

Blue consequences of the green bioeconomy: Clear-cutting intensifies the harmful impacts of land drainage on stream invertebrate biodiversity

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Abstract

1. Growing bioeconomy is increasing the pressure to clear-cut drained peatland forests. Yet, the cumulative effects of peatland drainage and clear-cutting on the biodiversity of recipient freshwater ecosystems are largely unknown.
2. We studied the isolated and combined effects of peatland drainage and clear-cutting on stream macroinvertebrate communities. We further explored whether the impact of these forestry-driven catchment alterations to benthic invertebrates is related to stream size. We quantified the impact on invertebrate biodiversity by comparing communities in forestry-impacted streams to expected communities modelled with a multi-taxon niche model.
3. The impact of clear-cutting of drained peatland forests exceeded the sum of the independent effects of drainage and clear-cutting, indicating a synergistic interaction between the two disturbances in small streams. Peatland drainage reduced benthic biodiversity in both small and large streams, whereas clear-cutting did the same only in small streams. Small headwater streams were more sensitive to forestry impacts than the larger downstream sites.
4. We found 11 taxa (out of 25 modelled) to respond to forestry disturbances. These taxa were mainly different from those previously reported as sensitive to forestry-driven alterations, indicating the context dependence of taxonomic responses to forestry. In contrast, most of the functional traits previously identified as responsive to agricultural sedimentation also responded to forestry pressures. In particular, taxa that live temporarily in hyporheic habitats, move by crawling, disperse actively in water, live longer than 1 year, use eggs as resistance form and obtain their food by scraping became less abundant than expected, particularly in streams impacted by both drainage and clear-cutting.
5. *Synthesis and applications.* Drained peatland forests in boreal areas are reaching maturity and will soon be harvested. Clear-cutting of these forests incurs multiple environmental hazards but previous studies have focused on terrestrial ecosystems. Our results show that the combined impacts of peatland drainage and clear-cutting may extend across ecosystem boundaries and cause significant biodiversity

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loss in recipient freshwater ecosystems. This information supports a paradigm shift in boreal forest management, whereby continuous-cover forestry based on partial harvest may provide the most sustainable approach to peatland forestry.

KEYWORDS

benthic invertebrates, clear-cutting, ecological integrity, forestry, freshwater, logging, peatland drainage, predictive modelling

1 | INTRODUCTION

The global climate crisis is increasing the demands for renewable energy sources. In forest-rich countries, increasing bioeconomy relies largely on wood production (FAO, 2020). In boreal regions, forests are harvested mainly by clear-cutting (Kuuluvainen et al., 2012) and extensive peatland areas have been heavily drained to enhance wood growth (Paavilainen & Päivänen, 1995). Many of these peatland forests are reaching maturity and will soon be harvested (Nieminen et al., 2015; O'Driscoll et al., 2016), raising concerns about consequences on greenhouse gas fluxes (Korkiakoski et al., 2019) and nutrient export (Nieminen et al., 2018). However, biodiversity impacts, and particularly those extending to adjoining freshwater ecosystems, have been largely neglected.

The adverse impacts of forestry on stream water quality and habitat structure have been addressed in a large number of studies. Clear-cutting and peatland drainage increase the inputs of fine sediments (Suurkuukka et al., 2014), nutrients (Nieminen et al., 2017; Schelker et al., 2016) and dissolved organic carbon (Nieminen et al., 2015), and alter the flow regime (Sørensen et al., 2009). Additionally, clear-cutting may increase light and temperature (Moore et al., 2005) and reduce the amount of large wood entering the channel (Gomi et al., 2006). These stressors and their combinations decrease biodiversity (Jyväsjärvi et al., 2014) and impair stream ecosystem functioning (Erdozain et al., 2018). The mechanisms causing these changes are poorly understood, but it is likely that forestry-related stressors induce strong environmental filtering, allowing only taxa with traits that afford tolerance to these stressors to persist (Thompson et al., 2009).

Inorganic and organic sedimentation is one of the most pervasive land-use stressors and a leading cause for in-stream habitat degradation in forestry-dominated boreal streams (Suurkuukka et al., 2014; Turunen et al., 2017). Current understanding of the trait-sedimentation relationships comes mostly from agricultural settings (e.g. Larsen et al., 2011; Wagenhoff et al., 2012), whereas similar research in forestry-impacted streams is rare. Several traits have been reported to be responsive to sedimentation. Long life cycle, active aquatic dispersal, prevalence of eggs as resistance form, shredding and scraping feeding habits, and relative richness of crawler and interstitial taxa are examples of traits sensitive to sedimentation (Brown et al., 2019; Larsen et al., 2011; Murphy et al., 2017) and therefore potentially responsive also to land drainage and clear-cutting.

The impacts of land drainage are typically stronger, more persistent and harder to mitigate than those of clear-cutting. For example,

peatland drainage can elevate nutrient concentrations in recipient fluvial networks even 60 years after draining (Nieminen, Sallantausta, et al., 2017), whereas harvesting typically increases nutrients only for 5–10 years (Futter et al., 2016). Also, the negative effects of clear-cutting alone are relatively manageable by retaining intact buffers between the stream and the harvested area (Kuglerová et al., 2020), whereas the impacts of forest harvest on drained peatlands are variable and extremely challenging to control (Nieminen et al., 2017). Rewetted peatland buffers, for instance, may decrease sediment and inorganic nutrient export but, simultaneously, increase the export of dissolved organic carbon and organic nutrients (Nieminen, Sarkkola, et al., 2017). Better understanding of the combined effects of clear-cutting and drainage on freshwater biodiversity is clearly needed as the growing bioeconomy is pushing harvesting activities towards peatland-dominated landscapes (O'Driscoll et al., 2013, 2016).

Bioassessment programmes typically focus on larger waterbodies while headwater streams are largely neglected, despite that they make up most of the riverine network (80%–90%; Bishop et al., 2008) and contribute greatly to biogeochemical cycling (Benstead & Leigh, 2012) and regional biodiversity (Finn et al., 2011). Furthermore, headwater streams are intimately linked with the surrounding terrestrial landscape, rendering them highly vulnerable to land-use impacts (Kuglerová et al., 2017) that may dilute towards larger downstream reaches (O'Driscoll et al., 2013). Alternatively, as forestry activities often occur simultaneously at multiple headwater catchments, their local impacts may accumulate and deteriorate habitats and biota at downstream reaches (Gomi et al., 2002; Kuglerová et al., 2017).

As the same catchments are typically managed for decades, no data are usually available before the impact, precluding a BACI-type (before-after-control-impact) approach and forcing researchers to rely on space-for-time substitution designs. These designs are based on the assumption that drivers of ecological change through time are the same as those that drive changes in space, and they typically suffer from uncontrollable variability caused by factors other than the factor of interest (Damgaard, 2019). Predictive multi-taxon niche modelling offers a tool for coping with such unwanted variability as it provides estimates of the composition of native biota expected in the absence of human impact (e.g. Hawkins & Yuan, 2016).

We quantified the impact of forestry-driven activities on benthic invertebrate biodiversity by comparing observed communities in forestry-impacted streams to native communities predicted using a multi-taxon niche model. To take this approach a step further, we also used the model outputs to derive expectations for species' trait

composition at impacted sites. We specifically examined (a) if (and how) catchment-scale clear-cutting and peatland drainage, separately and together, affect stream macroinvertebrate communities, (b) whether the response of invertebrates to forestry-driven catchment alterations is related to stream size; (c) which benthic taxa are most responsive to each forestry action and (d) whether functional traits (and which traits in particular) are more effective than individual taxa at detecting forestry impacts on stream biota. We expected drainage to exert a stronger control than clear-cutting on community composition, and that their combined effect would exceed the sum of individual stressor effects (i.e. synergistic interaction). We further expected headwater streams to be more affected by forestry than the larger downstream reaches. Finally, we expected that biological traits, particularly those related to tolerance of sedimentation, could increase understanding of the mechanistic linkages between a forestry pressure and community response.

2 | MATERIALS AND METHODS

2.1 | Study region

Our study streams are located in the boreal zone of Finland, between latitudes 61°35'N and 67°19'N (Figure S1). Their catchments are typically complexes of peatlands and mineral soils, growing mostly coniferous forests. The majority (67%) of Finland's land area is covered by forests, and nearly all (91%) of them are managed for wood production. A significant proportion (23%) of the forests grow on peatlands drained for forestry (Ihalainen et al., 2019).

2.2 | Data description and stream site groups

We used data from 116 streams (catchment area ≤ 100 km²), selected from a dataset maintained by the Finnish Environment Institute (SYKE) and University of Oulu. Altogether, 73 of the streams represent least disturbed reference conditions (*sensu* Stoddard et al., 2006; hereafter REF) and the remaining 43 streams drain forestry-impacted catchments (Figure S1). The REF sites were broadly similar to the impacted streams and differed only in the degree of forestry in their catchments (Table S1). Consequently, the REF sites had minimal anthropogenic pressure (clear-cut intensity <13%, drainage intensity <20%) in their catchments (Figure S2). No truly pristine catchments exist in the study region and the REF sites represent a compromise for having as little forestry impact as possible for modelling the near-native biota yet maintaining a sufficient number of sites for model calibration (Figures S1 and S2). We selected forestry-impacted sites based on their land use: (a) clear-cut catchments (hereafter CC, 18%–26% of catchment clear-cut) with minimal drainage (up to 11%), (b) drained catchments (D, 33%–55% of catchment drained) with minimal clear-cutting (up to 6%) and (c) catchments with both drainage and clear-cutting (D+CC, 27%–46% drained, 15%–35% of catchment clear-cut; Figure S2). As harvesting

activities in Finland are small scale and scattered within and across catchments, and distributed across multiple years, the overall harvest intensity in each catchment was estimated as percentage of forest area lost in 2001–2017 (loss-year data in Global Forest Change database, version 1.5; Hansen et al., 2013). Drainage intensity in each catchment was estimated as percentage of drained peatlands (drainage data, Finnish Environment Institute). We further divided the streams into small (catchment area ≤ 15 km²) and large (>15 km²) to examine whether the responses, if any, were related to stream (catchment) size. Group-specific sample sizes were as follows: 37 REF, 8 CC, 7 D and 6 D+CC for small headwater streams and 36 REF, 9 CC, 6 D and 7 D+CC for large streams.

2.3 | Environmental data

We obtained several environmental variables for model calibration and testing of model performance (Table S1). Catchment-scale variables were measured using GIS (ESRI, 2016, ArcGIS 10.4 software). Land use and land cover features (other than drainage and logging) were obtained from Corine Land Cover 2012 database (NLS) and water chemistry data from Hertta database (SYKE). Annual air temperature and precipitation data were derived from WorldClim database (Hijmans et al., 2005).

2.4 | Macroinvertebrate data and trait information

One autumnal benthic sample was collected at each site following the national standard protocol (Meissner et al., 2016). Each sample consisted of four 30-s subsamples taken from separate locations of a continuous riffle section using a kick-net (500- μ m mesh size). Macroinvertebrates were sorted and identified to the lowest possible taxonomic level, usually species or genus. Chironomids and Oligochaeta were not identified further and were therefore excluded.

We focused on a set of traits previously identified as sensitive to a key stressor in both agricultural and forestry-impacted streams, that is, sedimentation (Brown et al., 2019; Buendia et al., 2013; Descloux et al., 2014; Lange et al., 2014; Larsen et al., 2011; Murphy et al., 2017; Wagenhoff et al., 2012). To be included, a trait had to be reported as sensitive (or tolerant) to sedimentation of fine organic or inorganic particles in at least one (three out of 13 traits) but preferably in several (10 out of 13 traits) of the seven articles cited above. This resulted in 13 biological and ecological trait categories: feeding habits (scrapers, shredders and filter feeders), locomotion and substrate relation (temporarily attached, burrowers, crawlers and interstitial taxa), dispersal (aquatic active), life cycle length (life duration longer than 1 year), maximal size (≤ 0.5 cm), respiration (gill), reproduction (clutches, cemented or fixed) and resistance form (eggs/statoblasts). Information for each trait was compiled from Statzner et al. (1994), Dolédec et al. (1999), Usseglio-Polatera et al. (2000) and Schmidt-Kloiber and Hering (2015). Affinity of each taxon to each

trait category was described by an affinity score from 0 to 3 based on a fuzzy-coding approach (Chevenet et al., 1994). The higher the score, the higher the affinity of a taxon to the respective trait category. To give the same weight to each taxon and trait, we standardized the affinity scores so that their sum for a given taxon/trait equalled one. We then weighted the standardized affinity scores with \log_{10} taxa abundances (see Gayraud et al., 2003).

2.5 | Predictive modelling of macroinvertebrate communities

We used River Invertebrate Prediction and Classification System (RIVPACS)-type multi-taxon niche modelling (e.g. Hawkins & Yuan, 2016) to predict for each study site, the composition of macroinvertebrate community expected in the absence of forestry impact. RIVPACS-type models use environmental data to predict probabilities of observing the taxa in reference conditions established for a region. We provide a brief description of the modelling approach here (see Supporting information for a detailed description). The models are calibrated by first grouping the reference sites based on their biological dissimilarity. Then, environmental variables that best explain the site grouping are used to predict group membership probabilities for each site. Probabilities of capture of each taxon (altogether 122 taxa) for each site (p_i) in the absence of anthropogenic impact are calculated by weighting frequencies of each taxon within each group with group membership probabilities (Moss et al., 1987).

We used the modelling to predict expected \log_{10} abundance of each taxon for each site by weighting average \log_{10} abundances within each group with the group membership probabilities (Armitage et al., 1987). We included only taxa predicted to be locally common (p_i values ≥ 0.5 ; 34 taxa) because model performance is typically improved by excluding rare taxa (Van Sickle et al., 2007). We used the expected taxon abundances also to calculate expected abundances for traits using the procedure described above.

We quantified forestry impact at each site by comparing similarity between the observed and expected communities. For this purpose, we used Bray–Curtis dissimilarity values that were converted to similarity to improve interpretability (hereafter O/E-BC). An O/E-BC value close to 1.0 indicates community composition similar to that expected, whereas values less than 1 indicate disagreement between the observed and expected communities. We tested differences in O/E-BC values among the four stream groups (REF, CC, D, D+CC, small and large streams separately) using a two-way ANOVA, with drainage (minimal vs. intensive drainage) and clear-cutting (minimal vs. intensive clear-cutting) as independent variables. The O/E-BC values were ln-transformed prior to analysis to meet model assumptions. We interpreted the significant interaction using the directional classification system of Piggott et al. (2015) which combines the magnitude and direction of the cumulative response and the interaction effect (deviation from the additive model

prediction) to determine synergism or antagonism relative to individual stressors.

2.6 | Sensitive taxa and traits

We limited examination of taxon/trait sensitivity to forestry activities to the taxon/trait abundances that were reasonably well predicted by the model. These taxa/traits were defined as those whose 95% confidence intervals (CI) for the proportion of observed to expected abundances among the REF sites overlapped 100% (i.e. perfect abundance prediction). We then examined proportions of observed to expected abundances in each of the four stream groups (small and large streams separately) and defined taxa and traits sensitive to forestry activities if the CI among the forestry-impacted sites did not overlap the CI of the REF sites. All statistical analyses were conducted using R (version 3.5.0, R Core Team, 2018).

3 | RESULTS

3.1 | Benthic biodiversity

Predictive multi-taxon niche modelling resulted in an accurate and precise prediction of expected communities, improving prediction precision by about 16% from a null model (see Supporting Information for model performance details). Comparison of observed to expected community composition revealed negative effects of forestry in both small (Figure 1a; Table S2) and large streams (Figure 1b; Table S3). In small streams (Figure 1a), the interaction term (drainage \times clear-cutting) bordered at significance ($F_{1,54} = 3.63$, $p = 0.062$), indicating a synergistic effect between the two disturbances, with clear-cutting enhancing the negative effects of drainage (Table S2). In large streams (Figure 1b), drainage decreased O/E-BC ratio ($F_{1,54} = 12.29$, $p < 0.001$), whereas the main effect of clear-cutting ($F_{1,54} = 0.09$, $p = 0.765$) and the interaction between drainage and clear-cutting ($F_{1,54} = 1.83$, $p = 0.182$) were not significant (Table S3).

3.2 | Taxa sensitivity

Comparison of observed to expected abundances indicated 11 taxa (out of 25 modelled) as responsive to forestry activities. The number of responsive taxa was almost the same in small CC-, D- and D+CC-streams (Figure 2a), but in large streams the combined effect of D+CC increased the number of sensitive taxa compared to CC or D alone (Figure 2b). In small streams, the predatory stonefly *Diura* sp. was sensitive to clear-cutting while another predatory stonefly, *Isoperla* sp. was particularly sensitive to the sole impact of drainage (Figure 2a). The coleopterans *Hydraena* sp. and *Elmis aenea* were most likely to disappear from streams affected by both

FIGURE 1 Variation ($M \pm SE$) of O/E-BC-similarity between observed and expected (modelled) communities in each stream group in (a) small and (b) large streams. D, drainage and CC, clear-cutting intensity

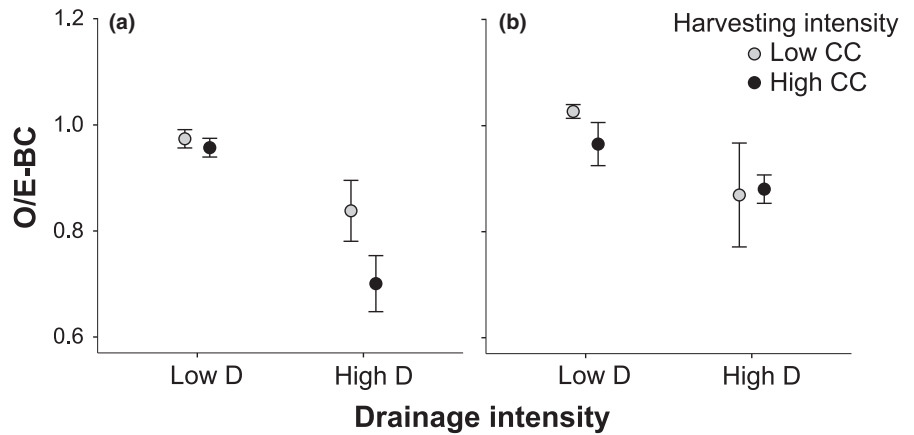
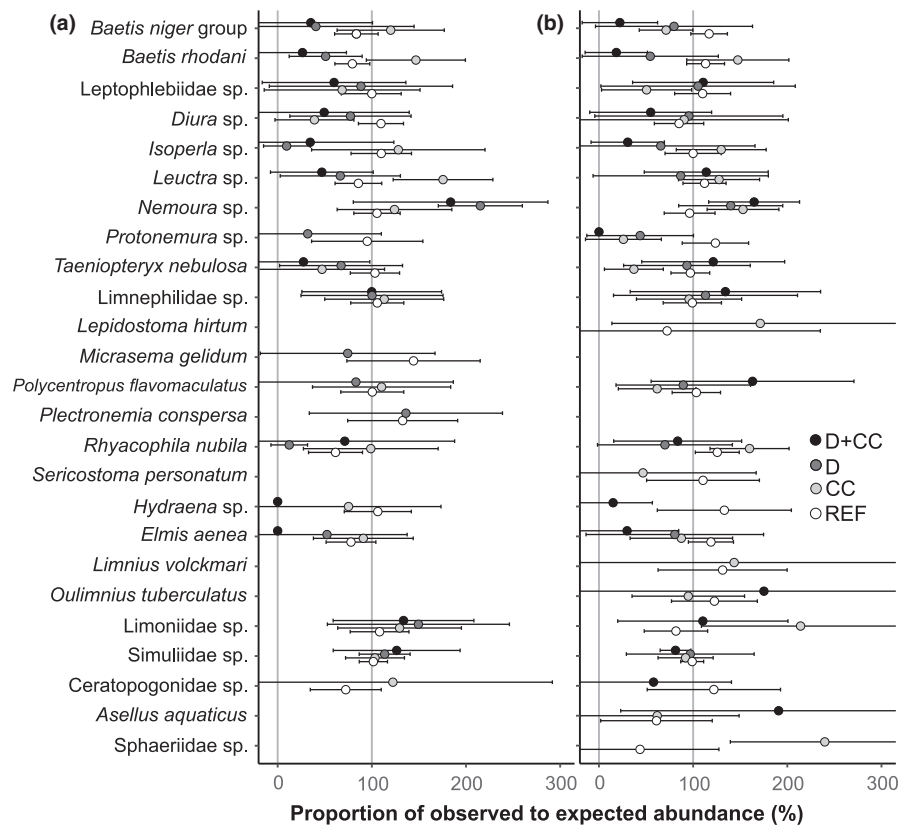


FIGURE 2 Proportion of observed to expected (modelled) abundance of benthic invertebrate taxa in (a) small and (b) large streams. Only taxa whose abundances were reasonably well predicted by the model (see text for details) are included. White dots represent mean ($\pm 95\%$ confidence intervals) among reference sites, depicting a model's ability to predict the abundance of each taxon while black and grey dots represent the proportion of observed to expected abundance (mean $\pm 95\%$ CI) of each taxon at sites impacted by different forestry activities. REF, minimally disturbed reference streams; CC, streams with mainly clear-cutting; D, streams with mainly drainage; D+CC, streams with both drainage and clear-cutting in their catchments



clear-cutting and drainage (Figure 2a). By contrast, the stonefly *Nemoura* sp. seemed to benefit from forestry actions, although significantly so only in drainage-impacted streams while the abundance of the stonefly *Leuctra* sp. was higher than expected in clear-cut streams (Figure 2a). In large streams, the shredding stoneflies *Protonemura* sp. and *Taeniopteryx nebulosa* showed the highest sensitivity to clear-cutting. No taxa responded significantly to drainage alone (Figure 2b), whereas five taxa (*Protonemura* sp., the mayflies *Baetis rhodani*, *Baetis niger* group, and the aquatic beetles *Hydraena* sp. and *Elmis aenea*) showed a strongly reduced abundance to the combined effect of D+CC (Figure 2b). The sphaerid clams (Sphaeriidae) were the only group with a strong positive response to any forestry action (in this case, clear-cutting) in larger streams (Figure 2b).

3.3 | Trait sensitivity

Comparison of the observed to expected trait abundances indicated 7 of the 13 sediment-sensitive traits to decline or increase due to forestry activities (Figure 3). Trait responses were clearly strongest to the combined effect of drainage and clear-cutting. In small streams, taxa that live temporarily in hyporheic habitats, move by crawling, are active aquatic dispersers, live longer than 1 year or lay clutches of cemented/fixed eggs declined the most (Figure 3a). Scrapers and taxa that respire with gills also declined in D+CC-streams but as their occurrence was not sufficiently well predicted, we cannot make strong inference about their responses (Figure 3a). In larger streams, two traits, taxa that obtain food by scraping and taxa that utilize eggs as resistance form, declined in streams affected by both

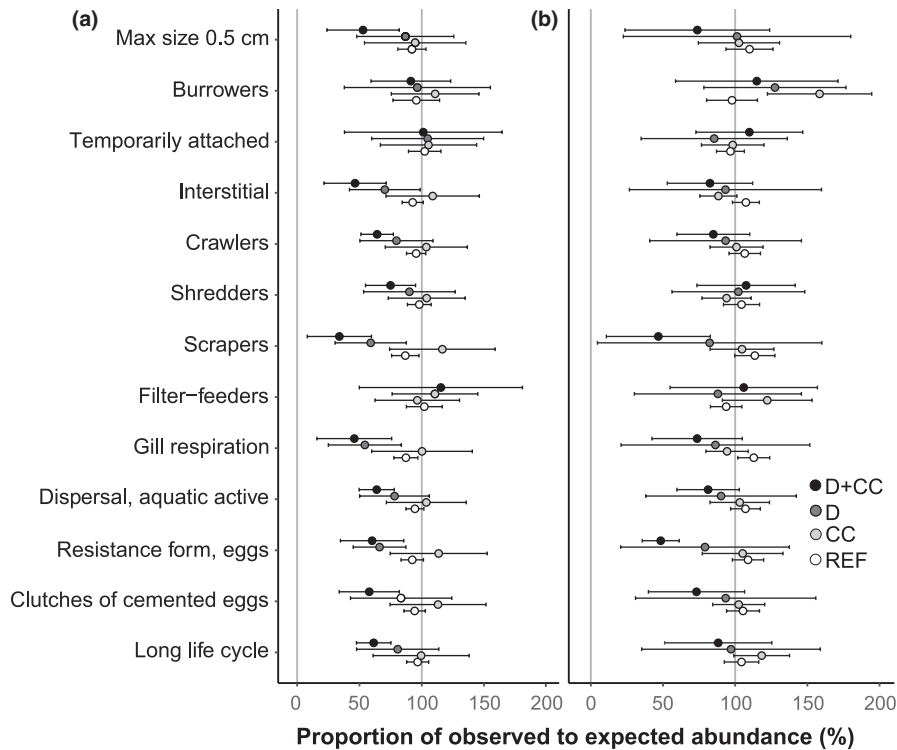


FIGURE 3 Proportion of observed to expected abundance of each sedimentation-related functional trait in (a) small and (b) large streams. For group identities, see Figure 2. Trait sensitivity was defined in the same way as taxa sensitivity (see Figure 2). The two upmost traits were expected to become more abundant and the others to decline in response to forestry activities

clear-cutting and drainage and one trait, taxa that burrow in fine sediment, increased in streams affected by clear-cutting (Figure 3b).

4 | DISCUSSION

With the growing bioeconomy, forest-rich countries increase their wood production, one reflection of which is the growing demand for clear-cutting of drained peatland forests. Yet, the cumulative effects of the two activities (land drainage, clear-cutting) on the biodiversity of recipient freshwater ecosystems are largely unknown. We showed that clear-cutting of drained peatland forests can impair the ecological integrity of stream ecosystems, with an overall impact that exceeds the effect of each disturbance alone. Here, the pattern was detected in small headwater streams. Peatland drainage alone induced a change of stream invertebrate biodiversity in both small and large streams, whereas the independent effect of clear-cutting was observed only in small streams.

Effects of clear-cutting on stream biodiversity have been highly variable, with individual studies showing negative, neutral or even positive effects on biodiversity (Richardson & Béraud, 2014). In this study, clear-cutting impaired macroinvertebrate communities only in small streams. Low responsiveness has been reported particularly where intact (or nearly so) buffer-strips were retained between the stream and the upland forest (e.g. Erdozain et al., 2018). The runoff of nutrients and suspended solids from a clear-cut can be mitigated by wide buffer-strips, but if the clear-cut is large (>30% of catchment), even a wide buffer (>30 m) may not protect the stream from stressors caused by land use (Palviainen et al., 2014). In this study, the estimated proportion of clear-cuts in non-drained catchments

did not reach 30% (18%–26%) and therefore the release of nutrients and sediments were likely controlled by riparian buffers. While information on exact buffer widths at our study sites was unavailable (i.e. they were not measured in situ), inspection of GFC (Global Forest Change, loss-year data in 2001–2017) maps revealed no clear-cuts in the immediate vicinity (within 30 m) of any of the sampling sites. In addition, a recent survey of buffer management in Finland demonstrated that intact buffers around streams were on average 15 m wide (Kuglerová et al., 2020). The impairment of macroinvertebrate communities in small but not in large streams potentially reflects higher connectivity of headwater streams to their catchments (Gomi et al., 2002; Kuglerová et al., 2017) and/or dissipation of elevated nutrient and carbon concentrations towards downstream reaches (Futter et al., 2010; Schelker et al., 2014, 2016).

Peatland drainage impaired macroinvertebrate communities in both small and large streams. Ramchunder et al. (2012) and Brown et al. (2019) detected a similar response in their studies on the impacts of peatland management (drainage, sheep grazing and rotational vegetation burning) on stream macroinvertebrate communities in headwater streams. In these two studies, organic sediment deposition and higher concentrations of suspended solids reduced benthic diversity. Thus far, the impacts of peatland drainage on biodiversity and stressor (i.e. sediments, nutrients, DOC) export have been studied mainly in the upmost headwater streams, yet our results suggest that the detrimental effects of drainage are also present in larger downstream sections.

In small streams, clear-cutting of drained peatlands caused an exceedingly high disturbance that surpassed the effect of drainage alone. Clear-cutting (and subsequent site preparation using heavy machinery) exposes the already eroding soils to further erosion, elevates groundwater table and flushes easily soluble and redox sensitive

elements (e.g. DOC, P and Fe) and fine sediments into ditches that drain towards the recipient streams (Nieminen, Sarkkola, et al., 2017). Congruent with our results, O'Driscoll et al. (2013) reported that clear-cutting of drained peatland forests impaired macroinvertebrate communities in headwaters but less so in downstream reaches, due in part to the initially elevated nutrient and suspended sediment concentrations that diluted towards larger water volumes in larger streams.

No individual taxa responded consistently to all forestry actions. The coleopterans *Hydraena* sp. and *E. aenea*, and the mayfly *B. rhodani* that reduced in abundance, or even disappeared, in D+CC-streams have been previously recorded as moderately sensitive to sedimentation (Larsen & Ormerod, 2010; Murphy et al., 2015; Wagenhoff et al., 2012). Additionally, *Nemoura* sp. that responded positively (although not always significantly) to all forestry actions have been characterized as tolerant (particularly *N. cinerea*) of both organic and inorganic sediment stress (Murphy et al., 2015).

Seven of the thirteen evaluated traits declined in D+CC-streams, and five of these in small streams, indicating that the cumulative stress caused by clear-cutting of drained peatlands was stronger than that of clear-cutting or drainage alone, and that it was stronger in small than in larger streams. Most of the traits that declined in the D+CC-streams were also identified as sensitive to organic sedimentation by Brown et al. (2019), with the exception that they also found leaf-shredding invertebrates to be selected against in sediment-stressed peatland streams, whereas in our study, shredder abundance did not differ from expected. Filter-feeders did not respond either, possibly due to antagonistic impacts of suspended solids that interfere with their filtering apparatus and increased availability of their main food source, fine particulate matter (Jones et al., 2012; Ramchunder et al., 2012). Tendency to lay fixed eggs and move by crawling were less prevalent in streams impacted by both clear-cutting and drainage. Both these traits suffer from sedimentation that decreases the availability of coarse substrates and clogs the interstitial spaces within the streambed (Murphy et al., 2017; Wilkes et al., 2019). Burrowing was the only trait that was positively associated to any forestry action, but significantly so only to clear-cutting.

Taxa responsive to sedimentation differed from those reported in most previous studies (e.g. Buendia et al., 2013; Larsen & Ormerod, 2010; Larsen et al., 2011; Murphy et al., 2015), whereas the majority of the functional traits previously identified as responsive to sedimentation also responded to forestry pressure. This result reflects the fact that traits are largely unaffected by differences in regional species pools (Bonada et al., 2007). A trait-based approach may be particularly useful for freshwater bioassessment also because traits may provide a mechanistic understanding of the trait–environment linkages related to particular stressors (Statzner et al., 2001). However, environmental filters act on trait combinations rather than on individual traits (Verberk et al., 2013), resulting in predominance of disturbance-tolerant trait syndromes under stressful conditions (Brown et al., 2019). Consequently, single-trait responses may yield such seemingly counterintuitive results as in our study where *Leuctra* sp. stoneflies became more abundant than expected in clear-cut streams and *Nemoura* sp. in drainage-impacted streams,

although they both represent some of the same sedimentation-sensitive traits as most of the taxa that declined in D+CC-streams (e.g. fixed eggs; movement by crawling).

Inadequate protection of headwater streams often results in degradation of downstream reaches (Kuglerová et al., 2017), potentially incurring great costs to restoration of downstream areas. In our study, however, forestry had a stronger negative impact on benthic biodiversity in small than in large streams, a result paralleled by previous studies for similar (O'Driscoll et al., 2013) as well as other types of land uses (Greenwood et al., 2012). Our results emphasize the importance of small streams in catchment-wide assessment of forestry impacts; these smallest and most isolated parts of the riverine networks are usually the first to suffer from forestry-related land uses.

There is some indication that continuous-cover forestry where single trees are harvested on a 15- to 20-year cycle may protect forest biodiversity and ecosystem services better than conventional rotation forestry (Peura et al., 2018). This kind of partial harvesting may also be the best management strategy for peatland forests as the rise of water table, excess nutrient input and soil erosion may be better controlled by harvesting only individual mature trees or small groups of trees (Nieminen, Sarkkola, et al., 2017). The severe impacts of clear-cutting of peatland forests on both freshwater (O'Driscoll et al., 2013; this study) and terrestrial (Remm et al., 2013) biodiversity and greenhouse gas emissions (Korkiakoski et al., 2019) impose a paradigm shift in boreal forest management and continuous-cover forestry with partial harvesting holds the greatest potential as an environmentally sustainable approach to the management of peatland forests for future bioeconomy.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the design of the study; M.R. built the predictive models and performed the statistical analyses; M.R. led the writing of the manuscript and all authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.95x69p8k7> (Rajakallio et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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