**Integrating passive acoustic monitoring and LiDAR for breeding bird habitat modelling in a working forest**

# Abstract

Accurately modelling bird species richness is essential for guiding conservation and forest management decisions; however, traditional ground-based surveys are often limited in spatial and temporal coverage. Here, we integrated passive acoustic monitoring and LiDAR-derived habitat covariates to model breeding songbird richness (composed of 40 target species) within the John Prince Research Forest, a 16,000 ha managed working forest in central British Columbia, Canada. Acoustic data were collected from 59 sites over three breeding seasons using autonomous recording units (ARUs) to inform site-level richness, which was then compared to 17 LiDAR covariates calculated using a 100-m buffer around each site. Our results showed that none of the LiDAR covariates strongly predicted richness of breeding songbirds, and only one covariate, the proportion of deciduous trees, showed a weak positive association for a species sub-group. Vertical canopy structure and other commonly used LiDAR metrics had limited explanatory power, likely reflecting the heterogeneous habitat preferences among breeding songbirds and the generally similar richness across sites. Overall, this study demonstrates the potential of integrating PAM and LiDAR to quantify biodiversity in working forests and highlights the importance of standardized approaches for large-scale acoustic monitoring.

**Introduction**  
Understanding the hotspots of bird species richness is crucial for identifying preferred habitats and guiding conservation priorities for different species (Francis and Currie 2003; Hawkins et al. 2003). Traditionally, estimates of richness relied on ground-based bird surveys that provided direct observations of species presence. To extend beyond surveyed locations, models have been developed to predict bird richness using habitat covariates, thereby linking biodiversity patterns to environmental drivers and supporting conservation and management decisions (Rahbek et al. 2006). In working forests, such models are particularly valuable for identifying priority areas for conservation, informing harvest planning, and evaluating the ecological impacts of forest management strategies (e.g., Maes et al., 2005).

Obtaining accurate and comprehensive data on bird richness, however, remains challenging. Ground-based surveys are labor-intensive, time-consuming, and often limited in spatial and temporal coverage, making it difficult to monitor large or remote areas effectively. Moreover, habitat covariates derived from conventional remote sensing methods, such as satellite imagery or aerial photography, generally emphasize horizontal landscape features. However, vertical habitat structure, such as canopy height, foliage density, and understory complexity, plays a critical role in shaping bird communities (Culbert et al. 2013). These vertical attributes are hard to capture with traditional remote sensing products, limiting the ecological relevance of bird–habitat models (Gottschalk et al. 2005).

Passive acoustic monitoring has emerged as a powerful and scalable tool for biodiversity assessment (Ross et al. 2023; Sugai et al. 2019). Autonomous recording units (ARUs) can collect continuous or repeated audio data over large spatial and temporal scales with relatively low human effort (Sugai et al. 2019). This approach enables detection of vocalizing bird species even in remote or difficult-to-access areas, thereby greatly expanding survey coverage. Numerous studies have demonstrated the effectiveness of acoustic monitoring for estimating species presence (e.g., Picciulin et al. 2019), vocal activity patterns (e.g., Pérez-Granados et al. 2021), density (Pérez-Granados and Traba 2021), and community composition (e.g., Mattmüller et al. 2022).

Light Detection and Ranging (LiDAR) technology provides a complementary perspective by offering detailed three-dimensional information on vegetation structure (Vierling et al. 2008). Unlike conventional remote sensing, LiDAR captures both horizontal and vertical habitat attributes, making it particularly well-suited for studying bird–habitat relationships (Bradbury et al. 2005; Tattoni et al. 2012). Previous research has demonstrated the utility of LiDAR-derived metrics in modeling bird diversity and habitat suitability across diverse ecosystems (Bakx et al. 2019). However, the integration of LiDAR with passive acoustic monitoring remains relatively unexplored, despite its potential to improve our understanding of the structural drivers of bird species richness.

In this study, we integrate passive acoustic monitoring and LiDAR remote sensing to model breeding bird richness within the John Prince Research Forest, a managed working forest in central British Columbia, Canada. Acoustic data were collected using autonomous recording units (ARUs) during three breeding seasons. LiDAR data provided structural habitat covariates characterizing vertical and horizontal forest complexity. Our objectives were to: (1) compile a comprehensive species list and estimate asymptotic site-level breeding bird richness, and (2) evaluate the associations between LiDAR-derived habitat covariates and bird asymptotic richness.

# Methods

## Study area and acoustic recording sites

The study was conducted in the John Prince Research Forest (~16,000 hectares in area), located in central British Columbia, Canada, within the dry sub-boreal spruce biogeoclimatic zone (**Fig. 1A**). Audio data were collected from 2020 to 2022 throughout the breeding season (early May to late July) between daily dawn chorus (4 am to 7am), using Audio Moth ARUs (Hill et al. 2019). ARUs were set to record for 1 minute, followed by 4 minutes pause, throughout the three hours recording period, resulting in 36 one-minute recordings per day per site. Each ARU was placed at least two kilometers apart to minimize spatial correlation. Variability in the number of active ARUs at each site/date (**Fig. 1B**) occurred due to setup logistics (e.g., accessibility of sites during early season) and field/equipment challenges (e.g., battery depletion, firmware issues, disturbances by wildlife). We excluded data from sites which had less than 15 days of ARU data to avoid potential bias due to low surveying effort. This resulted in data from 59 sites, with each site having an average of 106 ARU days across three years, ranging from 32 to 182 ARU days.

## Acoustic data processing and target species



**Fig. 1**. Spatiotemporal distribution of surveying effort. (A) ARU locations (central solid dots, with ARU days depicted in the size of the halo around the dot) during the surveying seasons and (B) yearly number of ARUs across the surveying period.

We analyzed collected acoustic data with the BirdNET Analyzer v2.4 model (BirdNET Team 2025), using the parameters listed in **Table 1**. The entire dataset, comprising 1.5 terabytes of audio, required approximately 72 consecutive hours of processing. An overall bird community list was generated in four steps: (1) BirdNET detections were initially filtered using a confidence threshold of 0.8. For each detected category, five recording segments with the highest confidence scores were manually reviewed. Sound categories with at least one confirmed vocalization were retained, resulting in 136 sound categories. (2) Non-bird categories, such as Car Engine, Red Squirrel, Wood Frog, and Slender Meadow Katydid, were removed, reducing the list to 129 sound categories. (3) Species not listed in the British Columbia Breeding Bird Atlas (Davidson et al. 2015), which documents species recorded in the Prince George area since 2008, were excluded, leaving 123 species. (4) Species detected at fewer than two sites or on fewer than two days in June (i.e., main breeding season) were excluded, resulting in a final list of 122 species (**Supplementary Table A**). The overall species list included a diverse range of bird taxa such as raptors, waterfowl, warblers, sparrows, flycatchers, woodpeckers, owls, and other families.

We further refined this overall species list to a target guild of passerine species that have confirmed breeding records in the study region, and which are known to be vocally active during the dawn chorus period. These criteria were used to avoid detection bias given that recordings were scheduled during the dawn chorus of the breeding season. We then assessed individual species-specific BirdNET confidence thresholds for the 40 species, following the methods of Tseng et al. (2025), to ensure the precision of detections. To do this, we used stratified sampling to select 360 recording segments in which BirdNET had detected each of the target species, with 20 segments drawn from each 0.05 detection confidence interval bin (ranging from 0.1 to 1.0). Each segment was then manually reviewed, by both listening to audio and viewing spectrograms in comparison with known exemplars of the species, to classify detections as true or false positives. For each species, a BirdNET confidence threshold was set that achieved a precision of 0.95, indicating that at least 95% of the retained detections were true positives (see Tseng et al. 2025 for the full workflow). These thresholds were set individually for each of the final list of 40 passerines target species included (**Table 2**).

**Table 1**. BirdNET algorithm arguments with default values and the values used in this study.

| Argument | Default value | Used value |
| --- | --- | --- |
| i | none | -- |
| o | none | -- |
| lat | -1 | same as default |
| lon | -1 | same as default |
| week | -1 | same as default |
| slist | none | same as default |
| sensitivity | 1.0 | same as default |
| min\_conf | 0.1 | same as default |
| overlap | 0 | same as default |
| rtype | table | r |
| threads | 1 | 4 |
| batchsize | 1 | 4 |
| locale | en | same as default |
| sf\_thresh | 0.03 | same as default |
| classifier | none | same as default |
| fmin | 0 | same as default |
| fmax | 15000 | same as default |
| output\_file | none | -- |
| skip\_existing\_results | FALSE | TRUE |

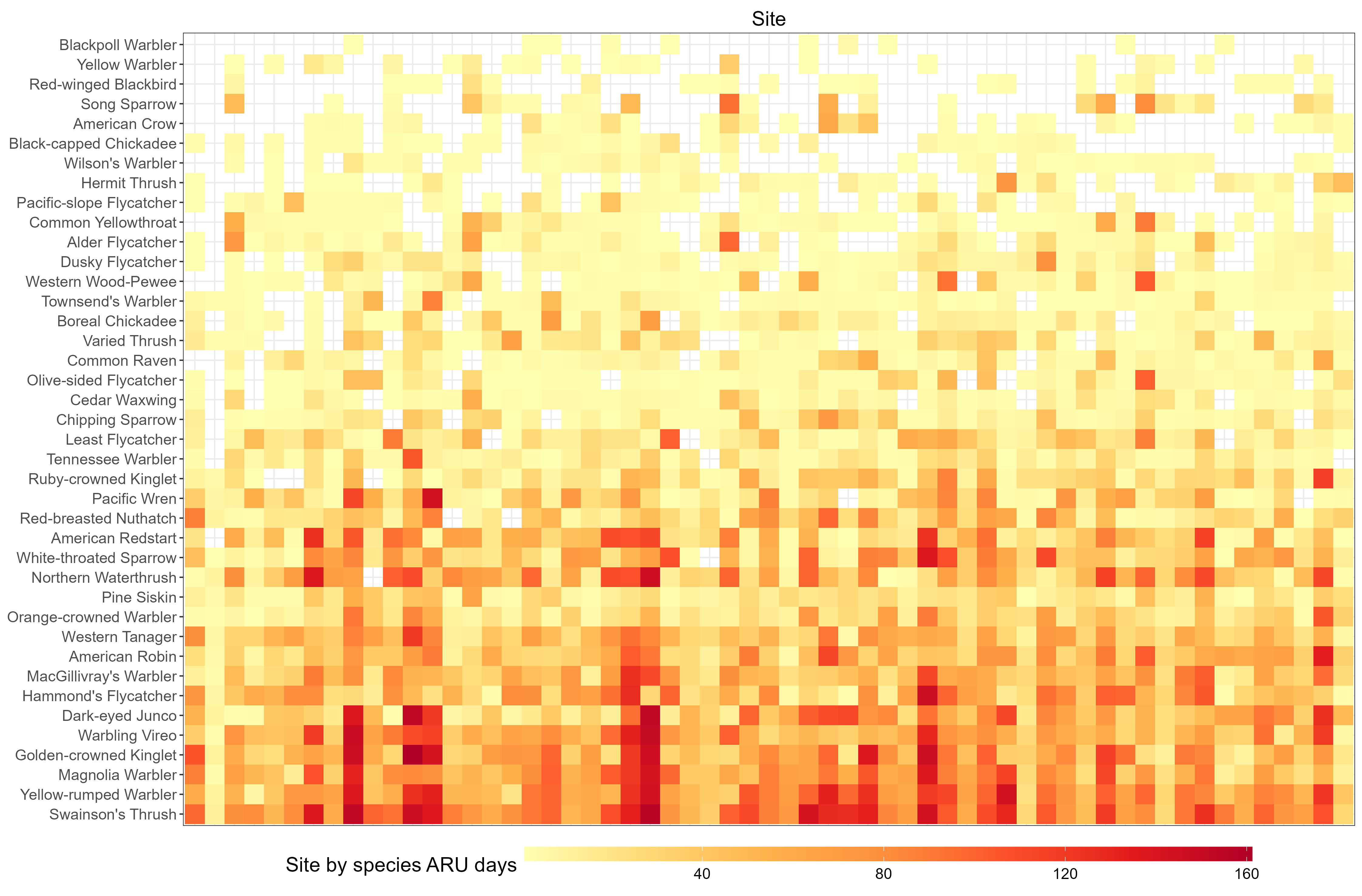
**Table 2**. The 40 species of breeding passerine birds detected during the dawn chorus and selected as target species. Sentence about where the data came from and number of sites. For each species, the table reports the total number of BirdNET detections and the number of sites where the species was detected. These values were calculated after applying species-specific BirdNET confidence thresholds that achieved 95% precision, and after excluding sites with fewer than 15 ARU recording days.

| Common name | Scientific name | Threshold (95%) | No. detections | No. sites |
| --- | --- | --- | --- | --- |
| Swainson's Thrush | *Catharus ustulatus* | 0.10 | 327234 | 59 |
| Hammond's Flycatcher | *Empidonax hammondii* | 0.10 | 140580 | 59 |
| Yellow-rumped Warbler | *Setophaga coronata* | 0.10 | 110942 | 59 |
| Warbling Vireo | *Vireo gilvus* | 0.10 | 86199 | 59 |
| Golden-crowned Kinglet | *Regulus satrapa* | 0.10 | 84229 | 59 |
| Magnolia Warbler | *Setophaga magnolia* | 0.10 | 74066 | 59 |
| Dark-eyed Junco | *Junco hyemalis* | 0.10 | 48329 | 59 |
| Western Tanager | *Piranga ludoviciana* | 0.10 | 39421 | 59 |
| American Robin | *Turdus migratorius* | 0.10 | 37644 | 59 |
| MacGillivray's Warbler | *Geothlypis tolmiei* | 0.10 | 30276 | 59 |
| Orange-crowned Warbler | *Leiothlypis celata* | 0.10 | 11907 | 59 |
| Pine Siskin | *Spinus pinus* | 0.10 | 6399 | 59 |
| Northern Waterthrush | *Parkesia noveboracensis* | 0.10 | 145743 | 58 |
| American Redstart | *Setophaga ruticilla* | 0.10 | 74866 | 58 |
| White-throated Sparrow | *Zonotrichia albicollis* | 0.10 | 42408 | 58 |
| Pacific Wren | *Troglodytes pacificus* | 0.10 | 60245 | 57 |
| Red-breasted Nuthatch | *Sitta canadensis* | 0.21 | 15373 | 57 |
| Tennessee Warbler | *Leiothlypis peregrina* | 0.10 | 36095 | 56 |
| Ruby-crowned Kinglet | *Corthylio calendula* | 0.10 | 13718 | 56 |
| Least Flycatcher | *Empidonax minimus* | 0.16 | 36919 | 55 |
| Chipping Sparrow | *Spizella passerina* | 0.10 | 5162 | 54 |
| Cedar Waxwing | *Bombycilla cedrorum* | 0.36 | 1994 | 53 |
| Olive-sided Flycatcher | *Contopus cooperi* | 0.31 | 9201 | 52 |
| Common Raven | *Corvus corax* | 0.10 | 4668 | 52 |
| Varied Thrush | *Ixoreus naevius* | 0.61 | 6693 | 51 |
| Townsend's Warbler | *Setophaga townsendi* | 0.24 | 3039 | 51 |
| Boreal Chickadee | *Poecile hudsonicus* | 0.20 | 2918 | 51 |
| Western Wood-Pewee | *Contopus sordidulus* | 0.10 | 10992 | 50 |
| Dusky Flycatcher | *Empidonax oberholseri* | 0.26 | 3495 | 49 |
| Alder Flycatcher | *Empidonax alnorum* | 0.10 | 21031 | 48 |
| Common Yellowthroat | *Geothlypis trichas* | 0.10 | 4153 | 46 |
| Western Flycatcher | *Empidonax difficilis* | 0.41 | 1306 | 37 |
| Hermit Thrush | *Catharus guttatus* | 0.79 | 3301 | 36 |
| Wilson's Warbler | *Cardellina pusilla* | 0.46 | 603 | 35 |
| Black-capped Chickadee | *Poecile atricapillus* | 0.26 | 606 | 32 |
| American Crow | *Corvus brachyrhynchos* | 0.10 | 1477 | 30 |
| Song Sparrow | *Melospiza melodia* | 0.10 | 3390 | 23 |
| Red-winged Blackbird | *Agelaius phoeniceus* | 0.10 | 204 | 23 |
| Yellow Warbler | *Setophaga petechia* | 0.40 | 394 | 21 |
| Blackpoll Warbler | *Setophaga striata* | 0.85 | 51 | 10 |

## Asymptotic richness detected by ARUs

We calculated the number of days on which each of the 40 target species was detected at each of the 59 sites (**Fig. 2**). To characterize similarities in site use among species, we applied k-means clustering to group species with comparable detection patterns across sites. Prior to clustering, we applied data normalization by dividing the number of species ARU days by the total number of ARU days per site, thereby accounting for variation in sampling effort. To determine the optimal number of clusters, we evaluated two approaches: the total within-cluster sum of squares (“elbow method”) using the *factoextra::fviz\_nbclust()* function (Kassambara 2017), and the gap statistic using the *cluster::clusGap()* and *factoextra::fviz\_gap\_stat()* functions (Kassambara 2017). Final clustering was performed using the *kmeans()* function in R (Lemenkova 2019).

Direct comparisons of observed species richness across sites (i.e., the number of coloured cells in each column of **Fig. 2**) can be misleading, as survey effort (i.e., number of ARU days) varied among sites. To account for this variation, we used asymptotic richness estimates as a standardized measure of site-level diversity (Chao et al. 2014). We calculated asymptotic richness using the iNEXT (iNterpolation and EXTrapolation) R package (Hsieh et al. 2016), which implements diversity estimation based on Hill numbers. Specifically, we used the *iNEXT::ChaoRichness()* function with incidence data to estimate asymptotic richness and its associated standard errors.



**Fig. 2**. Number of days each species was detected at each site using ARUs. Species in the lower part of the graph, such as American Robin, Dark-eyed Junco, and Golden-crowned Kinglet, were detected across most sites and likely represent generalists. In contrast, species toward the top of the graph, including Yellow Warbler and Red-winged Blackbird, were detected at fewer sites, potentially reflecting more specific habitat preferences.

## LiDAR covariates and model selection

LiDAR data were collected in 2015 during the leaf-off season, with a point density of XYZ. As all sites in the study had not undergone significant disturbance since 2015, the LiDAR covariates reflect the same relative habitat composition/shifts to allow for comparison with the audio data collected in (years x to y). We applied an area-based approach to rasterize the point clouds at a spatial resolution of 10 meters. For modeling purposes, we aggregated habitat covariates within a 100-meter radius around each ARU site to represent the area a bird might be using when detected (Pérez-Granados 2025). A total of 17 LiDAR-derived variables were considered as candidate covariates (**Table 3**). These covariates were classified following the framework outlined in Bakx et al. (2018), which highlights canopy structure and total vegetation metrics as the most commonly associated with bird species richness (see Fig. 4 in Bakx et al. 2019).

To reduce multicollinearity and ensure model stability, we calculated pairwise correlations among the covariates and removed those with correlations greater than 0.8. Furthermore, we computed variance inflation factors (VIFs) to ensure all the covariates having a VIF less than 5. This pre-selection ensured that only relatively independent covariates were included in the subsequent model selection. We then used an information-theoretical approach for model selection. Specifically, we fitted models using all possible linear combinations of the LiDAR covariates, calculating Akaike weights to quantify the relative support for each model. For each covariate, we then computed the sum of model weights by summing the weights across all models in which the covariate appeared. Covariates with high sum of weights (> 0.8) consistently appeared in the best-supported models, representing a high variable importance. This analysis was conducted using the *MuMIn::dredge()* function (Bartoń 2025), with the full model specified as a linear regression.

**Table 3**. LiDAR-derived habitat covariates used in the analysis, including measures of canopy structure, vegetation density, and ground features. Covariates retained after the correlation and multicollinearity screening are shown in bold (see **Results** section for details).

| Type | Name | Definition |
| --- | --- | --- |
| Topography/  Ground | **dem** | Average elevation |
| **slope** | Average slope |
| **aspect** | Average aspect |
| **d\_lid\_rip\_wet\_str\_le** | Distance to LiDAR stream, wetland (polygon), lake edge |
| **d\_vri\_polyedge** | Distance to VRI polygon stand edge |
| Canopy | **cc1\_3** | Average crown closure between 1 – 3 m |
| **cc3\_10** | Average crown closure between 3 – 10 m |
| **cc10** | Average crown closure above 10m |
| chm | Average canopy height |
| vdi\_95 | Vertical distribution if intercepted canopy elements ranging from 0 and 1 using 95% height |
| Total vegetation | less\_10 | Proportion of polygon with forest age less than 10 years |
| **age\_80** | Proportion of polygon with forest age greater than 80 years |
| **prop\_decid** | Proportion of deciduous tree counts for all trees having DBH > 10cm |
| decid\_dens | Number of deciduous trees per unit area |
| conf\_dens | Number of conifer trees per unit area |
| tree\_dens | Number of total trees per unit area |
| ba\_dens | Sum of basal area of all trees per unit area |

# Results

## Asymptotic richness estimates

Estimated asymptotic species richness across sites ranged from 29.66 to 48.79 species. Regardless of the number of ARU sampling days per site, species accumulation curves generally approached a plateau, indicating that the observed richness was close to the asymptotic estimate across all sampling effort (**Fig. 3**). The mean difference between estimated asymptotic and observed richness was 3.0 species for low-effort sites, 4.6 species for medium-effort sites, and 2.8 species for high-effort sites (Supplementary **Table B**).

A graph of different days

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**Fig. 3**. Rarefaction curves for sites with different survey efforts (i.e., ARU days): (A) fewer than 90 days, (B) between 90 and 120 days, and (C) greater than 120 days. Each semi-transparent line represents the curve for an individual site. The solid parts of the curve are interpolation of collected data while the dashed parts are extrapolation. If the solid line is already approaching the asymptote, it indicates that current sampling effort is sufficient in surveying richness.

## LiDAR covariate pre-selection

Pairwise correlations between the 17 LiDAR-derived covariates revealed several instances of high collinearity (|r| > 0.8; **Fig. 4A**). Specifically, several covariates representing canopy structure (**Fig. 4A** green highlight) and total vegetation (**Fig. 4A** yellow highlight) were strongly correlated. To reduce effects of multicollinearity among variables, we retained only the variables that were most interpretable and widely used in ecological studies, reducing the number of covariates from 17 to 10 (**Fig. 4B**). All retained variables had variance inflation factor (VIF) values below 5, indicating low levels of multicollinearity among variables (**Fig. 4C**; bolded variables in **Table 3**). Because aspect is a circular variable, we further decomposed it into its sine and cosine components, resulting in a total of 11 LiDAR covariates used in the subsequent model selection.

A close-up of a graph

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**Fig. 4.** Pre-selection of LiDAR covariates. (A) Correlation plot of the original set of 17 covariates. (B) Correlation plot of covariates retained after removing highly correlated variables (|r| > 0.8). (C) Final check showing that the variance inflation factors (VIF) for all variables were < 5.

## Asymptotic richness model with LiDAR covariates across all species

Among the 11? pre-selected LiDAR covariates, none had a sum of model weights exceeding 0.8 when predicting richness of all species combined (**Fig. 5A**). This finding indicates that no single covariate consistently appeared in the best-supported models, suggesting limited explanatory power of LiDAR covariates for overall asymptotic richness. The lack of strong covariate importance likely reflects differences in habitat preferences among species, which reduced the overall signal when analyzed together.

A graph of different colored and black lines

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**Fig. 5**. Sum of model weights for each LiDAR covariate across different species groups: (A) full species list (40 species of breeding songbirds), (B) purple group (13 species), (C) orange group (6 species), and (D) green group (21 species). The red line indicates a sum of model weights of 0.8, a commonly used threshold for identifying influential covariates.

## Asymptotic richness model with covariates for sub-groups of species

To account for the potential heterogeneity across all species, we grouped species based on their site-level occurrence patterns (**Fig. 2**) using k-means clustering (**Fig. 6**). This analysis identified three clusters comprising 13 (purple), 6 (orange), and 21 (green) species, respectively. Species within the same cluster exhibited similar distribution patterns across study sites, suggesting shared habitat associations or frequent co-occurrence.

All pre-selected LiDAR covariates had model weights lower than 0.8 for the purple (**Fig. 5B**) and green (**Fig. 5D**) groups. Even the covariates with the highest model weights, average crown closure above 10 m for the purple group and aspect for the green group, showed non-significant relationships with asymptotic richness (**Figs. 7A**, **7C**). For the orange group, the proportion of deciduous trees (prop\_decid) had a model weight greater than 0.8 (**Fig. 5C**) and showed a positive relationship with asymptotic richness (**Fig. 7B**). However, the effect size was small, and the relationship was only marginally significant, indicating a weak association.

A screenshot of a graph

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**Fig. 6**. K-means clustering of target species based on site-use patterns, visualized in principal component space. Species within the same cluster show similar distributions across study sites. The purple group includes 13 species, the orange group 6 species, and the green group 21 species.

A graph of a tree

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**Fig. 7**. Simple linear regression of the most influential LiDAR covariate for each species group in explaining asymptotic richness: (A) purple group – average crown closure above 10 m, (B) orange group – proportion of deciduous trees, and (C) green group – aspect. Note that even the most influential covariates showed weak or no association with richness within each group.

# Discussion

Our results showed that none of the LiDAR covariates effectively predicted overall breeding songbird asymptotic richness (**Fig. 5**), likely because species exhibit diverse habitat preferences that cannot be captured by a common set of structural features. When species were grouped based on similarities in habitat use, only one covariate, the proportion of deciduous trees, showed a weak positive association with richness for a single species group (**Fig. 7**). Rarefaction analyses indicated that surveying effort across study sites was generally sufficient, as observed richness closely approached estimated asymptotic richness (**Fig. 3**). This suggests that the number of ARU days at each site provided an adequate sampling of the local breeding songbird richness, which included 40 species in total. Overall, our large-scale acoustic survey provided a comprehensive assessment of the breeding bird community within the John Prince Research Forest in central British Columbia (**Supplementary Table A**).

Contrary to expectations from previous studies that identified canopy covariates as key drivers of bird richness (Bakx et al. 2019), LiDAR variables related to vertical canopy structure, such as average crown closure at different heights, showed limited explanatory power for asymptotic richness across all species. This discrepancy may reflect the composition of our focal community: the 40 species of dawn-chorus songbirds occupy a range of habitat types, which may have blurred any clear habitat association in the overall model. When analyzed by species groups, none of the covariates strongly predicted richness, as species richness was relatively similar across sites. Specifically, the 13 species in the purple group (**Fig. 6**) occurred at nearly all sites (**Fig. 7A**), and the 6 species in the orange group (**Fig. 6**) were also widespread across sites (**Fig. 7B**), resulting in low variation in asymptotic richness across sites. Overall, the weak relationships between asymptotic richness and LiDAR covariates likely reflect both heterogeneous habitat preferences among target species and the generally uniform species richness across sites.

Expanding analyses to include the full community species list could provide broader ecological insight, but presents several practical challenges. First, validating BirdNET detections requires substantial manual effort to establish species-specific thresholds (Tseng et al. 2025; Wood and Kahl 2024). Based on our workflow (see **Methods**), validating 360 song segments per species took approximately 4–8 hours, depending on factors such as vocal repertoire overlap (e.g., Varied Thrush vs. White-throated Sparrow; Alder Flycatcher vs. Hammond’s Flycatcher), frequency characteristics (e.g., the high-pitched songs of Brown Creeper and Golden-crowned Kinglet), and call length (e.g., short warbler calls). Scaling this process to 122 species would require roughly 100 person-days of effort. Second, even when focusing only on breeding songbirds, our results showed that LiDAR covariates were generally non-significant due to heterogeneous habitat preferences among species. Expanding the analysis to the full species list would probably further obscure any trends, requiring more complex models to disentangle covariate associations. Focusing on a subgroup of the community, the breeding songbirds, thus allows for a clearer understanding of the relationships between habitat structure and species richness.

One potential approach to reduce the validation effort and enable richness analyses across all species is the use of universal thresholds (Tseng et al. 2025), which apply a standardized BirdNET confidence threshold across species and aggregate results over longer temporal windows. Recent studies suggest that this strategy can yield community-level estimates comparable to expert validation while minimizing manual effort (Fairbairn et al. 2025). However, universal thresholds bypass species-specific error assessment, and their outputs should therefore be interpreted with caution. Without explicit quantification of precision or detection probability, such thresholds may be most appropriate for coarse-resolution analyses, where presence–absence data are aggregated over broad spatial or temporal scales (Fairbairn et al. 2025).

In conclusion, our findings showed none of the LiDAR covariate was strongly associated with the breeding songbird richness, resulting from the breeding songbirds in the study area exhibit varied habitat associations, and breeding songbird richness was generally similar across sites. Strategies such as universal thresholds could help facilitate broader community-level analyses, but they must be applied carefully due to the lack of species-specific error assessment. Future research could expand beyond richness to include other biodiversity metrics, such as evenness and abundance, though deriving these metrics from ARU data should be approached with caution. As acoustic monitoring becomes increasingly widespread for large-scale biodiversity assessments, the development of clear guidelines for using ARU-derived data is highly recommended. Such guidelines could include standardized procedures for generating species lists (as in our **Methods**), estimating richness across sites (e.g., using asymptotic richness), and deriving relative abundance for single or multiple species. Implementing these standardized practices will help ensure that acoustic monitoring can reliably inform biodiversity conservation and forest management decisions.

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# Supplementary Materials

**Table A**. The full list of 122 bird species detected by ARUs at the study site (do you mean study area? Elsewhere in the caption your refer to sites as ARU locations—would be good to keep language consistent!). For each species, the table includes the total number of detections identified by BirdNET and the number of sites where the species was detected. The values were calculated before applying species-specific thresholds (so species-specific thresholds applied to BirdNET detections) and before dropping unused sites from the analysis (what do you mean by unused sites? Do you mean sites where no birds were detected?). (This sentence represents Methods so don’t include in a caption)

| **Family** | **Scientific name** | **Common name** | **No. detections** | **No. sites** |
| --- | --- | --- | --- | --- |
| Accipitridae  (Hawks, Eagles, and Kites) | *Astur atricapillus* | American Goshawk | 4713 | 54 |
| *Buteo jamaicensis* | Red-tailed Hawk | 296 | 50 |
| *Buteo platypterus* | Broad-winged Hawk | 3302 | 57 |
| *Haliaeetus leucocephalus* | Bald Eagle | 398 | 30 |
| *Accipiter striatus* | Sharp-shinned Hawk | 116 | 38 |
| Pandionidae  (Osprey) | *Pandion haliaetus* | Osprey | 238 | 39 |
| Anatida  (Ducks, Geese, and Waterfowl) | *Anas platyrhynchos* | Mallard | 478 | 40 |
| *Branta canadensis* | Canada Goose | 788 | 39 |
| *Mergus merganser* | Common Merganser | 866 | 32 |
| *Bucephala clangula* | Common Goldeneye | 82 | 21 |
| *Anas crecca* | Green-winged Teal | 124 | 25 |
| *Lophodytes cucullatus* | Hooded Merganser | 75 | 13 |
| *Bucephala islandica* | Barrow's Goldeneye | 19 | 7 |
| *Cygnus buccinator* | Trumpeter Swan | 97 | 18 |
| *Spatula discors* | Blue-winged Teal | 24 | 7 |
| *Mareca americana* | American Wigeon | 23 | 4 |
| *Aythya collaris* | Ring-necked Duck | 144 | 14 |
| Trochilidae  (Hummingbirds) | *Selasphorus rufus* | Rufous Hummingbird | 177 | 24 |
| Caprimulgidae (Nightjars and Allies) | *Chordeiles minor* | Common Nighthawk | 469 | 45 |
| Laridae  (Gulls, Terns, and Skimmers) | *Chroicocephalus philadelphia* | Bonaparte's Gull | 31 | 6 |
| Scolopacidae  (Sandpipers and Allies) | *Actitis macularius* | Spotted Sandpiper | 297 | 33 |
| *Gallinago delicata* | Wilson's Snipe | 11401 | 37 |
| *Tringa solitaria* | Solitary Sandpiper | 94 | 23 |
| *Tringa melanoleuca* | Greater Yellowlegs | 994 | 48 |
| Alcedinidae  (Kingfishers) | *Megaceryle alcyon* | Belted Kingfisher | 462 | 51 |
| Falconidae  (Falcons and Caracaras) | *Falco sparverius* | American Kestrel | 143 | 42 |
| *Falco columbarius* | Merlin | 528 | 32 |
| Phasianidae  (Pheasants, Grouse, and Allies) | *Canachites canadensis* | Spruce Grouse | 15906 | 58 |
| *Bonasa umbellus* | Ruffed Grouse | 1000 | 49 |
| *Lagopus lagopus* | Willow Ptarmigan | 62 | 23 |
| Gaviidae  (Loons) | *Gavia immer* | Common Loon | 5530 | 57 |
| Gruidae  (Cranes) | *Antigone canadensis* | Sandhill Crane | 535 | 35 |
| Rallidae  (Rails, Gallinules, and Coots) | *Porzana carolina* | Sora | 3448 | 17 |
| Bombycillidae  (Waxwings) | *Bombycilla cedrorum* | Cedar Waxwing | 5771 | 59 |
| *Bombycilla garrulus* | Bohemian Waxwing | 151 | 40 |
| Cardinalidae  (Cardinals and Allies) | *Piranga ludoviciana* | Western Tanager | 39616 | 61 |
| *Pheucticus ludovicianus* | Rose-breasted Grosbeak | 3278 | 59 |
| Certhiidae  (Treecreepers) | *Certhia americana* | Brown Creeper | 15142 | 61 |
| Cinclidae  (Dippers) | *Cinclus mexicanus* | American Dipper | 1364 | 27 |
| Corvidae  (Crows, Jays, and Magpies) | *Perisoreus canadensis* | Canada Jay | 634 | 55 |
| *Corvus corax* | Common Raven | 4672 | 54 |
| *Corvus brachyrhynchos* | American Crow | 1477 | 30 |
| Fringillidae  (Finches, Euphonias, and Allies) | *Pinicola enucleator* | Pine Grosbeak | 1139 | 61 |
| *Spinus pinus* | Pine Siskin | 6400 | 60 |
| *Loxia leucoptera* | White-winged Crossbill | 6125 | 60 |
| *Coccothraustes vespertinus* | Evening Grosbeak | 552 | 58 |
| *Haemorhous purpureus* | Purple Finch | 10420 | 62 |
| *Leucosticte tephrocotis* | Gray-crowned Rosy-Finch | 1210 | 51 |
| *Haemorhous mexicanus* | House Finch | 4431 | 59 |
| *Loxia curvirostra* | Red Crossbill | 165 | 45 |
| Hirundinidae  (Swallows) | *Tachycineta thalassina* | Violet-green Swallow | 485 | 39 |
| *Tachycineta bicolor* | Tree Swallow | 1094 | 27 |
| Icteridae  (Troupials and Allies) | *Agelaius phoeniceus* | Red-winged Blackbird | 204 | 23 |
| *Molothrus ater* | Brown-headed Cowbird | 87 | 28 |
| *Euphagus carolinus* | Rusty Blackbird | 1395 | 36 |
| Motacillidae  (Wagtails and Pipits) | *Anthus rubescens* | American Pipit | 4368 | 58 |
| Paridae  (Tits, Chickadees, and Titmice) | *Poecile hudsonicus* | Boreal Chickadee | 4430 | 57 |
| *Poecile gambeli* | Mountain Chickadee | 12994 | 61 |
| *Poecile atricapillus* | Black-capped Chickadee | 1615 | 54 |
| Parulidae  (New World Warblers) | *Setophaga magnolia* | Magnolia Warbler | 74084 | 62 |
| *Setophaga coronata* | Yellow-rumped Warbler | 111092 | 62 |
| *Setophaga townsendi* | Townsend's Warbler | 7361 | 61 |
| *Setophaga striata* | Blackpoll Warbler | 4619 | 61 |
| *Geothlypis tolmiei* | MacGillivray's Warbler | 30304 | 61 |
| *Leiothlypis peregrina* | Tennessee Warbler | 36766 | 58 |
| *Setophaga ruticilla* | American Redstart | 74872 | 59 |
| *Seiurus aurocapilla* | Ovenbird | 5286 | 59 |
| *Cardellina pusilla* | Wilson's Warbler | 4738 | 60 |
| *Leiothlypis celata* | Orange-crowned Warbler | 11951 | 60 |
| *Parkesia noveboracensis* | Northern Waterthrush | 146613 | 60 |
| *Setophaga petechia* | Yellow Warbler | 3407 | 42 |
| *Geothlypis trichas* | Common Yellowthroat | 4153 | 46 |
| Passerellidae  (New World Sparrows) | *Spizella passerina* | Chipping Sparrow | 5162 | 54 |
| *Zonotrichia albicollis* | White-throated Sparrow | 42421 | 60 |
| *Zonotrichia leucophrys* | White-crowned Sparrow | 69534 | 62 |
| *Junco hyemalis* | Dark-eyed Junco | 48344 | 62 |
| *Passerella iliaca* | Fox Sparrow | 2861 | 60 |
| *Melospiza lincolnii* | Lincoln's Sparrow | 19790 | 59 |
| *Melospiza melodia* | Song Sparrow | 3390 | 23 |
| *Spizella pallida* | Clay-colored Sparrow | 228 | 39 |
| *Melospiza georgiana* | Swamp Sparrow | 1846 | 56 |
| *Zonotrichia atricapilla* | Golden-crowned Sparrow | 140 | 35 |
| *Pooecetes gramineus* | Vesper Sparrow | 456 | 32 |
| Regulidae  (Kinglets) | *Regulus satrapa* | Golden-crowned Kinglet | 84683 | 61 |
| *Corthylio calendula* | Ruby-crowned Kinglet | 13918 | 59 |
| Sittidae  (Nuthatches) | *Sitta canadensis* | Red-breasted Nuthatch | 23207 | 61 |
| Troglodytidae  (Wrens) | *Troglodytes pacificus* | Pacific Wren | 60989 | 59 |
| Turdidae  (Thrushes and Allies) | *Catharus ustulatus* | Swainson's Thrush | 327431 | 62 |
| *Ixoreus naevius* | Varied Thrush | 32529 | 61 |
| *Catharus guttatus* | Hermit Thrush | 52026 | 61 |
| *Turdus migratorius* | American Robin | 37737 | 62 |
| *Myadestes townsendi* | Townsend's Solitaire | 787 | 55 |
| *Sialia currucoides* | Mountain Bluebird | 1238 | 54 |
| Tyrannidae  (Tyrant Flycatchers) | *Empidonax difficilis* | Western Flycatcher | 12474 | 62 |
| *Empidonax hammondii* | Hammond's Flycatcher | 141949 | 62 |
| *Empidonax minimus* | Least Flycatcher | 44654 | 58 |
| *Empidonax oberholseri* | Dusky Flycatcher | 9356 | 58 |
| *Contopus cooperi* | Olive-sided Flycatcher | 17061 | 61 |
| *Empidonax flaviventris* | Yellow-bellied Flycatcher | 5815 | 61 |
| *Empidonax alnorum* | Alder Flycatcher | 21412 | 49 |
| *Tyrannus tyrannus* | Eastern Kingbird | 48 | 26 |
| *Contopus sordidulus* | Western Wood-Pewee | 10992 | 50 |
| Vireonidae  (Vireos, Shrike-Babblers, and Erpornis) | *Vireo gilvus* | Warbling Vireo | 87002 | 62 |
| *Vireo cassinii* | Cassin's Vireo | 6188 | 55 |
| *Vireo olivaceus* | Red-eyed Vireo | 600 | 35 |
| Ardeidae  (Herons, Egrets, and Bitterns) | *Botaurus lentiginosus* | American Bittern | 359 | 34 |
| Picidae  (Woodpeckers) | *Sphyrapicus varius* | Yellow-bellied Sapsucker | 5261 | 57 |
| *Sphyrapicus nuchalis* | Red-naped Sapsucker | 5182 | 57 |
| *Picoides arcticus* | Black-backed Woodpecker | 2928 | 60 |
| *Picoides dorsalis* | American Three-toed Woodpecker | 6417 | 62 |
| *Dryobates villosus* | Hairy Woodpecker | 1589 | 54 |
| *Dryocopus pileatus* | Pileated Woodpecker | 1910 | 56 |
| *Dryobates pubescens* | Downy Woodpecker | 331 | 49 |
| *Colaptes auratus* | Northern Flicker | 950 | 43 |
| Podicipedidae  (Grebes) | *Podiceps grisegena* | Red-necked Grebe | 26 | 8 |
| Strigidae  (Owls) | *Strix varia* | Barred Owl | 498 | 43 |
| *Bubo virginianus* | Great Horned Owl | 4902 | 57 |
| *Asio otus* | Long-eared Owl | 294 | 40 |
| *Strix nebulosa* | Great Gray Owl | 419 | 36 |
| *Aegolius acadicus* | Northern Saw-whet Owl | 2223 | 54 |
| *Glaucidium gnoma* | Northern Pygmy-Owl | 876 | 48 |
| *Aegolius funereus* | Boreal Owl | 5826 | 44 |

**Table B**. Estimated asymptotic richness for each site. "ARU days" refers to the number of days the ARU operated at a given site. "Species ARU days" indicates the accumulated number of days a species was detected, summed across all species detected at a site. LCL and UCL are the lower and upper boundary of the estimated asymptotic richness at 95% confidence level.

| Site | ARU days | Species ARU days | Observed richness | Asymptotic richness | No. of species added | LCL | UCL |
| --- | --- | --- | --- | --- | --- | --- | --- |
| N\_15 | 32 | 510 | 34 | 34.24 | + 0.24 | 34.01 | 38.62 |
| N\_25 | 50 | 463 | 31 | 35.41 | + 4.41 | 31.48 | 71.14 |
| N\_11 | 50 | 831 | 34 | 34.16 | + 0.16 | 34.01 | 37.49 |
| 14\_29 | 52 | 606 | 31 | 34.92 | + 3.92 | 31.55 | 59.22 |
| 14\_05 | 59 | 628 | 33 | 38.90 | + 5.9 | 34.05 | 66.10 |
| N\_19 | 65 | 641 | 31 | 48.72 | + 17.72 | 33.49 | 157.04 |
| 14\_02 | 66 | 115 | 19 | 19.49 | + 0.49 | 19.03 | 27.34 |
| N\_23 | 69 | 571 | 31 | 33.22 | + 2.22 | 31.26 | 49.80 |
| 14\_17 | 70 | 753 | 34 | 39.91 | + 5.91 | 35.05 | 67.18 |
| 14\_42 | 71 | 775 | 29 | 29.66 | + 0.66 | 29.06 | 36.72 |
| 14\_23 | 76 | 863 | 37 | 37.99 | + 0.99 | 37.09 | 47.94 |
| 14\_16 | 81 | 1100 | 34 | 34.00 | + 0 | 34.00 | 35.61 |
| N\_05 | 82 | 862 | 31 | 31.16 | + 0.16 | 31.01 | 34.50 |
| 14\_03 | 82 | 990 | 37 | 37.40 | + 0.4 | 37.03 | 42.26 |
| N\_08 | 83 | 453 | 32 | 36.45 | + 4.45 | 32.49 | 72.45 |
| N\_10 | 83 | 1034 | 35 | 41.17 | + 6.17 | 35.96 | 74.68 |
| 14\_35 | 85 | 570 | 31 | 31.10 | + 0.1 | 31.00 | 33.52 |
| 14\_41 | 85 | 959 | 32 | 34.63 | + 2.63 | 32.37 | 50.67 |
| N\_22 | 87 | 926 | 35 | 36.48 | + 1.48 | 35.17 | 47.76 |
| 14\_08 | 89 | 746 | 34 | 35.98 | + 1.98 | 34.27 | 48.23 |
| 14\_30 | 91 | 453 | 31 | 43.12 | + 12.12 | 33.18 | 98.45 |
| 14\_34 | 91 | 1134 | 34 | 34.49 | + 0.49 | 34.04 | 40.19 |
| 14\_21 | 92 | 870 | 36 | 37.48 | + 1.48 | 36.17 | 48.77 |
| N\_16 | 94 | 1012 | 33 | 37.45 | + 4.45 | 33.49 | 73.51 |
| 14\_15 | 98 | 641 | 31 | 35.12 | + 4.12 | 31.67 | 56.54 |
| 14\_19 | 101 | 1145 | 38 | 38.89 | + 0.89 | 38.10 | 46.30 |
| 14\_04 | 102 | 492 | 28 | 48.79 | + 20.79 | 33.02 | 114.06 |
| 14\_18 | 102 | 807 | 30 | 33.96 | + 3.96 | 30.55 | 58.46 |
| 14\_10 | 103 | 865 | 29 | 33.46 | + 4.46 | 29.49 | 69.54 |
| 14\_11 | 104 | 1077 | 34 | 42.91 | + 8.91 | 35.51 | 86.79 |
| 14\_31 | 105 | 1247 | 35 | 35.66 | + 0.66 | 35.06 | 42.75 |
| N\_14 | 105 | 1515 | 35 | 35.99 | + 0.99 | 35.07 | 49.30 |
| N\_21 | 108 | 1068 | 33 | 35.23 | + 2.23 | 33.26 | 51.88 |
| 14\_20 | 109 | 1015 | 35 | 38.96 | + 3.96 | 35.55 | 63.48 |
| 14\_24 | 109 | 1166 | 37 | 41.13 | + 4.13 | 37.67 | 62.56 |
| N\_18 | 111 | 533 | 29 | 31.64 | + 2.64 | 29.37 | 47.72 |
| N\_09 | 111 | 1421 | 36 | 41.95 | + 5.95 | 36.92 | 74.61 |
| 14\_28 | 114 | 985 | 34 | 37.10 | + 3.1 | 34.50 | 53.15 |
| 14\_06 | 115 | 748 | 27 | 31.46 | + 4.46 | 27.49 | 67.58 |
| N\_04 | 115 | 1654 | 35 | 36.98 | + 1.98 | 35.18 | 56.95 |
| N\_12 | 118 | 1645 | 35 | 39.46 | + 4.46 | 35.49 | 75.59 |
| 14\_01 | 121 | 915 | 31 | 38.93 | + 7.93 | 31.98 | 95.30 |
| N\_06 | 121 | 1665 | 36 | 45.92 | + 9.92 | 37.85 | 89.05 |
| 14\_33 | 124 | 1115 | 34 | 34.99 | + 0.99 | 34.09 | 44.99 |
| N\_24 | 137 | 1642 | 37 | 37.25 | + 0.25 | 37.01 | 41.71 |
| N\_13 | 139 | 834 | 35 | 36.49 | + 1.49 | 35.17 | 47.81 |
| 14\_07 | 139 | 1404 | 36 | 36.12 | + 0.12 | 36.01 | 38.91 |
| N\_17 | 139 | 1597 | 34 | 34.50 | + 0.5 | 34.03 | 42.39 |
| 14\_37 | 143 | 1300 | 36 | 37.49 | + 1.49 | 36.17 | 48.81 |
| 14\_40 | 143 | 1455 | 35 | 35.08 | + 0.08 | 35.00 | 37.26 |
| 14\_39 | 145 | 888 | 32 | 38.21 | + 6.21 | 32.97 | 71.87 |
| 14\_38 | 147 | 1393 | 35 | 36.49 | + 1.49 | 35.17 | 47.81 |
| N\_07 | 155 | 1180 | 33 | 34.49 | + 1.49 | 33.17 | 45.82 |
| 14\_25 | 155 | 1841 | 37 | 37.99 | + 0.99 | 37.07 | 51.35 |
| N\_01 | 155 | 1893 | 35 | 35.50 | + 0.5 | 35.03 | 43.40 |
| 14\_09 | 164 | 1990 | 37 | 37.99 | + 0.99 | 37.09 | 48.01 |
| 14\_14 | 167 | 1668 | 33 | 37.47 | + 4.47 | 33.49 | 73.68 |
| 14\_13 | 169 | 1877 | 35 | 42.95 | + 7.95 | 35.98 | 99.45 |
| 14\_26 | 182 | 1934 | 36 | 39.98 | + 3.98 | 36.55 | 64.58 |