Project Title: Montane Invertebrate Monitoring Project

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RESEARCH SUMMARY

In June and early July of 2021 and 2022, we sampled invertebrate and avian communities at a total of 42 high-elevation locations in Vermont (n = 15 on Mt. Mansfield; n = 16 on Bolton Mountain) and New Hampshire (n = 11 across the neighboring summits of Mount Martha and Mount Cherry); our goal was to elucidate the relationship between montane bird and invertebrate communities. Permitting delays prevented us from conducting full sampling during June of 2021, and instead, we treated early July of 2021 as a pilot season with permission from Jim Duncan. During the first few weeks of July 2021, we captured 312 specimens from 15 taxonomic orders in pitfall traps at eight locations on Mount Mansfield. We used that pilot season (which occurred outside of our proposed sampling period of June) to refine our techniques moving forward.

In 2022, our work benefited from the inclusion of two interns, an ECO Americorps member, and five community scientists. Our invertebrate sampling took place at 42 high high-elevation locations that were also a part of our long-term Mountain Birdwatch monitoring program where community scientists conduct point counts for montane birds each June. Via pitfall and aerial insect traps, we collected 5,458 invertebrates from at least 14 taxonomic orders in 2022, hiked them out, and painstakingly identified them under a microscope back in the lab. Invertebrate communities were relatively simple across the sampling locations, and some taxonomic groups were composed of few families or genera. For example, carabid and rove beetles compromised the vast majority of beetle specimens, *Arion* species likely represented all of the slugs we captured, and *Ceuthophius* (camel cricket) species likely represented most (or all) of the Orthoptera specimens.

Of those +5,000 invertebrates, almost 60% were flies and 18% were beetles. We were surprised at how similar the communities were across the 42 sites, but some subtle differences were suggestive in the principal components results between the three mountains. We now have the clearest image yet of the structure of the montane invertebrate community on these mountains. We related the invertebrate community composition to the occupancy probability of six relatively common bird species within the Mountain Birdwatch monitoring program of the spruce-fir forest zone. Contrary to our expectations, overall biomass of invertebrates was a poor predictor of occupancy for all six bird species, suggesting that overall food availability is less important than the abundance of individual taxonomic groups or community composition.

Instead, each bird species' abundance was associated with one or two specific groups of invertebrates or one principal component (representing combinations of invertebrate groups). For example, Swainson's Thrush [*Catharus ustulatus*] occupancy was lower at locations with abundant biomass of Hymenoptera (ants, bees, wasps, and sawflies), and also negatively related to the second principal component (which has strong negative correlations with millipedes, mites, slugs, and spiders). The White-throated Sparrow was the only species in our occupancy analysis where the null model (an intercept only model without any covariates describing the invertebrate community) was the parsimonious model—suggesting that none of the components that we measured or estimated were strongly related to their occupancy. It could be that White-throated Sparrow occupancy is driven more by elevation and/or vegetation characteristics then it invertebrate biomass. Although not our primary goal, we also were among the first folks to document more than a dozen invertebrate species in Vermont and New Hampshire, including *Pterostichus adstrictus* and *Metanomus insidiosus*.

The project continues, and we recently finished our 2023 field season in early July, revisiting those 42 high-elevation locations again. Those invertebrate samples have yet to be fully processed, and they are not included in this report. We are looking forward to the months it will take to sort and identify the contents of our 2023 field season efforts. A larger sample size of both avian (especially) and invertebrate data will enable a more complex analysis of the full dataset. With that expanded dataset we will continue to deepen our understanding of the interactions between birds and invertebrates within the spruce-fir ecosystem of Vermont and New Hampshire moving forward.

BACKGROUND

Invertebrates perform essential, irreplaceable ecological functions (e.g., pollination and seed dispersal) that increase the stability of ecosystems and provide invaluable ecosystem services (e.g., controlling agricultural pests, improving soil biochemical processes, and waste decomposition). Knowledge of the invertebrate communities occupying forested sites can lead to an enhanced understanding of defoliation and herbivory risk (e.g., Fleming 1996), future stand composition (Pureswaran et al. 2015), forest health (Coulson and Stephen 2006), and avian population dynamics (Drever et al. 2018, Cox et al. 2019).

Invertebrate populations throughout the globe, however, are likely experiencing precipitous declines in abundance and biomass, and terrestrial insect populations may be declining by as much as 9% per decade (Klink et al. 2020). The drivers of these apparent declines are not fully understood, but habitat destruction, insecticides, industrial agriculture and climate change are strongly suspected as being important factors (Sánchez-Bayo and Wyckhuys 2019). Understanding the pattern of these changes across the landscape and between taxonomic groups has been further complicated by the relative paucity of long-term monitoring programs for invertebrate populations (McDermott 2021).

Mountain ecosystems are already responding to climate change, and are expected to warm further rapidly (Rangwala and Miller 2012, Stewart et al. 2020, Halsch et al. 2021). Montane invertebrate populations, in particular, appear to be especially vulnerable to climate change, but a substantial increase in baseline data and monitoring efforts are immediately needed to understand the scale and severity of stressors to invertebrate populations (Montgomery et al. 2020, Halsch et al. 2021). A substantial portion of the existing monitoring efforts for montane invertebrates are narrowly focused on a handful of economically-important forest pests (e.g., Spruce Budworm [*Choristoneura* species complex] and balsam woolly adelgid [*Adelges piceae*]; (Vermont Department of Forests, Parks & Recreation 2018).

Here, our primary goal is to describe changes in abundance and biomass of invertebrates as climate change advances; this type of monitoring has the potential to be the most useful in understanding the drivers and extent of invertebrate declines (Hallmann et al. 2017, Wepprich et al. 2019). We will also document current patterns of invertebrate diversity, abundance, and dominance in the montane spruce-fir zone of the Northeast. These data would have tremendous standalone value; however, we have chosen monitoring locations in conjunction with another long-term monitoring project, Mountain Birdwatch. To fully comprehend and predict the future consequences of climate change on forest communities, we must document the population dynamics and phenology of interacting species, including birds, invertebrates, and plants (Miller-Rushing et al. 2010, Dunn and Møller 2014, McLean et al. 2016, Halsch et al. 2021).

Mountain Birdwatch

Since 2000, the Vermont Center for Ecostudies and our team of community scientists have been monitoring bird populations throughout the high-elevation spruce-fir forests of New

York and Northern New England. Our community science program, Mountain Birdwatch, provides the only region-wide source of population information for 10 high-elevation breeding bird species, including Bicknell's Thrush. Every June, more than 100 community scientists conduct repeated point counts at ~750 sampling stations located along hiking trails between 600 and 1300 m elevation from the Catskills to Katahdin.

Mountain Birdwatch has already provided invaluable insight into the population dynamics, regional abundance, and trends of montane bird species. Recently, using Mountain Birdwatch data, we published a paper estimating that the WMNF harbors nearly one-third of the entire U.S. population of Bicknell's Thrush—one of the most range-restricted bird species in North America. With these data, we also created fine-scale abundance maps predicting the population size of all Mountain Birdwatch species across all USFS lands in New Hampshire. Mountain Birdwatch data are curated by FEMC, openly available online, and permanently archived each year at KNB Data Repository (https://knb.ecoinformatics.org/).

2022 Sampling locations

In June and early July of 2022 (June 6th through July 4th), we successfully conducted invertebrate sampling at 42 locations. In Vermont, we expanded our 2021 efforts to an additional 7 locations on Mt. Mansfield (n = 15 sampling locations on Mt. Mansfield) and to 16 new locations on Bolton Mountain. The administrative control of three of these sampling locations occurred within the University of Vermont (UVM) Natural Area on the Mt. Mansfield ridgeline, with the remainder occurring solely within Mansfield State Forest. We did not deploy sampling equipment at the three Mountain Birdwatch sampling locations within the alpine area in the UVM Natural Area on the Mt. Mansfield ridgeline, because we could not hang our aerial traps, were unable to hide our equipment from visitors, and were greatly concerned about digging and disturbing those fragile soils. We also expanded our sampling efforts to New Hampshire in 2022, where we sampled at 11 locations across the connected summits of Mounts Cherry and Martha within the White Mountain National Forest.

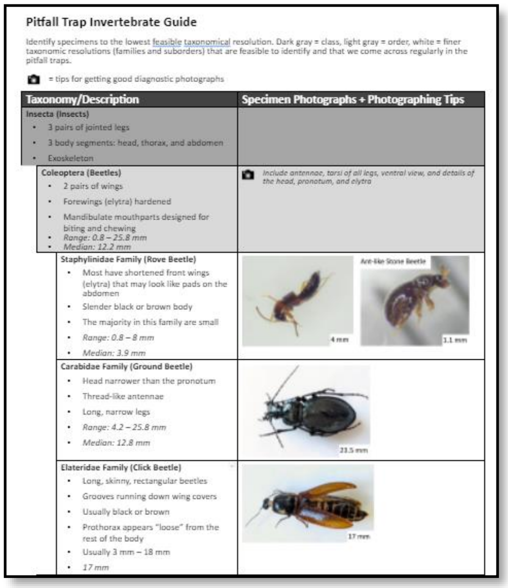
METHODS

Invertebrate sampling methods 2021

We captured and identified 312 specimens in pitfall traps from 15 invertebrate orders from eight locations on Mount Mansfield in July of 2021; these eight locations were all Mountain Birdwatch sampling locations as well. At each sampling location, we deployed four pitfall traps in the corners of a 5x5 m grid located ~25 m off of the established hiking trail. Each pitfall trap was covered with a lid held slightly above the trap using landscaping staples to keep bird predation of samples to a minimum and to prevent rainwater from filling the pitfall traps. Pitfall traps were partially-filled with propylene glycol as a killing agent and preservative. Propylene glycol (a common livestock food additive) is a viscous liquid that was chosen because it is not harmful if consumed by wild animals or the dogs of hikers (for example).

The duration that pitfall traps were deployed varied from one to several days in 2001 as we worked around community scientists' personal and professional schedules. We identified pitfall specimens using a dissecting scope back at our offices in White River Junction. Collectively, spiders (Araneae) and beetles (Coleoptera) comprised 50% of our samples, with fewer numbers of slugs (genus *Arion*, Stylommatophora, 12%), camel crickets (Orthoptera, 11%), flies (Diptera, 10%), and springtails (Collembola, 7%). We came to understand that counting, sorting and weighing springtails in the lab under the microscope was very difficult due to their small sizes (often ≤1 mm) and fragile bodies. We subsequently decided to not count, sort and weight springtails in 2022.

To facilitate future identification work, we created a photograph guide to the groups of invertebrates that we captured in our pitfall traps (Figure 1). We designed this guide to grow and improve as we encountered more invertebrate specimens in 2022 and beyond. We expect this guide to be useful for both researchers and community scientists, as dead specimens (viewed under a dissecting scope) often look quite different from their living counterparts.



Pitfall Trap Invertebrate Guide

Identify specimens to the lowest feasible taxonomical resolution. Dark gray = class, light gray = order, white = finer taxonomic resolutions (families and suborders) that are feasible to identify and that we come across regularly in the pitfall traps.

= tips for getting good diagnostic photographs

Taxonomy/Description	Specimen Photographs + Photographing Tips
Insecta (Insects) • 3 pairs of jointed legs • 3 body segments: head, thorax, and abdomen • Exoskeleton	
Coleoptera (Beetles) • 2 pairs of wings • Forewings (elytra) hardened • Mandibulate mouthparts designed for biting and chewing • *Range: 0.8 – 25.8 mm* • *Median: 12.2 mm*	*Include antennae, tarsi of all legs, ventral view, and details of the head, pronotum, and elytra*
Staphylinidae Family (Rove Beetle) • Most have shortened front wings (elytra) that may look like pads on the abdomen • Slender black or brown body • The majority in this family are small • *Range: 0.8 – 8 mm* • *Median: 3.9 mm*	4 mm Ant-like Stone Beetle 1.1 mm
Carabidae Family (Ground Beetle) • Head narrower than the pronotum • Thread-like antennae • Long, narrow legs • *Range: 4.2 – 25.8 mm* • *Median: 12.8 mm*	23.5 mm
Elateridae Family (Click Beetle) • Long, skinny, rectangular beetles • Grooves running down wing covers • Usually black or brown • Prothorax appears "loose" from the rest of the body • Usually 3 mm – 18 mm • *17 mm*	17 mm

Figure 1. First page of our invertebrate identification guide that we developed to facilitate the microscope identification of invertebrates.

In 2021, we also deployed a yellow sticky paper trap suspended from a tree at three test locations, but we quickly realized the need for a better sampling approach for the aerial insect community at our sampling locations. The yellow sticky traps were incredibly challenging to work with in a remote field setting. Once the plastic backing paper was removed, the traps glued themselves to anything that they came in contact with (e.g., researchers, tree branches and trunks). We secured the yellow sticky traps to the ground below and to a branch above with natural jute twine, as they were susceptible to being blown about by even slight winds. The traps, however, proved effective at attracting flighted insects—so much so that it made for difficult identification of insects. Insects were haphazardly stuck to the traps, often missing key body segments (either due to bird predation or parts of the insects breaking off due to the insect struggling in the glue), and specimens were often heavily layered atop of each other—making identification extremely difficult. We tried several approaches to hiking the yellow sticky traps out of the field (e.g., spraying them with non-stick cooking spray and reapplying the original plastic sheeting over the glue), but we quickly realized that the sticky trap approach was not suitable for our remote field conditions. By the time we got the sticky traps back to our lab for insect identification, the insects were badly mangled, making it difficult to identify insects even to taxonomic order.

We also developed a modified window trap built out of (largely) recycled materials (Figure 2). We chose recycled materials to keep costs low, and because of shipping and supply difficulties during the COVID-19 pandemic. However, our initial design proved to be difficult to hike into the field with, required greater reinforcement and greater assembly time than desired, and was prone to being dashed about in the wind and dumping the trap contents. We quickly realized that our sampling design was insufficient for our research needs.

Figure 2. Our initial attempt at developing a cost-effective modified window trap in 2021 for sampling aerial insects. Our design was prone to blowing about in the wind, and we attached weights (e.g., a filled water bottle) to increase the stability of our trap in the wind. ©Pete Kerby-Miller.

Invertebrate sampling methods 2022

We employed the same sampling methods at all 42 high-elevation locations in Vermont (n = 15 on Mt. Mansfield; n = 16 on Bolton Mountain) and New Hampshire (n = 11 across the neighboring summits of Mount Martha and Mount Cherry) during June in 2022; these locations are also a part of the Mountain Birdwatch community science program (see section below). At each Mountain Birdwatch location, we randomly chose a compass heading and headed in that direction until we were 25 m from the trail. We slightly adjusted this distance at some locations due to safety concerns with the topography or the visibility of our sampling equipment from the trail. In compliance with our research permits we 1) deployed our equipment out-of-site from the trail, 2) took steps to minimize evidence of our off-trail activities (as to not encourage other hikers from leaving the trail), 3) protected vegetation from being trampled, and 4) posted our contact information (and brief research summary) in a transparent, waterproof bag hung with our sampling equipment. No one contacted us in response to finding our sampling equipment, and there were no incidences of tampering with our survey stations. We deployed sampling equipment for a 7-day period at each site. Learning from our 2021 experience, we decided it was impractical to try and coordinate with community scientists for sampling equipment deployment during the week (when we were available, but the community scientists were not). Instead, sampling equipment was deployed by Jason Hill, Abbie Castriotta (VCE's 2021-2022 ECO Americorps member), Madison Sayers (VCE's 2022 Alexander Dickey Conservation Intern), and Latrice Hodges (VCE's 2022 Future Ecologist, an intern program reserved for Black, Indigenous, and People of Color applicants).

Pitfall traps: At each sampling site, we deployed four pitfall traps. One pitfall trap was placed at each corner of a ~5x~5 m grid centered around the modified window trap. To further reduce the possibility of small mammal bycatch (of which there was none), we changed the cups that were used as pitfall traps during our pilot season in 2021. The Solo cups that we used for pitfall traps in our pilot season of 2021, held 16 oz of liquid and were 4.625" tall with a 3.5" diameter opening. In 2022, we used 9 oz plastic cocktail cups that were only 2.75" tall but with the same diameter. The consistent cup diameter between years will allow for direct comparisons of sampling contents across years while further reducing the possibility of mammal bycatch.

We buried each pitfall cup flush with the ground, and we neatly piled the soil nearby so that we could fill in the hole after sampling was complete. Each pitfall trap was covered with a red plastic plate to protect the trap from filling up with rainwater. The plates were suspended ~1" above the surface of the pitfall trap using landscaping stakes that were inserted through tiny holes that we drilled around the perimeter of the plastic plates (Figure 3, 4 and 5). These red plates may have also served to visually attract insects, as we often saw flies and other insects landing atop the red plates immediately after deployment. The red color also helped us to relocate our pitfall traps in the forest understory.

Figure 3: Plastic plate cover suspended ~1" off the ground by two landscaping staples (one of which is visible) to protect the underlying pitfall trap from filling up with rainwater and leaves. The ¼" holes along the edge of the plate are for rain drainage. ©Jason Hill.

Figure 4: Pitfall trap (transparent cup) with its cover removed for photography. ©Jason Hill.

Figure 5: the red plastic plate (i.e., pitfall cover) also serves to make the pitfall trap visible in dense vegetation. ©Jason Hill.

Modified window traps: In 2022, we redesigned our improved and modified window trap to be smaller and easier to hike with in the forest (Figure 6). We chose recycled materials to keep costs low. The modified window traps allowed insects to fly into the plastic middle of the trap, and fall downward or fly upward into separate containers containing a 50-50 mix of water and propylene glycol. Propylene glycol is safe for vertebrate animals to consume and the solution serves as a preservative. Window traps capture insects by intercepting them in flight. Out of necessity, our window traps were several times smaller than the window traps used in many studies. Prior to the start of the 2022 field season, we experimented with inserting a yellow piece of paper into the middle of the window trap to serve as a visual attractant for some types of flying invertebrates. The yellow paper is sold as an insect attractant by a biological control company. The window traps without the yellow paper captured many fewer specimens in our tests, than did the traps with yellow paper. Therefore, we used the yellow attractant paper in all of our window traps during the regular field season of 2022 (and 2023). The insects could not reach the yellow sticky paper, which was left in its original plastic sheeting and sandwiched in the middle of the window trap.

Figure 6: Our modified window trap used to montane capture flying insects in 2022. ©Jason Hill.

Mustard water extraction: In late spring of 2022, prior to the start of our field season, we field-tested a mustard water sampling technique. We poured a litter of water, mixed with 1 tablespoon of mustard powder, onto a 25x25 cm section of ground beneath the modified window trap. Although we have successfully used this technique in other ecosystems, this sampling strategy proved ineffective for the spruce-fir environment. First, water was not readily available near our sampling stations, so we had to carry in 6 L of water per Mountain Birdwatch route. It was difficult to accommodate this much water in our backpacks alongside our personal water and other field equipment on our long hikes. Second, we did not capture any earthworms via this sampling technique in our field tests. We did capture a few ground beetles, but the pitfall traps are already highly effective at capturing ground beetles. Thus, we considered the mustard water extraction technique to be impractical, ineffective for sampling earthworms in the spruce-fir zone, and redundant (but inferior) with our pitfall traps for capturing ground beetles. Therefore, we did not use the mustard water extraction technique to capture invertebrates during our regular field season in 2022.

Hand searching: We also experimented with hand searching the mostly coniferous vegetation using the Caterpillar Count (Hurlbert et al. 2019) community science protocol. The Caterpillar Count protocol involves searching branches with living needles. Most of our sites, however, had few living branches within 2 m of the ground (see Figures 6 and 7), and we decided not to include hand searching in our 2002 field season; it was incredibly time-consuming (resulting in a 5X time increase at each station), but yielded few insects.

Figure 7. An invertebrate sampling plot on Mt. Mansfield showing a lack of live branches within 2 m of the ground, which was common at our sites.

Invertebrate specimen processing, 2022

After pitfall and aerial traps had been deployed for seven days, we returned to remove the traps and captured contents. In the field, invertebrate samples were transferred into watertight containers, and transported back to our office in White River Junction, VT. Under a dissecting scope, specimens were manually separated into taxonomic groups (typically taxonomic *order*). Sorting of specimens was laborious, but necessary for our project. Specimens from the same taxonomic group from a sampling station were then placed into a 5 cm^2 aluminum foil dish, dried in a biological oven for 30 hours at 60˚C. Dried specimens were then weighed on a digital balance to the nearest 0.0001 g. Weighing specimens in bulk had the benefit of reducing measurement error on the scale, because many of the specimens were (individually) near at the minimum measuring capability of the scale. Some groups of invertebrates (e.g., millipedes) could not be easily identified to taxonomic order every time, as they consist of multiple visually-similar taxonomic orders. The invertebrate groups that we detected in our 2022 samples are presented in Table 1.

Table 1. Invertebrate groups detected at 42 montane invertebrate sampling stations in 2022. Not all specimens could be reliably identified to taxonomic order (e.g., Millipedes). Therefore, we summarized specimens under the taxonomic grouping shown below. Groups demarcated with an asterisk were not used in our avian occupancy analysis due to their scarcity across sites.

Invertebrate group, common name	Taxonomic grouping (taxonomic level)
Beetles	Coleoptera (order)
Camel crickets	Orthoptera (order)
Flies	Diptera (order)
Harvestmen	Opiliones (order)
Ants, bees, wasps and sawflies	Hymenoptera (order)
Moths and butterflies	Lepidoptera (order)
Millipedes	Diplopoda (class)
Mites	Acariformes (superorder)
Common land slugs	Stylommatophora (order)
Spiders	Araneae (order)
True bugs	Hemiptera (order)
Caddisflies*	Trichoptera (order)
Stoneflies*	Plecoptera (order)
Scorpionflies*	Mecoptera (order)

Mountain Birdwatch

All 42 invertebrate sampling locations were also long-term Mountain Birdwatch locations. Mountain Birdwatch is a community science project, launched in 2000, that aims to elucidate the population trends of the spruce-fir avian community. Each June, observers volunteer to survey one of ~130 high-elevation Mountain Birdwatch routes across New England and eastern New York. Each route consists of 3-6 trail-based sampling stations where observers conduct repeated point counts for 10 species of birds and red squirrel (*Tamiasciurus hudsonicus*): a common nest predator of those bird species. The full Mountain Birdwatch protocol can be found on the Mountain Birdwatch website. Five community scientists and Abbie Castriotta (our 2021-2022 ECO Americorps member) conducted Mountain Birdwatch surveys on the eight routes where we also deployed our invertebrate sampling equipment; two of the community scientists and Abbie Castriotta surveyed two routes each.

The 2022 Mountain Birdwatch data were entered into the FEMC-hosted online database, and then shared with other scientists through the KNB Data Repository. An analysis of the stand-alone Mountain Birdwatch data is available at our State of the Mountain Birds Report website.

2022 Statistical Analysis

Principal components analysis: In Program R (R Core Team 2023), we performed principal components analysis (PCA) using the biomass of the invertebrate orders (n = 11) that were detected at 3 or more of the 42 sampling stations. The other three taxonomic groupings were too rare in our samples to be included in a fair model comparison exercise; models representing the biomass of those rare groups would have little chance of being selected over a null model. We retained principal components for use in our occupancy model selection that contributed to explaining >50% of the variance of the dataset (Bro and K. Smilde 2014).

Species Richness and Diversity: For each sampling station, we used the number of specimens from each invertebrate group to calculate species richness (total number of invertebrate groups present) and the Shannon Diversity Index—a way to measure the diversity of species in a community. A value of 0 indicates the community is composed of a single species (or taxonomic group in our case), while increasingly positive values indicate an increasingly rich and diverse community. We also considered using the Shannon Evenness Index, but both indices were highly correlated with each other (correlation coefficient of 0.96).

Occupancy modeling

We conducted single-season occupancy modeling in R using the *occu* function from package unmarked (Fiske and Chandler 2011). We choose occupancy models over N-mixture models due to our relatively small dataset; N-mixture models built using small sample sizes are unreliable, prone to violating model assumptions, and can generate spurious results (Kéry and Royle 2015). Occupancy models estimate the contribution of individual covariates to the occupancy probability of a species at a site, while accounting for imperfect detection of point count observers (Hayes and Monfils 2015). Mountain Birdwatch community scientists performed four five-minute back-to-back point counts at each of the 42 sampling locations. We transformed the counts of each bird species during a five-minute point count into 1 (one or more individuals of that species detected) or 0 (no individuals of that species detected). Typically, we would use multiple detection (e.g., point count start time, survey date, and background noise rating) and occupancy covariates to account for variation in the dataset; due to our relatively small dataset, we did not include covariates for detection. Every model (except the null model) contained elevation (m) as an occupancy covariate, because elevation is a strong predictor of occupancy for montane birds (Hill 2022). More complex structures often resulted in false or incomplete convergence of our models, yielding unreliable results. A more complex detection and occupancy model structure (stemming from a larger dataset) could benefit our results.

Some of the 10 avian Mountain Birdwatch species are uncommon or entirely absent at our montane invertebrate sampling locations, so for the purposes of the occupancy analyses we built models for a total of six species: Blackpoll Warbler, Bicknell's Thrush, Swainson's Thrush (*Catharus ustulatus*), Winter Wren (*Troglodytes hiemalis*), White-throated Sparrow (*Zonotrichia albicollis*), and Yellow-bellied Flycatcher (*Empidonax flaviventris*)

Occupancy model selection: We compared occupancy models using AICc in three suites of models (for ease of comparison), removed any model with uninformative parameters, and considered any model within 2 AICc units of the parsimonious model to be informative (Burnham and Anderson 2002, Arnold 2010). In the first suite we compared 15 models: 11 models each representing the biomass of one of the 11 groups of invertebrates, a model with all invertebratebiomass combined ("All Biomass"), a model with elevation as the only occupancy covariate, and a null model (with just an intercept for the occupancy portion of the model). In the second suite, we compared a total of eight models: a model with site-specific invertebrate group richness values, a model with site-specific Shannon's diversity values, four models with one of each of the first four principal components, and the elevation-only and null models. In the third and final suite, we compared all 20 models from suites 1 and 2 to facilitate comparison.

Occupancy modeling hypotheses: The diets of montane bird species in the northeastern U.S. are not well documented, partially due to the difficulties of observing these species in the dense spruce-fir forest (Bayly et al. 2021). Of the six Mountain Birdwatch species included in our analysis, Bicknell's Thrush has the most well-documented diet, which is thought to largely consist of beetles and Hymenoptera (especially ants) (Wallace 1939, Strong et al. 2004, Townsend et al. 2015). The known diet of Bicknell's Thrush, and the other five bird species in our project, are described from very small sample sets—for some of these species, their diet is known only from foraging observations or stomach content analyses of less than half a dozen individual birds. Furthermore, those observational techniques may be biased towards detecting larger prey items and those with relatively robust exoskeletons (e.g., beetles and ants)—those prey items that break down more slowly in the stomach.

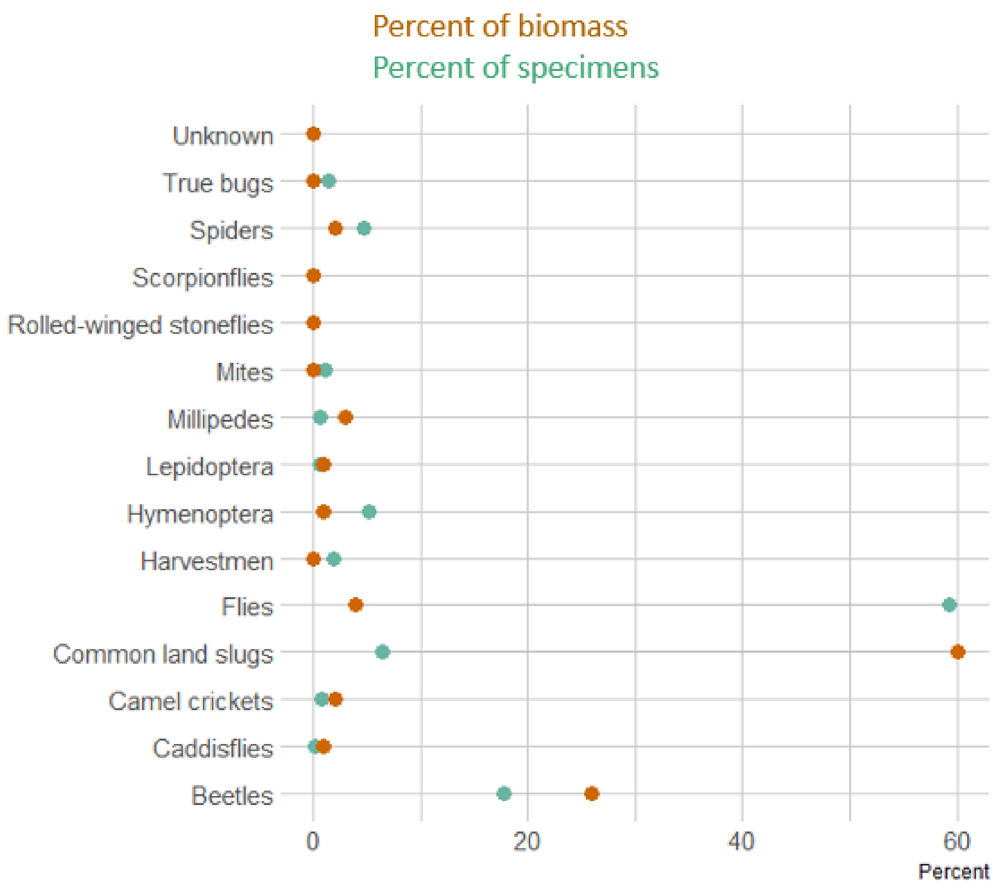
With these limitations in mind, we predicted that occupancy patterns of montane birds would be positively associated with overall biomass, species richness and Shannon's diversity index, because we speculated that those indices were overall indicators of food availability for birds. The diets of the montane birds in our project are not well known enough to warrant specific hypotheses for individual bird species* invertebrate groups. However, one might expect the occupancy of ground foraging species (e.g., thrushes) to be positively associated with ground-dwelling invertebrates like slugs and beetles, and for the occupancy of aerial foragers (e.g., Yellow-bellied Flycatcher) to positive associate with the biomass of aerial prey items such as flies.

2022 SAMPLING RESULTS & INTERPRETATION

Via pitfall and aerial insect traps, we collected just over 5,000 invertebrates representing at least 14 taxonomic groupings and 28.6 g of mass. Sorting through these specimens was labor-intensive and took more than a month of actual microscope time. Of those 5,458 captured invertebrates, almost 60% were flies and 18% were beetles (Supplementary Table). Less than 0.01% of specimens could not be identified to a taxonomic grouping—these were specimens that were partially eaten or damaged in the transport process. Hiking the specimens out of the field possibly degraded some samples. I can remember observing some well-preserved specimens in the fields (e.g., adult moths), but the sloshing inside the transport containers damaged the specimens and made higher resolution identification impractical. The percent of biomass and percent of specimen captures (Figure 8) were similar for most other groups except common land slugs (order

Stylommatophora), which were uncommon but relatively large and heavy specimens, and the numerically common (but lightweight) flies.

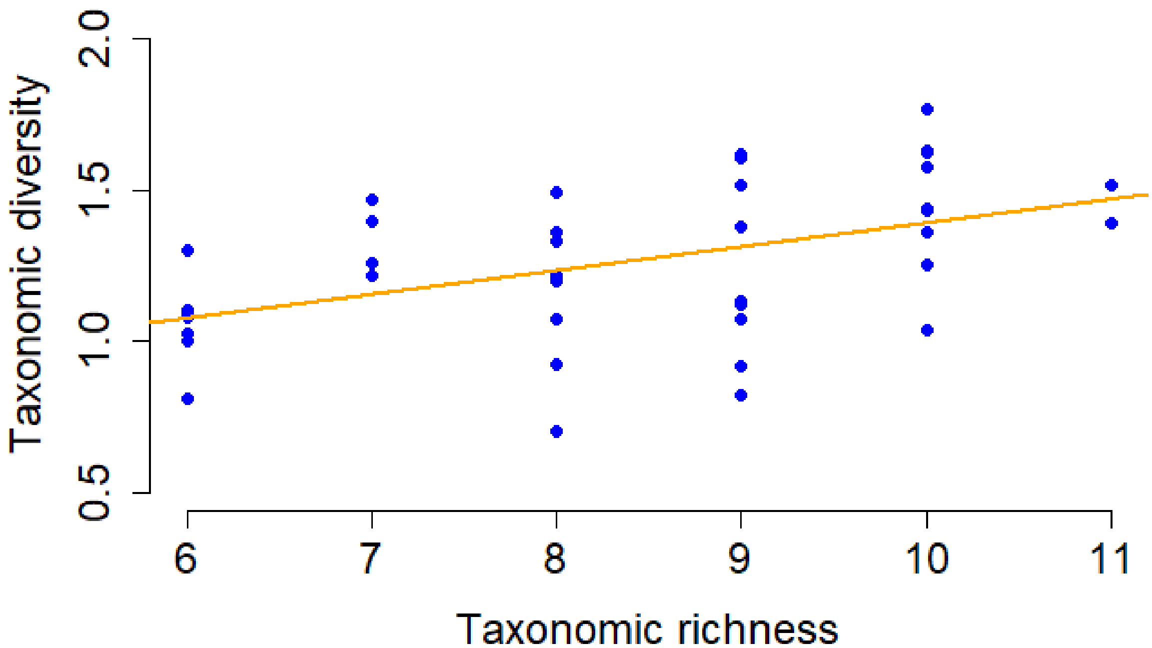
Figure 8: Percent of biomass (brown) and percent of specimen captures (green) for each taxonomic group represented within our 2022 samples of 5,458 invertebrates from 42 invertebrate sampling stations in Vermont and New Hampshire.



In general, taxonomic richness and evenness were positively (but not significantly) related to each other; not surprisingly, as taxonomic group richness increased at sampling stations so did the diversity index (Figure 9). Sampling station taxonomic group richness values ranged from 6 to 11 (median = 9), while Shannon diversity index values varied between 0.7

and 1.7 (mean = 1.2) out of a maximum possible value of 2.40 (2.4 = natural log of 11 [taxonomic groups]).

Figure 9: Taxonomic diversity vs. richness (blue dots) of the invertebrate community at 42 sampling locations; orange line shows the unsignificant (P = 0.08) positive relationship between diversity and richness from a simple linear regression.



Taxonomic richness values were consistent across elevations in our dataset (P = 0.65), but Shannon diversity index values significantly (but modestly) declined with elevation (P = 0.03, Figure 10). We had anticipated that invertebrate group richness would decline with elevation, but patterns between invertebrate richness and elevation vary with the range of the spatial scale examined (Gaston and Williams 1996), specific taxonomic group considered (Hodkinson 2005), plant community composition (Turner and Broadhead 1974, Lawton et al. 1987), and microclimate (Whittaker 1952). Similarly, diversity is also affected by climate (especially precipitation) (Hodkinson 2005), but diversity generally

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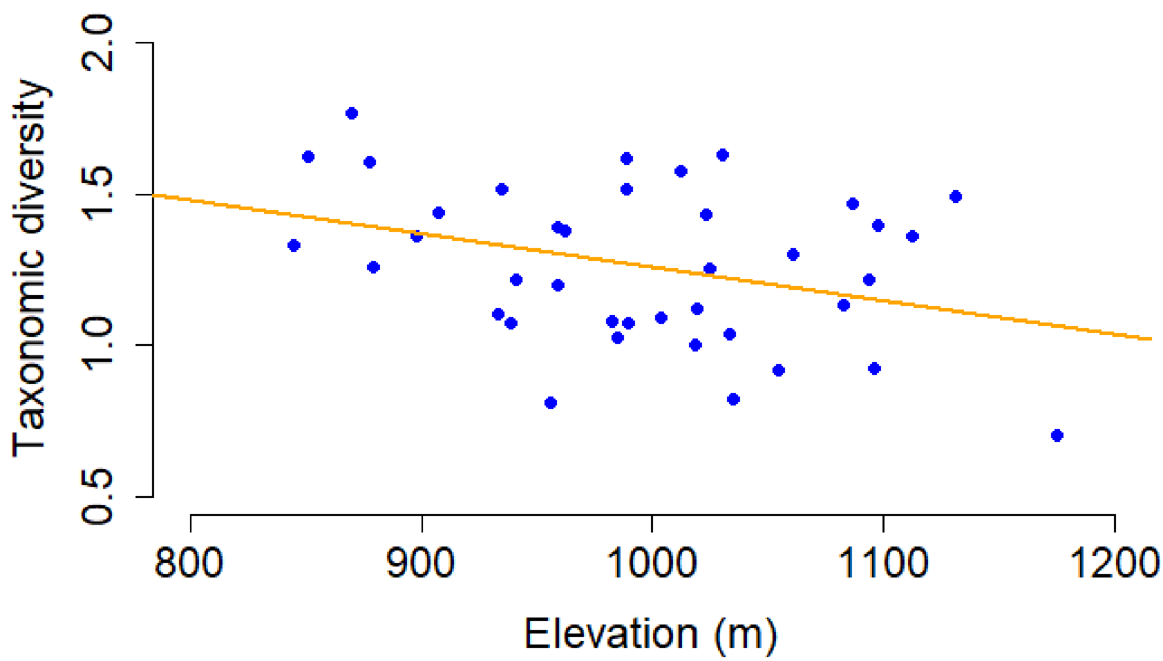
peaks at mid-elevation and declines above that in invertebrate communities (Janzen 2023 and references therein). We did not see an intermediate peak in diversity across the elevational gradient included in our study, but this might be a product of only sampling at higher elevations (i.e., above 800 m).

Figure 10. The significant (P = 0.03) relationship between Shannon diversity index values and elevation at our sampling stations (blue dots). Diversity declined by 0.001 units per meter (orange line).



In our dataset, the first four principal components explained 55.99% of the dataset variance (Figure 11), and we used these components (PC1, PC2, PC3 and PC4) in our occupancy model selection. The loadings for all 11 principal components are included in the Supplementary Table, but PC1 (for example), was strongly and positive associated with beetle and millipede biomass, and strongly and negatively associated with fly, slug, and true bug biomass. Principal components can be difficult to interpret, because the biomass of all 11 invertebrate groups are (in part) included in each of the 11 principal components (Figure 12). However, PCA portions the variance from each of these groups into unique configurations that likely better reflect the reality (and complexity) of the invertebrate community at our study sites compared to a single covariate with just the biomass of a single taxonomic group.

Figure 11: Scree plot of the variance explained by the principal components of the invertebrate community at 42 sampling locations in 2022. Eleven taxonomic groups were used in the PCA, and the first four were retained for use in the occupancy models. The orange line shows the cumulative variance explained with the inclusion of each additional principal component.

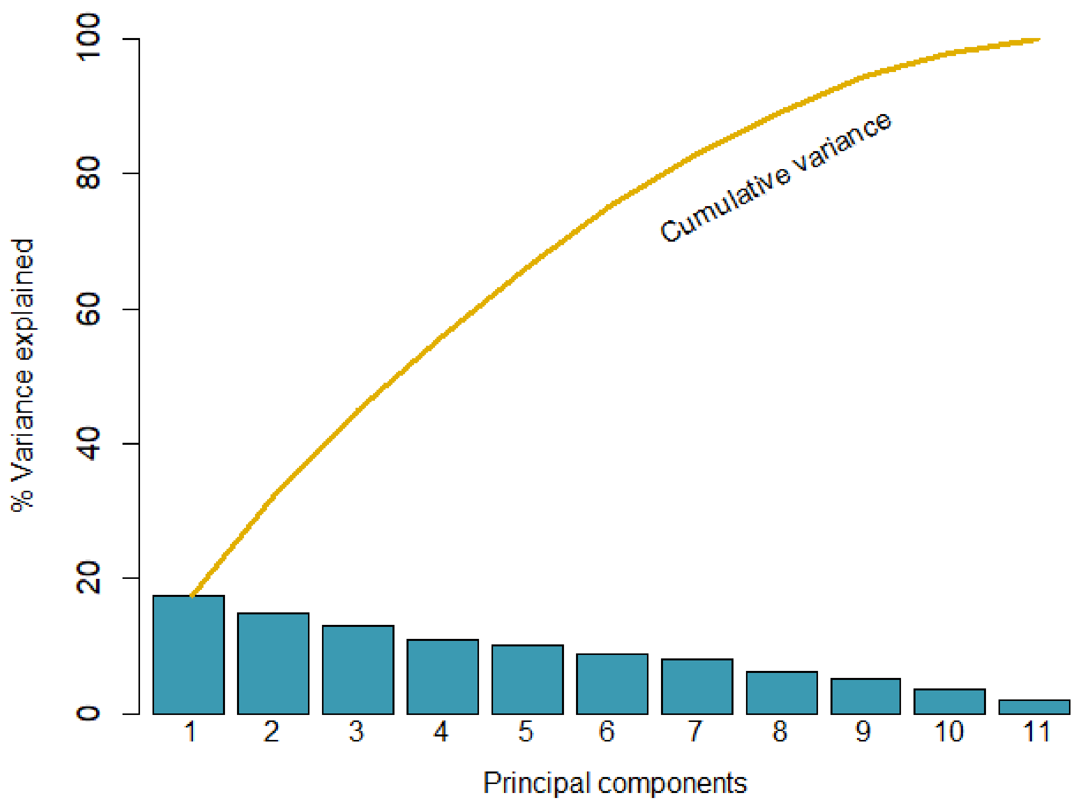
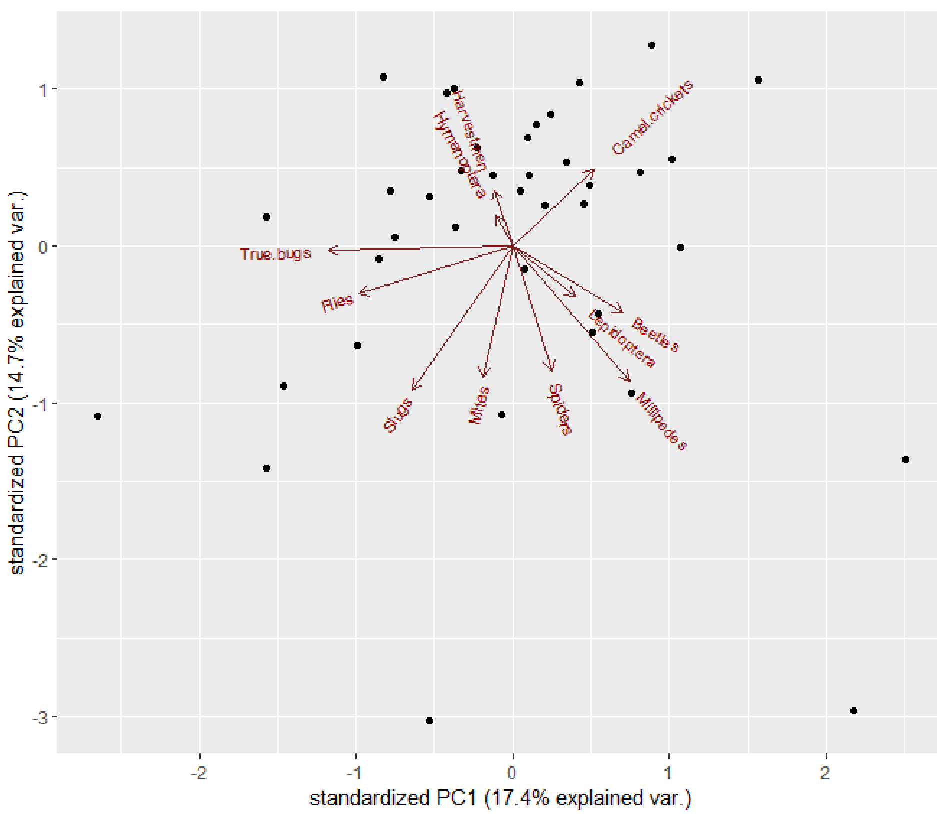


Figure 12. Biplot showing the vectors for the first two principal components of the invertebrate data. Variation in the dataset stemming from true bugs, for example, is barely represented by the second principal component (vector points towards zero on the y-axis), but true bug biomass is strongly and negatively correlated with the first principal component (vector points to the left [negative values] of the x-axis).



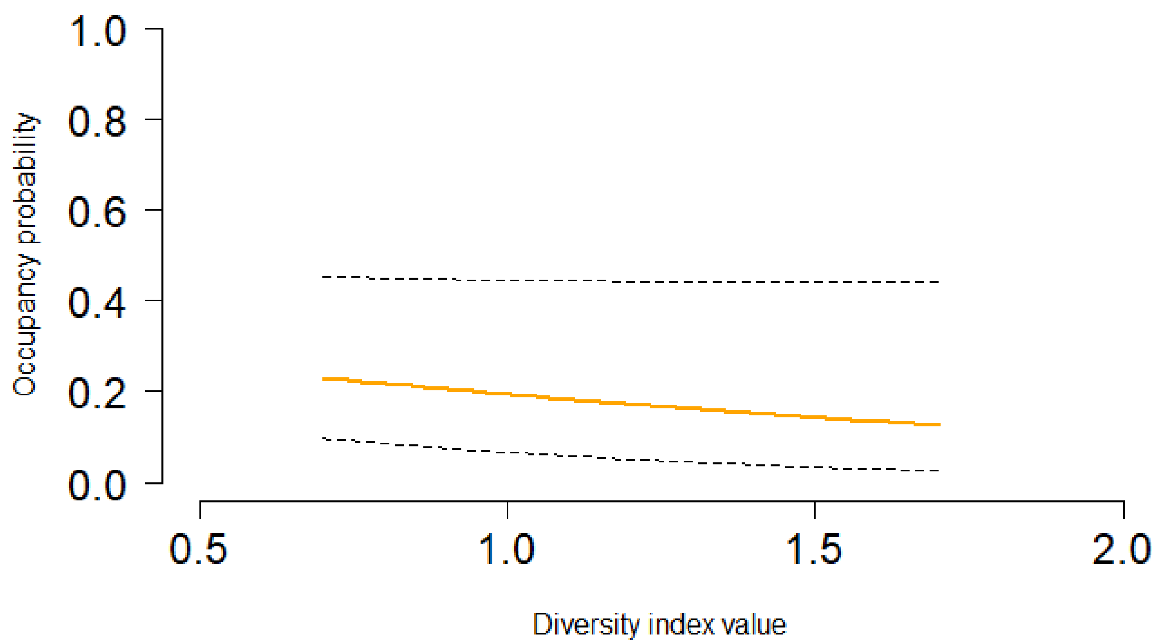
Occupancy Model Results

In contrast to our hypotheses, the occupancy probability of the six bird species in our analysis was unrelated to the total invertebrate biomass present within our samples from a sampling station. We were surprised by these results, because previous studies have linked overall invertebrate biomass to patterns of bird occupancy in multiple ecosystems (e.g., Studds and Marra 2005, Hussell 2012). In contrast, some studies of forest birds in the

Eastern U.S. have failed to find that pattern in the majority of species that they examined (Duren et al. 2017). In the Duren et al. (2017) study, for example, the researchers found patterns of occupancy in most forest bird species were better predicted by vegetation characteristics compared to invertebrate biomass. In our case, we hypothesized that an 'all biomass' model served as a proxy for total food availability in the local environment for birds, and that more biomass equated to greater food available and abundance. This might not be true for multiple reasons. First, although the diet of the bird species in our study is incompletely known, it is unlikely that all six bird species consume all of the 11 invertebrate groups included in our analyses. Second, our sampling took place within 2-m of the forest floor, out of convenience, whereas all of the bird species in our study spend at least some time foraging above that level. Fly biomass may be an important predictor for Yellow-bellied Flycatchers, for example, but Yellow-bellied Flycatchers typically forage at or above 2 m (J. Hill pers. Observation). It may be that our sampling methods favored other families of flies, that occur lower to the ground, than are typically a part of the Yellow-bellied Flycatcher diet. Hence our measurement of 'fly biomass' may not be a good approximation to the fly biomass available to Yellow-bellied Flycatchers or the canopy-foraging Blackpoll Warbler.

Our model selection procedure found a connection between invertebrate group richness and diversity for only two species. Swainson's Thrush occupancy was weakly and negatively related to invertebrate richness, while Yellow-bellied Flycatcher occupancy was negatively and marginally related to invertebrate group diversity (Figure 13). We had predicted positive relationships between occupancy and these metrics for all the species in our analysis. However, other studies of forest birds have also failed to find relationships between prey richness and diversity and avian occupancy, and have instead found support for habitat structure as the primary determinant of occupancy (Alexander 2023).

Figure 13. The occupancy probability (orange line, with dashed 95% confidence intervals) of Yellow-bellied Flycatcher was weakly and negatively related to the Shannon diversity index values, calculated from the invertebrates present in our samples at each site.



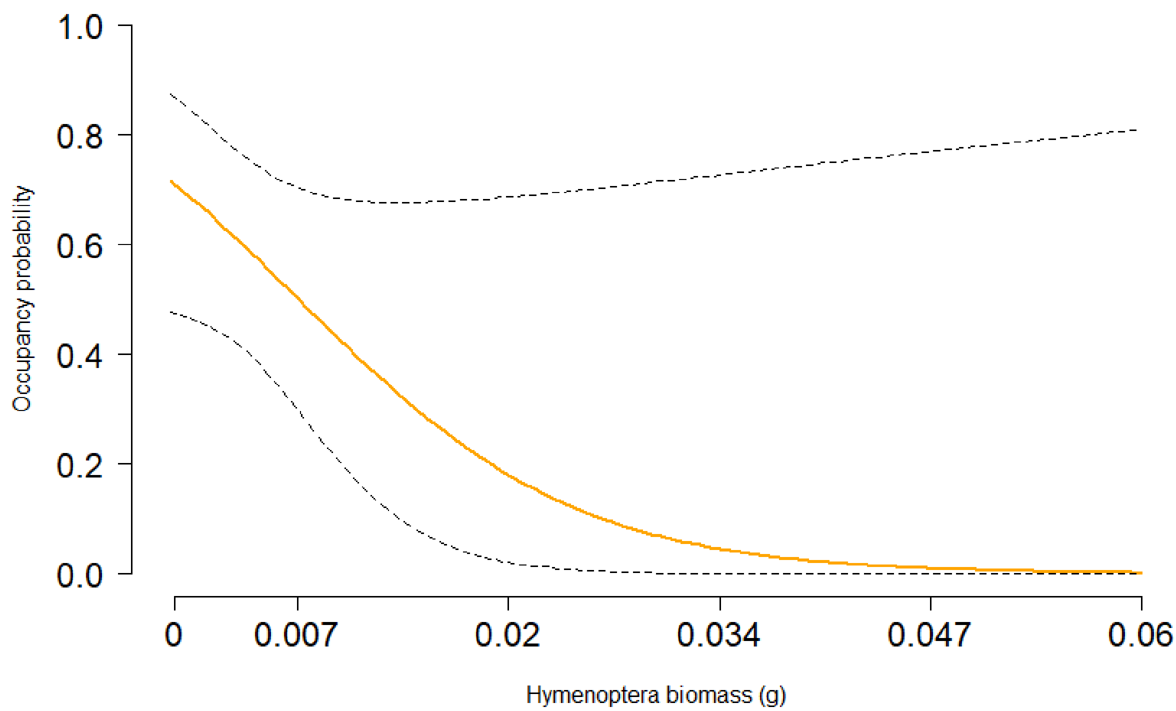
In our analysis, the occupancy probability of all but White-throated Sparrows was associated with the biomass from one or two specific groups of invertebrates (Supplementary Table): Blackpoll Warbler (+spiders), Bicknell's Thrush (+true bugs, +slugs), Swainson's Thrush (-Hymenoptera), Winter Wren (-camel crickets), and Yellow-bellied Flycatcher (-harvestmen, +true bugs). Some of these associations have been previously speculated (e.g., Blackpoll Warblers are known to eat spiders), but several of these findings are in direct contrast to what is previously known about the diets of some of those bird species.

Blackpoll Warblers primarily forage for adult and larval insects between 5 and 10 m above the forest floor (DeLuca et al. 2020). Although spiders are a documented component of their diet, lice, grasshoppers and crickets, lepidopteran larvae, ants and true bugs are all thought to be a more important staple of their diet (DeLuca et al. 2020). Spiders are thought to play important roles in suppressing the abundance of arthropods in ecosystems, in general (Michalko et al. 2019), but spider biomass was not significantly associated with any other group (or the combined biomass or all other groups) in our dataset. Bicknell's Thrush, a ground-foraging species, tends to favor ground beetles and ants in their diet (Townsend et al. 2015). Beetles (mostly ground and rove beetles) presented more than one-quarter of the biomass in our dataset, but instead we found correlations between Bicknell's Thrush occupancy and the biomass of slugs and true bugs.

The ecology of slugs in spruce-fir systems is not well known, but slugs have a complex relationship to birds and other animals in other ecosystems. A few species of birds (e.g., Rook [*Corvus frugilegus*] and feral pigeons [*Columba livia*]) have been documented predating slugs, but they are not thought to be a large dietary component of even those bird species (Feare et al. 1974, Dilks 1975). Carabid beetles are common predators of slugs, but when given the choice (in preference trails) carabids will usually chose alternative prey items (Ayre 2001, Mair and Port 2001). There is also some evidence that slugs (*Arion* sp.) are nest predators on ground-nesting birds in Europe, although it is uncertain how common this behavior occurs (Turzańska and Chachulska 2017).

Swainson's Thrush are near-ground foragers, primarily consuming beetles and ants in the Northeast forests, but also true bugs (Mack and Yong 2020). Surprisingly, we found no positive relationship between Swainson's Thrush occupancy and *any* invertebrate group, but Swainson's Thrush were <u>less likely</u> to occur in locations with abundant ant and other Hymenoptera biomass (Figure 14). Hymenoptera represented a very small portion (<2%) of the biomass in our dataset, so it is surprising to find any relationship between their biomass and the occupancy of any of the six bird species…let alone a species that is known to consume them as a regular part of their diet (Mack and Yong 2020).

Figure 14. The occupancy probability (orange line, with dashed 95% confidence intervals) of Swainson's Thrush was weakly and negatively related to the Hymenoptera biomass present at each of 42 sampling stations.



Similar to Swainson's Thrush, Winter Wren are ground foragers who primary consume beetles, true bugs, ants, flies and millipedes (Hejl et al. 2020), but their occupancy was negatively related to camel crickets (the only Orthopteran in our dataset). In contrast, Yellow-bellied Flycatchers are aerial foragers of the understory who primarily consume flying insects (e.g., midges [Chironomidae], stoneflies [Plecoptera], crane flies [*Tipula* spp.]) (Gross and Lowther 2020), but their occupancy was positively related to the biomass of true bugs and negatively related to the biomass of harvestmen in our study. Finally, White-throated Sparrow occupancy was unrelated to any of the invertebrate biomass covariates or indices that we considered (Supplementary Table), although they regularly take prey items from the invertebrate groups in our samples (Falls and Kopachena 2020).

While some bird species' occupancy was predicted by individual invertebrate groups in our study, others were better predicted by complex configurations of the invertebrate community: namely, principal components for Bicknell's Thrush (-PC1), Blackpoll Warbler (-PC2), and Winter Wren (+PC4). Principal components can be difficult to interpret, because they simultaneously represent all the invertebrate groups while representing some more than others. However, all the bird species in our study have diverse diets, and their occupancy patterns likely reflect that, rather than be driven solely be the biomass of individual invertebrate groups. The full principal component loadings are presented in the Supplementary Table.

CONCLUSIONS & FUTURE DIRECTIONS

With this project, we have initiated a novel undertaking in the Northeast—establishing a baseline monitoring program for montane invertebrates of the spruce-fir zone while generating high-quality data for other researchers as well (Figure 15). We now have the clearest understanding yet of the relationships between occupancy patterns of birds of the spruce fir zone as it relates to their diet and the invertebrate community. Many of the species-specific occupancy relationships were surprising, but we now suspect that invertebrate biomass and diversity are perhaps proxies of habitat quality in this ecosystem—rather than reflections of individual prey preferences. It may be that vegetation characteristics (not measured [currently] in our study are better measures of avian occupancy than are indices of the invertebrate community.

We just finished revisiting the 42 sampling locations in June of 2023, and we look forward to sorting through and identifying those specimens this autumn. Despite the careful and thoughtful design of our sampling procedures, identifying the specimens to taxonomic groups is labor- and time-intensive. It is difficult to imagine expanding our sampling regime to additional montane sites, simply due to the amount of time it takes to identify the specimens from our current sampling stations. In future seasons, we will explore non-lethal methods of sampling the invertebrate community as a way of reducing our microscope time and increasing our efficiency. If we can find non-lethal methods of sampling that are predictive of bird occupancy patterns, then we could 1) consider expanding to additional montane sites within Vermont and New Hampshire, and 2) create enhanced opportunities for community scientists to participate in our program.

Figure 15: Composite image of a few of the many invertebrates that were collected at the 42 sampling stations in 2022. Photographs were taken directly from the dissecting scope, which facilitated contributing to biodiversity projects (e.g., iNaturalist). ©Jason Hill

PERMITTING CHALLENGES

We underestimated the challenges and necessary lead times to secure permitting for our research. We successfully acquired the necessary permits for our research, but the permitting process itself poses as a potential barrier to further expansion of this research and monitoring project. In total, the Vermont Agency of Natural Resource and Mansfield

State Forest permitting process directly involved at least half a dozen individuals. We applied for our collection permit in early February of 2022, and received permission to sample invertebrates in early June.

Acquiring permission to conduct research in the UVM Natural Area was equally time-consuming and complex, due to staff vacancies and sabbatical leave. Ultimately, we secured permission from four different offices at UVM including the Real Estate Office, Vice Provost of Research Office, and the Legal Office. Obtaining these permissions also involved submitting a proposal to conduct research within the UVM Natural Area and recruiting a UVM entomologist to "sign off" on our methods and research questions.

In New Hampshire, the White Mountain National Forest oversees jurisdiction of Mounts Cherry and Martha; they ultimately decided that our research and monitoring activities did not require a US Forest Service Research or Collection Permit. However, the US Fish and Wildlife Service asked us to limit our sampling to Mounts Cherry and Martha—we had also proposed sampling at an additional 15 locations on Mount Moosilauke. We had already obtained permission from the White Mountain National Forest and Dartmouth (which also owns land on Mount Moosilauke where we proposed sampling activities) to conduct surveys on Mount Moosilauke. The US Fish and Wildlife Service was conducting sampling for northern bog lemming (*Synaptomys borealis*) on Mount Moosilauke during June of 2022, in response to an endangered species lawsuit. The US Fish and Wildlife Service was concerned that our sampling activities would interfere with their activities.

Mention of these permitting challenges is not meant to serve as a criticism of any of these agencies: state or federal. Without exception, the biologists and administrative folks who approved our research were welcoming and agreeable. The above paragraphs are instead, meant to simply acknowledge these difficulties and their effects on our research and monitoring: 1) as in 2021, we were not able to start sampling during June (the month when Mountain Birdwatch data are collected, and when we had access to community scientists) in Vermont and 2) we were not able to survey at all of the locations that we had gained permission for in New Hampshire through no fault of our own. These challenges have also made us rethink our plans for the future of this research and monitoring program, and the permitting delays greatly limit our ability to coordinate with community scientists and to plan for fieldwork in advance.

VERMONT CENTER FOR ECOSTUDIES COMMITMENT TO COMMUNITY SCIENCE AND DATA LEVERAGING

The Vermont Center for Ecostudies is an Open Science organization that values justice, equity, diversity, and inclusion, and we are committed to action that creates and sustains meaningful change, both within our organization and our broader sphere of influence. We annually engage thousands of community scientists via involvement in our many long-term community research projects, including Mountain Birdwatch (in its 23rd year), LoonWatch, Birder Broker, Vernal Pool Monitoring Project, Grassland Ambassadors, and the many projects of the Vermont Atlas of Life. As an organization, we have decades of experience sustaining community science projects and acquiring funding for long-term monitoring projects. We suspect these data will be directly beneficial to several FEMC projects, including Forest Health Monitoring and Monitoring Northeastern Forest Indicators for Signs of Climate-driven Change. As prioritized in the 2020 FEMC Work Plan, key objectives are to identify sentinel species, gaps in monitoring data, and existing monitoring efforts that could be replicated across the landscape. Our invertebrate monitoring project should directly facilitate FEMC in meeting these objectives.

ADDITIONAL DATA AND FILES

1) **Supplementary table (Excel) with species-specific occupancy modeling results and PCA results,**
2) **2022 taxonomic data,**
3) **2023 taxonomic data (anticipated ~November 2023)**

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