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Research article

Longhorn beetles (Coleoptera: Cerambycidae) community composition around different boreal infrastructures

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ABSTRACT

Wood processing, mining, and recreational infrastructures facilitate the transport and establishment of woodboring insects. Longhorn beetles (Coleoptera: Cerambycidae) are woodborers that typically develop in stressed or dead trees and are inadvertently transported in wood products, creating opportunities for exotic species to invade and expand their range around infrastructures. To understand how these infrastructures influence longhorn diversity, abundance, and potential invasions, we sampled longhorn beetles in 2021 and 2022 from 11 sawmills, 10 mines, 11 campgrounds, and 12 control (unmanaged) forest sites throughout northwestern Quebec (Canada) using broadly attractive blends of pheromone and host volatiles to assess infrastructure-related shifts in community composition compared to undisturbed forest stands. The most abundant species observed across all infrastructures was *Monochamus scutellatus scutellatus* Say, comprising over 60 % of the total individuals collected, followed by *Monochamus mutator* LeConte (17 %) and *Tetropium cinnamopterum* Kirby (7 %). We did not record any exotic species; this absence may reflect community-level resistance from diverse native longhorn assemblages. Sawmill sites had the highest diversity and evenness and showed increased abundance of several common native species. However, longhorn communities varied more with forest composition than infrastructure type. NMDS distinguished longhorns linked to balsam fir from those associated with Jack pine, like *M. mutator* and *Rhagium inquisitor* Linnaeus, and separated beetles in white spruce and pine, such as *Tetropium cinnamopterum* Kirby and *T. schwarzianum* Casey, from those in early-succession hardwoods. Increased abundance of longhorns near sawmills came from diverse forest types. We do not find evidence for increased invasion risk near infrastructures, but ongoing surveillance remains crucial.

1. Introduction

The infrastructure related to timber processing, mining, and recreation throughout the boreal forest in eastern Canada has significant risk impacts on surrounding boreal ecosystems, not least through the potential introduction and spread of invasive species. Timber harvesting and mining require the import of multiple commodities mainly from the Asia-Pacific region and Europe (Canadian Importers Database, n.d.; Global Affairs Canada, 2021; Jiang, 2022) that are often transported using wood packaging material. This packaging can inadvertently harbor woodboring longhorn beetles and forest pathogens, facilitating the introduction of nonindigenous pests despite regulatory treatments (CFIA, 2017; de Jong et al., 2004; Hulme, 2009). As these infrastructures are embedded in forested landscapes, they can act as source points for species introduction and range expansion. Understanding how these infrastructures influence native longhorn communities is critical for assessing their impact on biodiversity and forest health.

Exotic woodboring pests such as the Emerald Ash Borer (*Agrilus planipennis* Fairmaire; Buprestidae), Asian Longhorned Beetle (*Anoplophora glabripennis* Motschulsky; Cerambycidae), and Brown Spruce Longhorn Beetle (*Tetropium fuscum* Fabricius; Cerambycidae) were likely introduced to Canada through infested wood packaging materials and have since spread via the illegal movement of firewood (Haack et al., 2010, 2002; Poland et al., 1998; USDA-APHIS, 2011). Beyond

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economic losses, these pests disrupt the ecological balance of forests, altering biodiversity, weakening ecosystem resilience, and threatening essential forest ecosystem services such as carbon storage and habitat stability (Aukema et al., 2011; Haack et al., 2010; Liebhold et al., 1995).

Certainly, transport of infested logs to sawmills (as lumber) or to campgrounds (as firewood) could introduce large numbers of longhorn beetles and alter local communities. Freshly fallen trees/cut logs, especially conifer wood, are quickly colonized by these beetles, which can then reach high abundance and diversity in places where this wood accumulates (Bloin et al., 2022). Regional sawmills acquire and accumulate timber following natural disturbances such as insect outbreaks or wildfires, predominantly from local sources in Quebec, with supplementary provisions sourced sporadically from eastern Ontario (Bogdanski et al., 2020). The risk of non-native species introductions via log transport to mills is therefore low, but the risk of northward range expansions is more concerning.

Similarly, campgrounds constitute a significant focal point for the movement of longhorn beetles primarily through the informal transport of infested firewood by campers; a well-documented and potentially long-distance vector, combined with high visitor turnover, accelerates this dispersal, with up to 20 % of transported firewood containing live insect pests (Ali et al., 2015; Haack et al., 2010; Haack and Petrice, 2021; Jacobi et al., 2012; Koch et al., 2012; Solano et al., 2021). Although national and provincial parks implement firewood bans, compliance varies, and private campgrounds have less stringent regulations. Provincial campgrounds restrict outside firewood through exchange programs (e.g., SEPAQ in Quebec), but prolonged stockpiling (>3 weeks) in the collection bins may still increase pest risk. On the other hand, private campgrounds generally allow campers to bring their own firewood and rarely confiscate non-compliant wood, facilitating continued introductions (Gagné et al., 2017).

While long-distance transport of wood products is well understood to play a key role in the spread of invasive species, the impact of moving timber/cut logs on native woodboring communities is less well understood. Native longhorn beetle communities around sawmills and campgrounds can be altered by two different mechanisms, namely, transport of infested wood and oviposition in recently cut logs if accumulated for a longer period. Certain native pest longhorns, such as *Monochamus* and *Tetropium* spp, are quick colonizers of stressed, dying, and freshly fallen/cut logs, posing risks to the forest ecosystem of eastern Canada, potentially leading to severe ecological and economic consequences (Lidsky, 2003; Neidermeier et al., 2020). *Monochamus* species, commonly referred to as sawyer beetles, are also infamous for their role as vectors in the spread of pine wilt disease (Akbulut and Stamps, 2012; Boone et al., 2019; Vicente et al., 2021). Salvage logging increases the risk of logs arriving at the mill infested with longhorns.

In addition, the composition of forest stands plays an essential role in influencing these responses, as different longhorn species exhibit preferences for specific host trees (Traylor et al., 2022). Forests characterized by a high diversity of tree species and structures, including the presence of stressed, dying, freshly fallen trees and uneven-aged stands, tend to support longhorn communities that are more diverse and functionally intricate (de Quesada and Kuuluvainen, 2020; Leidinger et al., 2021). In contrast, alterations in forest composition due to management practices or the presence of invasive vegetation may diminish habitat heterogeneity and result in the simplification of communities. Hence, accumulated fallen trees (deadwood) and cut logs can modify local longhorn communities by altering the availability, type, and spatial concentration of suitable oviposition substrates. Since many longhorns utilize stressed, dying, freshly fallen trees and cut logs, infrastructures that aggregate such material may unintentionally modify species composition and increase the opportunities for colonization and range expansion. Many of these beetles can attack live trees as well, with important consequences for forest ecosystems (Gagné et al., 2017).

We predicted the longhorn beetle communities in forests adjacent to industrial and recreational facilities would differ from those in unmanaged forests, due, in part, to a greater risk of exotic species introductions (Rassati et al., 2015). By addressing this, we aim to elucidate how anthropogenic disturbances shape boreal longhorn insect communities and inform pest risk evaluations in the context of expanding human activity.

2. Methods

2.1. Study system

This study focused on longhorn beetles (Coleoptera: Cerambycidae), a group of woodboring insects known for their attack on stressed, dying, and dead trees, as well as degrading log quality, and facilitating the spread of wood-associated pathogens (Dodds et al., 2023; Saint-Germain et al., 2007). Females lay eggs on freshly fallen, dead, or cut logs, where larvae bore into wood, creating frass-filled galleries (Hulcr and Dunn, 2011; Krcmar-Nozic et al., 2000), and increase wood combustibility (Zhang et al., 2025).

We sampled forest stands throughout the three infrastructure types, camping, mining, and sawmills, which were predominantly conifer-dominated. Camping grounds, in our study, used as stopping points for camping, hunting, and fishing, were relatively continuous boreal forests with thick moss or lichen ground layers, scattered wetlands, and minimal understory regeneration. Most were dominated by *Picea mariana* (Mill.) B.S.P (black spruce), *Abies balsamea* (Linnaeus) Mill. (balsam fir), *Betula papyrifera* Marshall (white birch), or *Pinus banksiana* Lambert (jack pine), although several campgrounds featured older mixed stands with mature conifers and hardwoods. Northern Québec mines in our study area primarily extract gold and lithium, alongside growing production of copper, nickel, zinc, and titanium, commodities prioritized under Canada's critical mineral strategy (Ministère des Ressources naturelles et des Forêts, 2024). Forest stands adjacent to these mines were typically patchy but dense, conifer-dominated boreal forests with uneven canopies and limited understory light. Ground conditions were characterized by fallen logs, deadwood, and dense fallen branches in many cases, making access difficult. Sawmill-adjacent forest stands were also dense with uneven canopies; black spruce and balsam fir are the most prevalent species, often accompanied by jack pine, *Larix laricina* (Du Roi) K. Koch (tamarack), or scattered hardwoods like white birch, *Acer* Linnaeus (maples), and *Populus tremuloides* Michx. (trembling aspen).

These infrastructure-associated stands mostly occur on organic or glacio-lacustrine soils, with drainage conditions ranging from moderate to poor, aligning with ecological types typical of spruce–fir or birch–fir forests. Most are characterized as either even-aged or uneven-aged, encompassing age classes from 30 to 90 years and classified within the mid-successional to mature stages. Despite variations in origin and management practices, these stands tend to share a common pattern of closed-canopy, mid-successional coniferous forest structure, with minimal active management in recent decades. More detailed information about these infrastructures by site is compiled in supplementary file 2.

We sampled longhorn beetles from May 25 to August 19, 2021, and again from May 21 to August 26, 2022, across 44 sites throughout northwestern Quebec. Our transect covered over 750 km, with sampling sites spaced 10–50 km apart and located within 500 m of major highways or roads. We selected sites based on their use and surrounding activities, categorizing them into four groups: sawmills (11 sites), mines (10 sites), campgrounds (12 in total; 5 private and 7 provincial), and unmanaged forest as control sites (12 sites) (Supplementary file 2). To account for spatial variation, we grouped these sites into seven blocks: Mont-Laurier, Verendrye, Senneterre, Malartic-Val-d'Or, Rouyn-Cadillac, Amos, and LaSarre-Duparquet (Figure_1a). Due to construction and increased recreational activity, one campground site was excluded in 2022, reducing the total number of sampling locations to 43.

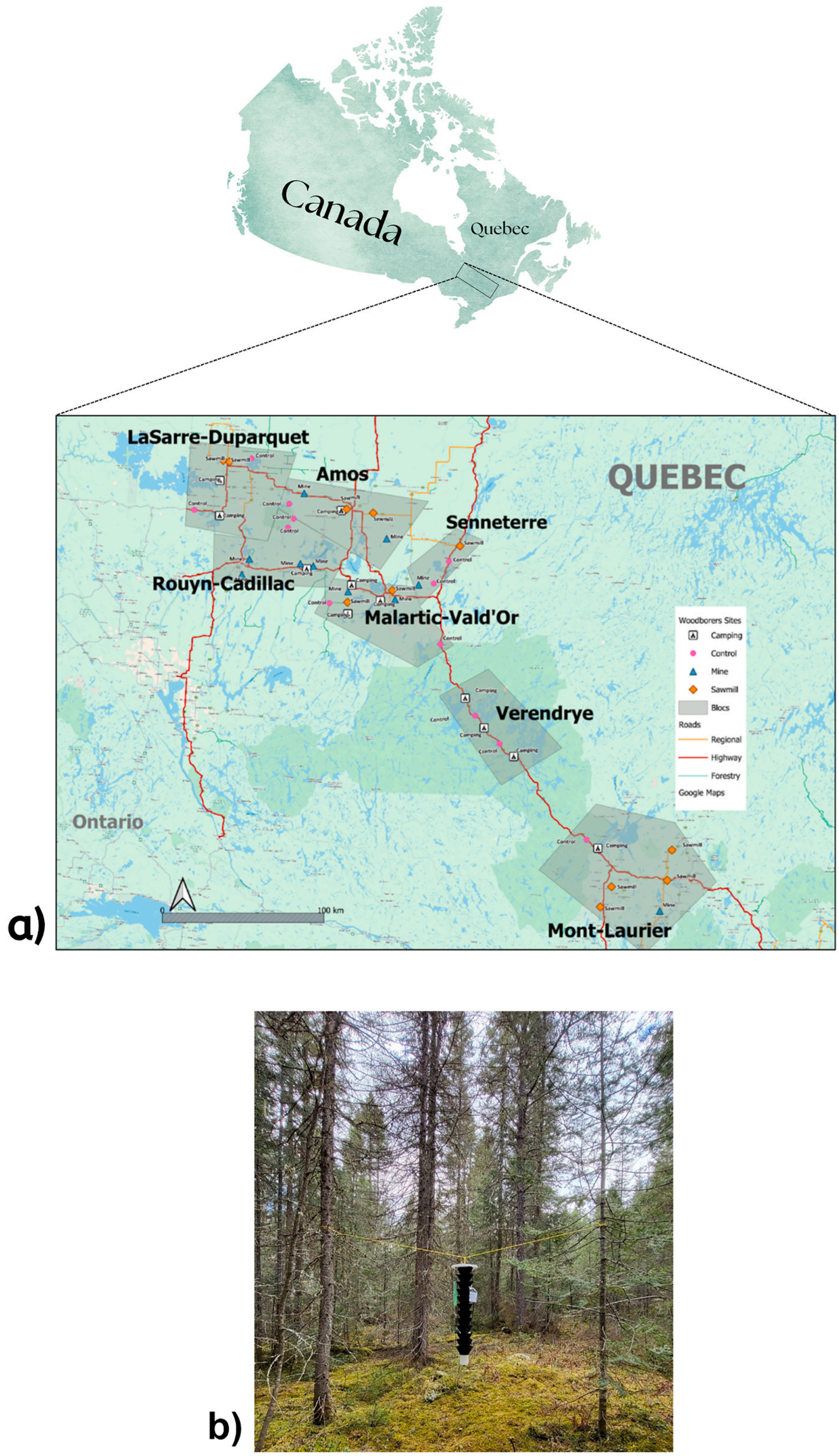

Figure_1. An overview of the study area, sampling sites, and sampling technique within Eastern Canada. **a)** Geographic distribution of the 44 study sites organized into 7 blocks across Northern Quebec, from Mont-Laurier to LaSarre-Duparquet, covering approximately 750 km. The shaded polygons represent the geographic limits for the blocks (displayed for understanding and don't delineate the regional boundaries), with a legend illustrating the treatment types through specific icons, block delineations, and the primary transport highway for context. The map scale indicates distances corresponding to real-world measurements, maintaining an accuracy of approximately ±10 %. **b)** Depiction of a typical Lindgren funnel trap setup used in the study, showing 12 units equipped with a wet collection cup and lures, deployed between two conifers about 5 m apart at one of the study sites.

2.2. Trapping system and lures

We used a 12-unit black Lindgren funnel trap system (Synergy Semiochemical Corp., Canada) to sample longhorn beetles. Traps were installed between two conifer trees that were spaced 5–8 m apart, and positioned 30–50 cm above the ground to minimize interference with understory vegetation (CFIA, 2019) (Figure_1b). Minor vegetation (under the trap), such as low shrubs or branches, was gently removed only when necessary to ensure a clear and unobstructed flight path. Trap placement was adjusted based on site conditions: reducing visibility in campgrounds away from campground paths, walking and cycling trails, maintaining distance from active log sorting yards at sawmills, minimizing disruptions near mines and setback from heavy equipment movement zones, and avoiding direct sunlight and excessive heat exposure. Placement of traps was timed to cover the phenological activity window of multiple native and non-native species. The traps were baited with a 'super-lure' pheromone blend (including Monochamol, fuscumol, fuscumol acetate, ultra-high release (UHR) EtOH, and α-pinene obtained from Synergy Semiochemical Corp., Canada), and propylene glycol served as the trapping solution (with 300–400 ml in each collection cup). All the traps were treated with fluon, which enhances insect capture and prevents the beetles from escaping the trap (Dong et al., 2023). Insects were collected every 3–4 weeks, and pheromones were replaced once after 45 days of trap operation during the summers of 2021 and 2022.

2.3. Species identification and data management

Trap contents were sorted, and all longhorn beetles were identified to species, and voucher specimen were deposited in the insect reference collection at Université du Québec à Montréal (UQAM). The finalized dataset from this study was uploaded to the UQAM data repository for accessibility and future reference.

2.4. Analysis

We employed diversity indices, ordination of community composition, and abundance modeling of the most common species to assess infrastructure effects on longhorn beetle assemblages and individual beetle species.

2.4.1. Diversity of longhorn beetles across infrastructures

We first used Hill numbers to compare alpha, beta, and gamma diversity between infrastructure types. These diversity metrics correspond to species richness ($q = 0$), relative abundance ($q = 1$; exponential of the Shannon index), and dominance ($q = 2$; inverse of Simpson index). Values were calculated via the hillR package (v 0.5.2; Daijiang Li, 2018). Sample-based rarefaction curves with simulation up to *2n* allowed us to estimate alpha and gamma diversity at q = 0, 1, and 2 with 200 bootstraps for 95 % confidence intervals. In sample-based methods, diversity is a function of the sample count, enabling standardized comparisons by sampling effort (Chao et al., 2023). This analysis was implemented in the iNEXT.beta3D package (v3.0.0; Chao et al., 2023).

2.4.2. Composition of longhorn beetles across infrastructures

Next, ordination was used to compare longhorn communities based on infrastructure type and forest characteristics. To ensure the standardization of capture data across diverse trapping durations and efforts, the catch rate was calculated by dividing the total abundance of a species at each site by the number of trap days (Apigian et al., 2006; Spence and Niemelä, 1994). Longhorns' catch rate (square-root transformed to reduce the influence of highly abundant taxa) was used in non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities (vegan package (Oksanen et al., 2001),) using $k = 2$ dimensions with a maximum of 500 iterations to optimize stress minimization. NMDS is an ordination method that ranks species composition dissimilarities in reduced-dimensional space without assuming normality. We also performed a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations to test if community composition differed by infrastructure type, using Bray-Curtis dissimilarity and the adonis2 function (Anderson, 2017). To evaluate the role of forest characteristics, we first examined pairwise Pearson correlation (linear relationship) coefficients among all candidate predictor variables and excluded those exhibiting strong correlations ($|r| \geq 0.7$) to reduce redundancy and potential collinearity effects (supplementary file 1; Fig. S3). Variables such as canopy density (in percentage), tree height (in meters), area (in hectares), age-class (in years), latitude, and forest species composition (percent-based cover of each species/group per site) obtained from the *Forêt ouverte* application (v16.12.1) and how these variables were recorded in *Forêt ouverte* application is provided in the supplementary file 1 (section A.2). We then used the envfit function with 999 permutations to identify significant environmental variables at $p < 0.001$ based on randomization tests. The forest species composition data included 21 tree species/groups and were only retained for visualization if significantly associated with NMDS in envfit ($p < 0.05$) or marginally associated ($p < 0.1$) and had comparatively high R^2. All envfit results for the 21 tree species/groups are reported in supplementary file 1 (Table S1). This included five tree species, particularly *Picea glauca* (Moench) Voss (white spruce), *Abies balsamea (*balsam fir), *Pinus strobus* Linnaeus (white pine), *Pinus banksiana* Lamb. (jack pine), and *Acer rubrum* Linnaeus (red maple), based on their significance in preliminary ordination analyses.

2.4.3. Species-specific responses across infrastructures

Finally, we compared the abundance of common longhorn species between infrastructure types with generalized linear models. To enhance statistical robustness and reduce the impact of rare species, only those species with a count of at least 50 individuals per site over the complete trapping duration (2021–2022) were considered ($N = 12$ species). For each beetle species, both negative binomial GLMMs (glmer.nb; lme4 package (v1.1-34, Bates et al., 2015) and GLMs (glm.nb; MASS package v7.3–60.0.1, Venables and Ripley, 2013) were fitted to account for potential overdispersion in count data. Fixed effects included latitude, infrastructure type, standardized by an offset term (log-transformed trap days) to control for differences in trapping effort, while block was incorporated as a random effect.

For each species, GLMMs and GLMs were compared using likelihood ratio tests (Chi-square test) and Akaike's Information Criterion (AIC). The best model for each species was selected based on two criteria: (a) the GLMM was retained if its AIC was lower by at least 2 units compared to the GLM, and (2) if AIC values were similar, the Chi-square test was used to determine whether including a random effect significantly improved model fit ($p < 0.05$). To assess the significance of variables, Wald χ^2 tests (type II/III) were performed using the Anova(.) function in the car package (Fox and Weisberg, 2019). Residual diagnostics were conducted via DHARMa package (v0.4.6, Hartig, 2016) using quantile-quantile plots and dispersion tests to ensure model assumptions were met.

All statistical analyses were conducted in RStudio (v4.3.1, R Core Team, 2023). Figures were produced using the ggplot2 package (v3.5.0, Wickham, 2016), and maps were generated via sf (v1.0-19, Pebesma, 2016), ggspatial (v 1.1.9, Dunnington, 2017) and rnaturalearth (v1.0.1, Massicotte and South, 2017) as well as in QGIS desktop (v3.32.3).

3. Results

We collected 24,753 longhorn beetles and classified them into 51 distinct species over four subfamilies, as depicted in Fig. 2. The most abundant species were conifer specialists, with *Monochamus scutellatus scutellatus* representing a majority (60 %) of all identified longhorns, followed by *Monochamus mutator* LeConte (17 %), and *Tetropium cinnamopterum* Kirby (7 %). *M. s. scutellatus* and *T. cinnamopterum* are

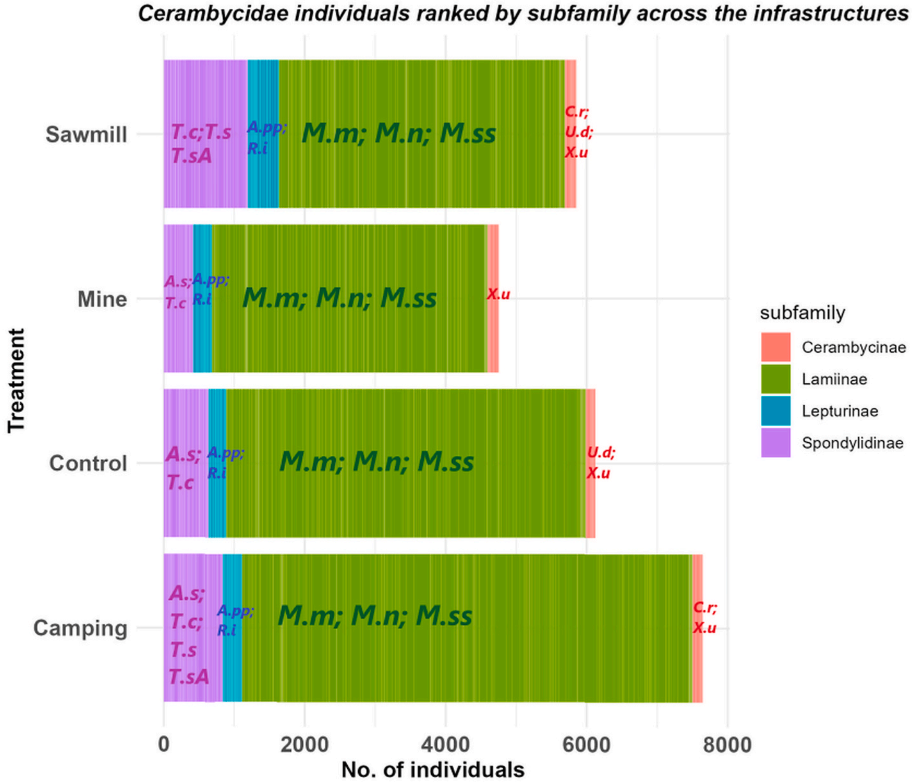

Figure_2. Longhorns' abundance plotted by subfamily across treatments in the eastern boreal forest of Quebec. The labels correspond to the significant species (12) identified by their initials, organized within their respective subfamilies across infrastructures, such as *A.pp = Acmaeops proteus proteus; A.s = Asemum striatum; C.r = Clytus ruricola; M.m = Monochamus mutator; M.n = Monochamus notatus; M.ss = Monochamus scutellatus scutellatus; T.c = Tetropium cinnamopterum; T.s = Tetropium schwarzianum; T.sA = Tetropium species A; U.d =Urographis despectus; X.u = Xylotrechus undulatus.*

important pest species attacking dead and dying conifers. Spatial distribution maps (supplementary file 1; Figure_S1) illustrate the widespread presence of *M. s. scutellatus* across all our sites. The highest longhorn abundance was encountered in campgrounds and the lowest in mines. Notably, no invasive species were detected during this sampling period.

3.1. Diversity of longhorn beetles across infrastructures

Alpha diversity at Hill number $q = 0$ showed an average of 16 species recorded in sawmills compared to 14 in mines, campgrounds, and control sites. However, on the rarefaction curves for $q = 0$ at alpha, and gamma levels (supplementary file 1; Figure_S2), overlapping confidence intervals suggest no significant richness difference between any of the infrastructures compared to control. Rarefaction curves at $q = 0$ showed that all treatments approached sufficient sampling; particularly, campground curves were notably flatter. For instance, extrapolating up to double the reference samples (15,000 individuals) suggests campground sites would yield only ~3 more species, whereas sawmills could still contribute ~5–8 additional species. The alpha- and gamma-level Shannon diversity, represented by $q = 1$, also appeared higher in sawmills than elsewhere; however, no differences were apparent between infrastructure types at $q = 2$ (Figure_S2).

3.2. Composition of longhorn beetles across infrastructures

Longhorn assemblages did not differ among infrastructures. The two-dimensional NMDS model converged after a maximum of 500 iterations, yielding a stress value of 0.17, indicating a good fit and reliability (>0.2; Buttigieg and Ramette, 2014). We assessed NMDS goodness of fit by correlating ordination distances with observed dissimilarities, resulting in a non-metric fit $R^2 = 0.98$ and a linear fit $R^2 = 0.95$. Stress plots confirmed that ordination distances closely matched observed dissimilarities, with low residuals (<0.013), indicating minimal distortion in species placement. PERMANOVA indicated no significant differences in longhorn beetle community across infrastructure types ($F = 0.69$, $p = 0.76$, $R^2 = 0.050$).

While infrastructure had little effect on the composition of beetle assemblages, catch rates of individual woodborer species reflected the latitudinal gradient and shifts in the relative abundance of tree species. A first NMDS axis separated balsam fir ($R^2 = 0.126, p = 0.057$) from jack pine ($R^2 = 0.278, p = 0.003$), whereas a second separated white pine ($R^2 = 0.303, p = 0.004$), white spruce ($R^2 = 0.207, p = 0.011$) and red maple ($R^2 = 0.393$, $p = 0.002$) communities with high canopy cover ($R^2 = 0.144, p = 0.049$) from those dominated by mixed hardwoods. Of the 12 common longhorn species investigated, 7–8 showed significant associations with different stand compositions (Figure_3). *Tetropium spA* ($R^2 = 0.763$, $p < 0.001$), *Tetropium cinnamopterum* ($R^2 = 0.331$, $p < 0.001$), and *Tetropium schwarzianum* Casey ($R^2 = 0.252$, $p = 0.005$) show a strong association on axis 2, aligning with forest trees such as white spruce and white pine, preferring dense, conifer-dominated stands. In contrast, *M. s. scutellatus* ($R^2 = 0.749$, $p < 0.001$) and *Acmaeops proteus proteus* Kirby ($R^2 = 0.333$, $p < 0.001$) were negatively associated with these stand types. *Monochamus mutator* ($R^2 = 0.692$, $p < 0.001$), *Rhagium inquisitor* Linnaeus ($R^2 = 0.319$, $p = 0.002$), and *Asemum striatum* Linnaeus ($R^2 = 0.538$, $p < 0.001$) showed orientation toward jack pine as a potential host preference.

3.3. Species-specific responses to infrastructures

Although overall longhorn beetle assemblage varied little among infrastructures, species-level GLMMs revealed eight of the 12 abundant species showed more pronounced patterns than community-wide metrics suggested (Table_1). Several of these species also show significant

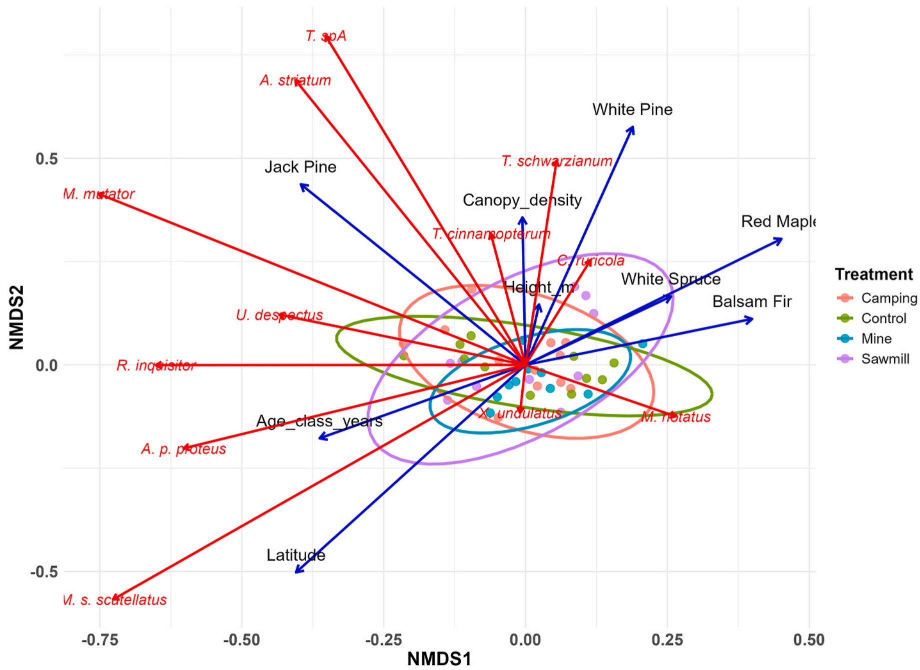

Figure_3. An NMDS plot illustrates the Bray-Curtis dissimilarities in the composition of longhorn beetle assemblages (square-root transformed catch rate) across various infrastructure types. Ellipses denote 95 % confidence intervals surrounding the group centroids, highlighting the dispersion of communities within each treatment. The environmental variables, particularly canopy density (%) and forest tree species, were found to be significant in shaping the longhorn beetle community within the studied infrastructures.

Table 1
A summary of the best-fitted generalized linear models (GLM) and generalized linear mixed models (GLMM) for the abundance and association of longhorn beetles (12 species; >50 individuals) with infrastructures. The model estimates (SE in parentheses) are provided for the three treatments, with the intercept (control forest stands) serving as a reference point. The table includes latitude influencing the longhorn beetles across infrastructures, the spatial variance of the block (σ), the AIC, and log-likelihood values. The level of significance next to the coefficients (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$, and + = $p < 0.1$) and a positive value indicates species that are more supported or promoted by specific infrastructure, as well as latitude.

	(Intercept)	Camping	Mines	Sawmills	Latitude	Random Effect of Block (σ)	AIC	Log. Like
Acmaeops proteus proteus	−42.910 (14.805) **	0.461 (0.378)	0.227 (0.394)	0.731 (0.411) +	0.827 (0.308) **	0.175	311.3	10.28
Asemum striatum	9.929 (8.899)	−0.174 (0.359)	−0.852 (0.383) *	−0.367 (0.371)	−0.248 (0.185)		351.3	16.49
Clytus ruricola	6.133 (12.596)	1.247 (0.567) *	0.555 (0.609)	1.731 (0.571) **	−0.231 (0.262)		213.0	5.30
Monochamus mutator	−34.668 (30.721)	0.623 (0.569)	−1.923 (0.561) ***	−0.231 (0.570)	0.702 (0.640)	0.493	467.6	116.93
Monochamus notatus	15.156 (16.351)	0.164 (0.325)	0.192 (0.348)	0.794 (0.318) *	−0.378 (0.341)	0.166	328.5	6.51
Monochamus scutellatus scutellatus	−33.389 (5.908) ***	0.151 (0.238)	−0.062 (0.250)	−0.018 (0.245)	0.710 (0.123) ***		588.1	218.53
Rhagium inquisitor	−51.013 (9.273) ***	−0.098 (0.356)	−0.372 (0.374)	0.928 (0.358) **	1.006 (0.193) ***		318.8	13.93
Tetropium cinnamopterum	−8.569 (8.539)	0.056 (0.348)	−0.044 (0.365)	1.108 (0.355) **	0.143 (0.178)		421.7	37.84
Tetropium schwarzianum	41.745 (16.795) *	0.433 (0.726)	−1.273 (0.930)	1.131 (0.722)	−0.974 (0.350) **		159.0	3.06
Tetropium spA	12.282 (14.593)	0.748 (0.593)	−0.911 (0.638)	0.570 (0.610)	−0.315 (0.304)		311.0	14.40
Urographis despectus	−1.601 (8.550)	−0.411 (0.351)	−0.350 (0.365)	0.005 (0.350)	−0.034 (0.178)		254.3	4.50
Xylotrechus undulatus	−6.094 (8.201)	−0.330 (0.326)	−0.030 (0.336)	−0.523 (0.339)	0.074 (0.171)		307.3	7.19

associations with the NMDS axes. Sawmills were associated with higher abundance of six species: *A. p. proteus* ($\chi^2(3) = 4.61$, p = 0.202), *Clytus ruricola* Olivier ($\chi^2(3) = 12.84$, p = 0.004), *Monochamus notatus* Drury ($\chi^2(3) = 7.32$, p = 0.062), *R. inquisitor* ($\chi^2(3) = 13.978$, p = 0.002), *T. cinnamopterum* ($\chi^2(3) = 15.10$, p = 0.001), and *T. schwarzianum* ($\chi^2(3) = 5.73$, p = 0.125; Figure_4). Campgrounds also promote the abundance of one of these species, *Clytus ruricola* ($\chi^2(3) = 12.84$, p = 0.004), relative to control sites. By contrast, the mines show a lower abundance of two common species, *Asemum striatum* Linnaeus ($\chi^2(3) = 5.62$, p = 0.131) and *Monochamus mutator* LeConte ($\chi^2(3) = 19.003$, p = 0.0002; Figure_5).

4. Discussion

Assemblages of longhorn beetles primarily reflected forest composition; however some abundant species responded to infrastructure presence. NMDS analysis showed species turnover across forest gradients, with certain beetles associated more strongly with jack pine and others with closed canopy stands of white pine, white spruce, and red maple. However, the overall composition of the longhorn assemblages did not differ across different infrastructure types. Hence, no infrastructure type is inherently more vulnerable to being colonized by non-native species based on the composition of resident woodborers. According to Hanks and Millar's, (2013, 2016) pheromone-free space hypothesis, native longhorns may reduce the likelihood of the

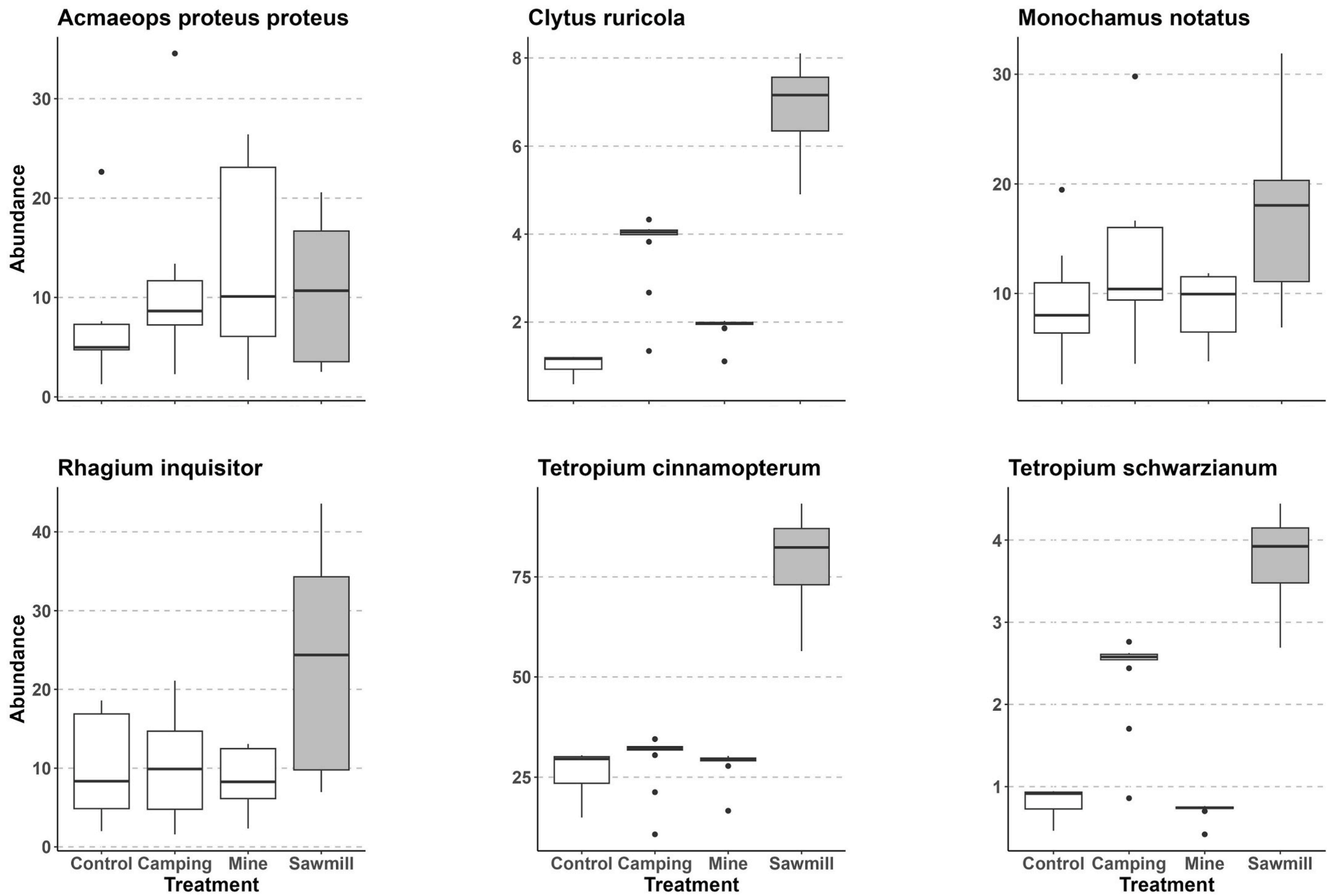

Figure_4. The abundance of longhorn species associated with sawmill (shown in grey-filled boxplots) infrastructures (as treatment on the x-axis) in the eastern boreal forest of Canada. The figure presents boxplots of model-predicted abundance (on y-axis), with corresponding medians, interquartile ranges, and outliers for *Acmaeops proteus proteus*, *Monochamus notatus*, *Rhagium inquisitor*, *Tetropium cinnamopterum*, and *Tetropium schwarzianum*. One of the species, *Clytus ruricola,* was found to be associated with both sawmills and campgrounds. The results indicate a significant positive association between species abundance and infrastructures (sawmills, campgrounds), as established by our generalized linear and mixed models.

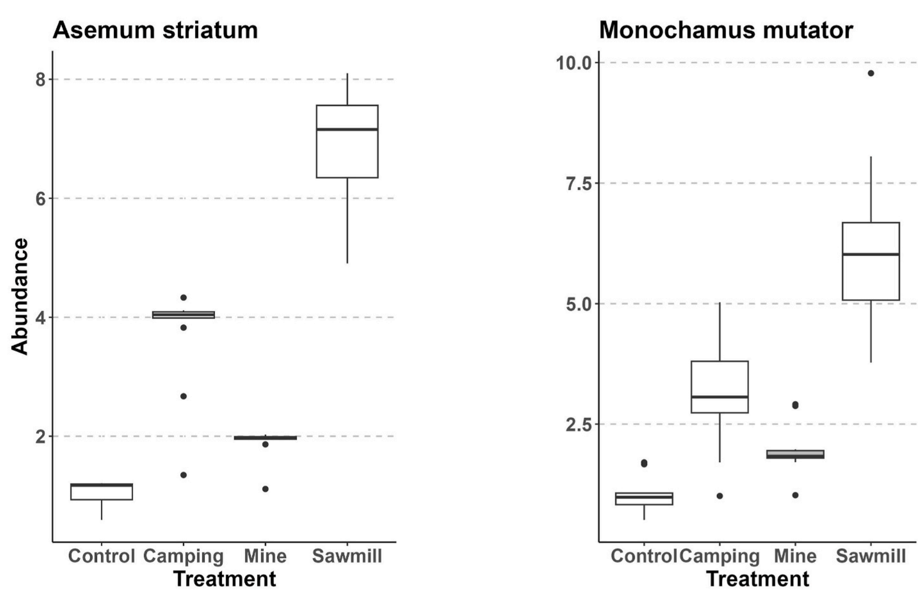

Figure_5. The abundance of longhorns with infrastructures in the eastern boreal forest of Canada. The plots display the predicted abundance with corresponding medians, interquartile ranges, and outliers for *Asemum striatum* and *Monochamus mutator*, which depicted a negative association with the mines (statistical significance determined by our generalized linear and mixed models).

establishment of invasive species through pheromone-mediated disruption, particularly when pheromone structures are similar across various species, supported by Rassati et al. (2021). We did not record any non-native longhorn or other beetles over the two years of this study, which might suggest community-level resistance, although it is also possible that no introductions occurred during the study period. Ongoing surveillance is still required to prevent incursions, as minor management lapses can lead to pest establishment when pathways align with host material (Aukema et al., 2011; Brockerhoff and Liebhold, 2017; Haack, 2006). Nonetheless, the shared semiochemical environment created by native species could plausibly hinder successful mate location and establishment by exotic congeners, especially when pheromone overlap results in cross-attraction or interference (Hanks and Millar, 2016). The diverse native longhorn communities we observed surrounding infrastructures may therefore could contribute to a biotic resistance, although this mechanism was not directly tested in this study. We also didn't record any red-listed species, suggesting no important conservation concerns.

Although traps were operated continuously throughout the main flight season (late May to late August) over two consecutive years, we acknowledge that deploying only one trap per site may still have underestimated local species richness. Previous work shows that increasing trap density can substantially increase the number of species detected (Flaherty et al., 2019), and rare or low-density species, including potential exotics, may therefore have gone undetected. In addition, the composition of the lure blend strongly influences which taxa are sampled. Our trapping strategy primarily targeted potential invasive congeners of *Monochamus* (Boone et al., 2019) and *Tetropium*, and the use of our lures combination likely favored capture of these genera. Inclusion of hydroxyketone- or hexanediol-based lures, or canopy-level traps, would likely have yielded a broader assemblage (Flaherty et al., 2019).

We observed responses to infrastructure at the level of individual longhorn species: six common species, including one frequent pest of freshly cut logs, *Tetropium cinnamopterum,* showed higher abundance at sawmills. These species showed various associations with diverse stand types, suggesting that beetles concentrated in mill yard log piles come from diverse ecological backgrounds. While assemblages were similar, differences in the relative abundance of specific dominant species may fine-tune the above-mentioned resistance, potentially enhancing or weakening it for particular invaders. For instance, higher numbers of native *T. cinnamopterum* at sawmills could reduce establishment likelihood for closely related invaders like brown spruce longhorn beetle (*T. fuscum*), should they arrive via wood packaging material. However, this interference is not guaranteed to prevent establishment. The invasive *T. fuscum* is considered established in the Canadian province of Nova Scotia, and a positive occurrence report is confirmed from eastern Quebec in the Beauce-Sartigan region (IPPC Secretariat, 2023). The exotic *T. fuscum* is considered a significant threat to Canadian conifer forests; it was not detected in our study, but its continued range expansion remains a threat.

In our study, all sites were dominated by *M. s. scutellatus* (over 60 % of the total individuals collected), and its relative abundance was not related to the presence of infrastructures. These results reflect its status as a generalist whose presence reflects microhabitat structures or the availability and/or condition of conifer deadwood rather than associations with specific tree species. These native conifer-feeding sawyers are considered serious pests that contribute to the decline of stressed trees, degrade the quality of harvested logs (Bousquet et al., 2017; Post and Werner, 1988) and potentially introduce wood-rotting fungi (Fierke et al., 2012). Bloin et al. (2022) showed that *M. s. scutellatus* rapidly colonizes freshly harvested conifer logs between mid-July to mid-September and suggest that harvesting of dead wood and processing at mills be timed in order to avoid *M. s. scutellatus* colonization. Logs harvested in spring and processed before July are less vulnerable; promptly handling and processing logs minimizes egg-laying opportunities. Although it is not particularly associated with any infrastructure in our study, it nonetheless poses a significant threat to harvested timber (Bloin et al., 2022) due to its ubiquitous high abundance, both at sawmills and throughout the region.

The NMDS showed how longhorn beetle communities were structured primarily by forest composition. Species grouped along two major axes: one separating balsam fir stands that are generally uneven-aged with high structural complexity from more even-aged Jack pine stands (Guimond et al., 2024; Hasan et al., 2023). The second distinguished high-canopy cover stands dominated by white pine, white spruce, and red maple from early successional hardwoods. *M. notatus* and *R. inquisitor* were associated with jack pine stands, while *A. striatum* showed a broader association with pines and canopy closure. *T. cinnamopterum* and *T. schwarzianum* aligned most strongly with mature white pine systems and closed canopy conditions. These patterns are consistent with broader findings that the composition of tree species and structural heterogeneity exert strong control over woodborer communities (de Quesada and Kuuluvainen, 2020; Leidinger et al., 2021; Traylor et al., 2022). Importantly, these stand-driven assemblage differences imply that infrastructure situated in different forest types, such as more northern jack pine versus southern white pine, will host different longhorn communities, even when infrastructure types are similar. Tree species composition is a key driver of longhorn beetle communities, as shown by Burner et al. (2021), and host preferences can shift regionally depending on the dominant tree species in the landscape (Müller et al., 2015). This has consequences for both biosecurity and wood product value. Invasion risk may vary regionally if exotic beetles arrive in areas where native congeners are abundant and share pheromone motifs or host preferences, potentially facilitating or inhibiting establishment (Hanks and Millar, 2013, 2016). Likewise, the potential for damage from native species may be forest-specific, depending on which longhorn beetles dominate local assemblages and how their phenology aligns with harvesting or timber storage practices.

Our study suggests an increase in diversity and evenness, but not in overall abundance, of native longhorn beetles near sawmills. Previous findings suggest that the presence of freshly harvested logs (Bloin et al., 2022) in mill yards leads to increased longhorn populations (Gandhi et al., 2019), potentially infesting nearby stressed live trees (Gandhi et al., 2009). Our work shows that different longhorns respond differently to the presence of sawmills: of the 12 common species investigated, 6 increased in abundance near sawmills. These are diverse in their associations with stand composition, and include species associated with both ends of the balsam fir – Jack pine axis (NMDS). Most show positive associations on the second axis, clustering around the closed canopy conifer forests rather than the earlier succession hardwood stands. These findings do not support any relationship between longhorns that concentrate in mill yards and any particular tree species; instead, they suggest that diverse longhorns with various ecological associations can use the resources furnished by sawmills. Longhorn beetles respond strongly to seasonal synchrony between their activity periods and the availability of freshly dead conifer wood, and these phenological differences could help explain differences in responses of longhorn species (Bloin et al., 2022).

Local longhorn increases around sawmills can occur by one of two mechanisms: first, attraction of local beetles to freshly cut logs accumulating in the mill yard, and second, transport of beetle larvae within logs from the locations where they were harvested. Thus, enriched sawmill longhorn communities may reflect both local attraction and passive introduction. Much of the wood in mill yards is harvested from natural disturbances like fire or defoliator outbreaks and therefore includes dead and dying trees that are at high risk of already being colonized by longhorns (Bloin et al., 2022), increasing the risk of passive introduction. However, at the mill, this wood undergoes processing that reduces beetle survival by exposing wood to high temperatures.

Concentration of longhorn beetles at mill sites nonetheless poses a potential risk to nearby standing timber. The most common pest species, *M. s. scutellatus*, was not affected by the presence of sawmills, but the second most common pest species, *T. cinnamopterum,* did increase around sawmills. Currently, many sawmills are surrounded by non-forested areas, like parking lots or sorting yards, limiting spillover effects. However, if future forest management leads to the establishment of intensively managed conifer plantations adjacent to sawmills' infrastructure, the proximity of growing stock to concentrated beetle activity could increase the vulnerability of plantation trees to infestation. This scenario is particularly relevant for species requiring sun-exposed (Jonsell and Rubene, 2024) or stressed wood, which may shift from mill yard stockpiles into nearby plantations. Thus, the combination of concentrated cut logs resources and susceptible young trees may create conditions that facilitate pest outbreaks if not carefully managed.

A few species showed increased abundance near other infrastructure types. *C. ruricola*, for example, was more common near sawmills and campgrounds, likely reflecting its association with hardwoods, particularly red maple, which was strongly correlated with longhorn community structure in our NMDS ordination. Campgrounds may offer increased access to stressed or dying maples, while canopy thinning in these areas may improve solar exposure and promote drying in upper branches, conditions that may benefit the canopy-dwelling oviposition behavior of this species (Vance et al., 2003).

Two conifer-associated longhorn species, *M. mutator* and *A. striatum*, showed decreased abundance near mining infrastructure. While this observation may imply modifications in habitat suitability, the underlying mechanisms are likely more complex than mere woody substrate depletion. Our field-based observations showed that adjacent forest stands were dense and patchy, characterized by heterogeneous canopies, the presence of coarse woody debris, and constrained light penetration. These conditions are insufficient to account for a reduction in deadwood resources directly. However, residual impacts stemming from anthropogenic land use activities, such as impediment from heavy equipment movement zones, contamination with heavy metals, or altered microclimatic conditions, could potentially degrade habitat quality through less conspicuous pathways. These observations align with existing research demonstrating the prolonged effects of mining operations on terrestrial insect communities, wherein beetle diversity and abundance remain diminished, attributable to alterations in soil composition and vegetation structure, as documented by Babin-Fenske and Anand (2011).

Reduced abundance of only two native beetle species in such altered zones could lower biotic resistance to relevant exotic congeners. As we discussed previously, Hanks and Millar (2013, 2016) emphasized that strong native assemblages, especially of closely related species, can inhibit establishment of invaders through competitive or chemical interference. Thus, infrastructure in such disturbed boreal sites may be doubly vulnerable, through habitat alteration and reduced native resilience, even if pathways for introduction (e.g., wood-packaged materials) are rare in remote mining regions.

5. Conclusion

Our study provides novel insights into how industrial and recreational infrastructures influence the diversity and community structure of longhorn beetles in boreal forests. *M. s. scutellatus* and *T. cinnamopterum*, important pests that degrade the quality of harvested wood, were found at high density at all sampling sites and thus pose a significant risk to both stressed pre-harvest trees and to logs accumulated at sawmills post-harvest. The longhorn beetle community was more affected by stand composition, while it did not vary much between the different infrastructure types. Species-specific responses to infrastructures show that several longhorn beetles with different ecological associations are concentrated around sawmills, whereas mining activities may negatively affect a few. No exotic beetles were detected during this study. However, as industrial activities proliferate in the boreal zone, the integration of ecological monitoring with sustainable forestry practices will be crucial in mitigating economic and biodiversity risks.

CRediT authorship contribution statement

Sabina Noor: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **Emma Despland:** Writing – review & editing, Resources, Funding acquisition. **Miguel Montoro Girona:** Writing – review & editing, Resources, Project administration, Funding acquisition. **Timothy Work:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of generative AI and AI-assisted technologies

During the preparation of this work, SN used Writefull's rephrasing tool to improve clarity and language. After using this tool/service, the co-authors, TM, ED, and MMG reviewed and edited the content as needed, and SN takes full responsibility for the content of the published article.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2026.128791.

Data availability

Data will be made available on request.

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