ECOSYSTEMS

Direct and Indirect Effects of Forest Anthropogenic Disturbance on Above and Below Ground Communities and Litter Decomposition

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ABSTRACT

Direct and indirect effects of habitat modification and changes in biotic interactions should be taken into consideration to understand the ecological consequences of forest anthropogenic disturbance on forest ecosystems. Few empirical studies assess indirect effects and consider multiple trophic levels, but recent statistical and theoretical advances provide new paths to do so. Here, we investigate direct and indirect effects of anthropogenic disturbances on multi-trophic soil communities in a boreal forest. We assessed the short term (2 years) abiotic and biotic responses to two anthropogenic disturbance intensities: conventional harvesting and harvesting followed by organic matter removal. We quantified the changes on eight groups of species, including vegetation and soil fauna, and their potential effects on leaf litter decomposition. We used a trait-based approach and structural equation modeling to quantify direct and indirect effects of disturbance intensity on environmental conditions, functional responses of the above and below ground biotic communities and leaf litter decomposition. Forest disturbance intensity was found to have a bottom-up effect on species community composition, from lower trophic levels (for example, detritivorous springtails) up to soil fauna top predators (for example, running spiders). Our results suggested some impacts of disturbance on leaf litter decomposition through changes in faunal

communities. Our study shows that a multi-trophic assessment of disturbance impacts provides an integrative understanding of ecosystem responses to environmental change.

Key words: Biodiversity; Ecosystem function; Biotic interactions; RLQ analysis; Soil processes; Structural equation modeling; Trait-based approach; Soil fauna.

HIGHLIGHTS

- Disturbance exerted direct and indirect effects on community functional composition.
- Disturbance exerted bottom-up effects on community functional composition.
- Our analyses suggest indirect effects of disturbance on leaf litter decomposition.

INTRODUCTION

Studies of biodiversity responses to disturbance have traditionally focused on direct effects on a single taxon and trophic level at a given point in time, neglecting potential interactions between species of other trophic levels (Werner and Peacor 2003; Barnes and others 2016; Brose and Hillebrand 2016). Despite this traditional focus, several studies have demonstrated how changes in food web structure could affect key ecosystem functions such as nutrient cycling (Ingham and others 1986; Hunt and Wall 2002) and productivity (Duffy and others 2007). Nonetheless, multi-trophic empirical studies of disturbances remain rare (Duffy and others 2007; Barnes and others 2017; Suding and others 2008). Although it is relatively simple to assess the effect of disturbances within a trophic level, it is significantly harder to evaluate their effects across several trophic levels. To adequately capture biodiversity responses to disturbances, multi-trophic studies require new techniques to capture the complexity of ecological network dynamics (Raffaelli and others 2002; Barnes and others 2016).

A network ecology perspective can be useful to demonstrate the importance of direct and indirect effects of disturbances on community structure and functioning (Montoya and others 2009). Species abundance is directly impacted by the abiotic environment and by biotic interactions such as a predator decreasing the abundance of its prey (top-

down effects). Species abundance can also be indirectly affected by interactions. For example, Hawes and others (2003) and Bohan and others (2005) documented cascading effects of changes in plant composition on the abundance and composition of herbivores, detritivores, predators and parasitoids (bottom-up effects). Changes in the predator community can indirectly affect basal trophic levels by modifying prey abundance and behavior, as well as ecosystem functions (Mulder and others 1999; Schneider and Brose 2013; Schmitz 2003). This could affect bottom-up and top-down regulation (Boyce and Anderson 1999; Wilmers and others 2006; Elmhagen and Rushton 2007), potentially affecting the functioning of the entire ecosystem (Pace and others 1999; Raffaelli and others 2002; Werner and Peacor 2003; Thébault and Loreau 2003).

Trait-based approaches, which have been used to assess changes in community composition effects on ecosystem functions (Lavorel and Garnier 2002; Cardinale and others 2012; McGill and others 2006; Suding and others 2008) have proven useful for understanding multi-trophic community functioning (Lavorel 2013; Moretti and others 2013). Trait-based approaches have recently been used in network ecology to assess interactions between species in various types of interaction networks (Morales-Castilla and others 2015; Bartomeus and others 2016; Brousseau and others 2018a; Laigle and others 2018), linking the characteristics of organisms to their position in the food web. For example, the functional composition of both vegetation and detritivore communities in soil food webs can influence important ecosystem functions such as leaf litter decomposition rates through both species complementarity (Handa and others 2014; Heemsbergen and others 2004; De Oliveira and others 2010) and selection mechanisms [for example, food preference of detritivores (Vos and others 2011; Rouifed and others 2010)]. Here, we propose to extend trait-based approaches to network analysis to assess direct and indirect effects of forest disturbance on leaf litter decomposition mediated by above and below ground multi-trophic community trait interactions.

Structural equation models (SEM) are powerful statistical methods designed to test hypothesized causal relationships between variables and to quantify indirect relationships between variables that are implied by such hypotheses (Grace and Keeley 2006; Eisenhauer and others 2015; Shipley 2016). For example, Henneron and others (2017) used SEM to show indirect effects of forest canopy removal on springtail functional groups mediated

through its direct effects on vegetation communities. Gotelli and Ellison (2006) used path analysis to reveal the direct and indirect effects of top predators on ecosystem response to habitat change. Although SEM has often been used to test direct and indirect effects of environmental changes on biodiversity and ecosystem processes, it has the potential to investigate the relative importance of direct and indirect effects of disturbances on the structure and functioning of complex food webs. This would give a more comprehensive understanding of the mechanisms driving species responses.

The North American boreal forest is prone to natural disturbance caused by large-scale fire and insect outbreaks (Gauthier and others 2009). These disturbances result in the addition of pulses of fresh woody debris to the forest floor (Stocks 1987; McRae and others 2001). After such a disturbance, large canopy openings provoke large changes in light availability at the forest floor and, on soil moisture and soil temperature regimes (Keenan and Kimmins 1993). In several geographic regions of the boreal forest, harvesting has now replaced fire as the primary disturbance (Cyr and others 2009). Movement of heavy machinery can create additional disturbances to the forest floor by compacting and mixing superficial soil layers (Marshall 2000; Frey and others 2011). Trenching, a common site preparation practice used to enhance planted tree survival and growth, further disrupts soil physical structure and function (Schmidt and others 1996). Together, these disturbances put a strong environmental filter on forest soil communities possibly cascading to ecosystem functioning.

An experimental site was designed collaboratively in this biome to better understand the impact of anthropogenic disturbance on biodiversity and ecosystem functioning and assess the sustainability of such practices (Kwiaton and others 2014; Aubin and others 2020). Several researchers investigated various aspects of environmental and biodiversity responses to forest anthropogenic disturbance intensity (for example, Webster and others 2016; Smenderovac and others 2017; Venier and others 2017; Rousseau and others 2018), providing an opportunity for integrative multi-trophic analyses. The expertise of each collaborator was essential for an efficient and synergic integration of the methods and for a transdisciplinary interpretation of the results. We combined a trait-based approach and a network analysis, implemented with SEM, to assess the direct and indirect effects of forest disturbance intensity on above and below ground communities of vegetation and soil fauna composition and rela-

tive abundance, and their potential effects on leaf litter decomposition, a possible key ecosystem function for boreal forest productivity (Prescott 2005). We hypothesized (Figure 1) that forest disturbances and resulting environmental changes (Figure 1; arrow 1) directly affect leaf litter decomposition through physical processes causing a shift in temperature and moisture and thus influencing litter decomposition (arrow 6a). Environmental changes are also expected to affect vegetation and soil fauna community assemblages (arrow 2) as revealed by previous studies done on several taxa independently, at the same experimental site (Webster and others 2016; Venier and others 2017; Rousseau and others 2018). Community changes are expected to cascade either through top-down effects when consumers change their resources abundance and composition, or through bottom-up effects when resources modify abundance and composition of their consumers (arrows 4 and 5, respectively). Soil fauna community can be further driven by changes in vegetation (arrow 3), which provides habitat and other resources. Ultimately, the shift in vegetation (not tested) and fauna community composition might then cascade to changes in leaf litter decomposition (arrow 6b).

METHODS

Study Site

The study took place in a jack pine-dominated forest stand (*Pinus banksiana*) at the Island Lake Biomass Harvest Experiment near Chapleau, Ontario, Canada ($47°\,50'$ N, $83°\,24'$ W) (Appendix 1). The mean annual temperature of the region is $1.7°$C with approximately 93 frost-free days and a mean annual precipitation of 797 mm (277 cm of snowfall; Environment Canada 2013). This experiment was originally designed to study the impact of a gradient of forest biomass removal on biodiversity and forest productivity. A 49-year-old second growth jack pine stand orinating from a harvest, was harvested in winter 2010–2011 using conventional and intensive harvesting techniques. In 2012, the site was prepared following conventional site preparation (mechanical disk trenching) creating, every 2.1 m, 50 cm wide trenches exposing the mineral soil. The site was then replanted with with jack pine and black spruce (*Picea mariana*). For more details about the study site, see Kwiaton and others (2014).

We compared an adjacent 51-year-old mature stand (hereafter called ''mature forest''), with two
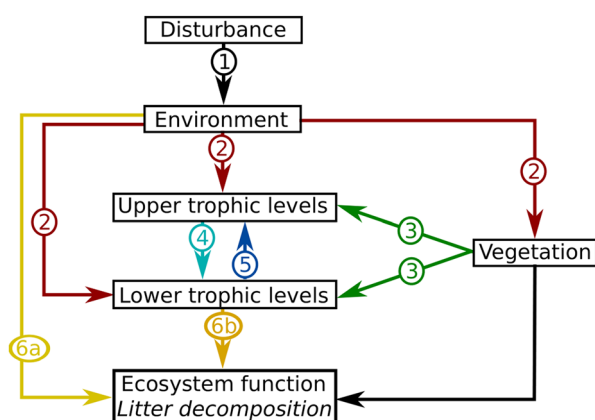
Figure 1. General a priori hypotheses on the direct and indirect effects of disturbances and resulting environmental changes on litter decomposition. Numbers and colors on arrows are related to the following hypotheses: (1) Forest anthropogenic disturbances are expected to affect environmental variables. (2) Environmental changes induced by such disturbances are expected to affect vegetation and soil fauna community abundance and functional structure. (3) Vegetation changes are expected to affect soil fauna community. (4) We expected that either changes in predator composition affect lower trophic levels (top-down effect), or (5) changes in prey composition affect upper trophic levels (bottom-up effect). (6a) Changes in environmental conditions directly affect leaf litter decomposition, and (6b) indirectly through changes in species composition at lower trophic levels. Leaf chemical and physical properties also influence decomposition, but this component was out of the scope of our study. Hypothesis 1 is tested in step 1 (Figure 2), hypothesis 2 is tested in step 2, hypotheses 6 are tested in step 3 and all the hypotheses are tested in step 4, in a global model.

disturbance treatments: (1) a full-tree biomass harvesting treatment (trunk, top, branches and non-merchantable trees harvested) followed by site preparation (hereafter called ''low intensity treatment''), and (2) a full-tree harvest followed by removal of all the organic matter, including woody debris, stumps and roots, forest floor and the upper 5 cm of the mineral soil (hereafter called ''high intensity treatment''). Treatments were replicated in five 70 × 70 m plots separated by at least 25 m following a randomized block design. Each plot was subdivided into four 35 m × 35 m subplots (Appendix 2). In August 2011, the two western subplots of each plot were hand sprayed with glyphosate herbicide (4 L/ha) to control vegetation. The herbicide subplots were not included in the assessment of community response to forest disturbance but were used to assess the influence of vegetation presence in the litter decomposition

experiment. In May 2012, the northern subplots were planted with jack pine, and the southern subplots were planted with black spruce at 1.8 m spacing. To reduce the edge effect, the five mature forest plots were embedded within an eight hectare tract of mature forest.

Sampling

Vegetation

In July 2013, we estimated the composition of vascular plants and mosses using a modified version of the point count technique (Fayle 1959). We set up seven 8 m parallel transects spaced 1 m apart, inside a 8 m × 6 m quadrat centered inside each non-herbicide subplot. We recorded species present within six 15 cm radius points at 1 m intervals along the transects, for a total of 56 points. We recorded every plant species with at least a fraction of its photosynthetic material within the point and a DBH (diameter breast height, that is, 1.4 m) less than 5 cm and a height less than 5 m. Individuals taller than 5 m were excluded from sampling. An occurrence value of 1 was attributed to species found within a point. Species present within the 8 m × 6 m quadrat but not in any of the 56 sampling points was given an occurrence value of 0.5. The sum of occurrences was divided by the total number of points (56) and then multiplied by 100 to get the percentage occurrence within a quadrat. We only identified vascular plants to the species level following the nomenclature of Gleason and Cronquist (1963). Presence of trees with DBH greater than 5 cm was noted as a Boolean variable.

Macrofauna

Ground dwelling invertebrates were collected every two weeks using pitfall traps (diameter 11.5 cm, depth 4.5 cm) between May 15th, 2013 and August 19th, 2013. We installed two traps, 10.6 m apart, and 50 cm outside the vegetation quadrat in each non-herbicide subplot for a total of 60 traps (see Venier and others 2017 for more details). They were filled with 150 ml of propylene glycol as a preservative, 150 ml of water and a small amount of detergent to break water surface tension. We covered the traps with suspended white plastic covers to prevent rainwater infiltration. We emptied trap contents at the end of each collection period and returned to the laboratory for sorting. We sorted specimens into four groups: ground beetles (Carabidae), spiders (Araneae), rove beetles (Staphylinidae) and macrodetritivores

including millipedes (Diplopoda) and slugs (Gastropoda) and stored them in 70% ethanol. We identified ground beetles according to Lindroth (1961, Lindroth and Freitag 1969) and named them using the nomenclature of Bousquet and Larochelle (1993). We identified rove beetles following Ashe (2001, Brunke and others 2011) and Seevers and Herman (1978). Only adult spiders were identified to species according to standard literature, following the nomenclature of Paquin and Buckle (2001). We excluded juveniles from the analysis as we could not identify them to species. We identified slugs and millipedes using Grimm (2009) and Hoffman (1999), respectively. We pooled the two traps per subplot to generate one sample per subplot. We standardized the samples of each subplot to the number of trap days during which the traps were open and not disturbed. If a trap was found disturbed during collection, the sample for the 2 week period was excluded.

Mesofauna

We collected springtails (Collembola) and oribatid mites (Oribatida) in each herbicide-free subplot using one soil core (PVC corers of 5-cm-diameter and 10 cm depth = 196 cm^3) from the soil surface, including organic horizons and the upper mineral soil (see Rousseau and others 2018). We also collected the living moss stratum which was only present in the mature forest, using a 10×10 cm square metal frame. Soil samples were transported in PVC soil corers, wrapped in aluminum foil and placed in Ziploc™ bags; moss samples were placed directly in bags. All samples were kept in coolers during field work, at $\pm 4°C$. Back in the laboratory, we extracted mesofauna from each soil and moss sample by placing them in a Tullgren dry-funnel for 2 days at 30°C, 2 days at 35°C and 2 days at 40°C in an air-conditioned room. Samples were preserved in 70% ethanol, then cleared with 88% lactic acid, mounted in Hoyer's medium, and identified using a contrast phase microscope Leica DM1000 (800× magnification). We combined the samples of the two non-herbicide subplots, and we standardized abundance by unit volume of the substratum (number of individuals per cm^3 of soil and moss strata, if present). We identified springtails according to Christiansen and Bellinger (1998) and Fjellberg (1998, 2007), and used Behan-Pelletier and Norton (2014) and Krantz and Walter (2009) for oribatid mite identification. We conducted the inventories in June 2013, August 2013 and May 2014. We used samples of springtails taken in 2014 to be consistent with decomposition measurements. However, only samples collected in 2013 were available for oribatid mites, due to time constraints.

A list of species and their summed abundance or occurrence from all the plots of the same treatment, can be found in Appendix J.

Species Traits

For each taxon, we selected a set of traits or proxies shown in the literature to be sensitive to environmental changes (for example, ecological preferences and mobility) and to influence species trophic interactions (for example, feeding guild; see Table 1). Trait values used were species average. For vascular plant traits, we measured traits known to have high intraspecific variability (for example, leaf nutrient concentration and specific leaf area; SLA) using sampling protocols detailed in Cornelissen and others (2003). We obtained remaining plant traits from the TOPIC database Aubin and others (2020)). Traits for non-vascular plants were not available. Ground beetle and spider traits were obtained from Venier and others (unpublished) and from the CRITTER database (Handa and others 2017). We obtained trait data of rove beetle from Klimaszewski and others (2013) and Stefani and others (2016). Traits of springtails and oribatid mites were measured by Rousseau and others (2019), on specimens sampled from the Island Lake experiment. We used several proxies of traits for macro-arthropods (for example, feeding guild and ecological preference) due to limited trait data availability. Likely feeding guild of springtails and oribatid mites was based on mouthpart morphology, and vertical soil distribution (microhabitat preference) was assessed using a combination of measured morphological traits (Rousseau and others 2019). Moss traits were not available, and we recorded only one species of millipede (*Uroblaniulus canadensis*, Prajulidae) and one genus of slug (*Arion sp.*, Arionidae); therefore, no traits were considered for these taxa, but only occurrence and abundance, because subsequent trait-based analyses could not be performed on a single species.

Environmental Variables

We sampled a series of environmental variables (Appendix 3) in each plot. We recorded mean and maximum soil daily temperature at a 10 cm depth with CR10x data loggers from August 21 to 27, 2014 (Venier and others 2014). We recorded the forest floor thickness (L, F, H horizons in the disturbance treatments and F, H horizons in the mature forest). We used the soil cores sampled by

Table 1. Traits or Trait Proxies Measured or Documented From the Literature

Taxa	Traits related to	Trait	Trait type	Description	Unit	Source
Vascular plants	Ecological preferences	Root depth	Ordinal	Deep rooting phanerophyte, superficial rooting phanerophyte, deep rooting non phanerophyte, intermediary rooting non phanerophyte, superficial rooting non phanerophyte	1, 2, 3, 4, 5	TOPIC
	Nutrition	Specific leaf area (SLA)	Continuous	One-sided area of fresh leaf, divided by its oven-dry mass	$m^2 kg^{-1}$	TOPIC
		Leaf Nitrogen Concentration (LNC)	Continuous	Percentage of Nitrogen in the leaf	%	TOPIC
	Other	Ligneous	Boolean	Ligneous (1), herbaceous (0)	0/1	TOPIC
		Seed production	Ordinal	1–20, 20–1000, > 1000 $g y^{-1}$	0, 0.5, 1	TOPIC
		Lateral extension	Categorical	Lateral root spreading: limited, clonal compact, clonal intermediate, clonal extensive	1, 2, 3, 4	TOPIC
		Plant height	Continuous	Shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level	cm	TOPIC
Springtails	Ecological preference	Vertical soil distribution	Categorical	Euedaphic, hemiedaphic, epiedaphic		Measured[1,3]
	Nutrition	Main feeding guild based on mouthpart structure	Ordinal	Reduced (mostly predator and necrophage), normal (mostly microbivore), complex (mostly detritivore)	0, 0.5, 1	Measured[1]
	Other	Average body length	Continuous	Mean of body length	mm	Measured[1]
Oribatid mites	Ecological preference	Vertical soil distribution	Categorical	Hemiedaphic, euedaphic, epiedaphic		Measured[1,3]
	Nutrition	Main feeding guild based on chelicerae shape	Categorical	Compacted (mostly detritivore), normal (mostly microbivore), elongated (mostly predators)		Measured[1]
	Other	Body length	Continuous	Mean of body length	mm	Measured[1]
Rove beetles	Ecological preference	Moisture preference	Ordinal	Dry, mesic, moist	0, 0.5, 1	Literature[2]
	Nutrition	Feeding guild	Categorical	Carnivore, fungivore		Literature[2]
	Other	Body length	Continuous	Minimum body length	Mm	Literature[2]
		Elytron length	Ordinal	Aborted elytron, reduced elytron, body covered by elytron	0, 0.5, 1	Literature[2]
Ground beetles	Ecological preference	Moisture preference	Ordinal	Dry, mesic, moist	0, 0.5, 1	Literature[4], CRITTER
		Light preference	Ordinal	Low, moderate, high	0, 0.5, 1	Literature[4], CRITTER
	Nutrition	Feeding guild	Categorical	Granivore, carnivore, not documented		Literature[4], CRITTER
	Other	Wing morphology	Ordinal	Brachypterous, dimorphic, macropterous	0, 0.5, 1	Literature[4], CRITTER

Table 1. continued

Taxa	Traits related to	Trait	Trait type	Description	Unit	Source
		Body length	Continuous	Average between the min and max body length	Mm	Literature[4], CRITTER
Spiders	Ecological preference	Moisture preference	Ordinal	From dry to moist habitats	0.1–1	Literature[4], CRITTER
		Light preference	Categorical	From shaded to bright habitats	0.1–1	Literature[4], CRITTER
	Nutrition	Hunting strategy	Categorical	runners, web builders, not documented (NA)		Literature[4], CRITTER
	Other	Body length	Continuous	Female body length (total length)	mm	Literature[4], CRITTER

Description of the traits or trait proxies used in this study for the six taxonomic groups. Source: TOPIC = Traits of Plants in Canada database (Aubin and others 2020), CRITTER database (Handa and others 2017), 1: Measured by Rousseau and others (2018), 2: Taken from Klimaszewski and others (2013), Stefani and others (2016), 3: Determined according to several traits (see Rousseau and others 2019 for details.), 4: Venier and others (unpublished dataset).

Rousseau and others (2018) to measure the following soil properties: forest floor moisture (gravimetric water content of soil and moss), soil bulk density (dried weight relative to sample volume) and forest floor pH. Fresh weight of these samples was measured before and after fauna extraction then dried in an oven for 24 h at 105°C. Soil samples were ground (< 2 mm) using a Pulverisette 6 classic line ball mill (Fritsch GmbH) prior to measuring soil pH in distilled water. We included in our analysis the ''Soil chemistry index'' defined by Rousseau and others (2018) based on the chemical properties of the organic and mineral soil horizons. At each plot, we combined line transect and fixed quadrat methods to estimate the mass of three decay classes of woody debris: recent coarse woody debris (''recent CWD'', > 2-cm-diameter), decayed coarse woody debris (wood without bark, ''decayed CWD'') and fine woody debris (''FWD'', $\leq 2cm$), summed in the variable ''Woody debris'' (Kwiaton and others (2014) for more detailed methods). We also recorded the relative occurrence of mineral soil exposure at the 56 vegetation points. Frequency of occurrence (%) of mineral soil exposure was calculated as the proportion of points in a subplot where it occurred.

Litter Decomposition Experiment

Litter decomposition was measured following Handa and others (2014) using 15-cm-diameter litter microcosms made from three different nylon mesh sizes (0.05, 2 and 5 mm). We used three mesh sizes to assess potential effects of detritivore community body size on litter decomposition. The increasing mesh sizes provided access to communities of increasing body size dominated by microbes and microfauna such as protists (< 0.1 mm), in addition to mesofauna such as springtails and mites (0.1–2 mm) and macrofauna (> 2 mm). Litter microcosms were made from modified black plastic flowerpots that were covered at the top and bottom with 0.05 mm nylon mesh that allowed rain to filter through microcosms but prevented litter fragment loss. We collected leaf litter of *Prunus pensylvanica* (pin cherry), the dominant deciduous tree species on site ($> 20\%$ cover in the low intensity treatment), using litterfall traps installed under *Prunus pensylvanica* trees over a two-week period during the fall of the previous year (2013). Leaves were oven-dried (40°C for 24 h) and frozen over the winter. Following Lorenz and others (2004), we installed 60 leaf litter microcosms filled with $6 \pm 1.5g$ of dried leaf litter in May 2014 and collected in October 2014 (144 days) in the five replicates of each of the three treatments. We placed a microcosm of each of the three mesh size in one of the two non-herbicide subplots (for a total of 45 microcosms). We also placed one 5-mm-microcosm in one of the two herbicide subplots to assess the effect of vegetation presence alone (for a total of 15 microcosms). We installed microcosms in a way to form a continuous litter layer, when present. In the mature forest, we manually removed 1 m² of vegetation to simulate herbicide application before installing the microcosm. We put Thermochron Ibuttons (Ds1922L-F5, Maxim Integrated Products) inside microcosms in three of the five treatment replicates, to measure daily temperature during the decomposition experiment (Fierer and others 2005). After collection, we dried the decomposed litter at 60°C, cleaned it to remove sand and other exogenous residues and weighed it to the nearest mg to assess mass loss. Litter decomposition in each litter microcosm was cal-

culated as the percentage of mass lost between the first and the last day.

Statistical Analyses

The data analysis was structured in four distinct steps (see Figure 2 for an overview) to assess the direct and indirect effects of the treatments on below ground communities and leaf litter decomposition. We selected environmental variables and species traits that responded the most to the treatments. According to these results, we tested hypotheses on causal relationships between environmental changes, species responses and litter decomposition.

In step 1, we determined environmental variables that captured most of the differences between the mature forest and the two disturbance treatments. We used a principal component analysis (R package ade4; Dray and others 2007) and Variance Inflation Factors (VIF) regression (Kutner and others 2004) with a cutoff value of 5 to detect collinearity between environmental variables (R package car; Fox and Weisberg 2019). We then used permutational MANOVA (999 permutations) followed by post-hoc pairwise comparisons and correction for multiple testing (fdr: false discovery rate) (Anderson 2001) to test the effect of the treatments on the selected environmental variables [R packages vegan (Oksanen and others 2016) and RVAideMemoire (Hervé 2016)]. These variables were subsequently used to mechanically assess how species responded to the disturbance.

In step 2, we assessed the changes in total abundance or occurrence of the eight groups according to treatments using a permutational ANOVA (999 permutations) (R package lmPerm; Wheeler and Torchiano 2016). We identified dissimilar treatments with a permutational pairwise t-test with fdr correction for multiple testing (R package RVAideMemoire). When we detected heteroscedasticity in the variance and non-normal distribution of the residues, we used a Kruskal–Wallis test. We then performed a RLQ analysis (Dolédec and others 1996; Dray and Legendre 2008) for each group (except slugs and mosses), to assess how species traits responded to changes in selected environmental variables (R package ade4). RLQ analysis combines the matrix of species traits (Q), species abundance (L) and environmental variables R. ''RLQ analysis performs a double inertia analysis of two arrays (R and Q) with a link expressed by a contingency table (L)'' (Dray and others 2007). Categorical traits were transformed to Boolean variables with one column for each cate-

gory. These analyses aimed at selecting taxonomic groups and traits that responded the most to environmental changes caused by the treatments.

In step 3, we used ANOVA and Tukey H.S.D corrections for multiple testing to determine whether litter decomposition (calculated as the percentage of litter mass loss) changed according to (i) treatment, litter microcosm mesh size, and their interaction, (ii) vegetation presence and its interaction with treatments. Given its potential impact on litter decomposition, we also tested whether temperature inside the microcosms differed between treatments and mesh sizes (Fierer and others 2005; Butenschoen and others 2011). We did not use an overall model since there was an unequal number of observations within each factor. This is because only 5-mm-mesh size microcosms were placed in herbicide subplots and four of them in the high intensity treatment were destroyed by animals or filled with sand because vegetation and litter cover was too scarce to avoid superficial water run-off. These analyses were used to determine whether vegetation, macrofauna or mesofauna had an influence on leaf litter decomposition.

In step 4, the most responsive abiotic and biotic variables were integrated into a multi-trophic trait-based analysis using structural equation models (Grace and Keeley 2006; Shipley 2016, more details about SEM in Appendix 4) [R package nlme (Pinheiro and others 2016) and piecewiseSEM (Lefcheck 2016)]. This allowed us to test causal hypotheses linking potential consumer's and resource's traits, abiotic variables and litter mass loss. For each plot, we considered the mean abundance of macrofauna and mean occurrence of vegetation in the two herbicide subplots of each plot, while abundance of mesofauna was already pulled by plot. Considering that soil fauna is mainly composed of opportunistic species (Hedde and others 2010; Wardle 2006; Digel and others 2014), we over-simplified the soil food web, and broadly assessed carnivore species diet on expert knowledge. Likely, we assumed that all detritivores consumed pin cherry litter. See Appendix 5 for the list of relationship tested in the SEMs. Treatments were considered as random effects. In this way, correlations between variables common to all treatments are elucidated even if their coefficients differ between treatments. We did not consider them as fixed effects because they do not represent a gradient, but three distinct treatments to which all environmental and biotic variables responded significantly. We then compared three a priori models testing causal relationships between the two selected environmental variables and traits. Species
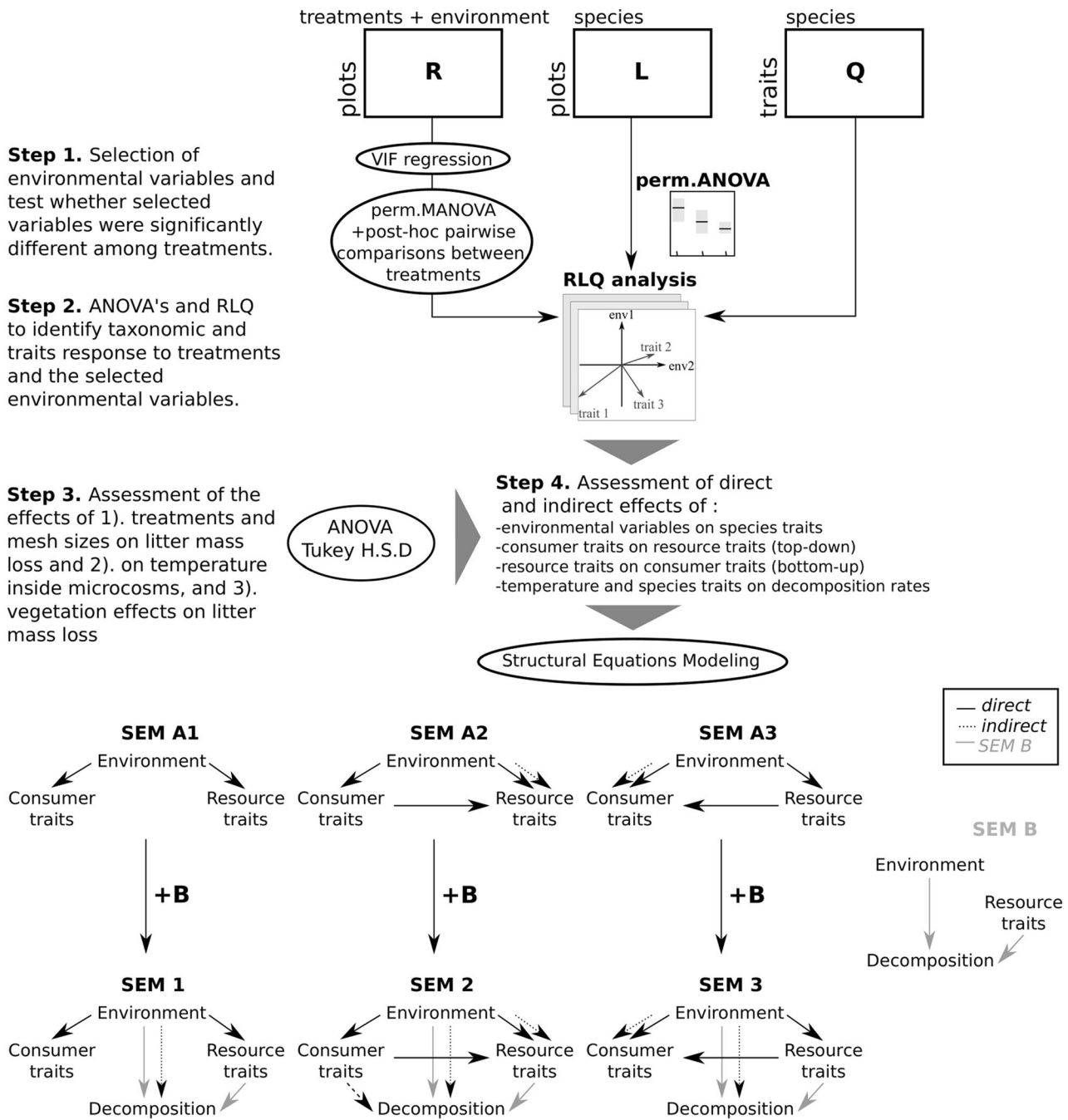
Figure 2. Diagram of the four analytical steps used to 1. assess the response of environmental variables to disturbance treatments (VIF = Variance Inflation Factor) and selection of the most responsive abiotic variables, 2. identify responses of taxonomic group abundance to treatments, functional responses to selected environmental variables and selection of the most responsive biotic variables, 3. assess treatments, temperature and microcosm mesh size effects on leaf litter decomposition, 4. test three distinct SEMs (SEM1 = direct effect; SEM2 = direct + indirect top-down effects; SEM3 = direct + indirect bottom-up effects) composed of one sub-model A (A1, A2, A3) and sub-model B to assess the direct and indirect effects of the selected biotic and abiotic variables on the leaf litter decomposition. An indirect effect between a variable 1 and 3 is assumed when variable 1 affects a variable 2 which affects variable 3. Analyses were based on the tables of environmental variables in each five replicates of the three treatments (Table R), species abundance or occurrence in each replicates of the three treatments (Table L), species traits (Table Q) and a table of litter mass loss in the microcosms. Tables L and analyses from step 2 were divided by taxa.

traits were included as a community trait mean values weighted by the abundance of the number of individuals of each single species in each community. Hence, for continuous trait, the trait variable is equivalent to the mean trait value of the community, and for categorical traits, the trait variable is equivalent to the summed abundance of species presenting the trait category. We added the presence (in the mature forest) or absence (in the disturbance treatments) of adult trees (diameter > 5 cm) as a Boolean variable in the models as it may explain a portion of species responses to environmental changes. The first sub-model (SEM A1, Figure 2) only includes environmental variables (with vegetation considered as habitat) as explanatory variables (testing for hypotheses 2 and 3 in Figure 1). In the second model (SEM A2, Figure 2), we added potential effects of consumers on their resources (testing for hypothesis 4, top-down effects, Figure 1) hence testing for indirect effects of disturbances on lower trophic levels. For the third model (SEM A3, Figure 2), we added potential positive effects of resources on their consumers (testing for hypothesis 5, bottom-up effects, Figure 1), testing for indirect effects of disturbances on upper trophic levels.

We considered full models to be the integration of the first sub-models (SEM A1-3) with a second sub-model (SEM B, Figure 2). SEM B was constant for the three full models and developed to test causal relationships between environmental variables and species traits on litter mass loss. SEM B was also comprised of four equations accounting for relationships between abiotic variables which were also included in SEM A1-3. Because SEM B was nested within SEM A1-3, we considered both sub-models (SEM A and B) as an overarching model for the purposes of biological interpretation. SEM B needed to be separated from SEM A as it included litter microcosm mesh sizes. When a taxonomic group was excluded from a microcosm based on mesh size, it was assigned a trait value of 0, which would have returned inaccurate results to sub-models SEM A1-3. The three microcosms from the same plot were related to the same environmental variables, with the exception of microcosm's temperature. We computed the marginal and conditional R^2 for each equation. Based on the results of the previous steps, we tested different combinations of variables to evaluate variable contribution to model accuracy. We first built SEM A1 according to correlations highlighted by RLQs. If mineral soil exposure or woody debris were cor-

related to higher abundance of taxa with specific trait values, we tested whether there were causal relationships between these variables. We also included vegetation according to observed associations. For instance, moss cover is typically more abundant under tree cover in this forest type. Relationships that decreased the significance of the model were removed. To build models A2 and A3, we tested causal relationships between animal traits when they responded in the same way to the environmental variables. For example, fungivorous rove beetle abundance was negatively correlated with mineral soil exposure but positively correlated with woody debris. Since carnivorous ground beetle abundance response pointed in the same direction as fungivorous rove beetles, we tested the relationships between this taxonomic group and fungivorous rove beetles. For model B, as the 5-mm-microcosms in the mature forest had the lowest temperature and the highest % mass loss, we tested whether temperature and detritivores, that were more abundant in the mature forest, influenced decomposition. We then compared the three models according to their p values and AIC. A p value > 0.05 indicates the model is acceptable while lowest AIC values indicate higher fits to the data.

All of the analyses were performed with R (v. 3.3.3; R Core Team 2015). The R script and data used for the analyses can be found in Appendix K and L, respectively.

RESULTS

Differences in Environmental Variables Among Treatments

We found that mineral soil exposure and above ground woody debris mass captured the differences between the mature forest, the low and the high intensity disturbance treatments (F test: $p = 1 \times 10^{-3}, R^2 = 0.91$, Appendix 7). The mature forest and the high intensity treatment were at opposite ends of the mineral soil exposure gradient, and both had low amounts of woody debris. The low intensity treatment, situated midway on the mineral soil exposure gradient, had the highest amount of woody debris. Mineral soil exposure was positively correlated with pH (VIF = 65), bulk density (VIF = 26) and soil mean and maximum temperature (VIF = 54 and VIF = 73, respectively), negatively correlated with the soil chemical index (VIF = 17), soil moisture (VIF = 43) and the forest floor thickness (VIF = 18), but not correlated with
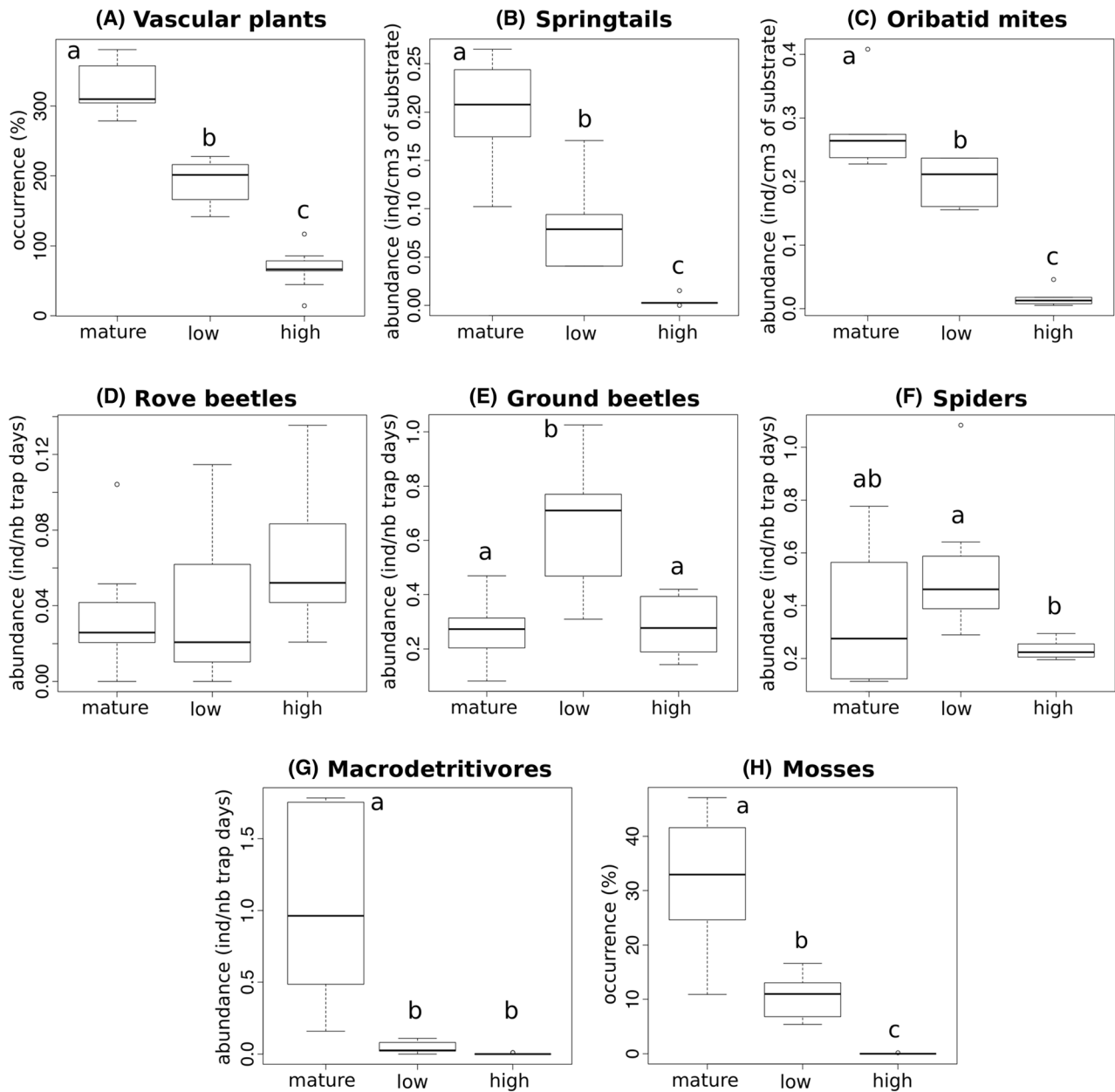
Figure 3. Total abundances or occurrence of the eight studied groups in the three treatments: **A** vascular plants (% occurrence), **B** springtails (ind/cm^3 of substrate), **C** oribatid mites (ind/cm^3 of substrate), **D** rove beetles (ind/number of trap nights), **E** ground beetles (ind/number of trap nights), **F** spiders (ind/number of trap nights), **G** macrodetritivores (ind/number of trap nights), **H** mosses (% occurrence). The letters above each box indicate significant differences between treatments at $p<0.05$ (permutational ANOVAs, and Kruskal–Wallis test for macrodetritivores). Only values inferior / superior to 1.5 multiplied by the value of the interquartile are represented inside the whiskers.

woody debris mass (VIF = 4.1) (Appendix 6). We then selected mineral soil exposure as an index of disturbance (removal of vegetation and the organic soil layer, and physical disturbance by heavy machinery) and the input of woody debris to investigate treatment effects on taxonomic groups.

Responses of Species Groups to Treatments and Resulting Environmental Changes

Total abundance or occurrence of vascular plants, springtails, oribatid mites, macrodetritivores and mosses decreased significantly with increasing
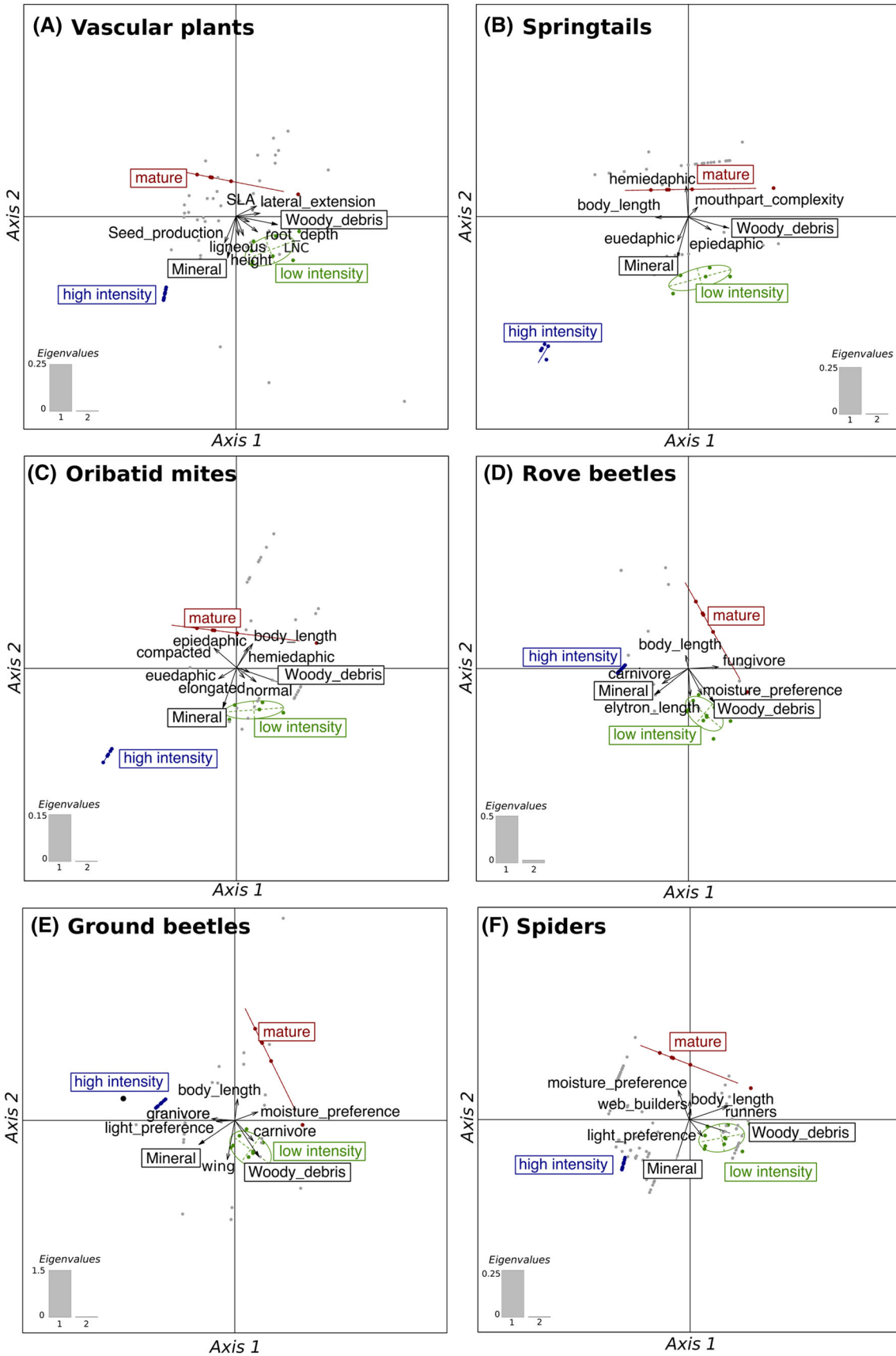
◄**Figure 4.** Biplots of the RLQ analyses of six taxonomic groups: arrows represent species traits (Table Q), and the two environmental variables selected from previous analyses (framed, Table R), and gray points represent species (Table L). Red, green and blue dots represent the five replicates (plots) of the mature, low and high intensity treatments, respectively, with ellipses indicating the dispersion of the plots. For a detailed description of species traits and environmental variables see Table 1 and Appendix 3.

intensity of disturbance. These groups were almost absent in the high intensity treatment (Figure 3A, B, C, G, H, respectively, $p<0.05$). Only one spring-tail species (*Tullbergia yosiii*) was recorded in the high intensity treatment. The abundance of rove beetles did not significantly vary among treatments (Figure 3D, $p = 0.16$). The abundance of ground beetles was the highest in the low intensity treatment, but was not significantly different between the mature forest and the high intensity treatment (Figure 3E, $p = 0.02$). Spider abundance was higher in the low intensity treatment compared to the high intensity treatment (Figure 3F, $p = 0.02$).

Several traits related to habitat and feeding guild were associated with the two selected environmental variables (Figure 4). In the mature forest, we found higher abundance of hemiedaphic springtails (Figure 4B), large epiedaphic oribatid mites with compacted mouthparts (mostly detritivores) (Figure 4C), fungivorous rove beetles (Figure 4D), as well as web building spiders and ground beetles without wings, both preferring shade and moist habitat (Figure 4E, F). In the low intensity treatment, where the soil was moderately exposed, and woody debris were the most abundant, rove beetles with long elytron and ground beetles with wings were more frequent (Figure 4D, E). It was also associated with runner spiders and carnivorous ground beetles (Figure 4F, E). In the high intensity treatment characterized by a great mineral soil exposure, we observed a higher occurrence of vascular plants with large seed production and low SLA (Figure 4A), higher abundance of carnivorous rove beetles and of granivorous ground beetles (Figure 4D, E). Deep rooted tall ligneous species, euedaphic mesofaunal species were less affected by environmental changes (Figure 4A–C). Soil position of mesofauna and feeding guild or hunting strategy of macro-arthropods was the most responsive to the treatments and resulting environment changes. Consequently, these were selected for the structural equation model (step 4).

Leaf litter decomposition response

Mass loss of leaf litter in the 5-mm-microcosms located in the mature forest was marginally significantly higher when compared to microcosms of 0.05 mm in the mature forest ($p = 0.08$) and significantly higher than both the microcosms of 2 mm in the mature forest and those located in the high and low intensity treatments ($p = 0.02$, $p<0.0001$ and $p = 0.001$, respectively) (Figure 5A). Litter mass loss was not affected by vegetation removal following herbicide application ($p = 0.70$; Figure 5B). The temperature inside the microcosms over the whole term of the experiment was higher (approximately 2 °C) in the two disturbance treatments compared to the microcosms in the mature forest ($p<0.05$; Figure 5C).

Direct and Indirect Effects of Disturbance on Leaf Litter Decomposition

In step 4, we tested three distinct a priori SEMs (SEM A1-3) to assess the direct and indirect effects of the selected variables on leaf litter decomposition. We selected SEM A3 (Fisher's $C = 183.27$, $df = 206$, $p = 0.87$, AICc = 143.9; Appendix 8—Table 3) as it has the lowest AIC values of the three models A, all of the path coefficients were significantly different from zero and in the correct direction according to hypotheses. This model codified the hypothesis that environmental changes directly and indirectly affect species from the bottom to the top of the food chain (Figure 6). SEM A1 codified the hypothesis that disturbance and resulting environmental changes only directly affect vegetation and fauna functional composition (Fisher's $C = 217.68$, $df = 214$, $p = 0.417$, AICc = 177.436; Appendix 9-a and 8—Table 1). SEM A2 codified the hypothesis that environmental changes directly and indirectly affect species from the top to the bottom of the food chain (Fisher's $C = 197.5$, $df = 198$, $p = 0.497$, AICc = 158.929; Appendix 9-b and 8—Table 2). The sub-model SEM B involving species traits, environmental variables and litter decomposition was accepted (Fisher's $C = 44.72$, $df = 52$, $p = 0.76$). All paths were significant ($p<0.05$) except effects from mineral soil exposure and decayed coarse woody debris on fungivorous rove beetles and slugs, as well as hemiedaphic springtail effects on decomposition, tree presence effects on moss cover, carnivorous rove beetles and running spiders. However, these effects were in the correct direction according to hypotheses and increased the fit of the resulting model (Appendix 8—Table 4).
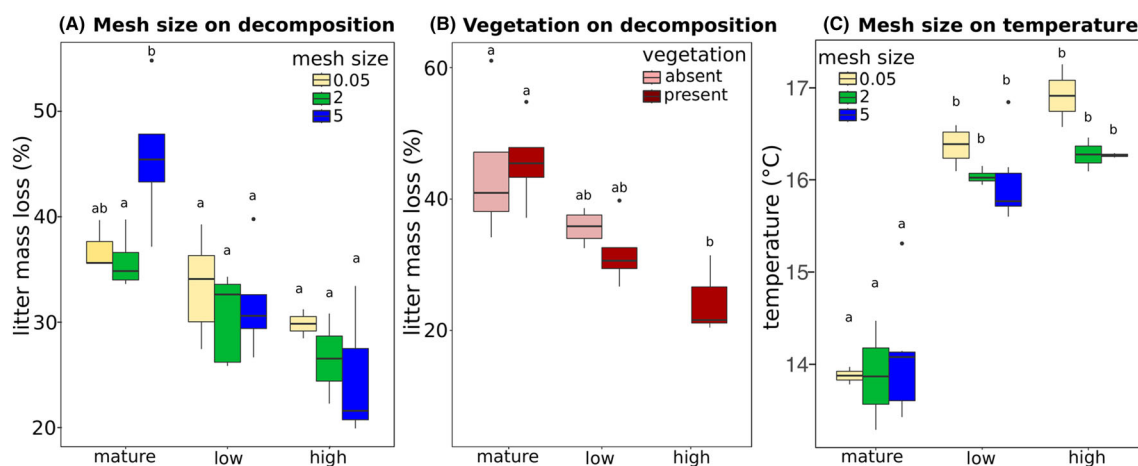
Figure 5. **A** Varying litter microcosm mesh size (0.05 mm, 2 mm, 5 mm) or **B** varying presence of vegetation shown as a function of the three treatments (mature, low intensity, high intensity disturbance) on litter decomposition (% mass loss). The letters above each box correspond to the result of the Tukey test, and boxes that do not share any letter are significantly different. **C** Varying litter microcosm mesh size shown as a function of treatments on temperature (°C) measured inside the litter microcosm. Only values inferior/superior to 1.5 multiplied by the value of the interquartile are represented inside the whiskers.

The full model SEM 3 revealed that forest disturbances and resulting environmental changes, measured as mineral soil exposure, directly affected several groups negatively including hemiedaphic springtails, web building spiders, carnivorous ground beetles, fungivorous rove beetles, tall plants and plants with high SLA value while positively affecting granivorous ground beetles (Figure 6). Carnivorous ground beetles were more abundant in the presence of plants with high SLA values. Low slug abundance was associated with low moss cover. Moss cover and carnivorous rove beetles were favored by the presence of a tree canopy layer in contrast to running spiders. Running spider, as well as fungivorous rove beetles, tall plants and slugs were positively related to the presence of woody debris, whereas its presence negatively affected hemiedaphic springtail abundance. Higher running spider abundance was associated with higher abundance of hemiedaphic springtails. Carnivorous ground beetles were more abundant with higher abundance of fungivorous rove beetles and running spiders. Carnivorous rove beetle abundance was positively related to the abundance of granivorous ground beetles. Finally, litter mass loss was positively related to the abundance of slugs and of hemiedaphic springtails, and negatively related to soil temperature which increased with mineral soil exposure.

DISCUSSION

By combining trait-based and network analyses, implemented through SEM, we reached a comprehensive assessment of the direct and indirect effects of treatments and resulting environmental changes on the food web structure and on leaf litter decomposition (Figure 6, SEM 3). In our specific boreal ecosystem (jack pine stand), we found these effects to be mainly mediated by changes in species at the lower trophic levels.

Direct Impacts of Forest Disturbance on Community Structure and Environment

We found that the two disturbance treatments resulted in several important environmental changes in comparison to the mature forest that can be summarized in two main categories: soil exposure as a result of vegetation and forest floor removal and site preparation, and the varying amounts of woody debris across treatments (none in the high intensity treatment and a higher amount in the low intensity treatment compared to the mature forest). Canopy removal drastically modifies microclimate, including light availability and soil temperature (Venier and others 2014, 2017). The high intensity treatment involving forest floor removal had the warmest growing-season temperatures and increased woody debris mass resulting from the low intensity treatment was also found to affect soil temperature and moisture (Fleming and others
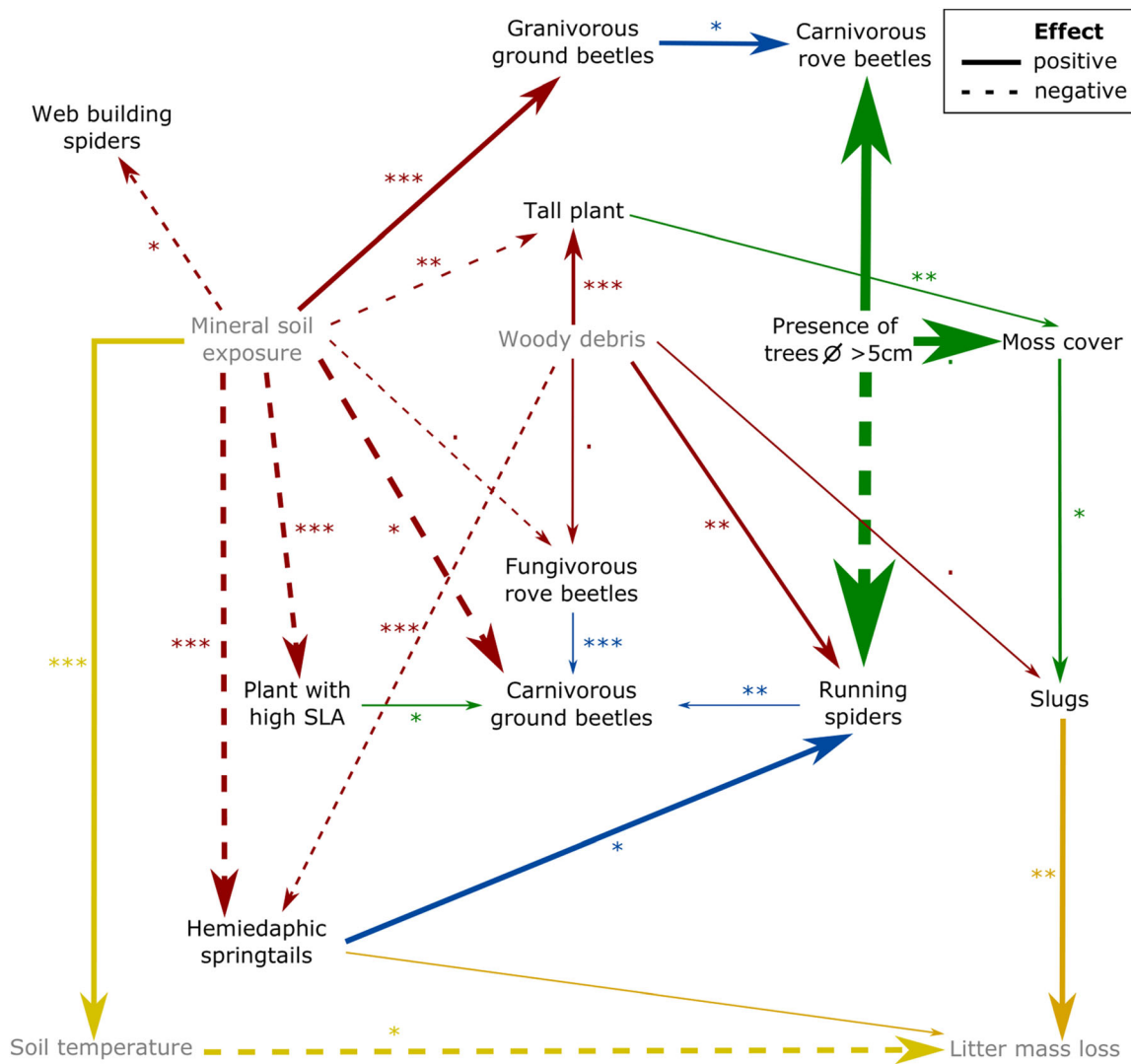
Figure 6. Full model SEM3 testing the ''bottom up'' effect of forest disturbance and induced environmental changes on litter decomposition as a result of the combination of sub-models SEM A3 and B (see Figure 1). Arrow widths are proportional to the standardized coefficient estimates of the relative structural equation (Appendix 8). Negative relationships are represented by dashed arrows while positive ones are represented by solid arrows. Colors refer to hypotheses tested in Figure 1. ***, **, *, and ''.'' indicate statistical significance at $p < 0.001$, 0.01, 0.05 and 0.10, respectively (for details of path standardized coefficients and p values, see Appendix 8).

2006; Webster and others 2016; Rousseau and others 2018). Working on the same experimental sites, Webster and others (2016) demonstrated that plots with higher biomass removal had lower retention levels of carbon and nutrients.

Simultaneous analysis of the species groups showed similarity of response among taxa, but also some important variations in the strength and direction of the responses to disturbance between taxa, suggesting different sensitivities within the food web. Mesofaunal communities were found to be highly sensitive to intensive soil disturbance. In contrast, mobile predators, such as several species

of spiders and ground beetles, benefit from the resources provided by the pioneer conditions/early successional stages and moderate mineral soil exposure. These responses are consistent with those reported after different types of forest disturbances, such as fire (for example, Moretti and others 2002, 2004; Buddle and others 2000, 2006) and windthrow (for example, Thorn and others 2016; Wermelinger and others 2017).

Intense soil disturbances and resulting environmental changes affected several species groups shortly after treatment, exerting selective pressure toward species with high dispersal abilities and

microhabitat requirements matching post disturbance conditions. Dispersal ability is an important factor for the colonization of disturbed areas for several taxonomic groups including ground beetles (Simons and others 2016) and spiders (Bell and others 2005). Species with lower dispersal ability and which require moist conditions were negatively affected. This could explain the extremely low abundance of the slug *Arion* sp. in the disturbance treatments (Getz 1959). We also observed lower abundances of springtail and oribatid mite species, both having low dispersal abilities (Rousseau and others 2019), in the intense disturbance treatments compared to the mature forest (Rousseau and others 2018). Hemiedaphic springtails are commonly found in thick forest floors (Farská and others 2013; Salmon and others 2014) and are therefore more likely to be affected by soil disturbance compared to epidaphic species which can better tolerate disturbed and xeric habitats (Makkonen and others 2011; Bokhorst and others 2012; Rousseau and others 2019). Running spiders were more abundant in the low intensity treatment, where higher amounts of woody debris provide foraging and nesting sites (Varady-Szabo and Buddle 2006). Similarly, web building spiders were less abundant in disturbance treatments where low amounts of woody debris and sparse vegetation provide limited attachment points (Castro and Wise 2009). Although understory vegetation was physically damaged by the treatments, large proportions of boreal forest species possess regeneration mechanisms to cope with such disturbances (Rowe 1983) and/or can re-establish rapidly from budbanks or seedbanks (De Grandpré and others 1993; Haeussler and others 2002).

Indirect Effects of Disturbance on Functional Composition and Ecosystem Functioning

The SEM 3 revealed some indirect impacts of disturbance treatments on food web structure mediated by lower trophic levels, which in turn affected upper trophic levels. Similar to Aubin and others (2013) we found granivorous ground beetles positively associated with disturbed habitats. As they are known to be rather opportunistic feeders (Kulkarni and others 2015), we suppose they can indirectly benefit from the lower abundance of other low trophic groups to colonize newly available niches. Consistent with Chen and Wise (1999), we also found carnivorous beetles and spiders to increase with prey availability. In contrast, our analysis suggests that negative effects of

increasing predators on their prey in disturbance treatments were not significant. Bottom-up control of the food web has also been demonstrated in other forests, such as mature deciduous forests of northern France (Ponsard and others 2000) and boreal forest of Central Sweden (Lenoir and others 2007). Additionally, in North American temperate and mixed forests, recent work has pointed to over one third spatial covariation of litter-dwelling detritivorous and predatory arthropods with their respective resources (Brousseau and others 2019; Raymond-Léonard and others 2019). These results suggest a dominance of bottom-up forces structuring the soil food web.

Our analyses suggested some indirect effects of environmental changes on the leaf litter decomposition. Although higher temperature may accelerate metabolic rate (Brown and others 2004), and thus increase litter decomposition rate in intact forest (Fierer and others 2005), it may also increase surface evaporation, reducing leaf litter moisture, thereby decrease microbial activity (Schimel and others 1999; Wan and others 2007; Butenschoen and others 2011). Working at the same study site, Smenderovac and others (2017) showed lower microbial biomass in the two disturbance treatments compared to the mature forest. Forest disturbance can also affect litter decomposition indirectly by changing species community composition. Species groups associated with decomposition according to the selected SEM, such as slugs and, to a lesser extent, hemiedaphic springtails, were found to be the most sensitive to disturbance treatments. The higher decomposition rate observed in the 5-mm mesh size in the mature forest condition may be related to the importance of soil fauna in this process, and especially large bodied species, as suggested by Handa and others (2014).

Limitations and the Way Forward

By combining a multi-trophic trait-based approach with network analyses, we were able to highlight some of the mechanisms driving the direct and indirect effects of changes in environmental conditions on a key ecosystem function. Numerous studies highlighted the need to incorporate biotic interactions, in particular between organisms of different trophic levels (Lavorel 2013; Brousseau and others 2018a; Seibold and others 2018), to better understand the effects of disturbance on ecosystem functioning (Werner and Peacor 2003; Thébault and Loreau 2003; Moretti and others 2013). Existing studies have largely remained in the theoretical realm (Kardol and others 2016;

Lortie and others 2016; Eisenhauer and others 2019), with very few investigating communities as networks comprised of multiple trophic levels via empirical means (Barnes and others 2016, 2017). Those studies which have tackled the effects of fauna on decomposition or nutrient cycling are either limited by the number of species (for example, De Oliveira and others 2010) or by their resolution, with organisms often coarsely grouped by their taxonomy or bodysize (Bradford and others 2002; Hunt and Wall 2002; Handa and others 2014; Ruiter and others 1993), rather than by their functions.

Our study showcases the potential of structural equation modeling to represent ecological networks comprised of numerous trophic levels of interacting species. The integration of traits into network analysis, as done in this study, allowed a mechanistic understanding of community changes in response to forest disturbance and their effects on ecosystem functioning. We use CWM in this study for its flexibility regarding type of traits, however several functional indices of community structure could be used. In this respect, our study provided empirical support of a bottom-up control in soil food webs by identifying effects of disturbance from the lower to the upper trophic levels. Despite the strong theoretical basis (Ponsard and others 2000), empirical studies looking at multi-trophic interactions have thus far only been able to find support for bottom-up controls in a handful of soil communities (Mikola and Setälä 1998; Rosemond and others 2001; Barnes and others 2017; Brousseau and others 2019; Raymond-Léonard and others 2019). From an applied perspective, our approach can help refine ecological succession assessments after natural and anthropogenic disturbances. Identification of environmental drivers of both direct and indirect impacts of disturbance is critical to the evaluation and improvement of forest policy and management guidelines. Across jurisdictions, large sums of money are spent monitoring a broad range of forest attributes such as regeneration, growth, biodiversity, forest health and wildlife populations. This information is typically analyzed separately to provide ''status and trend'' information, with little emphasis put on more holistic and mechanistic aspects of the assessments. For instance, if an overall mammal population decline is observed, it is then difficult, from this information alone, to attribute this decline to environmental changes resulting from a specific forest management activity, versus to natural changes in food supply, changes in cyclic predator/prey relationships, or the interaction of multiple factors. The approach described in our paper helps identify both the direct and indirect factors influencing these trends, providing managers with a holistic understanding about the plausible explanations for the observed trends, as well as any top-down or bottom-up trophic influences and interactions (see also Barnes and others 2017). As such, it would give supplementary information to forest managers to articulate more efficient forest policy and management guideline alternatives to help lessen or counteract these observed trends. In addition, our approach may also offer a way to select sets of indicator species and to identify important environmental drivers likely to be behind observed trends. Although the intensive research effort that has gone into the Island Lake experiment cannot realistically be implemented on broad regional scales, we can use the insight gained there to better define a focused set of indicator species and environmental variables. These would represent a cost-effective sampling strategy that could be used in broad-scale effectiveness monitoring programs that would treat management guidelines as hypotheses.

Despite recent significant advances in fauna trait selection and standardization across taxonomic groups (for example, Moretti and others 2017; Brousseau and others 2018b), work is still needed to make this approach fully operable. Large proportion of the available information remains derived from expert opinion-based metrics such as feeding guild and microhabitat preference. These metrics are of limited utility as they do not allow the identification of mechanisms underlying species assemblages and introduce circularity when derived from the environment (see trait definition by Violle and others 2007). Traits should, in fact, be selected among those that are expected to have a causal link with the focal stressor of interest (Brousseau and others 2018b). Traits like cuticle thickness and desiccation resistance (Moretti and others 2017) would be more informative on tolerance to hydric stress after disturbance than microhabitat preference (for example, Dias and others 2013). Trait matching between species interactions and information about ontogenetic niche shift during their life cycle are also often missing for most taxonomic groups. Feeding guild was the only information available addressing trophic interactions of several species, while we know that biomechanical and nutritional traits would have been more predictive of positive trophic interactions (Ibanez and others 2013; Brousseau and others 2018a, 2019). Another challenge we face is understanding how traits determine non-trophic

interactions. Most studies on species interactions focus on competition or predation (Montoya and others 2009; Brousseau and others 2018b; Berlow and others 2009). Still, other types of interactions like facilitation, symbiosis and ecosystem engineering can substantially affect biodiversity maintenance and ecosystem functioning, in soils in particular (Brooker and others 2008; Hedde and others 2010; Powell and Rilling 2018). Another challenge is the different taxonomic resolutions (Class, Family) at which these groups are traditionally studied, where in some cases, these differences could affect interpretations. For instance in our study, rove beetles and ground beetles (both Coleoptera) could have been merged and analyzed together, even though they demonstrate contrasting responses when investigated separately.

A true network perspective requires homogeneous documentation of all interacting species, which remains out of reach for empirical studies. A better understanding of fauna functional ecology and species interactions is necessary to provide a stronger framework for multi-trophic studies and improve a priori hypotheses. Implementation of such a holistic approach is a key challenge, but a step toward a comprehensive understanding of the ecological consequences of disturbance on ecosystems and their functioning.

ACKNOWLEDGEMENTS

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