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RESEARCH ARTICLE

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Boreal forest fertilization leads to functional homogenization of ground beetle assemblages

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Abstract

1. Intensive fertilization of young spruce forest plantations (i.e. 'nutrient optimization') has the potential to meet increasing demands for carbon sequestration and biomass production from boreal forests. However, its effects on biodiversity, other than the homogenization of ground-layer plant communities, are widely unknown.
2. We sampled ground beetles (Coleoptera: Carabidae) in young spruce forest plantations of southern Sweden, within a large-scale, replicated ecological experiment initiated in 2012, where half of the forest stands were fertilized every second year. We assessed multi-scale effects of forest fertilization on ground beetle diversity and community assembly, 4 years after commencement of the experiment.
3. We found that nutrient optimization had negative effects on ground beetle diversity at multiple spatial scales, despite having negligible effects on species richness. At the local scale, ground beetle species had lower variation in body size at fertilized sites, resulting in within-site functional homogenization. At the landscape scale, fertilized sites, with higher basal area and lower bilberry cover, filtered carabid traits composition to larger body sizes, generalist predators and summer breeding species.
4. *Synthesis and applications*. Fertilization of young spruce plantations is a strong filter for ground beetle assemblages, leading to functionally homogeneous communities in the short term, without changes in species richness. The large-scale functional impoverishment of carabid communities because of fertilization may have negative consequences on system resilience and on ecosystem service provision by this functionally diverse group. Large-scale establishment of nutrient optimization threatens ground beetle diversity in young conifer plantations, underlining the risks of introducing more intensive management schemes in already heavily managed forest landscapes.

KEYWORDS
biodiversity, community assembly, diversity apportionment, functional homogenization, ground beetles, intensive forest management, nutrient optimization, trait–environment relationship

1 | INTRODUCTION

Intensive forest management, including forest fertilization, has been proposed as a way of fulfilling increasing demands of fossil fuel replacement with woody biomass while contributing to increased carbon sequestration for climate change mitigation (Rytter et al., 2016). Nitrogen fertilization of mature boreal conifer stands is a common practice within intensive forest management, as a method for increasing wood production (Hedwall et al., 2014), overcoming the strong nitrogen limitation of boreal forests (Tamm, 1991). However, a more intensive form of forest fertilization (i.e. 'nutrient optimization', Bergh et al., 2008) has been proposed for implementation in 10%–15% of the productive forest land comprising young Norway spruce (*Picea abies* (L.) Karst.) plantations in Sweden (Larsson et al., 2009). Although nutrient optimization has the potential to meet the increasing demands for carbon sequestration and biomass production, it is watched with concern for its potential negative effects on the environment (Lindkvist et al., 2011).

Together with risks of nutrient leakage and acidification, the main concern regarding forest fertilization has focused on its negative effects on biodiversity (Hedwall et al., 2014). So far, the effects of boreal forest fertilization have focused on the response of understorey vegetation, including shifts in community structure and biodiversity loss. Long-term (>15 years) mature forest fertilization reduces cover of dwarf shrubs, lichen and mosses, favouring grasses and nitrophilous herbs (reviewed in Sullivan & Sullivan, 2018). Short-term nutrient optimization in young spruce plantations has similar negative effects to long-term mature forest fertilization (Hedwall et al., 2010, 2011).

However, the effect of forest fertilization on community structure and diversity of other trophic levels has received very little attention (Sullivan & Sullivan, 2018), which is especially true for research on community assembly mechanism of secondary consumers (Nijssen et al., 2017). Furthermore, given the large-scale focus of nutrient optimization, it is necessary to evaluate the mechanistic basis of fertilization effects at multiple spatial scales (i.e. from within stands to landscapes), linking local and regional effects on diversity through the study of variation in community structure (Socolar et al., 2016). The latter is especially important because short-term nutrient optimization causes plant community structure to become more similar (i.e. biotic homogenization) between forest stands (Hedwall et al., 2011), which may filter local consumer communities towards assemblages dominated with specific trait syndromes and with lower variation in the number of ecosystem functions provided (i.e. functional homogenization; Mori et al., 2018).

In this study, we sampled ground beetles (Coleoptera: Carabidae) to evaluate the relative importance of local and landscape environmental gradients shaped by nutrient optimization in driving consumer community assembly. Ground beetles are abundant, widely distributed and they are important contributors to pest suppression ecosystem services (Riddick, 2008). Moreover, carabids are functionally diverse, with traits related to ecosystem functioning and response to disturbance (Fountain-Jones et al., 2015), and as such, they have been extensively used as bioindicators (Rainio & Niemelä, 2003), with frequent application to forest management (Niemelä et al., 2007). The main objective of our work was to assess how young forest fertilization affects biodiversity and community assembly of ground beetles in the short term. Specifically, we addressed three main questions. First, given the short treatment time, did nutrient optimization affect taxonomic and functional diversity of ground beetles? Second, does carabid community structure suffer from homogenization at local and landscape scales, mirroring fertilization effects on ground-layer vegetation? Third, does forest fertilization filter carabid species traits towards functional homogenization, and is its effect dependent on spatial scale?

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

The study area is situated within the Asa Experimental Forest, southern Sweden (57°10′N, 14°47′E; Figure S1), in the hemiboreal zone (Ahti et al., 1968). The experimental forest comprises 6,000 ha of spruce-dominated forest in different age classes. All study sites were located in young-middle-aged (average ± *SD*: 27.78 ± 4.51 years) spruce-dominated stands with a field layer dominated by *Vaccinium* dwarf shrubs and grasses, and a bottom layer with mosses. Prior to the experiment, all sites were subjected to even-aged forest management, based on clear-cut followed by soil scarification, planting and pre-commercial thinning, 5 years after establishment (Roberge et al., 2020). The study includes 21 stands (range: 1.14–21.40 ha in size) of which 10 were managed according to an intensive fertilization regime and 11 were untreated control stands. Stands are separated by at least 276 meters (average ± *SD*: 1,459 ± 708 m) and geographically interspersed (Figure S1). The first fertilization took place in 2012, with subsequent fertilizations every second year. The total nitrogen, applied as NH_4NO_3, added from 2012 to 2016, ranged from 125 to 150 kg ha^{-1} $year^{-1}$. Phosphorous, potassium, calcium, magnesium, sulphur and boron were also added in variable amounts depending on nutrient concentrations from needle samples collected in the autumn before fertilization.

2.2 | Sampling and carabid traits

Ground beetles were sampled using 10 pitfall traps in each of the 21 sites, during three 6-week periods from mid-May to mid-September, 2016, covering most of the activity season in the region. Traps consisted of a 150-ml plastic container (65 mm in diameter) buried so that the edge was in level with the ground, and filled with 70% propylene glycol and a few drops of detergent. We placed a metal lid 3–5 cm above each trap to prevent rainwater from flooding the traps. In each site, traps were arranged with one trap at the site centroid, and the remainder in three transects with three traps each, heading north, southwest and southeast from the centre and separated by

15 m from the nearest trap. Due to the destruction of 58 samples by wild boar activity, we standardized the sampling to six traps per site with constant spatial location across the three sampling periods (Appendix S1). We pooled ground beetle abundance from three periods (local scale analysis), and from three periods and six traps (landscape-scale analysis). Carabid specimens were identified by an expert taxonomist. Carabid traits related to dispersal, resource acquisition, phenology, habitat affinity and life history were obtained from the literature (Table 1). A detailed account of carabid traits for this study plus sources of information are provided in Table S1 and Appendix S8.

2.3 | Environmental data

Data on forest structure and composition were sampled in 2017, measuring diameter, count and species identity of all trees with a stem with diameter greater than 2 cm, within ten 100 m^2 circular plots centred on pit fall trap location (Figure S2). We established three stem diameter classes: small (from minimum to median diameter, 2–9.8 cm, $N = 2{,}463$ stems), medium (from median to 3rd quartile diameter, 9.9–12.8 cm, $N = 1{,}188$ stems) and large (from 3rd quartile to maximum diameter, 12.9–42.3 cm, $N = 1{,}205$ stems). For each plot within sites, we calculated 24 variables based on field measurements on forest structure and composition (Table S2).

Quantitative data on ground vegetation were sampled in 2016, scoring relative abundances of all vascular plants and bryophytes using a modified version of the point intercept method (Appendix S2; Jonasson, 1988) on three 30 m transects per site (Figure S2). We obtained seven variables from the quantitative sampling of ground vegetation for each plot within sites (Table S2). Additionally, Ellenberg indicator values (Ellenberg & Leuschner, 2010) for light (L), temperature (T), moisture (F), pH (R) and nitrogen (N) were calculated for each plot as community-weighted means. Qualitative data on ground vegetation were sampled on 2016, identifying all ground-layer species within four 1-m^2 quadrats per site (Figure S2). Species richness of all species, dwarf shrubs, grasses, mosses and herbs was assessed as a measure of ground-layer community structure (Table S2).

2.4 | Data analysis

Statistical analyses were performed in R Version 3.6.0 (R Development Core Team, 2019). We assessed differences in carabid total (γ) diversity between fertilized and control sites by the use of rarefaction curves. Carabid total species richness and Simpson diversity were compared among treatments by rarefaction/extrapolation curves based on equal sample size per habitat, in the R-package iNEXT (Hsieh et al., 2020). We compared total functional diversity among treatments by sample-based rarefaction curves of Rao quadratic diversity (Rao, 1982) calculated from data on relative abundances (Ricotta et al., 2012).

We used additive apportionment of species richness, Gini–Simpson index (Lande, 1996) and Rao quadratic diversity (APQE; Pavoine & Dolédec, 2005) to quantify changes in taxonomic and functional diversity across hierarchical scales of trap within site (β_{trap}), and site within landscape (β_{site}) for each treatment. The apportionment of diversity allows us to explore the existence of biotic homogenization at different spatial scales when assessing β-diversity differences between treatments. Significances of diversity components α_{trap} (within-trap diversity), β_{trap} and β_{site} were assessed by comparison with appropriate null matrices depending on spatial scale (Appendix S3). Apportionment of species richness and Gini–Simpson

TABLE 1 Summary of carabid traits included in this study. A detailed account of carabid traits in Table S1, with data sources in Appendix S8

Trait	Type	Description
Body size	Quantitative	Relative body size in reference to the largest species, scored as 1.0
Wing development	Quantitative	Brachypterous (0), dimorphic (0.5), winged (1)
Food of adult	Nominal	Specialist predator, generalist predator, omnivorous, herbivorous
Eye–head ratio	Ordinal	Ratio eye–head surface: 1 (<10%), 2 (10%–25%), 3 (25%–50%)
Start of activity season	Ordinal	First catch on June–July (1), July–August (2), August–September (3)
Mean activity season	Ordinal	Catch on one, two or three sampling periods
Forest specialization	Nominal	Stenotopic, generalist on woody habitats, eurytopic
Moisture requirements	Ordinal	From 1–6: xeric, fairly dry, Mesic, Mesic-humid, moist, very wet
Light requirements	Quantitative	Low (0), moderate (0.5), high (1)
Breeding season	Nominal	Spring, Summer, Autumn
Overwintering stage	Nominal	Adult, mostly larva
Life cycle duration	Nominal	One or two years

index were implemented in the R-package VEGAN (Oksanen et al., 2019). APQE was conducted using R-codes adapted from those provided as Supporting Information in Pavoine et al. (2016). We assessed significance among diversity components as well as among total diversity of different treatments using *z*-tests on confidence interval overlap, following Schenker and Gentleman (2001).

We analysed the multi-scale environmental filtering of ground beetle species traits after forest fertilization by applying the methodology developed by Pavoine et al. (2011), in which species traits are connected with the environment, and environment is connected with spatial variation by an extension of the RLQ ordination analysis (Dolédec et al., 1996). This analysis uses three data matrices: matrix R (sites × environment), matrix L (sites × species) and matrix Q (species × traits), identifying main co-structures between traits and environmental variables mediated by species abundances (Thioulouse et al., 2018). In the current application, matrices R and L contain environmental factors and species abundances per trap within site (local RLQ) or forest site (landscape RLQ), depending on the scale of RLQ analysis.

We followed the procedures in Declerck et al. (2011), to obtain spatial predictors for geographically nested designs. The landscape scale was represented by a matrix filled with Moran's eigenvector maps (MEM; Dray et al., 2006), and by an inter-site spatial component, consisting of a matrix of dummy variables corresponding to forest site identity matrix (ID). The local scale was represented by a within-site spatial component consisting of a staggered matrix filled with MEM (more details on the computation of spatial matrices in Appendix S4). Matrix R is defined by the juxtaposition of a matrix E of standardized environmental variables (centred by the mean, scaled by *SD* and Box-Cox transformed), a matrix S of MEM, a matrix ID for the local RLQ and a matrix T (dummy variable for landscape-scale treatment) for the landscape RLQ.

We selected environmental and spatial variables that maximize the sum of trait–environment correlation (correlation L; Thioulouse et al., 2018) for the first two RLQ axes of environmental and spatial RLQs with all carabid traits considered. For every possible variable combination, we used a modification of procedures from Bernhardt-Römermann et al. (2008) to detect the optimal variable combination in E and S matrices (details in Appendix S5). After variable selection, we selected carabid traits by the application of the multivariate version of the fourth-corner analysis (S_{RLQ}), based on the sum of all eigenvalues of environmental RLQs for each trait separately (as in Pavoine et al., 2011). We used null model 4 from Dray and Legendre (2008) for testing S_{RLQ} significance, that is, permuting columns of matrix L. Significance under column permutation allows us to select traits linked to species distribution among traps or forest sites (Peres-Neto et al., 2017). Significance of RLQs was assessed by the use of both column (model 4) and row (model 2) permutation tests, considering a trait–environment link significant if *p* values from both tests are less than the nominal α level of 0.05 (ter Braak et al., 2012).

We partitioned the variation in environmental variables (matrix E) into their spatial and treatment components by redundancy analysis, and evaluated the contribution of components to trait–environment relationship following a modification of Pavoine et al.'s (2011) protocol (Appendix S6). We identified species clusters within RLQ ordination space (‘trait syndromes’, Appendix S7) following Kleyer et al. (2012). Analyses of the trait–environment relationship were implemented in R-package ADE4 (Dray et al., 2020).

3 | RESULTS

We collected 1,154 individuals of 25 ground beetle species from 8 fertilized (48 traps) and 10 control (60 traps) sites (Table S3). Fertilized forest sites were characterized by higher spruce basal area (corresponding to an average 7% increase in spruce canopy cover, following models from Korhonen et al., 2007), higher herb species richness and higher nitrogen indicator values. Control sites had much higher dwarf shrub cover, especially for heather and bilberry, and higher total moss cover, with *Hylocomium splendens* dominating on the basal layer (Table S2).

Total carabid species richness was not significantly different between control and fertilized sites ($z = 0.71$, $p = 0.869$). However, both Simpson ($z = 5.35$, $p =$ 9e-08) and functional diversity ($z = 8.01$, $p <$ 1e-15) were 1.5 and 1.2 times, respectively, higher in control compared with fertilized forest sites (Figure 1).

Additive apportionment of carabid species richness revealed β-diversity among sites as the main contributor to total species richness for both treatments, with no difference among diversity components between treatments (Figure 2a). Total Gini–Simpson index and Rao's quadratic entropy were mostly determined by α-diversity (Figure 2b,c). Control forest sites had higher β_{trap} than fertilized sites (Gini–Simpson index: $z = 2.35$, $p = 0.019$; Rao's *Q* index: $z = 2.51$, $p = 0.012$), with this difference accounting for the higher site and landscape Simpson and functional diversities of control sites. However, community variation among traps within sites (β_{trap}) was not different from the random expectation for all partitions, indicating lack of species aggregation nor differentiation within forest sites (Table 2).

We found a single trait (body size) linked with species distributions at the local scale (Table S4). The main contributor to ground beetle community assembly at this scale was the inter-site spatial component (matrix ID), which was the only environmental factor correlated with body size distribution among traps within sites (under both column and row permutation schemes, Table 3). Spatially structured environmental variation within sites accounted for a very small portion of trait–environment correlation (Table 3). Carabid functional groups were distributed along the first RLQ axis, with a higher variety of carabid size-groups distributed on control sites, and the largest size-groups mainly related to fertilized sites (Figure 3a).

At the landscape scale, we found three carabid traits correlated with environmental variables: body size, breeding season and food of adult (Table S4). There was a significant relationship between traits and environmental (spatial and environmental variables) and fertilization factors at this scale (Table 3). Environmental effects on community assembly were mediated by fertilization and forest

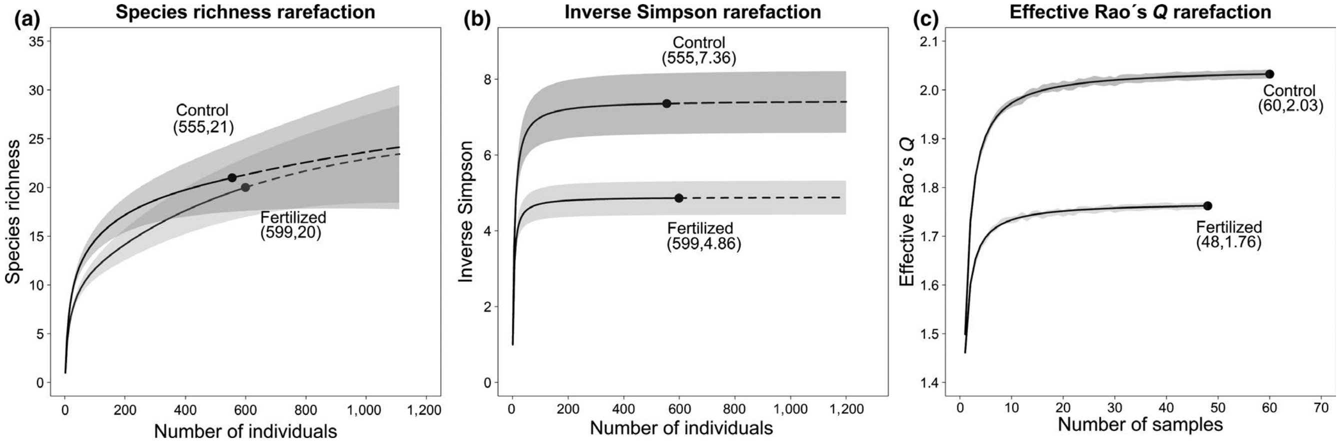

FIGURE 1 Rarefaction (solid line) and extrapolation (dashed line) plots with 95% confidence intervals (shaded areas) comparing (a) ground beetle species richness and (b) ground beetle Simpson diversity, and (c) effective functional diversity in fertilized and control forest sites. Reference (observed) samples are indicated by solid black dots. The numbers in parentheses show the x- and y-axis coordinates for each point

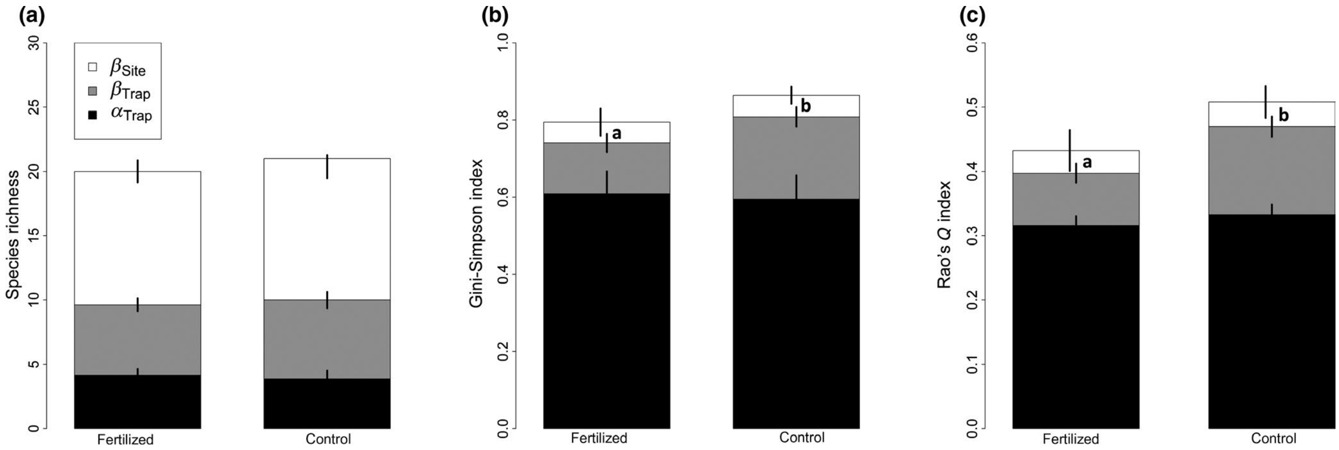

FIGURE 2 Mean α- and β-diversity values (± SE) for (a) carabid species richness, (b) carabid Gini–Simpson index and (c) carabid Rao's Q index. Diversity component α_{Trap} stands for average trap diversity, β_{Trap} for diversity among traps, within sites, and β_{Site} for diversity among forest sites. Different lowercase letters indicate significant differences in diversity components between each treatment

site geographical location (Figures S3 and S4). Fertilized sites had higher basal area and lower bilberry cover, filtering carabid traits composition to larger body sizes, generalist predation and summer breeding species (Figure 3b). Spruce stem density, related with pre-commercial thinning intensity, reinforced basal area effects on community assembly (Figure 3b; Table S3). Control sites contained higher diversity of body sizes, feeding guilds and breeding seasons for carabid species (Figure 3b; Table S5).

4 | DISCUSSION

Our study shows that intensive forest fertilization of young spruce plantations (i.e. nutrient optimization) has negative short-term effects on ground beetle diversity, revealing mechanisms of secondary consumer community assembly driven by forest fertilization. Nutrient optimization increases spruce basal area, which decreases light availability through increased canopy cover. Lower sunlight irradiation was found as the main filter of ground beetle community assembly, either directly, selecting species with larger body size, or indirectly, by changing understorey plant community structure. By filtering body size to larger species, fertilization causes local-scale functional homogenization, which, in turn, reduces functional diversity at the landscape scale.

We found that short-term nutrient optimization had negative effects on carabid site (α_{site}) and landscape (γ) abundance-weighted and functional diversities, a pattern consistent with the reduction in carabid diversity related to canopy closure (Koivula et al., 2002; Spake et al., 2016). Canopy closure has also been related to lower variation in carabid community structure among traps within forest sites (β_{trap}), with biotic homogenization of closed-canopy forests ascribed to lower levels of environmental heterogeneity (Niemelä et al., 1996). Our results show a similar pattern, with β_{trap} values in both control and fertilized sites that did not deviate from the random

TABLE 2 Hierarchical additive apportionment of species richness, Gini–Simpson index and Rao's *Q* index for carabid species. *p* values obtained by comparing observed values with the distribution of expected values taken from 999 randomizations. Bold type indicates significant results. Equivalent number of species and sites for Gini–Simpson index and APQE calculated following Pavoine et al. (2016)

Species richness^{a}		***p* value**^{b}	**Equivalent no**
Fertilized			
α_{trap}	4.146 (21%)	**0.001^{L}**	4.146
β_{trap}	5.479 (27%)	0.980	5.479
β_{site}	10.375 (52%)	0.071^{H}	10.375
γ	20		20
Control			
α_{trap}	3.883 (18%)	**0.001^{L}**	3.883
β_{trap}	6.117 (29%)	0.203	6.117
β_{site}	11.000 (52%)	**0.001^{H}**	11.000
γ	21		21
Gini–Simpson index^{a}			
Fertilized			
α_{trap}	0.609 (77%)	**0.001^{L}**	2.557
β_{trap}	0.132 (16%)	0.354	1.507
β_{site}	0.068 (7%)	**0.001^{H}**	1.262
γ	0.794		4.863
Control			
α_{trap}	0.594 (69%)	**0.001^{L}**	2.466
β_{trap}	0.213 (25%)	0.189	2.111
β_{site}	0.060 (6%)	**0.047^{H}**	1.413
γ	0.864		7.357
Apportionment of quadratic entropy (APQE)^{a}			
Fertilized			
α_{trap}	0.316 (73%)	**0.001^{L}**	1.461
β_{trap}	0.082 (19%)	0.312	1.135
β_{site}	0.035 (8%)	**0.001^{H}**	1.062
γ	0.433		1.762
Control			
α_{trap}	0.333 (65%)	**0.001^{L}**	1.499
β_{trap}	0.137 (27%)	0.361	1.258
β_{site}	0.038 (8%)	**0.019^{H}**	1.078
γ	0.508		2.033

[a] Percentage of total diversity for each component in brackets.

[b] Superscripts L and H indicate diversity component lower and higher than expected by chance.

expectation, suggesting environmental homogeneity within sites typical of dense plantation forests (Puetmann et al., 2009). However, fertilized sites had lower β_{trap} values than control sites, indicating even lower values for environmental heterogeneity within fertilized sites, which may be explained by levelled environmental conditions because of denser canopy cover (Nijssen et al., 2017), and increased spatial homogeneity of understorey vegetation following fertilization (Gilliam, 2006).

Nutrient optimization did not affect carabid species richness nor increased homogenization of community composition (i.e. incidence-based) in our system. This result is driven by the typical carabid species-abundance distribution in closed-canopy boreal forests, with very few dominant species, and absence of species of intermediate abundance (Niemelä, 1993). In our sites, forest fertilization mainly affected relative abundance of dominant species by trait filtering, driving functional homogenization by the selection of a very limited assortment of trait values.

At the local scale (i.e. within sites), body size was filtered by landscape-scale processes, with fertilized sites selecting for larger ground beetles. This pattern of ground beetle community assembly has been linked to predictions from the habitat templet theory (Southwood, 1977, 1988), in which species in predictable, adverse and spatially homogeneous habitats (e.g. fertilized forests) tend to be larger, and to have lower fecundity and lower dispersal abilities (Ribera et al., 2001). The carabid species that were dominant on fertilized sites in our system comply with predictions from the habitat template theory: they are large (Figure 3a, group E: average size = 30 mm, *Carabus glabratus* and *C. violaceus*; group D: average size = 24.5 mm, *C. hortensis* and *C. nemoralis*), have lower fecundity (Grüm, 1984) and are brachypterous with low dispersal abilities (Brouwers & Nweton, 2009). Furthermore, large carabid species from our sites are mainly nocturnal in Central Europe (Lindroth, 1992), so they may select closed-canopy forests because of lower detectability by predators, or because their lower surface–volume ratio may allow them to thrive in habitats with lower sunlight irradiation (Guevara & Avilés, 2013).

At the landscape scale, environmental gradients of basal area and bilberry cover structured by nutrient optimization, together with spatially structured gradients of spruce stem density and bilberry cover, act as dominant filters, organizing Carabidae community assembly. The first RLQ axis, explaining most of the variance in the environmental and trait data, followed a gradient of canopy cover, with fertilized sites associated with high total basal area (Figure 3b; Figure S3). At each extreme of the gradient in canopy cover, large, generalist predator species, breeding in summer (Figure 3b, Group B1) dominated in fertilized sites, while small, spring breeding omnivores (Figure 3b, Group D1) were most abundant in control sites. In between both extremes, other trait syndromes with greater trait diversity were mainly distributed in control sites, with larger species distributed also in fertilized sites (Figure 3b; Table S5). Cooler closed-canopy fertilized sites will favour the development of summer breeding species with overwintering larvae, reducing the risk of desiccation while spring breeding species with overwintering adults will favour warmer temperatures in more open habitats for the rapid development of their larvae (Butterfield, 1997).

The second landscape RLQ axis followed a gradient of bilberry cover structured both spatially and by nutrient optimization (Figure 3b; Table S4). Autumn breeding predatory species were associated with high bilberry cover in control sites (Figure 3b, groups A1,

TABLE 3 Results from RLQ ordination, depicting the association between environmental variables (E), spatial variation (S), site identity (ID) and treatment (T) with carabid traits at local (body size) and landscape (body size, food of adult and breeding season) scales

Site scale RLQ (among traps, within sites)	**Observed inertia 1st axis[a]**	**Observed inertia 2nd axis[a]**	**Correlation L 1st axis (ratio)[b]**	**Correlation L 2nd axis (ratio)[b]**	***p* value[c]**
All (E + S + T)	0.206 (100%)	—	0.403 (0.511)	—	**Mod2 = 0.001** Mod4 = 0.062
Environment (E)	0.173 (100%)	—	0.382 (0.485)	—	Mod2 = 0.909 **Mod4 = 0.037**
Pure environment (E | S + ID)	0.010 (100%)	—	0.338 (0.428)	—	Mod2 = 0.735 Mod4 = 0.188
Space (S)	0.164 (100%)	—	0.378 (0.479)	—	Mod2 = 0.849 Mod4 = 0.538
Site Id (ID)	0.173 (100%)	—	0.403 (0.211)	—	**Mod2 = 0.001** **Mod4 = 0.019**
Pure spatial (S + ID | E)	0.189 (100%)	—	0.375 (0.476)	—	**Mod2 = 0.001** Mod4 = 0.079
Spatially structured environment ($E \cap S + ID$)	1.8e-05 (100%)	—	0.387 (0.491)	—	**Mod2 = 0.001** **Mod4 = 0.002**
Landscape-scale RLQ (among sites)	**Observed inertia 1st axis[a]**	**Observed inertia 2nd axis[a]**	**Correlation L 1st axis (ratio)[b]**	**Correlation L 2nd axis (ratio)[b]**	***p* value[c]**
All (E + S + T)	1.089 (92.11%)	0.044 (3.7%)	0.413 (0.760)	0.182 (0.411)	**Mod2 = 0.001** **Mod4 = 0.004**
Environment (E)	0.471 (93%)	0.019 (3.8%)	0.392 (0.721)	0.142 (0.319)	**Mod2 = 0.001** **Mod4 = 0.001**
Pure environment (E | S + T)	0.039 (64.2%)	0.017 (28%)	0.165 (0.304)	0.157 (0.354)	Mod2 = 0.510 Mod4 = 0.268
Space (S)	0.412 (88.3%)	0.031 (6.6%)	0.406 (0.747)	0.168 (0.379)	**Mod2 = 0.009** **Mod4 = 0.024**
Treatment (T)	0.226 (100%)	—	0.321 (0.591)	—	**Mod2 = 0.010** **Mod4 = 0.033**
Pure spatial (S | E + T)	0.046 (66.6%)	0.012 (17.2%)	0.154 (0.284)	0.133 (0.299)	Mod2 = 0.951 Mod4 = 0.831
Spatially structured environment ($E \cap S$)	0.360 (100%)	—	0.404 (0.743)	—	**Mod2 = 0.001** **Mod4 = 0.002**
Fertilization structured environment ($E \cap T$)	0.341 (100%)	—	0.361 (0.644)	—	**Mod2 = 0.003** **Mod4 = 0.036**

[a] Observed inertia (trait–environment squared covariance), followed by % of total variation explained in brackets.

[b] Correlation L (trait–environment correlation) followed by ratio of observed to maximum correlation in brackets.

[c] Mod2 corresponds to matrix L row permutation test and Mod4 to matrix L column permutation test, bold type indicates significant results.

A2), and herbivore ground beetles were mainly distributed on sites with very low bilberry cover (Figure 3b, groups E1, E2). Short-term forest fertilization reduces bilberry cover by increasing canopy cover (Hedwall et al., 2010). Autumn breeder species association with high bilberry cover in our results suggests an alternative strategy for coping with high temperatures, benefiting from shrub shading, as they intergrade in phenology with summer breeder carabids in Scandinavia (Andersen & Hanssen, 2015). Reduction in bilberry cover from fertilized sites is associated with large reductions in moss cover because of direct toxicity (Kellner, 1993). Moss cover and habitat openness favour epigaeic Collembola species (Salmon et al., 2014), which are the preferred prey item for small oligophages (Hengeveld, 1980), dominating in control sites. Conversely, sites with low bilberry cover had larger relative abundance of herbs and grasses, which may favour seed feeder ground beetles (Lundgren, 2009).

5 | CONCLUSIONS

Large-scale intensive fertilization of young spruce forest plantations reduces ground beetle diversity at landscape scale through functional homogenization of local assemblages in the short term. This effect has high probability of being carried over time, as closed-canopy cover causes shifts in carabid functional composition, which are not alleviated by commercial thinning operations (Niemelä et al., 2007). Our results are especially relevant for boreal

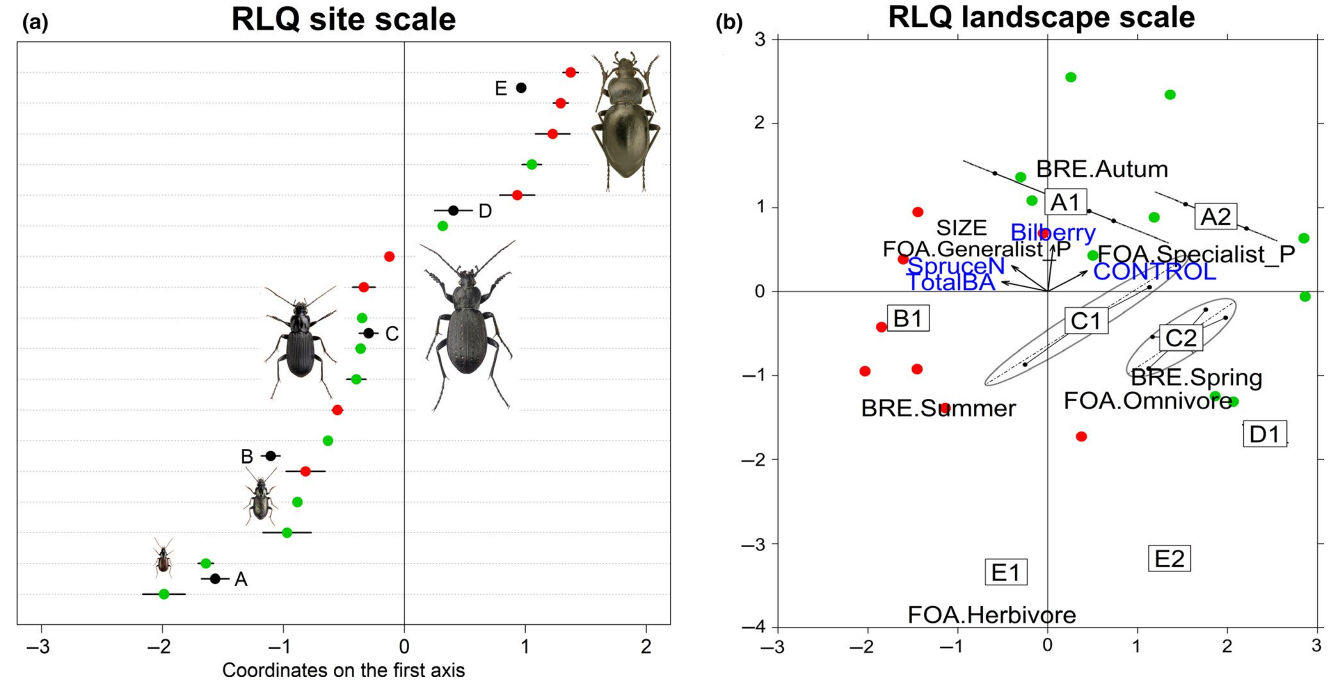

FIGURE 3 Effects of environmental variables and species traits with position of derived functional groups on (a) the first axis of local scale RLQ analysis and on (b) the ordination space of landscape-scale RLQ analysis. For the local scale RLQ (a), red and green dots represent average site coordinates from fertilized and control sites, with *SD* given by segment length. Inset pictures in (a) representing dominant carabid species for each functional group in the same size scale, from left to right (all pictures from SLU Artdatabanken): *Agonum fuliginosum* (group A), *Pterostichus oblongopunctatus* (group B), *Pterostichus niger* (group C), *Carabus hortensis* (group D) and *Carabus glabratus* (group E). Black dots in (a) represent average species scores for each functional group, with *SD* given by segment length. For the landscape-scale RLQ (b), red and green dots represent fertilized and control site scores, boxed labels stand for derived functional groups (Table S5 and Discussion section), black plain labels stand for species traits and arrows with blue plain labels stand for environmental variables. Abbreviations in (b) for traits and variables: FOA, food of adult; BRE, breeding season; SIZE, body size; Bilberry, bilberry cover; TotalBA, total basal area, SpruceN, spruce stem density; CONTROL, no fertilization

forest management landscapes in Fennoscandia, where large areas of forest are intensively managed (Hedwall et al., 2019), but trait filtering effects found in this study are probably applicable to other forest systems and management types involving canopy closure (Sklodowski, 2006). The implementation of nutrient optimization over large forest areas could have a potentially catastrophic effect on carabid resilience to disturbance, as functional homogenization of local communities across the landscape can increase vulnerabilities to large-scale disturbance events (Olden et al., 2004). Furthermore, changes in carabid functional composition are highly congruent with functional changes in other boreal forest taxa (Aubin et al., 2013), which can cause widespread functional homogenization, affecting the whole system resilience. Added to this, functional homogenization of carabid body size to larger size classes constraints the range size of consumed prey (Jelaska et al., 2014) and could impair forest pest regulation by this functionally diverse group of epigaeic arthropods.

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AUTHORS' CONTRIBUTIONS

T.L., J.S.t. and J.S.j. came up with the original idea for the study, and designed and initiated the field sampling; A.R., together with T.L. and A.-M.H., conceived the idea for the current study; A.R. planned and executed data analyses, and wrote the first draft of the manuscript as leading author. All authors contributed critically to the manuscript drafts and approval of the publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.t76hdr80j (Rodríguez et al., 2021).

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REFERENCES

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, *5*, 169–211. https://www.jstor.org/stable/23724233

Andersen, J., & Hanssen, V. K. G. (2015). The life cycles of carabid beetles (Coleptera, Carabidae) in wetlands and forests in Northern Norway. *Norwegian Journal of Entomology*, *62*, 140–153. http://www.entomologi.no/journals/nje/2015-2/pdf/nje-vol62-no2-140-153-andersen.pdf

Aubin, I., Venier, L., Pearce, J., & Moretti, M. (2013). Can a trait-based multi-taxa approach improve our assessment of forest management impact on biodiversity? *Biodiversity and Conservation*, *22*, 2957–2975. https://doi.org/10.1007/s10531-013-0565-6

Bergh, J., Nilsson, U., Grip, H., Hedwall, P.-O., & Lundmark, T. (2008). Effects of frequency of fertilization on production, foliar chemistry and nutrient leaching in young Norway spruce stands in Sweden. *Silva Fennica*, *42*(5), 225. https://doi.org/10.14214/sf.225

Bernhardt-Römermann, M., Römermann, C., Nuske, R., Parth, A., Klotz, S., Schmidt, W., & Stadler, J. (2008). On the identification of the most suitable traits for plant functional trait analysis. *Oikos*, *117*, 1533–1541. https://doi.org/10.1111/j.2008.0030-1299.16776.x

Brouwers, N. C., & Newton, A. C. (2009). Movement rates of woodland invertebrates: A systematic review of empirical evidence. *Insect Conservation and Diversity*, *2*, 10–22. https://doi.org/10.1111/j.1752-4598.2008.00041.x

Butterfield, J. (1997). Carabid community succession during the forestry cycle in conifer plantations. *Ecography*, *20*, 614–625. https://doi.org/10.1111/j.1600-0587.1997.tb00430.x

Declerck, S. A. J., Coronel, J. S., Legendre, P., & Brendonck, L. (2011). Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of high-Andes wetlands. *Ecography*, *34*, 296–305. https://doi.org/10.1111/j.1600-0587.2010.06462.x

Dolédec, S., Chessel, D., ter Braak, C. J. F., & Champely, S. (1996). Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics*, *3*, 143–166. https://doi.org/10.1007/BF02427859

Dray, S., Dufour, A.-B., & Thioulouse, J. (2020). *ade4: Analysis of ecological data: Exploratory and Euclidean methods in environmental sciences*. R-package version 1.7-15. https://cran.r-project.org/web/packages/ade4/index.html

Dray, S., & Legendre, P. (2008). Testing the species-traits environment relationship: The fourth-corner problem revisited. *Ecology*, *89*(12), 3400–3412. https://doi.org/10.1890/08-0349.1

Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: A comprehensive framework for principal coordinate of neighbor matrices (PCNM). *Ecological Modelling*, *196*, 483–493. https://doi.org/10.1016/j.ecolmodel.2006.02.015

Ellenberg, H., & Leuschner, C. (2010). *Vegetation Mitteleuropas mit den Alpen* (6th ed.). Verlag Eugen Ulmer.

Fountain-Jones, N. M., Baker, S. C., & Jordan, G. J. (2015). Moving beyond the guild concept: Developing a practical functional trait framework for terrestrial beetles. *Ecological Entomology*, *40*, 1–13. https://doi.org/10.1111/een.12158

Gilliam, F. S. (2006). Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, *94*, 1176–1191. https://doi.org/10.1111/j.1365-2745.2006.01155.x

Grüm, L. (1984). Carabid fecundity as affected by extrinsic and intrinsic factors. *Oecologia*, *65*, 114–121. https://doi.org/10.1007/BF00384473

Guevara, J., & Avilés, L. (2013). Community-wide body size differences between nocturnal and diurnal insects. *Ecology*, *94*(2), 537–543. https://doi.org/10.1890/12-0030.1

Hedwall, P.-O., Brunet, J., Nordin, A., & Bergh, J. (2011). Decreased variation of forest understory vegetation is an effect of fertilization in young stands of *Picea abies*. *Scandinavian Journal of Forest Research*, *26*(Suppl. 11), 46–55. https://doi.org/10.1080/02827581.2011.564397

Hedwall, P.-O., Gong, P., Ingerslev, M., & Bergh, J. (2014). Fertilization in northern forests – Biological, economic and environmental constraints and possibilities. *Scandinavian Journal of Forest Research*, *29*, 301–311. https://doi.org/10.1080/02827581.2014.926096

Hedwall, P.-O., Gustafsson, L., Brunet, J., Lindbladh, M., Axelsson, A.-L., & Strengbom, J. (2019). Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities. *Ecological Applications*, *29*(4), e01874. https://doi.org/10.1002/eap.1874

Hedwall, P.-O., Nordin, A., Brunet, J., & Bergh, J. (2010). Compositional changes of forest-floor vegetation in young stands of Norway spruce as an effect of repeated fertilization. *Forest Ecology and Management*, *259*, 2418–2425. https://doi.org/10.1016/j.foreco.2010.03.018

Hengeveld, R. (1980). Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). *Netherlands Journal of Zoology*, *30*(4), 564–584. https://doi.org/10.1163/002829679X00197

Hsieh, T. C., Ma, K. H., & Chao, A. (2020). *iNEXT: Interpolation and extrapolation for species diversity*. R-package version 2.0.20. https://cran.r-project.org/web/packages/iNEXT/index.html

Jonasson, S. (1988). Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, *52*, 101–106. https://doi.org/10.2307/3565988

Kellner, O. (1993). Effects on associated flora of sylvicultural nitrogen fertilization repeated at long intervals. *Journal of Applied Ecology*, *30*, 563–574. https://doi.org/10.2307/2404195

Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., Thuiller, W., & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: Which multivariate methods? *Journal of Vegetation Science*, *23*, 805–821. https://doi.org/10.1111/j.1654-1103.2012.01402.x

Koivula, M., Kukkonen, J., & Niemelä, J. (2002). Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation*, *11*, 1269–1288. https://doi.org/10.1023/A:1016018702894

Korhonen, L., Korhonen, K. T., Stenberg, P., Maltamo, M., & Rautianen, M. (2007). Local models for forest canopy cover with beta regression. *Silva Fennica*, *41*(4), 671–687. https://doi.org/10.14214/sf.275

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, *76*, 5–13. https://www.jstor.org/stable/pdf/3545743.pdf

Larsson, S., Lundmark, T., & Ståhl, G. (2009). *Möjligheter till intensivodling av skog. Slutrapport från regeringsuppdrag Jo 2008/1885*. Swedish University of Agricultural Sciences (SLU).

Lindkvist, A., Kardell, Ö., & Nordlund, C. (2011). Intensive forestry as progress or decay? An analysis of the debate about forest fertilization in Sweden, 1960–2010. *Forests*, *2*, 112–146. https://doi.org/10.3390/f2010112

Lindroth, C. H. (1992). *Ground beetles (Carabidae) of Fennoscandia. A zoogeographic study. Part I. Specific knowledge regarding the species*. Amerind Publishing.

Lundgren, J. G. (2009). The seed feeders. In *Relationships of natural enemies and non-prey foods*. Springer Nature. https://doi.org/10.1007/978-1-4020-9235-0_9

Mori, A. S., Isbell, F., & Seidl, R. (2018). β-diversity, community assembly and ecosystem functioning. *Trends in Ecology & Evolution*, *33*(7), 549–564. https://doi.org/10.1016/j.tree.2018.04.012

Niemelä, J. (1993). Mystery of the missing species: Species-abundance distribution of boreal ground-beetles. *Annales Zoologici Fennici*, *30*, 169–172. https://www.jstor.org/stable/23735394

Niemelä, J., Haila, Y., & Punttila, P. (1996). The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography*, *19*, 352–368. https://doi.org/10.1111/j.1600-0587.1996.tb01264.x

Niemelä, J., Koivula, M., & Kotze, D. J. (2007). The effects of forestry on carabid beetles (Coleoptera: Carabidae) in boreal forests. *Journal of Insect Conservation*, *11*, 5–18. https://doi.org/10.1007/s10841-006-9014-0

Nijssen, M. E., WallisDeVries, M. F., & Siepel, H. (2017). Pathways for the effects of increased nitrogen deposition on fauna. *Biological Conservation*, *212*, 423–431. https://doi.org/10.1016/j.biocon.2017.02.022

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community ecology package*. R-package version 2.5-6. https://cran.r-project.org/web/packages/vegan/index.html

Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, *19*(1), 18–24. https://doi.org/10.1016/j.tree.2003.09.010

Pavoine, S., & Dolédec, S. (2005). The apportionment of quadratic entropy: A useful alternative for partitioning diversity in ecological data. *Environmental and Ecological Statistics*, *12*, 125–138. https://doi.org/10.1007/s10651-005-1037-2

Pavoine, S., Marcon, E., & Ricotta, C. (2016). 'Equivalent numbers' for species, phylogenetic or functional diversity in a nested hierarchy of multiple scales. *Methods in Ecology and Evolution*, *7*, 1152–1163. https://doi.org/10.1111/2041-210X.12591

Pavoine, S., Vela, E., Gachet, S., de Bélair, G., & Bonsall, M. B. (2011). Linking patterns in phylogeny, traits, abiotic variables and space: A novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology*, *99*, 165–175. https://doi.org/10.1111/j.1365-2745.2010.01743.x

Peres-Neto, P. R., Dray, S., & ter Braak, C. J. F. (2017). Linking trait variation to the environment: Critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography*, *40*, 806–816. https://doi.org/10.1111/ecog.02302

Puetmann, K. J., Coates, K. D., & Messier, C. (2009). *A critique of silviculture. Managing for complexity*. Island Press.

R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.r-project.org/

Rainio, J., & Niemelä, J. (2003). Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, *12*, 487–506. https://doi.org/10.1023/A:1022412617568

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*, *21*, 24–43. https://doi.org/10.1016/0040-5809(82)90004-1

Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, *82*(4), 1112–1129. https://doi.org/10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2

Ricotta, C., Pavoine, S., Bacaro, G., & Acosta, A. T. R. (2012). Functional rarefaction for species abundance data. *Methods in Ecology and Evolution*, *3*, 519–525. https://doi.org/10.1111/j.2041-210X.2011.00178.x

Riddick, E. W. (2008). Ground beetle (Coleoptera: Carabidae) feeding ecology. In J. L. Capinera (Ed.), *Encyclopedia of entomology* (pp. 1742–1747). Springer Nature. https://doi.org/10.1007/978-1-4020-6359-6_1201

Roberge, J.-M., Fries, C., Normark, G., Mårald, E., Sténs, A., Sandström, C., Sonesson, J., Appelqvist, C., & Lundmark, T. (2020). *Forest management in Sweden. Current practice and historical background*. Rapport 2020/4. Skogsstyrelsen, Swedish Forest Agency.

Rodríguez, A., Hekkala, A.-M., Sjögren, J., Strengbom, J., & Löfroth, T. (2021). Data from: Boreal forest fertilization leads to functional homogenization of ground beetle assemblages. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.t76hdr80j

Rytter, L., Ingerslev, M., Kilpeläinen, A., Torssonen, P., Lazdina, D., Löf, M., Madsen, P., Muiste, P., & Stener, L.-G. (2016). Increased forest biomass production in the Nordic and Baltic countries – A review on current and future opportunities. *Silva Fennica*, *50*(5), 1660. https://doi.org/10.14214/sf.1660

Salmon, S., Ponge, J. F., Gachet, S., Deharveng, L., Lefebvre, N., & Delabrosse, F. (2014). Linking species, traits and habitat characteristics of Collembola at European scale. *Soil Biology & Biochemistry*, *75*, 73–85. https://doi.org/10.1016/j.soilbio.2014.04.002

Schenker, N., & Gentleman, J. F. (2001). On judging the significance of differences by examining the overlap between confidence intervals. *The American Statistician*, *55*, 182–186. https://doi.org/10.1198/000313001317097960

Seric jelaska, L., Franjevic, D., Jelaska, S. D., & Symondson, W. O. C. (2014). Prey detection in carabid beetles (Coleoptera: Carabidae) in woodland ecosystems by PCR analysis of gut contents. *European Journal of Entomology*, *111*(5), 631–638. https://doi.org/10.14411/eje.2014.079

Sklodowski, J. J. W. (2006). Anthropogenic transformation of ground beetle assemblages (Coleoptera: Carabidae) in Białowieża Forest, Poland: From primeval forests to managed woodlands of various ages. *Entomologica Fennica*, *11*, 296–314. https://doi.org/10.33338/ef.84349

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, *31*(1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, *46*, 337–365. https://doi.org/10.2307/3817

Southwood, T. R. E. (1988). Tactics, strategies and templets. *Oikos*, *52*, 3–18. https://doi.org/10.2307/3565974

Spake, R., Barsoum, N., Newton, A. C., & Doncaster, C. P. (2016). Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations. *Forest Ecology and Management*, *359*, 300–308. https://doi.org/10.1016/j.foreco.2015.10.008

Sullivan, T. P., & Sullivan, D. S. (2018). Influence of nitrogen fertilization on abundance and diversity of plants and animals in temperate and boreal forests. *Environmental Reviews*, *26*, 26–42. https://doi.org/10.1139/er-2017-0026

Tamm, C. O. (1991). Nitrogen in terrestrial ecosystems: Questions of productivity, vegetational changes and ecosystem stability. *Ecological Studies*, *81*, 1–116. https://doi.org/10.1007/978-3-642-75168-4

ter Braak, C. J. F., Cormont, A., & Dray, S. (2012). Improved testing of species traits–environment relationships in the fourth-corner problem. *Ecology*, *93*, 1525–1526. https://doi.org/10.1890/12-0126.1

Thioulouse, J., Dray, S., Dufour, A. B., Siberchicot, A., Jombart, T., & Pavoine, S. (2018). Relating species traits to environment. In *Multivariate analysis of ecological data with ade4*. Springer. https://doi.org/10.1007/978-1-4939-8850-1_11

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