

Biodiversity and community composition of ground-dwelling invertebrates across three disturbance regimes in a sub-boreal spruce forest

A. S. MITCHELL, D. P. W. HUBER*, AND L. M. POIRIER†

ABSTRACT

Natural and anthropogenic disturbances are closely tied to changes in biodiversity and ecological communities. Previous research has reported that ground-dwelling invertebrates exhibit a range of responses to different disturbance regimes. To investigate changes to community composition and biodiversity following forest harvest, we used pitfall traps to sample ground-dwelling invertebrates in the Aleza Lake Research Forest in British Columbia's Central Interior. We collected and compared pitfall trap catches using family-level identifications in new plantations (11 years since harvest), stands with a harvest history (> 40 years since harvest), and old-growth stands (no record of harvest). Community compositions differed among the three disturbance regimes, and Bray–Curtis dissimilarity indicated that β -diversity was highest in new plantation stands. A small but non-significant increase in α -diversity was also observed in new plantation stands compared to the other two forest types. These findings are consistent with previous work in the boreal forest, which reported increases in ground-dwelling invertebrate biodiversity following disturbance. Three families (Agriolimacidae, Formicidae, and Lycosidae) were significantly associated with new plantation stands and could potentially be used as indicators of forest disturbance or to monitor stand succession after harvest. This study provides a foundation for future work on invertebrate biodiversity in sub-boreal spruce forests, which would benefit from using species-level identifications and measuring environmental conditions associated with disturbance regimes.

INTRODUCTION

Understanding the effects of disturbance on biodiversity is critical in an era of growing human impacts (Wilson 2017). Although invertebrates have historically been overlooked in the context of conservation (Cardoso *et al.* 2011), recent evidence of insect declines (Hallmann *et al.* 2017; van Klink *et al.* 2020; Wagner 2020) has attracted considerable attention. Similar concerns about biodiversity loss have also been raised for other invertebrate taxa, such as mites (Sullivan and Ozman-Sullivan 2021). However, a lack of baseline data in natural systems makes distinguishing between natural variation and long-term trends difficult. Improved understanding invertebrate biodiversity and community structures is therefore crucial for assessing the cumulative impacts of disturbance.

University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9;
*dezene.huber@unbc.ca

†Deceased, October 2023

Indicator taxa are often used to assess the effects of disturbance due to the logistical challenges inherent to biodiversity sampling. Epigeic (ground-dwelling) invertebrates are useful for this purpose because they are abundant, easily sampled, and often exhibit predictable responses to environmental change (McGeoch 1998; Gerlach *et al.* 2013). A wide variety of taxa has been used or proposed as indicators, including ground beetles (Coleoptera: Carabidae), springtails (Collembola), harvestmen (Opiliones), slugs and snails (Gastropoda), and some groups of spiders (Araneae) (Rainio and Niemelä 2003; Gerlach *et al.* 2013). For example, arthropod taxa have been used to evaluate the effects of urban land use (McIntyre *et al.* 2001, the management of plantation forests (Oxbrough *et al.* 2010, and stand regeneration following forest harvest (Pohl *et al.* 2007).

The relationships between disturbance, biodiversity, and ecosystem function are complex, but in general, a positive relationship exists between species diversity and measures such as productivity and stability (Tilman *et al.* 2014; van der Plas 2019). Although disturbances are often associated with decreases in biodiversity, this is not always the case for invertebrate taxa. For example, invertebrate species richness in urban environments can vary considerably, with both increases and decreases observed at low to moderate levels of disturbance (McKinney 2008). Similarly, work in agricultural areas found that carabid richness and abundance were highest in the most disturbed, intensely managed sites (Vanbergen *et al.* 2005).

Invertebrate biodiversity may also increase following disturbance in forest environments. Natural forms of disturbance, such as gap formation, have been shown to influence arthropod community composition and increase family richness (Perry *et al.* 2018), and anthropogenic disturbances such as forest harvest have also been associated with such shifts. For example, clearcutting increased the biodiversity of some ground-dwelling invertebrate taxa and resulted in shifts in community structure between regenerating and mature stands in the Canadian boreal forest (Buddle *et al.* 2006; Pohl *et al.* 2007). However, biodiversity alone may not be a metric of ecosystem health or function in all cases. Although they may appear to be less biodiverse than disturbed stands, mature, unharvested forests can house unique species excluded from other habitats (Buddle *et al.* 2006). Niemelä *et al.* (1993) found that, although carabid beetles were most abundant in recently clearcut sites, species specialised for mature forest conditions decreased in abundance or disappeared from those areas.

Work done to examine such relationships in the Omineca region (Government of British Columbia, n.d.) in British Columbia's Central Interior has been limited. In a survey of carabid beetles in the Chun T'Oh Wudujut Provincial Park (53.76° N, -121.22° W), located in the Interior Cedar-Hemlock biogeoclimatic zone, Higgins (2019) found a positive relationship between forest harvest and biodiversity, with higher species diversity observed in clearcut stands than in old-growth sites. McColl (2010) also found that sub-boreal spruce stands with low canopy cover had greater carabid diversity and that forest harvest altered their community compositions. Research on ground-dwelling invertebrates in the urban centre of Prince George, B.C., also revealed similar trends. Specifically, highly disturbed industrial areas scored higher in biodiversity indices than

residential and greenbelt sites did, and each habitat type exhibited distinct community compositions (Huber *et al.* 2019).

Forests throughout the Omineca region have seen extensive alteration since the mid-19th century, including, but not limited to, industrial logging, outbreaks of forest pests such as the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and wildfire. The contributions of climate change to various forest disturbances are increasingly apparent, but a lack of baseline data in these biological systems makes the effects of such changes difficult to evaluate.

We examined the effects of forest harvest on epigeic invertebrates in the Aleza Lake Research Forest, about 70 km northeast of Prince George. Pitfall samples were collected from three forest types with variable histories of harvest representing distinct disturbance regimes. We hypothesised that new plantation sites, which represented the most recently disturbed areas, would display increased levels of biodiversity and distinct community compositions, consistent with past research performed in the Omineca region.

METHODS

Sampling area

The Aleza Lake Research Forest (ALRF; 54.095° N, -122.100° W) encompasses a roughly 9000-ha area northeast of Prince George, B.C. (53.894° N, -122.814° W). The ALRF was established in 1924 and includes areas with variable harvest histories and recovery times (Aleza Lake Research Forest Society 2019). Dominant tree species in the area are subalpine fir, *Abies lasiocarpa* (Hooker) Nuttall, and interior hybrid spruce, *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelmann (Bois *et al.* 2009), as is characteristic of the Sub-Boreal Spruce (SBS) biogeoclimatic zone.

Site selection

We sampled and compared replicated sites in three forest types representing various levels of disturbance (Table 1). *New plantation* stands had been logged relatively recently (2007–2008; 11 years previously) and replanted with interior hybrid spruce, with lodgepole pine, *Pinus contorta* Douglas ex Loudon var. *latifolia* Engelmann, also present. *Harvest history* stands had also been logged more than 50 years previously by thinning-from-above, meaning small-diameter trees were retained within the stand. These stands were not replanted after harvest and have instead regenerated naturally. Finally, *old-growth* stands had no recorded history of harvest since the establishment of the ALRF in 1924. They are identified as old forest by the Aleza Lake Research Forest Society (2019), which uses a cut-off of 140 years of age for coniferous-leading stands. One of the three sites was within the boundaries of the Aleza Lake Ecological Reserve, a provincial protected area established in 1978. Although the trees in these stands were not aged for this study, to our knowledge no stand-replacing disturbance events have occurred since record-keeping began. This was also true of new plantation and harvest history stands, in which forest harvest was the only disturbance known to have affected the stands as a whole. Replicated sampling areas (N = 3 for each forest type) were selected using harvest records and characteristic features of harvesting such as stumps or young trees.

Table 1. Information on sites from which ground-dwelling invertebrates were sampled in the Aleza Lake Research Forest, B.C. Three sites (1–3) were sampled in three forest types representing varying levels of disturbance from harvest. New plantation stands (NP) were clearcut and replanted, harvest history stands (HH) were thinned from above ~50 years previously and regenerated naturally, and old-growth stands (OG) had no history of harvest.

Site	Latitude	Longitude	Harvested
NP1	54.102	–122.090	2007–2008
NP2	54.096	–122.097	2007–2008
NP3	54.097	–122.097	2007–2008
HH1	54.083	–122.089	1959
HH2	54.093	–122.092	1967
HH3	54.095	–122.088	1967
OG1	54.083	–122.092	No harvest history
OG2	54.101	–122.087	No harvest history
OG3	54.091	–122.102	No harvest history

Sampling

Ground invertebrates were sampled using modified Norlander-style pitfall traps, consisting of a lidded plastic cup with 6-mm holes punched around the rim (Higgins and Lindgren 2012; Higgins 2019). Traps were buried so that their holes were flush with the ground and covered with duff and forest floor material to minimise detection and to simulate the surrounding environment.

Although pitfall traps are unable to discriminate between abundance and activity, they remain a valuable tool for invertebrate sampling due to their simplicity, low maintenance requirements, and efficacy at capturing certain taxa of ground-dwelling arthropods. While discussing the role of pitfall trapping in carabid sampling, both Niemelä *et al.* (1993) and Phillips and Cobb (2005) argue that despite these shortcomings, this method remains a useful tool for comparisons of community composition and diversity across habitats.

The traps contained 50% propylene glycol as a killing and preservative agent (Thomas 2008) with low toxicity to vertebrates. No attractants were used. Five traps were placed along a transect at each site, with each placed at least 10 m from other traps and at least 50 m from any trails or roads. In total, 45 traps were deployed across nine sites (three sites in each of the three forest types). Sampling took place over the summer of 2019, with traps placed in late May or early June and remaining in place until mid to late September, the period when sites were accessible. Trap contents were emptied between two and five times over this period as was permitted by weather and other access concerns. Contents were strained (mesh size: 1.25 mm) before being transferred to 100% ethanol in the field.

Sorting and data collection

Before the collection of count data, a survey of the collected samples was performed to prepare a catalogue of the taxa present. Photos were taken of each morphotype present, and keys (Lindroth 1961–1969; McAlpine *et al.* 1981; Marshall 2017) were used to identify them to at least family and to genus or species, where possible. Identification was aided by CO1 DNA barcoding

(Hebert *et al.* 2003) of 380 curated specimens by the Biodiversity Institute of Ontario (BOLD record available at dx.doi.org/10.5883/DS-ALEZA19). Using this catalogue and keys as needed, a second sort of the same samples was performed to obtain count data for analyses.

Statistical analysis

Taxonomic analyses were performed using family-level identifications, although sometimes morphotypes were used where morphological identification to family was difficult (e.g., earthworms were grouped into “Annelids”). Insect larvae were excluded from analyses when they could not be identified to family to avoid inflating biodiversity estimates. Springtails (Collembola) were also omitted due to their extreme abundance and because of losses that occurred when trap contents were strained in the field. All analyses were generated using R, version 4.0.2 (R Core Team 2020), and the *vegan* (Dixon 2003) and *indicspecies* (Cáceres *et al.* 2010) packages.

Sample-based rarefaction curves were used to assess sampling effort. This process is necessary to evaluate variations in sampling across study areas and is an important step before drawing comparisons between treatments (Gotelli and Colwell 2001; Buddle *et al.* 2005). Four curves were generated: one for the survey as a whole, and one for each of the three levels of harvest-related disturbance (Figs. 1 and 2). Diversity was compared at two scales: first, α -diversity was assessed as the family richness in each forest type, as well as the mean number of families found in each sampling area. Additionally, both Shannon and Simpson biodiversity indices were calculated for each sampling area. Differences between the mean ($n = 3$) index values were tested using a one-way analysis of variance. Second, β -diversity was determined using the Bray–Curtis dissimilarity index, with pairwise comparisons among sampling areas. Bray–Curtis indices were used to generate a cluster dendrogram (Fig. 3), where increased branch distance represents increasing dissimilarity between communities. Community compositions in each forest type were also compared using a non-metric multidimensional scaling plot (Fig. 4). Finally, indicator species analysis (Cáceres *et al.* 2010) was used to identify families associated with particular forest types and to suggest potential indicators of disturbance in the system.

RESULTS

Pitfall trapping between 22 May and 27 September 2019 yielded more than 15 000 invertebrates that represented three phyla and 94 families. Rarefaction curves did not reach asymptotes, suggesting that some rare families were not detected. However, curves approached asymptotes both in the survey overall (Fig. 1) and within each forest type (Fig. 2). Individual curves for each forest type also fell within 95% confidence intervals each other (Fig. 2).

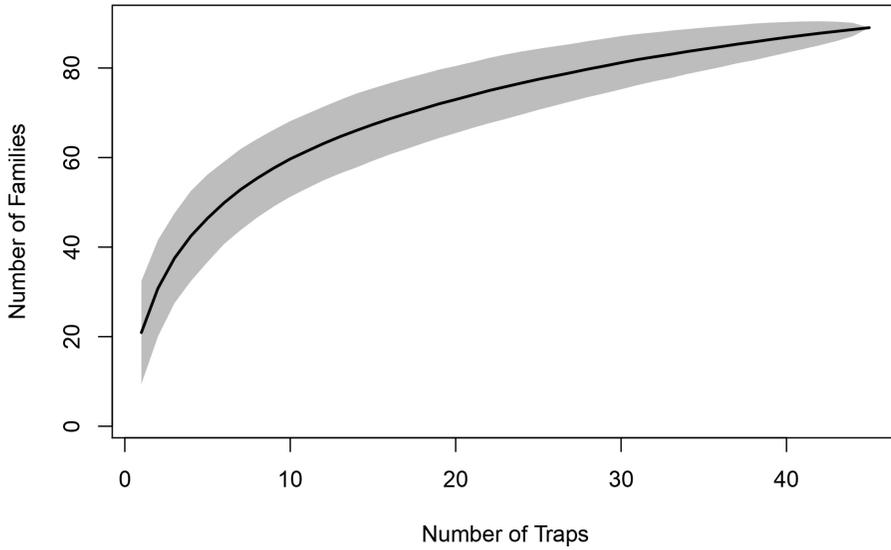


Figure 1. Sample-based rarefaction curve for all pitfall captures of ground-dwelling invertebrates (excluding springtails) in the Aleza Lake Research Forest, B.C. The rarefaction is based on 1000 permutations randomly generated from trap-catch data from all three levels of disturbance related to forest harvest sampled: new plantation, harvest history and old growth. The shaded area represents the 95% confidence interval.

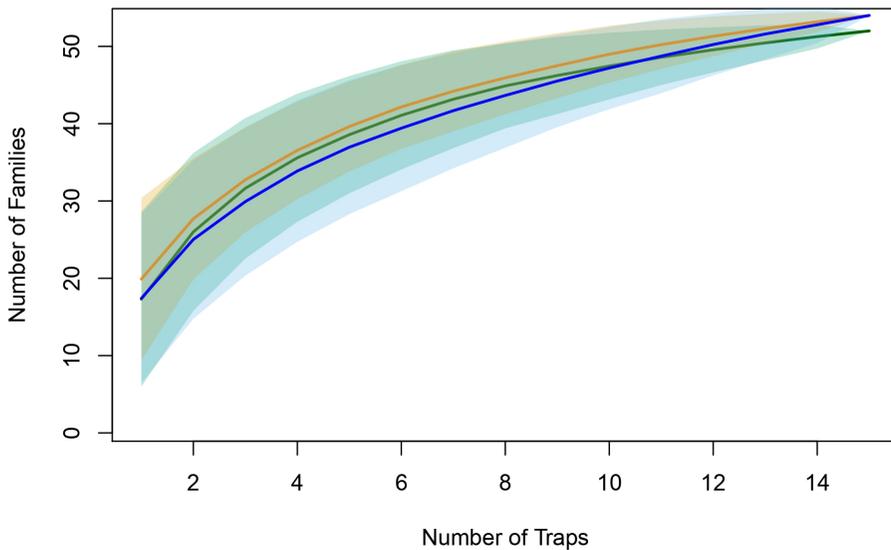


Figure 2. Sample-based rarefaction curves for pitfall captures of ground-dwelling invertebrates (excluding springtails) in three forest types in the Aleza Lake Research Forest, B.C. The rarefaction is based on 1000 permutations randomly generated from trap-catch data from each of the three levels of disturbance related to forest harvest. Curves for new plantation (orange), harvest history (blue), and old-growth (green) stands are shown with their 95% confidence intervals.

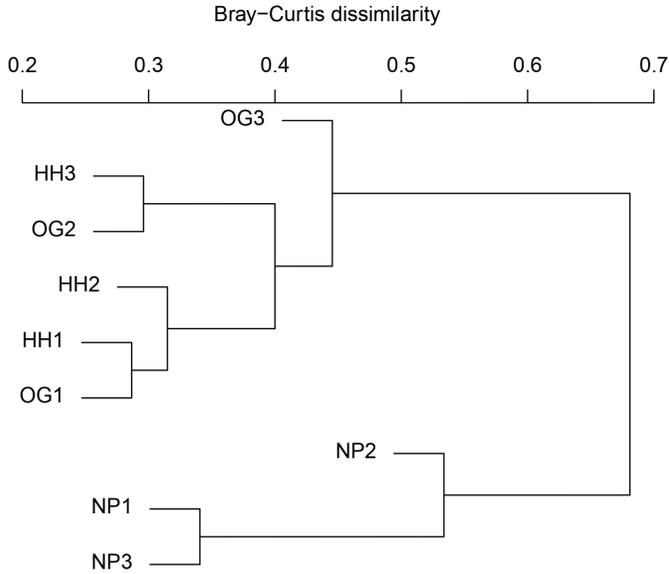


Figure 3. Cluster dendrogram of Bray-Curtis dissimilarity among sites from which ground-dwelling invertebrates were sampled in the Aleza Lake Research Forest, B.C. Greater distance on the tree indicates higher β -diversity when those two sites were compared and, consequently, higher dissimilarity between ground invertebrate communities in those sites. Bray-Curtis indices were calculated using pitfall trap captures excluding springtails. The level of harvest-related disturbance is indicated by the abbreviation (NP = new plantation, HH = harvest history, and OG = old growth) and individual sites are indicated by number (1, 2, 3).

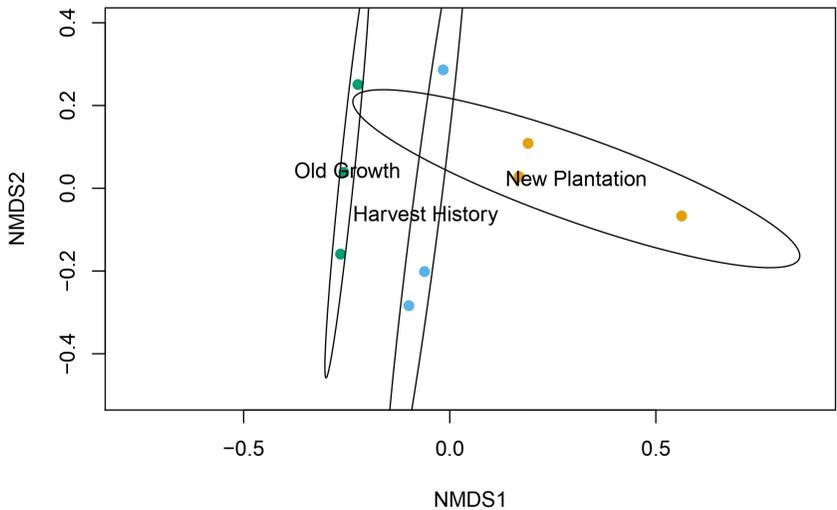


Figure 4. Non-metric multidimensional scaling plot for pitfall trap captures (excluding springtails) of ground-dwelling invertebrate families collected in the Aleza Lake Research Forest, B.C. Each point represents one of three sites for each level of disturbance related to forest harvest: new plantation (orange), harvest history (blue), and old growth (green), with ovals showing 95% confidence intervals. Stress value = 0.139.

Measures of α -diversity were consistent across forest types, with a total of 70 families identified in new plantation stands, 68 families in harvest history stands, and 65 families in old-growth stands. The mean numbers of families across the three sampling areas of each forest type were also similar: 47 (standard error = 3.2) in new plantation stands, 46.3 (standard error = 3.2) in harvest history stands, and 45.7 (standard error = 4.1) in old growth. Differences in the mean number of families detected in each of the three forest types were not significant (analysis of variance: $F_{2,6} = 2.7, P = 0.965$). The mean value of both Shannon and Simpson biodiversity indices (Table 2) was highest in new plantation forest, followed by old growth and then harvest history. However, differences between mean index values were not significant in either case (analysis of variance: Shannon: $F_{2,6} = 1.38, P = 0.321$; Simpson: $F_{2,6} = 1.096; P = 0.393$).

Table 2. Summary of Shannon (H) and Simpson (S) biodiversity indices by sampling site (1, 2, 3) for three forest types representing various levels of disturbance from harvest in the Aleza Lake Research Forest, B.C. New plantation stands (NP) were clearcut and replanted, harvest history stands (HH) were thinned from above approximately 50 years previously and regenerated naturally, and old-growth stands (OG) had no history of harvest.

	Sampling area								
	New plantation			Harvest history			Old growth		
	NP1	NP2	NP3	HH1	HH2	HH3	OG1	OG2	OG3
H	2.66	2.57	2.96	2.16	2.77	2.30	2.33	2.61	2.62
S	0.86	0.87	0.92	0.78	0.89	0.80	0.80	0.87	0.89
Mean H	2.73			2.41			2.52		
standard error	0.12			0.18			0.10		
Mean S	0.88			0.83			0.85		
standard error	0.02			0.03			0.03		

Differences between the three forest types were more apparent in measures of β -diversity and community composition. Bray–Curtis dissimilarity scores were highest in pairwise comparisons of new plantation stands and in those of the harvest history and old-growth categories, as shown by the separate clustering of the new plantation sites in Figure 3. This suggests that β -diversity increased with disturbance and is consistent with the changes observed in community composition. Non-metric multidimensional scaling ordination indicated there were differences in epigeic invertebrate community composition between the three forest types. As shown in Figure 4, old-growth and harvest history stands contained more similar ground-dwelling invertebrate communities, whereas new plantation sites contained the most dissimilar communities overall. Indicator species analysis produced four significant results ($\alpha = 0.05$). Three families were found to be significant indicators of the new plantation forest type, and one family was found to be an indicator of either harvest history or old growth (Table 3). Rove beetles (Staphylinidae) were non-significantly ($P = 0.68$) associated with the combination of harvest history and old-growth sites but are included in Table 3 due to previous work that suggests they are indicators of harvest in the boreal forest (Buddle *et al.* 2006).

DISCUSSION

Community composition of ground-dwelling invertebrates varied across the three types of forest sampled: new plantation, harvest history, and old growth. β -diversity and non-metric multidimensional scaling ordination (Figs. 3 and 4) indicated that communities in new plantation forest, representing the highest level of disturbance of the three types, were most distinct in their composition. Ordination also showed that harvest history stands, which had been logged 40 or more years before the new plantation stands, were more similar in their composition to the unlogged old-growth stands. Indicator species analysis (Table 3) also showed differences in assemblages between the new plantation sites and the other two forest types. Three of the four significant results were families that served as indicators of new plantation forest only (Agriolimacidae, Formicidae, and Lycosidae), whereas the fourth (Linyphiidae) was significant only when harvest history and old-growth sites were combined.

Table 3. Summary of indicator species analysis showing invertebrate families that were significantly ($\alpha = 0.05$) associated with three levels of disturbance related to forest harvest within the Aleza Lake Research Forest, B.C. “N” represents the total number of individuals within that family collected in the survey. No significant indicators were identified for harvest history or old-growth stands alone; however, one significant and one non-significant (*, cf. Buddle *et al.* 2006) indicator were found when they were considered in combination.

Forest Type	Potential indicator	N	Test	p
New plantation	Agriolimacidae	246	0.750	0.038
	Formicidae	448	0.816	0.038
	Lycosidae	170	0.838	0.038
Harvest history/Old growth	Linyphiidae	404	0.904	0.038
	Staphylinidae*	1583	0.725	0.068*

Interestingly, differences in α -biodiversity between the three forest types were small. Family richness was similar across both sites and forest types, and although new plantation stands had the highest mean Shannon and Simpson indices, the differences between these and the mean Shannon and Simpson indices for the harvest history and old-growth sites were not significant. This is consistent with Timms *et al.* (2013), who compared analyses of arthropod diversity in disturbed forests using family-, genus-, and species-level identifications. Family-level surveys were adequate to detect changes to community composition and β -diversity, but genus- or species-level data were required to detect significant effects of treatments on biodiversity (Timms *et al.* 2013).

Our findings are also consistent with other studies in the Omineca region. In this survey, the most recently disturbed sites (new plantation forest) were associated with a non-significant increase in biodiversity and distinct community compositions. Likewise, carabid biodiversity in the Chun T’Oh Wudujut Provincial Park (53.76° N, -121.22° W) east of Prince George was highest in recent clearcuts, which represented the most recently disturbed areas sampled (Higgins 2019). Similar trends were also observed in sub-boreal spruce stands, with carabid α -biodiversity reported as highest at low levels of canopy cover and

alterations to assemblages being associated with forest harvest (McColl 2010). Another study in the urban area of Prince George found that ground-dwelling invertebrate biodiversity was greatest in highly disturbed industrial sites and that those sites also contained distinct communities (Huber *et al.* 2019). The less pronounced differences in biodiversity in new plantation stands that we observed in the present study could be related to the comparatively long period (11 years) since harvest. In the Chun T'Oh Wudujut survey, two clearcut sites harvested eight years previously had greater carabid species richness and evenness compared to a third site that had been harvested 12 years previously (Higgins 2019). In the urban study, more pronounced effects of disturbance could be related to the intensity and frequency of disturbance events. Rather than a single large event such as forest harvest, industrial sites likely experience regular and less intense levels of disturbance that could affect biodiversity in those habitats more strongly.

Stand regeneration following harvest is associated with a wide range of environmental changes, and the intermediate community composition of harvest history stands compared to the other two forest types (Fig. 4) suggests that successional processes may be involved in differences observed between the three forest types. One such feature is spatial heterogeneity, which is related to the understorey vegetation, canopy cover, and other features of forest structure (McElhinny *et al.* 2005). Early seral plant communities often possess high structural richness due to a diversity of young trees, herbs, shrubs, and other shade-intolerant species (Swanson *et al.* 2011). Compared to natural forest disturbances, clearcutting and replanting reduce the complexity of these early seral systems (Swanson *et al.* 2011). Despite this, Butterfield (1997) found that carabid species diversity was highest in young plantations (5–22 years after planting) and that this period was also associated with increases in vegetation cover before canopy closure and increases in the diversity of other macroinvertebrates. Spatial heterogeneity within individual sites may also have created sampling variability and may have inflated observed levels of biodiversity. In a meta-analysis of within-site variation in pitfall trap captures, Niemelä *et al.* (1996) reported higher levels of sampling variability in young forest stands than in more mature ones. The mechanism driving this variability was not identified; however, the authors suggested it may reflect a high number of microhabitats due to the diversity of early seral plants (Niemelä *et al.* 1996). A similar dynamic could have contributed to the higher levels of biodiversity in new plantation sites observed in the present study.

Temperature variation between forest management types is also an important factor to consider when assessing these results. Harvesting mature trees removes their shading and temperature-moderating effects and leads to higher temperatures in recently logged areas, along with differences in snow accumulation and melting time. Because pitfall surveys are unable to discriminate between invertebrate abundance and activity between behaviourally dissimilar taxa, higher temperatures may have inflated catches in the new plantation sites by increasing the activity levels of invertebrates. Temperature has been shown to significantly influence capture rates of carabids (Saska *et al.* 2013) and would likely also affect other ground invertebrates because they are also ectothermic. This may have resulted in inflated biodiversity estimates by increasing total catch size and the likelihood that rare taxa encountered a trap.

The presence of canopy gaps in mature forest and the resulting spatial differences in temperature and moisture have been shown to influence ground invertebrate activity–abundance and taxon richness (Perry *et al.* 2018). As such, temperature variation could also explain differences observed between the old-growth stands and harvest history stands in which higher levels of biodiversity and distinct community compositions were observed.

The results of indicator species analysis may also be related to abiotic differences stemming from the three forest disturbance types. This is most clearly illustrated by the two families of spiders identified as potential indicator taxa: Lycosidae and Linyphiidae. McIver *et al.* (1992) tracked spider succession in recovering stands and found that diurnal predators like lycosids were gradually displaced by other feeding guilds, including linyphiids. A similar dynamic may have occurred in the present study because the harvest history stands recovered and became more structurally similar to the old-growth sites.

The two other significant results produced by indicator analysis were both associated with the more recently disturbed new plantation forest, which is consistent with their respective ecologies. In sub-boreal spruce forests, ants (Formicidae) appear to be excluded from less-disturbed forest stands, likely due to cooler temperatures and higher humidity (Higgins and Lindgren 2006). Higgins and Lindgren (2006) also found higher rates of coarse woody debris use in harvested stands compared to in unharvested stands, which could explain the strong association of this family with stands that had been clearcut relatively recently. Another possibility is that, in new plantation stands, traps were inadvertently placed closer to ant colonies. Pitfall trap captures of ants in sub-boreal spruce forests have previously been shown to be highly patchy, which has implications for the study of assemblages using this method (Higgins and Lindgren 2012).

Slugs (Agriolimacidae) captured in the ALRF were tentatively identified as *Deroceras reticulatum* (Müller) an introduced European species. A positive relationship between introduced slugs and disturbed sites has previously been demonstrated (Kappes and Schilthuisen 2014) and could explain the abundance of slugs in new plantation stands. Compared to other gastropods detected in this survey, these slugs were also relatively large, which may have increased their mobility and made it more likely for them to be sampled.

To provide additional sensitivity to disturbance effects, using genus- or species-level identifications would be beneficial in future studies. The selection of an appropriate indicator group would make this approach more feasible and could also yield additional insights from the samples collected in this present survey. Carabids are commonly used indicators of disturbance (Rainio and Niemelä 2003) and have previously been used in B.C.'s Central Plateau region (Higgins 2019); however, the results of this survey suggest other indicators may have more utility in the ALRF. One species, *Scaphinotus marginatus* (Fischer), was the dominant carabid across all forest types and represented about 90% of all carabids collected ($n = 369$ of 406 total). An alternative beetle family to investigate as an indicator taxon is Staphylinidae because members of this family were also abundant in the survey ($n = 1583$) and have previously been shown to respond to forest harvest (Buddle *et al.* 2006). Although they were not identified as a significant indicator in this study, Staphylinidae were associated more strongly with old-growth and harvest history stands than with new plantation

ones (Table 3), and further habitat associations would likely have been apparent if samples were identified to species. Spiders could also be a feasible indicator option because they too showed a clear response to harvest both in this study and in earlier studies (Buddle *et al.* 2000, 2006; Pinzon *et al.* 2011).

The present study demonstrated that recently disturbed areas can make important contributions to ground-dwelling invertebrate biodiversity at the landscape level. However, it is also important to note the importance of mature forest in providing habitat for specialist species, such as some carabid and staphylinid beetles (Niemelä *et al.* 1993; Spence *et al.* 1996; Buddle *et al.* 2006; Pohl *et al.* 2007). Taken together, these findings emphasize the importance of sampling across habitat types for biodiversity and including even highly disturbed areas in analyses. Collecting baseline biological data in B.C. Interior forests and identifying potential indicators of existing forms of disturbance would be useful when evaluating the ongoing effects of climate change. As the cumulative anthropogenic disturbance affecting ecosystems increases, being able to predict and mitigate effects wherever possible will become increasingly important. Doing so, however, requires a sound understanding of how organisms across taxonomic groups respond to changes in their environment.

ACKNOWLEDGEMENTS

Funding for this project was provided by the Aleza Lake Research Forest Society. We would also like to thank Colin Chisholm and Mike Jull at the ALRF for their help in selecting sites and in providing harvest records.

REFERENCES

- Aleza Lake Research Forest Society. 2019. Aleza Lake Research Forest Society Management Plan #3 [online]. Available from https://alrf.unbc.ca/?page_id=17 [accessed 3 April 2023].
- Bois, C.H., Janzen, D.T., Sanborn, P.T., and Fredeen, A.L. 2009. Contrasting total carbon stocks between ecological site series in a subboreal spruce research forest in central British Columbia. *Canadian Journal of Forest Research*, **39**: 897–907. <https://doi.org/10.1139/X09-018>.
- Buddle, C.M., Beguin, J., Bolduc, E., Mercado, A., Sackett, T.E., Selby, R.D., *et al.* 2005. The importance and use of taxon sampling curves for comparative biodiversity research with forest arthropod assemblages. *The Canadian Entomologist*, **137**: 120–127. <https://doi.org/10.4039/n04-040>.
- Buddle, C.M., Langor, D.W., Pohl, G.R., and Spence, J.R. 2006. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. *Biological Conservation*, **128**: 346–357. <https://doi.org/10.1016/j.biocon.2005.10.002>.
- Buddle, C.M., Spence, J.R., and Langor, D.W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography*, **23**: 424–436. <https://doi.org/10.1111/j.1600-0587.2000.tb00299.x>.
- Butterfield, J. 1997. Carabid community succession during the forestry cycle in conifer plantations. *Ecography*, **20**: 614–625. <https://doi.org/10.1111/j.1600-0587.1997.tb00430.x>.
- Cáceres, M.D., Legendre, P., and Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. *Oikos*, **119**: 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>.

- Cardoso, P., Erwin, T.L., Borges, P.A.V., and New, T.R. 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, **144**: 2647–2655. <https://doi.org/10.1016/j.biocon.2011.07.024>.
- Dixon, P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*, **14**: 927–930. <https://doi.org/10.1111/j.1654-1103.2003.tb02228.x>.
- Gerlach, J., Samways, M., and Pryke, J. 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*, **17**: 831–850. <https://doi.org/10.1007/s10841-013-9565-9>.
- Gotelli, N.J. and Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**: 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Government of British Columbia. n.d. Ministry of Forests Region & District Contacts. Ministry of Forests, Government of British Columbia, Victoria, British Columbia. Available from <https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/ministry-of-forests-lands-and-natural-resource-operations-region-district-contacts> [accessed 3 April 2023].
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., *et al.* 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS One*, **12**: e0185809. <https://doi.org/10.1371/journal.pone.0185809>.
- Hebert, P.D.N., Cywinska, A., Ball, S.L., and deWaard, J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences*, **270**: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Higgins, I. 2019. Ground beetles (Coleoptera: Carabidae) of the Chun T’oh Whudujut Park in eastern British Columbia, Canada, and their use as bioindicators of disturbance. MSc. thesis. University of Northern British Columbia, Prince George, British Columbia. <https://doi.org/10.24124/2019/59005>
- Higgins, R.J. and Lindgren, B.S. 2006. The fine-scale physical attributes of coarse woody debris and effects of surrounding stand structure on its utilization by ants (Hymenoptera: Formicidae) in British Columbia, Canada. *In* *Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology*. Edited by S.J. Grove and J.L. Hanula. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, United States of America. Pp. 67–74.
- Higgins, R.J. and Lindgren, B.S. 2012. An evaluation of methods for sampling ants (Hymenoptera: Formicidae) in British Columbia, Canada. *The Canadian Entomologist*, **144**: 491–507. <https://doi.org/10.4039/tce.2012.50>.
- Huber, D.P.W., Poirier, L.M., and Muir, A.M. 2019. Ground-dwelling invertebrate biodiversity patterns in a small, central British Columbia city support the intermediate disturbance hypothesis [online; poster]. *figshare*. <https://doi.org/10.6084/m9.figshare.8337635.v1>
- Kappes, H. and Schilthuizen, M. 2014. Habitat effects on slug assemblages and introduced species. *Journal of Molluscan Studies*, **80**: 47–54. <https://doi.org/10.1093/mollus/eyt043>.
- Klink, R. van, Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., and Chase, J.M. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, **368**: 417–420. <https://doi.org/10.1126/science.aax9931>.
- Lindroth, C.H. 1961–1969. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Parts 1–6. *Opuscula Entomologica, Supplementum*.
- Marshall, S.A. 2017. *Insects: their natural history and diversity: with a photographic guide to insects of eastern North America*. Firefly Books, Buffalo, New York, United States of America.

- McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., and Wood, D.M. (eds.). 1981. *Manual of Nearctic Diptera*. Volumes 1–3. Research Branch, Agriculture Canada, Ottawa, Ontario.
- McCull, D.A. 2010. Factors affecting carabid (Coleoptera: Carabidae) assemblages in successional sub boreal spruce forests, with special reference to their interaction with ants (Hymenoptera: Formicidae). MSc Thesis. University of Northern British Columbia, Prince George, British Columbia. <https://doi.org/10.24124/2011/bpgub710>
- McElhinny, C., Gibbons, P., Brack, C., and Bauhus, J. 2005. Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management*, **218**: 1–24. <https://doi.org/10.1016/j.foreco.2005.08.034>.
- McGeoch, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews*, **73**: 181–201. <https://doi.org/10.1111/j.1469-185X.1997.tb00029.x>.
- McIntyre, N.E., Rango, J., Fagan, W.F., and Faeth, S.H. 2001. Ground arthropod community structure in a heterogeneous urban environment. *Landscape and Urban Planning*, **52**: 257–274. [https://doi.org/10.1016/S0169-2046\(00\)00122-5](https://doi.org/10.1016/S0169-2046(00)00122-5).
- McIver, J.D., Parsons, G.L., and Moldenke, A.R. 1992. Litter spider succession after clearcutting in a western coniferous forest. *Canadian Journal of Forest Research*, **22**: 984–992. <https://doi.org/10.1139/x92-132>.
- McKinney, M.L. 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, **11**: 161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Niemelä, J., Haila, Y., and Punttila, P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography*, **19**: 352–368. <https://doi.org/10.1111/j.1600-0587.1996.tb01264.x>
- Niemelä, J., Langor, D., and Spence, J.R. 1993. Effects of clearcut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology*, **7**: 551–561. <https://doi.org/10.1046/j.1523-1739.1993.07030551.x>.
- Oxbrough, A., Irwin, S., Kelly, T.C., and O’Halloran, J. 2010. Ground-dwelling invertebrates in reforested conifer plantations. *Forest Ecology and Management*, **259**: 2111–2121. <https://doi.org/10.1016/j.foreco.2010.02.023>.
- Perry, K.I., Wallin, K.F., Wenzel, J.W., and Herms, D.A. 2018. Forest disturbance and arthropods: small-scale canopy gaps drive invertebrate community structure and composition. *Ecosphere*, **9**: e02463. <https://doi.org/10.1002/ecs2.2463>.
- Phillips, I.D. and Cobb, T.P. 2005. Effects of habitat structure and lid transparency on pitfall catches. *Environmental Entomology*, **34**: 875–882. <https://doi.org/10.1603/0046-225X-34.4.875>.
- Pinzon, J., Spence, J.R., and Langor, D.W. 2011. Spider assemblages in the overstorey, understorey, and ground layers of managed stands in the western boreal mixedwood forest of Canada. *Environmental Entomology*, **40**: 797–808. <https://doi.org/10.1603/EN11081>.
- Plas, F. van der. 2019. Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*, **94**: 1220–1245. <https://doi.org/10.1111/brv.12499>.
- Pohl, G.R., Langor, D.W., and Spence, J.R. 2007. Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. *Biological Conservation*, **137**: 294–307. <https://doi.org/10.1016/j.biocon.2007.02.011>.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/> [5 Aug 2020].

- Rainio, J. and Niemelä, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, **12**: 487–506. <https://doi.org/10.1023/A:1022412617568>.
- Saska, P., Werf, W. van der, Hemerik, L., Luff, M.L., Hatten, T.D., and Honek, A. 2013. Temperature effects on pitfall catches of epigeal arthropods: a model and method for bias correction. *Journal of Applied Ecology*, **50**: 181–189. <https://doi.org/10.1111/1365-2664.12023>.
- Spence, J.R., Langor, D.W., Niemelä, J., Cárcamo, H.A., and Currie, C.R. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici*, **33**: 173–184.
- Sullivan, G.T. and Ozman-Sullivan, S.K. 2021. Alarming evidence of widespread mite extinctions in the shadows of plant, insect, and vertebrate extinctions. *Austral Ecology*, **46**: 163–176. <https://doi.org/10.1111/aec.12932>.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., *et al.* 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, **9**: 117–125. <https://doi.org/10.1890/090157>.
- Thomas, D.B. 2008. Nontoxic antifreeze for insect traps. *Entomological News*, **119**: 361–365. <https://doi.org/10.3157/0013-872X-119.4.361>.
- Tilman, D., Isbell, F., and Cowles, J.M. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, **45**: 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.
- Timms, L.L., Bowden, J.J., Summerville, K.S., and Buddle, C.M. 2013. Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. *Insect Conservation and Diversity*, **6**: 453–462. <https://doi.org/10.1111/icad.12004>.
- Vanbergen, A.J., Woodcock, B.A., Watt, A.D., and Niemelä, J. 2005. Effect of land-use heterogeneity on carabid communities at the landscape scale. *Ecography*, **28**: 3–16. <https://doi.org/10.1111/j.0906-7590.2005.03991.x>.
- Wagner, D.L. 2020. Insect declines in the Anthropocene. *Annual Review of Entomology*, **65**: 457–480. <https://doi.org/10.1146/annurev-ento-011019-025151>.
- Wilson, E.O. 2017. Biodiversity research requires more boots on the ground. *Nature Ecology & Evolution*, **1**: 1590–1591. <https://doi.org/10.1038/s41559-017-0360-y>.