



Simulated extreme climate event alters a plant-frugivore mutualism

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ABSTRACT

Anthropogenic climate change is contributing to an increase in the frequency of extreme weather events. These extreme events may affect interactions in mutualisms that provide key ecosystem functions, especially when the event is rare for a given system and participants are differentially affected. The tropical hardwood hammocks of Key Largo, Florida, USA are inhabited by a highly specialized endangered rodent, the Key Largo woodrat (*Neotoma floridana smalli*), which may be an important seed disperser of many native fleshy-fruited plant species. Other potential mammalian dispersers are generalist omnivores, northern raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*), that are less selective. We sought to demonstrate that extreme climate events could alter seed dispersal mutualisms by differentially affecting fruit preference of potential dispersers. We designed a replicated cafeteria-style experiment across the entire range of the Key Largo woodrat with fruit from sixteen native plant species and simulated an extreme climate event by exposing half of the fruits to sub-freezing temperatures. Freezing temperatures are rare in this tropical environment, but increased frequencies of these types of extreme events are predicted with climate change. Using camera traps, we monitored the removal of fruit and seeds by woodrats and the generalist consumers, predicting that changes in fruit quality resulting from exposure to sub-freezing temperatures would reduce preference by the more specialized woodrat relative to its generalist consumers. Indeed, exposure to subfreezing temperatures decreased the probability of fruit and seed removal by woodrats while generalist consumers preferentially removed more of the fruits and seeds exposed to sub-freezing temperatures. These data provide evidence that extreme climate events may affect species preferences for food asymmetrically, which may shift the dynamics of seed dispersal mutualisms. Over time, increasing frequencies of extreme weather events could indirectly affect communities and ecosystem services by shifting interactions between organisms.

1. Introduction

Ecosystems in the Anthropocene are subject to frequent and pervasive change, often driven by human activity (Crutzen, 2002). Over the past few decades, a great deal of attention has been directed towards the effects of human-induced climate change on organisms (Trisos et al., 2020). Climate change research is often focused on the trend of increasing global temperatures (Garcia et al., 2014), however, the Intergovernmental Panel on Climate Change reports that extreme weather events, defined as observations rarer than the 10th or 90th percentile probability tails for an area, are also increasing in frequency, intensity, and duration (Seneviratne et al., 2021). These events can include very high or low daily temperatures, flooding, droughts, and

major storms (Easterling et al., 2000). They can have wide ranging effects on organisms and their interactions, ranging from changing the phenology of fruiting and flowering (Butt et al., 2015; Ma et al., 2015) to altering species distributions (Parmesan et al., 2000; Inouye, 2001) and causing mortality from exposure (Parmesan et al., 2000; Bojórquez et al., 2021; Choat et al., 2012). Unusual extreme cold events may be more prevalent in climates where they were previously rare as Arctic warming destabilizes jet stream patterns (Francis and Vavrus, 2015; Cohen et al., 2021). The effects of cold events may be highly disruptive in tropical and subtropical environments (Bojórquez et al., 2021), as rare events tend to cause substantial physiological stress on exposed organisms, which may lack the adaptations to accommodate those conditions, potentially leading to a disproportionate influence on species fitness and

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function (Augspurger, 2013; Buckley and Huey, 2016). This can lead to injury, reduced fitness, or mortality in vegetation (Inouye, 2001; Augspurger, 2013; Osland et al., 2020), while wildlife adapted for warmer climates also tend to fare poorly (marine life – Pirhalla et al., 2015; Leriorato and Nakamura, 2019; reptiles – Mazzotti et al., 2016; insects – Downing et al., 2016; Wang et al., 2016). Animals can also face indirect effects of extreme events even if they avoid exposure from influences on food supplies and cover (Inouye, 2001). As the ability of both plants and wildlife to function effectively can be altered by exposure to extreme weather, it is no surprise that plant-animal interactions such as pollination or seed dispersal can also be affected, which can lead to changes in the ecosystem services they provide (Mokany et al., 2014; McConkey and O'Farrill, 2016; Tylianakis et al., 2008; Teixido et al., 2022).

Animal driven seed dispersal (i.e., zoochory) is an important ecosystem service that influences the composition and genetic structure of plant populations at local and landscape scales (Farwig and Berens, 2012; Mason et al., 2022; Wang and Smith, 2002). This mutualism is vulnerable to asymmetrical effects of climate change as participating plants and animals respond to disturbances in different ways (Mokany et al., 2014). Plants are less able to avoid exposure to abrupt, extreme weather, while animals can mitigate the direct impacts of environmental stressors by utilizing refugia (Sunday et al., 2014; Martin et al., 2015). This leads to an asymmetry in which plants face the direct exposure effects of extreme weather, which could cause fruit or seed damage (Easterling et al., 2000; Bojórquez et al., 2021; Franklin et al., 2016), changes in phenology (Butt et al., 2015; McConkey and O'Farrill, 2016), or direct mortality (Bojórquez et al., 2021; Franklin et al., 2016; Niu et al., 2014); all of which can limit wildlife driven seed dispersal by reducing or shifting the timing of availability. Physiological and molecular plant adaptations to cope with their inability to avoid exposure to stressors prevent some impacts (Niu et al., 2014; Huey et al., 2002; Ahuja et al., 2010), though the ability of animals to alter their activity or movement patterns to avoid the same stressors may also lead to alterations in seed dispersal effectiveness as species are exposed to a variety of novel or unusual conditions (Mason et al., 2022; McConkey and O'Farrill, 2016; Schupp et al., 2010).

Species natural history may determine responses to extreme weather events. For example, seed dispersal effectiveness of both ungulates and mammalian carnivores declined during an unusual cold spell in China, but only carnivores resumed dispersal to previous levels following the event (Zhou et al., 2013). Because seed dispersal effectiveness varies widely between species of vectors (Wang and Smith, 2002; Jordano et al., 2007), asymmetrical effects of extreme weather events on potential vectors could have cascading indirect effects on plants through seed dispersal. Similar patterns have been reported with changes in relative abundance of vectors. For example, rodents can play a vital role as seed dispersers through epi-, endo-, and syn-zoochory (Godó et al., 2022), and declines in larger mammalian frugivores has led to increases in their relative seed dispersal effectiveness in some systems (Jansen et al., 2012; Corlett, 2017). Also, shifts in dispersal mutualisms due to biological invasions of competing vectors can cause cascading shifts in plant communities and associated ecosystem functions (Christian, 2001; Traveset and Richardson, 2006). Species specialized to geographic areas or diets appear to be more vulnerable to experiencing negative population or behavioral impacts from changes (Brook et al., 2008; Davies et al., 2004; Farwig and Berens, 2012) and potentially reducing their relative contributions to interactions. Shifts in the relative contributions of vectors can alter the dynamics of the seed dispersal process (González-Varo et al., 2018; Schupp et al., 2010; Mason et al., 2022), especially when functional redundancy within a system is low (Mouillot et al., 2013; Valiente-Banuet et al., 2015). Collectively, this suggests that plant-animal mutualisms may be particularly vulnerable to shifts in the relative importance of vectors following extreme climate events when the plant-animal mutualism is a specialized relationship with low functional redundancy and the vectors differ in their response to the weather event.

We sought to explore how a rare extreme cold event might affect the relative seed dispersal effectiveness of a specialized endangered rodent, the Key Largo woodrat (*Neotoma floridana smalli*), compared to potential competing generalist vectors in the hardwood hammocks of Key Largo, Florida, USA. We designed a replicated cafeteria style field-experiment, placing the fruit of 16 native plant species with and without exposure to sub-freezing temperatures, across the current range of the Key Largo woodrat. We predicted that exposure of fruits to sub-freezing temperatures would disproportionately reduce the likelihood of fruit and seed removal by woodrats because freezing alters fruit quality and likely increases fruit and seed perishability (USDA, 1951; Mello et al., 2011; Chassagne-Berces et al., 2010; Reid, 1996). Resource perishability is a critical component of selection by many species, particularly those that cache food (Kotler et al., 1999; Clayton and Dickson, 1998) and research in other woodrat species has demonstrated that they preferentially cache less perishable food items (Reichman, 1988; Post and Reichman, 1991). Contrastingly, the generalist consumers do not cache food, but instead readily consume it upon the initial encounter. Thus, we predicted that exposure of fruits to sub-freezing temperatures would have relatively little effect on the likelihood of fruit and seed removal by generalist fruit consumers.

2. Methods

2.1. Study area and study species

Tropical hardwood hammock on Key Largo consists of diverse vegetation including canopy species of gumbo limbo (*Bursera simaruba*), pigeon plum (*Coccoloba diversifolia*), poisonwood (*Metopium toxiferum*), with midstory comprised of wild coffee (*Psychotria undata*), marlberry (*Arisia escallonioides*), and snowberry (*Chiococca parviflora*), many of which provide fruit multiple times during the year (USFWS, 2015). The climate in the area is considered subtropical, with summer average temperatures of 29 °C and winter averages of 21 °C (Gore and Loggins, 2005) and an average rainfall of 1179 mm per year (Bancroft et al., 2000). Extreme cold events are rare throughout south Florida but not unprecedented: weather stations at cities near Key Largo show 11 instances of days where dry-bulb temperatures read below freezing over the past 50 years, with an additional 133 days where temperatures were less than 5 °C above freezing (NOAA, 2021). Verified reports of ice formation in the upper Keys are also available from the National Weather Service station in Key West from 1989, with more recent evidence of air temperatures approaching freezing also available (Pirhalla et al., 2015). The area more regularly experiences other extreme weather events, particularly hurricanes (Radabaugh et al., 2020). Our study took place in approximately 850 ha of hammock contained within two protected areas on the northern third of the island, Crocodile Lake National Wildlife Refuge and Dagny Johnson Botanical State Park. These protected areas are part of only a few locations in which development has not severely reduced natural hammock cover, and represent the entire range of the Key Largo woodrat (Fig. 1A).

These protected areas represent the majority of natural hammock cover not severely reduced by development and encompass the entire range of the endemic Key Largo woodrat, an endangered subspecies of the Eastern woodrat (*Neotoma floridana*). Like other members of their genus, they are ecosystem engineers, constructing large stick nests that can provide shelter (Wiley, 1980; Humphrey, 1992; Whitford and Steinberger, 2010) and function as a larder for cached food items (Post et al., 1993; Post et al., 2006; Alligood et al., 2011). Fruit comprises a substantial portion of their diet (averaging 42%, Kanine et al., 2015), and data from other woodrat species indicate that this group can be effective seed dispersers both through endozoochory of small seeds and deposition of seeds into small surface level caches (Chambers et al., 1999; Sommers and Chesson, 2016), though cached items in larders may be poor dispersal candidates (Vander Wall and Beck 2012).

Other potential mammalian dispersers throughout the study area

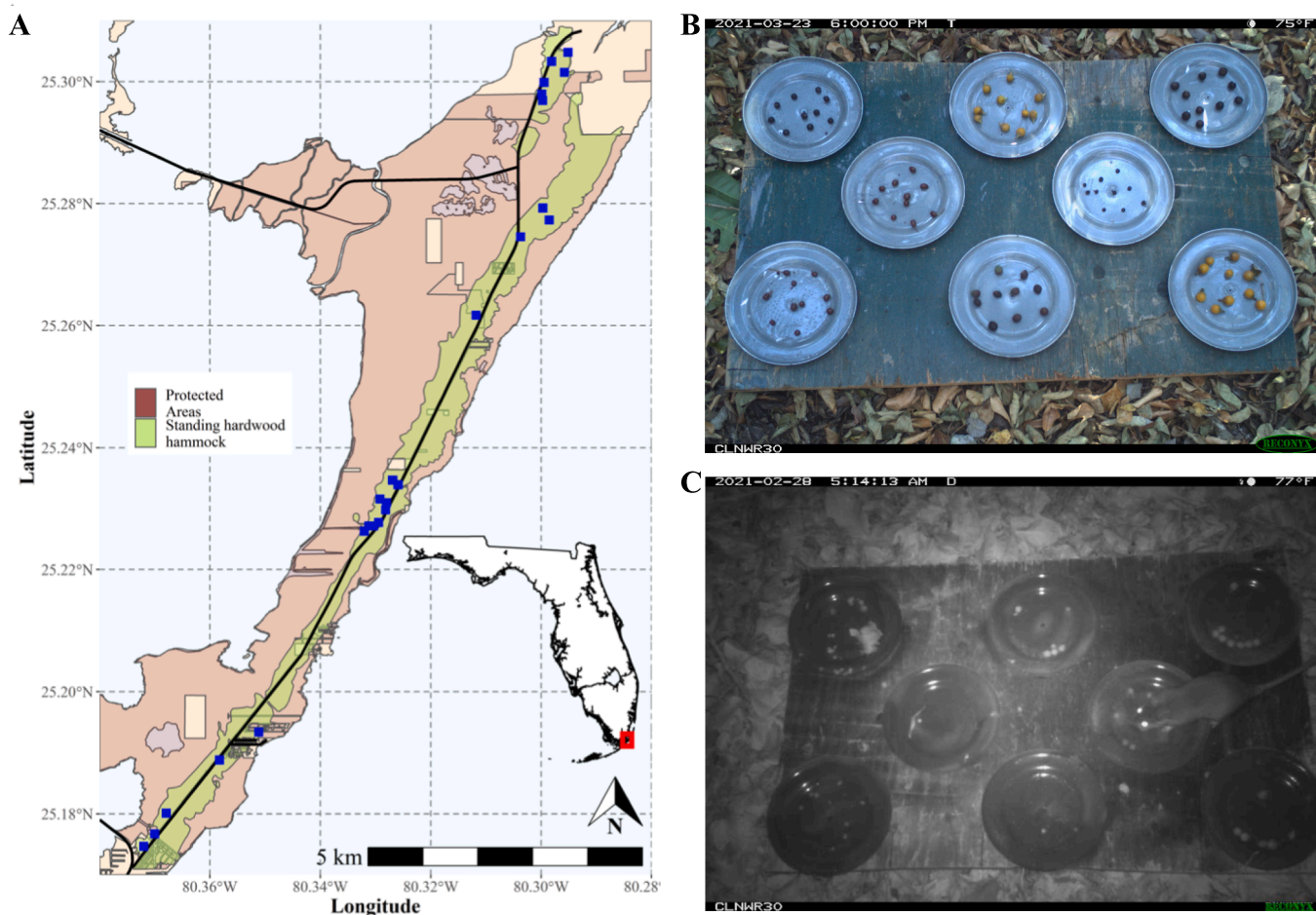


Fig. 1. Map of study area and food tray set up. A) Location of all sites where trays (blue squares) were deployed across study area, showing boundaries of hardwood hammock and protected areas. B) Example of food tray array set-up shortly after deployment. C) Photo of Key Largo woodrat removing fruit from tray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

List of all plant species used in analysis with baseline log hazard and the effect of freezing on fruit and seed removal. The treatment effect represents the difference in log-hazard for frozen fruit and seeds relative to fresh. Positive log hazard values correspond to higher risk of removal. Values marked with an asterisk have a significant relationship with the treatment.

Species	Number	Sites Used	Fruit Removed	Baseline Hazard	Treatment Effect	Seeds Removed	Baseline Hazard	Treatment Effect
Bahama Nightshade (<i>Solanum bahamense</i>)	40	2	7	-0.799	0.138	7	-0.58	0.138
Bahama Strongback (<i>Bourreria succulenta</i>)	100	5	82	1.394	0.780*	67	1.097	0.742*
Blackbead (<i>Pithecellobium keyense</i>)	100	5	15	-0.574	1.725*	14	0.095	2.220*
Crabwood (<i>Gymnanthes lucida</i>)	80	4	9	-1.608	2.519*	9	-1.395	2.519*
Greenbriar (<i>Smilax havanensis</i>)	141	7	69	0.828	1.285*	49	0.798	1.335*
Inkwood (<i>Exothea paniculata</i>)	60	3	59	1.534	1.480*	55	1.276	0.151
Marlberry (<i>Ardisia escallonioides</i>)	220	11	73	-1.833	-0.352	45	-1.524	-0.806*
False Mastic (<i>Sideroxylon foetidissimum</i>)	60	3	60	3.011	-2.927*	20	-0.16	0.641
Paradise Tree (<i>Simarouba glauca</i>)	181	9	172	2.658	0.780*	136	1.984	0.494*
Pearlberry (<i>Vallesia antillana</i>)	160	8	15	-2.124	-1.04	15	-1.582	-1.04
Pigeon Plum (<i>Coccoloba diversifolia</i>)	140	7	118	0.889	1.193*	70	-0.01	0.979*
Poisonwood (<i>Metopium toxiferum</i>)	100	5	8	-2.145	0.56	8	-1.592	0.56
Potato Tree (<i>Solanum elaeagnifolium</i>)	120	6	88	-0.941	1.261*	88	-0.068	1.261*
Shinyleaf Wild Coffee (<i>Psychotria nervosa</i>)	180	9	147	0.663	-0.291	135	0.99	0.112
Snowberry (<i>Chiococca alba</i>)	140	7	134	1.748	-1.026*	134	2.256	-1.026*
Wild Lantana (<i>Lantana involucrata</i>)	60	3	8	-2.702	-0.496	8	-1.585	-0.496

include northern raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), the endangered Key Largo cotton mouse (*Peromyscus gossypinus allapaticola*) and, to a lesser extent, the eastern gray squirrel (*Sciurus carolinensis*). Both raccoons and opossums are generalist meso-carnivores that have been demonstrated to disperse seeds (Wilson, 1993).

All aspects of study were approved under University of Florida Institutional Care and Use Committee #202010988 and U.S. Fish and Wildlife Service permits TE697819-4 and 41581-2020-01.

2.2. Experimental set-up

2.2.1. Fruit collection

Native fruits were collected throughout Crocodile Lake National Wildlife Refuge as encountered between January and May of 2021. Sampling days consisted of walking transects along reclaimed roads and trails throughout the refuge and collecting any ripe fruit visible. Upon encountering a fruiting plant, fruit samples were placed into zip lock bags labelled with the species and date of collection. Plant identification was verified using guidebooks (Hammer, 2004) and consultation with local U.S. Fish and Wildlife Service and Florida State Park staff. Plant species were only included in experiments if more than 40 individual fruits could be collected (Table 1). Where possible, fruits were collected from multiple individual plants of the same species. Any fruit showing signs of damage, such as evidence of invertebrates or shriveling, were not collected. Fruit collection occurred as ripe fruit was available, regardless of expected primary dispersal vector, i.e., by birds or mammals, if known. Half of the fruit collected for each species was frozen for a minimum period of 24 h. The remainder was refrigerated to maintain freshness for up to three weeks. Any fruit that showed signs of fermenting or rotting was discarded. No maximum period for frozen fruit retention was specified, though no fruit frozen for longer than 8 weeks was used in this study.

2.2.2. Site selection

A network of over 1000 supplemental nest structures has been deployed throughout protected areas in northern Key Largo as part of the Key Largo woodrat recovery effort (Cove et al., 2017). A subset of 197 nest structures were monitored with camera traps for rodent activity. Cameras were placed within three meters of nest structures and captured motion triggered photos on high sensitivity with no delay between triggers for at least one week. Twenty-four of those nest structures were selected to receive fruit trays, though due to uneven distribution of woodrats throughout the area, nest structures with evidence of rodent activity were given a higher weight in the pool of potential sites. To ensure independence of trials, sites with fruit deployed simultaneously had a minimum buffer of 100 m (Fig. 1A).

2.2.3. Tray and camera setup

Fruit tray design was modelled after Boggess et al. (2022) and consisted of eight plastic circular trays with a diameter of 18 cm fastened to a plywood board with 13 cm spacing between them (Fig. 1B). Four species of fruit from the currently collected stock were randomly selected for each array deployment, then each of the eight trays was randomly selected to have either 10 frozen or 10 fresh fruits. Trays were deployed before fruit was removed from storage, to minimize time frozen fruit was outside freezer. Fruit was transported in coolers and all trays received fruit within three hours of removal from freezer. Arrays were then monitored by camera traps (Reconyx Hyperfire II 850, RECONYX, Inc., Holmen WI, USA) on 127 cm tall tripods placed 25 cm from the edge of array. All cameras were set to record video when triggered by movement at high sensitivity, as well as take a time lapse photo every hour to ensure an accurate fruit count was maintained if a removal went undetected. Video was set to continue recording if sufficient animal activity persisted so that we could categorize how many fruits were removed during the total event. Arrays were placed within 5

m of supplemental nest structures with evidence of rodent activity. Arrays were placed at selected sites regardless of whether plants at ground level or in the canopy showed evidence of fruiting. Up to four arrays were deployed simultaneously over seven trials, with each site monitored for three to six days.

2.2.4. Camera video identification

We recorded the sequential times when individual fruits were removed from each tray and the wildlife species responsible. Removal events were categorized in two ways, the removal or observed complete or partial consumption of a fruit, regardless of seed fate, and the removal or observed consumption of seeds. This was because some wildlife species exhibited pulp-feeding behavior, which facilitated seed-foraging by other species and led to many occasions where seeds were removed from trays by a different species or individual than the individual responsible for pericarp consumption (Fedriani and Delibes, 2013). We assumed that the nutrition and energy gained through the consumption of the pericarp, seed(s), or all parts of available fruits were the primary interest of most consumer species, whereas dispersal of the seed was of interest from the plant perspective (González-Castro et al., 2022). To simplify identification of removal events and ensure removal counts were consistent across all species of fruit included, only a single seed was counted for each fruit. Each subsequent analysis was performed twice, once using fruit removal events, and again using seed removal events.

2.3. Analysis

2.3.1. Effect of exposure to sub-freezing temperatures on fruit and seed removal

The removal rates of different fruit species were compared using a mixed Cox proportional hazard analysis (Cox, 1972), incorporating the treatment effect of freezing fruit, and the species of fruit as fixed covariates. A nested random intercept of site ID within trial period was used to account for spatial and temporal variation. The most parsimonious of a set of five models, including a null model, a single variable model for treatment and another for fruit species, a multiple variable model with both, and a model with both variables and their interaction, was identified after selection using AIC_c scores, with a threshold of two Δ AIC_c for competing models, and model weights (Burnham and Anderson, 2004). Random effects were consistent across all models. The proportional hazards assumption of the Cox models was verified using a test of the Schoenfeld residuals. If this test failed, we used a two-step stratified Cox model approach (Mehrotra et al., 2012) to generate individual models for each group of any variable that failed to meet the proportional hazards assumption alongside a shared frailty model to generate a global effect (Beisel et al., 2017). This approach helps to address non-proportional hazards while also allowing for treatment effects to be heterogeneous among stratified groups.

2.3.2. Wildlife fruit and seed removal in response to treatment

Chi-square goodness of fit tests were performed for each wildlife species responsible for more than 5% of fruit removal events to evaluate species specific trends relative to the freeze treatment. Following this, a global Chi-square test of independence was performed on major species groups by the treatment, and partitioned (Bresnahan and Shapiro, 1966) to demonstrate differences in the response to the treatment across groups. Because raccoons and opossums are both adaptable generalists with similar sizes and diets, their responses were expected to be similar, and they were grouped together (Bateman and Fleming, 2012). Fruit was not replaced after removal from trays, so the proportions of fresh and frozen fruits removed by the first species to arrive at a site were compared using two-tailed T-tests and odds ratios to ensure there was no bias in selection due to a depletion of available resources for later arriving wildlife. Finally, a series of mixed logistic regressions were used to evaluate the probability a fruit was removed by a woodrat, by a generalist consumer, or by a cotton mouse. The treatment and time since

fruit trays were deployed were included as fixed effects while trial and fruit species were included as crossed random intercepts with time correlated slopes to account for variation in site and seasonal conditions as well as consumer preference.

All analyses were conducted in the statistical programming software R version 4.2.0 (R Core Team, 2022). The packages *coxme* (Therneau, 2020) and *survival* (Therneau, 2021) were used for the mixed Cox proportional hazard analysis, the package *MASS* (Venables and Ripley, 2002) was used for partitioning contingency tables, the package *lme4* (Bates et al., 2015) was used to construct regression models, and the package *AICModAvg* (Mazerolle, 2020) was used to generate model selection tables. Results were considered significant at p-values less than 0.05, and marginally significant at values between 0.05 and 0.1.

3. Results

A total of 36 native plant species were observed fruiting throughout the hardwood hammock within Crocodile Lake National Wildlife Refuge during the study. Sixteen of these species were included in the trials (Table 1). Across all arrays, 1064 individual fruits (56.5%) and 860 seeds (45.7%) were consumed directly or removed out of 1882 total fruits placed (Fig. S1). Eleven vertebrate species were observed in videos and photos, seven of which removed at least one fruit. Virginia opossums were the most frequently occurring species (Table 2). Some invertebrate species, including Cuban brown snails (*Zachrysia provisoria*) and Caribbean land hermit crabs (*Coenobita clypeatus*), also appeared to have consumed some fruit. Fruit and seed removal by observed species was highly variable across both fruit species (Table 1) and site (Table 2).

3.1. Effect of exposure to sub-freezing temperatures on fruit and seed removal

The best Cox proportional hazards models after model selection indicated models including fruit species and the interaction between fruit species and freeze treatment best explained removal risk for both fruits and seeds (Table S1). The treatment effect in the best models was an important predictor for fruit removal risk ($p = 0.018$), but not for seed removal risk ($p = 0.425$). A type II ANOVA indicated that fruit species ($p < 0.001$) and the interaction between fruit species and treatment ($p < 0.001$) were important predictors in both the best fruit and best seed models. The significant interaction between treatment and fruit species indicated that the effect of freezing fruit was inconsistent

across fruit species (Fig. S2). However, these models failed to meet the assumption of proportional hazards in a test of Schoenfeld residuals ($p < 0.001$), which was driven by the fruit species and interaction terms (Table S2). Shared frailty models addressed this assumption for both fruit ($p = 0.19$) and seed ($p = 0.52$) removal, generating an overall effect while still allowing for heterogeneous treatment effects, with individual models for each fruit species used to demonstrate species-specific treatment effects. Overall, both fruit and seeds that had been frozen were more likely to be removed than fresh controls ($p < 0.001$). When only considering fruit removal, frozen fruit was 24% more likely to be removed than fresh, while when seed removal was explicitly considered frozen fruit was 37% more likely to be removed than fresh (Fig. 2). Fruit species varied greatly in their baseline risk of removal and some species of fruit were less likely to be removed when frozen (Table 1, Fig. S2).

3.2. Wildlife fruit and seed removal in response to treatment

Four species, including the Key Largo woodrat, the Virginia opossum, the northern raccoon, and the Key Largo cotton mouse, were responsible for greater than 95% of the known removal events of both fruit and seeds. Opossums removed more fruit than any other species, followed by woodrats, though this relationship reversed when considering seeds (Fig. 3).

Opossums were also the first species to arrive at half of the sites. On average, the initial consumer to a site removed 20.9% (± 0.153 SD) of available fruit before another species arrived. The odds of a woodrat removing frozen fruit were 63.5% lower relative to fresh fruit ($OR = 0.47$, 95% $CI = [0.28, 0.79]$) when woodrats were the first consumer to arrive at a site. On average woodrats removed a slightly higher proportion of fresh fruit (0.300 ± 0.281 SD) relative to frozen fruit (0.181 ± 0.139 SD; $p = 0.216$). Generalist consumers odds of removal were 86.9% higher for frozen fruit relative to fresh fruit when they were the first to arrive ($OR = 1.87$, 95% $CI = [1.21, 2.89]$), and tended to remove a higher proportion of frozen fruit (0.270 ± 0.216 SD) relative to fresh (0.203 ± 0.144 SD; $p = 0.270$). This indicates the overall selection between treatments is not an artifact of the initial visitor exploiting available fruit. Indeed, these trends strengthened with subsequent visits, woodrats removed more fresh fruit ($\chi^2 = 9.8$, $p = 0.002$) and fresh seeds ($\chi^2 = 8.69$, $p = 0.003$) than expected (Table 3).

No other species differed from expected values for fruit, but both cotton mice ($\chi^2 = 4.05$, $p = 0.044$) and raccoons ($\chi^2 = 5.63$, $p = 0.018$) removed more frozen seeds than expected. Chi-square tests of independence show that freezing fruit had a differential effect on removal by generalist consumers both when considering only fruit removal ($\chi^2 = 15.47$, $p = 0.002$) and seed removal ($\chi^2 = 21.63$, $p < 0.001$; Table 3). Partitioned contingency tables reveal Key Largo woodrats respond differently compared to other species groups for both fruit ($\chi^2 = 10.01$, $p = 0.002$) and seed removal ($\chi^2 = 20.24$, $p < 0.001$), consistently removing more fresh fruit than frozen. Cotton mice and generalist consumers did not differ among each other in their response to the treatment for fruit ($\chi^2 = 2.44$, $p = 0.118$) or seeds ($\chi^2 = 0.206$, $p = 0.65$). The cumulative response of these species when only considering fruit had no apparent trend. When considering seeds, the response of these species shifted towards the removal of more frozen seeds. Overall, logistic regression models showed Key Largo woodrats were 58.3% less likely to remove frozen fruit ($\beta = -0.874$, $p < 0.004$) and 63.4% less likely to remove frozen seeds ($\beta = -1.005$, $p < 0.002$). The probability a fruit is removed by a woodrat decreases with time ($\beta = -3.703$, $p = 0.133$), varying widely across fruit species and trial (Fig. 4A) with a similar pattern when considering the probability of seed removal ($\beta = -3.371$, $p = 0.103$; Fig. 4B). Generalist consumers had a higher overall probability of removing both fruit (Fig. 4C) and seeds (Fig. 4D). They tended to remove more frozen fruit ($\beta = 0.259$, $p = 0.246$) and seeds ($\beta = 0.296$, $p = 0.199$) but were not more likely to remove one treatment group over the other. Cotton mice were more than 100% more likely to remove frozen fruit ($\beta = 0.847$, $p = 0.053$) and seeds ($\beta = 0.845$, $p =$

Table 2

List of major vertebrate species that removed fruit and seeds from trays.

Species	Sites observed	Visits	Fruit removed	Seeds removed
Mammals				
Key Largo woodrat (<i>Neotoma floridana smalli</i>)	9	61	245	234
Key Largo cotton mouse (<i>Peromyscus gossypinus allapaticola</i>)	12	54	60	80
Virginia Opossum (<i>Didelphis virginiana</i>)	18	66	311	199
Northern Raccoon (<i>Procyon lotor</i>)	6	13	99	86
Eastern Gray Squirrel (<i>Sciurus carolinensis</i>)	2	5	20	4
Birds				
Northern Cardinal (<i>Cardinalis cardinalis</i>)	1	3	6	0
Ovenbird (<i>Seiurus aurocapilla</i>)	3	4	3	2
Other*	16	22	12	5

*Other category includes herpetofauna (3 lizard species and one frog) and invertebrates (several insect species, one snail species, one hermit crab species). No herpetofauna removed any fruit or seeds, though a few invertebrates did.

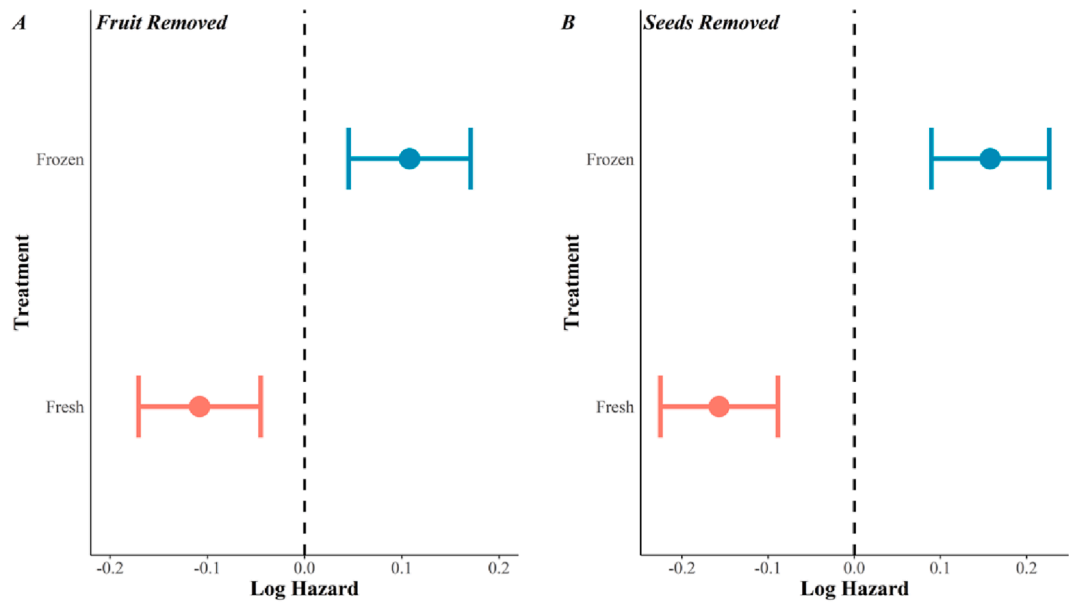


Fig. 2. Overall effect of freezing fruit and seeds on the risk of removal. A) shows removal of fruit regardless of seed fate while B) shows seed removal only. Vertical dashed line at log hazard of 0 represents baseline removal risk, regardless of treatment group. Positive log hazard values indicate an increased risk of fruit removal while negative values indicate a reduced risk of fruit removal.

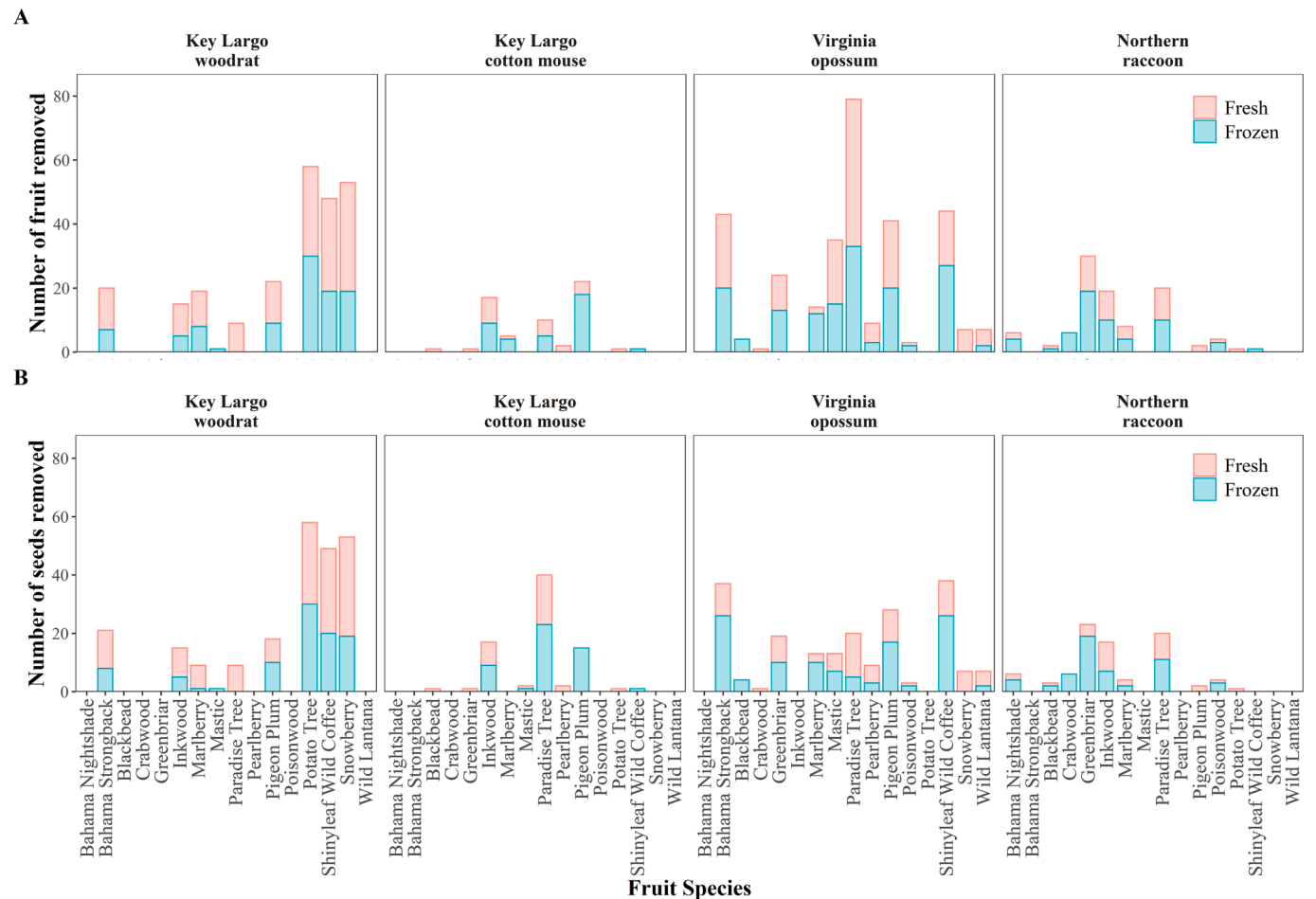


Fig. 3. Count of fruit and seeds of different plant species included in analysis removed by most frequently observed wildlife species. A) shows removal of fruit regardless of seed fate while B) shows seed removal only. Bars are colored to show effect of treatment on removal.

Table 3

Results of chi-square goodness of fit tests on treatment for single species, and test of independence on treatment for all species. Values with * are significant.

Analysis/Predator Species	Fruit Removed			Seeds Removed		
	Fresh	Frozen	χ^2	Fresh	Frozen	χ^2
<i>χ^2 Goodness of fit test</i>						
Key Largo woodrat	147	98	9.80*	139	94	8.69*
Key Largo cotton mouse	23	37	3.27	31	49	4.05*
Virginia Opossum	160	151	0.26	87	112	3.14
Northern Raccoon	41	58	2.92	32	54	5.63*
Other	20	21	0.02	4	7	0.82
<i>χ^2 Test of Independence</i>						
All species	391	365	15.47*	293	316	21.63*

0.030), and contrary to other species the probability of cotton mouse removal increased over time for both fruit ($\beta = 1.778$, $p = 0.233$; Fig. 4E) and seeds ($\beta = 2.995$, $p = 0.126$; Fig. 4F).

4. Discussion

We provide evidence that an extreme climate event could alter a seed dispersal mutualism by shifting the diet preferences of competing vectors. Exposure of native fruits to sub-freezing temperatures altered the decision process in food selection, resulting in a negative response by the endemic Key Largo woodrat relative to generalist consumers. Mutualisms built upon networks with many links can be robust to a reduction in effectiveness or loss of a given species due to the presence of redundant interactions (Bascompte et al., 2006; Tylianakis et al., 2008). However, rare species may disproportionately hold unique functional roles that are less easily replaced (Mouillot et al., 2013). In this system, the generalist consumers can contribute to dispersal, but they are omnivores that intake a much wider variety of potential resources as food, such as anthropogenic subsidies through waste (Gehrt, 2004; Beatty et al., 2014), than the woodrat, which is restricted to consuming local vegetation, including fruits and seeds. As the number of potential mammalian dispersers in the hammocks of the Florida Keys is limited, this may mean that woodrats hold a relatively important role in the dispersal process. In the event of extreme weather, the relative importance of woodrats on seed dispersal may be reduced in this system. It is unclear whether shifts in this mutualism toward the generalist consumers would have consequences to plant communities, but shifts in the relative preferences among consumers may have some negative impacts for the more specialized woodrats. In either case, our experiment provides evidence that extreme climate events have the potential to affect ecosystem processes by shifting the dynamics of mutualisms.

The disproportionate response of woodrats to the simulated extreme cold weather event relative to generalist consumers is likely the result of exposure to sub-freezing temperatures causing changes in fruit quality and perishability. The process of freezing alters the carbohydrate content of fruits and seeds (Mello et al., 2011) while also affecting texture and water content (Chassagne-Berces et al., 2010). Also, freezing is an unreliable method for removing microorganisms involved in the spoiling of food items (Golden and Arroyo-Gallyoun, 2012) and thawed foods may spoil faster than fresh foods. For species that cache food, such as woodrats, the perishability of collected items is important; cached food that spoils more quickly decreases the efficacy of hoarding (Gendron and Reichman, 1995). When presented with food items varying in perishability, eastern woodrats (*Neotoma floridana*) preferentially cached less perishable items first, even when the nutritional quality of the items was approximately identical and with the trend growing stronger in the presence of competitors (Reichman, 1988; Post and Reichman, 1991). Raccoons and opossums have a generalist diet and can consume a wide array of food resources with varying nutritional quality (Gehrt, 2004; Beatty et al., 2014), whereas woodrats are more restricted (Kanine et al., 2015). Perishability may appear to be of lower concern

than the immediate value of the fruit for the non-caching raccoons and opossums but may explain why they appeared to select slightly more frozen fruit and seeds relative to fresh than expected. Highly perishable items are eaten on site rather than cached (Clayton and Dickinson, 1998; Gendron and Reichman, 1995; Kotler et al., 1999), and this may apply to non-caching species as well, considering that delayed consumption could result in a missed opportunity. Because the strategies of woodrats and generalist consumers in relation to perishability differ, events that make foods more perishable may reduce woodrat fruit intake. Though it should be noted that in cases of food limitation, woodrats would likely consume perishable items as available. Cotton mice, which likely cache and hoard less than the larger woodrats based on the activity of other *Peromyscus* spp. (Sommers and Chesson, 2016; Hollander and Vander Wall, 2004; Post et al., 1993), selected frozen items more than fresh, offering further support that perishability is an underlying mechanism in fruit and seed selection among consumer strategies.

Our study has limitations, but we believe our design allowed us to make strong inferences about the system, and supporting literature provides evidence lending credence to our assumptions. We do not know the relative effectiveness of seed dispersers in the system or the fate of removed seeds, only the number of fruit and seeds removed by each species. However, metrics using the number of seeds removed by consumers can be efficient proxies of dispersal effectiveness (Vázquez et al., 2005). In addition, we made the simplifying assumption that each fruit only has a single seed, which is true for half of the plant species used in the analysis. This should have limited impact on our inferences on the relative prevalence of fruit and seed removal but could be an important aspect in dispersal effectiveness for some plant species. We were also unable to determine the fate of removed seeds. Larder hoarding in a central location, such as a nest, is typically considered a poor seed dispersal strategy compared to other caching mechanisms (Vander Wall and Beck, 2012). On rare occasions, the damage to nests as a result of hurricanes or overwash may partially mitigate some of the negatives of larder hoarding by freeing seeds stored in Key Largo woodrat caches. It should be noted that shifting seed dispersal to non-caching generalist consumers could also positively affect seed dispersal effectiveness of some plant species. Opossums frequently acted as pulp-feeders, consuming the flesh of fruits but leaving seeds; a common behavior among didelphids (Rebein et al., 2017; Cáceres and de Araújo Monteiro-Filho, 2007; Leiner and Silva, 2007). Seeds left behind by pulp-feeding animals can enhance foraging efficiency of seed-eating rodents (Fedriani and Delibes, 2013), and Key Largo cotton mice were often observed removing defleshed seeds later, presumably to consume rather than cache. Although there is evidence of several *Peromyscus* spp. contributing to seed dispersal through caching (Vander Wall et al., 2001; Hollander and Vander Wall, 2004), many are also implicated as seed predators (Wenny, 2000; Ostfeld et al., 1997). Though we observed few bird species removing fruit from our sample trays, several studies have cited birds as being the primary dispersal agents for a number of plants in South Florida's hardwood hammocks, including species used in this study or their close relatives (Bancroft et al. 2000; Zhou et al., 2008). The ultimate dispersal effectiveness of woodrats relative to other species in the system remains unknown, but our experiment demonstrates that extreme weather events could alter the relative importance of these vectors, which may be important for plant communities and the participating wildlife species. The effects of direct exposure to sub-freezing temperatures on the viability of seeds in this system remain unknown but have important implications for plants. This is likely a species-specific issue, as the seeds of some tropical plants fare poorly in cold conditions (Chandel et al., 1995), while others appear to be more tolerant (Mello et al., 2011). If freezing kills the seed outright, the resulting changes in the relative importance of vectors would be a moot point from the plant's perspective. The direction of fitness consequences of our results to plants in this study should be interpreted with caution, but a change in seed dispersal effectiveness is likely.

Finally, our experiment represents only one piece of a complex

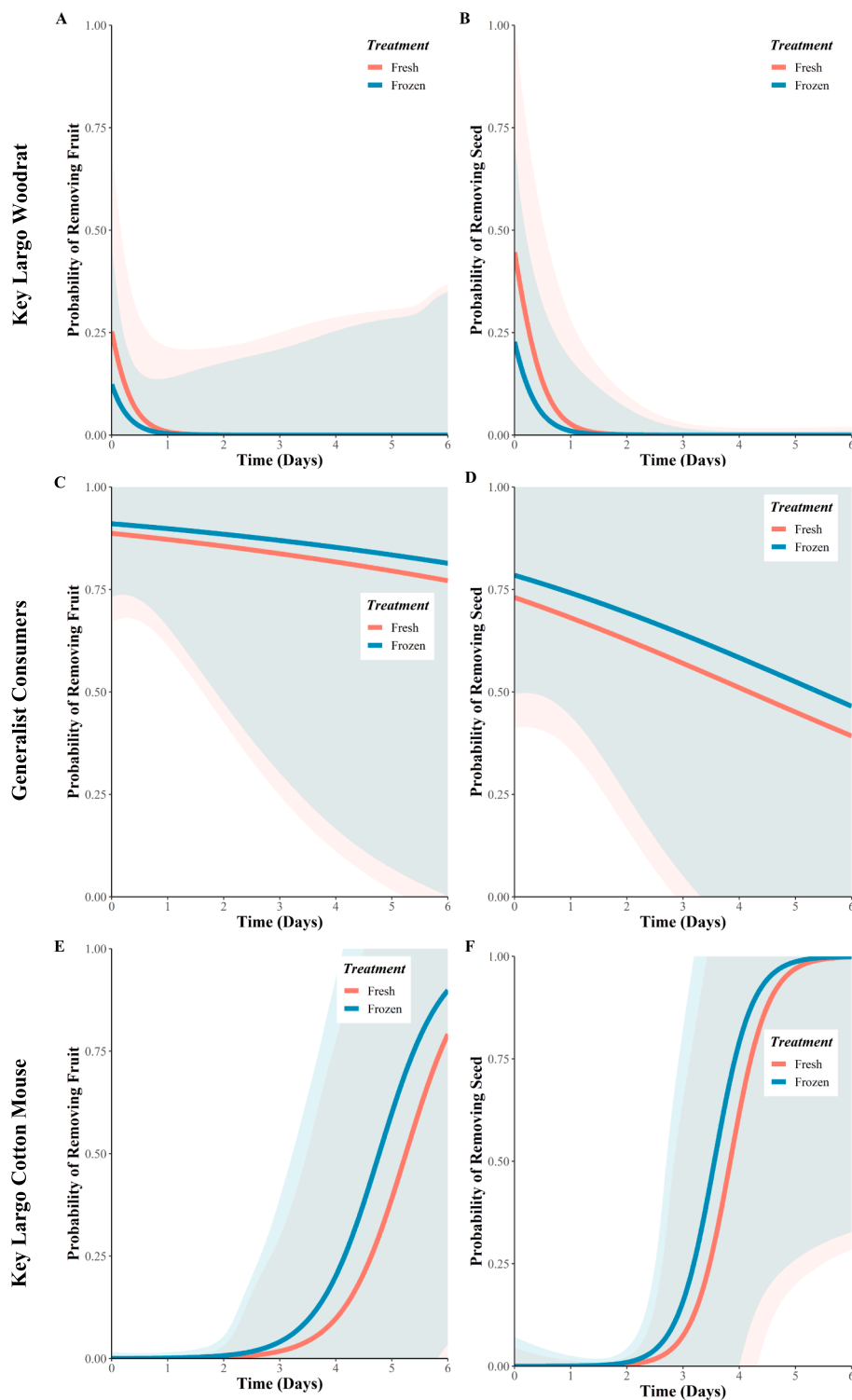


Fig. 4. Probability of frequently observed wildlife species removing a fruit or seed out of all removal events. A) and B) show the probability of the removal of fruit or seeds respectively by Key Largo woodrats over time. C) and D) show the probability of the removal of fruit or seeds respectively by generalist consumers (i.e., opossums and raccoons). E) and F) show the probability of the removal of fruit or seeds by Key Largo cotton mice over time. Semi-transparent bands around lines in all plots represent bootstrapped 95% confidence intervals. High variation is due to different preferences for individual fruit among species and inconsistent observations of wildlife species across sites and trials.

system. We assume that in the event of extreme weather, such as a freeze, fruit will be available on plants but the quality may be altered affecting wildlife preference and removal. However, stress from an extreme event can result in alterations of phenology (Butt et al., 2015, Ma et al., 2015), leading to delays or the absence of fruit on the landscape altogether. A similar extrapolation can be made for wildlife, exposure to unusual conditions, either the direct impacts of an extreme event or indirect effects related to changes to resources as a result, such as changes in food availability, might result in changes in food selection

(Zhou et al., 2013). For example, more generalist consumers could switch to non-fruit items in the event fruit was limited or had reduced quality. In reality, an animal's decision to consume or move a fruit or seed is based on both the state of the animal and a number of additional environmental factors beyond the simplified system we have presented here. That said, our experiment had the strength that we isolated one factor (i.e., the effect of freezing fruits) on the fruit selection process. Our data suggests that consumers may respond differently to shared events, which may indicate that the relative role of consumers in the

dispersal process could change as a result.

Our study demonstrates that extreme weather events can indirectly and asymmetrically affect the preferences of potential vectors. Over time this is one of several related factors that could alter seed dispersal mutualisms as the ability of species to acclimate to changing conditions varies. Shifts in the relative importance of dispersers may ultimately contribute to concurrent shifts in local plant communities and biodiversity (Schupp et al., 2010; Mason et al., 2022), particularly when there is low functional redundancy (Mouillot et al., 2013). Increasing prevalence of extreme weather worldwide due to climate change (Seneviratne et al., 2021) creates a potential for broad impacts as these stochastic events affect species and their interactions. These events do not occur in a vacuum either, other aspects of global change, such as urbanization, are disrupting ecosystems simultaneously and can interact with climate change factors to affect important processes like seed dispersal (Zhou et al., 2013) and drive community shifts in complex ways (Brook et al., 2008; Farwig and Berens, 2012; Tylianakis et al., 2008). It is therefore important to continue to build an empirical understanding of how important ecological processes are affected by extreme weather and other elements of global change moving forward.

CRediT authorship contribution statement

Brandon W. McDonald: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Carolina Baruzzi:** Formal analysis, Writing – review & editing. **Robert A. McCleery:** Formal analysis, Writing – review & editing. **Michael V. Cove:** Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. **Marcus A. Lashley:** Conceptualization, Methodology, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Brandon McDonald, Marcus Lashley, Michael Cove reports financial support and equipment, drugs, or supplies were provided by United States Fish and Wildlife Service.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121294>.

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