RESEARCH ARTICLE

Successional patterns of terrestrial wildlife following deglaciation

Mira L. T. Sytsma[1] | **Tania Lewis**[2] | **Jonathan D. Bakker**[1] | **Laura R. Prugh**[1]

[1]School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA

[2]Glacier Bay National Park and Preserve, Gustavus, Alaska, USA

Correspondence
Mira L. T. Sytsma
Email: mirasytsma@gmail.com

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Abstract

1. Disturbance is a key driver of community assembly and patterns of diversity. Whereas successional changes in vegetation have been well-studied, postdisturbance successional patterns of wildlife communities remain poorly understood.

2. Here, we investigated the roles of site age and habitat in shaping community assembly and the diversity of terrestrial mammals in Glacier Bay National Park, Alaska (GBNP), which has undergone the most rapid and extensive deglaciation in the world since the Little Ice Age. Deglaciation has extensively altered the landscape, opening up new habitat for recolonization by plants and animals.

3. We used camera traps, small mammal trapping and vegetation surveys to investigate the patterns of mammalian succession and beta diversity following deglaciation, using a space-for-time substitution across 10 sites during summers 2017 and 2018. Site age and habitat characteristics were not strongly correlated ($r < 0.46$), allowing the influences of time since disturbance and habitat changes to be distinguished.

4. PERMANOVA analyses indicated that mammal community assembly was more strongly influenced by site age than habitat, whereas habitat and age had similar effects on beta (between site) diversity. Beta diversity was higher for smaller, less mobile mammals than larger, more mobile mammals and was primarily driven by species turnover among sites, whereas relative turnover was much lower for larger mammals. A comprehensive review of historical distributions of mammals in GBNP supported our findings that species turnover is a driving influence of community assembly for smaller mammals.

5. Our results indicate that body size of mammals may play an important role in shaping colonization patterns postdisturbance, likely via size-related differences in mobility. Patterns of wildlife community assembly may therefore not track vegetation succession following disturbances if there are barriers to movement or if dispersal ability is limited, highlighting the importance of incorporating landscape connectivity and species traits into wildlife conservation efforts following disturbances. This knowledge may improve predictions of mammalian community assembly following major disturbance events.

1 | INTRODUCTION

Disturbance is a fundamental process controlling diversity (Huston, 1994). Disturbance is defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment" (White & Pickett, 1985). There is widespread agreement that climate change will influence the magnitude and frequency of disturbances, making it imperative to understand how biotic communities respond to these events (Sergio et al., 2018). When a disturbance significantly reduces the diversity of a region, the starting point for community assembly processes is essentially reset (Turner et al., 1998). Many studies have documented patterns of vegetation succession in response to these events, but animal community successional patterns are not as well understood (Monamy & Fox, 2010).

The importance of habitat suitability to the establishment of wildlife populations following disturbance has been long recognized in ecology (Sousa, 1984; White & Pickett, 1985). Habitat metrics are often used as a surrogate for changes in wildlife assemblages postdisturbance (Barton et al., 2014), and models often assume uniform rates of recolonization (Mutz et al., 2017). For example, the habitat accommodation model (HAM; Fox, 1982) for animal succession proposes that wildlife species appear on a landscape undergoing successional change when the vegetation community reaches a threshold of suitable habitat. This model assumes animal succession does not follow site age per se, but rather follows changes in vegetation (Fox et al., 2003). Habitat development and site age may be correlated due to plant succession (Clements, 1916), but barriers to seed dispersal or differential proximity to seed sources could decouple these factors. Quantifying the relative importance of site age and habitat would increase our understanding of the processes driving postdisturbance wildlife community assembly.

In this paper, we used remote cameras, small mammal livetrapping, and vegetation surveys to investigate the roles of site age and habitat characteristics on patterns of mammalian community assembly and beta diversity in Glacier Bay National Park (GBNP) following glacial recession. Glacier Bay has undergone the most rapid deglaciation in the world since the Little Ice Age (LIA; Kohls et al., 2003), resulting in a marine fjord and a time-since-deglaciation chronosequence along the shoreline ranging from zero at the glacier faces to about 270 years at the mouth of the bay. Studies in GBNP during the last century have examined soil development (Crocker & Major, 1955), plant succession (Chapin et al., 1994), and successional patterns of microcrustaceans, macroinvertebrates and fish (Milner et al., 2000). Despite the history of extensive scientific inquiry on postglacier successional processes in GBNP, mammal colonization and distributions have not been systematically examined. GBNP

provides a unique opportunity to tease apart the relative importance of site age and habitat characteristics on postdisturbance community assembly, because these factors are not closely correlated in this system and colonization by mammals is recent and ongoing (Buma et al., 2019).

We examined patterns of beta diversity and species composition to identify key processes influencing postglacial mammal community successional dynamics. Species turnover—when species in one site are substituted by different species in other sites—is a key component of beta diversity. It reflects ecological sorting whereby species are "filtered" by local environmental conditions and occur only at sites with suitable habitat (Svenning et al., 2011). The magnitude of turnover can provide insight into the importance of ecological sorting compared to dispersal. Turnover can also be calculated in absolute terms and relative to total beta diversity. Considering both metrics can clarify whether the importance of turnover depends on the overall amount of beta diversity (Baselga & Orme, 2012).

We expected site age and habitat characteristics to play important roles in shaping postglacial mammalian successional patterns. Studies of plant succession in GBNP found that distance to seed source and seed dispersal ability played a large role in shaping early establishment patterns of plants (Fastie, 1995), and we hypothesized that mammalian recolonization could face a similar limitation. Larger mammals are generally better dispersers and therefore may be able to access suitable habitat inaccessible to smaller mammals. Because of this, we expected that habitat would influence community assembly and beta diversity of larger mammals more so than for smaller mammals. Conversely, we expected community assembly and beta diversity of small mammal communities would be more closely tied to site age. Because high dispersal rates can homogenize community composition and thereby reduce beta diversity (Vanschoenwinkel et al., 2013), we expected total beta diversity to be lower for larger mammal communities.

2 | MATERIALS AND METHODS

2.1 | Study system and site selection

Glacier Bay National Park and Preserve is a 13,000 km^2 protected area in Southeast Alaska (Figure 1). The deglaciation of GBNP has exposed several hundred square kilometres of glacial till and outwash plain to plant and animal colonization. Today, Glacier Bay proper is a marine fjord with east and west arms that split about 45 km from the mouth. It is 80 km long from the mouth to the top of the east arm and 100 km long from the mouth to the top of the west arm. Glacier Bay is surrounded by mountains, glaciers, ice fields and temperate rainforest.

FIGURE 1 Location of Glacier Bay National Park, AK and study sites (1–10). See Tables 1 and 2 for site details.
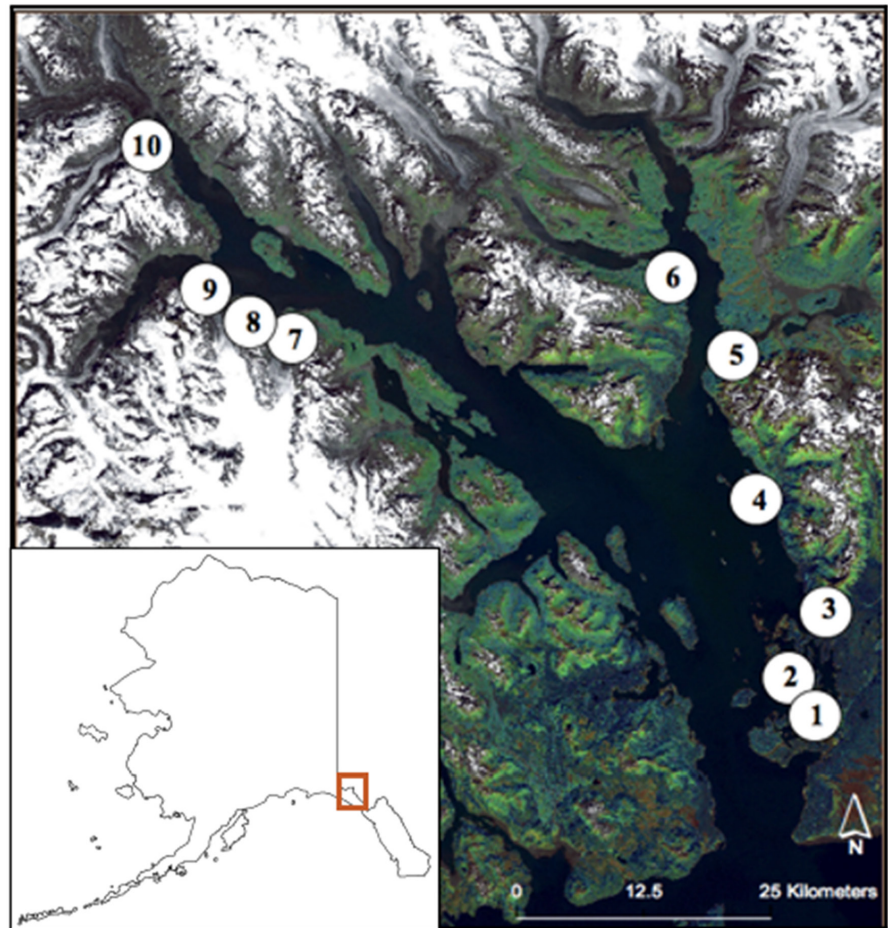
The plant communities in GBNP differ dramatically from north to south. The most recently deglaciated sites occur in the north and are dominated by dwarf scrub dryas *Dryas drummondii*. Proceeding south, habitats transition to open and closed scrub dominated by willow *Salix* spp. or alder *Alnus* spp. and then to young forests dominated by Sitka spruce *Picea sitchensis*. The plant communities of the east and west sides of the bay also differ: the more rapid and earlier retreat of glaciers on the west side facilitated early dominance of willow due to their abundant seed rain, relatively light seeds and rapid growth (Buma et al., 2017). Conversely, Sitka alder and Sitka spruce dominate on the east side (Fastie, 1995). Areas to the southeast and west of Glacier Bay that were not glaciated during the LIA (Lewis, 2012) are mature forests dominated by hemlock *Tsuga heterophylla* and likely served as refugia for animals during the LIA.

We selected 10 sites spanning a gradient of time-since-exposure (Figure 1, Table 1). Sites needed to be accessible by boat with shoreland and inland habitats accessible by foot. Six sites were on the east side of Glacier Bay (hereafter "east"): four on the east side of the main channel (sites 1–4) and two on the east arm (sites 5–6). Four sites were on the west side of the main channel (sites 7–10; hereafter "west"). Time-since-exposure-related variables gathered for each site via ArcGIS included distance to the mouth of Glacier Bay (*DistanceMouth*), distance to the glacier that previously covered each site (*DistanceGlacier*; Figure 1), and northing (*Northing*). Approximate

years-since-deglaciation (*Age*) was determined from maps provided by the National Park Service. These variables were highly correlated ($r = 0.87$–0.99; Figure S1), so we used *Age* in analyses because it was the most direct measure of time-since-exposure.

2.2 | Data collection

2.2.1 | Vegetation surveys

We conducted vegetation surveys during 2018 at ten 1 m^2 plots in the inland habitat at each site. Plots were approximately 10 m apart along the diagonal of each site's small mammal trapping grid (Figure S2). We recorded percent cover of substrates and understory vegetation in each plot and grouped those covers into seven functional groups: bare ground, low scrub, tall scrub, dwarf scrub, graminoid-herbaceous, forb-herbaceous and bryoid-herbaceous (Viereck et al., 1992). Average cover was calculated for each functional group in each site, and total cover as the sum of the average covers of all functional groups. We made four densiometer readings per plot and used the average as our measure of canopy cover. We measured tree diameter at breast height (DBH) of the four trees closest to each plot centre, and calculated average basal area (BA, m^2) for each site.

TABLE 1 Characteristics of sites in Glacier Bay National Park (GBNP). Site numbers correspond to Figure 1. *Easting* and *Northing* are in meters and are from UTM zone 8N. Time-since-exposure-related variables gathered using ArcGIS included distance to the mouth of the Glacier Bay fjord (*DistanceMouth*), distance to the glacier that deglaciated each site (*DistanceGlacier*; Grand Pacific in the west and Muir in the east; Figure 1), and *Northing*. Approximate time-since-exposure was determined from maps provided by the National Park Service (*Age*). *Side* indicates whether the site is on the east (E) or west (W) side of Glacier Bay.

Site #	Site name	Easting	Northing	DistanceGlacier (km)	DistanceMouth (km)	Age (years)	Side
1	Bartlett Cove	447,413	6,478,484	72.42	13.36	218	E
2	Lester Island	449,123	6,480,711	69.54	15.60	208	E
3	Beartrack Cove	451,084	6,495,758	62.43	25.72	188	E
4	South Sandy	443,038	6,509,206	48.30	36.52	156	E
5	Adams Inlet	439,723	6,524,048	34.22	51.55	118	E
6	Hunter Cove	434,970	6,531,360	25.00	59.93	118	E
7	Reid East	395,729	6,523,717	27.56	71.35	148	W
8	Reid West	394,833	6,525,799	25.79	73.01	148	W
9	Lamplugh	389,140	6,530,393	20.09	79.47	118	W
10	Upper Tarr	382,799	6,544,135	4.56	94.20	108	W

2.2.2 | Small mammal trapping

We trapped small mammals on two grids per site using 50 large and 50 small folding Sherman traps (Model LFA; 3 × 3.5 × 9″ and 2 × 2.5 × 6.5″; H.B. Sherman Folding Traps, Inc.) per grid, with traps placed 10 m apart in a grid (Figure S2). One grid was placed in inland habitat and the second in shore habitat, approximately 0.5 km apart. Traps were baited using bird seed, oats, apples, dried mealworms and cotton batting. Trapping sessions lasted 3 days and two nights, with traps checked each morning and evening. Captured individuals were weighed, measured, identified to species and sex, and marked with a Sharpie near the base of the tail. Capture and handling procedures were approved under University of Washington's Institutional Animal Care and Use Committee #4381-01 and Alaska Department of Fish and Game permit #17-113. We calculated the Minimum Number Alive (MNA; Krebs, 1966) for each species as an index of population size and summed the MNA across habitat types as a site-level estimate of abundance. We were unable to identify shrews to species in the field, and 97 mortalities were sent to the University of Alaska Museum of the North for identification (Table S2). MNA for each shrew species was calculated by multiplying the total number of shrews caught per site by the proportion of museum-identified individuals represented by that species.

2.2.3 | Camera trapping

We installed four cameras (Reconyx HC600 Hyperfire Covert IR) at each site (40 total cameras), two in shoreline habitat and two in inland habitat. Cameras were approximately 0.5 km away from one another—forming a square grid at each site—and were installed approximately 0.5 m above the ground on trees or t-posts along the shoreline, game trails or other expected areas of wildlife concentration. Cameras took a burst of three photos when triggered (the "rapid-fire" setting). Two cameras per site also took "timelapse"

photos every 15 min regardless of if they were triggered. We processed photos using Timelapse2 (Greenberg & Godin, 2015), identifying individuals to species for each photo.

We screened photos so that photographic events of the same species at a camera were considered independent if separated by more than 30 min (Carter et al., 2012), using both timelapse and motion triggered photos. The number of independent events for each species was then summed across the four cameras at each site as a measure of its abundance.

2.2.4 | Historical data

We examined and compiled records of historical mammal detections and distributions originating from the 1899 Harriman Expedition and the 1907 Alexander Alaska Expeditions (Heller, 1909). We also reviewed publications and field notes from W. Cooper and D. Lawrence (Buma et al., 2019) and Goldthwait et al. (1966), as well as GBNP ranger observations from 1952–1969 (NPS unpublished data). These observations consisted of only general locations, did not have corresponding information about the vegetation, and were not recorded in a systematic manner comparable to our data collection. We therefore qualitatively examined historical occurrence patterns to provide additional insights into species community assembly patterns. An abridged version of these records can be found in Table S8, and a full data set is in a Dryad Digital Repository: https://doi.org/10.5061/dryad.t1g1jwt5r.

2.3 | Statistical analyses

2.3.1 | Vegetation community analysis

We used a Similarity Profile Analysis (SIMPROF; Clarke et al., 2008) in the R package CLUSTSIG (Whitaker & Christman, 2014; version 1.1)

to determine the number of significant vegetation clusters within GBNP. This analysis used hierarchical agglomerative clustering with Ward's linkage method, grouping observations to maximize similarity. Data were relativized by species maxima so that all species contributed equally to dissimilarities among sites and expressed with the Bray–Curtis dissimilarity measure.

Because of the large number of potentially correlated habitat-related variables (n = 10, Table S1), we used Principal Component Analysis (PCA) to reduce these variables to a small number of uncorrelated principal components (PCs) (Figure 2). The first three PCs together explained 81% of the variance in the full set of habitat-related variables and were used as explanatory variables in subsequent analyses. Based on the loadings (Table S3), PC1 was most strongly associated with the bryoid-herbaceous and bare ground variables, PC2 was strongly associated with dwarf scrub and tall scrub, and PC3 was highly associated with graminoid-herbaceous and total cover. *Age* was weakly correlated with the three habitat PCs ($r < 0.46$ and $p > 0.05$; Figure S1).
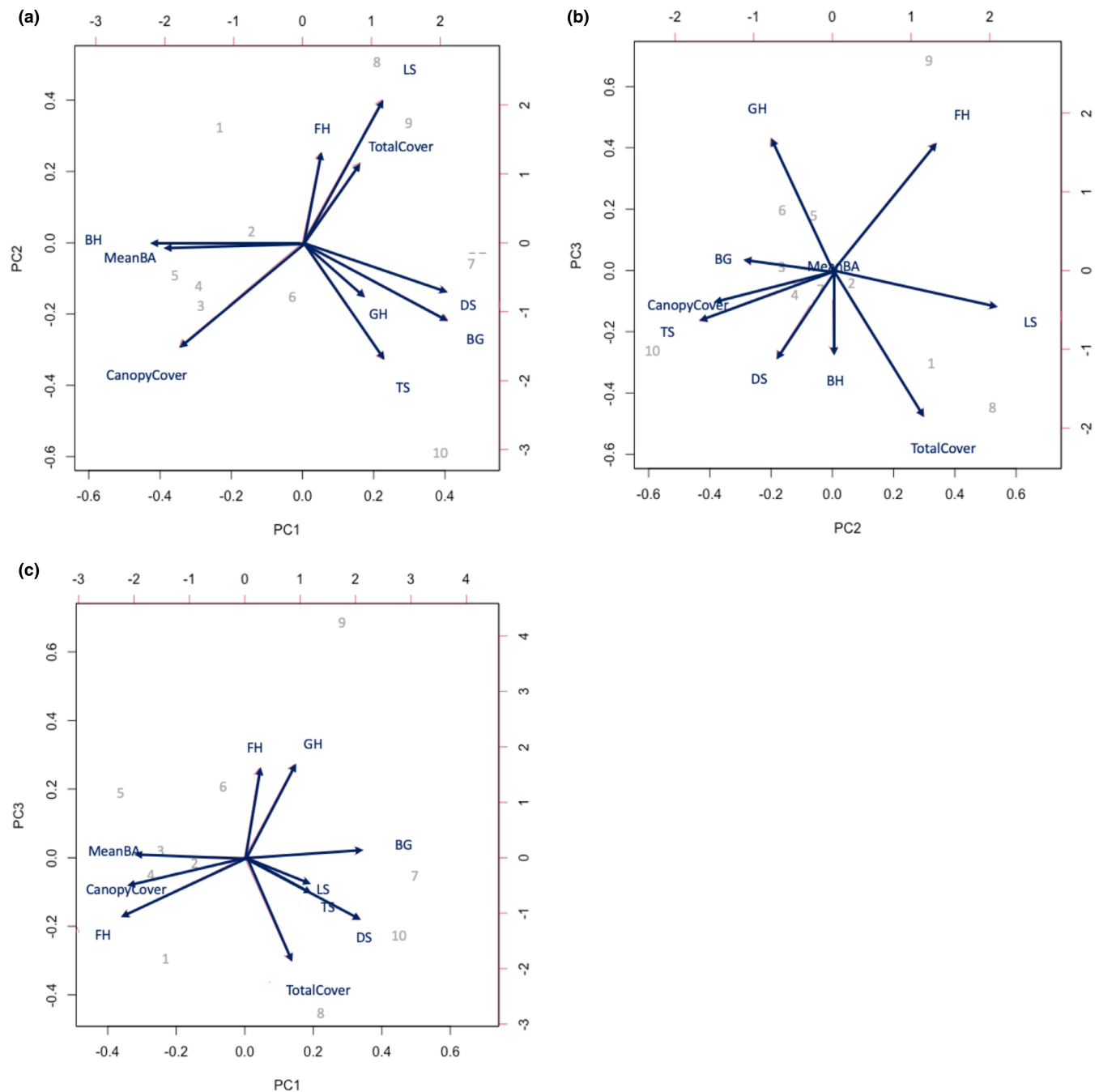

FIGURE 2 PCA of 10 habitat-related variables, comparing (a) PC1 to PC2, (b) PC2 to PC3, and (c) PC1 to PC3. Variables are defined in Table S2. PC1 explained 39.3% of the variation, PC2 explained 23.2%, and PC3 explained 18.8%. Loadings are reported in Table S3. Grey numbers refer to sites (Table 1).

2.3.2 | Mammal community composition

Mammal community composition was expressed as the number of individuals (small mammals) or independent photo events (large mammals) per species. Data were relativized by species maxima and were therefore unitless. We performed a hierarchical cluster analysis using Ward's linkage and Euclidean distances. We then used a tanglegram (DENDEXTEND package; Galili, 2015; version 1.9.0) to compare the clusters within the mammal community to the clusters identified in the vegetation community.

To evaluate the influence of dispersal ability on community assembly, we classified mammal species as good or poor dispersers based on average adult body mass (Jones et al., 2009). Dispersal ability is proportional to body mass (Lindstedt et al., 1986). To verify this with our taxa, we obtained home range size estimates (an indicator of movement ability) for 15 species from Jones et al. (2009); body mass and home range size were strongly correlated ($r = 0.90$). Similarly, maximum recorded dispersal distances (Prugh et al., 2008) were correlated with body mass ($n = 12$, $r = 0.74$). Finally, we examined how sensitive the results were to the body mass cutoff used to classify species as good or poor dispersers: varying the cutoff from 200–10,000 g did not change the results qualitatively (Table S4). Here, we classified species with body mass > 8000 g (i.e. river otter [*Lotra canadensis*] and larger) as good dispersers (8 species) and < 8000 g (i.e. porcupine [*Erethizon dorsatum*] and smaller) as poor dispersers (10 species).

We used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to assess the influence of *Age* and habitat characteristics (PCs) on the mammal community. This procedure provides a multivariate equivalent to the F-ratio with significance determined from permutations (Newman et al., 2014). Each explanatory variable (*Age* and all three PCs) was tested separately with 999 permutations. We conducted PERMANOVAs using three community matrices: (1) the entire mammalian community, (2) good dispersers, and (3) poor dispersers. PERMANOVAs were run using relativized abundance data and Euclidean distances. We also ran the PERMANOVAs using species occurrence data and found similar results, though habitat-related variables had a slightly larger effect on species occurrence than abundance (Table S5). All predictor variables were continuous. To better understand the contribution of individual species to the community-level patterns, we used linear regression to estimate the amount of variation in the abundance of each species explained by *Age* and by each PC.

2.3.3 | Beta diversity

We used the R package BETAPART (Version 1.5.2; Baselga et al., 2018; Baselga, 2010) to calculate overall beta diversity (β_{sor}; Sørensen dissimilarity, Equation 1) and Simpson dissimilarity (β_{sim}; spatial turnover, Equation 2),

$$\beta_{sor} = \frac{\max(b,c) + \min(b,c)}{2a + \min(b,c) + \max(b,c)}, \tag{1}$$

$$\beta_{sim} = \frac{\min(b,c)}{a + \min(b,c)}, \tag{2}$$

where *a* is the number of species shared by two sites, *b* is the number of species unique to site 1, and *c* is the number of species unique to site 2. Baselga's (2010) approach also calculates the amount of beta diversity that is due to nestedness but we focused on turnover because it is more straightforward to interpret and more directly relevant to our research questions (Ulrich et al., 2009). We focused on three metrics: overall beta diversity (Equation 1), turnover (Equation 2) and relative turnover (equation 2/equation 1). These metrics were calculated for the entire mammalian community, good dispersers, and poor dispersers.

To assess the effects of *Age* and habitat on patterns of beta diversity, we ran PERMANOVAs on each metric for each aspect of the mammalian community. As above, each explanatory variable was tested separately.

3 | RESULTS

3.1 | Vegetation community composition

Approximate years-since-deglaciation (*Age*) ranged from 108 years (Upper Tarr) to 218 years (Bartlett Cove; Table 1). The cluster analysis of the vegetation community data yielded two distinct groups corresponding to the east and west sides of Glacier Bay (Figure 3). Sites in the east were characterized by moss (*BH*) and trees such as Sitka spruce, Black cottonwood *Populus trichocarpa*, and Western hemlock (Table S1). Sites in the west were characterized by bare ground (*BG*) and early successional species such as willow (*LS*) and dryas (*DS*).

3.2 | Mammal community composition

Six small mammal species were captured (Tables 2 and 3). There were 284 total captures, and we captured a minimum of 275 individuals, of which 72% were montane shrews *Sorex monticolus*. Our remote cameras detected 12 mammal species (Tables 2 and 3), yielding 1709 independent detections; black bears were most frequently detected, followed by brown bears and porcupines.

The number of species detected generally increased with *Age*, ranging from six species at the youngest site to 13 species at the oldest sites (Table 2). Similarly, the number of sites each species was detected at generally increased with body mass ($n = 18$, $R^2 = 0.41$; Tables 2 and 3). For example, the two largest species, brown bears and moose *Alces alces*, were detected at all sites. Coyotes *Canis latrans*, porcupines and red squirrels *Tamiasciurus hudsonicus* were detected only on the east side, and marmots *Marmota caligata* and wolverines (one site only) were detected only on the west side. We generally detected more poor dispersers on the east side than the west side, however Keen's mice *Peromyscus keeni*, long-tailed voles *Microtus longicaudus* and montane shrews were distributed across the youngest sites on the west side.
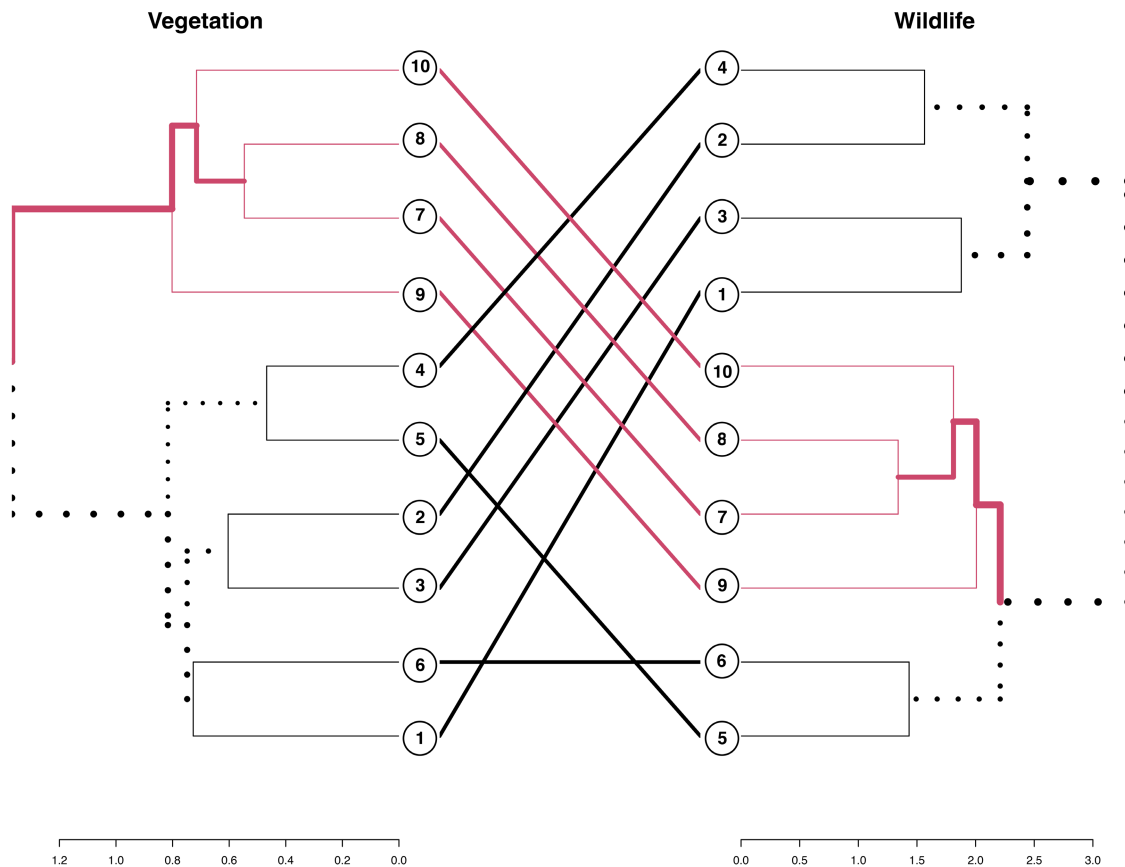
FIGURE 3 Tanglegram comparing the vegetation communities (left) and wildlife communities (right) at each site. The two groups in the vegetation cluster analysis correspond to the east and west arms of Glacier Bay. The lines between the two dendrograms connect the same site in each. Pink lines indicate similar compositional patterns for both communities (here, sites 7–10). Patterns that are not consistent between communities are shown by dashed lines in the dendrograms and black lines connecting them. If the vegetation and mammal communities followed the same successional patterns, the cluster dendrograms would be mirror images of each other. Numbers represent sites (Table 1).

Mammal community composition was closely tied to habitat in the west, but these communities were not as closely associated in the east (Figure 3). *Age* explained 27% ($F_{1,8} = 3.009$, $p = 0.001$; Table 4, Table S6) of the variation in the mammal community, while PC1 explained 18% ($F_{1,8} = 1.802$, $p = 0.042$) and neither PC2 nor PC3 were statistically significant (Table 4). *Age* also had a stronger influence on community assembly of good and poor dispersers than any of the PCs, explaining 26%–35% of the variation in these communities. Comparatively, PC1 explained about 19% of the variation, PC2 ranged from 6%–9% and PC3 from 8%–12% (Table 4). At the individual species level, PC1 and PC2 did not significantly affect the abundance of any species, whereas PC3 significantly affected two species (American marten (*Martes americana*) and moose; Table S7). *Age* significantly affected the abundance of common shrews (*Sorex cinereus*), red squirrels, Sitka black-tailed deer *Odocoileus hemionus* and black bears.

3.3 | Historical data

Historical data from the early 1900s indicated that tundra voles *Microtus oeconomus* were common on the east and west sides

of Glacier Bay, while red squirrels were common only on the east (Table S8). In the mid-1900s, Goldthwait et al. (1966) documented that montane shrews were early arrivers to more recently deglaciated areas in the east arm and were replaced by common shrews in older sites. The same study also reported Keen's mice, red-backed voles *Myodes rutilus*, long-tailed voles and tundra voles in the east arm of the bay. Ranger observations from the same time indicate hoary marmots were present in the east arm, coyotes were present near the upper west arm, and red foxes *Vulpes vulpes* were detected in the lower bay (Table S8).

3.4 | Beta diversity

Turnover largely drove patterns of beta diversity across sites (relative turnover = 86%; Table 4). Good dispersers had relatively low beta diversity and low relative turnover (0.571 and 55%, respectively; Table 4, Table S9). *Age* explained 53% of the variation in overall beta diversity of good dispersers while PC1 accounted for 53% of the variation. Poor dispersers had higher beta diversity and relative turnover (0.761 and 90%, respectively; Table 4, Table S9).

TABLE 2 Species detected at each site (site numbers defined in Table 1). Species are separated into poor (top) and good (bottom) dispersers and organized by increasing body mass. Number of species in each category and totals for each site are also shown.

Species	1	2	3	4	5	6	7	8	9	10
Poor dispersers										
Common shrew	X		X	X						
Montane shrew	X	X	X	X	X	X	X	X	X	
Tundra vole					X		X	X		
Keen's mouse					X	X				X
Red-backed vole		X	X	X			X			
Long-tailed vole	X							X	X	X
Red squirrel	X	X	X	X	X					
American marten	X		X		X	X			X	
Marmot							X	X	X	
Porcupine	X	X	X	X	X					
Good dispersers										
River otter	X		X							
Coyote	X	X	X	X	X					
Wolverine										X
Wolf		X	X	X	X	X	X	X	X	X
Sitka black-tailed deer	X		X							
Black bear	X	X	X	X		X			X	
Brown bear	X	X	X	X	X	X	X	X	X	X
Moose	X	X	X	X	X	X	X	X	X	X
Number of poor dispersers	6	4	6	5	6	3	4	4	4	2
Number of good dispersers	6	5	7	5	4	4	3	3	4	4
Total number of species	12	9	13	10	10	7	7	7	8	6

Age explained 33% of the variation in poor dispersers while PC1 explained 37%. *Age* and PC1 explained 38% and 46% of the variation in beta diversity of all mammals considered together. Meanwhile, *Age* and PC1 explained similar amounts of variation in total turnover and beta diversity for each of the three community groups (entire, good dispersers, poor dispersers), but none of the explanatory variables significantly affected relative turnover (Table 4, Tables S9 and S10). No measures of beta diversity were significantly related to PC2 or PC3 (Table 4, Figure 4, Table S10).

4 | DISCUSSION

Mechanisms driving whole-community responses of mammals to disturbance remain poorly understood (McKelvey, 2015), and while habitat undoubtedly has a strong effect on wildlife community assembly postdisturbance, the extent to which wildlife recovery mirrors habitat recovery is poorly known (Barton et al., 2014). GBNP was established in part to facilitate scientific documentation of terrestrial community development postglaciation (Lewis & White, 2016), however wildlife community responses to glacial recession remain under-studied. In this paper, we show that mammalian communities increase in diversity over time, similar to plant and stream communities. However, changes in wildlife communities do not directly track changes in habitat, particularly if communities consist of species with differing dispersal abilities. Community assembly was more strongly related to site age than habitat, whereas beta diversity was similarly affected by both factors (Figure 4). Additionally, beta diversity was lower for good dispersers, highlighting the role dispersal can play in homogenizing communities. Overall, our findings indicate that caution should be used when inferring changes in wildlife communities based on habitat succession alone, as landscape connectivity and the dispersal abilities of local species may be important drivers of wildlife community succession following disturbances.

Site age had a larger impact on the postglacial mammal community assembly than habitat-related variables, which was contrary to predictions made by the habitat accommodation model in post-fire systems (Fox, 1982). It is generally difficult to separate habitat characteristics and site age in studies of community succession due to the inherent correlation between the two (Clements, 1916), but GBNP provides a unique opportunity to differentiate between them. For example, sites 5 and 6 in northeastern GBNP were similar in age to sites 9 and 10 in the northwest but had different plant communities, as indicated by the vegetation cluster analysis (Figure 3). Buma et al. (2017) similarly found different patterns of plant succession

TABLE 3 Species scientific names, common names and average body mass for mammals captured in this study. Capture method, home range size, maximum dispersal distance, the number of captures/detections, and the number of sites at which each species was detected are shown. Mammals were classified as poor or good dispersers based on body mass. Data that were not available are indicated by 'N/A'. Captures/detections are the minimum number alive from live trapping and the number of detections from remote camera data, respectively. See Table S2 for shrew mortality data.

Scientific name	Common name	Capture method	Body mass (g)	Home range (km²)	Maximum dispersal distance (km)	Captures/ detections	Number of sites detected
Poor dispersers							
Sorex cinereus	Common shrew	Live trap	4	0.005	5.090	19	3
Sorex monticolus	Montane shrew	Live trap	6	0.002	8.508	197	9
Microtus oeconomus	Tundra vole	Live trap	17	0.002	N/A	7	3
Peromyscus keeni	Keen's mouse	Live trap	22	0.003	N/A	31	3
Myodes rutilus	Red-backed vole	Live trap	26	N/A	N/A	13	4
Microtus longicaudus	Long-tailed vole	Live trap	37	N/A	5.693	8	4
Tamiasciurus hudsonicus	Red squirrel	Camera	200	0.008	1.610	38	5
Martes americana	American marten	Camera	874	3.910	158.000	10	5
Marmota caligata	Marmot	Camera	2254	N/A	N/A	113	3
Erethizon dorsatum	Porcupine	Camera	7420	0.110	N/A	270	5
Good dispersers							
Lontra canadensis	River otter	Camera	8087	16.950	200.000	38	2
Canis latrans	Coyote	Camera	11,989	19.910	232.200	125	5
Gulo gulo	Wolverine	Camera	12,793	363.580	300.000	2	1
Canis lupus	Wolf	Camera	31,757	43.130	809.000	68	9
Odocoileus hemionus	Sitka black-tailed deer	Camera	84,561	2.850	11.710	10	2
Ursus americanus	Black bear	Camera	196,288	34.070	225.000	429	6
Ursus arctos	Brown bear	Camera	371,704	333.820	471.000	419	10
Alces alces	Moose	Camera	461,901	73.260	N/A	229	10

between the east and west sides of the fjord and highlighted the impact that distance to seed source has had on plant succession in GBNP. Mammal communities did not closely mirror vegetation communities, indicating successional trajectories of plants and animals are not tightly coupled in this system.

As with plants, wildlife succession postdisturbance is affected by the distance to source population as animals colonize newly uncovered land from glacial refugia. Unfortunately, there is no information regarding which mammal species may have survived in various refugia surrounding GBNP's glaciers during the LIA, but dispersal ability and distance from these refugia may have an unmeasured influence on mammalian community assembly across the chronosequence. Structural connectivity has likely played a large role in shaping wildlife communities in GBNP, due primarily to two major barriers to wildlife movement. First, the bay itself has inhibited wildlife movement from glacial refugia and funnelled dispersal northward from eastern and western glacial refugia (Lewis et al., 2015). Second, glacier-covered mountains and ice fields likely hinder wildlife movement, particularly on the west side, which is dominated by the Fairweather mountain range and the Brady ice field. The east side has low-lying mountains that have facilitated wildlife movement from eastern glacial refugia (Schoen & Albert, 2016). These barriers

to wildlife movement prevent both black bears and brown bears from genetically mixing in southeast Alaska (Lewis et al., 2015, 2020; Peacock et al., 2007) and likely affect other species as well.

Our results indicate that certain species may have recolonized GBNP only from one side of the bay: coyotes and marmots were only detected on the east and west side, respectively (Table 2, Figure S3). However, historical observations show that coyotes were present in the west arm in the late 1960s (Table S8), indicating some level of turnover in larger mammals. Similarly, red foxes were common in Bartlett Cove in the 1960s but were not observed anywhere along the shoreline areas in our study (Table S8). Brown bears, moose and wolves *Canis lupus* were distributed across almost all sites, indicating that these species are able to disperse greater distances despite the fragmented landscape, and/or that they recolonized from refugial populations on both sides of the bay. While brown bears and wolves have been observed on the GBNP shoreline for 75–100 years, moose are a relative newcomer—arriving from the east in the late 1960s (Table S8, Dryad Digital Repository)—supporting a lower level of turnover in large mammals as well. Interestingly, some of the smallest mammal species were also widely distributed: montane shrews were detected at nearly all sites, and Keen's mice were detected on both sides of the fjord. Patterns of landscape heterogeneity and

TABLE 4 Results from PERMANOVAs conducted to assess the separate influence of habitat (PC1, PC2, PC3) and time since exposure (Age) on community assembly and beta diversity. Results are separated based on PERMANOVAs conducted on the entire species matrix, and on good and poor dispersers separately. Statistically significant effects ($p < 0.05$) are in bold. Total beta diversity, total turnover and relative turnover are listed. Detailed results for the beta diversity analyses are located in the Appendix (Tables S6 and S9).

Metric	Category	Variable	R^2	p value	Turnover	Relative turnover	Total
Assembly							
	All species						
		PC1	0.18	**0.04**			
		PC2	0.07	0.86			
		PC3	0.10	0.56			
		Age	0.27	**0.02**			
	Good dispersers						
		PC1	0.19	0.07			
		PC2	0.09	0.60			
		PC3	0.08	0.70			
		Age	0.35	**0.01**			
	Poor dispersers						
		PC1	0.18	0.08			
		PC2	0.06	0.87			
		PC3	0.12	0.47			
		Age	0.26	**0.02**			
Beta diversity							
	All species				0.596	86%	0.696
		PC1	0.46	**<0.01**			
		PC2	0.11	0.40			
		PC3	0.01	0.96			
		Age	0.38	**0.01**			
	Good dispersers				0.315	55%	0.571
		PC1	0.53	**0.01**			
		PC2	0.06	0.54			
		PC3	−0.03	1.00			
		Age	0.53	**0.02**			
	Poor dispersers				0.682	90%	0.761
		PC1	0.37	**0.01**			
		PC2	0.14	0.29			
		PC3	0.02	0.89			
		Age	0.33	**0.02**			

structural connectivity are likely key aspects of postdisturbance wildlife recolonization as dispersal barriers may prevent wildlife from tracking environmental changes (Caplat et al., 2016).

While historical mammal observations in Glacier Bay were not systematic enough to facilitate quantitative comparisons to our data on contemporary distributions, these records provide insights about successional patterns over time that are rarely possible to obtain in studies using a space-for-time substitution such as ours. Both current and historical distributions of small mammals indicate that species turnover is a driving influence of community assembly. Goldthwait

et al. (1966) proposed that montane shrews and deer mice were the first pioneer mammal species to colonize the east arm after deglaciation but that the mice were unable to persist after spruce forest developed, whereas common shrews arrived after forest development. Our results generally support this: montane shrews were found at all but one site, mice only at upper bay sites, and common shrews only at lower bay sites. Tundra voles were common on both sides of the lower Bay in the early 1900s (Heller, 1909) but were only found in the upper east and west arms in our study. Red-backed voles were largely found in older sites and long-tailed voles in newer

FIGURE 4 Variation explained by time-since-exposure (Age) and habitat (PCAs) in (a) community composition and (b) beta diversity of good dispersers (orange bars) and poor dispersers (blue bars) based on PERMANOVA analyses. Full statistical results are in Tables S6 and S9. Statistical significance ($p < 0.05$) is indicated by a (*).
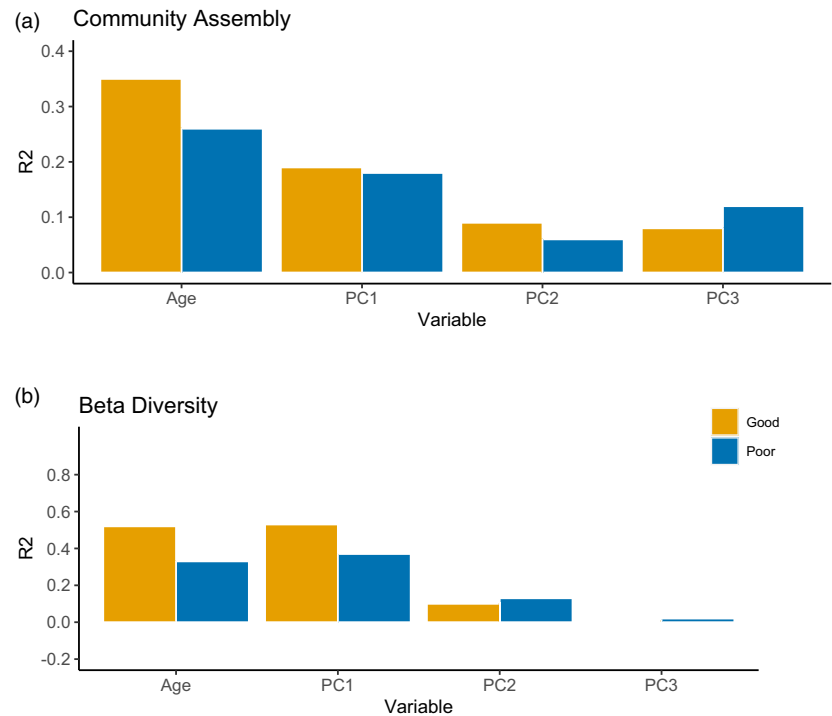
sites. These patterns suggest a relationship between species occupancy and habitat that leads to turnover for poorly dispersing small mammals. However, the current distribution of small mammals calls to question the assumption that these animals are indeed poor dispersers; although they may lack the ability to cross marine fjords on their own, they could disperse across fjords via logs or even vessels.

Patterns of beta diversity were similarly impacted by *Age* and habitat-related variables (Table 4, Figure 4) for the entire community and for good and poor dispersers separately. Increasing community dissimilarity with geographic distance, or distance decay, has long been recognized in ecology (Whittaker, 1975). Dispersal ability can impact distance decay via recolonization from refugia, and dispersal limitations can increase community dissimilarity as geographic distance between patches increases (Tornero et al., 2018). Further, dispersal between these patches via habitat connectivity features can have large impacts on the distribution of species and communities (Harrison, 1991), and while the influence of patch isolation on community composition is small relative to habitat quality (Grimbacher & Catterall, 2007; Thomas et al., 2001), most of the studies reporting this have been conducted on insects. However, our results are consistent with other studies in GBNP that found that species richness generally increases with time-since-deglaciation. Milner et al. (2000) found that the number of microcrustacean and macroinvertebrate taxa was significantly greater in older streams, and our results show a similar pattern: the total number of species detected at each site increased with site age (Table 2). Additional research is needed to understand the explicit role that habitat connectivity features and species traits play in community assembly and recolonization of disturbed landscapes by higher vertebrates.

Patterns of community composition and beta diversity are driven by multiple ecological processes (Soininen et al., 2007), and

substantial variation in the mammal community of GBNP was unexplained by site age or habitat. A study of primary succession in GBNP similarly concluded that "no single factor or mechanism fully accounts for primary succession" (Chapin et al., 1994). Indeed, patterns of mammalian community assembly in GBNP in response to habitat and time-since-exposure were not always straightforward. *Age* had generally stronger effects on assembly than habitat metrics, and larger-bodied species occurred at more sites than smaller-bodied species—supporting the importance of dispersal as a key process. However, relative turnover was high (86%), which is more consistent with habitat filtering as a key process. Furthermore, the similar patterns between the impacts of *Age* and habitat-related variables on total beta diversity and turnover indicate that turnover may be driving overall beta diversity effects (Table S10). Relative turnover was much lower for good than poor dispersers (Table 4), contrary to our initial expectation but in alignment with a study showing that the proportion of postglaciation beta diversity attributable to turnover neared 50% for good dispersers (in this case, birds) compared to a higher percentage for species with poorer dispersal ability (Dobrovolski et al., 2012). In GBNP, larger species with greater dispersal ability were likely able to recolonize ice-free areas faster following deglaciation. This could have generated a richer species pool, contributing to the patterns we found here: that total turnover was about half of total beta diversity. Our findings of high relative turnover in less vagile mammals (Table 4) are similar to those from other studies showing that turnover increases with declining dispersal ability (Baselga et al., 2012; Griffiths, 2017). Overall, these findings indicate that key processes driving assembly likely differ among species groups within animal communities, and that dispersal ability is a key species trait influencing the relative importance of these processes.

While our findings highlight the importance of body size and associated impacts on mobility, species-specific differences in habitat specialization likely also influence the development of biotic communities following disturbance. For example, red squirrels, porcupines, and black bears are often associated with forest cover and were largely found in forested sites during this study. Habitat generalists can often outcompete habitat specialists in disturbed landscapes (Marvier et al., 2004). Brown bears, for example, may be able to outcompete black bears in younger terrain through resource defence competition (Lewis, 2012). Competition and facilitation probably play a role in shaping mammal communities in GBNP as they do in plants (Connell & Slatyer, 1977) but were not explicitly tested for in this study. Our surveys likely missed some rare species and therefore may have underestimated species richness, though this issue should have impacted all sites equally and minimally impacted diversity metrics, and thus is unlikely to have strongly affected our findings. A detection of a species also does not necessarily mean the species has established at a site—it is possible we detected individuals that were passing through an area but had not technically recolonized it. To our knowledge, this is the first study to investigate the impacts of contemporary glacial recession on the successional dynamics of terrestrial mammals, thus making it difficult to compare our results to other studies of this kind, or to articulate the extent to which these results can be generalized to other systems. While substituting space for time, as we have done here, has its limitations (Johnson & Miyanishi, 2008), it is often necessary when attempting to understand long-term disturbance-related impacts to wildlife communities (McKelvey, 2015). To resolve key processes driving successional patterns postdisturbance, additional research that uses systematic, repeated surveys of mammalian communities and incorporates landscape characteristics, species life history traits, interspecific relationships, source population dynamics, and evolutionary processes is warranted.

AUTHOR CONTRIBUTIONS

Mira L. T. Sytsma, Laura R. Prugh and Tania Lewis conceived the ideas, designed methodology and collected the data; Mira L. T. Sytsma analysed the data with guidance from Jonathan D. Bakker; Mira L. T. Sytsma and Laura R. Prugh led the manuscript writing. All authors contributed to drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t1g1jwt5r (Sytsma et al., 2022).

ORCID

Mira L. T. Sytsma https://orcid.org/0000-0002-4250-7286
Tania Lewis https://orcid.org/0000-0001-5687-3722
Jonathan D. Bakker https://orcid.org/0000-0002-8973-2771
Laura R. Prugh https://orcid.org/0000-0001-9045-3107

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Habitat characteristics of each site in GBNP, based on 10 vegetation plot surveys per site. Site numbers explained in Table 1 and shown in Figure 1. Mean percent cover in each of 7 categories (following Viereck et al., 1992) are listed. *BG*=bare ground, *LS*=low scrub, *DS*=dwarf scrub, *GH*=graminoid-herbaceous, *FH*=forb-herbaceous, *BH*=bryoid-herbaceous, and *TS*=tall scrub. Total cover, tree basal area (m^2; mean (standard deviation)), and canopy cover (mean (standard deviation)) are also listed. Tree spp indicates which and how many of each tree species were surveyed at each site (A=alder spp., BC=black cottonwood, SS=Sitka spruce, WH=western hemlock). There were 40 total tree measurements taken at each site except site 10, which only had two trees within the vegetation survey area, and sites 7, 8 and 9 which had no trees.

Table S2. Details of the 97 shrew mortalities that were sent to the University of Alaska Museum of the North. Site number, species name and accession numbers are provided.

Table S3. Loadings from the PCA for all habitat-related variables (Table 2). PC1 was most strongly associated with the *BH* (bryoid-herbaceous) and *BG* (bare ground) variables, PC2 was strongly associated with *LS* (low scrub) and *TS* (tall scrub), and PC3 was highly associated with *GH* (graminoid-herbaceous) and *TotalCover*.

Table S4. Sensitivity analysis of different body mass cutoffs for determining good and poor dispersers. Turnover, relative turnover and total beta diversity are shown for each category within each cutoff group, followed by the Pearson correlation coefficients (R) and associated p-value (P) for the correlation with time since exposure (Age), PC1, PC2 and PC3. Statistically significant effects (P <0.05) are in bold. The number of species in each category is also reported.

Table S5. Results from PERMANOVAs testing the impact of habitat-related principal components (PCs) and time since exposure-related variables (Age) on occurrence-based community assembly data for all species, good dispersers, and poor dispersers. Degrees of freedom (DF), sum of squares (SS), R^2 values, F-statistics and p-values are shown. The beta diversity PERMANOVAs were run on species occurence data to begin with and are therefore unchanged. Statistically significant effects (P <0.05) are in bold.

Table S6. Results from PERMANOVAs testing the impact of habitat variables (PC1, PC2, and PC3) and time since exposure (Age) on abundance-based community assembly for all species, good dispersers, and poor dispersers. Degrees of freedom (DF), sum of squares (SS), R^2 values, F-statistics, and p-values are shown. Statistically significant effects (P <0.05) are in bold.

Table S7. Results from linear regressions examining the effect of habitat characteristics (PC1, PC2, and PC3) and time since exposure (Age) on abundance of each species across the 10 sites (DF = 9 for all regressions). Values are the R^2 for each relationship; statistically significant relationships are highlighted in bold. Dispersal ability is explained in Table 3, and relationships with Age are shown in Figure S3.

Table S8. Historic mammal observations in GBNP. The table shows a subset of observations from the 1907 Alexander Alaska Expeditions (Heller, 1909); and field notes from W. Cooper and D. Lawrence (Buma et al., 2019) and Goldthwait et al. (1966), as well as National Park Service ranger observations from 1952-1969 (NPS unpublished data). A more comprehensive list of observations and specimen records—from the 1899 Harriman Expedition (the National Museum of Natural History, Smithsonian Institution https://collections.nmnh.si.edu/search/mammals/?ark=ark:/65665/366c02eac148e46d782bbf096b878bf42, keyword search "Glacier Bay" on 11/4/2022)—can be found in the Dryad digital repository: https://doi.org/10.5061/dryad.t1g1jwt5r

Table S9. Results from the PERMANOVAs testing the impact of time since exposure (Age), and habitat variables (PC1, PC2, and PC3) on the beta diversity of all species, good dispersers, and poor dispersers. Degrees of freedom (DF), sum of squares (SS), R^2 values, F-statistics, and p-values are shown. Statistically significant effects (P < 0.05) are in bold.

Table S10. Results from the PERMANOVAs testing the impact of time since exposure (Age), and habitat variables (PC1, PC2, and PC3) on the total turnover and relative turnover of all species, good dispersers, and poor dispersers. R^2 values and p-values are shown. Total turnover was calculated using Simpson dissimilarity and relative turnover was calculated as the difference between total beta diversity (Sørensen dissimilarity) and total turnover. Statistically significant effects (P < 0.05) are in bold.

Figure S1. Correlation matrix between all possible explanatory variables. PC1, PC2 and PC3 represent the first three principal components from the Principal Component Analysis conducted on all habitat-related variables across the 10 sites (Table S1). Correlations between time since exposure (*Age*) and each principal component

were weak (r <0.46 for all correlations), and none were statistically significant. Positive correlations are displayed in blue and negative in red. Circle size indicates how strong the correlation is.

Figure S2. Diagram of the layout of a study site. Vegetation surveys occurred on the diagonal of the small mammal trapping grid, with the camera in the center. This diagram represents one of the two small mammal trapping grids placed at each site, and one of the two vegetation surveys (shore and inland). Only inland vegetation survey data were used for analysis. Four cameras were installed at each site, two of which did not have vegetation surveys or small mammal trapping grids placed at them. Sites 1, 4, 6, 8, and 9 were trapped during the summer of 2017, and the remaining sites were trapped in 2018.

Figure S3. Abundance of each species as a function of time since exposure (*Age*) across the 10 sites. Abundance was relativized for each species so that the maximum value possible was 1. All species are shown regardless of total abundance. Statistical results are summarized in Table S7. Species are shown in order of increasing body mass.