Environmental Entomology, 53(3), 2024, 383–397
https://doi.org/10.1093/ee/nvae017
Advance Access Publication Date: 28 March 2024
Research

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Community Ecology

Distinct communities under the snow: describing characteristics of subnivium arthropod communities

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Subject Editor: Talbot Trotter

Received on 9 October 2023; revised on 2 January 2024; accepted on 13 March 2024

Arthropods are active during the winter in temperate regions. Many use the seasonal snowpack as a buffer against harsh ambient conditions and are active in a refugium known as the subnivium. While the use of the subnivium by arthropods is well established, far less is known about subnivium community composition, abundance, biomass, and diversity and how these characteristics compare with the community in the summer. Understanding subnivium communities is especially important given the observed and anticipated changes in snowpack depth and duration due to the changing climate. We compared subnivium arthropod communities with those active during the summer using pitfall trapping in northern New Hampshire. We found that compositions of ground-active arthropod communities in the subnivium differed from those in the summer. The subnivium arthropod community featured moderate levels of richness and other measures of diversity that tended to be lower than the summer community. More strikingly, the subnivium community was much lower in overall abundance and biomass. Interestingly, some arthropods were dominant in the subnivium but either rare or absent in summer collections. These putative "subnivium specialists" included the spider *Cicurina brevis* (Emerton 1890) (Araneae: Hahniidae) and 3 rove beetles (Coleoptera: Staphylinidae): *Arpedium cribratum* Fauvel, 1878, *Lesteva pallipes* LeConte, 1863, and *Porrhodites inflatus* (Hatch, 1957). This study provides a detailed account of the subnivium arthropod community, establishes baseline information on arthropod communities in temperate forests of northeastern North America, and explores the idea of subnivium specialist taxa that are highly active in winter and might be especially vulnerable to climate change.

Key words: arthropod, pitfall trap, subnivium, winter, climate change

Graphical Abstract

A temperate deciduous forest in winter and summer, including a cross-sectional view of the snowpack and leaf litter. The subnivium, a space between the snowpack and the soil surface that acts as a refuge for winter arthropods (and other taxa), is represented by the thin dark layer in the left panel. The arthropod community differs between seasons in composition, biomass, and abundance. The 5 arthropods presented on each side of the illustration, in winter (left) and in summer (right), are representative of groups commonly captured during their respective collection period. On the winter panel, from left to right, the arthropods shown here are a centipede (family Linotaeniidae), a spider (Cicurina brevis; family Hahniidae), a beetle larva (likely belonging to the family Cantharidae), a rove beetle (family Staphylinidae), and a wingless fly (genus Chionea). In the summer panel from left to right, the arthropods are a rove beetle (family Staphylinidae), a carrion beetle (family Silphidae), a cricket (family Rhaphidophoridae), a fly (family Phoridae), and a ground beetle (family Carabidae). The leaf litter layer and the arthropods depicted are magnified in this illustration for effect.

Introduction

Insects and other arthropods are poikilothermic animals that depend on physiological and behavioral strategies to endure or avoid freezing. The production of antifreeze-like substances (polyols, sugars, proteins) to prevent intracellular freezing, and the localization of ice formation within intercellular spaces are components of a strategy employed by a range of winter-active freeze-tolerant insects (Bale 2002, Sinclair et al. 2003, Morgan-Richards et al. 2023, Teets et al. 2023). Freeze avoidance strategies include long-distance migration, most common in the Odonata and Lepidoptera (Reppert et al. 2010, May 2013), and dormancy (including facultative or obligate diapause), often in a life stage with elevated cold tolerance and/or in microrefugia (Gill et al. 2017). Other arthropods remain active within thermally buffered refugia, such as inside plant material, human structures, or the soil. Some of these refugia remain remarkably thermally stable, such as beneath ice in aquatic environments or under the snow in the subnivium (Aitchison 1987, Kirchner 1987, Hågvar and Hågvar 2011).

The subnivium is a space beneath the snowpack and above the soil surface created by sublimation, or the conversion of ice or snow directly to the gas phase (Pauli et al. 2013). This space remains relatively stable so long as deep snow (about 15–20 cm) is maintained (Pruitt 1970, but see Thompson et al. 2018). The subnivium acts as a winter refuge for many organisms as it provides a unique microhabitat with consistent, near-freezing temperatures (0 °C) and relative humidity of around 100% (Petty et al. 2015, Rossi et al. 2019). These conditions allow small mammals, fungi, plants, and even arthropods to remain active during the winter (Aitchison 1984a, Starr and Oberbauer 2003, Schmidt et al. 2008, Pauli et al. 2013, Scott et al. 2022). In fact, a complex subnivium food web exists beneath the snowpack, with arthropods likely filling various functional roles spanning the brown and green web, acting as decomposers/detritivores, bacterivores, fungivores, herbivores, and predators. Shrews or other small insectivorous mammals often act as apex predators in these systems (Aitchison 1984a, Hågvar and Hågvar 2011). While many arthropods are active primarily in the summer and enter facultative diapause during winter (Gill et al. 2017), a number of arthropods are known to remain active in the subnivium, with spiders, beetles, mites, and collembola among the most commonly collected groups (Aitchison 1984a, Hågvar and Hågvar 2011).

Anthropogenic climate change threatens the subnivium microhabitat and the communities that depend on it (Thompson et al. 2018, Zuckerberg and Pauli 2018, Harvey et al. 2023). Winters in many regions of the world are getting warmer, resulting in more variable snowpacks that are thinner, less insulative, and present for fewer days per year (Templer et al. 2011, Petty et al. 2015). For overwintering arthropods, reduced snowpack increases exposure to harsh and fluctuating ambient conditions. So, paradoxically, as winters get warmer, many overwintering arthropods may experience colder and more variable temperatures (Lombardero et al. 2000, Groffman et al. 2001, Brown and DeGaetano 2011). As a result, some arthropod populations or communities may decline or shift dramatically in composition. Presumably, other species that remain active at or near-freezing temperatures may enter dormancy under reduced snowpack, resulting in altered winter food webs and energy budgets, extended development times, or reduced reproductive rates. Conversely, some arthropods may benefit from reduced snow cover, especially if this decreases winter predation or competition for resources.

Arthropod decline, and more specifically insect decline, has entered the spotlight as researchers have documented significant declines in richness and abundance across disparate regions of the world (Conrad et al. 2006, Shortall et al. 2009, Schuch et al. 2012, Hallmann et al. 2017, Harris et al. 2019, Powney et al. 2019, Sánchez-Bayo and Wyckhuys 2019, van Strien et al. 2019). Though causal mechanisms remain elusive and likely vary regionally, reduced snowpack has been cited as a hypothesized driver of arthropod decline in temperate regions. Harris et al. (2019) found that species richness and abundance of summer-active beetles in a north-temperate forest declined sharply over a 45-yr period, with the most dramatic declines in beetle abundance and diversity at lower elevations where the duration of winter snow cover markedly declined. Templer et al. (2011) experimentally removed snow from forest plots and found that winter soil frost depth increased, and overall summer arthropod richness and abundance decreased, with some taxonomic groups being more affected than others. While these studies were not focused on subnivium arthropod communities, they demonstrate that snowpack decline may be correlated with arthropod decline.

Subnivium arthropod communities have been characterized in previous studies (Näsmark 1964, Aitchison 1974, 1978, 1979a, 1979b, 1979c, 1979d, 1984a, 1984b, 1984c, Koponen 1976, Olynyk and Freitag 1977, Leinaas 1981, Merriam et al. 1983, Schmidt and Lockwood 1992, Addington and Seastedt 1999, Vanin and Turchetto 2007, Hågvar and Hågvar 2011). To our knowledge, however, no study has systematically compared arthropod communities on the forest floor during summer and winter. Better knowledge of winter and summer invertebrate communities may be especially important in northeastern North America, where winters are changing faster than any other season (Karmalkar and Bradley 2017). In this study, we collected and compared invertebrates that are active on the forest floor during summer (in July and August) and in the subnivium during winter (January–March). The study system was a large, minimally disturbed secondary forest in northern New Hampshire, USA, with a history of winters with deep, persistent snow cover. We hypothesized that (H1) most invertebrates would be dormant and inactive in the winter and therefore subnivium communities would have lower diversity, lower abundance, and less overall biomass relative to summer communities and (H2) subnivium communities would represent a subset of the summer arthropod community that remain active in the winter.

Materials and Methods

Site Description

We conducted our study in the Second College Grant (SCG), a township and Dartmouth College property located in northern New Hampshire along the Maine border. This remote property, which is within a temperate-boreal transition zone at 44.9 °N, 71.1 °W, is about 11,000 ha of forested land. The land is managed for recreation, wildlife, and forest production. Dominant hardwood tree species of the SCG include American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), quaking aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and yellow birch (*Betula alleghaniensis*). Dominant softwood species include balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and white spruce (*Picea glauca*) (Nagel et al. 2017).

Pitfall trap sampling was conducted across a large geographic area; thus, a range of elevations was sampled (471–667 m above sea level). The mean elevation (± standard deviation) of the sampled areas within the SCG was 564 ± 61.5 m a.s.l. Sampling occurred over 2 winters and one summer. Mean daily low and high annual temperatures from 1990 to 2022 in a nearby area were 0.2 ± 0.9 °C and 12.2 ± 0.8 °C. Mean annual precipitation over this 33-yr period was 108.3 ± 15.6 cm, with roughly 20% of that falling as snow, and the average annual snow depth was 8.1 ± 3.5 cm (NOAA weather station ID: USC00270690) (Menne et al. 2012a, 2012b). Winter sampling occurred during 2 consecutive winters from late January to mid-March in 2020–2021 (“winter 1”) and 2021–2022 (“winter 2”), while summer sampling consisted of 2 separate, 2-week-long sampling periods in 2021, the first in late July (“summer 1A”) and the second in late August (“summer 1B”). During the winter collections, the average daily winter temperature was −7.5 ± 6.5 °C, with an average daily temperature range of −21.5–5 °C. During the summer collections, the average daily temperature was 17 ± 3 °C with an average daily temperature range of 12.5–21.5 °C (unpublished weather station data, Dartmouth College Woodlands). The mean snow depth measured for the 2 winters during mid-winter (late January) was 35 ± 5.5 cm with a range of 23–52 cm. The mean snow depth decreased for late-winter measurements (mid-March) with mean snow depth at 32.5 ± 6.5 cm with a range of 12–49 cm. Comparisons of our study years using climate data from a nearby NOAA station indicated that weather conditions were within the norms for 1990–2022.

Pitfall traps were deployed within 4 forested blocks (Fig. 1) representative of mid- to late-successional northern forests of the area. Distributed across each of the four 10.5-ha blocks were 8 pitfall traps set up in pairs, 5–10 m apart. Blocks were separated by 1–6 km, and a total of 32 traps were used across all blocks. Two of the traps in block 4, however, were lost and removed from further consideration. These forest blocks also serve as the control (unmanaged) treatments within the Adaptive Silviculture for Climate Change (ASCC) experiment (Nagel et al. 2017, Palik et al. 2022).

Pitfall Trap and Sampling Design

Ground-active arthropods were collected using pitfall traps modified to withstand snow and improve trap catch during both the winter and summer (Fig. 2). The exterior structure of the trap, the walls and roof, were built from 0.45-cm-thick black corrugated plastic sheets pinned to the ground with 15.2 cm long garden stakes. Each of the 4 wall sections of the structure measured 61 cm in length and 7.62 cm in height. The roof was a 25.4 × 25.4 cm square. The “X” shaped design maximized arthropod catch by intercepting passing arthropods, forcing them to walk along the walls and towards the cup containing preservative fluid (Boetzl et al. 2018).

Two cups, inner and outer, formed the pitfall and were made from durable plastic containers (Placon, Madison, WI, USA). The larger outer cup (946 ml, 14 cm height) held the preservative fluid. We limited the bycatch of larger nontarget animals by using a shallow inner cup (355 ml, 5.7 cm height) that occupied the upper volume of the outer cup. The inner cup had two 2.54-cm-diameter holes cut at the bottom of the cup at opposite edges to allow arthropods to fall into the larger outer cup (Supplementary Fig. S1). The opening of both cups, and therefore of the pitfall trap itself, measured 11.43 cm in diameter.

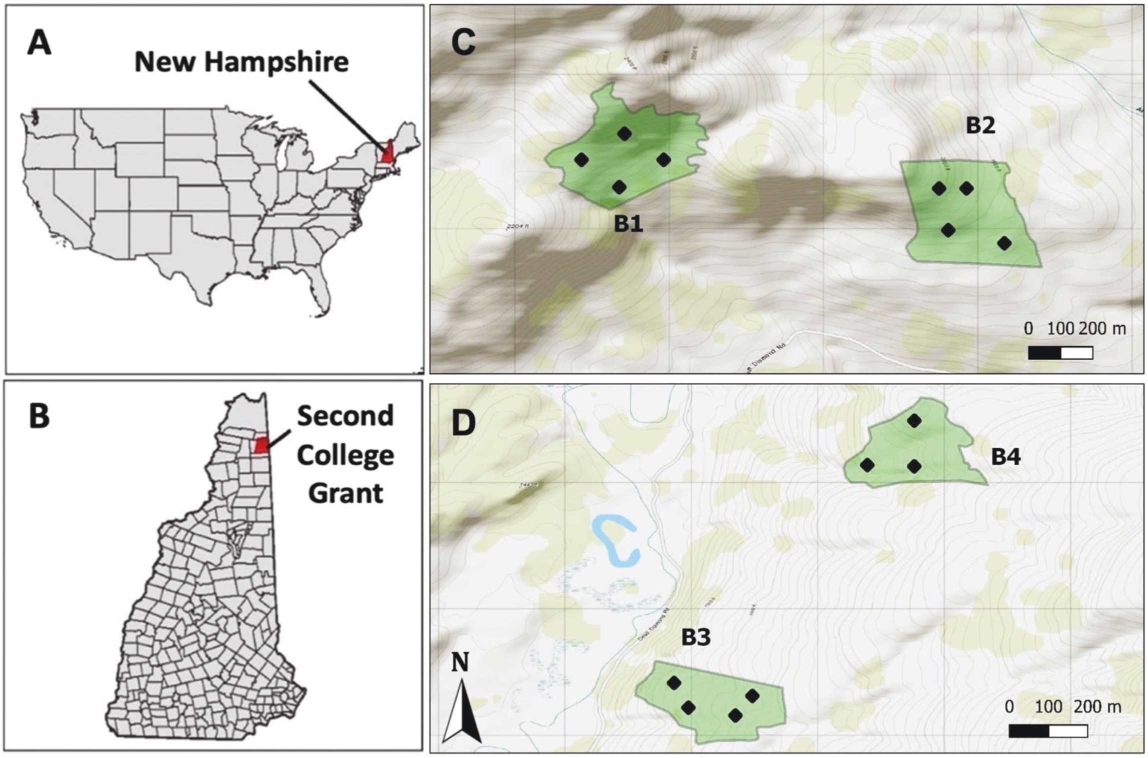

Fig. 1. Topographic map depicting the location of the SCG and the 4 blocks from which samples were collected. The blocks are represented by the polygons and have B1-4 labels next to them. The boxes within the polygons represent a "sampling site" where a set of pitfall traps are located. Blocks 1 and 2 were located roughly 6 km southwest of blocks 3 and 4.

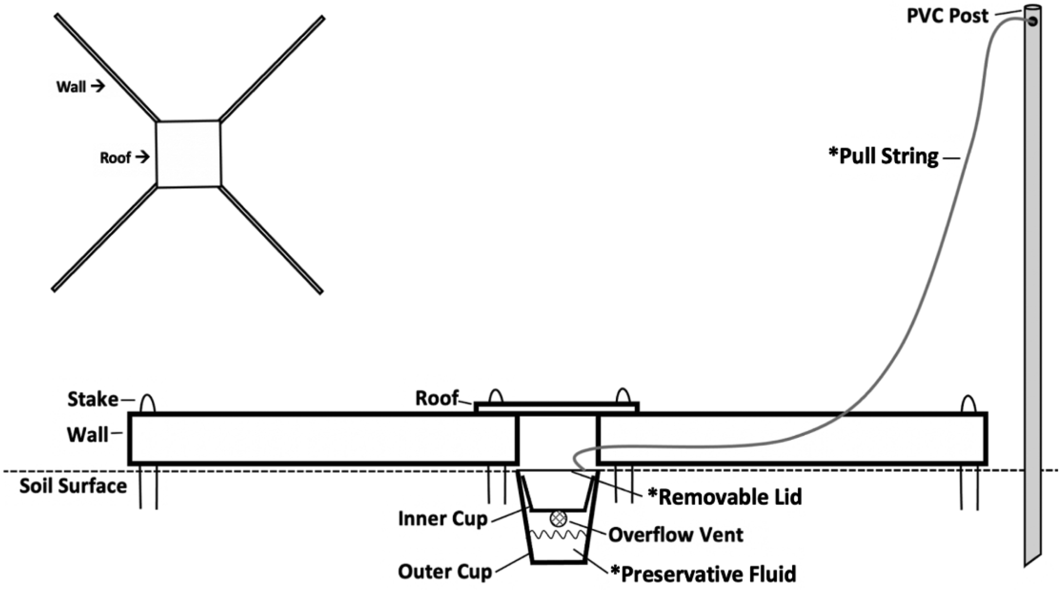

Fig. 2. Cross-sectional diagram of the modified pitfall trap before being activated/opened. An aerial view of the modified pitfall trap is in the top left corner and demonstrates the "X" shape design. *The components that change between summer and winter collections (Supplementary Appendix A).

This is a unique pitfall trap design that incorporates components of existing designs (Merriam et al. 1983, Boetzl et al. 2018).

In the winter, we used 500 ml of propylene glycol-based, glycerin-free antifreeze mixed with a few drops of odorless dish soap as the preservative fluid in each trap. This substance is harmless to vertebrates and does not freeze at temperatures present within the subnivium. For summer collections, we used a salt solution instead of antifreeze to limit attractiveness to bears or racoons. The summer preservative for each trap included 297 ml of water, 3 ml of Tween 80 (Thermo Fisher Scientific Inc., Waltham, Massachusetts), and 9 water softener salt pellets (Morton, Chicago, Illinois). See Supplementary Appendix A for more details on the traps.

For the winter sampling, the traps were deployed in November, but each was covered with a plastic lid to prevent arthropod capture. Traps were activated for sampling in January of each winter once a deep snowpack had formed (~0.5 m). Traps were activated without disturbing the subnivium by pulling a prepositioned string that was accessible from above the snow (Fig. 2; Supplementary Fig. S2). Winter trapping continued from late January to mid-March for a total of 56 days each winter. During both winter sampling periods, there was constant snowpack present across the sampling locations. The traps were only collected once during the winter, at the end of the 56-day period, to avoid disturbing the snowpack. Typically, pitfall trap samples are collected more frequently than this to avoid sample degradation and to prevent the traps from overflowing with water, rendering them ineffective. These issues, however, are less prominent during winter sampling. Near-freezing temperatures and the use of propylene glycol as a preservative fluid prevented the samples from degrading, allowing the traps to remain active throughout the entire winter. We collected the traps before snowpack termination occurred at the end of winter, ensuring that the traps were only collecting arthropods that were active under the snowpack. See Supplementary Appendix B within supplemental materials for more details on sampling.

Sample Processing, Arthropod Identification, and Biomass Calculation

We sorted all arthropods into morphospecies with the aid of a dissecting microscope. Representatives from each morphospecies were photographed, assigned a code, and later identified taxonomically to the family level. We were only able to identify immature arthropods to the order level. When possible, all rove beetles (family Staphylinidae) from every sample were identified at the species level. Spiders (order Araneae) from a subset of 16 randomly selected traps per collection (winter 1 and 2, summer 1A and 1B) were also identified to the species level when possible, primarily using Ubick et al. (2017), Paquin and Dupérré (2003) and following taxonomy accepted in the World Spider Catalog (WSC) (2023). These 2 groups, spiders and rove beetles, were selected to be identified as species because initial sample processing indicated that they were abundant in winter sample collections and noticeably large compared to other winter-collected taxa. As spiders and many groups of rove beetles are known to be predators, they may also play a uniquely important role in the winter arthropod community. We freeze-dried and weighed representatives for nearly all morphospecies and then calculated a mean dry mass per individual for each morphospecies, which we then multiplied by abundance to get estimates of biomass for different groups of arthropods across the different collections and total biomass for each collection. About 35% of the morphospecies were too rare or had no intact representatives to accurately calculate mean biomass; for these rare taxa, we used estimates of mass based on similarly sized and taxonomically related morphospecies. Error in the estimation of these weights is presumed to have had negligible effects on calculations of overall biomass, given their low relative abundances in samples. Biomass is ecologically relevant (e.g., from a food web/energy flux perspective) and is likely more directly comparable than abundance across taxa with highly divergent body sizes.

Data Analysis

For simplicity and to allow for a more nuanced insight into the arthropod community, when appropriate for analyses and figures, insects and noninsect arthropods (hereafter, "other arthropods") were considered separately. Since winter and summer collections had a different number of collection days, abundance and biomass data were divided by the number of days the traps were active to make samples and results more comparable across seasons. Sample collections were pooled for each pair of traps, so data were expressed as captures · trap-pair^{-1} · collection day^{-1} (Fig. 1C and D). Most analyses were conducted in R (Version 4.0.3; R Core Team, 2020) using package *vegan* (Oksanen et al. 2022) for analysis and *ggplot2* (Wickham 2016) for figures; mixed modeling was conducted in JMP (Version 16. SAS Institute Inc., 2021). The R package "iNEXT" was used to calculate rarefied (to 60 individuals per trap-pair) estimates of all arthropods for species richness (S), the exponent of Shannon's diversity index ($e^{H'}$), and Simpson's diversity index (D) (Chao et al. 2014, Hsieh et al. 2016). Prior to testing differences in indices between collections, they were checked for normality using the Shapiro–Wilk's test and homoscedasticity using Levene's test. Simpson's and Shannon's indexes were square root and log+1 transformed, respectively, which fixed issues with heteroscedasticity. The rarefied richness and other diversity estimates were analyzed with mixed model analysis using the restricted maximum likelihood estimation. The statistical model for each index, abundance, and biomass, included collection date, block, and their interaction as fixed effects and trap-pair as a random effect nested within the block.

To examine patterns in morphospecies composition, we used a Bray–Curtis dissimilarity matrix and constructed nonmetric multidimensional scaling (NMDS) ordinations (Bray and Curtis 1957). The NMDS was 3-dimensional as this allowed the stress level to be within an acceptable range (<0.20) while limiting the complexity of more dimensions. For repeatability, we used a seed value of 1,151,997 for the NMDS, which produced results that were indistinguishable from those of using a random seed. Rare morphospecies that appeared in fewer than 2 trap pairs were removed from the dataset prior to analysis. The species abundance matrix for all arthropods was transformed prior to analysis using the Hellinger method (Legendre and Gallagher 2001). Differences in arthropod communities across collections and blocks were assessed with permutational multivariate analysis of variance (PERMANOVA) using the *adonis2* function in *vegan*. Where statistical differences were found (at $\alpha < 0.05$), we conducted pairwise comparisons among factor levels using Tukey's Honestly Significant Difference (HSD) to correct for Type 1 error. Data from this study are available in the Environmental Data Initiative Repository (EDI) (Ziadeh et al. 2023).

Results

Abundance and Biomass

Just over 20,000 arthropods were collected (Supplementary Table S1). By abundance, insects represented about 18% of winter collections and 25% of summer collections (Fig. 3E); the rest were other arthropods. From the total arthropods collected, 94% of winter collections and 95% of summer collections consisted of adults, while the remaining 5%–6% were immature arthropods. During the first winter, the most abundant order of arthropods (individuals per day) was Poduromorpha (Collembola; 19 per day). Oribatid mites (Acari, Acariformes) were the most abundant in the second winter collection (15 per day). Summer 1A and 1B were dominated by Entomobryomorpha (Collembola; 109 per day) and mesostigmatid mites (Acari, Parasitiformes; 235 per day), respectively (Fig. 3C; Table 1). In total, summer traps collected around 6-fold more arthropods per trapping day than winter traps (59 and 78 per day in the first and second winter collections vs. 400 and 466 per day in the summer collections; Fig. 4A). A similar pattern for abundance was observed when insects and other arthropods were considered separately (Supplementary Fig. S3).

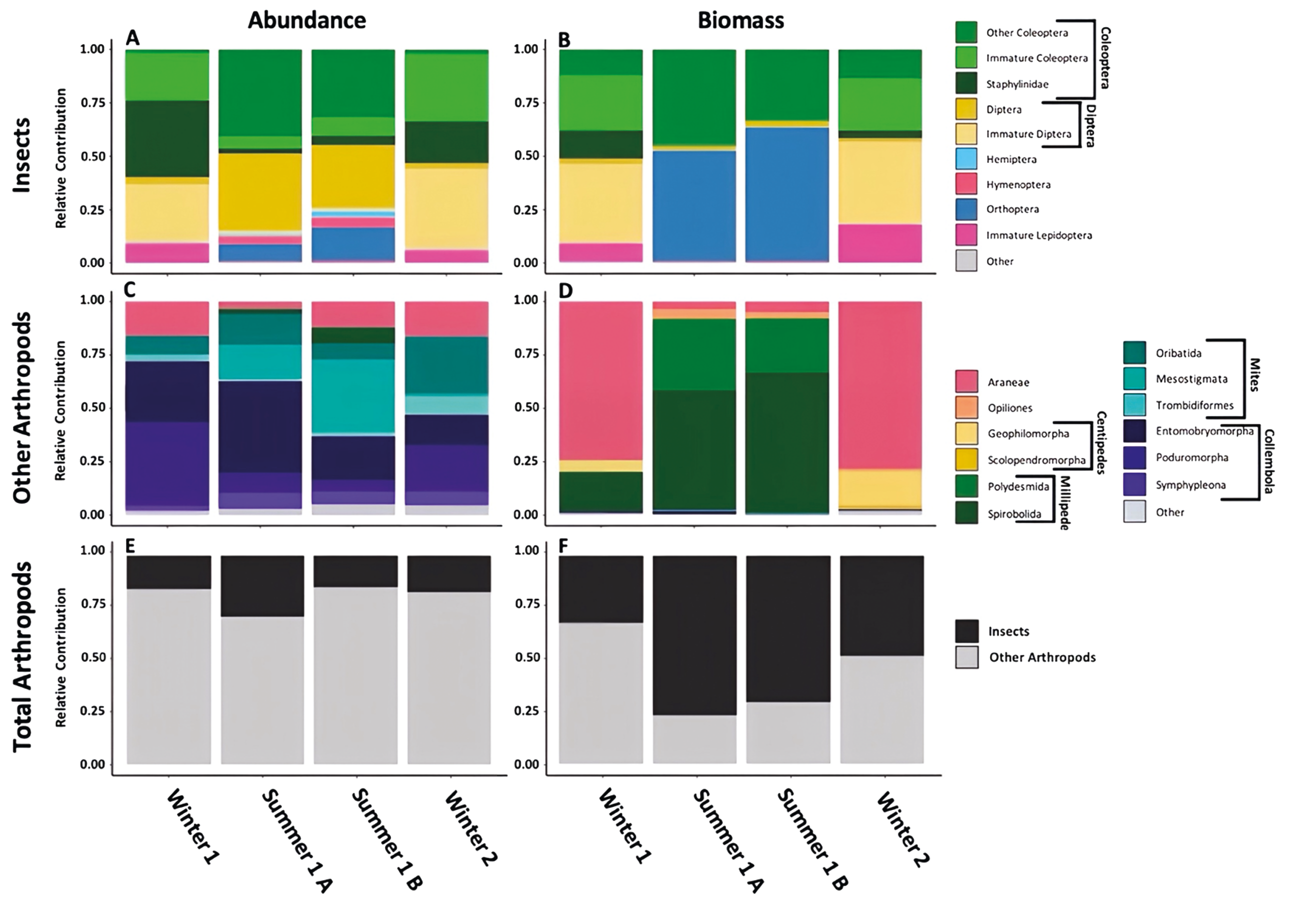

Fig. 3. Multipaneled stacked bar plot showing relative abundance and biomass of different arthropod groups in the 4 collections, separated into insects (Parts A and B), other arthropods (Parts C and D), and total arthropods (Parts E and F). Any group that represented less than 5% of a stacked bar was assigned to the "Other" category. Absolute abundance and biomass are presented in Fig. 4. For a more comprehensive account of what arthropods were collected in which seasons, refer to Supplementary Appendix C, Table S1.

Mean total biomass per day was about 69-fold higher in the summer collections (1161.3 and 1,850 mg/day) vs. in the winter collections (17.5 and 26.3 mg/day) (Fig. 4B). A similar pattern for biomass was observed when insects and other arthropods were considered separately (Supplementary Fig. S3). Spiders (Araneae) had the greatest biomass across both winters (winter 1 = 8.78 mg/day; winter 2 = 10.58 mg/day) (Fig. 3D). Orthoptera had the highest biomass for summer 1A (428.91 mg/day), and summer 1B (584.88 mg/day) (Fig. 3B). Morphospecies that we identified as predators based on mouthparts and natural history, accounted for 31.5% of the biomass in the winter and 26.4% of the biomass in the summer. The mean mass/individual (±SD) of arthropods without considering the abundance of each taxon (i.e., the overall mean mass of a season when adding together one individual from each morphospecies collected), was 1.91 ± 5.84 mg in the summer and 0.69 ± 3.30 mg in the winter. The greater mean mass/individual of arthropods in the summer collections relative to winter was statistically significant ($t_{(214)} = 3.20$, $P = 0.002$).

Mixed model analyses of arthropod abundance and biomass confirmed that collection season, chiefly winter vs. summer, was the main driver of observed patterns. The model for total arthropod abundance per day accounted for 88% of the variance in arthropod abundance, with the effect of random trap-pair accounting for 29% of this variation. The collection variable was highly significant ($F = 73.4$; df = 3, 33; $P < 0.001$); pairwise analysis showed higher abundances in summer, with no apparent differences between collections within each season (Fig. 4). Collection, more specifically the underlying variable of season, was likewise the only significant parameter when predicting daily abundance for insects and other arthropods separately (insects: $F = 145.5$; df = 3, 33; $P < 0.001$; other arthropods: $F = 39.9$; df = 3, 33; $P < 0.001$). The same pattern was observed when mean abundance per trap was examined for insects ($R^2 = 0.923$; Random trap-pair effect = 13%) and other arthropods ($R^2 = 0.835$; Random trap-pair effect = 38%).

The mixed model for total arthropod biomass accounted for 98% of the variance ($R^2 = 0.983$), with the random trap-pair effect accounting for 48% of this variance. From the fixed effects, the collection was the only significant factor for total arthropod biomass ($F = 627.0$; df = 3, 33; $P < 0.001$), of with differences occurring between collections different seasons. In the biomass mixed model for insects ($R^2 = 0.963$; random trap-pair effect = 12%) and other arthropods ($R^2 = 0.960$; random trap-pair effect = 54%), biomass was again statistically similar between collections of the same season and dissimilar between seasons and greater in the summer collections relative to winter collections (Fig. 4B) (insects: $F = 331.7$; df = 3, 33; $P < 0.001$; other arthropods: $F = 237.2$; df = 3, 33; $P < 0.001$). No significant block effects were detected for either abundance or biomass.

Richness and Diversity

Taxonomic richness and diversity were not as different between winter and summer as abundance and biomass (Fig. 5). Mixed model analyses showed a significant collection effect across all rarefied diversity estimates (Table 2), reflecting, in some instances, differences

Table 1. The number of individuals collected in each season is standardized for the number of trap days across the 4 collections, which are specified mainly according to the order level. Abundance per trap was rounded to the nearest integer. The right side shows the relative contribution of each group to the corresponding collection (Group Abundance/Collection Abundance × 100). For a similar table that specifies groups to the family level, see Supplementary Appendix C

			Abundance/trap days				Relative contribution to collection			
			W 1	S 1A	S 1B	W 2	W 1	S 1A	S 1B	W 2
Insects	Coleoptera	Other Coleoptera	1	55	43	1	0.3	13.7	9.2	0.4
		Immature Coleoptera	2	7	8	4	3.4	1.8	1.7	5.6
		Staphylinidae	3	3	4	3	5.6	0.7	0.8	3.5
	Diptera	Diptera	3	46	26	1	4.8	11.5	5.6	0.5
		Immature Diptera	3	3	2	5	4.3	0.7	0.4	6.7
		Hemiptera	1	1	2	1	0.1	0.3	0.5	0.1
	Hymenoptera	Other Hymenoptera	1	4	3	1	0.1	1.1	0.7	0.1
		Hymenoptera (ants)	0	1	1	1	0.0	0.1	0.2	0.0
		Orthoptera	0	10	14	0	0.0	2.5	3.0	0.0
	Lepidoptera	Lepidoptera	0	1	1	0	0.0	0.0	0.0	0.0
		Immature Lepidoptera	1	1	1	1	1.4	0.1	0.2	0.9
Other arthropods		Araneae	8	9	23	10	12.6	2.2	5.0	12.5
		Opiliones	1	4	5	1	0.0	1.0	1.0	0.1
	Centipedes	Geophilomorpha	1	0	0	2	0.8	0.0	0.0	2.1
		Scolopendromorpha	0	1	1	1	0.0	0.1	0.1	0.2
	Millipedes	Polydesmida	0	3	4	0	0.0	0.7	0.9	0.0
		Spirobolida	1	6	14	0	0.1	1.5	3.0	0.0
	Mites	Oribatida	4	36	15	15	6.4	9.0	3.1	20.1
		Mesostigmata	0	55	235	1	0.3	13.6	50.0	1.0
		Trombidiformes	1	3	4	5	2.3	0.7	0.9	6.6
		Ixodida	1	1	1	1	0.4	0.1	0.0	0.0
	Collembola	Entomobryomorpha	14	109	39	8	22.2	27.0	8.2	10.6
		Poduromorpha	19	24	11	13	30.5	6.0	2.3	16.6
		Symphypleona	1	19	11	4	1.8	4.6	2.4	4.9
		Anostraca	1	0	0	1	0.5	0.0	0.0	1.0
		Pseudoscorpiones	0	1	0	0	0.0	0.1	0.0	0.0
		Siphonaptera	0	0	1	1	0.0	0.0	0.0	0.0
		Psocodea	0	1	0	1	0.0	0.2	0.0	0.0

between collections from different seasons and, in others, differences between collections from the same season. The highest rarefied richness (Fig. 5A) and Shannon diversity index (Fig. 5B) estimates were from summer 1B and the lowest from winter 1, with summer 1A and winter 2 between these. Mean Simpson diversity index for winter 2 and summers 1A and 1B did not differ statistically, but winter 1 had a statistically lower value than winter 2 and summer 1B (Fig. 5C). There was no effect of block or block × collection on estimates of richness, Shannon diversity index, or Simpson diversity index. The same pattern was apparent when the diversity indices of insects and other arthropods were analyzed separately, with the collection being the only fixed factor of importance and differences always occurring between the collections of different seasons and occasionally between collections of the same season (Table 2; Supplementary Fig. S4).

Community Composition

Total arthropod community composition differed strongly between winter and summer seasons (PERMANOVA pseudo-$F = 48.4$; df = 1, 35; $P = 0.001$; $R^2 = 0.455$; Fig. 6). There was also a significant difference in composition between all collections, although the differences were greatest between seasons (Fig. 6; Table 3). Composition varied substantially between winter and summer for insects and noninsect arthropods considered separately (Supplementary Fig. S5; Supplementarty Table S2). Certain taxonomic groups were disproportionately represented in the summer or winter, contributing to the major seasonal differences in NMDS grouping (Fig. 6). Arthropods that were relatively abundant in the winter were immature beetles (Coleoptera), rove beetles (Staphylinidae), immature flies (Diptera), spiders (Araneae), Oribatida (mites), Trombidiformes (mites), and Poduromorpha (Collembola). In the summer, arthropods that were relatively abundant included nonstaphylinid beetles (Coleoptera, other), adult flies (Diptera), and crickets (Orthoptera) (Fig. 6, lower; Fig. 3A; Table 1).

Rove Beetles and Spiders

Rove beetles (Staphylinidae) and spiders (Araneae) were particularly prominent in the winter samples. Across both winter collections, rove beetles represented approximately 26.6% of insects collected, while in the summer, it was approximately 14.6%. In the winter, the most abundant species of rove beetle was *Arpedium cribratum* Fauvel 1878. The species of rove beetles most abundant in the summer was *Quedius peregrinus* (Gravenhorst 1806) (Table 4). Spiders were also a relatively abundant group in all the collections, but like the rove beetles, they had a greater relative abundance

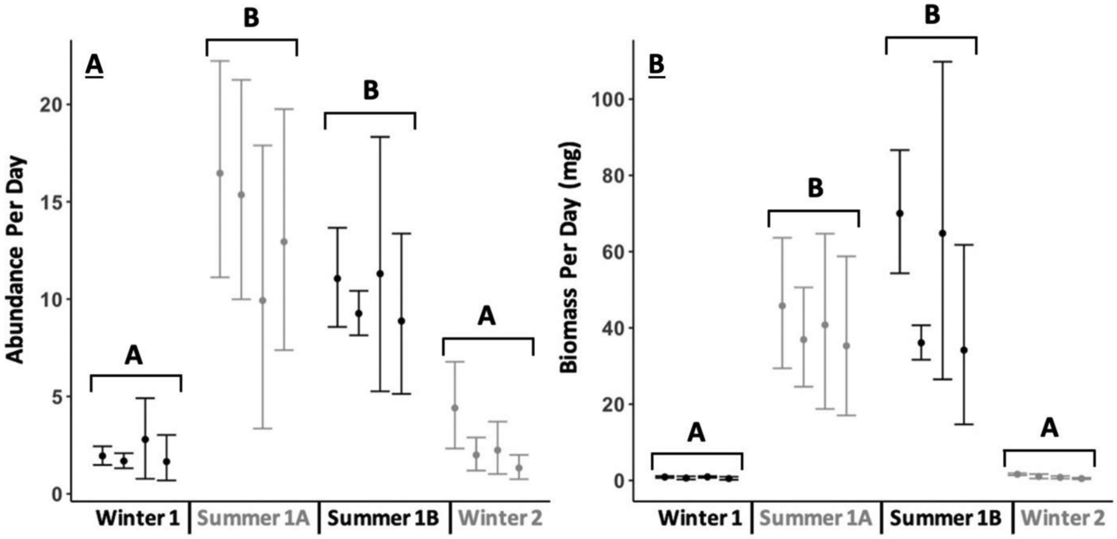

Fig. 4. Mean abundance (Part A) and biomass (Part B) for all arthropods, separated by collection and, within each collection, separated by block (1–4) (see Fig. 1). Error bars represent 95% confidence intervals; shading is for readability. Results of Tukey's HSD tests are indicated by letters, with different letters signifying differences between collections.

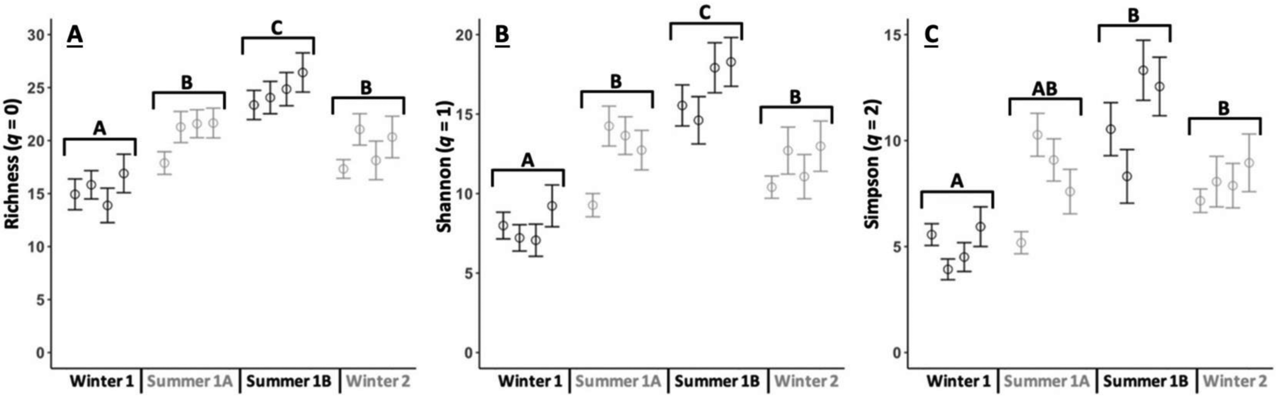

Fig. 5. Mean richness (Part A), Shannon's diversity index (Part B), and Simpson's diversity index (Part C) for each block (1–4) in each collection rarefied to 60 individuals from the observed individuals using iNEXT. The *q* numbers along the *y*-axis refer to the Hill numbers used in calculating these values. Error bars represent the lower and upper control limits calculated by iNEXT, and coloration or text and points are simply aesthetics. Results of Tukey's HSD tests are indicated by letters: collections differed if they are shown with no letters in common.

Table 2. Results of mixed model analyses for richness, Shannon diversity, and Simpson diversity. Results for total arthropods, insects, and other arthropods are all shown

		R^2	Random trap-pair effect	*F*	df	*P*
Total	Richness	0.605	0.138	14.3	3, 33	<0.001
	Shannon	0.639	0.240	13.6	3, 33	<0.001
	Simpson	0.601	0.270	9.1	3, 33	<0.001
Insects	Richness	0.619	0.080	13.2	3, 33	<0.001
	Shannon	0.601	0.001	11.8	3, 33	<0.001
	Simpson	0.640	0.013	11.7	3, 33	<0.001
Other arthropods	Richness	0.433	0.048	5.5	3, 33	0.004
	Shannon	0.620	0.316	5.9	3, 33	0.002
	Simpson	0.610	0.172	4.3	3, 33	0.012

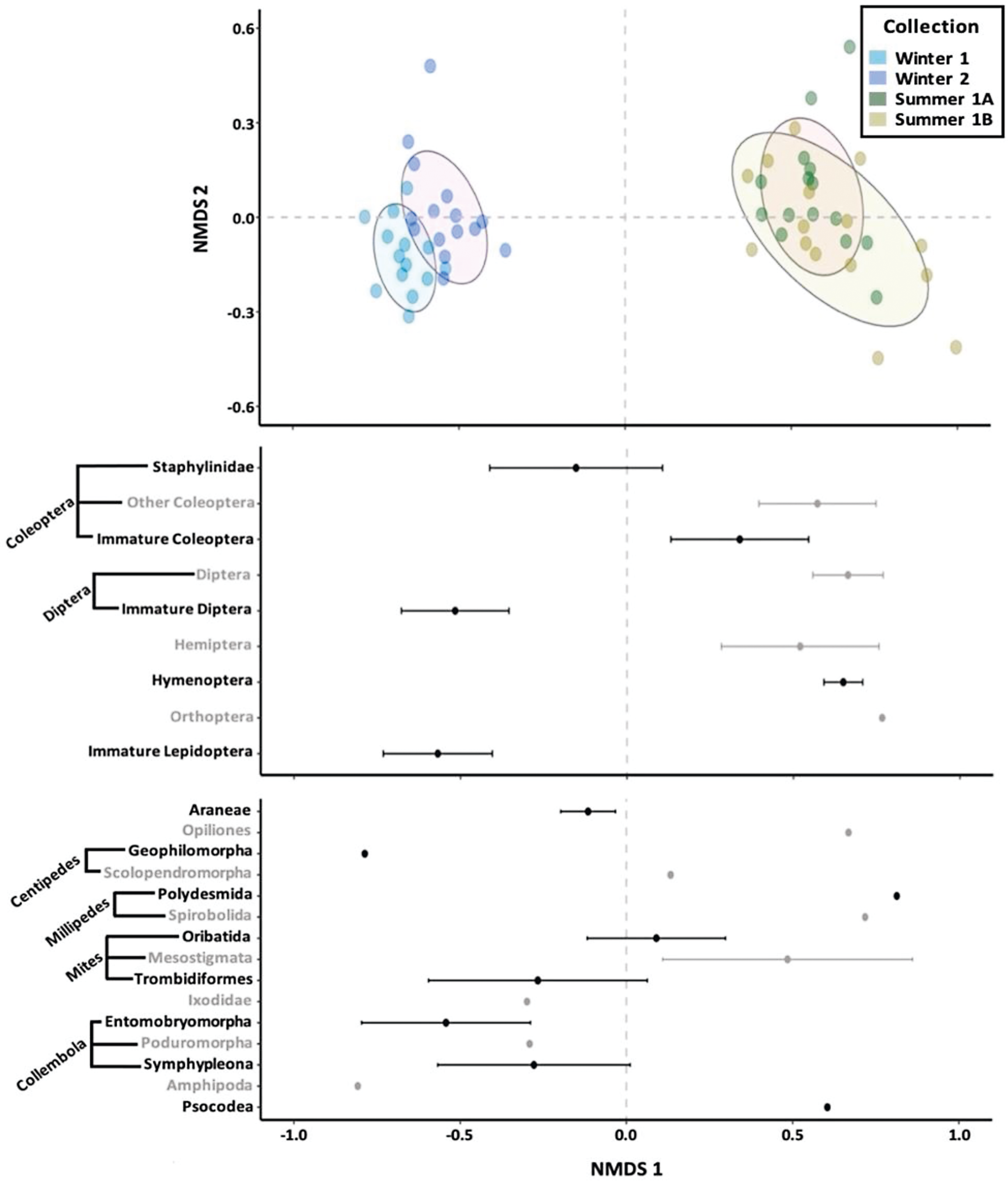

Fig. 6. Nonmetric multidimensional scaling (NMDS) of sampling sites and seasons in species space (upper). The bottom 2 panels show the different groups of arthropods and how they aligned along the divergent axis (NMDS 1), with error bars representing the variation of different morphospecies within the group. Bray–Curtis dissimilarity was used, and the resulting figure has a stress level of 0.112 and is a 3D solution, of which 2 axes are displayed here.

during the winter compared to summer. Across winters, spiders represented 12.6% of all arthropods collected, while in the summer, this percentage was only about 3.7%. The most abundant spider species in the winter was *Cicurina brevis* (Emerton 1890), and in the summer it was *Neoantisea magna* (Keyserling 1887), both species currently assigned to the family Hahniidae (WSC 2023). In general, more male spiders were captured than females for most species across both seasons, with the male:female ratio being about 6:1 in the winter and 2:1 in the summer (Table 5). Approximately 37% of spider specimens from the subset of traps could not be identified to the species level due to sexual immaturity or because they were in poor condition. The unidentified spider specimens were not included in Table 5, but many were still identified at the generic level (Supplementary Appendix C). These included small numbers of juveniles belonging to families not represented in Table 5: Araneidae (*Neoscona arabesca* (Walckenaer 1841), summer), Tetragnathidae

(*Tetragnatha* sp., winter), and Thomisidae (*Ozyptila* sp., summer and winter) (Supplementary Table S3).

Discussion

Overall Findings

The results indicated significant numbers of arthropods are active during winter within the subnivium habitat of the forest floor in our study area (Figs. 3 and 4). Furthermore, the community composition of active arthropods differed greatly between winter and summer (Fig. 6). We therefore reject the hypothesis (H2) that winter-active communities are simply a subset of summer-active communities overwintering. While there was a nontrivial degree of overlap among morphospecies captured across the 2 seasons, there were numerous taxa that were relatively abundant in winter collections and were absent or very rare in summer collections. Overall, 89 distinct morphospecies were captured in pitfall traps during winter. Not surprisingly, total and per trap day abundance were considerably lower in winter, this fact supports half of our hypotheses (H1) about lower abundance metrics during the winter. This must be partly due to reduced movements at low ambient temperatures but probably also reflects some differences in life history and phenology. The arthropods active in the subnivium were also considerably smaller in mass on average than the arthropods active in the summer. Rarefied diversity indices were, on average, higher in summer than in winter, which partially supports the other half of our hypothesis (H1) about winter having lower diversity metrics. Differences in diversity between collection seasons, however, were not as clear cut as anticipated as our early summer collection did not differ from the second winter (Fig. 5). Interestingly, richness was reduced more strongly in winter for insects than for other arthropod richness.

Table 3. Results of the pairwise analysis comparing composition of all arthropods among collections

Comparison	df	F. model	R^2	*P*
W1 & S1A	1	29.349	0.512	0.001
W1 & S1B	1	26.72	0.488	0.001
S1A & W2	1	29.0192	0.509	0.001
S1B & W2	1	27.396	0.495	0.001
W1 & W2	1	3.232	0.104	0.001
S1A & S1B	1	3.763	0.119	0.002

Comparison to Previous Subnivium Studies

This is the first study that we know of to directly compare metrics of arthropod diversity and composition across summer and winter arthropods, so there are no studies with which to directly compare our results. We are, however, able to compare what we found in the winter portion of our study to other subnivium research of arthropods. From both winter collections, we collected about 7,250 individual arthropods belonging to 89 morphospecies and 47 families using 30 traps that were active for 56 days and replicated for 2 consecutive winters. On average, during the winter, we collected about 2 individuals per day in each trap, with new morphospecies appearing in each trap about every 75 days and a new family appearing around every 143 days. The rates of capture of individuals and new morphospecies and higher taxonomic ranks were roughly in line with other studies of subnivium arthropods (Merriam et al. 1983, Schmidt and Lockwood 1992). This degree

Table 4. Additional taxonomic specificity was possible for morphospecies within the rove beetles (family Staphylinidae: identifications by Don Chandler), including the number of individuals collected in each season (Abundance) and the number of individuals collected when number of trap days is considered (A/TD). Relative contribution (%) of each species to the total number of Staphylinidae collected in each season is also shown

					Summer			Winter		
Subfamily	Tribe	Genus	Species	Authority	Abundance	A/TD	%	Abundance	A/TD	%
Aleocharinae	Athetini	—	—	—	53	1.89	57.0	43	0.38	12.4
Omaliinae	Anthophagini	*Acidota*	*subcarinata*	Erichson 1840	0	0.00	0.0	1	0.01	0.3
Omaliinae	Anthophagini	*Arpedium*	*cribratum*	Fauvel 1878	0	0.00	0.0	136	1.21	39.2
Omaliinae	Anthophagini	*Lesteva*	*pallipes*	LeConte 1863	0	0.00	0.0	109	0.97	31.4
Omaliinae	Anthophagini	*Porrhodites*	*inflatus*	(Hatch 1957)	0	0.00	0.0	40	0.36	11.5
Paederinae	Lathrobiini	*Lathrobium*	*fauveli*	Duvivier 1883	3	0.11	3.2	2	0.02	0.6
Paederinae	Staphylinini	*Tympanophorus*	*puncticollis*	(Erichson 1840)	1	0.04	1.1	0	0.00	0.0
Proteininae	—	*Proteinus*	—	—	1	0.04	1.1	12	0.11	3.5
Pselaphinae	Trichonychini	*Bibloplectus*	*integer*	(LeConte 1878)	0	0.00	0.0	1	0.01	0.3
Pselaphinae	Tychini	*Lucifotychus*	*testaceus*	(Casey 1884)	1	0.04	1.1	0	0.00	0.0
Scaphidiinae	Scaphisomatini	*Scaphisoma*	—	—	3	0.11	3.2	1	0.01	0.3
Scydmaeninae	Glandulariini	*Euconnus*	—	—	6	0.21	6.5	0	0.00	0.0
Scydmaeninae	Glandulariini	*Parascydmus*	—	—	1	0.04	1.1	1	0.01	0.3
Staphylininae	Staphylinini	*Laetulonthus*	—	—	1	0.04	1.1	0	0.00	0.0
Staphylininae	Staphylinini	*Quedius*	*peregrinus*	(Gravenhorst 1806)	20	0.71	21.5	0	0.00	0.0
Tachyporinae	Tachyporini	*Tachyporus*	—	—	3	0.11	3.2	1	0.01	0.3

Table 5. Additional taxonomic specificity was possible for morphospecies within the Order Araneae (identifications by Christopher Ziadeh with oversight from Mark Townley), including the number and sex of adult individuals collected in each season and the total abundance of each species when trap days are considered, (A/TD). The relative contribution (%) of each species to the total number of Araneae collected in each season is shown

				Summer				Winter			
Family	Genus	Species	Authority	♀	♂	A/TD	%	♀	♂	A/TD	%
Agelenidae	*Wadotes*	*calcaratus*	(Keyserling 1887)	15	38	1.89	37.9	0	2	0.02	0.5
Amaurobiidae	*Amaurobius*	*borealis*	Emerton 1909	0	0	0	0	2	4	0.05	1.6
Amaurobiidae	*Callobius*	*bennetti*	(Blackwall 1846)	1	0	0.04	0.7	0	0	0	0
Clubionidae	*Clubiona*	*bishopi*	Edwards 1958	1	2	0.11	2.1	0	0	0	0
Cybaeidae	*Cybaeota*	*calcarata*	(Emerton 1911)	0	2	0.07	1.4	0	0	0	0
Gnaphosidae	*Zelotes*	*fratris*	Chamberlin 1920	0	1	0.04	0.7	0	0	0	0
Hahniidae	*Cicurina*	*brevis*	(Emerton 1890)	1	2	0.11	2.1	39	277	2.82	84.7
Hahniidae	*Cicurina*	*pallida*	Keyserling 1887	3	2	0.18	3.6	2	17	0.17	5.1
Hahniidae	*Cicurina*	*robusta*	Simon 1886	0	0	0	0	0	1	0.01	0.3
Hahniidae	*Neoantistea*	*magna*	(Keyserling 1887)	12	47	2.11	42.1	6	1	0.06	1.9
Linyphiidae	*Bathyphantes*	*pallidus*	(Banks 1892)	1	0	0.04	0.7	0	0	0	0
Linyphiidae	*Centromerus*	*persolutus*	(Pickard-Cambridge 1875)	0	0	0	0	1	3	0.04	1.1
Linyphiidae	*Ceraticelus*	*fissiceps*	(Pickard-Cambridge 1874)	0	0	0	0	1	0	0.01	0.3
Linyphiidae	*Ceraticelus*	*minutus*	(Emerton 1882)	0	0	0	0	1	0	0.01	0.3
Linyphiidae	*Gnathonaroides*	*pedalis*	(Emerton 1923)	0	0	0	0	0	1	0.01	0.3
Linyphiidae	*Helophora*	*insignis*	(Blackwall 1841)	0	0	0	0	2	0	0.02	0.5
Linyphiidae	*Lepthyphantes*	*intricatus*	(Emerton 1911)	3	0	0.11	2.1	0	0	0	0
Linyphiidae	*Mermessus*	*maculatus*	(Banks 1892)	0	0	0	0	1	0	0.01	0
Linyphiidae	*Pityohyphantes*	*subarcticus*	Chamberlin and Ivie 1943	1	0	0.04	0.7	0	0	0	0
Linyphiidae	*Sisicus*	*penifusifer*	Bishop and Crosby 1938	0	0	0	0	0	2	0.02	0.5
Linyphiidae	*Tenuiphantes*	*zebra*	(Emerton 1882)	0	0	0	0	1	4	0.04	1.3
Linyphiidae	*Walckenaeria*	*castanea*	(Emerton 1882)	1	0	0.04	0.7	0	4	0.04	1.1
Linyphiidae	*Walckenaeria*	*directa*	(Pickard-Cambridge 1874)	1	0	0.04	0.7	0	0	0	0
Linyphiidae	*Walckenaeria*	*pallida*	(Emerton 1882)	2	0	0.07	1.4	0	0	0	0
Liocranidae	*Agroeca*	*ornata*	Banks 1892	2	2	0.14	2.9	0	0	0	0
Theridiidae	*Robertus*	*riparius*	(Keyserling 1886)	0	0	0	0	0	1	0.01	0

of congruence is surprising given the difference in habitats, trap designs, and geographic regions involved.

Summer vs. Subnivium Ground-Active Communities

A majority (63%) of the morphospecies that we detected in winter were also found in summer. However, some species, morphospecies, and larger taxonomic groups appeared predominantly or exclusively in the subnivium during winter. Of the 89 morphospecies present in the winter, 33 (37%) were exclusively found in the winter, not appearing at all in our summer sampling. This suggests that many arthropods specialize in exploiting subnivium habitats and may preferentially utilize the subnivium habitat over those present in the summer. The impact of this previously unreported, distinct temporal niche partitioning on important ecological processes is not known. There would be value in understanding the impacts of winter-active invertebrates on nutrient cycling in the plant–soil interface and energy flow through the brown food web(Cordone et al. 2020), as it seems possible that there are effects one could not easily predict from knowledge of summer-active invertebrates alone.

Patterns in Key Taxonomic Groups

Spiders.

Spiders were a dominant group in the subnivium, accounting for 13% of arthropods collected in winter compared with only 4% in summer (Fig. 3C; Table 4). Spiders are known to be active in the winter on top of the snow and in the subnivium (Merriam et al. 1983, Aitchison 1984b, 1987, Kirchner 1987, Schmidt and Lockwood 1992, Vanin and Turchetto 2007, Hågvar and Hågvar 2011, Ingle et al. 2020, Hågvar and Aakra 2006). They have unique biological traits that may contribute to the ability of winter-active species to feed at temperatures in the range of 2 °C to −2 °C (Aitchison 1984c). For example, digestion in spiders is extra-oral, and the liquefied products of this digestion are filtered in the mouth such that only particles about a micron or less in size enter the gut (Collatz 1987, Foelix 2011). This liquid diet may reduce the likelihood of suitable ice-nucleating sites existing in the gut, helping to prevent freezing (Aitchison 1987).

Species of the sheet web spiders (family Linyphiidae) had a moderately higher richness in our winter samples than in our summer samples (Table 5). There have been previous reports of sheet web spiders being diverse and sometimes abundant in the subnivium (Olynyk and Freitag 1977, Merriam, Wegner, and Caldwell 1983, Aitchison 1984b, Schmidt and Lockwood 1992, Hågvar and Aakra 2006, Vanin and Turchetto 2007, Hågvar and Hågvar 2011, Ingle et al. 2020). The greater richness of sheet web spiders could, in part, reflect the vertically restricted space available within the subnivium. Sheet web spiders would need to interact with the ground level more often in the subnivium than during the summer, increasing their likelihood of being collected by a pitfall trap. Additionally, sheet web spiders may be less likely to build prey-capture webs in the subnivium, or the webs may be more ephemeral than those in the summer due to changes within the snowpack (e.g., melting, sublimating, compression), prompting the spiders to move more often. Whatever the explanation, in this study, it was the hahniid genus *Cicurina* that was the most abundant subnivium spider group (90.1%), with the species *Cicurina brevis* alone representing nearly 85% of all spiders in the winter collections, and these were rare but present in the summer samples. *Cicurina* was transferred from the family Dictynidae to the Hahniidae in 2017, with a proposal that it become the type genus of a new family, Cicurinidae (Murphy and Roberts 2015), not accepted (see WSC 2023). Other genera more traditionally placed within Hahniidae—*Hahnia*, *Antistea*, and *Neoantistea*—as well as a former hahniid genus, *Cryphoeca* (now in Cybaeidae (WSC 2023) but included by Murphy and Roberts (2015) in their Cicurinidae), have also been found to be active in the subnivium or to be winter-active (Aitchison 1984b, Hågvar and Aakra 2006, Vanin and Turchetto 2007, Hågvar and Hågvar 2011, Ingle et al. 2020; this study), but only a couple studies have reported finding the genus *Cicurina* (Aitchison 1984b, Vanin and Turchetto 2007). To our knowledge, no other subnivium studies have recorded collecting *C. brevis*, which is interesting considering how common it was in this study and its relatively large known geographic range (Exline 1936, Chamberlin and Ivie 1940, Paquin and Dupérré 2003). There is little information on the life history of *C. brevis*. For species of *Cicurina* generally (Exline 1936, Chamberlin and Ivie 1940), adult individuals can be found throughout the year, and eggs are likely laid in the spring, with sexual maturity reached in the fall (Kaston 1981). This potentially explains why *C. brevis*, and more specifically, the males of this species, are so active in the winter that they may be searching for a mate in the subnivium. Additionally, many species belonging to the genus *Cicurina* are cave dwelling and have evolved characteristics typical of cave arthropods (Gertsch 1992, Paquin and Dupérré 2003). It is interesting to note that conditions in caves share some striking, if superficial, similarities with the conditions present in the subnivium.

Rove beetles.

A few groups of rove beetles also appeared to be common in the subnivium (Table 4; Supplementary Table S4). Rove beetles as a family are known to be active in the subnivium, having been found in previous subnivium studies as abundant (Aitchison 1979b, Merriam et al. 1983, Schmidt and Lockwood 1992, Slatyer et al. 2016). The taxonomy of Staphylinidae is difficult, and few other subnivium studies have identified rove beetles beyond the family level, though Aitchison (1979b) reported the subfamilies Aleocharinae and Tachyporinae as being active in the subnivium, as we found here. Species belonging to the tribe Anthophagini from the subfamily Omaliinae, including the species *Arpedium cribratum* Fauvel, 1878, *Lesteva pallipes* LeConte, 1863 and *Porrhodites inflatus* (Hatch, 1957), appeared exclusively during the winter and in relatively high abundance (Table 4). Members of Anthophagini are known to be active during cooler seasons, with some present in mountainous regions or the Arctic (Newton et al. 2000), suggesting low-temperature adaptations are widespread in this group. *Arpedium cribratum* lives in leaf litter and has a previously reported range from Iowa to Ohio (Newton et al. 2000). Thus, our finding extends their known distribution to at least northern New Hampshire. Members of *Lesteva pallipes* are active predators that live in leaf litter and have been known to inhabit caves (Newton et al. 2000). As with *Cicurina*, the presence of cave-inhabiting rove beetles in the subnivium supports the concept that some traits that are adaptive in caves are also adaptive in the subnivium. *Porrhodites inflatus,* another of our winter-active rove beetles, also lives in leaf litter, where it likely feeds on fungal spores and was previously known to be active under the snow (Crowson 1982, Newton et al. 2000). Other than rove beetles, few adult beetles were active in the subnivium (Table 1).

Immature arthropods.

Immature arthropods were present in all collections, but both immature beetles and immature flies accounted for a much higher percentage of total trap catch in the subnivium than they did in the summer. The immature morphospecies in the subnivium were likely among the dominant taxa found in the summer, just in an immature stage, and the subnivium provides them with favorable conditions for foraging until the return of warmer weather. Beetle larvae from the families Cantharidae and Carabidae have been reported as abundant in other subnivium studies (Aitchison 1979b, Merriam et al. 1983, Schmidt and Lockwood 1992). Fly larvae have also been reported, with the families Trichoceridae and Stratiomyidae noted as more abundant than others (Merriam et al. 1983, Schmidt and Lockwood 1992). Adult flies were nearly absent in our winter collections, with a few exceptions. Individuals of the genus *Chionea* (snow flies) appeared during both winter collections, with 5 individuals in winter 1 and 8 in winter 2. This unique group of wingless crane flies is known to be winter-active, being found both on top of the snow and in the subnivium (Schmidt and Lockwood 1992, Hågvar 2010). Snow flies both mate and lay eggs during winter (Hågvar 2010). Other than adult flies and beetles outside of rove beetles, large groups that were absent or rarely collected in the subnivium but were otherwise relatively abundant in the summer included Orthoptera and millipedes (orders Polydesmida and Spirobolida) (Fig. 3; Table 1).

Microarthropods.

Microarthropods were abundant in both winter and summer, but the relative proportion of mites (Acari) and Collembola were highly variable between collections, and abundances were highly aggregated. However, subgroups within the mites and Collembola did show evidence of seasonal partitioning (Fig. 3C; Fig. 6). For example, parasitiform mites belonging to Mesostigmata were present during both seasons but were much more abundant in the summer and scarce during the winter. Acariform mites belonging to Oribatida were relatively abundant during both winter and summer, especially members of Galumnidae. Other acariform mites belonging to Trombidiformes were also found in both summer and winter but had slightly higher relative abundance in the winter. Families within Trombidiformes that were more abundant in the winter than in summer included Bdellidae, Microtrombidiidae, and Rhagidiidae. Mesostigmatid and oribatid mites have previously been reported to be active in the subnivium, including the family Phthiracaridae, which we also reported in this study (Aitchison 1979c, Hågvar and

Hågvar 2011). Collembola of the orders Entomobryomorpha and Symphypleona seemed to be equally abundant in both winter and summer, with Entomobryomorpha highly abundant in both seasons. However, among the Entomobryomorpha, the family Isotomidae was relatively more abundant in the summer, while the family Tomoceridae was relatively more abundant in the winter. Collembola order Poduromorpha, specifically the family Hypogastruridae, was present in both seasons but accounted for a greater contribution in abundance to winter collections than to summer collections. Other subnivium studies that looked at Collembola also found that the orders Entomobryomorpha and Poduromorpha were active in the subnivium, but, except for the family Hypogastruridae, they reported different families from these groups than we did (Aitchison 1979a, Hågvar and Hågvar 2011).

Advantages for Arthropods in the Subnivium

It is at least a bit surprising that there is a distinct community of poikilothermic animals active in the forest floor beneath the winter snow. We hypothesize several potential benefits of being active in the subnivium. While we know subnivium arthropods must be mobile because they can be collected using pitfall traps, it is unlikely that they are moving and foraging at any great speed. Major components of the subnivium community are predators, especially spiders, centipedes, and rove beetles. These predators would not need to be very fast because there is likely an abundance of immobile prey in the subnivium. Grazers, fungivores, and omnivores in the subnivium likely also find themselves in a food web with reduced competition relative to what is present in the summer. Consequently, slower metabolism or energetic costs associated with the maintenance of low-temperature tolerance and adaptations may be offset by the relative ease of foraging and/or abundance of resources. Being smaller in size also seems to be advantageous to subnivium arthropods. One possible explanation for this difference in size between winter and summer arthropods is that the constricted subnivium space makes it more difficult for larger arthropods to move about. The fact that winter-active species are frequently undetectable during summer suggests the possibility of a tradeoff between traits that promote success in winter and summer.

Subnivium Specialists

We identified 4 species that we consider subnivium specialists, including *C. brevis*, *A. cribratum*, *L. pallipes*, and *P. inflatus*. We define subnivium specialists as arthropods that are not only present in the subnivium but are seemingly dominant components of the community that spend a large portion of their adult life stage in the subnivium and are rare or not active during the summer. An alternative hypothesis to these arthropods being metabolically dormant during warmer seasons is that they could simply be going elsewhere in the environment, like up into the canopy, and therefore are not (or rarely) detected in summer pitfall traps. However, the 4 species we identified as subnivium specialists are all known to reside in leaf litter, and neither they nor others in their clades have ever been reported as being arboreal. Therefore, the subnivium specialist concept seems like a more likely explanation. If we had been able to identify more arthropods to species, we would have undoubtedly identified other subnivium specialists beyond the 4 discussed here. While the loss of snowpack and the associated thermal refugium will likely have major impacts on all arthropods that spend winter on the ground, even subtle changes in structure, duration, or predictability of the subnivium will likely disproportionately impact subnivium specialists. This impact on subnivium specialists could possibly result in a decrease in the abundance of winter-active arthropods with potential for cascading effects on the subnivium food web.

Conclusion

The arthropod fauna in the subnivium make up a relatively diverse and distinct community, with numerous taxa using this space for foraging, dispersal, and finding mates. The uniqueness of the community, as revealed by this study, together with the likelihood that winter activity represents an important component of forest food webs and energy transfer across trophic levels, raises additional concerns as climate change threatens the subnivium habitat. It is highly likely that subnivium arthropod communities will be diminished in a global band as winter snowpacks decline from climate warming in temperate and boreal forests (Contosta et al. 2019, Burakowski et al. 2022). A better understanding of the ecology and natural history of winter-active forest arthropods would be valuable.

Acknowledgments

We would like to thank Dartmouth College for letting us use the Second College Grant property and its facilities, especially the Director of Woodlands Operations, Kevin Evans. We appreciate the Adaptive Silviculture for Climate Change project for allowing us to conduct our research within their larger study design, especially Tony D'Amato. Don Chandler, the expert who identified all the rove beetles, was an immense help. Thank you, Naiade Caparelli, for making the graphical abstract. This project was a major physical undertaking, and we owe a sincere thank you to the people who helped in the field and those who helped with the process of sorting samples. We would like to thank lab and field technicians, including Charlie Farrell, Deanna Flood, Casey Coupe, Jessica Grondine, and Al Searing. Additionally, several graduate students and postdocs, including Caroline Kanaskie, Kenneth Windstein, and Todd Johnson, took time out of their busy schedules to help us out. We also had assistance from a few unpaid volunteers outside of the ecological research realm, including Mark Medeiros, Tim Ziadeh, Brian Taylor, Alexa Kip Smith, and Whitney. Finally, we would like to thank the 2 anonymous Reviewers for taking the necessary time and effort to evaluate this paper; we sincerely appreciate all the valuable comments, suggestions, and positive feedback. All authors declare that they have no conflict of interest.

Funding

Partial support was provided by NSF LTER 1637685.

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acquisition [lead], Methodology [supporting], Resources [equal], Software [equal], Supervision [lead], Validation [lead], Writing—review & editing [supporting])

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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