effect on spider α-diversity (Fig. 4). Canopy closure had a negative effect on FR ($p = 0.031$), and percentage of bare ground had an overall negative effect on both spider α-diversity and RED ($p = 0.047$ and $p < 0.001$, respectively). No other variables included in spider sub-models had direct or indirect effects on spider FR, RED, or α-diversity.

The SEM for vascular plants responses indicated a good fit with the selected data (Fisher's $C = 24.053$, $p = 0.153$). The SEM for vascular plants (Fig. 5) showed that an increase in buffer density and higher percent canopy closure had a negative effect on plant FR ($p = 0.030$ and $p = 0.021$, respectively). In contrast, higher α-diversity of vascular plants had a positive effect on plant FR ($p < 0.001$). Vascular plant RED was negatively influenced by plant FR and Ellenberg derived fertility values ($p < 0.001$ and $p = 0.004$, respectively). Finally, α-diversity, as a positive driver of vascular plant FR, was influenced by distance from the stream edge. Post-hoc testing showed a significantly higher α-diversity at 0 m compared to 15 and 30 m (4.67 ± 1.01 and 4.45 ± 1.02, respectively) (Fig. 6). Buffer category had no effect on vascular plant α-diversity (Fig. 7) and no other variables included in the sub-models had a direct or indirect effect on vascular plant FR, RED; or α-diversity.

Null models showed that mean observed FR were not significantly different from mean randomized FR for both spiders and vascular plants.
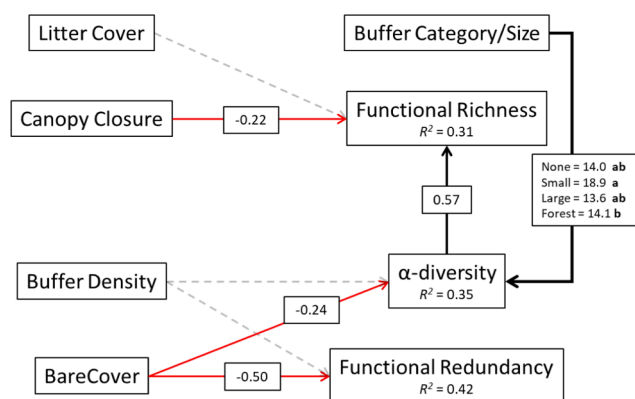

Fig. 2. Piecewise structural equation model showing direct and indirect effects of buffer category and environmental variables on spider FR, RED, and α-diversity. Solid arrows represent significant ($p < 0.05$) interactions between variables. Red and black arrows denote negative or positive standardized coefficients, respectively. Standardized coefficients for continuous variables are in boxes over each significant arrow. Buffer category/size reports estimated marginal means of α-diversity for each buffer type. Letters after each marginal mean indicate significant differences between buffer categories based on post-hoc tests. Dashed arrows signify no influence of environmental variables on the responses ($p > 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

In this study, although buffer size had a small effect on spider α-diversity, overall species diversity was similar across all buffer types for both spiders and vascular plants. Our models show a distinct effect of bare ground cover on spider α-diversity and functional redundancy (RED). We found buffer density and soil fertility had an effect on plant functional richness (FR) and RED and both spider and plant FR was affected by canopy closure. We found strong linkages between α-diversity and functional richness for both spiders and plants, which was not surprising as α-diversity is strongly correlated with different measures of functional diversity (Petchey & Gaston, 2002; Petchey, 2004). We confirmed this effect in our null models where our observed FR did not differ from the mean null functional richness for both spiders and plants. In our sites, it is clear that FR is being driven by the α-diversity within each sampling unit, and by using SEM models, we are able to show the linkages between the environmental drivers of α-diversity connected to FR.

Spider α-diversity was negatively affected by bare ground coverage and showed minimal response to buffer size category. We found higher bare ground coverage in sampling units with low vegetation cover suggesting that the decrease in spider α-diversity at these sites is linked to a decreased structural diversity in litter and vegetation. It is known that spider communities are sensitive to the structural complexity of their habitats, as different feeding guilds require specific conditions to thrive (Rypstra et al., 1999; Jiménez-Valverde & Lobo, 2007), and litter depth and coverage are important for spider α-diversity (Uetz, 1979; Bultman & Uetz, 1982; Castro & Wise, 2009). Small and fully forested buffers had a different mean number of species in each sampling unit. However, the absence of a mean difference in species between clear cuts and large buffers compared to small and forested buffer sites suggests that there is very little difference in overall α-diversity between buffer types. A *meta*-analysis by Prieto-Benítez and Méndez (2011) points out that land uses in forests did not have a clear negative effect on spider species richness. Similarly, Ramberg et al. (2020) found no difference between non-buffered, buffered, and fully forested sites for spider species richness. Our results do not support our hypothesis of larger buffers supporting higher spider α-diversity as such an effect is more closely related to the environments within the buffers.

Spider FR was positively affected by α-diversity and negatively affected by canopy closure. Post-hoc community analysis showed clear-cut sites with distinct spider species that prefer open light and low humidity, conditions commonly found in clear-cuts. In contrast, four different spider species were more closely associated with all sizes of forested buffers and were mostly absent in clear cuts with those species preferring higher humidity and shade, both conditions provided by forested buffers regardless of size category. The structure and habitat across different forest types and clear-cuts has been shown to support different spider assemblages (Pearce et al., 2004; Oxbrough et al., 2005). Canopy coverage is an important factor as it both regulates light reaching the vegetation and ground levels, as well as affects other microclimatic conditions important to spiders (Samu et al., 2014). In contrast to our findings, Košulič et al. (2016) recorded a peak in spider functional diversity in more closed canopies, although oak dominated production forests in their study have a different light regime and harbor very different spider assemblages compared to coniferous production forests where our study was performed (Pearce et al., 2004; Finch, 2005). Other studies have shown that canopy thinning greatly increases spider FR and can restore and maintain functional diversity as a regular forest management practice (Šipoš et al., 2017; Vymazalová et al., 2021). This is consistent with our hypothesis that environmental variables within the buffers have a direct effect on functional diversity measures.

Spider RED was negatively affected by bare ground coverage. Increasing bare ground coverage lowers spider abundance and favors specialist species (Costello & Daane, 1998; Horváth et al., 2015)
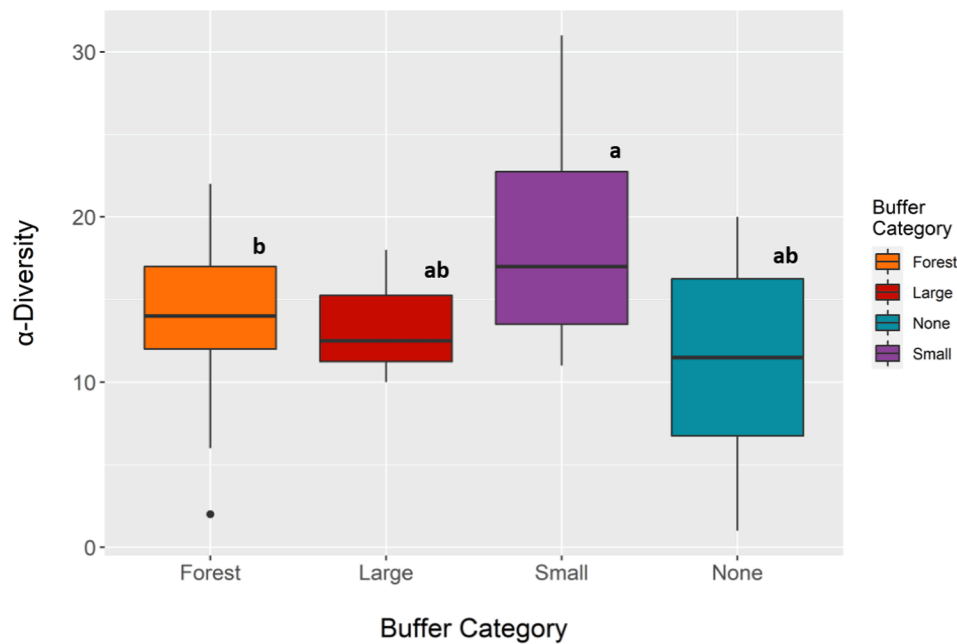
Fig. 3. Boxplots showing significant differences between mean spider α-diversity within each buffer category. Letters above each box plot indicate significant differences calculated in post hoc analysis using pairwise comparisons of estimated marginal means.

Fig. 4. Boxplots showing significant differences between mean spider α-diversity at each sampling distance from the stream edge. Letters above each box plot indicate significant differences calculated in post hoc analysis using pairwise comparisons of estimated marginal means.
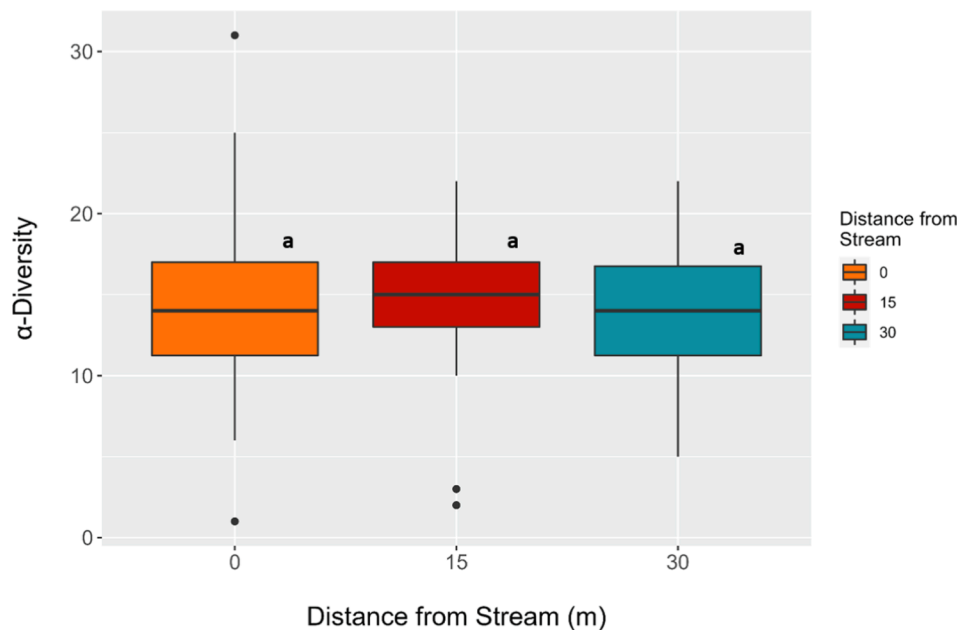
resulting in fewer overlapping species guilds and thus reduced RED. Land use is a disturbance that has been shown to decrease RED (Roubinet et al., 2017; Potapov et al., 2020). Košulič et al. (2016) suggested that intensive post-harvest forest management affecting litter and woody debris created homogenized habitats leading to an overall decrease in spider species redundancy. Our findings suggest that forestry management at our sites is affecting RED, regardless of buffer width, but consistent with other studies where local factors lead to overall reductions in RED.

Plant FR was positively influenced by α-diversity and negatively influenced by buffer density and canopy closure. This agrees with Petchey & Gaston (2002) stating that α-diversity is the most important

driving factor for the FR values, and was further confirmed by our null models. In addition, as new species are added to a system, the chances of adding new traits increases and the functional diversity will increase (Poos et al., 2009). The negative effects found in our models may be explained by the increased buffer density and canopy closure having a direct effect on the forest habitats (Biswas et al., 2019; Hedwall et al., 2019). Forest harvest can have significant negative impacts on plant diversity (Elliott and Vose, 2016; Oldén et al., 2019a) and directly impact forest density and canopy closure. However, even under a negative impact, plant diversity in small or disturbed buffers can create a more heterogeneous community and increase the overall species diversity over time (Elliott & Vose, 2016), thus increasing functional
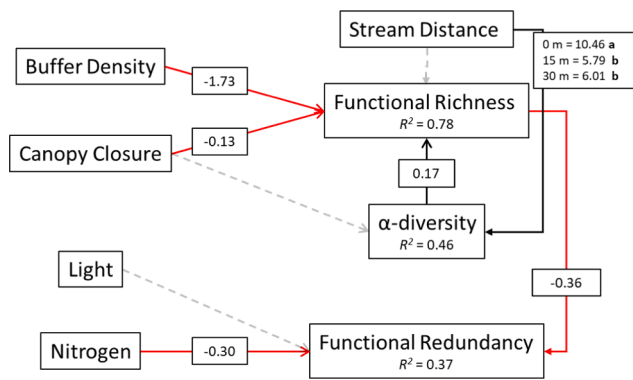
Fig. 5. Piecewise structural equation model showing direct and indirect effects of buffer category and environmental variables on vascular plant FR, RED, and α-diversity. Solid arrows represent significant ($p < 0.05$) interactions between variables. Red and black arrows denote negative or positive standardized coefficients, respectively. Standardized coefficients for continuous variables are in boxes over each significant arrow. Stream Distance reports estimated marginal means of α-diversity for the distance each sampling unit was from the stream. Letters after each marginal mean indicate significant differences between stream distances based on post-hoc tests. Dashed arrows signify no influence of environmental variables on the responses ($p > 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversity. The variables influencing FR in our study have further highlighted how α-diversity and local abiotic factors affect functional diversity in buffered systems.

Vascular plant α-diversity was linked to the distance from the edge of the stream. We believe the higher number of species closest to the stream is related to the extent of the riparian zones. Based on our post hoc species community analysis, 15 species of vascular plants were strongly associated with only the stream edges. Each plant species associated with the stream edge was classified as having a moisture value of>5 (mesic-moist), as defined by Ellenberg et al. (2001) with most of the plants between 7 and 10 suggesting an environment that was consistently moist to nearly always inundated with shallow water. In production forest settings along small streams, stream edges and the

adjacent riparian zone will have a higher α-diversity resulting in higher functional richness. These areas with higher α-diversity should be key areas for protection or forestry practices that maintain such functional diversity.

Plant RED was negatively affected by plant FR and fertility, which was expected as adding new species is likely to introduce new traits into a community, thus reducing the amount of trait overlap, and create a less redundant plant assemblage. In this study, we assume that plant RED is related to spider habitat and function and we chose the plant traits for this comparison (see: Fonseca & Ganade, 2001 regarding trait selection). Therefore, we argue that the increase in plant FR creates an environment that is less functionally redundant in support of spider assemblages. Further, Cornwell and Grubb (2003) concluded that species richness of shade-tolerant plants is higher in nutrient-rich forest sites and we believe that our more fertile sites may have a positive effect on plant species richness. This does not necessarily translate to a decrease in spider FR, but disturbances that negatively affect plant RED may also have direct effects on spider communities (Scheidler 1990; Horváth et al., 2009; Moretti et al., 2013).

An increase in canopy closure was, as the single environmental variable, associated with a decrease in both spider and plant FR. Decreased forest canopy cover is linked to plant species richness increase (Spitale et al., 2009; Widenfalk & Weslien, 2009) and plant functional structure changes (Lanta et al., 2019), both often having a direct linkage to species FR. The direct effects of canopy closure on both spider and plant FR provides an important functional linkage between spider community assemblage and vegetative diversity and structure.

5. Conclusions

Using a fine-level trait-based approach to measure functional diversity, our study showed that forested buffers have a minimal overall impact on spider FR and RED. However, we show that it is important to maintain high levels of α-diversity to preserve and promote both spider and plant FR in production forests. We suggest that forest management practices in and around riparian systems focus on creating environments that conserve and encourage high levels of α-diversity to increase overall functional diversity. Even though we found no direct effect of buffer size on the functional diversity measures of spider or vascular plants,
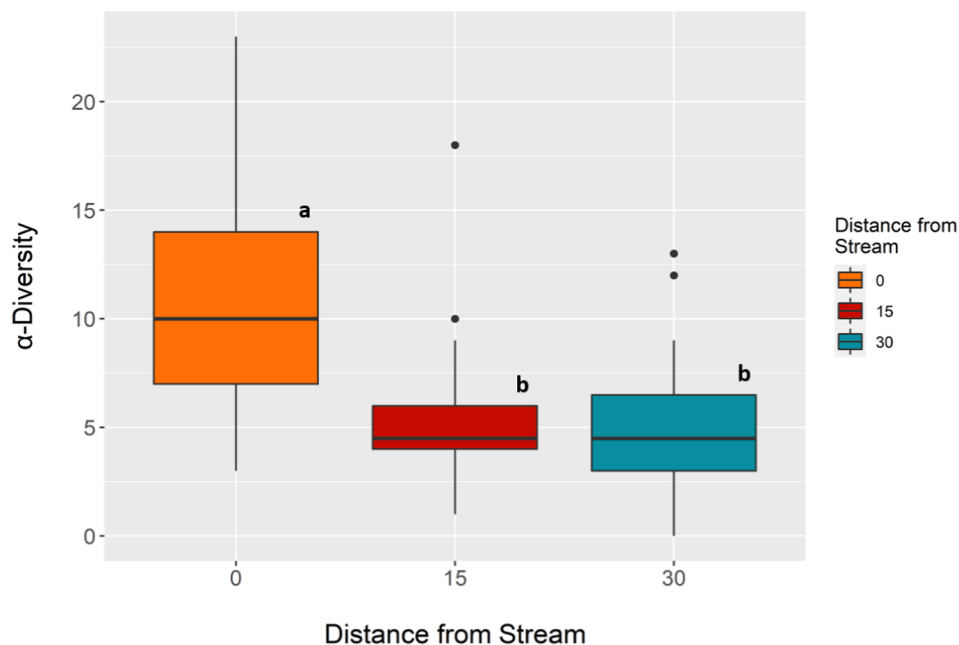

Fig. 6. Boxplots showing significant differences between mean vascular plant α-diversity at each sampling distance from the stream edge. Letters above each box plot indicate significant differences calculated in post hoc analysis using pairwise comparisons of estimated marginal means.

Fig. 7. Boxplots showing significant differences between mean vascular plant α-diversity within each buffer category. Letters above each box plot indicate significant differences calculated in post hoc analysis using pairwise comparisons of estimated marginal means.

riparian buffer strips remain critical to control and maintain riparian zone temperatures, canopy coverage, and humidity–factors that are important to both animal and plant community assemblages (Larrivée et al. 2008; Oldén et al. 2019a; Oldén et al., 2019b). Management of riparian forests through thinning or selected clearing could create a mosaic habitat producing a forested buffer complex enough to maintain high ecological function and heterogeneous enough to provide a wide range of habitats and structure to maximize spider and vascular plant α-diversity, functional diversity, and functional redundancy (Sebek et al., 2016; Gallé et al., 2017). Spider and vascular plant diversity in and around riparian systems in production forests provide a critical piece of the overall ecosystem function and should be part of a multi-taxon monitoring approach (Flensted et al., 2016; Brunbjerg et al., 2018; Lelli et al. 2019). Our study shows a crucial link between species richness and functional diversity, with both direct and indirect abiotic and spatial drivers, and conservation focused forest management can be implemented to maximize species richness (Chaudhary et al., 2016).

Data Availability Statement.

Data are available from Zenodo (https://doi.org/10.5281/zenodo.6997226).

CRediT authorship contribution statement

Jeffery Marker: Methodology, Investigation, Writing – original draft, Formal analysis, Visualization. **Eva Bergman:** Supervision, Writing – review & editing. **Rolf Lutz Eckstein:** Investigation, Supervision, Writing – review & editing. **Denis Lafage:** Conceptualization, Investigation, Funding acquisition, Writing – review & editing, Supervision.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120599.

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