RESEARCH ARTICLE

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Divergent Tree Communities across Ridge, Cliff, and Talus Relate to an Association between Diaspore Weight and Micro-Topography at Mohonk Preserve, New York

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ABSTRACT: Ecological study of cliff environments has steadily increased in the last three decades. However, plant communities on many cliffs have yet to be investigated, and there remains uncertainty about the mechanisms that drive vegetation patterns on cliffs. On the Trapps cliff, a renowned rock-climbing destination within Mohonk Preserve, New York, we recorded tree species and surface micro-topography ("sloping," "level," "incut") along seven rappel transects. In two study areas, we also sampled the ridge and talus areas above and below the cliff transects, and in one of those areas, we included a separate lateral survey along a prominent ledge on the cliff. We used estimated diaspore (seed or fruit) weights and chi-square analyses to test for association between diaspore weight class and topographic categories across the entire study. The cliff tree communities were dominated by mature pitch pine (*Pinus rigida*) and more frequent but smaller-diameter sweet birch (*Betula lenta*). Sweet birch, a species with light-weight, wind-dispersed seeds, was disproportionately frequent on the cliff and on sloping surfaces on the cliff, while heavier, gravity-dispersed diaspore species (especially oaks) were underrepresented on the cliff in general, but disproportionately associated with level micro-topography on the cliff. Our results suggest that diaspore weight and associated dispersal mechanisms may play a role in the assembly of cliff tree communities that are divergent from the ridge above, or talus below. Management implications include protecting adjacent plant communities (ridge, talus) that are likely diaspore sources that sustain plant communities on cliffs.

Index terms: cliff, diaspore, forest community composition, seed, topography

INTRODUCTION

Ecological study of cliff environments has steadily increased in the last three decades (Larson et al. 2005; Holzschuh 2016), however, plant communities on many cliffs have yet to be investigated. Cliffs are targets for research and conservation because they are relatively free from anthropogenic impacts and may harbor rare plant species and unique plant communities (Larson et al. 2005). There is growing attention to studying vegetation patterns on cliffs to reveal the mechanisms that drive those patterns.

The protected lands in northern Shawangunk Mountains are valued for their rugged, varied terrain, and unusually high plant diversity, which includes three globally rare, and eight state rare, plant communities (Thompson and Huth 2011). A focal point in the Shawangunks are cliffs and rocky ridgelines, which harbor rare, old-growth forest remnants dominated by pitch pine (*Pinus rigida* Mill.) (Cook and Jacoby 1977; Abrams and Orwig 1995). The Trapps cliff, located within Mohonk Preserve, is a visually striking, mostly sheer rock wall renowned as a rock-climbing destination. Although Mohonk Preserve has a legacy of ecological monitoring dating back to the late 1800s, information on the specific composition of plants on the cliffs at Mohonk Preserve is limited to visual tallies from the base of the cliffs (Thompson 1999).

Variation in cliff angle, surface micro-topography, and associated microsite conditions can affect plant establishment, germination, and seedling growth in surprising ways on cliffs. For example, vertical cracks which may appear to be harsh growing environments may actually be well-watered and well-drained "safe sites" for plants due to water seepage from areas above the cliff. In contrast, ledges, despite having some soil or sediment build-up, may lack reliable water during the dry seasons (Larson et al. 2005; Matthes and Larson 2006). Cliff microsites may also differ in light and temperature (Larson et al. 2005). Gravity plays a unique role in creating microsite variety on cliffs by concentrating nutrients and soil on ledges and in cracks (Larson et al. 2005). For these reasons, cliff faces with high micro-topographic complexity may have higher species richness, plant functional group richness, or overall plant abundance (Haig et al. 2000; Graham and Knight 2004; Kuntz and Larson 2006b; Carmo et al. 2016). The effect of surface micro-topography on the presence, absence, or relative abundance of particular species is not clear, however.

A number of studies have documented differences between tree community composition on cliffs and adjacent tree communities above and below the cliff (Larson et al. 1989; Fuls et al. 1992; Camp and

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Knight 1998; Graham and Knight 2004; Harkey 2013), stimulating interest in the underlying mechanisms that drive plant community composition on cliffs. "Community assembly" refers to the process by which plant communities are assembled from a local or regional species pool that passes through a sequence of "filters" to produce the final pattern of community composition (Drake 1990; Booth and Larson 1998; Götzenberger et al. 2012). Poschlod et al. (2013) described four filter stages for plant communities as dispersal, seed bank persistence, germination, and establishment. Primary dispersal from parent trees is responsible for diaspore rain (seeds or seed-bearing fruit) into new sites, a first filter for determining community composition. The fate of a newly arrived diaspore at a given site is influenced by the potential for subsequent movement or "secondary dispersal" (Chambers and MacMahon 1994). For diaspores that leave seeds in the seed bank, successful germination depends on seed characteristics, microsite conditions, and weather/seasonal effects. Successful establishment and survival of seedlings is a final filter, and depends on the match between the abiotic conditions of the site, the physiological requirements and stress tolerance of the individual species, and biotic interactions with competitors, herbivores, and pathogens.

Studies of plant community assembly rarely study all the filters for a given community due to the labor and time required. There is, therefore, a need to explore keystone traits that may correlate with overall probability of successful establishment (Laughlin 2014). For cliffs, only one intensive study of plant community assembly has been conducted to date (Booth and Larson 1998, 2000a, 2000b). Although all assembly filters may act in unique ways in a cliff environment, early filters (primary and secondary dispersal of diaspores) may play an especially important role on cliffs because the steep or vertical habitat provides limited sites for successful seedbank establishment. The fate of seeds that arrive and persist in plant communities is driven mainly by diaspore morphology (size, special structures) and dispersal mechanism (e.g., wind, gravity, animals) (Chambers et al. 1991; Chambers and MacMahon 1994; Willson and Traveset 2000; Poschlod et al. 2013). Because gravity and wind are likely to be important forces affecting primary and secondary dispersal on cliffs (Booth and Larson 2000a), diaspore weight (Westoby et al. 1996) and dispersal mechanisms that act on diaspore weight (wind and/or gravity) could be especially important. In addition, diaspores typically dispersed by animals could move greater distances in a cliff environment due to gravity acting on weight alone, although animals could modify these effects by moving or consuming fruit or seeds (Vander Wall 1992). Despite the plausibility of these mechanisms, the role of diaspore weight and associated dispersal mechanisms in determining plant communities on cliffs has received little attention.

Our objective in this study was to describe the tree community composition of the Trapps cliff at Mohonk Preserve and look for patterns in community composition relating to surface micro-topography on the cliff. We sought to quantify and explain the differences between the cliff tree community, including a specific community along a prominent ledge (the "Grand Traverse" or "GT" ledge) compared to adjacent communities on the ridge above the cliff and in the talus below. We reasoned that gravity and wind may be important forces acting on diaspores on a cliff, and focused our analyses on the relative differences in diaspore weight between tree species that could affect the arrival and persistence of different seeds at microsites. This reasoning suggests that heavy diaspores would likely be excluded from sloping and vertical faces, though possibly protected by level or incut surfaces. Conversely, light diaspores may be more likely to land and stick in cracks on vertical or sloping surfaces, but be more likely to be blown off level surfaces by wind.

Based on these ideas, we predicted that species that were disproportionately more frequent on the cliff in general as well as disproportionately represented on sloping surfaces in particular, would have lightweight diaspores reliant mostly on wind for dispersal. In contrast, we expected heavy-diaspore species to be underrepresented on the cliff as whole, but disproportionately more frequent on level and incut surfaces compared to sloping surfaces.

METHODS

Site Description

The Shawangunks are a folded ridge of hard quartz conglomerate rock overlaying a softer shale and sandstone layer that has eroded over time to create exposed cliffs with broken talus slopes at their base (Kiviat 1988). The Trapps is a southeast-facing cliff, located within Mohonk Preserve, a protected area at the northern end of the Northern Shawangunks Ridge. The cliff is accessed via a gravel carriage road that either runs through the talus area, or in some places, runs directly at the base of the cliff. The ridge above the cliff is also accessible via a steep climber's footpath. In the northern section of our study area, the ridge area above the cliff is a narrow, southeast-sloping or terraced bench extending from a distinct ridgetop down to the cliff edge. The ridge area in the southern section of our study area is bounded above by rock outcrops and slopes gently to the south, somewhat oblique to the cliff edge. The cliff height across our study area ranges from 50 to 75 m.

Field Sampling

In fall of 2013 and 2014, seven rappel routes (Bunny, Apoplexy, Betty, Jackie, Three Pines, Updraft, CCK) were selected to study the relationship of surface micro-topography to tree species composition on the cliff (Figure 1). These initial routes were chosen to spread our sampling generally across the breadth of the Trapps climbing area within Mohonk Preserve. Climbing difficulty ratings associated with these routes ranged from 5.3 to 5.9 (Swain 1995). During our initial sampling, we became interested in species composition differences across the ridge–cliff–talus system, and in particular along the GT ledge, a lateral cliff feature that intersected several of our initial rappel routes. Ridge and talus tree communities were sampled above and below the cliff face in two study areas, Jackie/Betty and CCK/Updraft, named for

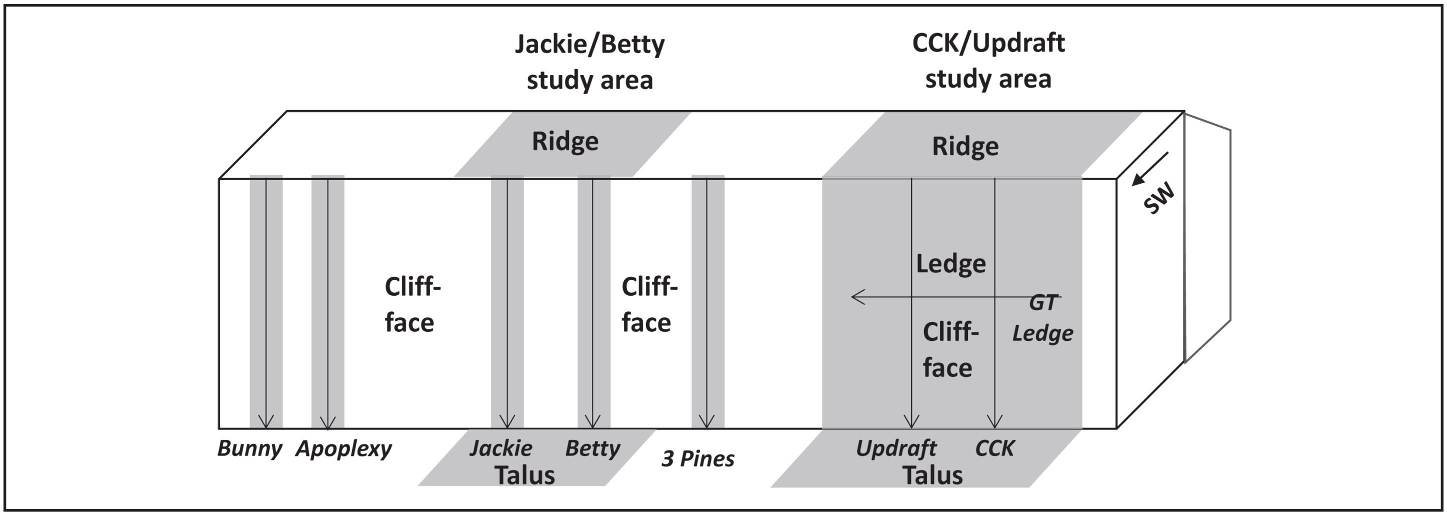

Figure 1. Schematic diagram showing relative locations of study areas and names of climbing/rappel routes and cliff features at Mohonk Preserve, Trapps area. Shading indicate areas sampled (by belt transects, augmented by binocular survey at CCK/Updraft). Arrows indicate rappel and ledge belt transects. Not to scale, actual dimensions of transects and sampling areas are in Table 1.

the rappel routes we used for sampling the cliff faces in each area (Figure 1). Talus and ridge areas were not sampled for the other three rappels because talus or ridgeline tree communities were either fragmented by the carriage road or inaccessible (Bunny, Apoplexy) or the rappel was too distant from other rappels (Three Pines). The GT ledge was sampled at CCK/Updraft only, because other portions of the ledge were deemed not passable either because of safety concerns, or, in one case, the obstacle of an active falcon nest.

Rappels were each sampled along a single route from the top of the cliff to the bottom using established rappel anchor stations. Approximate transect lengths are given in Table 1. Observations were dictated into a digital voice recorder for later transcription. Trees and woody shrubs were identified within a visually estimated 6-m belt transect—approximately 3 m on either side of the rope line. Woody plants were identified to species, except for northern red oak (*Quercus rubra* L.) and eastern black oak (*Quercus velutina* Lam.), which we did not distinguish in all instances, and lumped for analysis purposes. For trees that could be safely reached, diameters were measured at a stem height at or near breast height (1.37 m), using a forester's diameter tape. Some trees were not measured by tape, but visually designated into diameter size classes (< 2.5 cm, 2.5–10 cm, 10–25 cm, >25 cm). On the rappels, detailed descriptions of the ground surface micro-topography at the base of each tree were recorded, including descriptions of slope, soil, sediment, sand, and rock structures. These descriptions applied to a spatial scale of approximately 10 cm^2 to 1 m^2. For analysis, the transcribed descriptions were grouped into three categories: "sloping" (greater than ~2° outward slope), "level" (~0–2° slope in any direction), and "incut" (greater than ~2° inward slope).

We sampled the GT ledge at CCK/Updraft using a lateral transect, running north and south of a fixed rope anchor station located along the CCK rappel route. The ledge itself was an average of 1–1.5 m wide and the total lateral distance sampled was approximately 50 m. All trees along this ledge transect were classified as having "level" micro-topography. Diameters were measured using the same procedures described above. Trees on the cliff face, outside the ledge and rappel transects, were identified using binoculars from vantage points on the GT ledge and from the ground, resulting in a continuous survey of the cliff face at CCK/Updraft (Figure 1). Micro-topographic data were not recorded for trees identified using binoculars. Because the GT ledge was not accessible at Jackie/Betty, binoculars were not used to extend the cliff sampling from ledge vantage points, and cliff sampling was limited to the two rappel transects in that study area.

We used natural boundaries and topography to delineate ridge–cliff–talus sampling areas that were potentially interconnected by diaspore dispersal. Because wind- or animal-dispersed diaspores have the potential to cross all topographic positions, we focused on the likely movement of gravity-dispersed diaspores as a criterion for determining boundaries of sampling areas. Ridge sampling areas consisted of areas gently sloping toward the cliff edge but below a higher natural boundary (the ridgetop at CCK/Updraft and a rock outcrop at Jackie/Betty). A lateral-running belt transect 10 m wide was determined to sufficiently capture the ridgeline tree community within these boundaries for both study areas. In the talus, we reasoned that gravity-dispersal downslope from the cliff base would be limited by the discontinuous surface of broken talus rock. We used 5-m wide belt transects in the talus for both study areas. Lengths of ridge and talus sampling areas were determined by the lateral extent of cliff face sampled in each area (Table 1). Within the ridge and talus sampling areas, all trees >1 cm diameter were identified and placed into size classes as above. Diameters >25 cm were measured using a forester's tape. Dominant woody shrub cover was also estimated at regular 5 × 10 m sections along the ridge, and individual woody shrubs were recorded in the talus and on the cliffs, but because

Table 1. Study areas and sampling information for cliff study at Mohonk Preserve.

Study area	Topographic position (& cliff feature)	Route names	Sampling method/transect widths	Approx. transect lengths (m)	Approx. total area sampled (m^2)	# of trees	# tree species detected
CCK/Updraft	Ridge		One 10-m belt transect	70	700	191	14
	Cliff (face)	CCK, Updraft	Two 6-m belt transects, binocular survey	75	5250	43	8
	Cliff (ledge)	GT Ledge	One 1 - 1.5-m belt transect	50	63	34	7
	Talus		One 5-m belt transect	75	375	91	7
Jackie/Betty	Ridge		One 10-m belt transect	40	400	62	8
	Cliff	Jackie, Betty	Two 6-m belt transects	50	600	36	4
	Talus		One 5-m belt transect	30	150	34	5
Other rappels	Cliff	Apoplexy, Bunny, Three Pines	Three 6-m belt transects	30 - 50	720	41	9

our study focused on trees, these data were not analyzed.

Data Analysis

To compare tree community composition related to topographic position, we separated our data into two focal study areas (CCK/Updraft, Jackie/Betty) where we had contiguous ridge–cliff–talus data, and an additional category of other rappels (Figure 1, Table 1). The two study areas were further subdivided based on the topographic positions/cliff features sampled within each study area: ridge, cliff face, cliff ledge, and talus at CCK/Updraft; ridge, cliff, and talus at Jackie/Betty (Table 1). Within each focal study area (Jackie/Betty, CCK/Updraft), all recorded tree data were pooled within each topographic position/cliff feature.

Relative frequencies of tree species were calculated by dividing the total counts of each species by the total number of trees counted within that sampling area (study area × topographic position/cliff feature). Basal areas for each tree were calculated by assuming circular stems and using measured diameters or the mid-point of estimated diameter size classes. Overall relative basal areas of each species were calculated by summing all basal areas for each species and dividing by the total basal area of all trees in the sampling area. Relative importance values for each tree species within each sampling area were calculated as relative density plus relative basal area divided by 2 (Curtis and McIntosh 1951).

For Jackie/Betty and CCK/Updraft, we used modified rank-abundance charts to visualize patterns of tree establishment on the cliff (depicted as tree relative frequency) and the relative strength of diaspore sources (initially depicted as tree relative importance or tree relative basal area) from adjacent ridge and talus communities. Overall patterns of abundance were similar whether relative importance values or relative basal area values were plotted. We chose to plot relative importance values because the slight weighting of smaller stem species (generally <5% higher values than basal area values) allowed easier visualization of the entire ridge and talus tree communities in the figures. Tree species were ranked along the horizontal axes by estimated diaspore weight and bars were coded by diaspore dispersal mechanism. For CCK/Updraft, the cliff relative frequencies were further subdivided by "ledge" vs. "face." We also plotted diameter size-class distributions (with 2.5, 10, 25, >25 cm bins) of four tree categories (sweet birch, pines, oaks, hickories) across the three topographic positions (ridge, cliff, talus) using data pooled across the entire study.

Estimated mean seed dry-weights were calculated for each tree species from values obtained from the TRY database (Kattge et al. 2011); these values were used to estimate diaspore weight for seed-dispersing species (Table 2). For fruit-dispersing species, we adjusted seed weight values as follows: we used published records of seed weight/fruit weight ratios to estimate diaspore weight for juneberry (*Amelanchier arborea* (F. Michx.) Fernald) (Brinkman and Strong 2008) and black cherry (*Prunus serotina* Ehrh.) (Grisez et al. 2008). Similar information for sassafras (*Sassafras albidum* (Nutt.) Nees) and sourgum (*Nyssa sylvatica* Marshall) was not obtained, so we made an approximate estimate of

Table 2. Tree species recorded on ridges, cliffs, and talus slopes at Trapps area, Mohonk Preserve, New York, with estimated seed and diaspore weights, diaspore weight class grouping schemes, and methods used to calculate diaspore weights. Codes for dispersal mechanisms: W = wind, WG = wind & gravity, WA = wind & animals, A = animals, GA = gravity and animals.

Common Name	Scientific Name	Diaspore type / dispersal mechanism	Mean seed dry wgt. (mg)[1]	Diaspore dry wgt. (mg)	Log diaspore dry wgt. (mg)	Diaspore weight class - grouping scheme 1	Diaspore weight class - grouping scheme 2	Method for estimating diaspore dry weight
bigtooth aspen	*Populus grandidentata*	seed/W	0.16	0.16	-0.8	light	light	seed dry weight
sweet birch	*Betula lenta*	seed/W	0.81	0.81	-0.09	light	light	seed dry weight
pitch pine	*Pinus rigida*	seed/WG	7.62	7.62	0.88	medium	medium	seed dry weight
eastern white pine	*Pinus strobus*	seed/WA	16.4	16.4	1.22	medium	medium	seed dry weight
red maple	*Acer rubrum*	seed/W	19.8	19.8	1.3	medium	medium	seed dry weight
eastern red cedar	*Juniperus virginiana*	fruit/A	10.3	23	1.36	medium	medium	mean of 10 dried fruits collected in the field
striped maple	*Acer pensylvanicum*	seed/W	38.9	38.9	1.59	medium	medium	seed dry weight
white ash	*Fraxinus americana*	seed/W	43.3	43.3	1.36	medium	medium	seed dry weight
juneberry	*Amelanchier arborea*	fruit/A	5.67	283.6	2.45	medium	heavy	[2]seed wgt./fruit wgt.
sassafras	*Sassafras albidum*	fruit/A	92.8	464.2	2.67	medium	heavy	seed wgt./fruit wgt. of *Prunus serotina*
black cherry	*Prunus serotina*	fruit/GA	95	475.1	2.68	medium	heavy	[3]seed wgt./fruit wgt.
sourgum	*Nyssa sylvatica*	fruit/GA	129.9	649.5	2.81	medium	heavy	seed wgt./fruit wgt. of *Prunus serotina*
pignut hickory	*Carya glabra*	seed/GA	2609	2609	3.42	heavy	heavy	seed dry weight
black/red oak	*Quercus velutina/rubra*	seed/GA	2790	2790	3.45	heavy	heavy	seed dry weight
American chestnut	*Castanea dentata*	seed/GA	3729	3729	3.57	heavy	heavy	seed dry weight
chestnut oak	*Quercus montana*	seed/GA	4534	4534	3.66	heavy	heavy	seed dry weight
shagbark hickory	*Carya ovata*	seed/GA	4547	4547	3.66	heavy	heavy	seed dry weight

[1] Reported seed dry weight values accessed through the TRY database. Original sources include Wirth & Lichstein 2009, Green 2009, Kuhn et al. 2004, Moretti & Legg 2009, Cornelissen et al. 2003.

[2] Reported seed/fruit weight ratio, Brinkman & Strong, 2008.

[3] Reported seed/fruit weight ratio, Grisez et al. 2008.

fruit weight for these species using the seed weight/fruit weight ratio for black cherry. For eastern red cedar (*Juniperus virginiana* L.), we used the average of 10 field-collected fruits. Species were also classified into one of five primary diaspore dispersal mechanisms (wind, wind and gravity, animals, wind and animals, gravity and animals) based on published information (Burns and Honkala 1990a, 1990b; USDA-FEIS 2017).

Chi-square analyses were used to test for association between diaspore weight and topographic variables. To keep expected cell values above 5 for the tests involving fewer trees, three diaspore weight classes ("light," "medium," "heavy") were chosen. Cutoff values between weight classes were based on where the largest gaps occurred between estimated diaspore weights ranked on a logarithmic scale (Baker 1972) (see Table 2). We used chi-square analyses to test if the proportion of species in each diaspore weight class differed from expected (i.e., equal proportions) in (1) each of the three topographic positions ("ridge," "cliff," "talus") using data pooled across all sampling areas, (2) each of the three surface micro-topographies ("sloping," "level," "incut") using data pooled across all cliff sampling areas, and (3) between cliff-face and ledge at CCK/Updraft. *Z*-tests with Bonferroni corrections were used to test for significant differences between diaspore weight classes within topographic positions, micro-topography categories, and cliff features ("face" vs. "ledge"). Because cliff areas sampled in "other rappels" did not have directly associated ridge and talus sampling areas, we repeated the test for association with topographic position with a dataset that excluded trees from the "other rappels" and compared results. In addition, because the cutoff between the medium and heavy diaspore weight class depended on approximate estimates of diaspore weights for several fruit-dispersed species, two alternative diaspore weight grouping schemes were generated by placing these species in either the medium or heavy weight class (Table 2). We repeated all the tests with each grouping scheme and compared results. SPSS 24.0 software was used for all statistical tests.

RESULTS

Across the entire study, we recorded a total of 532 trees—253 on the ridge, 154 on cliffs, and 125 in talus (Table 1). We detected a total of 17 tree species for the study as a whole. Across both CCK/Updraft and Jackie/Betty study areas, most tree species encountered on the cliff were also detected on either the ridge or in the talus (Figures 2 and 3). One species, big-tooth aspen (*Populus grandidentata* Michx.) was not detected on ridges or talus but was found on the cliff at CCK/Updraft. White ash (*Fraxinus americana* L.), black cherry, sourgum, shagbark hickory (*Carya ovata* (Mill.) K. Koch), and American chestnut (*Castanea dentata* (Marsh.) Borkh.) were found rarely on the ridge or talus, and were not detected on cliffs. Woody shrubs, listed in order from most to least abundant, were high-bush blueberry (*Vaccinium corymbosum* L.), scrub oak (*Quercus ilicifolia* Wangenh.), witch-hazel (*Hamamelis virginiana* L.), mountain laurel (*Kalmia latifolia* L.), winged sumac (*Rhus copallinum* L.), and staghorn sumac (*Rhus typhina* L.) on the ridges; scrub oak, high-bush blueberry, mountain laurel, and staghorn sumac on the cliff; and witch-hazel and mountain-laurel in the talus.

Based on visual inspection of rank-abundance charts (Figures 2 and 3), relative frequencies for several tree species on cliffs were divergent from their importance values on either ridges or in talus. Sweet birch was the most frequent tree species on cliffs in all sampling areas, with relative frequencies above 60% on the cliff at Jackie/Betty (Figure 2), 35% at CCK/Updraft (Figure 3), and 37% on other rappels (not shown). Sweet birch was a very minor component of ridge communities, but an important component in talus. However, chestnut oak was more abundant with higher importance values than sweet birch in the talus of both areas (Figures 2 and 3). Pignut hickory was absent on the cliffs at CCK/Updraft and Jackie/Betty despite having the highest importance value on the ridge at CCK/Updraft (Figure 3), although it was not found on the ridge at Jackie/Betty (Figure 2). Pignut hickory was found at the very top of one rappel route (Three Pines) but was never observed on the main faces of any cliff in any of the sampling areas. Black/red oak and chestnut oak (*Quercus montana* Willd.) were important components of both ridge and talus at both CCK/Updraft and Jackie/Betty. Oaks had relative frequencies above 10% on the cliff at CCK/Updraft, although most of these trees were on the GT ledge (Figure 3, middle panel). Black/red oak was less frequent, and chestnut oak was not detected on the cliff at Jackie/Betty, where the GT ledge was not sampled. Red maple (*Acer rubrum* L.) was relatively infrequent on the cliffs despite moderate importance values on ridges and in talus. Several other tree species (juneberry, pitch pine, eastern white pine [*Pinus strobus* L.], sassafras) had relative frequencies on the cliff that appeared to be generally consistent with their relative importance on ridges and/or talus, although there was some variation between the study areas (Figures 2 and 3).

Sweet birch on the cliff was mostly in the smallest size class (<2.5 cm diameter), although some larger sweet birch did occur on the cliff (Figure 4). Pitch pine on the cliff was more evenly distributed between size classes than sweet birch (Figure 4) and had higher relative basal area on the cliff across the entire study (results not shown). Large oaks also occurred on the cliff (Figure 4); however, most of these were on the GT ledge (Figure 3, middle panel). Hickories occurred in all but the largest size class on the ridge at CCK/Updraft (Figures 3a and 4).

Light- to medium-weight diaspore species common on the cliff are either completely or partly wind-dispersed (sweet birch, big-tooth aspen, eastern white pine, pitch pine), with some animal-dispersed species (juneberry, eastern red cedar, sassafras). Sweet birch, the most frequent cliff species, has very lightweight seeds and is wind dispersed, with high importance only in the talus, below the cliffs and not on the ridge above. Black/red oak and chestnut oak, present on cliffs, but especially on the GT ledge, are heavier-seeded species dispersed by gravity and animals (Figures 2 and 3). However, pignut hickory, a heavy-seeded, gravity/animal-dispersed species was absent on cliffs at Jackie/Betty

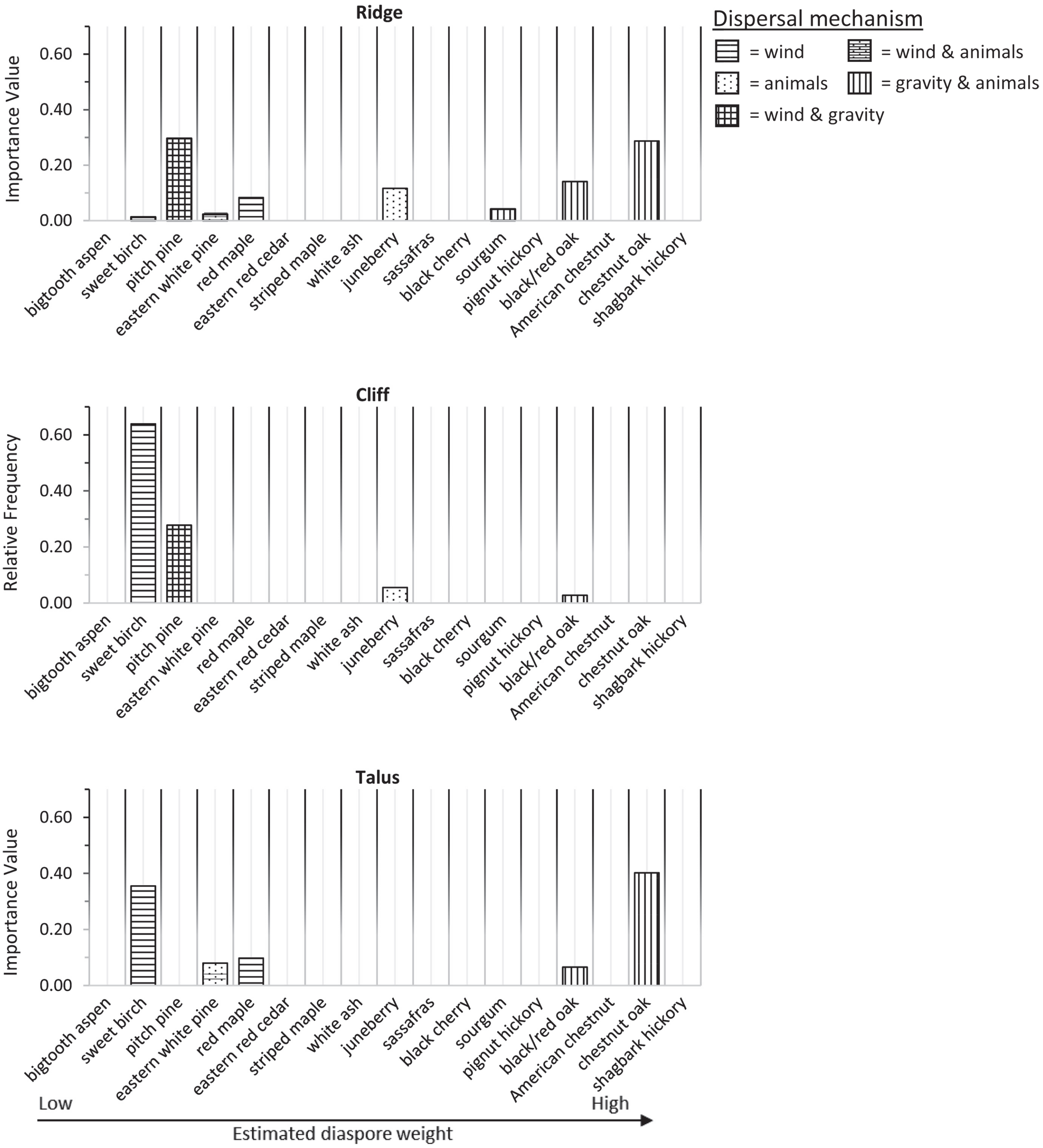

Figure 2. Jackie/Betty tree relative frequencies (cliff) and relative importance values (ridge, talus) ranked by estimated diaspore weight (left to right, low to high). Primary diaspore dispersal mechanisms for each species are indicated by pattern on bars. Sample sizes are in Table 1.

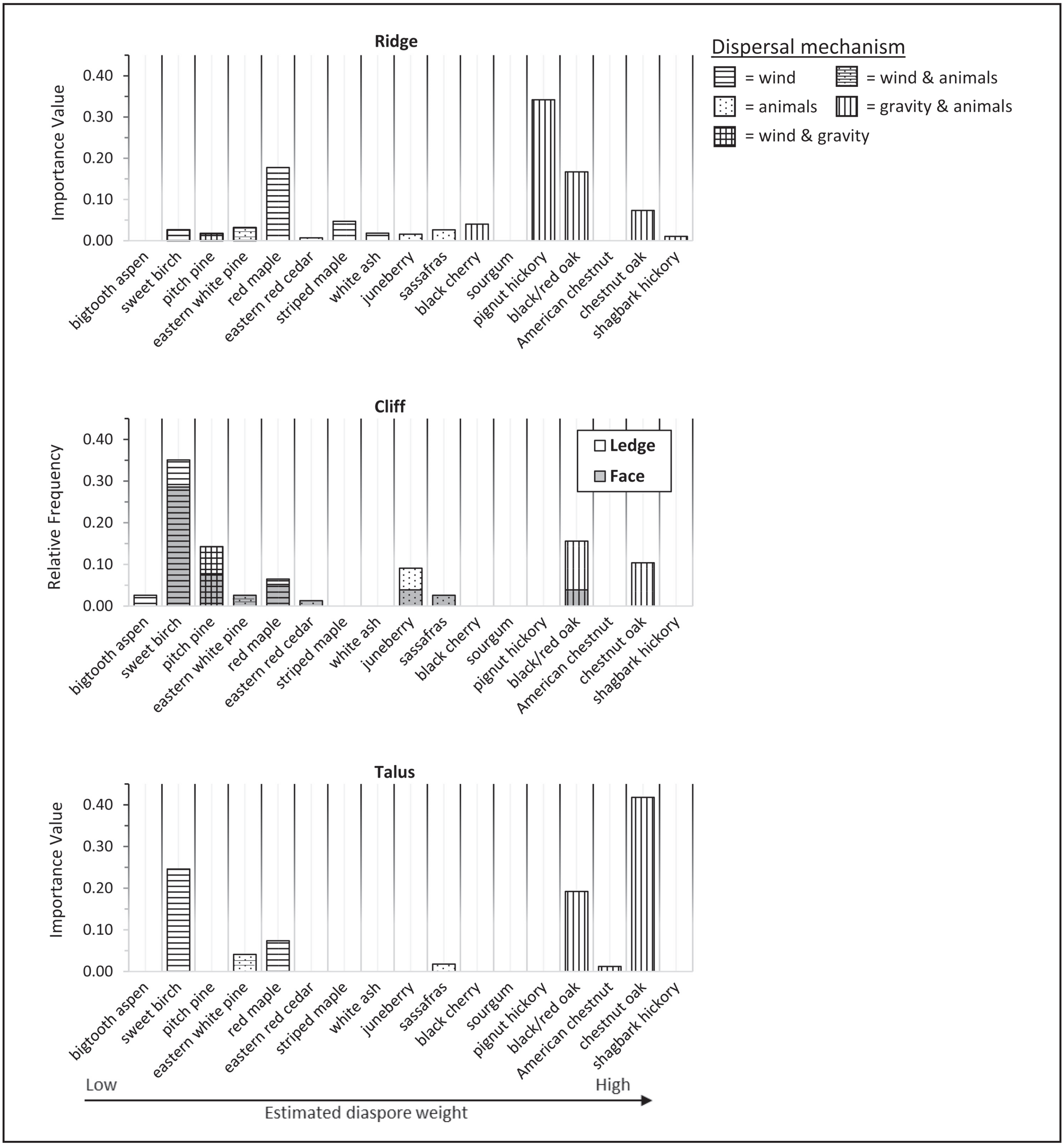

Figure 3. CCK/Updraft tree relative frequencies (cliff) and relative importance values (ridge, talus) ranked by estimated diaspore weight (left to right, low to high). Primary diaspore dispersal mechanisms for each species are indicated by pattern on bars. Relative frequencies on the cliff are divided into "ledge" vs. "face." Sample sizes are in Table 1. Note vertical scale is adjusted compared to Figure 2.

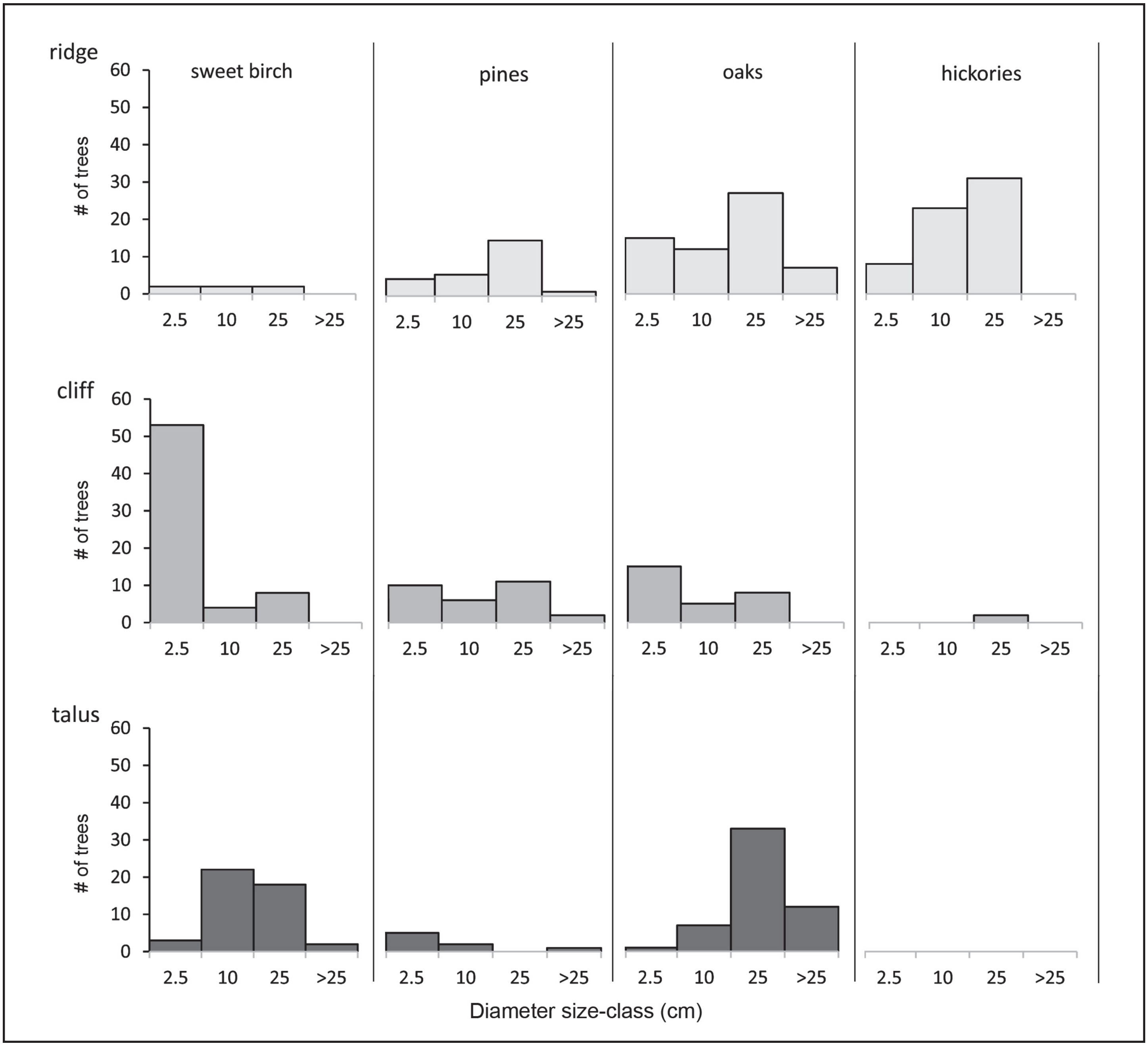

Figure 4. Size-class distributions of sweet birch, pines (eastern white, pitch), oaks (black, red, chestnut), and hickories (pignut, shagbark) on the ridge, cliff, and in the talus, using data pooled across all sampling areas. Diameter values (in cm) on horizontal axes are upper limits of each bin. Trees on the GT ledge are included in the cliff trees.

and CCK/Updraft, including on the GT ledge, despite having the highest relative importance on the ridge above the ledge at CCK/Updraft.

Across the entire study, diaspore weight class was significantly associated with topographic position ($\chi^2 = 127.2, P < 0.000$; Figure 5a, based on grouping scheme 1). Species with lightweight diaspores (big-tooth aspen, sweet birch) were disproportionately associated with the cliff, while both larger diaspore weight classes were disproportionately underrepresented on the cliff, with the heaviest weight class significantly less associated with the cliff compared to both medium and light weight classes. Results, including *Z*-test results, were the same in a second test that excluded trees from the "other rappels" category ($\chi^2 = 125.6$, $P < 0.000$; results not shown). Results were also similar for both tests when grouping scheme 2 was used ($\chi^2 = 115.0$, $P < 0.000$ for full dataset, 117.1, $P < 0.000$ excluding other rappels; results not shown) except that proportions of medium and large weight classes on the cliff were not significantly different.

Among tree species found on cliffs, diaspore weight class was significantly asso-

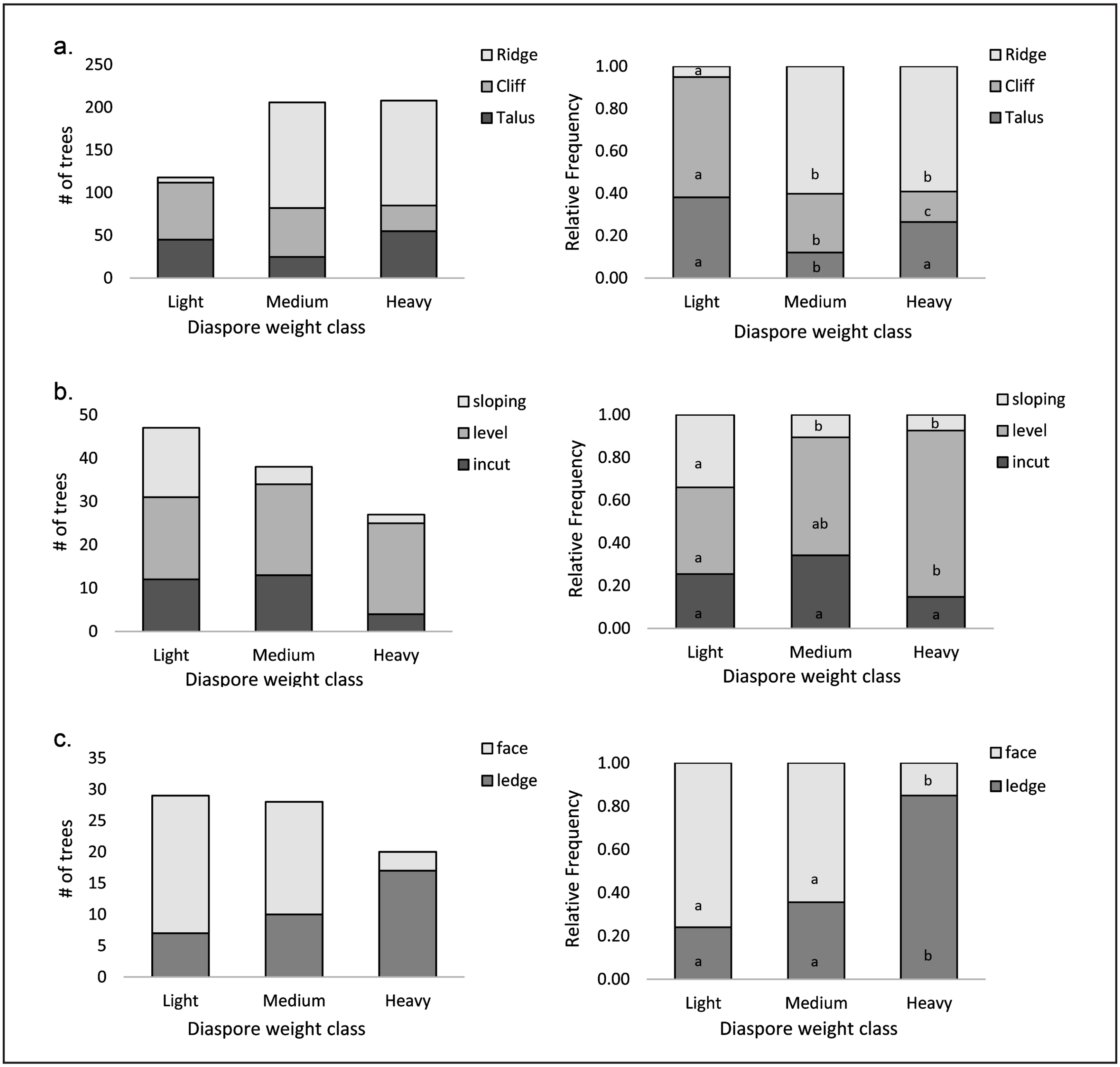

Figure 5. Relative counts (left) and frequencies (right) of trees within three diaspore weight classes (light, medium, heavy) across (a) three topographic positions (ridge, cliff, talus), (b) three cliff-face micro-topographic surface types (sloping, level, incut), and (c) two cliff features at CCK/Updraft (face, ledge). Significant differences in frequencies between diaspore weight classes within each topographic variable/cliff feature are indicated on the right-side graphs by different letters (*Z*-test with Bonferroni corrections, $P < 0.05$).

ciated with surface micro-topography ($\chi^2 = 15.32$, $P = 0.004$; Figure 5b, based on grouping scheme 1). Species with light-weight diaspores (big-tooth aspen, sweet birch) were disproportionately associated with sloping surfaces, while medium and heavy weight classes were disproportionately underrepresented on sloping surfaces. Conversely, heavy diaspore species were disproportionately associated with level surfaces compared to the lightest diaspore weight class. Similarly, at CCK/Updraft, heavy diaspore species were disproportionately associated with the ledge and underrepresented on the cliff face ($\chi^2 = 19.05$, $P < 0.000$; Figure 5c). Chi-square results, including all *Z*-test results, were the same with grouping scheme 2 (results not shown) for both surface micro-topography ($\chi^2 = 13.03$, $P = 0.011$) and ledge vs. cliff face at CCK/Updraft ($\chi^2 = 15.323$, $P < 0.000$).

DISCUSSION

Despite increasing interest in cliff ecology, cliffs remain one of the least studied ecosystems. To our knowledge, ours is the first rope-assisted study of the woody plant community on the Trapp's cliff, a focal point of Mohonk Preserve, and a unique geological feature of the region. The cliff tree communities in our study areas were dominated by mature pitch pine and more frequent but smaller-diameter sweet birch, with red/black oak and eastern white pine as sub-dominant species and less-frequently occurring chestnut oak, juneberry, red maple, sassafras, big-tooth aspen, and eastern red cedar. Species with light diaspores, dominated by sweet birch, were disproportionately frequent on the cliff compared to heavier diaspore species (Figure 4a). On the cliff, lightweight diaspore species were disproportionately frequent on sloping surfaces, while the heaviest diaspore weight class was disproportionately associated with level surfaces in general (Figure 4b), and with the GT ledge at CCK/Updraft in particular (Figure 4c).

Our findings raise the possibility that an association between diaspore weight and cliff micro-topography plays a role in assembling a cliff tree community that is divergent in composition from the ridge above, or talus below. The high relative frequency of sweet birch on the cliff compared to its importance in adjacent ridge and talus areas (assessed visually from Figures 2, 3, and 5) may be related to an association of lightweight diaspores (seeds in this case) with mostly sloping and vertical micro-topography on cliff faces. Similarly, the lower relative frequency of heavy diaspore species (e.g., oaks) on the cliff compared to the importance values of these species in adjacent areas, may be due to the association of heavy diaspores with level surfaces that are generally rare on the cliff. This reasoning is supported by the opposite pattern observed on the level GT ledge, where heavy-seeded oaks were the most abundant trees.

Dispersal mechanisms, and the topographic position (ridge vs. talus) where individual species have high importance values, may explain patterns of relative abundance on the Trapps cliff face. Sweet birch was not abundant on the ridge in our study, but is generally abundant in talus areas across the Shawangunks (Kiviat 1988; Thompson 1999) and had relatively high importance values in talus in our study. Wind dispersal, which can move lightweight seed upwards, against gravity, may be an important mechanism moving birch seeds from talus to cliff. Pitch pine is generally associated with shallow, rocky or sandy soil across the region (Bernard and Seischab 1995; Seischab and Bernard 1996), and dominates the Shawangunk rocky ridgelines (Kiviat 1988; Thompson and Huth 2011). Pitch pine may be especially important directly on cliff edges, an optimal location for seed dispersal to cliffs below. Oaks have heavy seeds (acorns) that probably move mainly by gravity between ridge and talus, with the possibility of reaching some microsites on the cliff, notably level microsites and ledges, in our study. Species categorized as animal-dispersed in our study are most likely dispersed by birds (Stiles 1980; Burns and Honkala 1990a, 1990b), which suggests that seeds could arrive at the cliff from either ridge, talus, or more distant locations. However, in the unique vertical environment of cliffs, these diaspores may be more likely to be moved by wind or gravity than in non-cliff environments. Although seed-dispersing animals are known to visit cliff faces (Matheson 1995), little is reported on the role of animals in the primary and secondary dispersal of seeds on cliffs.

The association we found between diaspore weight and patterns of community composition in different microsites is consistent with a manipulative study by Booth, who monitored persistence of different seed types placed on ledges and in crevices on the cliff face of the Niagara Escarpment (Booth 1999). In general, Booth found that small seeds remain in microsites longer than large seeds and dense seeds are removed from crevices faster than less-dense seeds. Although our study only considered weight (and not size or density), in the Booth study seed size and density were both correlated with seed weight. Consistent with the patterns in our study, Booth found that acorns of heavy-seeded oaks were lost quickly from crevices, but persisted on ledges, while light-seeded paper birch (*Betula papyrifera* Marshall) and white cedar (*Thuja occidentalis* L.) had higher persistence in crevices. Despite findings of seed persistence related to seed sizes at the microsite level, Booth reported no correlation between seed size, shape, or dispersal spectra with differences in community composition between cliff and talus or ridge. In contrast, our study found an association between diaspore weight and topography both at the level of microsite and broader topographic position.

A striking pattern at CCK/Updraft was the lack of pignut hickory on the cliff, despite its high importance on the ridge above. This was especially surprising on the GT ledge, where we found no pignut hickory, despite the presence of red oak and chestnut oak both on the ledge and in the ridgeline community. It is possible that an older cohort of oaks had established on the GT ledge, preempting subsequent establishment from a possible younger hickory cohort on the ridge above (Davis 1951; Matthes and Larson 2006). It is also possible that pignut hickory is less adapted to the potentially harsh conditions of the ledge, a conclusion that is supported by the fact that red oak, and especially chestnut oak, tend to be more dominant in shallower and drier, nutrient-poor soils than pignut hickory across the Shawangunk mountains (Thompson and Huth 2011). The abundance of pignut hickory along the ridgeline at CCK/Updraft may be something of an anomaly, perhaps due to deeper soils in the bench-like terrain between the cliff edge and the ridgeline at CCK/Updraft. On the ridge at Jackie/Betty, which lacked this bench-like terrain, pignut hickory was absent, and pitch pine was dominant.

Community assembly and the possibility that plant community composition on cliffs may be related to seed dispersal has only been extensively investigated at one cliff worldwide (Booth and Larson 1998, 2000a). On the Trapps cliff, we found an association between diaspore weight and cliff micro-topography that may partially explain patterns of community composition across the cliff system. However, our conclusions must be tempered by caution due to the small scope of our study and challenges we faced within our field sampling.

Our cliff face sampling areas differed in whether binoculars were used, which produced a large increase in the calculated area surveyed at CCK/Updraft. However, the number of trees detected on the cliff face was similar across study areas (Table 1). This is because most of the calculated cliff face area sampled at CCK/Updraft was bare rock. It is likely that steeper cliff angles reduced surface heterogeneity at CCK/Updraft, decreasing the number of sites for trees (Clark and Hessl 2015). Therefore, a wider survey of the cliff was deemed necessary to make an accurate assessment of the cliff face tree community. Consequently, longer lateral distances (and larger areas) on the ridge and talus were needed at CCK/Updraft. In contrast, at Jackie/Betty, the two adjacent rappels alone detected almost as many trees as the continuous cliff face area at CCK/Updraft. Consequently, less ridge and talus area was surveyed above and below the cliff face at Jackie/Betty. In addition to differences in sample area size, we were also not able to sample ridge and talus areas above and below the "other rappel" cliff-face transects (Figure 1). However, we believe these sampling limitations do not crucially affect our broader conclusions, because the association between diaspore weight and topographic categories (Figure 5) was based on data pooled across the entire study, tested in several different ways. For example, the association between diaspore weight and topographic position was statistically significant, even when we excluded the "other rappels" where we did not have complete ridge–cliff–talus observations.

Community assembly is complex, and variables we did not include in our analyses, acting at any stage of community assembly process (dispersal, seed bank persistence, germination, establishment, survival) are likely affecting final community composition. For example, the lack of pignut hickory on the cliff at CCK/Updraft could be related to failure at the seed germination or seedling recruitment filter stages, due to hickory being outside its fundamental niche on the cliff. Competitive effects may also play a role in determining the final community composition in cliff systems. For example, the relatively high occurrence of sweet birch on the cliff may be due to release from competition, which reduces its abundance on the ridge. Based on size-class distributions (Figure 5), it is also possible that sweet birch, unlike pitch pine, is less likely to grow to large sizes on the cliff, suggesting a filter at a later survival stage for sweet birch. In addition, our categorization of surface micro-topography was somewhat coarse, and was based on visual assessment rather than physical measurements of slope or soil/sediment characteristics. Despite these limitations, the strong theoretical relationship between diaspore weight and gravity or wind makes it plausible that the association we report is affecting species composition at our site and could be a mechanism on other cliffs.

The popularity of the Trapps cliff as a climbing destination raises the question of how climbing impacts are affecting plant community composition in our study. All of our study areas include popular climbing routes, probably receiving approximately equal use from climbers. Therefore, although climbers may be impacting vegetation on the Trapps cliff, these impacts are unlikely to be significantly different across the sampling areas in our study. Although negative effects of rock climbing on cliff vegetation have been reported (Kelly and Larson 1997; Camp and Knight 1998; McMillan and Larson 2002), more recent work has found that these effects may be due to systematic differences in cliff terrain between climbed and unclimbed cliffs related to the preferences of climbers (Kuntz and Larson 2006a; Clark and Hessl 2015; Holzschuh 2016). Actual climber impacts may be comparatively small compared to physical variables such as cliff angle (Clark and Hessl 2015). However, given the popularity of the Trapps, the patterns we report here should be tested and corroborated at other sites, especially sites where climbing intensity could be included as a test variable.

As managers of protected areas with cliffs focus attention on conservation of cliff plant communities, there will be an increasing need for explanatory mechanisms to inform management. Our study is the first of its kind at a regionally important cliff in a protected area with high recreational value. Our results suggest that diaspore weight and/or associated dispersal mechanisms may play a role in the assembly of cliff tree communities. This possibility, though not highlighted in the literature, is consistent with other work and deserves broader and more extensive testing. Future research should also consider animals as potential seed dispersal agents on cliffs and the role of plant seed sources across cliff systems in supporting food webs that ultimately sustain focal cliff species such as peregrine falcons (*Falco peregrinus* Tunstall). Our study also suggests that protection of the talus slope, which can be especially vulnerable to human impacts in climbing areas (Rusterholz et al. 2011), may be important for maintaining wind-dispersed seed sources that sustain plant communities on the cliff.

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