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# Ecological function maintained despite mesomammal declines

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Mid-sized mammals (i.e., mesomammals) fulfill important ecological roles, serving as essential scavengers, predators, pollinators, and seed dispersers in the ecosystems they inhabit. Consequently, declines in mesomammal populations have the potential to alter ecological processes and fundamentally change ecosystems. However, ecosystems characterized by high functional redundancy, where multiple species can fulfil similar ecological roles, may be less impacted by the loss of mesomammals and other vertebrates. The Greater Everglades Ecosystem in southern Florida is a historically biodiverse region that has recently been impacted by multiple anthropogenic threats, most notably the introduction of the Burmese python (*Python molurus bivittatus*). Since pythons became established, mesomammal populations have become greatly reduced. To assess whether these declines in mesomammals have affected two critical ecosystem functions—scavenging and frugivory—we conducted experiments in areas where mesomammals were present and absent. We did not observe significant differences in scavenging or frugivory efficiency in areas with and without mesomammals, but we did observe significant differences in the communities responsible for scavenging and frugivory. Despite the observed evidence of redundancy, the changes in community composition could potentially lead to indirect consequences on processes like seed dispersal and disease dynamics within this ecosystem, emphasizing the need for further study.

Vertebrates, especially mammals, are declining precipitously across the globe from overharvesting, habitat loss, and invasive species<sup>1,2</sup>. In particular, larger mammals appear vulnerable to these anthropogenic impacts, and their declines can drive changes that radiate across the ecosystem<sup>3,4</sup>. Mesomammals (i.e., mid-sized mammal species weighing between 1 and 25 kg as adults) are thought to be more resilient<sup>5</sup>, and may even benefit from the removal of larger predators and competitors<sup>6</sup>. However, not all mesomammal species are robust to anthropogenic environmental changes, and an increasing number of species in this size class are experiencing population declines<sup>7</sup>.

The decline of mesomammals is concerning because they fulfil vital ecological roles<sup>8</sup>. Given their varied diets, mesomammals are important consumers of carrion and fruit<sup>9,10</sup>. The loss of carnivorous mesomammals may lead to an increase in prey populations (e.g., rodents)<sup>11</sup>, a decrease in scavenging (i.e., carrion removal), and alterations in nutrient cycling<sup>12</sup>. Moreover, mesomammal declines may disrupt the consumption, dispersal, and germination of seeds<sup>13,14</sup>. However, ecosystems with high functional redundancy—characterized by the co-occurrence of multiple species capable of fulfilling similar ecological roles—may be less impacted by the loss of mesomammals and other vertebrates<sup>15–17</sup>. In such systems, it is possible that surviving species will compensate for the services provided by declining populations, thereby maintaining ecosystem functions<sup>18,19</sup>. For example, small-bodied frugivores may consume sufficient fruit to compensate for the absence of larger frugivores, preserving seed ingestion rates<sup>20</sup>. Similarly, despite the importance of mammals as seed predators, fungi and insects have been observed to compensate for the absence of vertebrates in enclosure experiments, resulting in comparable seedling establishment rates across treatments<sup>19</sup>. Accordingly, functional redundancy contributes to ecological stability by buffering important functions in the context of species loss<sup>21</sup>.

Although species loss is a global phenomenon, few places have experienced sharper declines of historically common mesomammals than the Greater Everglades Ecosystem (GEE) in Florida, USA. Starting in the early 2000s, native mesomammals—including opossums (*Didelphis virginiana*), skunks (*Mephitis mephitis*; *Spilogale putorius*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), rabbits (*Sylvilagus palustris*; *Sylvilagus floridanus*) and foxes (*Urocyon cinereoargenteus*; *Vulpes vulpes*)—declined precipitously, likely as a result of the establishment and spread of non-native Burmese pythons (*Python molurus bivittatus*) which were introduced via the pet trade<sup>22–25</sup>.

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However, the impact of mesomammal declines on scavenging and frugivory efficiency in the GEE, as well as any potential secondary changes to related processes, remain poorly understood.

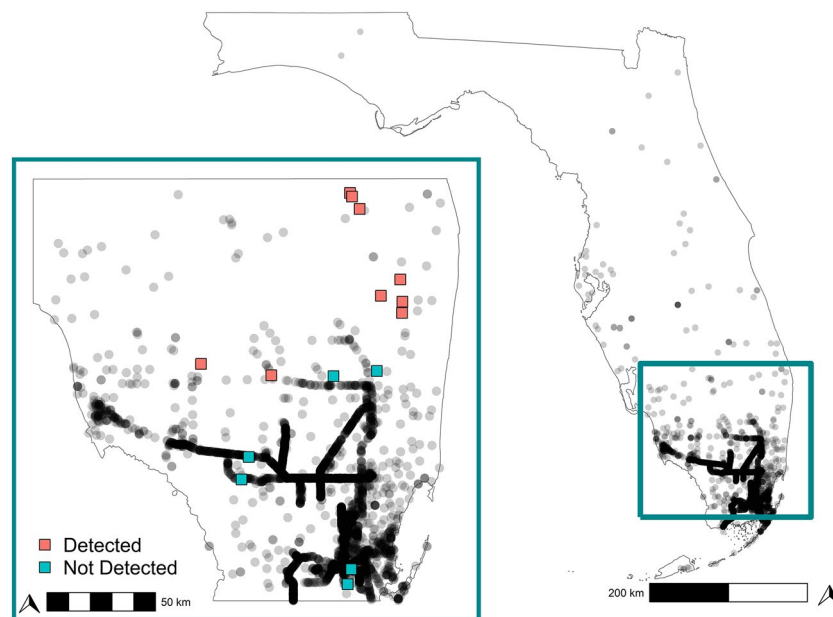
If mesomammal declines have altered scavenging and frugivory rates in the GEE, the ecological ramifications could be far-reaching. However, the GEE has been identified as a system with high functional diversity and redundancy, which theoretically should enhance its resilience<sup>26</sup>. Additionally, there is a need to understand whether and how functionally redundant systems can mitigate the loss of mammals and other vertebrates<sup>27</sup>. To address this knowledge gap, we leveraged the documented gradient in mammal diversity within the GEE<sup>24,25,28,29</sup> to assess the influence of mesomammal declines on two critical ecosystem processes, scavenging and frugivory. Specifically, our objectives were to—(1) evaluate differences in scavenging and frugivory rates between areas where mesomammals were and were not detected and (2) compare communities of scavengers and frugivores between areas that vary in their level of mesomammal activity. Based on the diversity and potential for redundancy in the GEE<sup>26</sup>, we predicted that carrion and fruit removal rates would not change in areas without mesomammals due to compensation by remaining taxa.

## Results

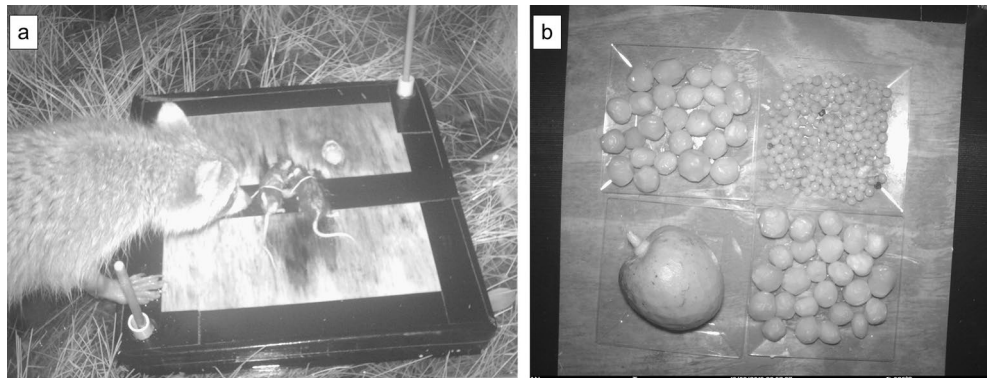
Using a previously established gradient in mammal diversity that appears to be linked to python establishment<sup>22,25,28,30</sup>, we conducted scat surveys and 14 trap nights of camera surveys at 15 sites throughout the GEE. Although mesomammals were detected at all 15 of these sites in 2014<sup>30</sup>, we detected mesomammals at only nine of these sites in 2019<sup>25</sup>. We failed to detect mesomammals at the remaining 6 sites from our passive sampling and with the additional 36 trap nights associated with scavenging and frugivory experiments<sup>30</sup> (Fig. 1). Conversely, we observed mesomammals at scavenging or frugivory stations at 8/9 sites we categorized as “mesomammal detected” from our passive sampling.

### Scavenging

To compare scavenging efficiency in sites where mesomammals were present or absent, we experimentally placed 2 rat carcasses at each scavenging station ( $n = 3/\text{site}$ ) for 7 nights (Fig. 2a). We placed cameras at each scavenging station to monitor rat decomposition and identify the species responsible for scavenging activity. In total, we documented 160 scavenging bouts by 14 species from 10 different families (Table 1). We found little evidence that the occurrence of mesomammals influenced scavenging rates. Seventy percent of rat carcasses (19/27) were visited by scavengers at sites where mesomammals were detected and 66.7% of carcasses (12/18) were visited at sites where mesomammals were not detected. Using a Cox proportional hazards model, we did not find a significant difference ( $z = -0.22$ ;  $df = 1$ ;  $p = 0.83$ ) in the estimated median time it took wildlife to detect and begin consuming the bait at scavenging sites where mesomammals were detected (49.0 h, 95% CI = 30.2-NA) and at sites where mesomammals were not detected (50.7 h, 95% CI = 30.2-NA) during passive sampling (Fig. 3a). Additionally, we did not observe a significant change ( $z = -0.17$ ;  $df = 1$ ;  $p = 0.86$ ) in consumption time—i.e., the time required for the carcass to be completely consumed to the point that no visible portion remained on camera—for



**Figure 1.** Map of python removals that occurred between 1979 and 2019 across Florida with study region in Greater Everglades Ecosystem outlined in turquoise. Inset: Map of 15 sampling sites on public lands within the GEE study region. Mesomammals were detected at all 15 sites in 2014 surveys but were detected at only 9 of 15 locations in the sampling conducted in 2019. This figure was created using ArcGIS Pro 3.1.0 (<https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview>).



**Figure 2.** (a) Scavenging and (b) frugivory station stations deployed at 15 sites in the Greater Everglades Ecosystem (Florida, USA). Scavenging stations were baited with two rat carcasses. Frugivory stations included the fruit of three native species, American beautyberry, cocoplum, and pond apple.

Mesomammals not detected		Mesomammals detected	
Species	Number of bouts	Species	Number of bouts
Cotton rat ( <i>Sigmodon hispidus</i> )	65	Raccoon ( <i>Procyon lotor</i> )	28
Cottonmouth ( <i>Agkistrodon piscivorus</i> )	11	Turkey vulture ( <i>Cathartes aura</i> )	10
Turkey vulture ( <i>Cathartes aura</i> )	6	Black racer ( <i>Coluber constrictor</i> )	7
Black vulture ( <i>Coragyps atratus</i> )	2	Opossum ( <i>Didelphis virginiana</i> )	7
Red-shouldered hawk ( <i>Buteo lineatus</i> )	2	Alligator ( <i>Alligator mississippiensis</i> )	4
Marsh rice rat ( <i>Oryzomys palustris</i> )	2	Marsh rice rat ( <i>Oryzomys palustris</i> )	4
American alligator ( <i>Alligator mississippiensis</i> )	1	Cotton rat ( <i>Sigmodon hispidus</i> )	4
Black bear ( <i>Ursus americanus</i> )	1	Cotton mouse ( <i>Peromyscus gossypinus</i> )	3
		Cottonmouth ( <i>Agkistrodon piscivorus</i> )	1
		Common garter snake ( <i>Thamnophis sirtalis</i> )	1
		Spotted skunk ( <i>Spilogale gracilis</i> )	1
<i>Total Scavenging Bouts</i>	90	<i>Total Scavenging Bouts</i>	70

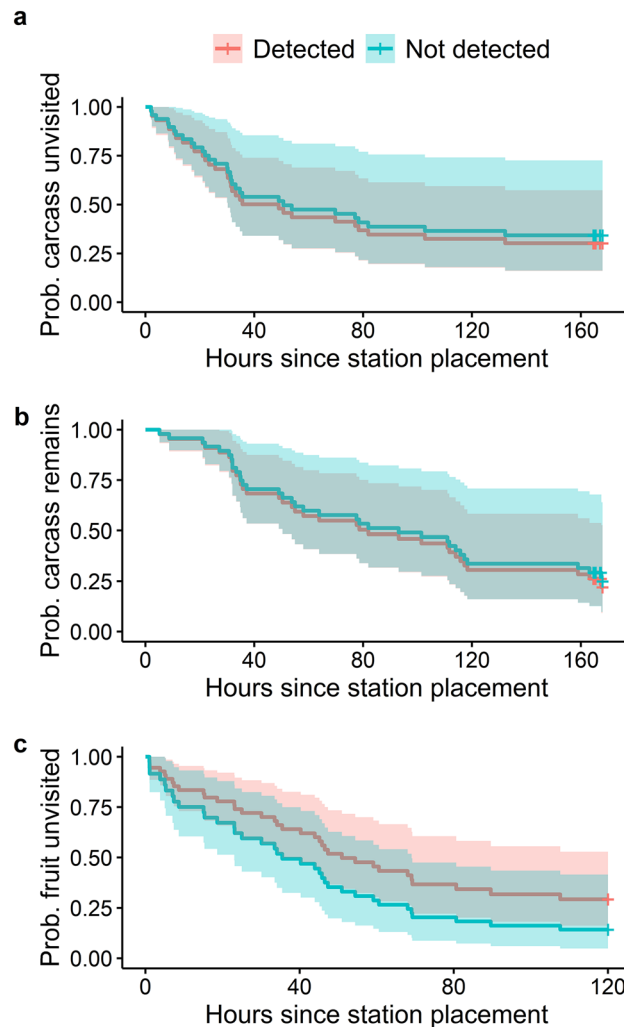
**Table 1.** Species observed consuming carrion during scavenging experiments conducted at 15 sites within the Greater Everglades Ecosystem (Florida, USA) along a gradient of python activity. Sites were categorized based on whether mesomammals (e.g., raccoons, opossums, foxes, etc.) were detected in camera and scat surveys in 2019 passive sampling. Mesomammals were detected at all locations in 2014.

rat carcasses between sites where mesomammals were and were not detected during passive sampling. Our Cox proportional hazards model estimated that it took a median of 81.9 h (95% CI = 50.4-NA) for a carcass to be completely removed in sites where mesomammals were detected and 93.1 h (95% CI = 50.4-NA) in sites where mesomammals were not detected in passive sampling (Fig. 3b).

Although we did not observe a significant difference in scavenging efficiency between sites where mesomammals were detected and not detected, a PERMANOVA revealed a significant difference in scavenger communities ( $F = 2.81$ ,  $df = 1$ ,  $p = 0.03$ ). We recorded 90 scavenging bouts conducted by 8 species at sites where mesomammals were not detected and 70 bouts by 11 species at sites where mesomammals were detected during passive sampling (Table 1). Rodents were the dominant scavenging group at sites where mesomammals were not detected (74.4%), while mesomammals were dominant at sites where they were detected in passive surveys (51.4%; Fig. 4a).

### Frugivory

To assess fruit removal rates at sites with and without mesomammals detected with passive sampling, we placed three native fruit species at each frugivory station ( $n = 3/\text{site}$ ; Fig. 2b). Using cameras mounted above the frugivory station, we monitored the proportion of fruit remaining and the amount of time required for a species to arrive and consume fruit (i.e., visiting latency). Additionally, we used camera traps to record the number of one-minute frugivory bouts and to identify the species responsible for each bout. In total, we recorded 757 one-minute frugivory bouts by 9 species from 7 families across all sites (Table 2). Similar to scavenging, we found little evidence that frugivory metrics changed with mesomammal detection. Frugivores arrived at 70.4% of stations (19/27) where mesomammals were detected and 88.9% (16/18) of stations where mesomammals were not detected in passive sampling. The Cox proportional hazards model estimated the median visiting latency in frugivory experiments was 50.9 h (95% CI = 35.5-NA) for sites where mesomammals were detected and 35.5 h



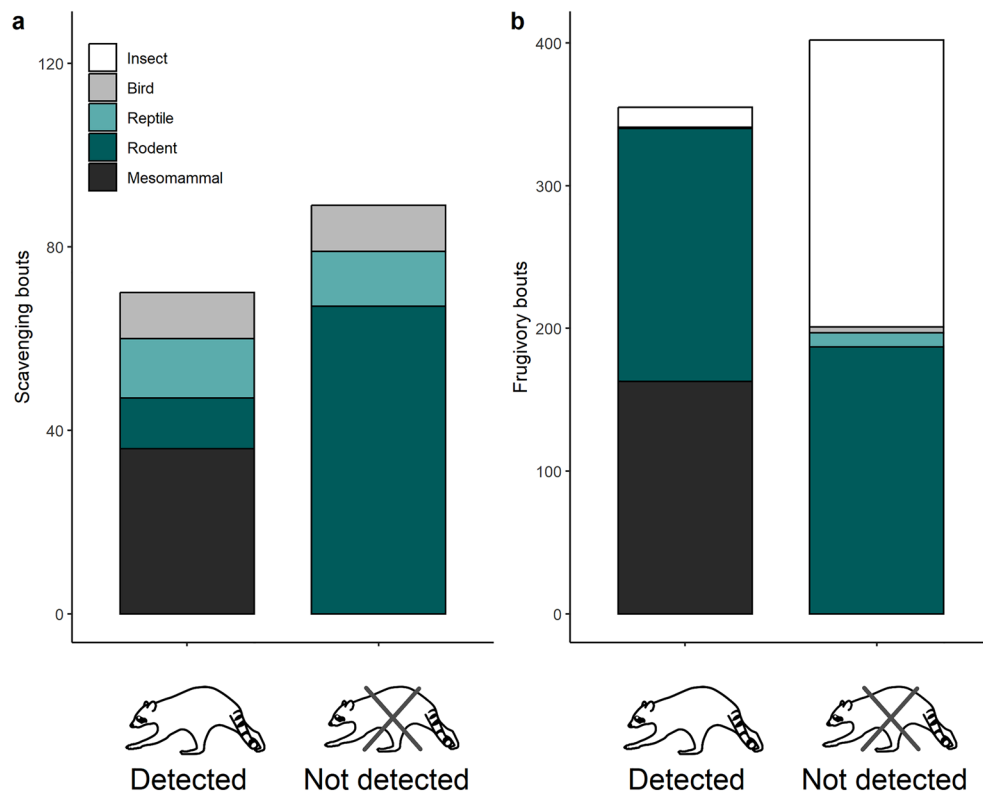
**Figure 3.** Cox proportional hazards survival curves with 95% confidence intervals representing the probability that (a) the carcass remained unvisited; (b) the carcass was not completely consumed; and (c) that fruit remained unvisited as a function of hours since station placement. Line color reflects whether mesomammals were detected or not detected at the site in passive sampling.

(95% CI = 23.1–69.1) at sites where mesomammals were not detected with passive sampling (Fig. 3c). However, these differences were not statistically meaningful ( $z = 1.25$ ;  $df = 1$ ;  $p = 0.21$ ). The proportion of fruit consumed was similar across sites with and without mesomammals (Fig. 5). The linear mixed model used to analyze fruit removal revealed that the proportion of fruit consumed at stations varied by fruit type ( $\chi^2 = 48.46$ ,  $df = 2$ ,  $p < 0.0001$ ). *Cocoplum* (*Chrysobalanus icaco*) was consumed at higher rates than American beautyberry (*Callicarpa americana*;  $t = 4.75$ ,  $df = 118$ ,  $p < 0.0001$ ) and pond apple (*Annona glabra*;  $t = 6.78$ ,  $df = 118$ ,  $p < 0.0001$ ). However, there was no significant relationship between mesomammal presence in passive sampling and the proportion of fruit consumed ( $\chi^2 = 0.30$ ,  $df = 1$ ,  $p = 0.58$ ). Similarly, there were no interactive effects between mesomammal presence and fruit type ( $\chi^2 = 0.70$ ,  $df = 2$ ,  $p = 0.71$ ).

Although frugivory rates were similar between sites where mesomammals were and were not detected, we observed differences in the frugivore communities. We observed 402 frugivory bouts conducted by 5 species at sites where mesomammals were not detected during passive sampling and 355 bouts by 7 species where mesomammals were detected (Fig. 4b, Table 2). A PERMANOVA revealed these differences to be significantly different ( $F = 3.18$ ,  $df = 1$ ,  $p = 0.02$ ). Raccoons were the most common fruit consumers at sites where mesomammals were detected during passive sampling, accounting for 25.4% of the frugivory bouts. Lubber grasshoppers (*Romalea guttata*) were responsible for the majority of frugivory bouts at sites where mesomammals were not detected, accounting for 50.0% of the frugivory bouts (Table 2).

## Discussion

A diverse community of animals contributed to the functional redundancy of scavenging and frugivory services, compensating for the reduction of mesomammals across the GEE. Despite notable shifts in community composition, we did not find any significant decreases in scavenging and frugivory rates. Compensation by remaining



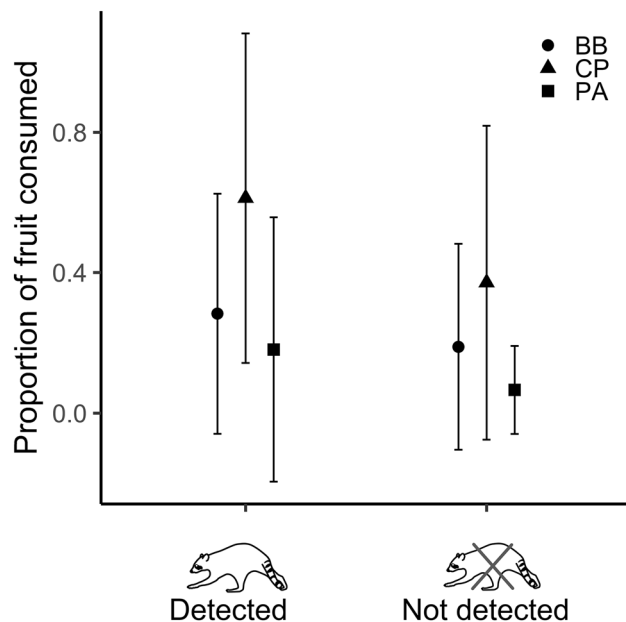
**Figure 4.** Number of (a) scavenging and (b) frugivory bouts by group in sites where mesomammals were detected versus not detected in passive surveys conducted at 15 sites in the Everglades (Florida, USA). A single scavenging bout by a bear was also recorded at a site where mesomammals were not detected but is not represented in the figure.

Mesomammals Not Detected		Mesomammals Detected	
Species	Number of bouts	Species	Number of bouts
Lubber grasshopper ( <i>Romalea microptera</i> )	201	Raccoon ( <i>Procyon lotor</i> )	90
Cotton rat ( <i>Sigmodon hispidus</i> )	130	Cotton mouse ( <i>Peromyscus gossypinus</i> )	79
Rice rat ( <i>Oryzomys palustris</i> )	57	Opossum ( <i>Didelphis virginiana</i> )	73
Brown basilisk ( <i>Basiliscus vittatus</i> )*	10	Black rat ( <i>Rattus rattus</i> )*	62
Turkey vulture ( <i>Cathartes aura</i> )	4	Rice rat ( <i>Oryzomys palustris</i> )	33
		Lubber Grasshopper ( <i>Romalea microptera</i> )	14
		Cotton rat ( <i>Sigmodon hispidus</i> )	3
		Turkey vulture ( <i>Cathartes aura</i> )	1
<b>Total Frugivory Bouts</b>	<b>402</b>	<b>Total Frugivory Bouts</b>	<b>355</b>

**Table 2.** Species observed consuming fruit during frugivory experiments conducted at 15 sites within the Greater Everglades Ecosystem (Florida, USA) along a gradient of python activity. Sites were categorized based on whether mesomammals (e.g., raccoons, opossums, foxes, etc.) were detected in camera and scat surveys in 2019 passive sampling. Mesomammals were detected at all locations in 2014. \*Invasive species.

species in the GEE provided a degree of redundancy that has buffered these ecosystem services against some of the impacts associated with the establishment of Burmese pythons. This finding illustrates how functional redundancy can contribute to ecosystem resilience following disturbance, lending additional support to similar patterns shown in other systems<sup>21</sup>. However, because scavengers and frugivores vary in many aspects of their biology, compositional changes to scavenger and frugivore communities may still impact the ecosystem, even if scavenging and frugivory rates remain stable. As such, additional research into related processes, such as seed dispersal, plant germination rates, and disease dynamics, is warranted.

For both ecosystem functions, smaller organisms (i.e., rats, insects) compensated to maintain scavenging and frugivory rates where mesomammals were rare or absent. This pattern highlights a broader global trend in trophic downgrading, where larger species are chronically removed from ecosystems<sup>31</sup>. With larger species removed,



**Figure 5.** Proportion of each fruit type, beautyberry (BB), cocoplum (CP), and pond apple (PA) consumed during frugivory experiments. Error bars indicate standard deviation.

relatively smaller species may only compensate for some of the functions performed by larger species<sup>32</sup>. Consequently, trophic downgrading can indirectly influence diverse ecological processes ranging from an ecosystem's susceptibility to fire or its potential for carbon sequestration<sup>31</sup>. In terms of scavenging specifically, carcass size greatly influences scavenging efficiency and scavenger community composition<sup>33</sup>. Although small scavengers (e.g., rodents, snakes), were able to efficiently remove rat carcasses deployed in this study, it is unlikely that they would be able to efficiently consume large carcasses<sup>34</sup>. Increased persistence of these larger carcasses could result in excess localized nutrient flows to soils, increased risk of pathogen spread, or reduced water quality<sup>35,36</sup>.

Our observation that mesomammal absence did not impact scavenging efficiency of small carcasses aligns with prior research showing little change in scavenging rates despite the experimental exclusion of mesomammals<sup>37</sup>. As with our study, other taxa were able to compensate for the absence of mesomammal scavenging guilds<sup>37</sup>. However, in anthropogenically-impacted systems, the loss of mesomammals and other key scavengers, resulted in reduced scavenging efficiency. Several studies reporting declines in scavenging rates were conducted in disturbed landscapes, such as urbanized areas<sup>38</sup> and agricultural lands<sup>39,40</sup>, where the potential for functional redundancy may already have been limited. Although the GEE has faced a history of degradation<sup>41</sup>, it includes over 1.2 million ha of protected land and has also been the subject of extensive restoration with > \$8 billion in investment<sup>42</sup>. Therefore, our study system, like other protected areas, may have a greater capacity for redundancy than areas that have already faced significant biodiversity loss<sup>43,44</sup>. As development continues to impact natural areas, important ecosystem functions such as scavenging may lack the resilience needed to withstand further biodiversity loss<sup>45,46</sup>. High connectivity between protected areas may slow the loss of ecosystem function by facilitating the movement of species between sites<sup>47</sup>, creating opportunities for functionally redundant species to recolonize sites following declines. However, habitat connectivity could also facilitate the spread of introduced species<sup>48</sup>, such as the Burmese python, complicating efforts to slow the spread of this apex predator.

We found the process of fruit removal was also robust to changes to the frugivore community<sup>20,49</sup>. However, plant-frugivore relationships are complex. Consequently, studies that have focused on patterns of seed dispersal and predation, rather than fruit/seed removal, have observed less resilience following frugivore community changes<sup>50,51</sup>. Frugivore traits affect many aspects of seed germination and dispersal<sup>52,53</sup>. For example, the impact of gut passage on seed germination rates of a particular plant varies depending on the species consuming it<sup>54,55</sup>. Additional research is required to understand how different frugivores impact seed germination rates of plants in the GEE. In general, large-bodied frugivores have longer retention times and larger home ranges than smaller species, increasing their effectiveness as dispersers<sup>56</sup>. Losses of large-bodied frugivores therefore can reduce diversity and alter evolutionary trajectories of plant species, ultimately decreasing forest resilience<sup>57,58</sup>. Because we observed a shift to smaller species consuming fruits, dispersal services may be disrupted in areas where mesomammals were lost.

Despite little change in scavenging and frugivory metrics, the shifts in species responsible may affect secondary ecosystem processes that were outside the direct focus of our study. For example, we recorded a high number of scavenging bouts conducted by rodents at sites where mesomammals were absent. This finding is consistent with recent research suggesting that the functional role of rodents as scavengers may be understated<sup>34</sup>. If rodents experience increased access to high-protein food resources when potential predators/competitors are reduced, such provisioning may increase rodent populations<sup>59</sup> or aggregate individuals around carcasses, thereby increasing opportunities for pathogen transmission<sup>60</sup>. Because rodents are carriers/reservoirs for many pathogens, a shift

to rodent-dominated scavenging communities could potentially increase pathogen transmission and ultimately pose a threat to human health<sup>36,61</sup>. Already, changing mammal community composition in the GEE has been linked to increased disease risk for humans<sup>29</sup>. Similarly, insects were responsible for the majority of frugivory bouts in sites where mesomammals were absent. However, insects remove fruit pulp but do not usually disperse seeds<sup>62</sup>. Reductions in seed dispersal can disrupt gene-flow within plant communities, decrease plant diversity, and slow regeneration<sup>63,64</sup>.

In addition to quantifying scavenging and frugivory rates, our study adds additional evidence that mesomammals are declining in this region<sup>22,25</sup>. Baiting camera traps generally improves detection probability<sup>65–67</sup>. However, we consistently failed to document mesomammals during passive sampling<sup>25</sup> or over the course of scavenging and frugivory experiments, providing compelling evidence that mesomammals were absent or rare at these locations. We do not believe that additional trap nights would have yielded detections of mesomammals at sites in the areas where we consistently failed to detect them. However, additional replication of these experiments at different times of year might elucidate seasonal patterns in the efficiency of fruit/carrion removal and could potentially identify differences in the community composition of compensating taxa. For example, insects and reptiles might be less able to contribute to these functions in winter months. Finally, replication of such experiments over time could identify subsequent changes in community composition that may unfold as a result of pythons or other environmental impacts, particularly as pythons continue their range expansion<sup>25,68</sup>.

Despite widespread mammalian declines following the introduction of Burmese pythons<sup>22–24</sup>, scavenging and frugivory rates were maintained, indicating the potential for resilience in communities with reduced mesomammal populations. Importantly, pythons established in the GEE relatively recently (i.e., in the last three to four decades)<sup>23,69</sup>. As such, the consequences of this introduction are still unfolding<sup>25</sup>. Taxa such as rodents initially appeared resistant to python-associated declines<sup>70,71</sup>. However, some native rodents may be declining in regions where pythons have been established the longest<sup>25</sup>. Additional declines in this region have the potential to erode previously robust functions, decreasing the resilience of the system as a whole. The ongoing vulnerability of compensating taxa to pythons and other threats highlights an important caveat to the concept of functional redundancy. Functional redundancy has been described as “insurance against the loss of function,” and this insurance policy weakens as each species declines<sup>72</sup>. Therefore, continued monitoring of the GEE and its evolving ecosystem dynamics is essential to better understand and address the complex challenges posed by introduced species and their impacts on biodiversity. As pythons continue to expand their range and impact additional taxa<sup>68</sup>, the development of proactive management efforts may support preservation of key functions.

## Methods

### Study area

The GEE is a subtropical wetland located in southern Florida, USA. Extending from Lake Okeechobee to the tip of peninsular Florida, the GEE supports many vertebrates, including at least 35 species of terrestrial mammals<sup>73</sup>. This ecosystem faces numerous threats, including urban development, altered hydrology, and agricultural contamination<sup>41</sup>. In the early 2000s, the effects of Burmese pythons became a concern following their establishment in Everglades National Park (located in the southernmost portion of the GEE) and subsequent northward expansion<sup>25,69</sup>. Native to Southeast Asia, these large constrictors have been consistently implicated in mammal declines<sup>22–24</sup>. Although pythons are impacting many species, mesomammals appear especially vulnerable<sup>70</sup>.

### Site selection and categorization

To assess whether mesomammal declines have altered ecosystem processes, we investigated scavenging and frugivory rates in areas that varied in their diversity of mammals. We established clusters of experimental scavenging and frugivory stations at 15 sites on public lands, covering a latitudinal gradient of known mammal diversity, with diversity increasing south to north (Fig. 1)<sup>25</sup>. For this study, we used a random subset of established mammal sampling locations that covered the same gradient of mammal diversity while also facilitating access<sup>25,28,30</sup>. The original sites were established in vegetation communities that were most likely to support high mammal diversity (e.g., hardwood hammocks and tree islands). All our experimental sites recorded mesomammals in 2014 but varied in mesomammal detection in 2019<sup>25,28,30</sup>. Prior to the initiation of our scavenging and frugivory experiments, we assessed mammal community composition using a combination of scat surveys and motion-activated camera traps (See Taillie et al.<sup>25</sup> for details; Appendix S1). We deployed two motion-triggered cameras for 7 nights, resulting in 14 trap nights/site. We reviewed all scat records and photos to categorize sites as either “mesomammal detected” if we documented at least one mesomammal species—including opossums, raccoons, foxes, skunks, bobcats, rabbits, minks (*Mustela vison*) and/or otters (*Lontra canadensis*) or “mesomammal not detected” if we failed to detect at least one mesomammal species during the passive sampling period (Fig. 1).

### Sampling design

After passive sampling had concluded at each site, we conducted scavenging and frugivory experiments to quantify how mesomammal presence affected frugivory and scavenging rates. To assess these processes, we monitored the persistence of carrion and fruit using motion triggered cameras. We deployed three scavenging and three frugivory stations at each of the 15 sites between May 6 and October 31, 2019 (see Appendix S1 for sampling dates by site) and placed stations  $\geq 100$  m apart to minimize spatial dependence<sup>74</sup>. We placed a Spartan SR2 Trail Camera with a 40-cm focal distance at each station (Spartan Camera, Duluth, GA) and set the camera to record 3 pictures followed by a 60-s delay between bursts. We reviewed photos to identify species and determine if they consumed carrion/fruit. Although there were additional photos of animals at stations (e.g., walking through frame), we limited our analysis to photos that documented animals consuming carrion/fruit. We filtered photos so that each record represented a one-minute scavenging or frugivory bout. Using the photos collected at stations,

we also investigated the composition of animal communities responsible for scavenging and frugivory. Research was approved by and conducted in accordance with the University of Florida's Institutional Animal Care and Use policies (permit #202,111,381). Although Animal Research: Reporting of In Vivo (ARRIVE) guidelines were developed for laboratory and formal test settings<sup>75</sup>, we attempted to adhere to these guidelines to the extent possible. Fruit collection on federal lands was permitted by the Department of the Interior (OMB #1024-0236). The collection and use of plants adhered to all pertinent guidelines.

### Scavenging experiments and analysis

To quantify scavenging rates, we secured carrion to a 40 × 40 cm board at each station (Fig. 2a). Because rodent carcasses are commonly used to assess scavenging rates of mid-sized vertebrates<sup>9</sup>, we used two lab-grade rat carcasses (*Rattus norvegicus domestica*) as bait.

Rat carcasses were sourced from Layne Laboratories (Arroyo Grande, CA), a USDA-accredited facility recognized for providing high-quality carcasses to meet the dietary needs of captive wildlife. Layne Laboratories follows humane handling practices and uses a carbon dioxide chamber for euthanasia, adhering to the recommendations of the American Veterinary Medical Association.

To monitor scavenger activity, we mounted the camera onto a post 1 m away from the carcasses. We deployed cameras for 7 nights, after which point the carcasses became too decomposed to accurately monitor with photographs. Consistent with previous investigations of scavenging efficiency<sup>76,77</sup>, we recorded detection time (the elapsed time between deployment and the first scavenger's arrival) and consumption time (the elapsed time between deployment and the complete consumption of the carcass). In cases where we never observed the arrival of the scavenger or full consumption of the carcass, we recorded the endpoint as the completion of the study and marked the record as censored. Censored observations—i.e., observations where the event of interest is not observed—still contain important information such as the minimum time during which the event did not occur. Analytical techniques that can incorporate both censored and observed data points have long been used in industry and medicine, but are increasingly applied to ecological questions<sup>78</sup>.

To evaluate differences in these 2 scavenging metrics, we used Cox proportional hazards regression models<sup>79,80</sup>. This approach is well-suited for analyzing time-to-event data in scenarios with censored observations<sup>78</sup>. To account for multiple stations at the same site, we included site as a cluster variable in our model using the “survival” package<sup>81</sup> in R. From these models, we deemed variables to be significant if the p-value associated with their Wald statistic was less than 0.05. We also reported median survival for each analysis with 95% confidence intervals of these estimates. In many cases, upper limits of confidence intervals are NA (infinity) in survival analysis due to the right skew of the data<sup>82</sup>. For each regression, we tested the assumption of proportional hazards by creating plots of Schoenfeld residuals and testing model fit with *cox.zph* function in the “survival” package (Appendix S2)<sup>81</sup>.

### Frugivory experiments and analysis

Because frugivores may select fruits of a given size<sup>83</sup>, we collected fruits from 3 native plant species for our experiments: American beautyberry (3–9 mm diameter), cocoplum (20–50 mm diameter), and pond apple (50–150 mm diameter). We placed fruits on four 11.5 × 11.5 cm plastic trays that were secured to a 40 × 40 cm board (Fig. 2b). Trays contained 50 cocoplums, one whole pond apple, and one 10 × 10 cm partition uniformly filled with a single layer of beautyberry. We concluded the experiment after 5 nights to avoid decomposition and ensure fruit remained palatable throughout the experiment.

To quantify frugivory rates, we used 2 metrics. The first metric, visiting latency (the time elapsed between the fruit availability and first feeding event<sup>84</sup>), is an important aspect of frugivory, because microbes colonize fruits over time, sometimes making them unpalatable to potential dispersers<sup>85</sup>. For visiting latency, we calculated the number of hours that elapsed between the placement of fruit and the arrival of the first frugivore. The second metric, relative removal (the proportion of fruits removed), is an important aspect of plant reproductive success and a common metric of efficiency in plant–frugivore systems<sup>86</sup>. We estimated relative removal using photo data from the end of each trap-night to visually estimate the proportion of beautyberry or pond apple consumed and to count the number of cocoplums removed. At the end of the five-day deployment, we summed the amount of fruit consumed during the experiment as an estimate of fruit removal for each station.

As with the scavenging metrics, we analyzed visiting latency using Cox proportional hazards regression—see scavenging section for details. For relative removal, we used linear mixed models. Using relative removal as the response variable and mesomammal detection/non-detection as independent fixed variables, we fit models assuming a Gaussian distribution using packages “lme4”<sup>87</sup> and “car”<sup>88</sup>. We included site as a random effect to account for multiple replicates at each location. We considered models that included fruit type as an additive or interactive effect with mesomammal detection to determine if fruit type affected this metric. We conducted Tukey pairwise comparisons using package “emmeans” to assess differences between fruit types<sup>89</sup>. We tested the assumption of normally distributed residuals with the Shapiro–Wilk normality test. Although we did not find significant deviations from normality, we conducted additional analyses, such as beta regression and linear regression with arcsin transformation of observations, to ensure our findings did not differ between approaches (Appendix S3). Because our findings were consistent across all regressions, we report only the analysis with the original untransformed data.

### Scavenger and frugivore community composition analysis

To understand broad changes in scavenger and frugivore communities, we aggregated species into taxonomic groups—large carnivores, birds, insects, mesomammals, reptiles, and rodents—at the site level. To determine if there were shifts in the composition of communities that scavenged and consumed fruit on sites with and



without the detection of mesomammals, we used multivariate methods commonly used to understand ecological communities<sup>90</sup>. Using the number of scavenging or frugivory bouts for each group, we first log-transformed the data and then calculated a dissimilarity matrix using a Ruzicka (quantitative Jaccard) distance metric<sup>91,92</sup>. We then conducted permutational multivariate analysis of variance (PERMANOVA) with 99,999 permutations on the calculated distances to determine if there was a significant difference in scavenging and frugivore communities where mesomammals were detected/not detected during the passive survey<sup>93</sup>. We used the “vegan” package<sup>92</sup> for these calculations.

## Data availability

Scavenging and frugivory efficiency data is available as part of this data release: <https://doi.org/10.5066/P98RTNTU94>.

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## Author contributions

RAM, PT, and KH conceived of the research idea and secured funding. CL, AS, and PT developed field methodology and collected data. RKM and RAM analyzed the data. RKM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-66534-8>.

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