The Canadian Entomologist (2023), **155**, e16, 1–19
doi:10.4039/tce.2022.50

Published on behalf of the Entomological Society of Canada

ARTICLE

Coleoptera associated with intermittent streams and their riparian zones in south coastal British Columbia

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(Received 10 June 2022; accepted 7 November 2022)

Abstract

Intermittent streams that periodically cease surface flow have long been understudied in ecology and underrepresented in conservation policy. However, they currently account for 30–50% of the global river network, and that number is rising due to anthropogenic water extraction, land-use change, and climate change. We explored the Coleoptera biodiversity of the south Pacific coast region of British Columbia, Canada, using pitfall traps at perennial and naturally intermittent stream reaches, in shoreline, dry streambed, and riparian habitats, in both flowing (spring and early summer) and nonflowing (late summer) phases. We found that habitats around perennial reaches had significantly greater abundance of Coleoptera individuals than did those around intermittent reaches. However, neither habitat type nor flow regime was a significant predictor of taxon richness, and intermittent stream sites featured unique taxa that were not found near perennial streams. This aligns with recent results from other taxonomic groups; that is, finding that intermittent ecosystems can host high taxonomic diversity of Coleoptera, on par with or even greater than that of perennial streams. Because intermittent streams will likely become more prevalent within the global river network, a better understanding of how different species use these habitats is needed to inform appropriate biodiversity conservation efforts and flow management.

Introduction

Intermittent streams are characterised by periodic cessation of surface flow, resulting in either the complete drying of the streambed or the formation of isolated pools. This reoccurring pattern of flow cessation and onset may take place annually, based on seasonal changes, or every few years and supports dynamic aquatic–terrestrial ecosystems and habitat heterogeneity (Datry *et al.* 2014). Intermittent streams are common globally, existing on every continent. Estimates on the total length of intermittent streams vary widely, ranging from a conservative 30% of the global river network (Tooth 2000) to more than 50% if accounting for all low-order streams (Messager *et al.* 2021). Despite their global presence, intermittent streams have historically been overlooked in water legislation (Sullivan *et al.* 2019; Walsh and Ward 2021) and understudied ecologically compared to perennial streams, particularly in wetter biomes

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Subject editor: Jeff Battigelli

such as temperate zones, where their presence and ecological importance have been underestimated (Buttle *et al.* 2012; Stubbington *et al.* 2017).

Despite the variable and sometimes harsh environmental conditions of streams that dry, the biodiversity associated with these ecosystems may be on par with or even greater than that of perennial streams (Meyer *et al.* 2007; Perkin *et al.* 2021). Stream drying can promote high species turnover in stream and associated riparian invertebrate communities both directly, based on water availability, and indirectly, by providing habitat for migration and additional sources of nutrients for consumption (Larned *et al.* 2010). Studies done to date on intermittent stream biodiversity have primarily focused on aquatic species (*e.g.*, Valente-Neto *et al.* 2020; Bunting *et al.* 2021; Gill *et al.* 2022), but patterns of drying affect riparian communities as well, particularly terrestrial invertebrates (Corti and Datry 2014; Sánchez-Montoya *et al.* 2016, 2020). Many riparian invertebrates rely on aquatic invertebrates as prey, pursuing them either by swimming or by burrowing into the substrate to extract them (Hering 1998; Paetzold *et al.* 2005). Other taxa prey on emergent insects as they transition from aquatic to terrestrial and aerial stages (Ramey and Richardson 2017). Terrestrial invertebrates are therefore an entry point for aquatically derived energy and nutrients into terrestrial food webs. Prey availability, and thus energy flux into the food web, may be affected by flow intermittence; for example, drying can initially trigger emergence of adult insects from aquatic larval forms (Larned *et al.* 2010), which terrestrial predators can then feed on, but may ultimately lead to a loss of aquatic resources. Some evidence suggests that aquatic food webs may be maintained during dry phases by groundwater inputs (Burrows *et al.* 2018), providing a mechanism through which aquatic-to-terrestrial energy flows could be maintained despite drying. However, other work has found no loss of predatory terrestrial taxa after stream drying when compared to perennial streams over the same time period (Corti and Datry 2014).

Intermittent streams are becoming more common as water extraction, land-use change, and climate change alter hydrology and increase the likelihood and duration of drying (Datry *et al.* 2014; Tramblay *et al.* 2021). The extent of intermittent streams and the duration of flow cessation for these streams will increase, with the extent of this increase varying among regions (Larned *et al.* 2010; Jaeger *et al.* 2014; Pumo *et al.* 2016). A better understanding of intermittent stream ecology is necessary given ongoing global changes to the hydrological cycle. Riparian invertebrates are an important piece of this puzzle because they link aquatic and terrestrial habitats through trophic processes (Paetzold *et al.* 2005).

We explored the relationship between biodiversity and flow cessation in headwater streams by examining environmental characteristics and surveying terrestrial invertebrates. Specifically, we investigated the abundance and taxonomic richness of beetles (Coleoptera) in British Columbia, Canada, in a temperate region with numerous intermittent headwater streams. Beetles are abundant in riparian habitats and play a variety of trophic roles (Ramey and Richardson 2017; Steward *et al.* 2022). Some beetle species are able to colonise streambeds after drying, whereas others may specialise in riparian habitats (Ramey and Richardson 2017). Previous studies in British Columbia and the Pacific Northwest region of the United States of America have compared beetle abundance and diversity in riparian areas to those in upland areas (Rykken *et al.* 2007, 2011; Sultaire *et al.* 2021); however, we are unaware of any published research that addresses how beetles use stream-edge and dry-streambed habitat in British Columbia. Here, we asked how beetle abundance and taxonomic richness compare across stream types (perennial *versus* intermittent), flow phases (flowing *versus* nonflowing), and riparian *versus* streambed habitats. Specifically, we predicted that Coleoptera abundance and taxonomic richness would differ between riparian, shoreline, and dry-streambed habitats due to differences in habitat conditions and resource availability and that shifts in abundance and richness from flowing to nonflowing phases would be more pronounced around intermittent streams than around perennial streams because of greater shifts in abiotic conditions and resources.

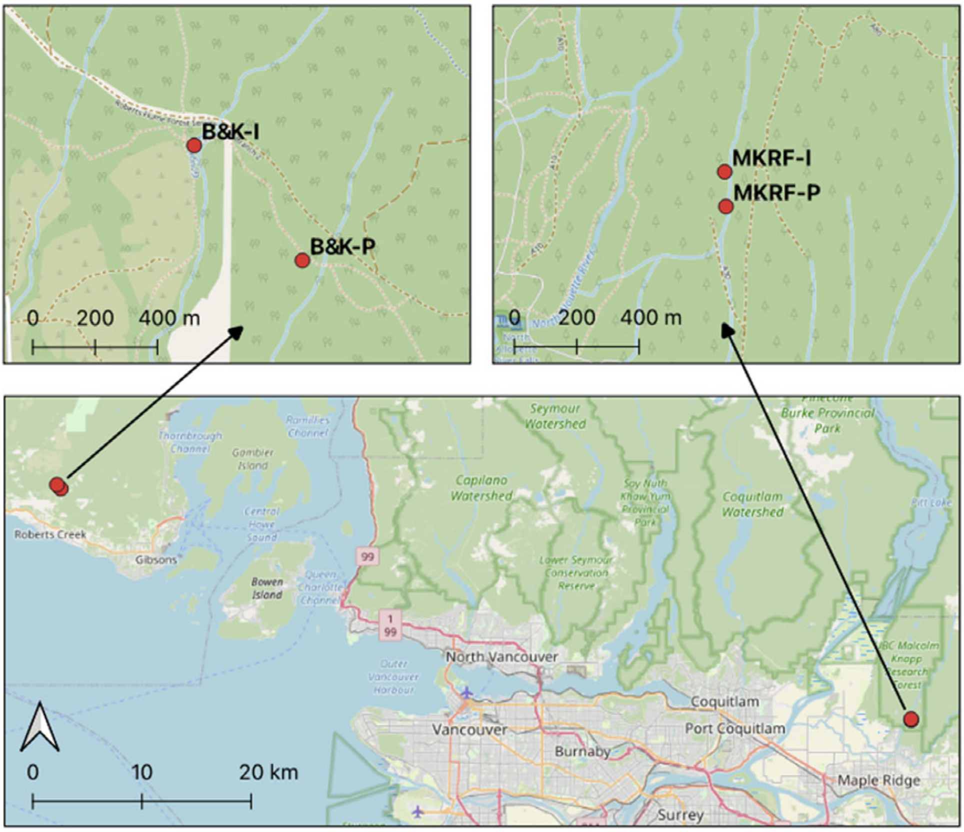

Fig. 1. Map of the four study sites in southern British Columbia: top left, the study areas of B&K, and (top right) those in the Malcolm Knapp Research Forest (MKRF). Map orientation is the same in inset panels as in larger panel. Background map data © OpenStreetMap contributors via Open Data Commons licence (www.opendatacommons.org/licenses/odbl).

Methods

Study areas

We established study sites in two areas in the south coast region of British Columbia, in the Coastal Western Hemlock Dry Maritime biogeoclimatic subzone: the Malcolm Knapp Research Forest and the area around the B&K multi-use trail system (referred to hereafter by its name, "B&K"). At both the Malcolm Knapp Research Forest and B&K, a perennial reach and an intermittent reach were selected from the headwaters of the same stream, totalling four study sites (Fig. 1).

The Malcolm Knapp Research Forest is a 5157-ha area managed by the University of British Columbia (Vancouver, British Columbia, Canada). The research forest is located in Maple Ridge, east of Vancouver, in the Coast Mountain foothills, on the traditional territory of the Katzie First Nation. The research forest experiences high levels of precipitation, ranging between approximately 2200 and 3000 mm per year (University of British Columbia 2004). The forest was extensively logged through the 1930s and more selectively since then as part of research operations (University of British Columbia 2004). One perennial reach ("MKRF-P") and one intermittent reach ("MKRF-I") were selected at the following coordinates: 49° 16' 06.6" N, 122° 33' 33.8" W and 49° 16' 10.02" N, 122° 33' 34.0" W, respectively. Both reaches are in the headwaters of a small unnamed tributary to the Alouette River, with MKRF-I being upstream of MKRF-P. The riparian areas had not been cut in the last two decades.

B&K is an area of forest and multi-use trail systems in Roberts Creek, on the Sunshine Coast, British Columbia, most of which lies in the swiya (territory) of the shíshálh Nation. The nearest climate station with long-term data, in Sechelt (roughly 10 km away), recorded 1010 mm of precipitation in 2021, which is roughly consistent with previous years' data from Sechelt and nearby Gibsons (Government of Canada, https://climate.weather.gc.ca/historical_data/search_historic_data_e.html). The area has been logged historically; the stand around the selected perennial site ("B&K-P") was 101–120 years old at the time of study, and that at the intermittent site ("B&K-I") was 21–60 years old (Sunshine Coast Regional District 2018). The B&K-P site is located at 49° 27' 29.8" N, 123° 37' 44.6" W, and the B&K-I site is located at 49° 27' 41.7" N, 123° 38' 01.8" W. Both reaches are located within the Gough Creek watershed but on separate tributaries.

For site selection, a reach qualified as intermittent if it was expected to experience flow cessation or complete drying of surface water at some period during the year. Because site selection occurred during the flowing phase, MKRF-I and B&K-I were selected by consulting land survey records and people with knowledge of the areas to identify reaches that would likely become intermittent later in the summer. We aimed to select reaches with lengths 10 times the channel widths. In each study area, the paired perennial and intermittent reaches were separated by at least 100 m in order to sample independent communities. In addition to the 100-m separation, we also aimed for the perennial–intermittent pair to have similar physical and environmental characteristics, which meant locating them in close proximity to one another (< 500 m). All sites were small headwater streams removed from urbanisation, with low chances of human disturbance of the sampling equipment. The MKRF-P site was moved slightly downstream between the flowing and intermittent sampling visits due to low flow during the extreme heat wave in the summer of 2021 (see Discussion).

Environmental variables and habitat characteristics

We visited each site in the summer of 2021 during both the flowing phase (spring, wet season: May 14–21, Malcolm Knapp Research Forest; June 3–11, B&K) and the nonflowing phase (late summer, dry season: August 20–27, Malcolm Knapp Research Forest; July 21–27, B&K). During the first site visit, percent cover of substrates across the reach was estimated visually. Substrate categories were as follows: silt–mud, sand (< 0.25 cm), gravel (0.25–2.5 cm), cobble (2.5–20 cm), boulder (> 20 cm), and bedrock (as in Little and Altermatt 2018). Morphological characteristics of each site were first assessed during the flowing phase, when we measured reach length, active channel width, and floodplain width. In the nonflowing phase, we noted whether complete drying of the reach had occurred or if isolated pools were present. Active channel width was also remeasured during the intermittent phase.

Riparian canopy cover was estimated once per phase at each site, using a modified spherical densiometer, because canopy cover was assumed to be changeable over the growing season. In addition, riparian vegetation was assessed through two other metrics: the three most abundant species (in terms of percent cover) at each site were identified visually, and the presence and absence of herbs, shrubs, and trees were each noted.

Sediment and soil moisture were calculated at each site during each phase. A 100-g sample was collected from the first 10 cm of sediment or soil at locations adjacent to each deployed pitfall trap (see *Terrestrial beetle diversity* subsection, below). The six riparian samples were then pooled, as were the six streambed or shoreline samples, resulting in one 600-g composite sample from riparian soil and one 600-g composite sample from streambed sediment or shoreline for each reach in each flow phase (representing a total of 16 composite samples throughout the course of the study). Samples were kept in sealed plastic bags in coolers with icepacks while they were being transported to the laboratory, where they were sieved at 2 mm. To determine moisture content, the sieved samples were then weighed, dried for 24 hours at 60 °C, and then reweighed (Corti and Datry 2014). Wet mass (m_{wet}) and dry mass (m_{dry}) of a given sample were used to calculate percent moisture content of the soil or sediment (MC), as shown in equation 1. To determine organic matter content, 5-g subsamples of the dried samples were weighed and combusted at 550 °C for four hours before reweighing. This process removes organic matter from the soil, leaving only "ash." Ash-free dry mass ("$AFDM$") was determined using the values of ash mass (m_{ash}) and soil mass before combustion (m_{dry}), as shown in equation 2:

$$MC = \left(\frac{m_{wet} - m_{dry}}{m_{dry}} \right) \times 100\% \tag{1}$$

$$AFDM = \left(\frac{m_{dry} - m_{ash}}{m_{dry}} \right) \times 100\% \tag{2}$$

Terrestrial beetle diversity

Pitfall traps were deployed at each site, in both the flowing phase and the nonflowing phase. Pitfall traps are an imperfect biodiversity surveying method because they are biased towards collecting individuals that are more active and move farther, typically those with larger body size (Hancock and Legg 2012). However, pitfall trapping is widely used because it is fairly efficient: pitfall traps can be left in the field for many days and require little to no monitoring in the meantime, and many replicates can easily be deployed in a single study due to their size, low cost, and ease of set-up. We deployed 12 pitfall traps per site – six riparian and six streambed or shoreline if the bed was not dry (similar to the method used by Sánchez-Montoya *et al.* 2020) – equalling 96 pitfall traps in total throughout the study. Three spots on each side of the stream were chosen for trap deployment, separated along the stream edge by a distance of at least twice the width of the stream channel, and a trap was set up in both the riparian and the streambed or shoreline habitats associated with that spot. Shoreline traps were placed 10–20 cm from the water's edge, and streambed traps during the nonflowing phase were placed in the centre of the stream channel. Riparian traps were placed above the high-water mark, at least 2 m from the shoreline trap. Traps consisted of three-ounce (88.7-mL) clear plastic cups, three-quarters filled with 1,2-propylene glycol-based antifreeze (Absolute Zëro RV Waterline Antifreeze, Recochem, Montréal, Québec, Canada). Propylene glycol is an attractant for carabid beetles but less so for other families (such as Silphidae), which potentially biases our results (Knapp *et al.* 2016). The cups were inserted into holes in the sediment so that the tops of the cups were flush with the ground surface. Plastic lids were positioned over the top of each cup opening and propped up using small twigs placed in the soil or sediment: this prevented rain and debris from entering the cups while still allowing invertebrates to enter. Although guidance barriers have been suggested as a method to more comprehensively survey arthropod biodiversity using pitfall traps (Boetzl *et al.* 2018), our traps were placed on uneven and rocky ground in the shoreline and riparian zones, making this technique unwieldy.

Pitfall traps were left for 6–8 days before specimens were collected from each trap. One streambed pitfall trap at MKRF-I during the nonflowing phase was discarded due to flooding when rainfall returned water to the stream. Therefore, specimens from 95 pitfall traps were collected throughout the course of the study. All specimens from the riparian traps at each site and phase were pooled, and the same was done with specimens from the streambed and shoreline traps. The pooling step is recommended in order to overcome trap-by-trap variability and bias inherent in pitfall trap studies (Boetzl *et al.* 2018). Doing this resulted in 16 pooled sample types, categorised by site, habitat, and flow phase – for example, "MKRF-P, riparian, flowing." Pooled samples were preserved in ethanol until they could be sorted and identified.

In the laboratory, specimens in each pooled sample were sorted based on morphological appearance visible without magnification, at which point specimens of the order Coleoptera were selected. Published keys and guides (Scudder and Cannings 2005; Peterson 2018; Avis *et al.* 2021; University of British Columbia 2021) were then used to identify Coleoptera specimens to the lowest possible taxonomic level. Identifications were checked against distribution maps to confirm that their presence in the study locations was reasonable (Global Biodiversity Information Facility, https://www.gbif.org). Whenever possible, we identified individuals to the species level. Due to lack of taxonomic information or detailed keys for some species, some individuals could only be identified to the genus or family level.

Analyses

Coleoptera specimens were analysed based on abundance (the number of individuals in a pooled sample) and taxon richness (the number of distinct taxa in a pooled sample). We analysed differences in total abundance and taxonomic richness using generalised linear mixed-effects models in the package "lme4," version 1.1-27.1 (Bates *et al.* 2015). In models of both response variables, we chose a Poisson distribution because the data represented counts. Because we were primarily interested in differences among reach types (intermittent *versus* perennial), flow period, and habitat, we included these factors as fixed factors and considered study area ("MKRF" or "B&K") as a random effect. We assessed the significance of fixed factors using likelihood ratio tests. Where likelihood ratio tests indicated a fixed factor was an important component of the model, we calculated the prevalence ratio associated with the fixed factor by extracting the estimated effect and its Wald 95% confidence interval and then back-transforming these by exponentiation. Where likelihood ratio tests did not indicate a fixed factor was an important component of the model, we did not provide estimates or confidence intervals.

We explored differences in community composition among sites and time periods using nonmetric multidimensional scaling (NMDS). We used two-dimensional NMDS on abundance data from the pitfall traps, and we performed separate analyses at the lowest identifiable–taxon level and at the family level using the "vegan" package, version 2.5-7 (Oksanen *et al.* 2020) in R, version 4.0.3 (R Core Team, Vienna, Austria, https://www.r-project.org).

We used paired *t*-tests to assess whether soil moisture and ash-free dry mass of soils and sediments changed at the sites from the flowing phase to the nonflowing phase. We then used Pearson's correlation test to assess whether beetle abundance or taxon richness was associated with soil and sediment moisture.

Results

Environmental characteristics

We successfully selected sites with similar environmental and physical characteristics (Table 1). Cobble was the substrate type with the most coverage at every site except MKRF-I, where sand covered 50% of the substrate area. At MKRF-I, disconnected pools formed in the nonflowing phase, whereas B&K-I experienced complete drying of the streambed.

In terms of vegetation, canopy cover increased at all sites between the flowing and nonflowing phases. It was also high across all sites and flow phases, ranging from 78 to 96%, with a mean of 87%. Herbs, shrubs, and trees were present at all sites. Western redcedar, *Thuja plicata* (Cupressaceae), and salmonberry, *Rubus spectabilis* (Rosaceae), were particularly abundant at all sites.

Table 1. Summary of environmental variables recorded at each of the four study sites: intermittent (I) and perennial (P) reaches in two study areas, Malcolm Knapp Research Forest (MKRF) and B&K (described in the Methods section). F denotes the flowing phase and NF the nonflowing phase at each site.

	MKRF-I		MKRF-P		B&K-I		B&K-P	
Variable	F	NF	F	NF*	F	NF	F	NF
Active channel width (m)	2.9	2.1	2.6	1.8	1.5	0	2.1	1.9
Floodplain width (m)	6.8		4.2	5.0	1.9		3	
Reach length (m)	18		25	18.5	10.0		15.3	
% cover silt/mud	0		0	0	0		0	
% cover sand (< 0.25 cm)	50		5	2	1		1	
% cover gravel (0.25 2.5 cm)	18		30	10	6		20	
% cover cobble (2.5 20 cm)	22		40	80	83		59	
% cover boulder (> 20 cm)	10		20	8	10		20	
% cover bedrock	0		0	0	0		0	
Canopy cover %	85	86	83	90	78	93	86	96
Riparian vegetation	Herbs, shrubs, and trees		Herbs, shrubs, trees	Herbs, shrubs, trees	Herbs, shrubs, trees		Herbs, shrubs, trees	
Dominant riparian species	*Thuja plicata*, *Gaultheria shallon* (Ericaceae), and *Rubus spectabilis*		*Thuja plicata*, *Rubus spectabilis*, *Blechnum spicant* (Blechnaceae), and *Polystichum munitum* (Dryopteridaceae)	*Thuja plicata*, *Rubus spectabilis*, and *Vaccinium parvifolium* (Ericaceae)	*Gaultheria shallon*, *Polystichum munitum*, and *Rubus spectabilis*		*Pseudotsuga menziesii* (Pinaceae), *Thuja plicata*, *Blechnum spicant*, and *Polystichum munitum*	
Type of drying (if intermittent stream)	N/A	Disconnected pools	N/A	N/A	N/A	Complete drying	N/A	N/A

*The MKRF-P site was moved slightly downstream between the flowing and intermittent sampling visits; therefore, certain environmental variables were re-recorded at the new site during the nonflowing phase.

Percent moisture content in soil and sediments decreased significantly ($t = 2.40$, $df = 7$, $P = 0.004$) between the flowing and nonflowing phases (Table 2); however, the shoreline habitats of the perennial reaches MKRF-P and B&K-P had 33% and 18% higher moisture, respectively, in the nonflowing phase than in the flowing phase. Percent moisture and ash-free dry mass were highly correlated ($r = 0.74$, $df = 14$, $P < 0.001$); however, no overall difference in ash-free dry mass was detected between the flowing and nonflowing phases ($t = 0.53$, $df = 7$, $P > 0.1$). Ash-free dry mass was significantly higher in riparian habitats (range: 9.9–37.6%) than in streambed and shoreline habitats (range: 2.6–6.2%; $t = 5.3919$, $df = 7$, $P = 0.001$; Table 2).

Terrestrial beetle diversity

We collected 894 individual specimens of Coleoptera during the study. These were sorted into 25 distinct taxa (Table 3), with 6.5% of individuals identified to species, 23.7% to genus, 65.4% to subfamily, and 4.4% to family. Of the 25 taxa collected, 14 (56%) were present in only one of the 16 pooled samples. Three taxa stood out with high frequencies of occurrence across the samples: Aleocharinae spp. (present in 81.25% of samples), *Pterostichus* spp. (present in 81.25% of samples), and *Scaphinotus angusticollis* (present in 75% of samples; Table 3). The most abundant taxon was Aleocharinae spp., of which 526 individuals were collected throughout the study (representing 59% of all individuals).

The individuals collected in pitfall traps belonged to 10 families: Carabidae (ground beetles), Cerambycidae (long-horned beetles), Coccinellidae (lady beetles), Curculionidae (snout and bark beetles), Dytiscidae (predaceous diving beetles), Elateridae (click beetles), Lampyridae (fireflies), Mycetophagidae (hairy fungus beetles), Nitidulidae (sap beetles), and Staphylinidae (rove beetles). Of these, four families appeared in only one sample each (Coccinellidae, Elateridae, Lampyridae, and Nitidulidae). Four other families (Carabidae, Curculionidae, Mycetophagidae, and Staphylinidae) were present in each study area, stream type, flow phase, and habitat. Cerambycidae, Lampyridae, and Nitidulidae were found only in habitats around intermittent reaches, whereas Coccinellidae and Elateridae were found only in habitats around perennial reaches. Staphylinidae was the most abundant family, with 701 individuals (including the 526 Aleocharinae spp. individuals), or 78.4% of the total collected. This is largely attributed to a single sample (B&K, perennial, riparian, flowing) that contained 482 Staphylinidae individuals. Carabidae were the second-most abundant family, with 158 individuals, or 17.7% of the total collected.

Beetle abundance and richness

The B&K study area had a higher abundance of Coleoptera than the Malcolm Knapp Research Forest study area did, with B&K accounting for 91.7% of the total specimens collected and 11 times more individuals per sample (mean abundance per pooled sample: 9.25 individuals at Malcolm Knapp Research Forest, 102.5 individuals at B&K). Reach type, habitat, and flow period were all significant predictors of total beetle abundance in pitfall traps (Figs. 2 and 3; Table 4; generalised linear mixed-effects models, likelihood ratio test $P < 0.001$ for all three variables). All three factors remained significant predictors of total beetle abundance when the outlier data point (B&K, perennial, riparian, flowing) that contained 482 Staphylinidae individuals (and 54% of individuals collected across the entire study) was removed from the data set and models were re-run (generalised linear mixed-effects models, likelihood ratio test $P < 0.001$ for reach type and habitat, $P = 0.04$ for flow period). Beetle abundance was fourfold higher in perennial reaches than in intermittent reaches (exponentiated model coefficient = 4.25, 95% confidence interval = 3.60–5.03), after accounting for the random effect of study area and the other two parameters of interest. Beetle abundance was threefold higher

Table 2. Percent moisture and ash-free dry mass (AFDM) content in collected soil and sediment samples at two research areas, Malcolm Knapp Research Forest (MKRF) and B&K.

Site	Sample	Flow phase	Percent moisture (%)	% Change in moisture	Percent AFDM (%)	% Change in AFDM
MKRF-P	Riparian	Flowing	93.5	−62.3	21.3	−3.0
		Nonflowing	35.3		20.7	
	Stream/shore	Flowing	33.8	30.0	6.0	−18.2
		Nonflowing	44.0		4.9	
MKRF-I	Riparian	Flowing	110.3	−61.0	37.6	−73.7
		Nonflowing	43.1		9.9	
	Stream/shore	Flowing	60.0	−62.5	6.2	−35.6
		Nonflowing	22.5		4.0	
B&K-P	Riparian	Flowing	37.7	−2.0	12.3	51.8
		Nonflowing	37.0		18.6	
	Stream/shore	Flowing	22.3	19.0	4.6	−26.1
		Nonflowing	26.5		3.4	
B&K-I	Riparian	Flowing	76.6	−39.2	18.4	60.1
		Nonflowing	46.6		29.4	
	Stream/shore	Flowing	21.8	−74.1	4.2	−37.5
		Nonflowing	5.6		2.6	

Table 3. Coleoptera taxa collected in all pitfall traps, their abundance, and their frequency of occurrence (percentage of the 16 pooled samples in which the taxon was found).

	Family	Identified taxon	Habitats where found	Abundance (# of individuals)	Frequency of occurrence
1	Carabidae	*Nebria* spp.	Riparian, stream/shore	87	37.5
2		*Omus dejeani* (Reiche)	Riparian	2	12.5
3		*Promecognathus crassus* (LeConte)	Riparian	1	6.25
4		*Pterostichus* spp.	Riparian, stream/shore	26	81.25
5		*Pterostichus lama* (Ménétriés)	Stream/shore	1	6.25
6		*Scaphinotus angusticollis* (Mannerheim)	Riparian, stream/shore	41	75.0
7	Cerambycidae	Cerambycidae sp. 1	Riparian	1	6.25
8		*Plectrura spinicauda* (Mannerheim)	Riparian	1	6.25
9	Coccinellidae	Coccinellidae family	Stream/shore	3	6.25
10	Curculionidae	Curculionidae spp.	Stream/shore	2	6.25
11		Molytinae sp.	Riparian	1	6.25
12		*Scolytus rugulosus* (Müller)	Riparian	1	6.25
13		*Steremnius carinatus* (Boheman)	Riparian	5	12.5
14	Dytiscidae	Dytiscidae family	Stream/shore	5	25.0
15	Elateridae	Elateridae family	Stream/shore	2	6.25
16	Lampyridae	*Ellychnia* sp.	Riparian	1	6.25
17	Mycetophagidae	Mycetophagidae spp.	Riparian, stream/shore	7	37.5
18		*Typhaea stercorea* (Linnaeus)	Riparian	5	12.5
19	Nitidulidae	Nitidulidae family	Riparian	1	6.25
20	Staphylinidae	Aleocharinae spp.	Riparian, stream/shore	526	81.25
21		Staphylinidae sp.	Stream/shore	18	6.25
22		*Stenus* sp.	Stream/shore	1	6.25
23		Tachyporinae spp.	Riparian, stream/shore	58	18.75
24		*Tachinus* sp.	Riparian, stream/shore	97	56.25
25		*Tasgius ater*	Riparian	1	6.25

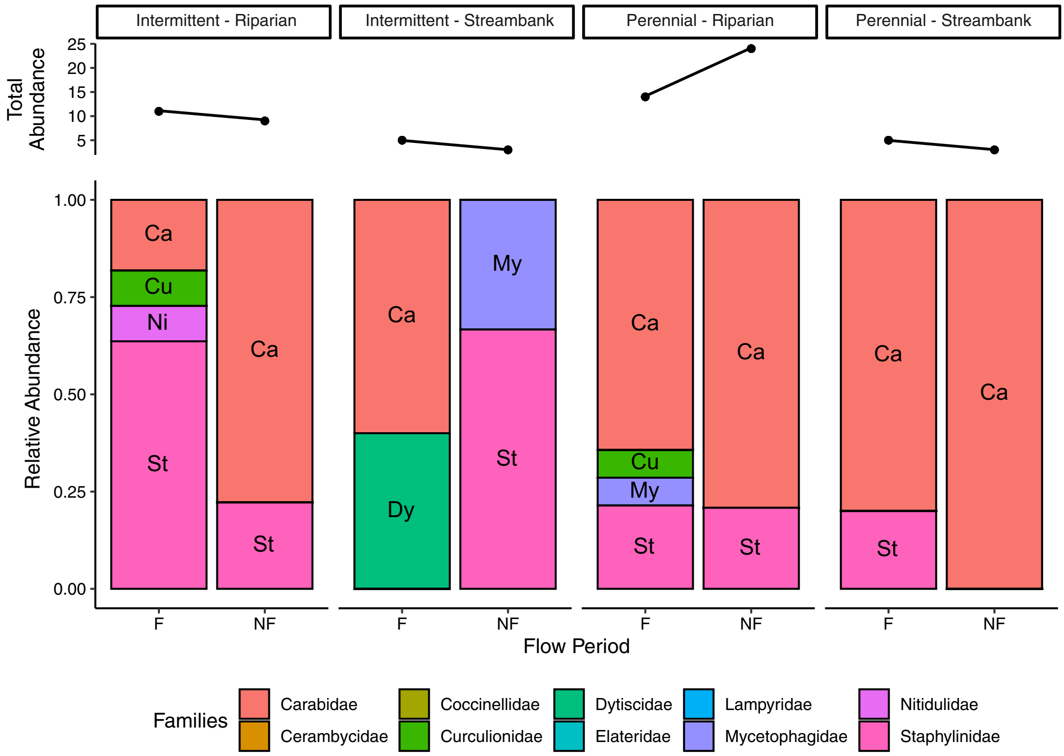

Fig. 2. Top panel, total abundance in number of individuals per pooled sample, and bottom panel, relative (proportional) abundance in the sample of different families of Coleoptera at different site types in Malcolm Knapp Research Forest. F, flowing phase; NF, the nonflowing phase. Sections of the relative abundance bars are labelled with the first two letters of the family name making up that portion of the relative abundance: Ca, Carabidae; Cu, Curculionidae; Dy, Dytiscidae; Ni, Nitidulidae; St, Staphylinidae.

in the nonflowing phase than in the flowing phase (exponentiated model coefficient = 3.26, 95% confidence interval = 2.79–3.80). However, abundance on streambanks and in dry streambeds was only about one-quarter that of riparian habitats, after accounting for the effects of flow period, reach type, and study area (exponentiated model coefficient = 0.23, 95% confidence interval = 0.20–0.28).

Taxon richness in B&K was also higher than in the Malcolm Knapp Research Forest, with 21 taxa found at B&K compared to 13 at the Malcolm Knapp Research Forest. However, none of reach type, habitat, nor flow period were significant components of models of taxonomic richness found in pitfall traps (Table 4; generalised linear mixed-effect models, likelihood ratio test $P > 0.10$ for all three variables).

Across study sites, soil moisture conditions were not correlated with total abundance nor with taxon richness ($|r| < 0.15$, $df = 14$, $P > 0.5$; Fig. 4).

Beetle community composition

At the family level, few clear patterns were detected in community similarity and dissimilarity among study areas, site types, habitats, and flow phases (Fig. 5A). However, family-level community composition was similar between the riparian habitats of intermittent reaches during the flowing phase at both study areas and between the streambank habitats of intermittent reaches during the flowing phase in both study areas (Fig. 5A). These site pairs were much more dissimilar during the nonflowing phase.

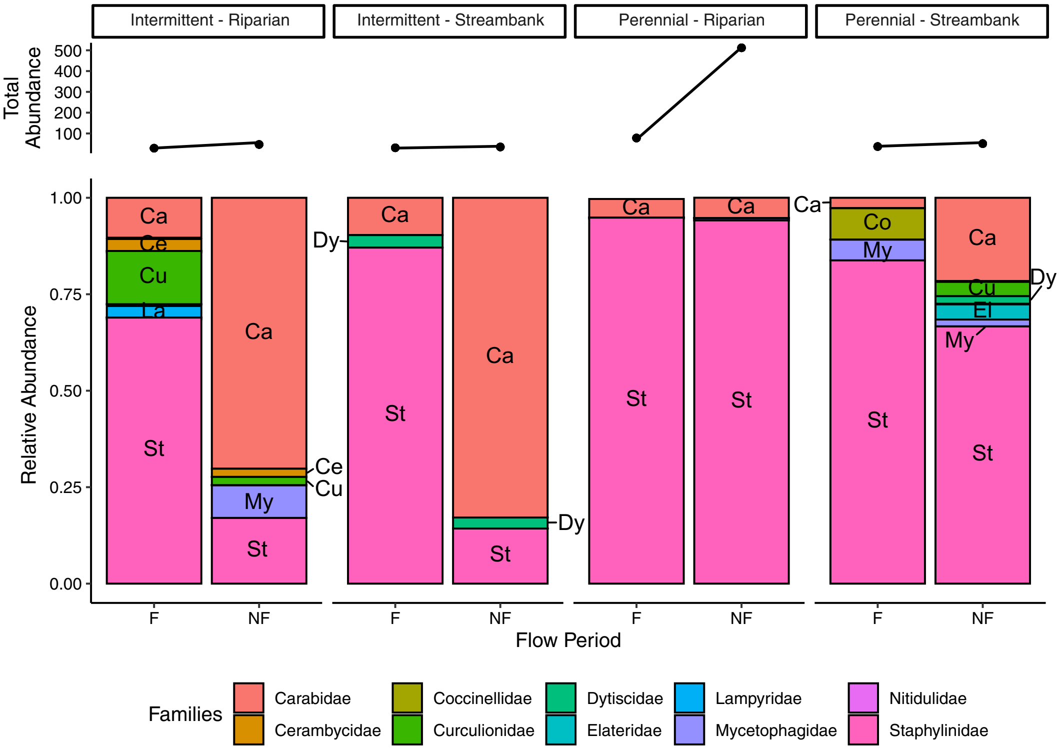

Fig. 3. Top panel, total abundance, number of individuals per pooled sample, and bottom panel, relative (proportional) abundance in the sample of different families of Coleoptera at different site types in the B&K study area. F, flowing phase; NF, nonflowing phase. Sections of the relative abundance bars are labelled with the first two letters of the family name making up that portion of the relative abundance: Ca, Carabidae; Ce, Cerambycidae; Co, Coccinellidae; Cu, Curculionidae; Dy, Dytiscidae; El, Elateridae; La, Lampyridae; Ni, Nitidulidae; St, Staphylinidae. Where relative abundance is too small to fit a text label on the bar, labels are placed beside the bar, and lines indicate which section of the bar the label refers to. Note the different y-axis scale for total abundance compared to Figure 2.

With the added detail of identifying taxa to subfamily, genus, and species level where possible, it appeared that communities were dissimilar between the flowing phase and the nonflowing phase, with most sites clustered in the lower left corner of the NMDS space (Fig. 5B). In the nonflowing phase, communities were more similar among perennial stream sites than they were among intermittent stream sites, where communities varied more in composition, including more divergence within habitat types (Fig. 5B).

Discussion

Overall, our results indicated that intermittent streams can host substantial coleopteran diversity, comparable to perennial reaches in richness but including different taxa. The study revealed high rates of taxa turnover associated with stream flow, location, habitat, and flow phase with regard to Coleoptera abundance and taxonomic richness in headwater riparian zones in coastal British Columbia.

One of our most notable findings was that, in our study area, taxon richness was identical between perennial and intermittent streams, despite abundance being four times greater in the former than in the latter. These results are consistent with findings from more arid zones (Sánchez-Montoya *et al.* 2016, 2020; Moody and Sabo 2017) and from a temperate river basin in Europe (Corti and Datry 2014). Within each study area, community composition varied

Table 4. Results of generalised linear mixed-effect models, using the Poisson distribution with a log link function. Estimates for the intercept and the effect of each parameter of interest are reported from the full generalised linear mixed-effect models for each response variable, and parameters that were significant ($P < 0.05$) according to likelihood ratio tests are indicated with asterisks. Study area (Malcolm Knapp Research Forest or B&K) was considered a random effect, and the variance associated with this random effect and the among-area standard deviation (in parentheses) is reported in the bottom row of the table.

Parameter	Total abundance	Taxonomic richness
Intercept	2.189	1.672
Reach type	1.449*	0.140
Habitat type	–1.449*	–0.329
Flow period	1.181*	0.140
Location	*1.446 (1.203)*	*0.031 (0.178)*

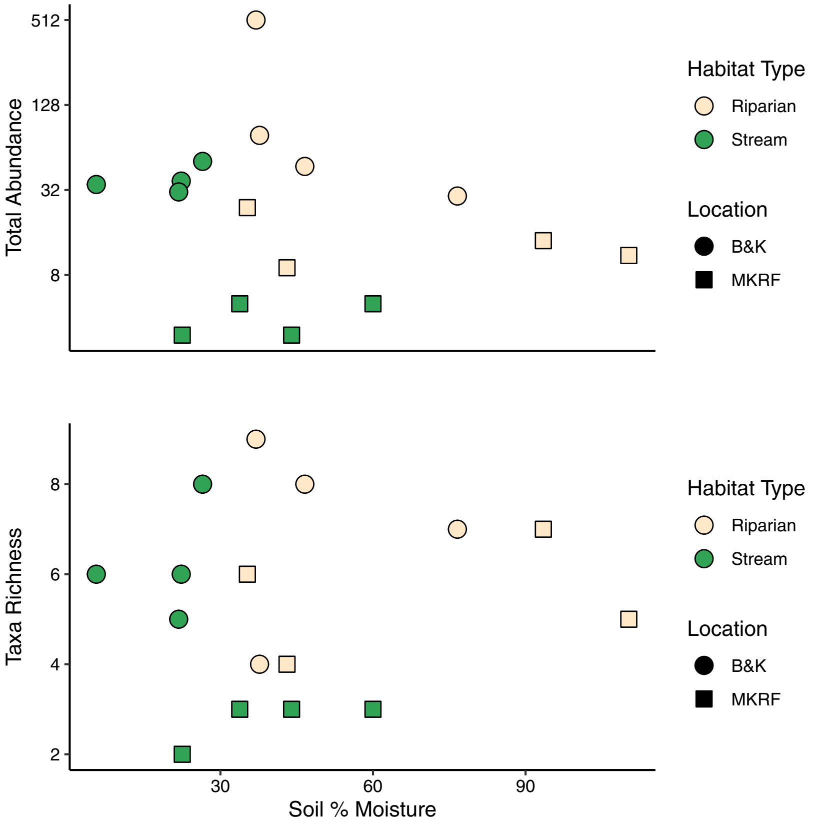

Fig. 4. Total abundance, or number of individuals per pooled sample, and taxa richness, or number of taxa, of Coleoptera caught in pitfall traps throughout the survey period at the two study locations. Colours indicate samples from riparian habitats and from streambank or streambed habitats. Circles indicate samples collected from the B&K study area, and squares indicate samples collected from the Malcolm Knapp Research Forest (MKRF) study area.

among sites and between time periods, despite intermittent and perennial sites being within 100–400 m of one another and, according to our assessment, presenting comparable environmental variables. This result is inconsistent with research on riparian invertebrates in European basins, where communities were very similar in perennial and intermittent reaches

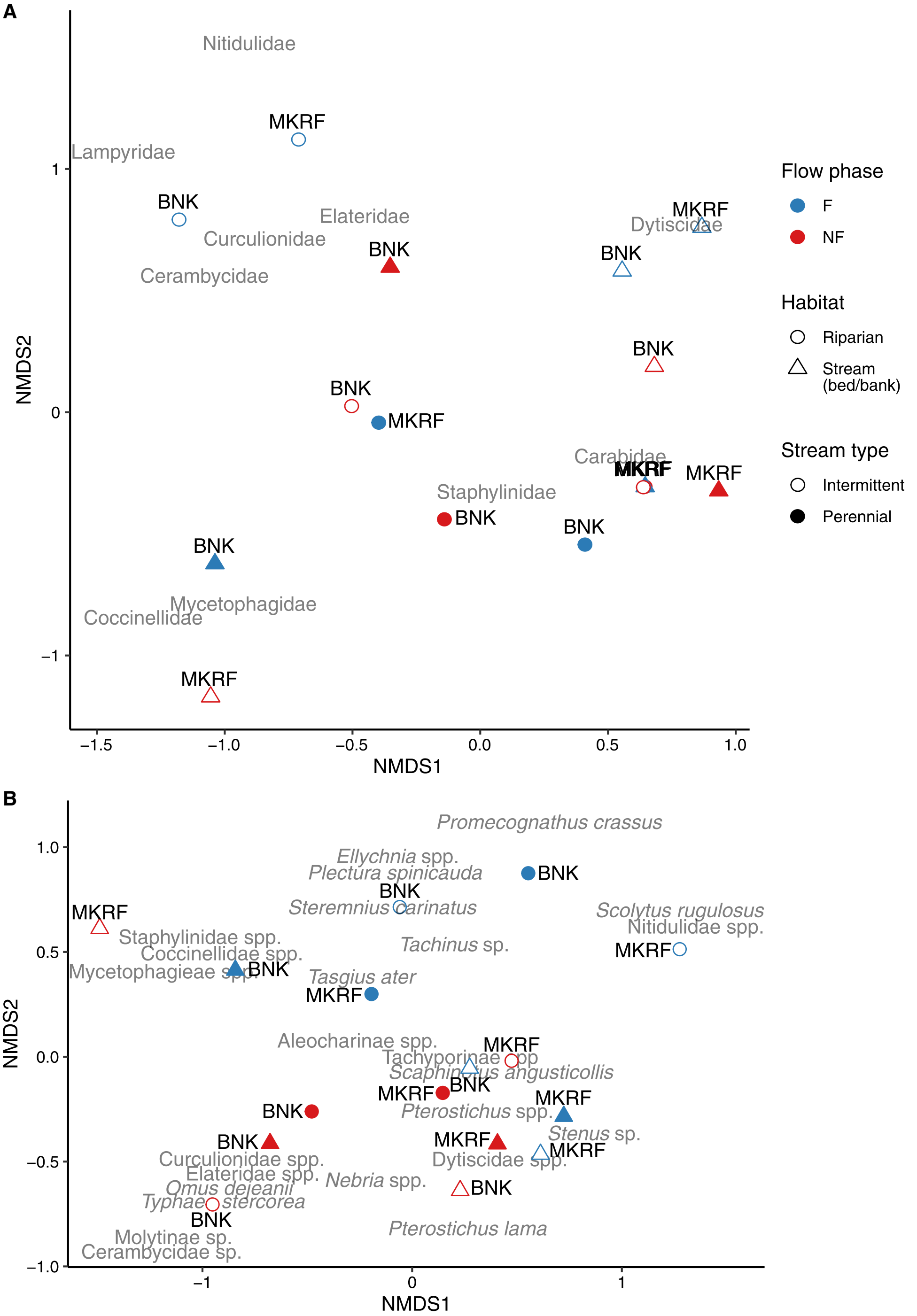

Fig. 5. Nonmetric multidimensional scaling (NMDS) of Coleoptera communities collected in pitfall traps, at the level of **A**, family (stress = 0.136), and **B**, lowest identifiable taxon (stress = 0.114). Colours of open and closed shapes indicate the flow phase when the community was collected: blue, flowing (early summer); red, nonflowing (late summer). Filled shapes indicate communities around perennial stream reaches, and open shapes indicate communities around intermittent stream reaches. Circles represent communities from the riparian zone, and triangles represent communities from streambank or (for intermittent streams during the nonflowing phase) streambed locations. Shapes are labelled with the study area where they were collected: MKRF, Malcolm Knapp Research Forest; BNK, B&K.

during the flowing phase (Corti and Datry 2014). During the flowing phase at both of our study sites, unique taxa were found at the intermittent site that were not present in the same habitat type (streambank, riparian zone) at the nearby perennial site. Previous research has attributed the dissimilarity between stream types to high taxa turnover due to the unique conditions created by patterns of flow cessation and onset (Moody and Sabo 2017). In our study, taxa from Cerambycidae, Lampyridae, and Nitidulidae were found only in habitats around the intermittent reaches. These taxa were rare in our data set but represent important functional diversity. For example, many Nitidulidae taxa feed on decaying material, and Cerambycidae are decomposers – functional roles that are less well represented among the taxa common across all study sites; these latter were often scavengers or predators. We therefore conclude that intermittent streams in British Columbia can harbour unique biodiversity not common around perennial streams.

We also found that streambank and streambed habitats had lower abundance of Coleoptera than riparian habitats did, especially at the Malcolm Knapp Research Forest. The presence of microhabitats and microclimates can strongly influence beetles' habitat choices (Lavallee and Richardson 2010). Diverse microhabitats can reduce competitive exclusion and encourage habitat specialisation in invertebrates (Ramey and Richardson 2017). The dynamic patterns of flow cessation and onset drive habitat heterogeneity (Larned *et al.* 2010; Datry *et al.* 2014), including the formation of microhabitats and microclimates, particularly in riparian zones (Ramey and Richardson 2017). This could explain the higher abundance and greater response to drying shown in the riparian sites of the present study. Near perennial reaches, Coleoptera abundance also increased from the flowing to the nonflowing phase. British Columbia experienced an extreme heat wave during the summer of 2021, and our study locations experienced short-term moderate to severe drought (Agriculture and Agri-Food Canada 2021). This likely reduced soil moisture and water availability in terrestrial ecosystems and pushed organisms into riparian zones near streams, where temperatures were likely cooler (Brosofske *et al.* 1997).

Despite the Malcolm Knapp Research Forest and B&K having similar environmental conditions and being only 85 km apart in a straight line, the two study areas returned notably different abundance and taxon richness results. For example, 91.7% of all Coleoptera individuals were collected at B&K. More different families were also found at B&K than at the Malcolm Knapp Research Forest. This may be a sampling effect, related to the overall higher number of individuals sampled due to the differences in abundance between the two study areas, or it may represent a true underlying difference in diversity. Despite their close straight-line distance, the fractal-like nature of British Columbia's coastline means that the sites were functionally distant from one another for dispersing beetles, with major rivers, inlets, and sounds presenting obstacles to land-based or short-distance aerial dispersal. As a result, the two locations may have different local species pools. However, regionally common taxa such as *S. angusticollis* were found at all four study sites.

Because B&K experienced complete drying during the nonflowing phase and the Malcolm Knapp Research Forest's intermittent reach retained disconnected pools, we could have expected that dynamics of the Coleoptera communities around the streams in those locations would be different. Previous studies have reported decreases in riparian invertebrate abundance in response to complete drying, due to aquatic invertebrates being removed as a food source (Burdon and Harding 2008; Corti and Datry 2014). This pattern was not revealed in our findings: the site in our study that experienced complete drying (B&K) had higher abundance. Across all habitat types and reaches, Coleoptera abundance declined by 25% from flowing to nonflowing phases at the Malcolm Knapp Research Forest and increased by 36% at B&K. This suggests that total abundance changed only moderately at intermittent sites in either location from the flowing to nonflowing phases and did not entirely collapse when flow ceased completely. Meanwhile, family-level community composition underwent a much larger shift at the Malcolm Knapp Research Forest than at B&K. At Malcolm Knapp Research Forest, at least 50% of the families found during the flowing phase were not present when we resampled during the nonflowing phase, and only one of the four sites (the riparian zone at intermittent reach) had new families found in the nonflowing phase that had not been found there in the flowing phase. At B&K, on the other hand, only two sites lost the presence of any families from the flowing to the nonflowing phase. Because the nonflowing phase was measured at different times (both in the Julian calendar and in terms of time since flow cessation) in the two locations, it is possible we were comparing communities at different points in their responses to drying (Sánchez-Montoya *et al.* 2016); this may partly explain the divergent results we obtained during the nonflowing phase at the two locations.

As shown in this study, intermittent streams are complex, dynamic systems, capable of hosting communities with unique taxonomic diversity. Historically, they have not been well protected in environmental legislation nor necessarily seen as valuable habitat. Yet our results indicate that intermittent streams and their riparian zones are important for many beetle taxa. Investigating the environmental conditions of different microhabitats associated with intermittent and perennial streams and their riparian areas would provide further insight into Coleoptera abundance and richness in these areas. Sampling over longer timescales, including during the wet winter months, would reveal whether community composition is stable in these different stream areas; for example, it could show whether the unique taxa found near intermittent streams are present there year round or they opportunistically disperse to intermittent stream areas during the summer months. Sampling over a greater geographic range would reveal whether the patterns that we found, such as the different taxa found around intermittent and perennial reaches, are general or not. Intermittent waterways and lower-order perennial streams may be increasingly important in regulating temperature and moisture under ongoing climate change, and these effects will influence the distribution of terrestrial invertebrates. In order to prepare effective conservation efforts in anticipation of the effects of climate change on global river networks, more research is needed on intermittent streams and the unique habitats and patterns of biodiversity associated with them.

Data availability. Data used in this manuscript have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.rfj6q57f5; Little and Schutz 2022).

Acknowledgements. The authors sincerely thank the shíshálh Nation for granting us permission to conduct field research within their swiya. They are also grateful to Ionut Aron at the Malcolm Knapp Research Forest for facilitating our research there and to John Richardson for invaluable advice in identifying study sites there. They thank Sage Dillabough for her help in processing soil and sediment samples and Thibault Datry for catalysing this research and providing a sampling protocol through the 1000 Intermittent Rivers project. The authors are grateful to the three anonymous reviewers who helped improve this manuscript. This project was funded by a Discovery Grant from the Natural Sciences and Engineering Council of Canada.

Conflicts of interest. The authors declare no conflicts of interests.

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Cite this article: Schutz, Z.B.D. and Little, C.J. 2023. Coleoptera associated with intermittent streams and their riparian zones in south coastal British Columbia. The Canadian Entomologist. https://doi.org/10.4039/tce.2022.50.