ABSTRACT

FLY ON THE WALL: COMPARING ARTHROPOD COMMUNITIES BETWEEN ISLANDS WITH AND WITHOUT HOUSE MICE (*MUS MUSCULUS*)

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Northern Illinois University, 2021
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Invertebrates are key to island ecosystems, but impacts from invasive mammalian predators are not well documented or understood. Given this knowledge gap, we studied terrestrial arthropod communities in the presence of a common invasive rodent (house mice, *Mus musculus*) on a subtropical atoll—Midway Atoll National Wildlife Refuge (MANWR). Here, invasive mice recently began to attack and depredate nesting seabirds, prompting a mouse eradication. Although eradication planning efforts are underway, uncertainty remains regarding the ecosystem's response to mouse removal. As part of a pre-eradication investigation, we conducted a baseline survey of MANWR's arthropod community structure and diversity, comparing islands with and without mice. From April 2018 to February 2020, we used pitfall traps to monitor ground-dwelling arthropods on MANWR's Sand Island (mice present) and Eastern Island (mice absent). During our study, we captured over 450,000 specimens from 24 taxonomic units. Arthropods on MANWR form six community clusters and differ between islands and habitats. Richness is relatively similar among clusters and islands, but diversity of common and dominant taxa is significantly higher on Sand Island, as well as in

anthropogenically built habitats. Arthropod communities and diversity vary marginally throughout the year; temperature and rainfall are minor environmental drivers. Additionally, anthropomorphic landscape-level alteration of MANWR may still influence arthropod communities today. Continued monitoring and research will provide better insight into how arthropod communities recover following invasive mouse eradications. Our study contributes to the body of knowledge of arthropods in the Northwestern Hawaiian Islands, arthropod community ecology, and potential mouse impacts on islands.

NORTHERN ILLINOIS UNIVERSITY
DEKALB, ILLINOIS

MAY 2021

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BY

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A THESIS SUBMITTED TO THE GRADUATE SCHOOL

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE

MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

Thesis Director:
Holly P. Jones

ACKNOWLEDGEMENTS

I would like to thank the U.S. Fish and Wildlife Service and Island Conservation for allowing me to collaborate on innovative research to better understand the impacts of invasive house mice on Midway Atoll National Wildlife Refuge. I would also like to acknowledge the organizations that funded my graduate research: the National Science Foundation, AmeriCorps, Sigma Xi, the Elwood and Ruth Briles Memorial Fund, and the Northern Illinois University Graduate School. This project could not have been completed without the dedication of many Northern Illinois University undergraduate students who assisted in lab work; I am very grateful to Nikolas Ballut, Kristin Chapman, Paige DuBois, Gian Feniza, Brittany Guzy, Christopher Holliday, Megan Harris, Austin Lahman, Sarah Naughton, Matthew Nordin, Erick Pacheco Grande, Juliana Peschke, Michaela Plagwitz, Dana Romaniak, and Kaylee Rosenberger for identifying and counting pitfall trap contents. I would also like to thank Marti J. Anderson and Christy N. Wails for providing feedback and advice on statistical analyses. I am grateful to Sheldon Plentovich, Daniel Simberloff, and Forest and Kim Starr for their feedback and comments, which greatly benefitted this thesis. I would like to thank my committee members, Richard B. King and Wesley D. Swingley, for their assistance and advice in developing specific parts of this project. I am deeply grateful to my family and my fiancé, Matthew Nissenbaum, for their patience, optimism, and support throughout this entire process. Finally, I would like to make a very special thank you to my advisor and thesis committee chair, Dr. Holly Jones, for guiding and joining me in this wild adventure of research and helping me become the scientist I never thought I could be.

Arthropod specimens for this project were collected under permit #PMNM-2019-005 by the U.S. Fish and Wildlife Service and Island Conservation. Material in this thesis is based upon work supported by the National Science Foundation Graduate Research Fellowship Program, Grant No. DG#-1842161. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and does not necessarily reflect the views of the National Science Foundation, U.S. Fish and Wildlife Service, or Island Conservation.

DEDICATION

This thesis, and all the hard work, dedication, and passion involved, are dedicated to my family, my fiancé Matthew Nissenbaum, and my Midway *ohana*. I also dedicate this thesis to my great uncle, Kees (C.) Swennen, who shared a deep desire for seabirds and their conservation.

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CHAPTER 1

INTRODUCTION

Islands have long been celebrated and studied as biodiversity hotspots as well as exceptional areas of endemism (Kueffer et al. 2014). Unfortunately—and most challenging in terms of conservation—61% of recent extinctions were island species (Jones et al. 2016). Seabirds comprise a quarter of those extinctions and are considered the most endangered marine group (Spatz et al. 2014, 2017; Doherty et al. 2016). Specifically adapted to a life at sea and typically breeding on remote, isolated islands, seabirds are particularly vulnerable to introduced mammalian predators because they lack appropriate anti-predator behavior and response (Blackburn et al. 2004; Gaston 2004; Duncan and Blackburn 2007; Howald et al. 2007; Phillips et al. 2016). Invasive rodents are likely responsible for the greatest number of island bird extinctions as well as disrupted ecosystem functions (Atkinson 1996; Towns et al. 2006; Howald et al. 2007).

Rats are usually the focus of island restoration and conservation interventions, yet house mice also have ecosystem-altering ramifications (Crafford 1990; Fukami et al. 2006; Wanless et al. 2007; Angel et al. 2009). Initially thought to pose minimal risk to seabirds, mice recently entered the spotlight of island conservation when they were discovered depredating seabirds (adults and chicks alike), in some cases leading to a significant decline in species' breeding success (Cuthbert and Hilton 2004; Wanless et al. 2007, 2009, 2012; Jones and Ryan 2009;

Duhr-Schultz et al. 2018; Jones et al. 2019). Starting in 2015, house mice (*Mus musculus*) were discovered to depredate breeding albatross on Midway Atoll National Wildlife Refuge (MANWR, Pihemanu and Kuaihelani in Hawaiian), a subtropical atoll in the north Pacific Ocean (Duhr-Schultz et al. 2016). MANWR is the largest nesting colony of Laysan and Black-footed Albatross (*Phoebastria immutabilis* and *P. nigripes*, mōlī and ka'upu in Hawaiian) in the world, providing breeding grounds for 73% and 36% of these albatross species' global populations, respectively (Duhr-Schultz et al. 2018; USFWS 2019).

Invasive house mice and black rats (*Rattus rattus*) were inadvertently introduced on MANWR around 1943 (Hadden 1941; Seto and Conant 1996). Black rats were successfully eradicated from MANWR in 1996, leaving mice as the only invasive mammalian rodent in the Northwestern Hawaiian Islands (NWHI; Seto and Conant 1996; PMNM 2008; Duhr-Schultz et al. 2018; USFWS 2019). Mouse predation of albatross on Sand Island was first observed in 2015 (Duhr-Schultz et al. 2016). In the following winter, the extent, number, and severity of attacks and depredations increased. Mouse aggression incidents have been severe enough to prompt USFWS to plan a mouse eradication for the summer of 2022.

Predation of seabirds and other at-risk wildlife is a direct and alarming impact of mice—but there is more than meets the eye with these widespread rodents. Mice directly and indirectly affect insular ecosystems via consumption of seeds, plants, and invertebrates, both above and below ground (Jones et al. 2003; St Clair 2011; Wanless et al. 2012; McClelland 2013; Dilley et al. 2015; Rogers et al. 2017; Cuthbert et al. 2018). As opportunistic omnivores, mice can significantly change island species distributions, densities, and persistence, which in turn alters or disrupts nutrient cycles, symbioses between species, and other major ecosystem processes

(Fukami et al. 2006; Angel et al. 2009; Phiri et al. 2009; Mulder et al. 2011). In particular, mice can substantially affect insular invertebrate communities, both directly through predation and indirectly via interactions with invertebrate competitors, predators, prey, hosts, or other ecosystem engineers associated with regulating invertebrate abundance (St Clair 2011). Because insular invertebrates play key roles in ecosystem functions and structure as detritivores, primary consumers, predators, prey, competitors, mutualists, pollinators and disease vectors, shifts in invertebrate community composition, diversity, and/or abundance have repercussions for various ecosystem components (Towns et al. 2009; St Clair 2011; Thoresen et al. 2017). Moreover, when mice are the sole (introduced) predatory mammal on island ecosystems, they may exhibit "rat-like" behaviors and the magnitude of their ecological impacts may be amplified (Angel et al. 2009; Nathan et al. 2015; MacKay et al. 2019). Without taking these impacts into consideration—through understanding both diet of mice and broader ecological effects—the continued presence of mice on islands can hamper or possibly prevent the success of attempted restoration or conservation efforts (Zavaleta et al. 2001; Rauzon 2007; Chown et al. 2008; Smith 2008).

Like MANWR's house mice, terrestrial arthropods and invertebrates of this unique atoll system are not well understood and their broader impacts on ecosystem functions are mostly a mystery due to their cryptic nature. Yet many island ecosystems (as well as the dynamics and regulations of ecosystems functions) are dominated by arthropods (Copson 1986; Crafford and Scholtz 1987; Smith and Steenkamp 1990, 1992; Chown and Smith 1993; Huyser et al. 2000; Le Roux et al. 2002; Smith et al. 2002; Jones et al. 2003; Chown et al. 2008). Arthropods are also key to ecosystem structure and function via their roles in pollination, decomposition, nutrient cycling and mineralization, and more (St Clair 2011). While most attention on invasive island mammals has focused on their impacts on other vertebrates, very few studies have examined and quantified impacts on arthropods and other invertebrates and the larger implications for the ecosystems impacted.

On oceanic islands (mainly Southern Ocean Islands), food webs are commonly detritus-based and largely regulated (or dominated) by decomposer arthropod species (Le Roux et al. 2002; Chown et al. 2008). Arthropods play a pivotal transition role between nutrient deposition (via guano from seabirds; e.g., Mulder et al. 2011) and consequent use for primary production by vegetation (Smith and Steenkamp 1992). In nutrient-limited systems—which are especially common in Southern Ocean Islands due to harsh environmental conditions that reduce the rates of natural decomposition and mineralization—several studies point to arthropods being the key mediator in maintaining nutrient requirements by mineralization of nutrients present in detritus and organic matter (e.g., Smith and Steenkamp 1993). In fact, it is posited that decomposition (via fragmentation and digestion by detritivores as well as microbial decomposition) is the focal "bottleneck" in nutrient recycling on islands (Crafford and Scholtz 1987; Rowe-Rowe et al. 1989; Crafford 1990; Smith and Steenkamp 1992). Terrestrial arthropods and invertebrates are known to be vulnerable to rodent predation (St Clair 2011). Given that endemic entomofauna communities are usually depauperate (e.g., Chown et al. 2008; PMNM 2008) and little redundancy exists within functional groups, the risk for changes or loss of ecosystem functions (such as pollination or decomposition) is greatly increased with the presence of rodents on islands. Consequently, any disturbance or suppression to arthropods via predation pressure and indirect effects by rodents can have greater consequences on island species distributions, densities, and persistence as well as major ecosystem processes.

Invasive species can influence native fauna through cryptic and indirect channels (McClelland 2013). For example, increasing populations of invasive rodents on islands can lead to increased predation on arthropods, causing declines in nutrient cycling rates and—by extension—lower primary production (Smith and Steenkamp 1990). Consequently, changes in island arthropod communities can lead to widespread changes in vegetation community composition, structure, abundance and succession (Gleeson and Van Rensburg 1982; Crafford 1990; Smith and Steenkamp 1990). Changes in vegetation structure and populations can also have complex feedback loops for arthropod communities, in that plants provide habitat (Phiri et al. 2009; St Clair 2011). For example, Phiri et al. (2009) detailed the use and destruction of the cushion plant (*Azorella selago*) by house mice on Marion Island as nesting habitat; structural damage to this plant species is also detrimental to the many arthropod species that rely on this plant for habitat and cover.

MANWR's arthropod community is little studied, in comparison to other island systems, and collections from that atoll are rare. Since the earliest documented record of insect collecting on MANWR back in 1890, only three studies have systematically surveyed the terrestrial arthropods of MANWR, namely Bryan (1926), Suehiro (1960), and Nishida and Beardsley (2002). Among the Northwestern Hawaiian Islands, native terrestrial arthropods and land snail communities are the least well studied among all taxa, but they are also thought to be the most heavily impacted by human activities and invasive species introductions (PMNM 2008). Given the lack of native or endemic species on MANWR as well as its highly altered landscape and high degree of exotic species, the impact of invasive house mice in MANWR on endemic arthropods may not necessarily be a detectable or biologically significant effect. However, relationships between house mouse and pollinator arthropod species for native plant species (in light of notoriously low plant recruitment and difficulties in propagating native species) or suppression of potential biosecurity hazards (like the Emerald Beetle, *Protaetia pryeri*) may change drastically post-eradication. It could also be that certain arthropod and invertebrate species constitute important diet components of other terrestrial species (e.g., St Clair et al. 2011), notably endangered Laysan Ducks, and that mice are directly competing for resources with native wildlife. Thus, examining the relationships between mouse impact on arthropod communities may help to predict post-eradication phenomena, such as trophic cascades within terrestrial arthropod and invertebrate communities (and related implications), and inform best management practices (St Clair 2011).

"Knock-on" or cascading effects of terrestrial arthropod and invertebrate suppression (via rodents) can impact other ecosystem processes and properties, including demography of island species, symbioses between species, soil processes, and nutrient cycling, and also decrease resilience of a system as a whole in light of additional invasion events (Huyser et al. 2000; Zavaleta et al. 2001; St Clair 2011). Invasive rodents—such as mice—on islands are able to catalyze trophic cascades (Wardle et al. 2004; McClelland 2013). Even through the predation of intermediate organisms, such as arthropods, invasive rodents can still indirectly affect the abundance and composition of the vegetation communities (Wardle et al. 2004; Phiri et al. 2009; McClelland et al. 2018). Because terrestrial arthropods and invertebrates are thought to be primary drivers of nutrient cycling and energy flow on islands, any changes to arthropod communities can have broader impacts on nutrient limitation in island ecosystems (McClelland 2013). Indeed, as found by Fukami et al. (2006), the below-ground component of island ecosystems is functionally important to ecosystem processes and also links strongly to above-ground components via diverse ecological interactions. Thus, the relationships between nutrient cycling and ecosystem function are complex and can even be affected indirectly.

In the case of MANWR, arthropods may serve as primary drivers in nutrient cycling and energy flow in the atoll's islands, as is the case with terrestrial arthropods and invertebrates of the Southern Ocean Islands (e.g., Smith et al. 2002). In light of the need for better informed and effective conservation interventions such as invasive island mammal eradications, a greater understanding is needed of the functional roles (and their magnitude) of island arthropod communities and the indirect consequences of rodent invasion and eradication (ranging from impacts on individual species to ecosystem functions (St Clair et al. 2011). With the pending eradication of house mice on MANWR, it is also important to predict "surprise effects" following this conservation intervention in that there could be unexpected population irruptions of previously suppressed species, which may cause negative consequences and setbacks for ongoing restoration and recovery efforts on native island flora and fauna (Zavaleta et al. 2001; Watari et al. 2011).

In Chapter 2, I begin by comparing arthropod community structure and diversity between MANWR's two main islands in order to obtain baseline knowledge of arthropod communities both exposed to and isolated from mice. Specifically, I describe patterns in arthropod community composition and diversity among habitats and islands as well as trends along temporal scales and environmental gradients. In Chapter 3, I conclude by broadly discussing my findings in the context of invasive house mouse effects on MANWR as well as the implications of ecosystem recovery post-eradication. Furthermore, I detail the ongoing research efforts to understand mouse effects on the MANWR ecosystem via diet analyses, which will be completed through the complementary use of eDNA metabarcoding of mouse fecal samples and stable isotope analysis of mouse hair samples.

CHAPTER 2

FLY ON THE WALL: COMPARING ARTHROPOD COMMUNITIES BETWEEN ISLANDS WITH AND WITHOUT HOUSE MICE (*MUS MUSCULUS*)

Introduction

Many island ecosystems, communities, interactions, and functions are dominated by invertebrates (Chown et al. 2008; Smith 2008; Houghton et al. 2019). As linchpins in island food webs, invertebrates participate in nearly every trophic level and ecological function, ranging from generalist foragers (Formicidae; Hölldobler and Wilson 1990) to keystone detritivores (*Pringleophaga* spp.; Crafford and Scholtz 1987). Island invertebrates contribute substantially to insular biodiversity and are central to ecosystem structure and function via their roles in pollination, decomposition, nutrient cycling and mineralization, primary productivity, and more (Burger 1978; Smith and Steenkamp 1993; Cardoso et al. 2020). In particular, island food webs are commonly detritus based and largely regulated (or dominated) by invertebrate detritivores (Le Roux et al. 2002; Lawrence and Samways 2003). Consequently, invertebrates play a pivotal transition role between nutrient deposition (via guano and carcasses from seabirds; e.g., Mulder et al. 2011) to use for primary production by vegetation (Smith and Steenkamp 1992).

Despite the ecological importance of island invertebrates, knowledge of invertebrate communities and interactions on islands is deficient (St Clair 2011); this is especially true in regard to ecological restoration, which is heavily biased towards conserving charismatic vertebrates (Clark and May 2002; Holmes et al. 2019). Naturally, depredation of seabirds and other vulnerable island fauna is a direct and alarming impact of invasive mammals (see Courchamp et al. 2003; Doherty et al. 2016). On the other hand, these direct impacts can often be remediated through eradications (Jones 2010). Focusing solely on conserving island vertebrates via invasive mammal eradications, however, neglects understanding the composition and ecological functions of native invertebrate communities. In turn, the absence of pre-eradication data and limited post-eradication monitoring have directly led to knowledge gaps on both the impacts of invasive species on invertebrates as well as invertebrate response following eradication (Towns et al. 2006; Croll et al. 2015).

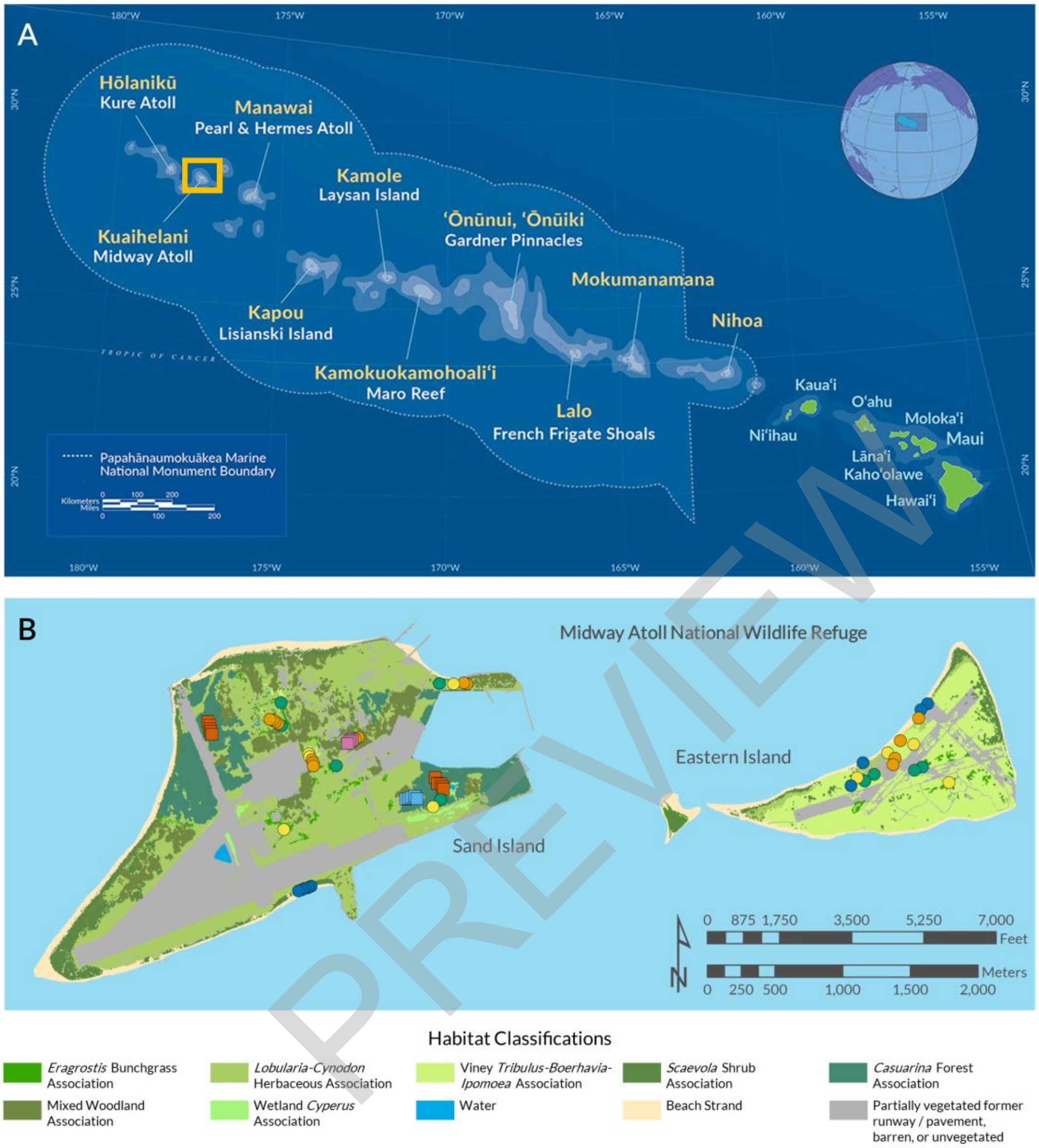
To address this knowledge gap, we present a case study focused on terrestrial arthropod communities in the presence of a common invasive mammal (house mouse, *Mus musculus*) on a subtropical atoll—Midway Atoll National Wildlife Refuge (MANWR). Containing the world's largest albatross colony (USFWS 2019), MANWR is also home to invasive house mice, which were inadvertently introduced to one of the atoll's three islands in 1943 (Fisher and Baldwin 1946). Decades later, in winter of 2015, mice began to attack and depredate hundreds of adult breeding albatross (Duhr-Schultz et al. 2018; Work et al. 2021). Planning is underway to eradicate mice in the near future, but a critical uncertainty remains regarding island ecosystem response to this conservation intervention. MANWR provides an ideal experimental set-up because mice are present on Midway's Sand Island, but not on Eastern Island (the atoll's other main island). The effects of invasive mice on MANWR arthropods have never been studied. Pre-eradication research on mice, arthropods, and other ecological components is ongoing to obtain baseline data (USFWS 2019); anticipated post-eradication research will evaluate how the atoll's fauna and flora respond and recover following mouse removal.

Here, we present the results from our pre-eradication research, providing a snapshot of arthropod communities and diversity on MANWR. Although descriptive, our study gives a comprehensive overview of the ground-dwelling arthropod community structure as well as a comparison of arthropod communities among islands, habitats, and environmental gradients. Since environmental variables can influence arthropod community composition (see Lessard et al. 2011; Allen 2016; Torode et al. 2016; Tao et al. 2019), we also included measurements of temperature, precipitation, distance inland, and edaphic variables (such as soil texture) in our study. Overall, our research provides the baseline data needed for a rigorous BACI (Before-After-Control-Impact) study post-eradication.

Materials and Methods

Study Site

Midway Atoll National Wildlife Refuge (MANWR, also known as Pihemanu, Kuaihelani: 28°11′41″–28°16′50″ N and 177°18′38″–177°25′38″ W) is part of the Northwestern Hawaiian Islands (NWHI), a 2,400-kilometer chain of islands, atolls, coral reefs, and seamounts located in the subtropical north Pacific Ocean (Figure 1A). Remote and isolated, the NWHI collectively constitute one of the oldest and highest latitude coral reef ecosystems (PMNM 2008; Dale et al. 2011) and are protected by one of largest conservation areas in the world—



Pitfall Trap Sampling Points by Habitat Association

Island	*Eragrostis* Bunchgrass	*Lobularia-Cynodon* Herbaceous	Viney *Tribulus-Boerhavia- Ipomoea*	*Scaevola* Shrub	*Casuarina* Forest	Mixed Woodland	Wetland *Cyperus*
Sand Island	5	11	5	5	10	3	5
Eastern Island	4	4	4	4	–	–	–
Total	*9*	*15*	*9*	*9*	*10*	*3*	*5*

Figure 1: Map of the Hawaiian Archipelago in the north Pacific Ocean, including the Papahānaumokuākea Marine National Monument. Midway Atoll National Wildlife Refuge is outlined in yellow (map credit: NOAA). B) Map of Midway Atoll National Wildlife Refuge's islands and habitats, including pitfall trap sampling point locations; habitat classification data generated from WorldView-3 (2015) imagery and 2010 USGS LiDAR and eCognition (map credit: Khem So/USFWS).

—the Papahānaumokuākea Marine National Monument (PMNM; EO No. 13022, Presidential Proclamation No. 8031). MANWR is situated near the northwestern end of the NWHI and consists of an atoll and three coral islands: Sand (457.7 ha; mean elevation 3.2 m), Eastern (136.4 ha; mean elevation 2.6 m), and Spit (5.1 ha; mean elevation 1.5 m) (PMNM 2008; Reynolds et al. 2017; Figure 1B). MANWR features a subtropical climate with relatively even temperatures year-round and pronounced wet/dry seasons (Duhr-Schultz et al. 2018; Appendix A). MANWR's islands are largely covered with salt-tolerant and drought-resistant vegetation, including low-growing forbs, grasses, and vines surrounded by a perimeter of coastal scrub vegetation (Figure 1B). In addition, large parts of MANWR's Sand Island are dominated by introduced tree species, such as *Casuarina* spp. (Figure 1B). Collectively, MANWR has seven distinct habitat associations (hereafter called "habitats"; USFWS 2015; Appendix B). MANWR also has large barren areas owing to widespread landscape modification during wartime efforts, including runways, concrete foundations, asphalt, buildings, piers, and other structures (Figure 1B).

Midway Atoll's location halfway across the Pacific has led to a complex history of landscape modification and disturbance. Claimed as a US territory in 1859, Midway Atoll remained largely unoccupied by human inhabitants until 1903, when the atoll became an integral link in the first trans-Pacific telegraph cable and a cable station was established on Sand Island (Rauzon 2001). In the late 1930s, the atoll became a landing site for Pan Am Clippers crossing the Pacific Ocean and a luxury travel destination (Hadden 1941). During WWII, Midway Atoll was developed into a key US naval and submarine base. In turn, imported military materials and infrastructure heavily altered the atoll's flora, fauna, and geographic extent (Fisher 1949;