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Terrestrial Gastropod Grazing on Macrolichens in a Northern Broadleaf–Conifer Forest

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Abstract - Herbivory by terrestrial gastropods, particularly *Arion* spp. (a slug), can alter epiphytic lichen communities; however, little is known about this interaction in forests of North America. We used 3 lines of evidence to explore this interaction: field grazing assessments on lichen thalli, a 10-y re-measure of gastropod abundance, and gastropod feeding trials in a montane forest at Hubbard Brook Experimental Forest (HBEF) in northern New Hampshire. Grazing damage by terrestrial gastropods was widespread, though few sites had severe grazing. Grazing damage was significantly higher on flatter terrain and on broadleaf trees. Slug densities were significantly lower in 2016 than in earlier surveys (1997–2006) on 4 of 6 plots. In feeding trials, 2 common lichens, *Hypogymnia physodes* and *Platismatia glauca*, were grazed more heavily by both native and non-native slugs than other lichen species. However, the Succineidae (amber) snails preferred *Lobaria pulmonaria*, a lichen that has been declining at HBEF in the last decade. Overall, lichen communities in the HBEF were moderately impacted by terrestrial gastropod grazing, but potential effects of the non-native slugs at higher elevations and impacts on lichen health of widespread, moderate grazing deserve further study.

Introduction

Epiphytic lichens face many stressors, including the legacy of air pollution and acid rain (Gauslaa 1995, Gilbert 1970), loss and fragmentation of habitat through forest harvest, and targeted herbivory by invertebrates. In the last decade, we have noticed a decline in the presence and health of the large and conspicuous lichen, *Lobaria pulmonaria* (L.) Hoffm. (Lung Lichen), at our study site, Hubbard Brook Experimental Forest (HBEF) in north-central New Hampshire. Pollution inputs have greatly decreased (Likens et al. 1984, 1996) and lichen diversity and abundance appear better explained by plot traits than pollution indicators (Cleavitt et al. 2019); thus, we explored an alternative explanation for this decline. Studies from Europe have demonstrated impacts of gastropod grazing as an alternative driver of lichen species abundances (Asplund and Gauslaa 2008, Vatne et al. 2010), and, in the Northeast, the presence of non-native slugs may accentuate this impact. For example, *Arion* is a gastropod genus containing competitive European slug species that were introduced to the US by humans (Martin 2000), and they have been recognized as a potential threat to plant conservation (Moss and Hermanutz 2010). Lichens and fungi are known to be a relatively high proportion of their diet (Asplund and Gauslaa 2008, Hotopp et al. 2013, Martin 2000).

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Gastropod grazing on lichens in forests of northeastern North America has received little study, although concern has been raised in Nova Scotia (Cameron 2009). In particular, the potential impact of the non-native slugs *Arion* spp., has been largely unexplored. Thus, we addressed 3 questions: (1) Has the abundance of gastropods in the HBEF increased in recent years compared to surveys conducted during 1997–2006 (Skeldon et al. 2007)? (2) Does grazing damage to lichen thalli vary across the landscape in relation to tree species composition and topographic factors such as elevation and slope angle? (3) Do non-native *Arion* spp., differ from native gastropods in their preference for lichen species, potentially resulting in impacts on epiphytic lichen community composition?

Methods

Field-site description

The HBEF is a Long-term Ecological Research (LTER) site in Grafton County, NH (43°56'N, 71°45'W) with an average January temperature of -8 °C, an average July temperature of 19 °C, and mean annual precipitation of 140 cm (Bailey et al. 2003). The HBEF encompasses 3160 ha of mixed northern hardwood–conifer forest spanning elevations of 252–1015 m. The dominant tree species in the HBEF are *Fagus grandifolia* Ehrh. (American Beech), *Betula alleghaniensis* Britt. (Yellow Birch), *Acer saccharum* Marsh. (Sugar Maple), *Picea rubens* Sarg. (Red Spruce), and *Abies balsamea* (L.) P. Mill. (Balsam Fir), with the conifer species being most abundant at higher elevations (Schwarz et al. 2003). The forest was widely disturbed by logging and hurricane damage in the late 19th and early 20th century. The soils are mostly well developed, acidic Spodosols. A preliminary assessment of diversity and abundance of epiphytic lichens at the HBEF documented 67 species of macrolichens (Cleavitt et al. 2019).

For this study, we used 3 sites with long-term monitoring plots within the HBEF. A network of 0.05-ha circular plots spans the entire valley and is designated as the valley-wide (VW) plots (Schwarz et al. 2003; Fig. 1). We selected 51 of these VW plots for the present study, representing the variety of forest composition, elevation, and topography within the HBEF (see Table S1 in Supplemental File S1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n26-2-N1664-Cleavitt-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1664.s1). To evaluate recent changes in gastropod abundance, we resampled 6 plots in the HBEF that were used by Skeldon et al. (2007) to quantify the effects of restoring soil calcium on gastropod abundance. These plots are located in a reference site (REF; 3 plots) for watershed studies at the HBEF (Fahey et al. 2005) and an adjacent, experimentally treated watershed, W1 (here designated "CAL", 3 plots; Fig. 1). The REF plots are representative of the ~100-year-old forest along the elevation gradient on the south-facing, gaged watersheds (Fahey et al. 2005). The CAL plots have a similar history, but received a treatment of wollastonite ($CaSiO_3$) equivalent to 1.6 tons calcium/ha in October 1999 (Peters et al. 2004, Skeldon et al. 2007). We added 1 plot in the CAL site to our 51 VW plots for a total of 52 plots assessed for gastropod grazing pressure.

Grazing damage assessment.

On each of the 52 plots, we chose up to 10 trees (>10 cm diameter at breast height [DBH]) nearest to the center of the plot for assessment to randomize the samples of lichen communities and tree species assessed and to assure that plot characteristics were coordinated with the grazing data. Six plots had low levels of lichen presence and we could only assess 8–9 trees (hence, a total of 513 trees). To obtain a representative sample, on each tree in the trunk with 3 or more thalli present, we scored grazing on lichens within an area 0.5–1.5 m off the ground. We distinguished gastropod herbivory from other forms of damage by the presence of grazing trails and often by slime deposits. We assessed herbivory on lichens in the field with the aid of a hand lens (10x magnification) and used a visual scale for the extent of herbivory damage at the genus level that had 4 possible scores: 0 = no damage on any thalli of the genus, 1 = grazing marks visible for 1 or more thalli (at 10x magnification), 2 = grazing damage visible with the naked eye on 1 or more thalli, and 3 = grazing damage obvious and extensive on most or all thalli.

We analyzed grazing scores using Proc Glimmix in SAS 9.4. We reduced scores to a binary score of little to no grazing (field scores 0 and 1) and obvious to severe grazing (field scores 2 and 3). The model had a binomial distribution with a logistic-link function. Plot, tree, and lichen were random variables, and elevation, plot steepness, tree density, and tree composition group (conifer or broadleaf) were fixed variables in the model.

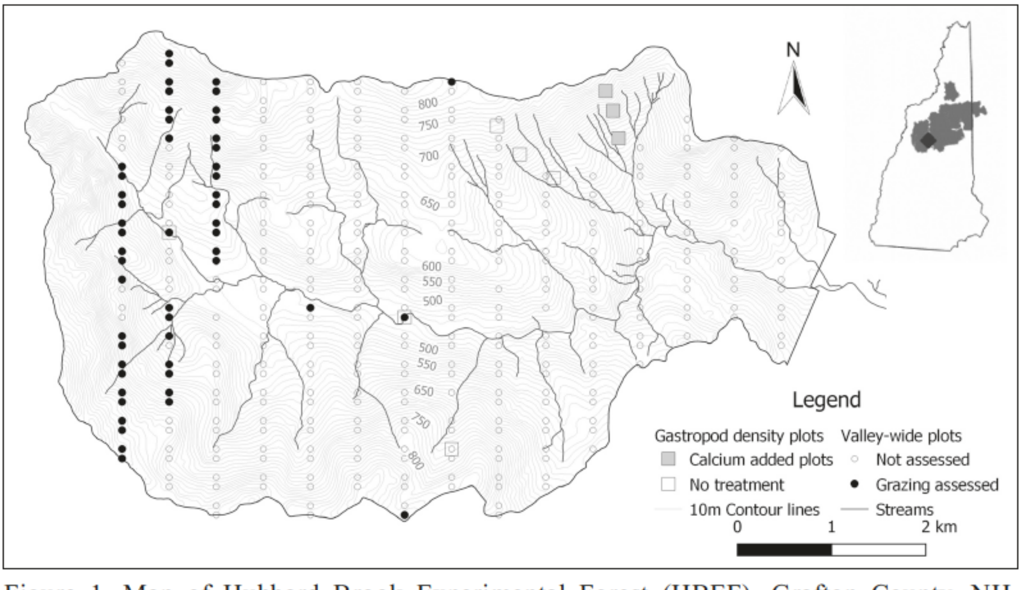

Figure 1. Map of Hubbard Brook Experimental Forest (HBEF), Grafton County, NH, showing the location of study plots for gastropod density counts (n = 9 plots) and grazing assessments (n = 52 plots). On the state inset, the location of the White Mountain National Forest is shown by dark gray filled area and HBEF is depicted by a diamond. Plot descriptions are provided in supplemental Table S1 (see Supplemental File S1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n26-2-N1664-Cleavitt-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1664.s1).

Gastropod density measurement.

We measured gastropod densities at 3 elevations (520 m, 610 m, 700 m) in each of 3 sites (REF, CAL, and VW; Fig. 1). Skeldon et al. (2007) surveyed 2 of the sites (REF and CAL) during 1997–2006, and we added 3 of the VW plots at corresponding elevations to broaden the sample. We surveyed the gastropods using the cardboard-sheet method with the dimensions of the materials, timing of surveys, and other parameters precisely replicating the previous surveys that took place in 1997–2006 (Skeldon et al. 2007). We briefly outline the methods here and recognize the same caveats on the method in terms of not fully capturing the terrestrial gastropod diversity (Skeldon et al. 2007). After removing fallen branches and other debris, we placed sheets of paperboard (n = 15 per plot; surface area = 0.56 m^2, thickness = 0.7 mm) in direct contact with the litter layer in late May 2016 (Skeldon et al. 2007). We left the boards to naturally mold to the forest floor for at least 28 d before surveying. After >7-mm rain events on 30 June 2016 and 2 August 2016, field crews surveyed the 3 areas simultaneously. To minimize potential biases, we conducted the late-June survey from low-to-high elevation plots and the early August survey from high-to-low elevation plots; we shuffled crew members and assigned new locations for the 2 surveys. During the surveys, each board was carefully turned over and we counted only gastropods that adhered directly to the underside of the board itself (i.e., not to leaf litter attached to the board) (Skeldon et al. 2007). Crews recorded counts of individuals in 3 categories: native slugs, non-native slugs, and total snails. The most common taxa (*Arion* spp., *Philomycus* spp., *Discus catskillensis* Pilsbry, and snails of Succineidae family) were collected for laboratory preference-feeding trials (see below). We followed Watson and Dallwitz (2005), White-McLean (2011), and Hotopp et al. (2013) to identify the terrestrial gastropods.

We conducted temporal comparisons with previous surveys (Skeldon et al. 2007) using analysis of means (ANOM) for ranks by plot (for REF and CAL only). We tested whether the gastropod densities in 2016 were significantly above or below the long-term average densities by plot. Using only the 2016 data for all 3 sites (VW, REF, and CAL), we tested for spatial differences by Wilcoxon matched pairs with counts matched by board within plot for native versus non-native slugs and for total snails versus total slugs.

Preference feeding trials

We used feeding trials to evaluate consumption of lichens by native (*Philomycus* spp.) and non-native (*Arion* spp.) slugs and the most common snail species present, *Discus catskillensis* and amber snails (Succineidae). After we collected the gastropods from the boards, we fed them lettuce in outdoor shaded conditions prior to the start of the first feeding trial. Lichen species used in the main feeding trial were: *Hypogymnia physodes* (L.) Nyl., *Lobaria pulmonaria*, *Myelochroa aurulenta* (Tuck.) Elix & Hale, and *Punctelia rudecta* (Ach.) Krog. We noted that these species differ in frequency, abundance, and grazing damage in the field. *Hypogymnia* was found the most frequently and most often had minimal to moderate grazing damage (Table 1). *Lobaria* is the least common and always exhibited moderate grazing damage targeted to cephalodia. *Myelochroa* and *Punctelia* were intermediate in frequency of occurrence, and both experienced moderate to severe grazing damage (Table. 1). These lichens differ in tissue chemistry, though all except *L. pulmonaria* contain atranorin (Table 1; Hinds and Hinds 2007)). We selected all lichens for their abundance and relative ease of collection at the HBEF except for *L. pulmonaria*, which was shipped from Maine where it is much more common. The observed decrease in abundance and health of *L. pulmonaria* at the HBEF in

Table 1. Level of grazing damage scored on epiphytic lichens on conifer (con.) and broadleaved (broad.) trees in Hubbard Brook Experimental Forest, NH. "Scored" is the number of trees on which thalli of that genus were scored. The scoring categories are no grazing, minimal grazing (min.: grazing on 1 thallus on the tree), moderate grazing (mod.: grazing visible with magnification on many thalli on the tree), and severe grazing (grazing visible without magnification on all or almost all thalli on the tree). Lichen chemistry is summarized from Hinds and Hinds (2007). Asterisks (*) denote lichens that were included in the feeding trials.

				Grazing				
Lichen	Scored	On con.	On broad.	No	Min.	Mod.	Severe	Chemistry
Candelaria	11	0	11	11	0	0	0	Calycin, pulvinic dilactone
Cetrelia	1	0	1	0	0	1	0	Atranorin
Cladonia	122	65	57	41	34	46	1	Fumarprotocetraric acid
*Flavoparmelia**	1	1	0	1	0	0	0	Usnic and protocetraric acids
*Hypogymnia**	91	82	9	22	29	37	3	Atranorin, physodic, protocetraric, 3-hydroxyphysodic, physodialic acids
Imshaugia	43	42	1	14	15	14	0	Thamnolic acid, Atranorin
Leptogium	7	0	7	1	4	2	0	None reported
*Lobaria**	2	0	2	0	0	2	0	Stictic and norstictic acids
Melanelia, sensu lato	120	27	93	22	37	56	5	Variable by species includes lecanoric acid for *M. subaurifera* and fumarprotocetraric, protocetraric and atranorin for *M. halei*. The 2 most common species on our plots.
*Myelochroa**	42	1	41	1	10	28	3	Atranorin, secalonic, zeorin and leucotylic acids
Normandina	1	0	1	1	0	0	0	None reported
Parmelia	119	83	36	28	40	48	3	Salazinic and consalazinic acids
Parmeliopsis	37	33	4	10	13	14	0	Usnic and divaricatic acids
Phaeophyscia	187	3	184	59	61	59	8	Skyrin
Physconia	12	0	12	3	3	5	1	None reported
*Platismatia**	13	12	1	10	3	0	0	Atranorin and caperatic acid
*Punctelia**	18	4	14	0	1	11	6	Atranorin and lecanoric acid
Pyxine	4	0	4	0	1	3	0	Atranorin
*Usnocetraria**	209	170	39	52	76	79	2	Usnic, caperatic, lichesternic, protolichesteric, secalonic acids
Vulpicida	5	4	1	5	0	0	0	Usnic, pinastric and vulpinic acids
Xylospora	10	3	7	4	6	0	0	Lecanoric acid
All lichens	1055	530	525	285	333	405	32	

the last decade was a primary motivation for this study and therefore the inclusion of this species in the feeding trials was justified.

We removed lichen thalli from their substrate and dried (40 °C for 48 h) and weighed them prior to the start of the feeding trials. We conducted 10 trials for each of the 4 gastropod taxa. We weighed and distributed individual gastropods into plastic, rectangular food-storage containers (343.5 cm^2), the lids of which had been punctured in several places for air exchange. We covered the bottom of each container with wetted unbleached paper towel (Türke and Weisser 2013, White-McLean and Capinera 2014) and arranged the lichens equidistant from the gastropods upon placement of the gastropods into the center of the containers (White-McLean and Capinera 2014). Containers were kept in natural light conditions in a shaded outdoor location. The feeding trials lasted for 4 d, and we sprayed the containers to maintain humidity at least every 8 h. At the end of the trials, we removed gastropods and fecal matter from the remaining lichen scraps, which we then dried at 40 °C for 48 h and re-weighed.

We conducted a second set of feeding trials for just the slugs with 3 additional lichen species, *Flavoparmelia caperata* (L.) Hale, *Platismatia glauca* (L.) W.L. Culb. & C.F. Culb., and *Usnocetraria oakesiana* (Tuck.) M. J. Lai & C. J. Wei; these species had low grazing damage in the field (Table 1). Also, we included *Punctelia rudecta* in both feeding trials as a reference to check comparability of the results with the previous trials. For these trials, we did not completely remove substrate material from the lichens. We conducted these trials in the laboratory using 12 h of light, and slugs were not fed overnight prior to starting the experiment. In all other respects, these trials were identical to the first set.

We analyzed the 2 feeding trials separately, but used the same model structure. The response variable for tests of preference was total thallus biomass consumed (post-trial dry mass determined after drying at 60 °C for 24 h) for each lichen species. We examined the variables with a linear mixed model, with both total amount consumed for all species and mass of individual gastropods nested within container as random variables. This model structure accounted for the lack of independence between consumption of the 4 lichen samples within the containers and for differences in the size of gastropod individuals, respectively. Fixed effects were gastropod taxon, lichen species, and their interaction. We examined significant effects with a Tukey's HSD post hoc multiple comparison test. We ran all statistical tests in JMP Pro 13 for Windows (SAS Institute Inc., Cary, NC).

Results

Pattern of grazing damage under natural field conditions.

Based on scores of 1055 lichen genera occurrences on 513 trees in 52 plots, grazing damage was best predicted by tree group (conifer vs. broadleaf) ($F_{1,980}$ = 6.42, P = 0.0115) and plot steepness (average slope %) ($F_{1,980}$ = 7.47, P = 0.0064). Grazing was significantly more severe for lichens on broadleaf trees and flatter plots (Fig. 2). Thallus assessments on conifer and broadleaved trees were roughly equal; a little over a quarter of the thalli had no grazing damage (Table 1). Overall, moderate grazing damage was the most commonly scored damage class and only 32 of the 1055 assessments found severe grazing damage of the thalli (Table 1). Three genera, *Melanelia* (sensu lato), *Myelochroa*, and *Punctelia*, were notable in having more high scores relative to low scores for grazing (Table 1). Reproductive

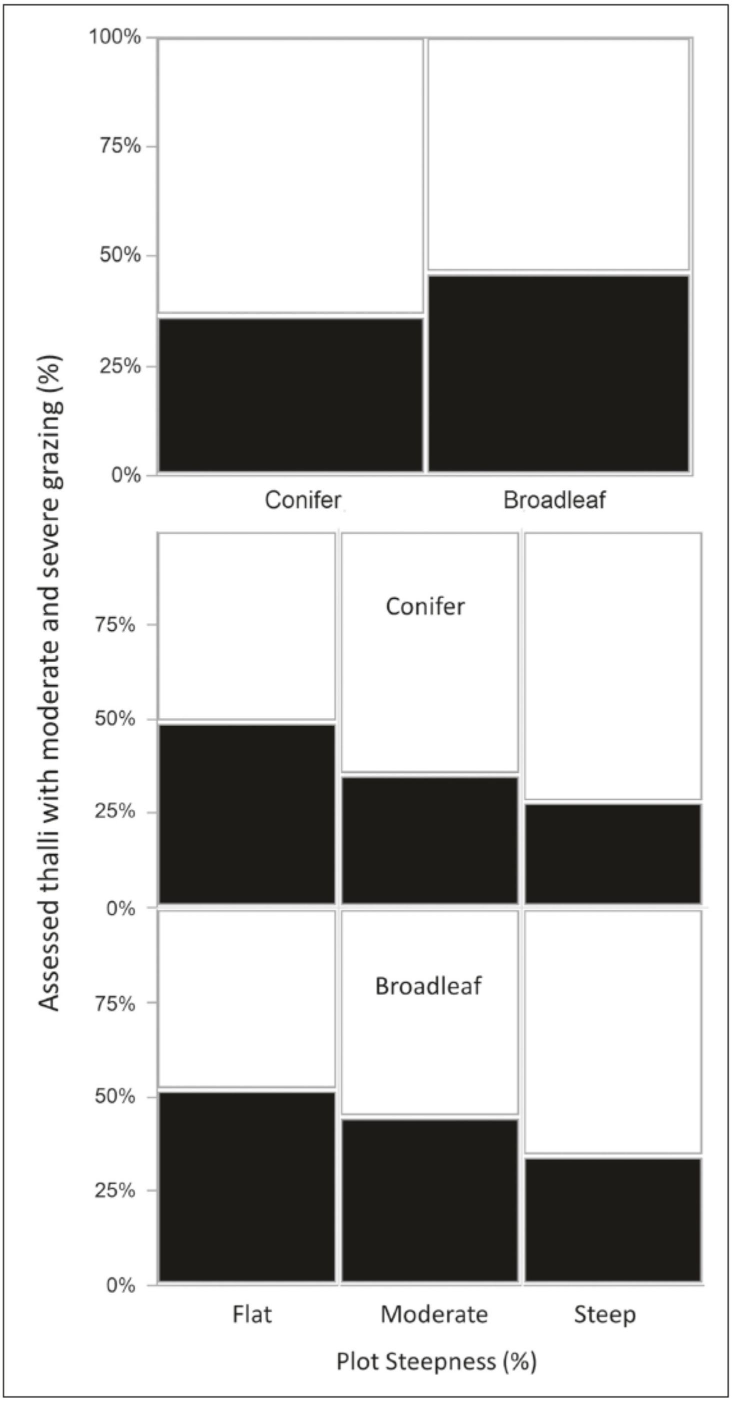

Figure 2. The relationship between moderately and severely grazed thalli (% of all thalli scored) occurring in Hubbard Brook Experimental Forest, NH, with the predictor variables tree group (conifer or broadleaf) and plot steepness (%). The top panel shows differences by tree groups and the bottom panel shows differences by tree group and plot steepness where plot steepness (a continuous variable) has been summarized as flat (0–14 %), moderate (14–21%), and steep (21–48%). Grazing damage was scored on 1055 generic-level groups of thalli occurring on 513 trees over 52 plots. Lichen generic summary is given in Table 1.

structures, soralia and apothecia, were preferentially eaten in 8 thalli scorings. We noted slime trails as still present on 19 thalli groups.

Gastropod density surveys.

Gastropod density surveys had 2 separate objectives: (1) to examine temporal differences in 2 areas where surveys were done previously, and (2) to examine spatial variation by adding 3 additional plots from the valley-wide network. The most notable pattern in comparisons with measurements colleted during 1997–2006 (Skeldon et al. 2007) was significantly lower slug abundance in 2016 at 4 of the 6 plots compared to the earlier long-term mean (Table 2). In the spatial comparison, snails greatly outnumbered slugs, and most of the slugs were non-native in 2016 (Table 2); however, the greater abundance of *Arion* spp. was significant only for the 3 VW sites ($F_{1, 89} = 13.83$, $P < 0.0001$), particularly at higher elevation ($F_{1, 89} = 12.01$, $P < 0.0001$). Despite the greater individual mass of slugs, snails still dominated the terrestrial gastropod community when biomass was estimated as the product of average individual mass values and counts (Table 2).

Gastropod feeding trials.

We conducted 2 feeding trials. The first trial included both slugs and snails, while the second trial focused only on slugs. In all analyses, we accounted for the conflict of only being able to graze 1 lichen at a time and the difference in body mass of the gastropods by including random variables in the model (see Methods for details). Overall, the slugs ate more than the snails, although the difference between the

Table 2. Summary of terrestrial gastropod counts (mean with standard deviation in parentheses in units of number per m^2 board surface) and mean estimated biomass (dry mass per m^2 board area) based on paper-board surveys (n = 15 boards per plot, i.e., at each elevation within a site) in July and August 2016 for 3 study sites in Hubbard Brook Experimental Forest, NH. Two sites, a reference site (REF) and a calcium addition site (CAL), were previously surveyed using the same methods during the period 1997–2006 (Skeldon et al. 2007). The CAL site had a calcium addition in October 1999. For these 2 sites only, superscripts denote significant decrease (^{A}) or increase (^{B}) from the long-term (1997–2006) densities in these areas. Past data are not shown here and are available online at (http://data.hubbardbrook.org/data/dataset.php?id=126). Lack of a superscript signifies no difference at α = 0.05 from the long-term mean densities. We included the 3rd site to look at spatial variability in snail and slug counts only in 2016 and is denoted as VW (valley-wide) (refer to Fig. 1).

					Biomass		
Site	Elevation (m)	Snails (#/board-m^{-2})	Slugs (#/board-m^{-2})	Gastropods (#/board-m^{-2})	Snail (mg/m^{-2})	Slug (mg/m^{-2})	Gastropod (mg/m^{-2})
REF	520	10.89 (8.37)	0.42 (1.01)	11.31 (8.05)	125.0	23.8	149.0
	610	6.07 (7.60)^B	0.71 (1.53)	6.79 (8.21)	69.8	72.6	142.0
	700	4.58 (4.11)	0.83 (1.22)^A	5.42 (4.39)	52.7	100.0	153.0
CAL	520	4.17 (4.79)^A	0.30 (0.82)^A	4.46 (4.68)	47.9	11.4	59.3
	610	8.99 (7.74)	0.54 (1.16)^A	9.52 (7.67)	103.0	14.2	117.0
	700	17.08 (14.07)^B	0.48 (1.23)^A	17.56 (14.22)	196.0	54.5	250.0
VW	520	3.05 (2.58)	0.86 (1.21)	3.92 (2.97)	35.1	39.6	74.7
	610	14.10 (12.86)	0.62 (1.10)	14.72 (12.98)	162.0	52.3	214.0
	700	10.95 (8.73)	3.04 (2.93)	13.99 (9.06)	126.0	122.0	248.0

amount consumed by the native slugs and *Discus* snails was not significant (Fig. 3, Table 3). Preference for *L. pulmonaria* was only apparent for Succineidae snails, while *Discus* snails were the only group to show no feeding preference (Fig. 3). Results of the 2 trials for the reference species, *P. rudecta,* were nearly identical with very low consumption in both trials, suggesting that methodological differences between the 2 trials were not important. Both slug taxa consumed the most of *P. glauca* and *H. physodes,* and the native slug consumed more *M. aurulenta* (Fig. 3).

Discussion

Although gastropods grazed widely on lichens, the majority of grazing was minimal to moderate, and the density of terrestrial gastropods was lower in 2016

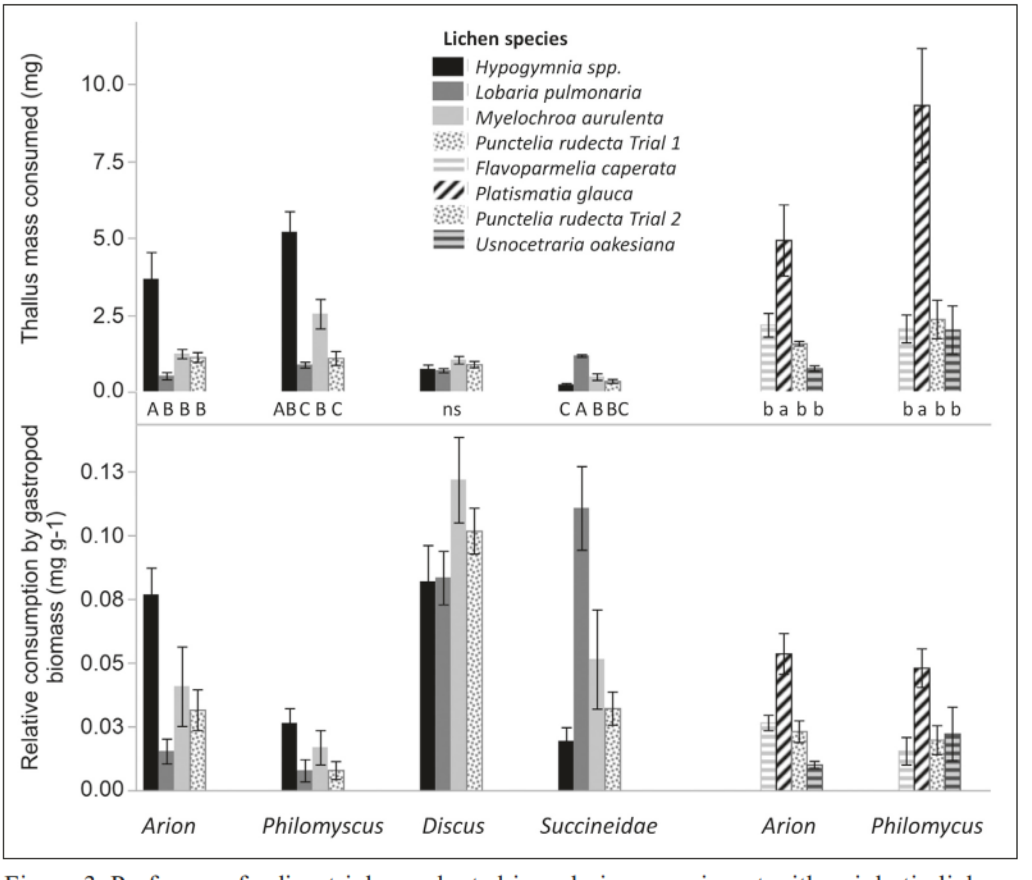

Figure 3. Preference feeding trials conducted in a choice experiment with epiphytic lichens and terrestrial gastropods. Top panel shows consumption (mg) of lichen thalli by 4 terrestrial gastropods and bottom panel shows consumption relative to individual gastropod live mass consumption (mg g^{-1}). The second trial is shown to the far right and only involved slug taxa. Values are mean (± SE) for all graphs with letters below the bars denoting significant post hoc differences at $\alpha = 0.05$ for lichen preference. Capital letters relate to differences in the first trial and lowercase letters to the second trial. There were no significant differences in lichen consumption by *Discus* snails (ns). Linear mixed model results are given in Table 3.

than during the 1997–2006 surveys. Variation in grazing damage corresponded to both landscape-level (slope angle) and tree-level (broadleaf versus conifer) factors. However, our results did not support a differential impact of the non-native slugs compared to the native slugs. In the feeding trials, the native snails in the family Succineidae preferred *L. pulmonaria*, and their impact on this lichen, which has been noted as declining in the HBEF (N.L. Cleavitt, pers. observ.), deserves further study, particularly because snails dominate the terrestrial gastropod fauna of HBEF.

Grazing damage by terrestrial gastropods on epiphytic macrolichens was widespread within the HBEF, but only 32 out of 1055 assessed thalli had severe grazing (Table 1; see also Table S2 in Supplemental File S1, available online at http://www.eaglehill.us/NENAonline/suppl-files/n26-2-N1664-Cleavitt-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1664.s1). Moderate grazing was most often observed and more study should be given to how this level of grazing impacts lichen survival, growth, and reproduction. Interestingly, slope steepness was the strongest predictor of grazing damage, with a higher percent of ungrazed thalli on steeper plots, suggesting that gastropods avoided or could not access steep plots. One possible explanation of this relationship is that lower soil-water retention and a flashier moisture regime on steeper slopes (Burt and Butcher 1985) may make steeper plots less suitable habitat for terrestrial gastropods; however, relationships of soil moisture and topography are quite complex at HBEF (Bourgault et al. 2017). The importance of plot steepness for gastropod grazing pressure on lichens has not been reported previously and offers another factor to explain landscape patterns in lichen–herbivore dynamics. Tree group (broadleaf versus conifer) was also significant; there was higher grazing of lichens growing on broadleaf trees. Greater grazing on lichens in broadleaf compared to conifer-dominated forests has also been found in Europe (Asplund and Gauslaa 2008, Vatne et al. 2010).

Our gastropod surveys recorded particularly low slug densities compared to historical densities recorded during 1997–2006, with significantly lower values on 4 of the 6 plots (Table 2; Skeldon et al. 2007). This observation may be influenced

Table 3. Linear mixed model results for fixed effects of gastropod choice feeding trials with 4 lichen species. The first trial included 2 slug and 2 snail taxa, while the second trial included only the 2 slug taxa. Significance of the effects is indicated by superscripts as: $P \geq 0.05$, ns; $P < 0.05$, *; $P < 0.001$, **; $P < 0.0001$, ***. Random effects in the model were total amount of lichen consumed per container and weight of the individual slug or snail. The lichen species used and post-hoc differences are shown in Figure 3.

	Degrees of freedom (numerator, denominator)	*F*-ratio
Slugs and snails		
Gastropod spp.	3, 36.3	9.20^{**}
Lichen spp.	3, 118.2	28.84^{***}
Gastropod spp.* Lichen spp.	3, 118.2	15.57^{***}
Slugs only		
Slug spp.	1, 54.4	1.32ns
Lichen spp.	3, 67.1	21.64^{***}
Slug spp.* Lichen spp.	3, 67.1	3.02^{*}

by protracted drought conditions in 2016 (NIDIS 2018) as terrestrial gastropods are vulnerable to drying out and are active mainly during periods of high humidity (Riddle 1983). Earlier gastropod surveys at the HBEF noted higher slug densities at higher elevation sites, but we did not detect this pattern in 2016 except in the VW plots (which were not surveyed in the earlier study; Table 2). Higher slug densities at higher elevation sites would match with feeding a preference of these gastropods for 2 lichen species commonly more abundant in higher elevation plots, *H. physodes* and *P. glauca* (Cleavitt et al. 2019). For the 3 plots (1 at CAL, 2 at VW) with both gastropod density counts and grazing damage assessments of lichen thalli, the 2 measures qualitatively suggested that grazing damage increased with higher gastropod densities. Future studies would be strengthened by overlapping these measures on more plots.

Notably, non-native slugs, *Arion* spp., were abundant at the HBEF and mostly outnumbered the native slugs. However, feeding-trial results suggested that *Arion* were not more aggressive consumers of lichens than the native slugs, and that snails may be equally or more important than slugs as lichen herbivores in this forest. Snails were more abundant than slugs in terms of both numbers and biomass (Table 1), and although we could not distinguish grazing by slugs from that by snails in the field surveys, in the feeding trials, snails consumed similar or higher amounts of lichen than slugs relative to their body mass (except for *Hypogymnia*; Fig. 3). The earlier study on the CAL and REF sites at the HBEF demonstrated that restoration of soil calcium significantly increased snail abundance (Skeldon et al. 2007). Whether changes in snail abundance associated with de-acidification of soils in the Northeast could cause increased snail grazing on lichens deserves further study particularly given the appetite of Succineidae snails for the declining *L. pulmonaria*.

In comparison to the earlier terrestrial gastropod surveys, *Striatura exigua* Stimpson, a snail species that increased significantly in response to the calcium addition on CAL, was far less common in our 2016 surveys (Skeldon et al. 2007). This species has been shown to respond positively to increased soil calcium and negatively to increase in elevation in the Adirondacks where it was quite abundant (Beier et al. 2012). The decline in this species may relate to decrease in available calcium in the litter layer 17 y after the treatment application (Shao et al. 2016), but additional sampling is needed.

In the feeding trials, there were no notable differences in lichen preferences of the native versus non-native slug taxa, which both consumed more of the common lichens, *H. physodes* and *P. glauca* (Cleavitt et al. 2019). This result agrees with those of other studies using feeding trials, which have demonstrated the preference of terrestrial gastropods for more abundant lichen species (Baur et al. 1995, Boch et al. 2015). In terms of lichen chemistry, lichens with atranorin, such as *Hypogymnia*, *Melanelia*, *Myelochroa*, and *Punctelia*, were more often severely grazed, while yellow species, *Candelaria*, *Flavoparmelia*, and *Vulpicidia*, were not grazed at all (Table 1, Fig. 3).

The relationships between terrestrial gastropods and epiphytic lichens are very complex, including long-term, indirect effects of grazing on competitive interactions (Boch et al. 2016) and vertical distribution of species (Asplund et al. 2010), lack of short-term grazing on growth rates (Gauslaa et al. 2006), and interactions between factors affecting lichen chemistry and palatability including presence of parasitic fungi (Asplund et al. 2016). We often observed grazing specifically on reproductive structures such as the apothecia of *Melanohalea halei* and the capitate soralia of *Phaeophyscia pusilloides*. Such targeted grazing could either limit the ability of lichens to reproduce or aid in dispersal (McCarthy and Healy 1978).

Our work represents a first approximation of patterns in terrestrial gastropod grazing on epiphytic lichens in montane forests of northeastern North America. The results suggest that landscape factors influence the impact of terrestrial gastropods. Lichen epiphytes located on flatter plots and on broadleaf trees are likely to experience greater grazing damage than those on steeper plots and on coniferous trees. Minimal and moderate grazing of lichen thalli were the conditions most often observed, and more study should be given to how these levels of grazing impacts lichen survival, growth, reproduction, and dispersal. The non-native slugs, *Arion* spp., are not significantly different than the native slugs in terms of lichen preference, though they may be more abundant particularly at higher elevation sites, and more study is warranted on their potential impacts on lichen communities.

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