



Longitudinal trends of the small mammal community of the Apostle Islands archipelago

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Abstract

Documenting longitudinal changes in small mammal communities provides insights into ecosystem dynamics. We examined changes in small mammal communities of the Apostle Islands archipelago (Wisconsin, USA) since the establishment of the Apostle Islands National Lakeshore in 1970. We trapped small mammals from 20 of the 22 islands of the archipelago (2017–2020) and compared those results to historical (1961–2004) records. *Microtus pennsylvanicus* ($p=0.0076$) and *Sorex cinereus* ($p=0.0268$) exhibited significant changes in distribution. *Microtus pennsylvanicus* was likely extirpated from 10 of the 11 islands where it was previously detected, while *S. cinereus* increased in distribution. *Peromyscus* spp. colonized at least three islands since the establishment of the National Lakeshore, potentially through human-facilitated dispersal (i.e., boating, kayaking). *Myodes gapperi* remained widespread and abundant. Recent trends (2003–2004 to 2017–2020) in abundance indicated that *S. cinereus* may be declining locally on the islands, whereas *Tamiasciurus hudsonicus* may be increasing. Community diversity was driven by island size, regardless of variation over time. Long-term changes in small mammal populations across the archipelago likely reflect reduction of human extractive activities following the establishment of the National Lakeshore and the corresponding succession of vegetative communities. Our work suggests that even though small mammal communities of the archipelago have changed over time, larger islands may be able to better retain species that have been lost on others; therefore, island size remains an important predictor of community diversity.

Keywords Island biogeography · *Myodes gapperi* · *Microtus pennsylvanicus* · *Peromyscus* · *Sorex cinereus*

Introduction

Small mammals contribute to the health and biodiversity of ecosystems (Ryszkowski 1975) enhancing soil structure and composition (Golley et al. 1975), influencing vegetation diversity, regeneration, and density (Martin 2003),

dispersing seeds (Hamilton 1941), affecting invertebrate populations (Hamilton 1941), and influencing the abundance and distribution of predators that rely on them (Ryszkowski 1975). Thus, fluctuations in small mammal populations can alter community dynamics (Hamilton 1941).

Longitudinal trends in small mammal populations can provide important insights into ecosystem dynamics. In addition to being relatively widespread and abundant, small mammals respond quickly to changes in their environment (Franci and Small 2013). Therefore, small mammals are ideal for examining drivers of ecosystem dynamics. Disturbances such as timber harvest, fire, and herbivory alter habitats, affecting the distribution of small mammal populations across a landscape (Martell 1983; Briani et al. 2004; Busch 2008). Small mammal abundance can also be affected by predator presence, prey abundance, and interspecific competition (Clark et al. 1987; Ruggiero 1994). Observed changes within small mammal communities may therefore

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be indicators of changes in habitat or species composition within an ecosystem.

The Apostle Islands archipelago consists of 22 islands within Lake Superior. The islands experienced extensive human activity as natural resources, such as timber, fish, and brownstone, were extracted during the early 1900s (Busch 2008; Jordahl 1994; Feldman 2011) altering habitat and disrupting ecological processes (Feldman 2011). In 1970, the Apostle Islands National Lakeshore was established, leading to restrictions of certain anthropogenic activities, resulting in ecological succession (Feldman 2011). Thus, the Apostle Islands National Lakeshore provides an opportunity to examine longitudinal change in the small mammal community composition and the factors driving it within the archipelago.

To gain a better understanding of small mammal community dynamics, we live-trapped small mammals on 20 islands within the Apostle Islands archipelago. We compared our data to historical data from prior small mammal trapping efforts within the archipelago to identify changes that have occurred within the small mammal community since the establishment of the Apostle Islands National Lakeshore. However, because the Apostle Islands National Lakeshore is an island system, it is also important to consider how island biogeography may be influencing the dynamics of small mammal communities.

The equilibrium theory of island biogeography predicts that smaller more isolated islands will contain fewer species than larger and less isolated islands due to differences in extinction and immigration rates (MacArthur and Wilson 1967). Understanding the impact that island biogeography has on species richness can aid in effective conservation efforts (Sax and Gaines 2011). For example, Allen et al. (2019) determined that island biogeography variables, including island size and distance from the mainland, were important drivers of carnivore community composition within the Apostle Islands archipelago. However, few researchers have tested the effects of island biogeography on small mammal communities, especially in temperate archipelago systems (Lomolino 1984). Therefore, we also expected island biogeography variables to be important drivers of small mammal community composition and dynamics within the archipelago. Specifically, we expected greater species richness of small mammals on larger and less isolated islands, and we expected these patterns to be consistent over time.

Our main goal was to identify long-term, species-specific changes within the small mammal community of the Apostle Islands archipelago and explore how island biogeographic factors influenced the small mammal community at different time periods. We compared the distribution of species between three different time periods, 1961–1983, 2003–2004, and 2017–2020, and changes in species relative

abundance between 2003–2004 and 2017–2020, the only two time periods with comparable abundance data. Lastly, we examined the influence of island biogeography on the small mammal communities within the archipelago over all three time periods.

Methods

Study area

The Apostle Islands National Lakeshore is located in southwestern Lake Superior, Wisconsin, USA (46°42′–47°05′ N; 90°24′–91°03′ W), and encompasses 21 of the 22 islands within the Apostle Islands archipelago (Fig. 1). Madeline Island, the largest island of the archipelago (59.9 km²), is not included in the National Lakeshore and is developed with roads and mostly privately owned. Islands within the National Lakeshore range in size from 0.01 km² (Gull Island) to 40.69 km² (Stockton Island) (Fig. 1), and island distance from the mainland ranges from 1.48 km (York Island) to 23.83 km (Outer Island). Annual temperature within the archipelago ranges from –18 to 27 °C with a mean of –4.5 °C. Average precipitation across the islands is 76 cm of rain and 145 inches of snow (Apostle Islands National Lakeshore 2015).

Prior to the establishment of the National Lakeshore, logging and other human disturbances altered vegetative communities throughout much of the archipelago (Busch 2008; Judziewicz and Koch 1993). Before these disturbances, mixed hardwoods and conifers dominated 90% of the islands (Fredrick and Rakestraw 1976). Currently, most islands support secondary forests that are dominated by white birch (*Betula papyrifera*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), balsam fir (*Abies balsamea*), and white cedar (*Thuja occidentalis*) (Judziewicz and Koch 1993). Eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), and red oak (*Quercus rubra*) are also common (Judziewicz and Koch 1993). Canada yew (*Taxus canadensis*) has persisted within the archipelago and continues to dominate the understory on many of the Apostle Islands (Judziewicz and Koch 1993; Mudrak et al. 2009) despite being largely extirpated on the mainland.

Since 2014, there have been a variety of surveys observing the presence of mammal species within the Apostle Islands archipelago (Pichler et al. *in review*, including this work). Data from camera trapping, small mammal live trapping, and acoustic bat monitoring have confirmed the presence of 27 mammal species; six bat species, 7 small mammal species, and 14 medium-large mammal species (Pichler et al. *in review*). No invasive terrestrial vertebrate species are known within this ecosystem (Jackson 1961).

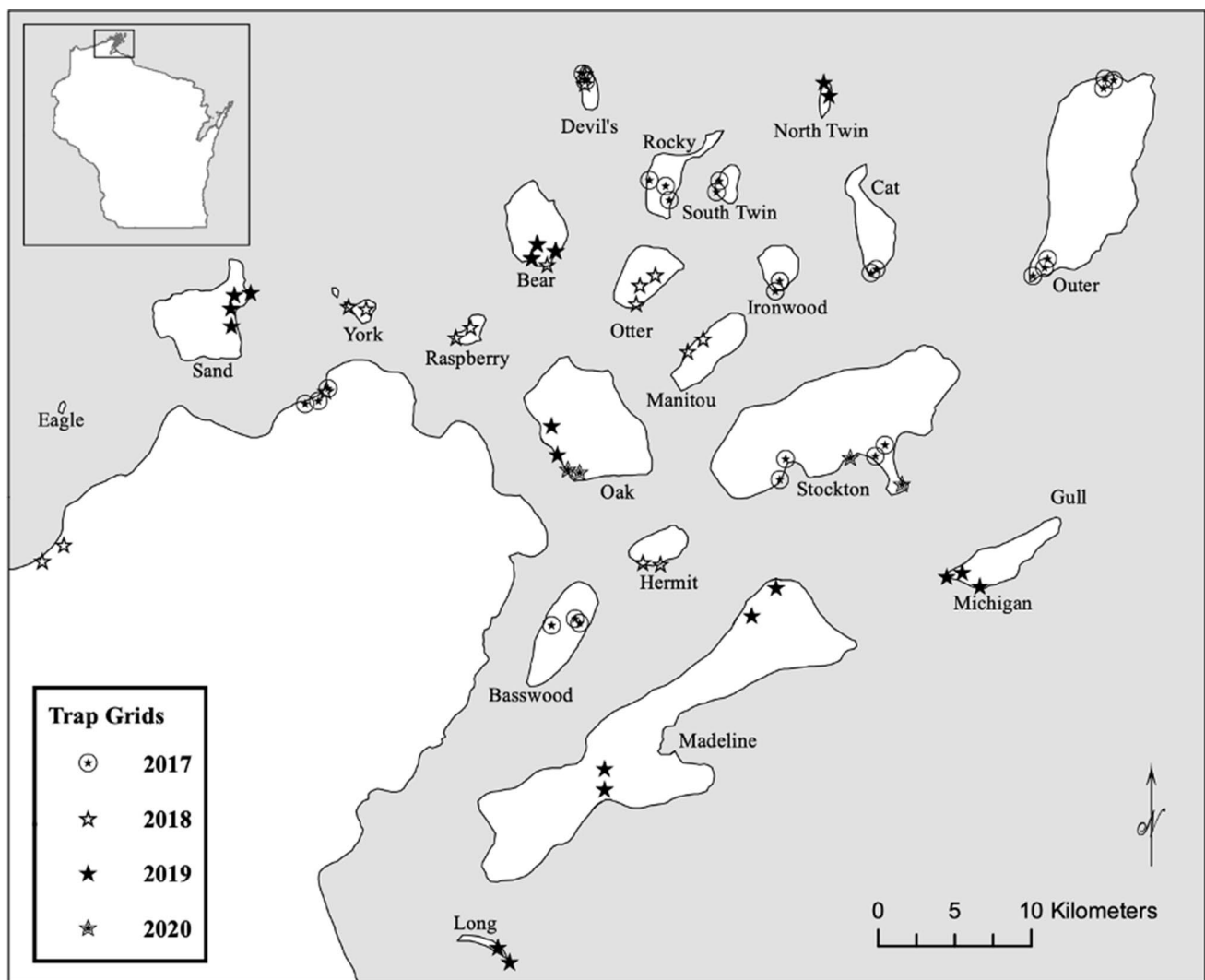


Fig. 1 Study area with small mammal live trap grid locations within the Apostle Islands archipelago, Wisconsin, USA (2017–2020)

Field methods

During four field seasons, we surveyed a portion of the mainland and 20 of the 22 islands within the Apostle Islands archipelago (Fig. 1). Trapping occurred from mid-June to late August (2017–2020) except for Oak Island in 2019, which we trapped in October to avoid trap disturbance by black bears (*Ursus americanus*). Oak Island was surveyed again in June of 2020 with minimal damage from bears, allowing us to expand our dataset. Oak Island small mammal data were relatively similar when comparing trapping done in October of 2019 and June of 2020, suggesting that our trapping window of June–October was acceptable. Small mammal trapping in the Apostle Islands has occurred sporadically since the 1960s (Jackson 1961; Patzoldt 1975; Schuls 1976; Kantak 1978; Brander et al. 1978; Anderson et al. 1978; Meierotto 1979; Smith and Maragi 2004; Smith

and Fawver 2005). Various field techniques were used during these efforts, although detailed information on field methodology for studies conducted prior to the 2000s is scarce. Descriptions of Smith and Maragi (2004) and Smith and Fawver (2005) were more detailed, allowing us to replicate their methods.

Following Smith and Maragi (2004) and Smith and Fawver (2005), we deployed 36 Sherman 3310G and LFA live traps (H.B. Sherman Traps, Inc., Tallahassee, FL, USA) in a 6 × 6 grid, spaced 10 m apart to form a 3600 m² grid (Online Resource 1). We set four Tomahawk 106 live traps (Tomahawk Live Trap, Hazelhurst, WI, USA) in a stratified fashion, with one trap placed opportunistically in each of the four separate quadrants of each grid. In addition, we deployed two Tomahawk 102 live traps (Tomahawk Live Trap, Hazelhurst, WI, USA) at opportunistic locations within each grid. In 2017, we only deployed two large (106)

and two small (102) Tomahawk live traps opportunistically throughout the grid. We baited the Sherman live traps with a mixture of peanut butter and oats and the Tomahawk live traps with apple slices. To avoid attracting nuisance bears on Oak Island in 2019 and 2020, we used a mixture of sunflower seeds, apple, and oats (Fryxell et al. 1998). We placed cotton batting in each Sherman live trap to provide animals with bedding material during all trapping efforts (Masters et al. 1998; Phelps and McBee 2009). Trapping protocols were reviewed and approved by an institutional animal care committee at the University of Wisconsin–Madison (protocol number: A005801-R01).

We spaced trap grids at least 700 m apart and using satellite imagery, attempted to locate trap grids in different habitats when selecting grid locations. We chose 700 m as the minimum distance between trap grids to enhance independence of sampling sites while also accounting for logistical restraints. The home range size of *M. gapperi* (red-backed vole) is estimated to be between 0.004 and 0.013 km² (Tisell et al. 2019); therefore, it is unlikely that *M. gapperi* and other small mammal species similar in size were able to move between grids. This also applies to the largest species captured, *T. hudsonicus* (American red squirrel), with a mean home range size between 0.009 and 0.01 km² (Goheen and Swihart 2005). We factored in island size (x , km²) when determining trap grid density (y , grids/km²) per island using the following power law curve equation:

$$y = 1.9172x^{-0.695}$$

Smaller islands had a minimum of two trap grids, while additional trap grids were deployed on larger islands, scaling with island size (Allen et al. 2019). We collected habitat information from each trap grid location, including vegetation present in the canopy and understory, as well as presence of downed woody debris. Typically, trap grids were run simultaneously with few exceptions. We trapped small mammals at each site for 3 trap nights and checked traps twice daily: once in the morning and once in the afternoon.

Each individual small mammal was identified to species level according to Reid (2006). For each individual small mammal captured, we recorded weight (g), sex, hind-foot length (cm), tail length (cm), body length (cm), and ear length (mm) (Stephens et al. 2014). We marked each individual captured with two #1005-1 Monel ear tags (National Band and Tag Co., Newport, Kentucky, USA) to identify recaptures (Rosenstock 1996; Edalgo and Anderson 2007). We took photographs of each new species found on an island. Using these photographs, two mammalogists independently verified field identification of each species. Two species of *Peromyscus* inhabit northern Wisconsin—*P. maniculatus* (Deer mouse) and *P. leucopus* (White-footed mouse). Both species are extremely similar in appearance

and can only be differentiated via morphological measurements or genetics (Stephens et al. 2014; Ridenhour and Cramer 2015). For field identification, we identified *Peromyscus* spp. to species in the field based on an ear length threshold of < 17 mm for *P. leucopus* according to Stephens et al. (2014; J. Pauli, pers. comm.). We quality assured *Peromyscus* spp. identification using the classification models presented by Stephens et al. (2014). All animal trapping and handling was done in accordance with the American Society of Mammalogists guidelines for use of wild mammals in research (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016) and the approved UW protocol (above).

Data analysis

We summarized the total number of trap nights for each island. A trap night represents a night where a Sherman live trap was either open or contained a captured mammal. Traps that were sprung and closed but did not have a capture, and traps that were damaged by black bears or other species were subtracted from the total number of trap nights. We calculated a relative abundance index (RAI) for each species for each island as:

$$RAI = \left(\frac{C}{TN} \right) * 100$$

where C is the total number of captured individuals (excluding recaptures) for that species and TN is the total number of trap nights for that grid or island (Hopkins and Kennedy 2004). *Tamiasciurus hudsonicus* was the only small mammal species captured in the Tomahawk live traps; therefore, we excluded Tomahawk traps from the total trap nights calculation for all species except *T. hudsonicus*. We calculated grid- and island-scale RAI for each species (Edalgo and Anderson 2007).

To examine the dynamics of small mammal communities within the archipelago over time, we compared the distribution of small mammal species to historical data from previous studies. Prior to our studies, trapping efforts occurred sporadically from 1961 through 1987 (Jackson 1961; Patzoldt 1975; Schuls 1976; Kantak 1978; Brander et al. 1978; Anderson et al. 1978; Meierotto 1979) as well as in 2003 and 2004 (Smith and Maragi 2004; Smith and Fawver 2005). To ensure an adequate representation of these study periods in our analyses, we split the data into three different time periods: pre-2000, early 2000s (2003 and 2004) and our recent efforts (2017–2020). Since sampling methods and efforts varied between studies, historical data were considered only in terms of the presence and absence of species. Since the islands were first studied in 1961, *M. gapperi*, *Peromyscus* spp. (mice spp.), *M. pennsylvanicus* (meadow vole), *B. brevicauda* (short-tailed shrew), and *S. cinereus* (masked

shrew) have consistently been reported. Although historical data indicated that only *P. maniculatus* was present on the islands, this species can easily be confused with *P. leucopus* (Stephens et al. 2014). Thus, early efforts to identify *Peromyscus* to species were likely insufficient, and therefore, we classified all previously detected *P. maniculatus* as *Peromyscus* spp. We used multiple studies from each time period, and we examined species presence at coarse temporal and spatial scales.

To identify changes in small mammal distribution across the islands, we performed a two-tailed McNemar's Chi-squared test comparing the pre-2000 data to data collected in the 2000s (i.e., early 2000s and this study). The McNemar's Chi-squared test is designed to detect directional change from repeated measures data (i.e., islands with and without a certain species pre-2000s and post-2000; (Siegel 1956)). We tested the marginal homogeneity of the following dichotomous variables: (1) number of islands that each species had either appeared or disappeared on since the pre-2000s; (2) number of islands that each species was either present or absent on during both time periods (Harney and Dueser 1987). Prior to our trapping efforts, Long Island and Madeline Island had never been surveyed; thus, we excluded them from this analysis. Again, we excluded *T. hudsonicus* for this analysis.

To determine changes in species abundance over time, we compared species *RAI* in the early 2000s to species *RAI* during our efforts for a subset of islands with abundance data from both time periods using a two-tailed *t* test. Data collected prior to the 2000s were not used in this analysis because it did not include the information necessary to calculate species *RAI*. We used *RAI* because it is considered an accurate index of abundance (Parsons et al. 2017; Palmer et al. 2018) or site use (Sollmann 2018) for some mammals. Sollmann (2018) indicated that *RAI* is sensitive to differences in sampling design. However, because we used the same sampling design as the surveys completed in the early 2000s, our use of *RAI* to examine changes in species abundance is reliable, especially for common species. Because of their low abundance on the islands, *B. brevicauda* and *M. pennsylvanicus* were not included in this analysis; however, we integrated *T. hudsonicus* into this analysis because *RAI* for this species was reported by Smith and Maragi (2004) and Smith and Fawver (2005) in 2003 and 2004.

To examine the effects of island biogeography theory, we tested three a priori generalized linear models: (1) island size, (2) island isolation, and (3) an interactive model with both island size and isolation, for each dependent variable (species richness for all time periods combined and species richness for each individual time period) using the R 3.6.1 package *MuMIn* (Barton 2019) to predict small mammal species richness across the archipelago. We ranked models according to second-order Akaike information criterion

(Allen et al. 2019) and generated full model-averaged coefficients (i.e., full averages; (Barton 2019)). We determined the significance of the coefficients based on whether the corresponding 95% confidence intervals overlapped zero (Olson et al. 2019). *Tamiasciurus hudsonicus* presence was not recorded in studies conducted prior to the 2000s; therefore, *T. hudsonicus* was not included in this analysis. Typically, researchers use distance to the mainland or the nearest island as a metric of isolation (e.g., Allen et al. 2019; Allen et al. 2018, Farmer et al. *in review*). To determine island isolation, we calculated an isolation metric based on the average distance to all neighboring landmasses using the shore protection manual (SPM) method in the WAVES fetch simulation model (e.g., Rohweder et al. 2012; Olson and Ventura 2012; Online Resource 2). We first used the WAVES fetch simulation model in order to estimate fetch from eight cardinal and inter-cardinal directions. We then averaged the eight fetch rasters with the raster calculator tool in ArcMap 10.7.1 (Redlands California, USA) to get the mean fetch for each 30-meter cell in Lake Superior (Olson and Ventura 2012). An average shoreline fetch for each island was calculated by averaging the fetch values within 100 meters around each island shoreline to create the island isolation metric used in our analysis (Online Resource 2; Pichler et al., *in review*).

Results

We had 1366 captures of 876 individual small mammals (Online Resource 3) over 7672 total trap nights (2017–2020). All islands had a trapping effort between 192 and 630 trap nights, with a mean of 295 (SD = 108) trap nights per island. Ten small mammal species were captured, three of which were only detected on the mainland (Online Resource 4). The mainland had the highest species richness with eight species detected. Among the islands, Madeline had the highest diversity of small mammals with six species detected, whereas Cat, Ironwood, Bear, and Manitou Islands had the lowest species diversity with only one species detected.

Historical comparisons

When comparing species presence on the islands from the pre-2000 sampling period to the post-2000 sampling period, *M. pennsylvanicus* distribution decreased significantly ($p=0.013$, $\chi^2=6.125$, $df=1$), whereas *S. cinereus* increased significantly ($p=0.027$, $\chi^2=4.90$, $df=1$). *Microtus pennsylvanicus* was detected on nine islands that were surveyed prior to the 2000s and on Rocky and Basswood Islands by Smith and Fawver (2005). During our recent efforts, we captured *M. pennsylvanicus* on Stockton Island; however, we did not capture them on any of the other islands they were previously been detected on (Fig. 2). We did capture

M. pennsylvanicus on Madeline Island and the Mainland during recent survey efforts, although these locations were not surveyed previously. *Sorex cinereus* has been detected on nine additional islands since the pre-2000 sampling period. (Fig. 2). *Peromyscus* spp. distribution expanded slightly since pre-2000s, although not significantly ($p=0.248$, $\chi^2=1.33$, $df=1$), with detections on three additional islands

and detections on all islands with historical presence (Fig. 2). *Blarina brevicauda* has only ever been detected on three islands, Oak and Stockton Islands prior to the 2000s and Oak and Basswood Islands during the 2000s. Due to a small sample size, we did not test for directional change in *B. brevicauda* distribution. *Myodes gapperi* distribution

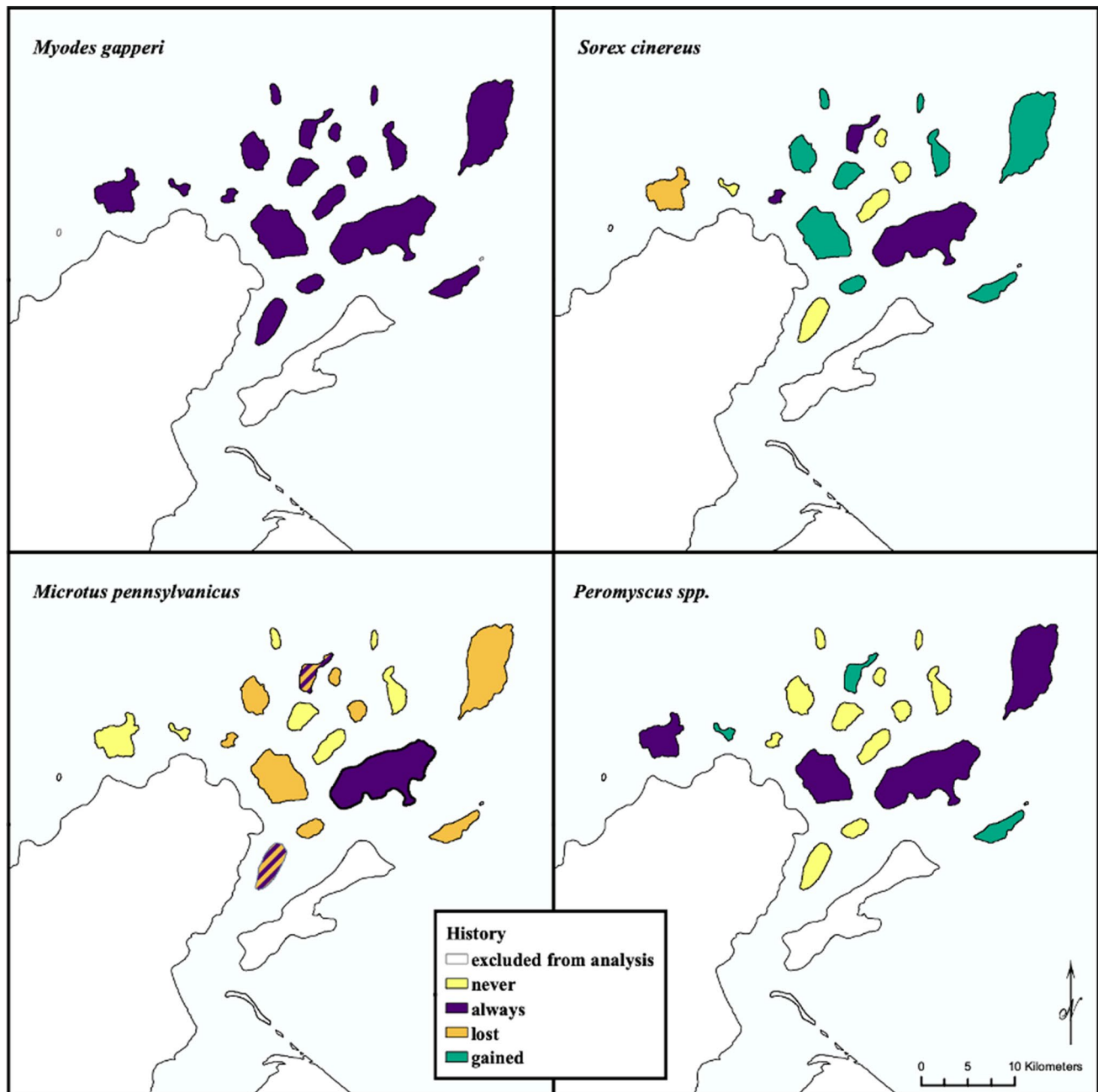


Fig. 2 Changes in select small mammal species distribution over time (from 1961–1983 to 2003–2020) within the Apostle Island National Lakeshore of northern Wisconsin, USA (never=never detected in any survey; always=detected in both time periods; lost=detected in the first time period, but not detected in the second time period;

gained=not detected in the first time period, but detected in the second time period; orange and purple stripes indicate islands where *M. pennsylvanicus* was detected in the pre-2000s and early 2000s but not in 2017–2020)

remained stable, having been detected on every island with historical presence (Fig. 2).

Regarding more recent changes in species abundance, *S. cinereus* has declined significantly ($p=0.04$, $t=2.242$, $df=14$, $n=8$) in abundance on all islands assessed since 2003 and 2004 (Table 1). No other species experienced a significant increase or decrease in abundance (Table 1). *Peromyscus* spp. abundance has increased slightly on two islands and decreased on one since 2003 and 2004, but no significant archipelago-wide trend was detected (Table 1). The abundance of *M. gapperi* has remained fairly stable, increasing on four islands and decreasing on four since the early 2000s (Table 1). *Tamiasciurus hudsonicus* has experienced an increase in abundance on four islands and a slight decrease in abundance on two islands (Table 1).

Island biogeography

Island size was a significant predictor of species richness and had over ten times as much support as any other model (AIC_c weight = 0.86, $\beta = 0.692 \pm 0.306$) (Tables 2 and 3) when combining data from all three time periods (1961–1983, 2003–2004, 2017–2020) (Fig. 3). Island size was our top model for predicting species richness prior to the 2000s (AIC_c weight = 0.88, $\beta = 0.718 \pm 0.431$) (Tables 2 and 3) and during our efforts (AIC_c weight = 0.96, $\beta = 0.778 \pm 0.325$) (Tables 2 and 3). However, island size was not significant in predicting species richness during the early 2000s. For each of the dependent variables, neither the island isolation model or interactive model was significant in predicting species richness (Tables 2 and 3).

Table 1 Captures per trap night for small mammal species on select islands within the Apostle Islands archipelago during 2003 or 2004, and 2017–2020. The archipelago-wide decline for *SOCI*¹ was significant at $p=0.04$

Island	MYGA ^a 03,04	MYGA ^a 17,18,19,20	PE spp. ^a 03,04	PE spp. ^a 17,18,19,20	SOCI ^a 03,04	SOCI ^a 17,18,19,20	TAHU ^a 03,04	TAHU ^a 17,18,19,20
Rocky	3.7 →	10.0	* →	2.8	4.2 ←	*	2.3 ←	0.6
South Twin	4.1 →	44.2	*	*	*	*	0.6 →	0.8
Stockton	2.5 →	3.5	1.3 →	4.6	1.0 ←	0.2	1.8 →	3.3
Basswood	13.1 ←	5.9	*	*	9.0 ←	*	* →	1.4
Cat	15.8 →	23.1	*	*	2.0 ←	*	*	*
Devils	22.7 ←	4.2 (1.9) ^b	*	*(*) ^b	0.9 ←	*(*) ^b	* →	2.8 (0.4) ^b
Outer	12.9 ←	8.3	9.4 ←	1.0	3.0 ←	0.5	1.2 ←	0.9
North Twin	30.7 ←	11.2	*	*	0.6 ←	0.5	*	*

^aMYGA = *Myodes gapperi*, PE spp. = *Peromyscus* species, SOCI = *Sorex cinereus*, TAHU = *Tamiasciurus hudsonicus*

^bIn this analysis Devils Island was the only island surveyed at the same grid locations in 2017 and 2018, thus, captures per trap night for 2018 are in parentheses

*Indicates species was not detected; → increasing abundance, ← decreasing abundance

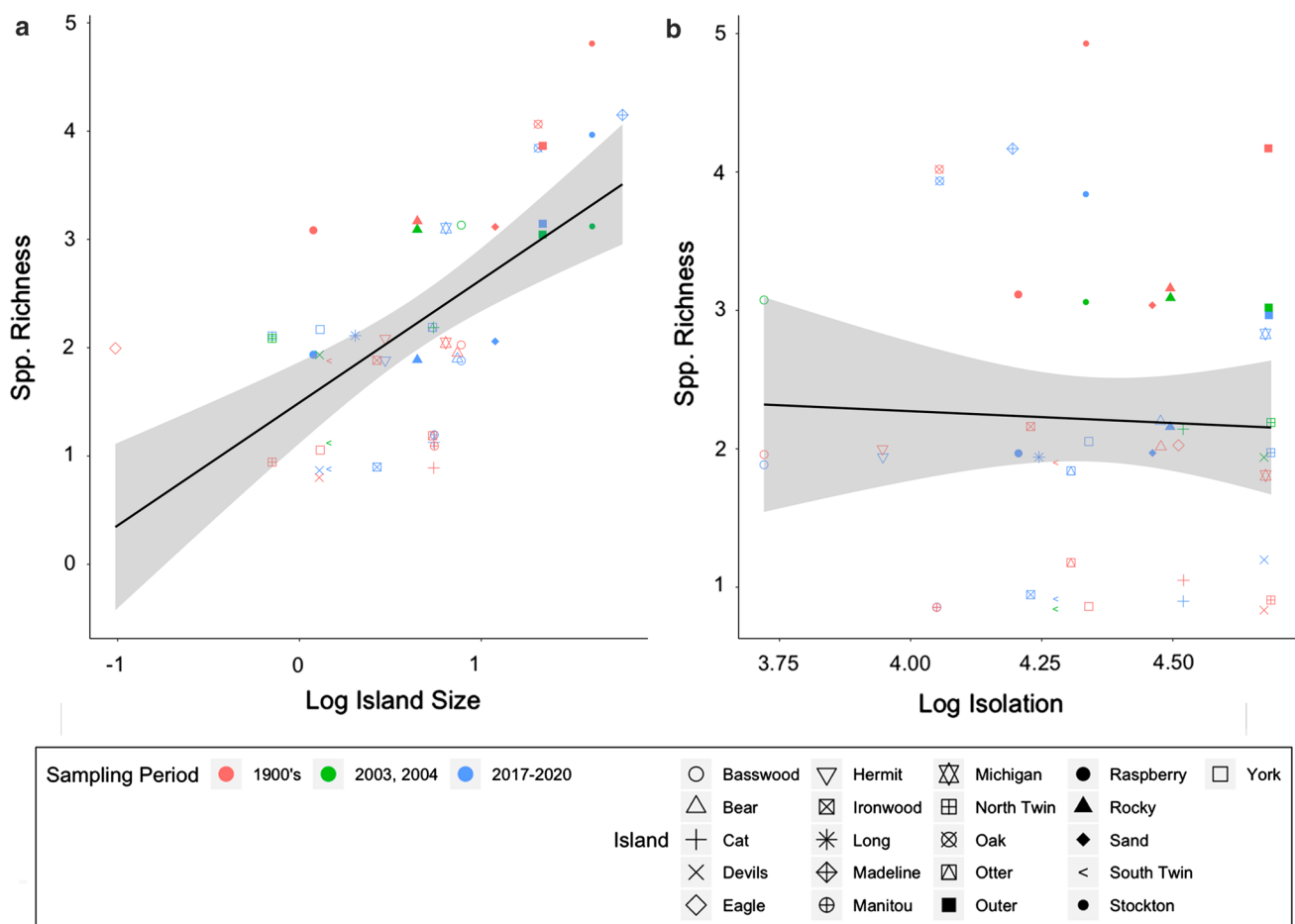
Table 2 Model comparison results for possible factors influencing small mammal species richness within the Apostle Islands archipelago

Dependent variable	Model	ΔAIC_c	AIC_c weight	k
Species richness for all time periods	Island size	0.00	0.86	3
	Island size * Island isolation	3.69	0.14	5
	Null	32.70	0.00	2
	Island Isolation	34.84	0.00	3
Species richness prior to the 2000s (1961–1983)	Island Size	0.00	0.88	3
	Island size * Island isolation	4.07	0.12	5
	Null	15.76	0.00	2
	Island Isolation	18.12	0.00	3
Species richness in the early 2000s (2003–2004)	Null	0.00	0.71	2
	Island Size	2.09	0.25	3
	Island isolation	5.53	0.05	3
	Island size * Island isolation	30.02	0.00	5
Species richness from this survey (2017–2020)	Island size	0.00	0.96	3
	Island size * Island isolation	6.42	0.04	2
	Null	16.18	0.00	5
	Island Isolation	18.95	0.00	3

Table 3 Model averaged unconditional parameter estimates for possible factors influencing small mammal species richness within the Apostle Islands archipelago

Dependent variable	Model	β coefficient	$\pm 95\%$ confidence interval
Species richness for all time periods	Island size	0.692	0.306
	Island Isolation	-0.010	0.112
	Island size * Island isolation	0.037	0.263
Species richness prior to the 2000s (1961–1983)	Island size	0.718	0.431
	Island Isolation	-0.027	0.192
	Island size * Island isolation	0.054	0.367
Species richness in the early 2000s (2003–2004)	Island size	0.148	0.598
	Island Isolation	-0.001	0.172
	Island size * Island isolation	0.000	0.002
Species richness from this survey (2017–2020)	Island size	0.778	0.325
	Island Isolation	0.001	0.080
	Island size * Island isolation	0.006	0.162

Values in boldface type have 95% confidence intervals that do not overlap 0

**Fig. 3** Small mammal species richness relative to **a** island size and **b** island isolation within the Apostle Islands archipelago from 1961 to 2020. Black line = best fit line based on simple linear regression; gray shaded region = 95% confidence interval for best fit line

Discussion

Our results indicate that small mammal communities on the Apostle Islands have experienced significant changes over time. We performed a meta-analysis to detect trends in the distribution and abundance of five small mammal species that have consistently been reported within the archipelago since 1961. These longitudinal trends are likely the result of changes in ecological processes following the establishment of the Apostle Islands National Lakeshore in 1970.

Of all small mammal species found across the archipelago, *M. gapperi* has remained the most widely distributed and abundant small mammal species over time. The abundance of *M. gapperi* on the mainland has consistently been less than that of the islands (Smith and Maragi 2004). *Myodes gapperi* has been detected on every island assessed (Fig. 3) and has the highest capture success rate when compared to other small mammals captured on the islands. Contrarily, *M. gapperi* was not detected during any trapping efforts on the mainland unit of the Lakeshore prior to the 2000s. *Myodes gapperi* was captured on the mainland in 2003 but low in abundance (Smith and Maragi 2004; Online Resource 5). In 2003, *M. gapperi* constituted 66% of captures on the islands but only 12% of captures on the mainland (Smith and Maragi 2004). When combining data from 2017 to 2020, 13% of all captures on the mainland were *M. gapperi* compared to 74% of captures being *M. gapperi* across the islands.

Many factors could be influencing the success of *M. gapperi* on the Apostle Islands. A relatively simplified small mammal community could suggest reduced competition for *M. gapperi*. Additionally, a major difference between the islands and the mainland is the presence of *T. canadensis* (Mudrak et al. 2009; Beals et al. 1960). According to a study by Windels and Flaspohler (2011), small mammal diversity and abundance was greater in northern hardwood forest understories containing dense *T. canadensis*. Smith and Maragi (2004) and Smith and Fawver (2005) also concluded that most *T. canadensis* dominated grids on the Apostle Islands had a higher *M. gapperi* biomass. The presence of *T. canadensis* may provide foraging substrate and structural cover for *M. gapperi* (Windels and Flaspohler 2011). Mallinger et al. (2020) also documented a significant positive correlation between *M. gapperi* abundance and understories dominated by *T. canadensis* using the data for the Apostle Islands archipelago from the surveys reported herein. Thus, the widespread distribution and high abundance of *M. gapperi* within the archipelago could be due to unique habitat features or reduced competition.

Blarina brevicauda has remained relatively rare within the islands system, and due to the low sample size, it was

difficult to determine longitudinal changes. Of the five small mammal species that have been consistently captured across the islands, *B. brevicauda* are the least abundant and have only been detected on three islands (Oak, Stockton, and Basswood; Online Resource 5) since 1961. *Blarina brevicauda* were also detected on the mainland for the first time during the 2018 trapping efforts (Online Resource 5). The limited number of detections of *B. brevicauda* could be explained by the fact that our protocol and the majority of historical protocols (Kantak 1978; Meierotto 1979; Smith and Maragi 2004; Smith and Fawver 2005) did not include pitfall traps which have been reported to have higher success rates for capturing shrews (Bury and Corn 1987; Nicolas and Colyn 2006; Chung-MacCoubrey et al. 2009; Stromgren and Sullivan 2014). Thus, given even our coarse spatiotemporal examination of presence, issues of imperfect detection for this species likely exist and may affect the value of abundance indices for this species (Stokes 2013).

Two species appear to have increased in distribution across the archipelago, *S. cinereus* and *Peromyscus* spp. *Sorex cinereus* distribution increased significantly in comparison with historical observations, yet recent data (2017–2020) suggest that *S. cinereus* has been declining in abundance in recent years. Although *S. cinereus* is relatively difficult to detect, it is possible that its population is declining due to predation. *Martes americana* has recently (Smith et al., *in review*) recolonized the archipelago and was recently detected on seven islands (Allen et al. 2018; Allen et al. 2017), six of which support *S. cinereus*. Two of the six islands, Bear Island and Otter Island, were not trapped in the early 2000s; thus, information on abundance over time is unknown for these two islands. The other four islands (i.e., Outer, Cat, Rocky, Stockton) have experienced a decline in *S. cinereus* abundance (Table 2). According to Carlson et al. (2014) in the Chequamegon–Nicolet National Forest in northern Wisconsin, *S. cinereus* appeared to be one of the main food resources for *M. americana*. Hence, abundance of *S. cinereus* could be declining due to the increasing presence of *M. americana* across the islands. However, we did observe declines in *S. cinereus* abundance on Devils and Basswood Islands, where *M. americana* has not been detected. Additionally, it is suspected that *S. cinereus* was one of the main food resources for *M. americana* in the Chequamegon–Nicolet National Forest, in part, because *M. gapperi* were less prevalent (Carlson et al. 2014). The relatively high abundance of *M. gapperi* within the archipelago would likely reduce predation pressure on *S. cinereus*. Thus, an alternative explanation could be that the absence of pitfall traps diminished our abilities to adequately assess changes in relative abundance for this species over time (Bury and Corn 1987; Nicolas and Colyn 2006; Chung-MacCoubrey et al. 2009; Stromgren and Sullivan 2014).

Peromyscus spp. also seem to be increasing in distribution and abundance. *Peromyscus* spp. have been detected on three more islands since the 1970s (Fig. 3). These new colonizations could be due to human boat traffic, considering that the newly colonized islands are more randomly distributed. Furthermore, recent colonizations occurred on relatively small islands, one of which is considered highly isolated (Michigan Island). *Peromyscus* spp. are well known for occupying human structures and equipment such as boats and vehicles (Timm and Howard 1994). Thus, we hypothesize that *Peromyscus* spp. may be hitchhiking on boats to various islands throughout the archipelago.

Microtus pennsylvanicus is the only small mammal species that has experienced a significant decline in both abundance and distribution across the archipelago. *Microtus pennsylvanicus* was present on at least 11 islands since the 1970s and in the early 2000s was detected on only two (Fig. 2). More recently, *M. pennsylvanicus* was not detected on any of the islands except for Stockton Island, Madeline Island, and the mainland (Online Resource 5). Abundance of *M. pennsylvanicus* was likely high in the 1970s due to a relatively greater availability of open habitat following historical human uses of the archipelago (Busch 2008; Judziewicz and Koch 1993). *Microtus pennsylvanicus* are adapted to living in disturbed patches and appear to prefer habitat edges (Brander and Bailey 1983; Bowers 1982). Following the establishment of the National Lakeshore, secondary forests replaced open habitat (Judziewicz and Koch 1993), resulting in a decline of suitable habitat for *M. pennsylvanicus*. In fact, Brander (1983, p. 111) “expected that the meadow vole [*M. pennsylvanicus*] will become increasingly rare as the forests of the islands recover from the logging era.”

We detected two individual *M. pennsylvanicus* in a ruderal grassland habitat on Stockton Island in 2020. This specific habitat has only been reported nominally on Basswood, Oak, Sand, and Stockton Islands (Hop et al. 2010), all of which were heavily logged prior to the establishment of the National Lakeshore (Busch 2008). In addition, Basswood, Oak, and Stockton Islands have the highest abundance of *Odocoileus virginianus* (white-tailed deer) in the archipelago apart from Long Island (Pichler et al. *in review*). *Odocoileus virginianus* consume a substantial amount of understory vegetation and can inhibit tree regeneration (Bradshaw and Waller 2016); thus, *O. virginianus* browse could play an important role in shaping available habitat on these islands. In addition to Stockton Island, we captured *M. pennsylvanicus* on Madeline Island and the mainland in 2019 (Online Resource 5) and during the early 2000s *M. pennsylvanicus* were detected on Basswood and Rocky. In 1956, Beals et al. (1960) determined that Rocky, Stockton, Basswood, and Madeline Islands had more *O. virginianus* browse than other islands; however, *O. virginianus* likely experienced a decline in abundance on Rocky Island due

to poor browse conditions following a population peak that occurred two years prior to the survey (Beals et al. 1960). Hence, the absence of *M. pennsylvanicus* on Rocky Island during our recent efforts could be related to the decline in *O. virginianus* abundance. On Basswood Island in 2017, we initially suspected that we captured *M. pennsylvanicus* in the field, although further evaluation by multiple mammalogists determined these individuals were *M. gapperi*. We did not survey much open habitat on Basswood Island; therefore, it is possible that *M. pennsylvanicus* still exists on the island, but, if present, its range would likely be constricted to the few areas containing grassland habitats. Grant (1971) suggested that *M. pennsylvanicus* will inhabit woodlands in the absence of competitor and predator species. Moreover, Grant (1971) noted that *M. pennsylvanicus* will spend significantly more time in open habitat when *M. gapperi* and *Peromyscus* spp. are present in woodlands. Thus, the loss of open habitat due to succession of vegetative communities, along with the presence of competitors, may be the reason why *M. pennsylvanicus* are blinking out of this island system.

Tamiasciurus hudsonicus appears to be widespread throughout the island archipelago, and Brander (1983, p. 106) stated that this species was “in the primeval fauna of the islands”. *Tamiasciurus hudsonicus* recently has increased in abundance across a subset of islands when comparing data from the early 2000s to our data (Table 2). *Tamiasciurus hudsonicus* has increased in abundance on South Twin Island and Stockton Island (Table 2). Distribution and abundance of *T. hudsonicus* is likely influenced by the availability of principle seed foods, cones from *Abies* spp., *Thuja* spp., and *Pinus* spp. (Brander and Bailey 1983; Riege 1991). *Abies balsamea* and *T. occidentalis* dominate areas of the islands that were previously logged (Busch 2008), suggesting that increasing *T. hudsonicus* abundance could be due to changes in resource availability.

Despite the establishment of the National Lakeshore and the subsequent reduction in the human footprint, island size appears to mitigate the dynamics of the small mammal community. Species richness tended to be greater on larger islands for the combined dataset (i.e., all time periods combined), as well as during two separate time periods (Table 1). The lack of a significant effect for island size from the early 2000s dataset is likely due to the reduced sample size (i.e., fewer islands surveyed) for that time period. Stockton Island is the largest island, aside from Madeline, that has been sampled and is the only island where all five small mammal species were detected (Fig. 3). Outer Island is slightly smaller than Stockton, and four species have been detected there (Fig. 3). However, even the larger islands of the archipelago supported only a subset of the small mammal species detected on the mainland. Our results support island biogeography theory, with larger islands supporting a wider variety of species. The distribution of one of the less common

small mammals, *B. brevicauda*, also supports island biogeography theory; *B. brevicauda* has only been detected on three islands that are close to the mainland and larger in size (Stockton, Basswood, and Oak; Online Resource 5). In comparison, most of the smaller islands (Eagle, North Twin, South Twin, York, and Devils; Fig. 3) only had two species detected, further supporting island biogeography theory. Similar to other studies, our data demonstrate that degree of island isolation has no apparent significant effect on species richness, but that island size remains a powerful predictor of the mammal community of the Apostle Islands archipelago (Allen et al. 2019; Allen et al. 2018; Bowers 1982; Belant and Van Stappen 2002) (Table 1; Fig. 3).

Conclusion

Our work suggests that the small mammal community of the archipelago has changed since the establishment of the Apostle Islands National Lakeshore in 1970. Small mammals fulfill many roles within ecological communities and contribute to the health and biodiversity of ecosystems. Thus, understanding the factors influencing changes within small mammal populations can provide insight into larger ecosystem dynamics. Our results show that a high abundance of *M. gapperi* on the islands has remained stable over time, whereas *M. pennsylvanicus* distribution has declined dramatically. The abundance of both species was likely influenced by the availability of suitable habitat and competition. Furthermore, *T. hudsonicus* has recently experienced an apparent increase in abundance across a subset of islands which could possibly be related to resource availability as a result of successional changes in vegetation. *Sorex cinereus* and *Peromyscus* spp. have increased in distribution over time, possibly due to the reduction of resource extraction or in the case of *Peromyscus* spp., an increase in human recreational boat traffic. Island size remains an important predictor of small mammal community diversity despite island-level factors causing species-specific changes following the establishment of the Apostle Islands National Lakeshore. Therefore, island size is potentially mitigating the dynamics of the small mammal communities of the Apostle Islands archipelago. To better understand the long-term dynamics of the Apostle Islands archipelago, we recommend repeated survey efforts every 5–10 years. Such data will provide managers with a glimpse into the long-term spatiotemporal dynamics of the small mammal community of the archipelago.

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Authors contributions ECM and ERO managed the development of the manuscript. All coauthors contributed to the manuscript. ERO conceived the original idea. ECM, MM, MJF, and BK conducted fieldwork with guidance from ERO. ECM and ERO were responsible for statistical analysis and figure development; BK provided additional statistical analysis. TRV, JV, and ERO coordinated the overall project and acquired funding to support the project.

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Availability of data and material The datasets generated during or analyzed during the current study are available from the corresponding author on reasonable request. See also the supplemental material.

Code availability Custom code is available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethics approval Trapping protocols were reviewed and approved by an institutional animal care committee at the University of Wisconsin—Madison (protocol number: A005801-R01).

Consent to participate NA.

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