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Spatiotemporal Patterns of Mammalian Use of Everglades Tree Islands

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

SPATIOTEMPORAL PATTERNS OF MAMMALIAN USE OF EVERGLADES TREE ISLANDS

A dissertation submitted in partial fulfillment of
the requirements for the degree of
DOCTOR OF PHILOSOPHY
in
EARTH SYSTEMS SCIENCE
by
Marcel Bozas

2024

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Marcel Bozas, and entitled Spatiotemporal Patterns of Mammalian Use of Everglades Tree Islands, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Hong Liu, Committee Member

Jennifer Rehage, Committee Member

Alessandro Catenazzi, Committee Member

Craig van der Heiden, Committee Member

Michael Ross, Major Professor

Date of Defense: April 25, 2024

The dissertation of Marcel Bozas is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Senior Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2024

DEDICATION

I dedicate this dissertation to best friends and mentors Nick and Corky Gonzalez. Even as a young boy I knew I wanted to work with animals and be outdoors, but it was not until I met Nick and his father Corky that I experienced the outdoors much more intimately. It was through the countless hours we spent hunting, fishing, hiking, camping, and simply enjoying nature that my childhood desire grew into a passion to develop a deeper understanding of the natural world. The man I have become and life path I have chosen is in no small part thanks to the relationships we have forged over time, inviting me into your family, and all you have taught me about the outdoors, wildlife, the inseparability of human nature from the rest of the natural world, and how to be the best person you can be. Truly, had I not met you two, I could not imagine where else I may be in my life, and I have come to realize I wouldn’t want to be anywhere else.

I would also like to dedicate this dissertation to my mother, Julie Van Enk. Throughout my life you have been by my side to help, protect, and guide me. That has certainly continued throughout my time in grad school, as you always sought to assist me and alleviate the everyday stressors I was juggling. Without your support, I would not have been able to pursue this goal and complete my dissertation. As I move into my career, make my way through life, and begin a family of my own, I know I will have your everlasting love and support. For that, I cannot thank you enough.

ACKNOWLEDGMENTS

I would like to acknowledge the support and intellectual guidance my committee members have offered me throughout my time here at Florida International University and especially throughout the development of my dissertation. When forming my committee, I wanted to ensure my committee members had distinct research backgrounds so that their unique expertise and perspectives may broaden my understanding and shed light on new thinking about an issue. Certainly, you all excelled in doing so and I am very grateful for all the insights you provided.

I would especially like to thank Dr. Michael Ross and Craig van der Heiden. Your continuous support and the regular discussions we had about plant communities, wildlife behavior, ecological interactions, etc. really helped me build up and refine my ideas. Sincerely, I thank you both for your commitment, dedication, and all the opportunities you have provided to me.

I owe a tremendous thank you to the Miccosukee Tribe of Indians of Florida for supporting me throughout my years of pursuing this PhD. The resources, equipment, trainings, and personnel that the Tribe made accessible to me is what allowed me to develop and complete this research project. I also owe a thank you to the personnel who assisted me with field work and never griped about getting baked by the sun, poked in the eye by branches, stung by caterpillars and wasps, eaten alive by mosquitos, swarmed by bees almost trampled by deer, and chased up trees by alligators: Greg Evans, Daniel Hagood, Tadeo Monterubio, Yunelis Perez, Brandon Davis, Kenton Finkbeiner, Nicholas Gonzalez, Thomas Kelly, Jonathan Pinkas, Nicholas Hurst, Alex Crow, and Dion Bert.

ABSTRACT OF THE DISSERTATION

SPATIOTEMPORAL PATTERNS OF MAMMALIAN USE OF EVERGLADES TREE ISLANDS

by

Marcel Bozas

Florida International University, 2024

Miami, Florida

Professor Michael Ross, Major Professor

Tree islands are spatially discrete ecosystem patches of woody vegetation that developed from natural processes within a matrix of dissimilar vegetation. Tree islands ecosystems are distributed across the globe and occur in a remarkably wide range of environmental conditions, but share a common mechanism of formation and maintenance: tree islands form in stressful landscapes by colonizing microsites where environmental stress is low enough to permit survival of woody species, then positive feedbacks stimulate endogenous growth. Another common thread shared by tree islands, globally, is that most of the regional wildlife is heavily dependent on tree islands for habitat and other resources. Five years of monitoring the mammal metacommunity on tree islands in the Florida Everglades supported this concept and revealed species differentially used tree islands primarily based on hydrologic stress and functional connectivity of the landscape. Marsh amplitude, patch size, and percent area of neighboring tree island patches influenced metacommunity structure and species distributions, but these effects paled in comparison to that of local marsh water depth. Tree islands with low levels of hydrologic stress (i.e., local marsh water depth) supported diverse mammal communities and exhibited higher levels of habitat use. Mammal diversity and habitat use steadily declined as hydrologic stress increased, until the community was predominantly composed of myomorphs and black bear, as these species are particularly well-suited for occupying mesic sites and traversing deeply inundated matrices. Further investigation of black bears' spatial and temporal use of Everglades tree islands indicated that despite bears' ability to cope with mesic or inundated conditions, bears selected for tree islands with shallower marsh depths and cubs were especially sensitive to tree island hydroperiod. Bears also increasingly used tree islands with large patch sizes, as these sites provide more space and resources. The most important resource to bears in the Everglades appeared to be the availability of soft mast forage. Spatiotemporal variation of this resource was strongly related to bear distribution and habitat use. Temporal changes in soft mast availability were also synchronous with changes in bears' biological seasons; thus, these effects could not be fully teased apart.

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CHAPTER I. TREE ISLANDS OF THE WORLD

INTRODUCTION

In the book “Tree Islands of the Everglades” by Sklar et. al, a chapter by Wetzel (2002) described the different tree island ecosystems of the world. Patterns and processes of tree island formation, development, and maintenance were compared to identify geological and ecological commonalities. Wetzel’s work, and the rest of the tree island book, remain unique as there has not been another global review of tree islands, nor such an extensive review of a single tree island ecosystem. The publication of the book catalyzed a wave of tree island research across the world, especially in the Everglades. Many of the uncertainties and unanswered questions Wetzel brought to light, have been addressed by these newer publications (e.g., how hydrology affects tree island development, what are the water depth tolerances of major tree species, how do nutrients accumulate on tree islands, and how do animals use tree islands spatiotemporally). Thus, for the remainder of the first chapter of my dissertation, I have provided an updated review of tree island ecosystems of the world. This review is not intended to rehash the foundational concepts and knowledge discussed by Wetzel (2002) but to expand and advance the body of knowledge from where he left off.

This literature review incorporated a systematic approach to ensure reproducibility, transparency, and minimize bias (Lame, 2019). A systematic approach also helped ensure the literature search was comprehensive and thorough enough to identify nearly all global tree island ecosystems that are available in the literature. To ensure the search effort was comprehensive, the list of search terms was allowed to dynamically expand as the literature search progressed and novel (i.e., previously unsearched) terms were encountered (refer to the Appendix for search criteria, terms, and a list of all identified tree

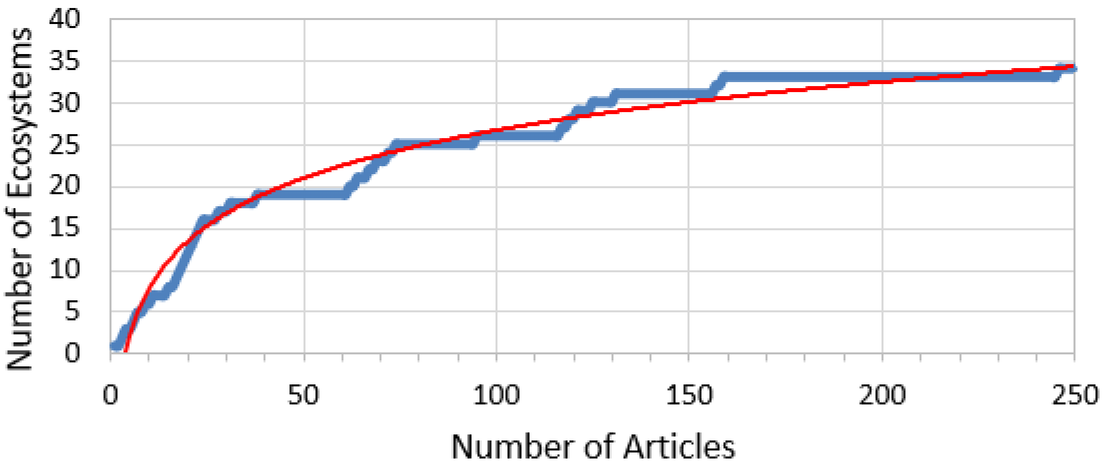

Figure 1. The search effort curve, above, corresponds to search string #2 for non-Everglades tree island ecosystems (refer to Table 3 in the Appendix). The x-axis displays the number of scientific articles that were deemed relevant to the search and reviewed. The y-axis displays the number of "new" (i.e., not yet encountered with the current search string) tree island ecosystems that appeared in the search. The solid blue line depicts the raw number of new ecosystems encountered per unit search effort. The solid red line is the best-fit, logarithmic, trendline.

island systems). To ensure the search effort was thorough, a search effort curve was produced in real-time to track how many ecologically and geographically distinct tree island complexes were encountered as the number of reviewed articles from a particular keyword search increased (for example, Fig. 1).

Ecologists have repeatedly offered nuanced definitions of the term "tree island", most of which were tailored to their study systems and research questions. Proposed definitions include patches of trees in wetland matrix, in matrix of dissimilar vegetation, matrix of herbaceous vegetation, single tree in matrix, two or more trees in matrix, single or cluster of trees as fungal or microbial community hotspots, etc. (Resler & Stine, 2009; Pansing, 2014; Glassman et al., 2017; Christmann et al., 2021; Ross et al., 2021). Wetzel (2002) defined tree islands as "patches of woody vegetation within a freshwater wetland matrix that is dominated by non–woody species". Wetzel's definition was well suited for its context because all the book's compiled literary works focused on the Everglades ecosystem, making other freshwater wetland tree island ecosystems most comparable. However, in the global context, tree island ecosystems commonly occur in matrices of other forest types, savanna, tundra, desert, and montane settings (Schade & Hobbie, 2005; Weiss *et al.*, 2005; Houle *et al.*, 2006; van der Valk & Warner, 2009; Bader *et al.*, 2021; Christmann *et al.*, 2021; and many others). The broad range of matrix habitat types and hydrologic conditions that tree islands naturally occur in warrants the use of a more encompassing definition that does not omit non-wetland tree islands.

Wetzel (2002) also specifies that to be considered a wetland, the matrix' water depth must average ≤ 2m to be considered a wetland; this cutoff value is consistent with many ecological and legal definitions of wetland. However, to include systems where the matrix's water depth is ≤ 2 m but exclude systems > 2 m water depth appears to be an arbitrary cutoff for tree island classification because it is irrelevant to the functional ecology and processes occurring in these systems. For instance, a riverine tree island system with average water depth ≤ 2 m would be considered a "wetland" and included in the tree island definition used by Wetzel, but the processes that control tree island formation do not differ whether water depth is ≤ 2 m or > 2 m in riverine systems. Water depth does not fundamentally alter the processes, but it can impact the likelihood and rate of tree island formation because as average river depth increases, so does the transport of logs and other material that often serve as points of tree island nucleation. However, the number of retentive sites, like sediment bars or islands, that can receive the nucleating material decreases (Welber *et al.* 2013; Ruiz *et al.*, 2016).

As for seed dispersal and plant colonization processes, matrix water depth is unlikely to be an important factor within a tree island landscape because most species' seeds disperse across the matrix and to other tree islands by floating in the air column, on the surface of water, or by faunal dispersers. The first method of dispersal (anemochory) is completely unaffected by water depth. The successful dispersal of floating seeds (hydrochory) will be strongly affected by the presence or absence of water, but the depth is less relevant. Seed dispersal by wildlife (zoochory) is likely to be limited by matrix water depth but the ability and efficiency of a species to successfully distribute seeds is species-specific (contingent upon body size, mobility, ability to fly or swim, and other movement-related behaviors and life history traits). Small mammals and other fauna must swim to disperse even in very shallow water (i.e., < 0.25 m). At depths > 1 m, the water would be too deep for nearly all wildlife to walk across so they would have to swim or fly to disperse. In this regard, a 2 m cutoff would not be widely acceptable.

At a finer spatial scale, water depth can still impact plant species' distributions on seasonally inundated tree islands and shallow depth environments, such as the tree island-marsh ecotone, because species have unique flood tolerances that profoundly affect post-dispersal seedling establishment, survival, and growth rates (Palta *et* al., 2003; Jones *et al.*, 2006; Sousa *et al.*, 2007; Stoffella *et al.*, 2010). Thus, water depth can affect the prevalence of tree islands on the landscape by altering conditions for nucleation, but the formational processes are the same. Plant and, to a greater extent, animal dispersal processes can be affected by water depth, but not necessarily by a 2 m cutoff. It should be recognized that water depth variably impacts ecological processes, but the processes are still fundamentally the same and there are no grounds to exclude tree island systems from a definition based on matrix water depth.

Inconsistent use of the term "tree islands" across the literature warrants the adoption of a single definition that can be universally applied and encompass a full range of environmental conditions. Upon reviewing the multitude of definitions and descriptions of tree island ecosystems globally, I propose tree islands be defined as spatially discrete ecosystem patches (i.e., islands) of woody vegetation that developed from *natural* processes within a matrix of dissimilar vegetation. For tree islands to be considered “natural” and be included in this definition, they must arise from self-organizational or degradational processes that are not anthropogenically induced; however, the point of formation they occur on may be of natural or anthropogenic origin. For example, patches of trees that successionally colonized Native American midden piles would be considered tree islands, but forest fragments that exist solely because they are planted forest patches, remnants of deforestation or erosion, or products of other anthropogenic actions would not be considered “tree islands” because the processes that led to their formation were anthropogenic. Also, note that this definition requires tree islands to have more than one constituent tree because patches of single trees lack the functionality, network of interactions, and emergent properties of forest communities. Although such forest patches are excluded from this definition and will not be given more attention from hereon, it is worth noting that many of the properties, functions, processes, and dynamics of natural tree islands (e.g., biodiversity, animal movement, seed dispersal, metapopulations and -communities) may be relevant and readily applicable to these tree island-like systems in ecologically meaningful ways.

It is important to use a broad and inclusive definition for tree islands because overly restrictive defining criteria pose the risk of omitting valuable knowledge and insight. By instead acknowledging the nuances and dissimilarities between tree island systems, the foundational characteristics of tree islands will be brought to light and help scientists synthesize a greater understanding of these ecosystems. Subcategorizing and analyzing a subset of tree island systems might be quite useful and make comparison of one’s study system more feasible but other, less similar, tree islands systems should not necessarily be overlooked nor excluded because all tree island systems form and maintain themselves through similar processes and share similar ecological characteristics.

One such characteristic is that tree islands tend to be hotspots for biogeochemistry, as well as microbial, fungal, floral, and faunal communities. Recognition that tree islands exert strong controlling forces on ecosystem processes and biodiversity has led them to be increasingly studied and prioritized in ecosystem and biodiversity conservation, globally. The ecological importance of tree islands highlights the need for a better understanding of what environmental factors and processes characterize tree islands so that scientists, land managers, government agencies, and non-governmental organizations can conserve or restore these ecosystems in a way that improves ecosystem functions and biodiversity.

FORMATION, DEVLOPMEMT, AND MAINTENANCE

Tree island ecosystems are widespread across the globe and across gradients of temperature, water availability, edaphic conditions, and other basal ecosystem properties. Despite the extremely diverse geographic and environmental range tree islands exist in, their formational characteristics, processes, and structure are remarkably similar. For such fundamental traits to be shared among tree island systems globally, there must be some common force underlying the origin and existence of all tree islands.

Researchers from several ecological subdisciplines and tree island systems have independently theorized and reported mechanized conditions for tree island formation, growth, maintenance, and degradation. A widespread and increasingly robust theory of tree island development is that tree islands nucleate and maintain themselves through a balance of formational and degradational positive and negative feedbacks that regulate tree island growth (Alftine & Malanson, 2004; Givinish et al., 2008; Roush, 2009; Sullivan, 2011). Stark boundaries with the matrix occur at the interface where formational feedbacks that promote tree island expansion meet degradational feedbacks that promote matrix expansion (i.e., tree island mortality) (DeAngelis, 2012). In cases in which the balance becomes increasingly skewed towards degradational feedbacks, often a result of anthropogenic alterations to the system, tree island processes become destabilized and may lead to abrupt tree island loss as the system shifts to an alternative stable state. This has been well documented in the Everglades, where alterations in hydrology have caused excessive flooding and drought-induced fires that damage tree islands. When Everglades tree islands are disturbed beyond some critical threshold, trees occupying the islands die, soil and elevation is lost, and only a footprint of the former islands (i.e., "ghost islands" and "skeleton islands") remain (D'Odorico *et al.*, 2011; Ruis et al., 2013). Despite the seemingly sensitive balance of ecological conditions that tree islands require, they have developed and remained an integral ecosystem within the landscapes they comprise for, in many cases, thousands of years (Langstroth, 1996; Willard *et al.*, 2006; Bernhardt, 2011; McCarthy et al., 2012).

1.1. Landscape Heterogeneity

Microtopography and microsite conditions at the landscape scale are key determinants of where tree islands and their "points of formation" occur on the landscape. All points of formation occur in local patches where stresses from the disturbance regime are absent or have been reduced to a colonizable level. Wetzel (2002) gives many examples of common points of formation in wetland systems: high points in bedrock, infilled bedrock depressions, minerotrophic groundwater outflows, floating peat mats, termite mounds, large woody debris, log jams, and linguoid dunes. Like points of formation in wetland tree islands, those in non-wetland environments are often associated with localized topographical high spots or areas of nutrient concentration. For instance, ribbon-shaped tree islands in montane settings tend to form on microtopographic relief, whether it be a solifluction terrace, bedrock ridge, or outcrop (Buckner, 1977; Bekker & Malanson, 2008; Kharuk *et al.*, 2017). Tree islands in the Nylsvley savanna in South Africa formed on soil patches with high nutrient concentrations, an artifact of Iron Age human settlements (Blackmore et al., 1990). Tree islands in the nearby Soutpansberg savanna, like many other tree island systems, formed on active and abandoned termite mounds (Mourik *et al.*, 2007).

Contrastingly, points of formation in some non-wetland systems have seemingly no relationship with topography or soil nutrient content. These points of formation simply occur in patches where stresses have been locally reduced. This is typically the case with tree islands growing in environments with frequent or extreme disturbance regimes, such as in montane subalpine environments with harsh winds and severe cold temperatures. Here, points of formation are located only a few meters downwind of rocks, boulders, or other structures functioning as windbreaks (Bekker, 2005; Resler, 2006; Daley, 2009; Sindewald *et al.*, 2020). In landscapes where fire is a dominant disturbance, burned areas may be converted into a matrix of tree mortality or fire-tolerant vegetation. Meanwhile, unburned forest patches can remain as tree islands of fire-intolerant vegetation. The location, size, and shape of these tree islands are the legacies of where past fires did not burn (Calandriello, 1999; Houle *et al.*, 2006; Krawchuk *et al.*, 2020).

1.2. Endogenous Growth

The characteristic self-organizing nature exhibited by tree islands is resultant of endogenous factors that accelerate tree island growth. Most commonly, a positive feedback loop forms between soil accumulation and retention, increased nutrients, increased plant biomass, and increased tree recruitment (see Fig. 2, below). The relationship typically begins with a tree island developing a slightly elevated mound of soil that can originate from autochthonous and allochthonous sources. Organic soil accumulates on tree islands because plant biomass production is higher and deposited woody material retards the rate of decay on tree islands compared to the surrounding matrix, resulting in a net increase of soil organic matter (Rodriguez, 2013). Soil can also accumulate from aeolian, or water transported sediment, which are the dominant mechanisms in arid and riverine tree island systems, respectively (Ravi et al., 2007; Francis et al., 2009).

Differential soil formation, aeolian deposition, and water-transported sediment are the most common causes of soil accumulation and mounding on tree islands, but they are not mutually exclusive and are often co-occurring within tree island ecosystems and even on a single tree island. The tree islands of the Okavango Delta in Botswana exemplify this nicely because they primarily originate from termite mounds or fluvial sedimentation. These mounds continue to grow through the interaction of differential soil formation, mineral precipitation via evapotranspirational pumping, and aeolian deposition of dust (Humphries et al., 2014). In contrast, tree islands in the Canadian arctic develop soil mounds from upheaved sediment as permafrost forms and thickens, not from the aforementioned mechanisms of soil accumulation (Scott & Hansell, 2002); this example is unique and the only known exception to the typical tree island soil mounding mechanisms.

The same mechanisms that are responsible for soil accumulation on tree islands also drive nutrient accumulation. As organic soil forms on tree islands, plant matter decomposes, releasing stored nutrients that stimulate plant growth (Troxler & Childers, 2009). Aeolian deposition of nutrients also occurs as particles are transported in air currents until dry fallout is captured by trees intersecting the air column (Ju & DeAngelis, 2009, Humphries et al., 2014, Wetzel et al., 2017). Surface and subsurface flows bring additional nutrients to tree islands, which are drawn closer to the soil surface through evapotranspiration and can be used directly by plants (Wang et al., 2011; Wetzel et al., 2005).

The preferential use of tree islands by wildlife also concentrates nutrients on tree islands. Wildlife tend to spend more time on tree islands than in the matrix habitat, increasing the likelihood that fauna will add nutrients to the tree islands via excretion, deposition of antlers or other material, and post-mortem decomposition (Blackmore et al., 1990, Coultas *et al*., 2008; Piercey-Normore, 2008; Desbiez *et al*., 2009; Wetzel *et al*., 2017). In some tree island ecosystems, like the Everglades, indigenous people visited and inhabited tree islands over thousands of years. Their preferential use of tree islands, like wildlife, increased nutrients and soil material on tree islands primarily through the deposition of assumedly consumed animal bones, shells, pottery, and tools (Coultas *et al*., 2008; Irick et al., 2013).

The combined effect of soil and nutrient accumulation on tree islands facilitates growth of existing trees and other plants. The increased plant biomass reciprocally increases the strength of the mechanisms driving soil and nutrient accumulation, establishing a positive feedback loop for tree island growth. Hypothetically, increased plant biomass is expected to simultaneously increase litterfall production, aeolian and hydrologic sediment capture, evapotranspirational pumping, faunal habitat use, and nutrient availability in the rhizosphere (Krah & McCarthy, 2004; Wetzel et al., 2011; Humphries et al., 2014). All of these processes contribute to soil accretion and/or nutrient accumulation, further stimulating growth of tree island vegetation (Fig. 2).

In some cases, the formation of tree islands may be induced by anthropogenic activity, but the same processes that naturally develop and maintain tree islands (soil accumulation, focused nutrient redistribution, and increased plant biomass) are required for these anthropogenic islands to persist. Blackmore et al. (1990) documented anthropogenically induced tree island formation in the Nylsvley savanna of South Africa. Iron Age settlements of the Tswana tribe substantially increased nutrient concentrations in the soil beneath them, primarily through the deposition of dung from domestic cattle, charcoal from spent firewood, bones, pottery, and other artifacts. Clear agreement between archaeological, geological, and ecological evidence strongly supported the hypothesis (and disproved other hypotheses) that the localized nutrient accumulation associated with these sites functioned as points of tree island formation once the settlements were abandoned. However, anthropogenic activity alone was insufficient to maintain these tree islands and some other mechanism of nutrient import, likely herbivory and increased faunal use, was required to facilitate their development (Blackmore et al., 1990).

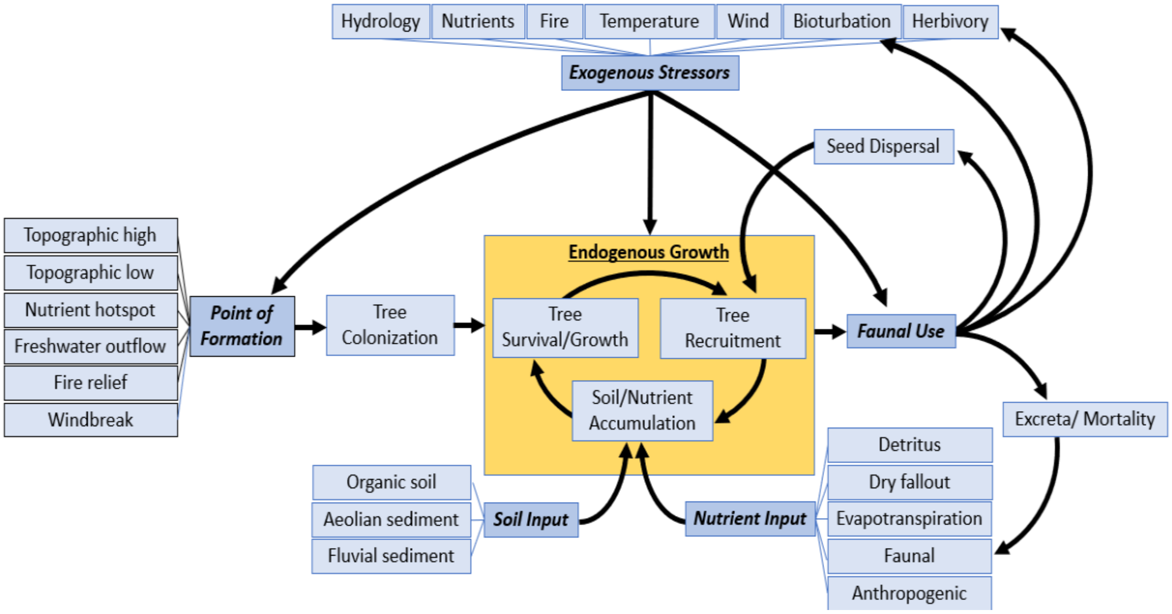

Figure 2. Conceptual model of how ecosystem processes and interactions form/develop tree islands.

Similarly, excavated tree islands in the Llanos de Moxos region of Bolivia revealed multiple layers of shells, animal bones, charcoal, and human burials that extend ~1.5 m below the present-day soil surface. These middens were incrementally deposited 10,600 - 4000 BP, building up the soil surface and becoming points of tree island formation (Capriles et al., 2019). As previously mentioned, anthropogenic activity of Native Americans on pre-existing tree islands in the Florida Everglades has been found to stabilize and even speed up tree island growth. Midden piles of artifacts and ecofacts (such as pottery or tools, and bones or shells from consumed animals, respectively) added nutrients, soil material, and in some cases contributed to the formation of a calcrete layer (Carr, 2002; Bernhardt, 2011).

1.3. Exogenous Stressors

Tree island presence, dynamics, growth, and distribution can partially be explained by ecological conditions having disparately stressful impacts across distinct landscapes features. Periodic abiotic stresses, like wind, fire, or flooding, cause mortality along tree islands' borders and limit outward expansion. Tree islands can only expand when formational/growth processes outweigh external stressors such that conditions along the tree island-matrix edge become suitable habitat for colonization of trees and other tree island lifeforms. The disturbance regime and directionality of external stressors are largely responsible for controlling tree island expansion and contraction, but they also have a strong influence on tree island shape.

Many environmental stressors impact the landscape without exerting a directional force or disproportionately affecting a particular side of tree islands (e.g., low soil nutrients, seasonal drought, fires). Under this regime, tree islands expand radiatively outward because stress evenly or randomly limits growth along the islands' periphery, giving islands a circular or irregular shape, respectively. When external stressors follow a linear pattern (e.g., fluid shear from flowing water in Everglades), then tree islands will be sculpted parallel to the directional stress, and tree island expansion will occur primarily at the downstream or leeward side of the island (Wetzel, 2002). Tree islands can also be linear but perpendicular to the directional stressor (e.g., prevailing winds in montane tree islands). This occurs when multiple stressors interact to create very harsh conditions at the upstream/windward and downstream/leeward ends of the tree island, and conditions suitable for outward expansion only occur on the lateral sides of the island, resulting in perpendicular growth (Bekker & Malanson, 2008).

Perpendicular tree islands are far less common than parallel, circular, or irregularly shaped tree islands. Much of the literature regarding perpendicular tree islands pertain to the string shaped tree islands in northern latitude peatlands that run parallel to land contours and perpendicular to water flow, originally discussed in detail by Foster et al.

(1983) and revisited by Wetzel (2002). Ribbon shaped tree islands are also prevalent in the literature but were not covered in the original review by Wetzel (2002) because they are not wetland tree islands. Ribbon islands form in montane systems with high snow input and high wind speeds that transport snow and push snowdrifts. Ribbons form on microtopographic high points such as rocky outcrops or terraces along mountain faces because thinner snow depth provides habitat conducive for tree growth. Once trees colonize, snowdrifts accumulate at the windward side of ribbon tree islands, increasing snow depth such that ribbon islands cannot expand windward. Decreased wind speeds at the leeward ends of ribbon islands also accumulate an excess of snow, preventing leeward expansion. However, scouring winds along the sides of ribbon islands prevent deep snow accumulation, allowing the ribbons to expand perpendicular to wind speed (Buckner, 1977; Bekker & Malanson, 2008).

Perpendicular tree islands, locally referred to as “tzekeles”, also occur in the northwest Yucatan, near Chunchucmil. Tzekeles are oriented parallel to the coastline, perpendicular to coastward water flow. However, the shape of tzekeles do not appear to be governed by current ecological or geological processes. Tzekeles are “fossilized beach ridges”, estimated to have been deposited 129,000 – 120,000 years ago when wave action, the directional stressor at the time, deposited sediment along and parallel to the historic coast (Hixson 2011). Over millennia, the tzekeles’ limestone differentially eroded, leaving remnant forested hillocks embedded in the footprints of ancient beach ridges (Van Sweetwood, 2008, Hixson et al., 2017).

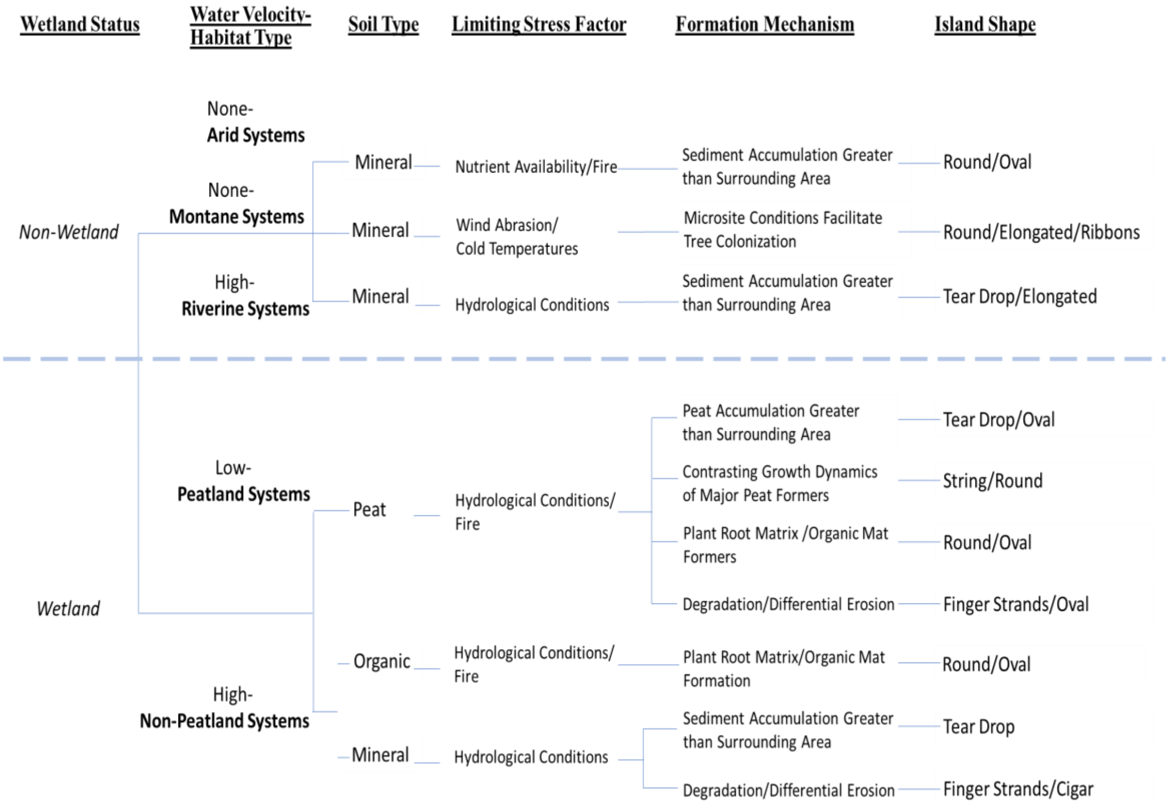

Figure 3. Classification system for tree islands found throughout the world (Modified from Wetzel, 2002).

ENVIRONMENTAL CONDITIONS

1.4. Climate

Tree islands are strongly influenced by localized ecological stressors at short and long temporal scales, but changes in environmental conditions at larger spatial scales (i.e., regional or global) are also important in modulating tree islands’ condition and growth. Analyses of tree rings and other metrics of tree growth have been used to reveal how changes in climate have directly influenced tree and tree island expansion in the past several hundred years (Vallée & Payette, 2004). Although these methods are practical for analyzing the effects of recent climatological shifts on tree islands, the data are limited to the lifespan of the trees from which the metrics are acquired. To expand our analyses and understanding of climate-tree island relationships beyond short temporal scales, the geologic and pollen record can be used. Several studies have already taken this approach and discovered that periods of enhanced tree island expansion and contraction are closely related to climate patterns at large spatial and temporal scales. Willard *et al.* (2006) found that episodic expansion of Everglades tree islands was synchronous with multi-decadal droughts caused by the southward migration of the Intertropical Convergence Zone. The droughts extended into Central and South America, where similar tree island systems exist and likely experienced similar climate induced growth. However, long-term growth of tree islands via favorable climatological conditions can abruptly be reversed by rapid die-offs from unpredictable, extreme climate events such as severe winter or summer storms, avalanches, volcanic eruptions, etc. (Holtmeier, 2009; Bernhardt, 2011).

A wide array of ecological conditions, stressors, and disturbances are exerted on tree islands because tree islands are widely distributed across the globe and exist in a surprising breadth of climates and biomes but some distributional patterns are apparent. One such pattern is that most tree island systems recorded in the literature exist above the Tropic of Capricorn (see Fig. 4, below). More specifically, tree island systems extend latitudinally from ~70°N to 23.5°S (Tropic of Capricorn). The lack of tree island ecosystems south of this latitude seems unrelated to climate patterns because tree island ecosystems are abundantly distributed north of the tropics, so similar climate patterns south of the tropics should not restrict tree island formation. Instead, the absence of tree islands is likely because only 8% of Earth’s landmass is situated south of the Tropic of Capricorn. Their southward absence may merely be from chance and not some limiting climatic or geographic factor.

Figure 4. Blue circles represent wetland tree island ecosystems; orange circles represent non-wetland tree island ecosystems. The size of each circle is scaled to the number of published scholarly articles where the study area lied within that tree island ecosystem. All tree island ecosystems depicted above were found during the literature search (Table 4 in the Appendix for a complete list of tree island systems).

Another notable pattern is that most tree island systems were found within North America, and to a lesser extent South America. This may have to do with the limited accessibility of scientific articles from foreign nations and articles not being translated to English, resulting in most of the tree island systems I have documented being from the Americas. It is also possible that tree island ecosystems outside of the Americas appeared less frequently in the literature review because a different term, besides "tree island" and the other search criteria, is used by the people or scientists of that region (refer to Table 3 in the Appendix for search terms). For example, people refer to tree islands as "murundus" in the cerrado region of Brazil, "cordilheiras" or "capaoes" in the Mato Grosso region of Brazil, and "petenes" in the Yucatan. Although many synonymous terms for "tree island" were discovered in the literature search, I acknowledge that it is possible some tree island systems went undetected because scientists from foreign nations, especially non-English speaking nations, may be unaware of and use an alternative term to describe tree islands.

1.5. Hydrology

Hydrology often plays an important role in tree island distribution, formation, maintenance, and related ecological processes. The importance of hydrology is especially true in the case of wetland and riverine systems. This is partly because hydrology controls flow and sedimentation rates surrounding tree islands, which are determinants of their location, shape, and size (Bazante *et al.*, 2006; Francis *et al*., 2009). The interaction between topography and hydrology also affects island elevation relative to the water level, a determinant of whether trees can establish, survive, and grow on potential tree island sites (van der Valk *et al.*, 2007; Stoffella *et al*., 2010).

Hydrology is also important to non-wetland tree islands, such as those in montane systems. However, unlike other tree islands, important hydrologic factors in montane systems are typically related to snow. Krummholz tree islands provide well-studied examples of this and exist throughout many mountain ranges. Krummholz islands are a subcategory of montane tree islands that occur above the timberline and are characterized by trees' stunted growth, asymmetry, and wind-sculpted form, which can be genetically determined or induced by harsh climatic conditions (Bekker & Malanson, 2008). The survival and growth of krummholz islands are highly dependent on increased snowpack and snowmelt, which insulate the trees during the winter and promote better growing conditions in the spring, respectively. Drought is another important hydrologic factor in montane tree islands because low soil moisture limits tree growth and island expansion during the growing season (Williamson, 2020).

In semi-arid to arid environments (hereon, referred to as arid), soil moisture is the most important hydrologic factor affecting tree island distribution and ecological processes. Soil moisture is generally very low in arid tree island ecosystems, even under sheltered microsites, and it fluctuates with seasonal rainfall patterns (Schade & Hobbie, 2005). Rainfall and rainwater runoff are the primary sources of water for plants growing on arid tree islands and are the major determinants of tree island growth. At the landscape-scale, runoff preferentially flows through the bare soil matrix but when arid tree islands impede the flow path, flow is reduced, causing fine sediment and nutrients to be deposited along the outer edges of the islands. Within-patch rainwater runoff also contributes to island expansion. Rain that lands directly on an arid tree island tends to runoff towards the outer edge of the island because fine sediment beneath the canopy has a low infiltration rate; when the runoff reaches the matrix soil at the outer extent of the island, water readily infiltrates into the ground. The combined effects of matrix and within-island runoff depositing nutrients and increasing belowground water availability results in growth of existing plants and outward expansion of the island as new plants colonize its edge. (Ravi *et al*., 2007)

1.6. Fire

Drought-induced fires are disturbances characteristic of all tree island ecosystems. Fire return intervals can vary drastically between different tree island systems (e.g., 10-14 years in the matrix surrounding Everglades tree islands and +150 years in that of the Lake Agassiz peatlands), but in general, fires are more frequent in sub-tropical peatland tree island systems because they experience seasonal dry downs and lightning events (Wetzel, 2002).

Fires occur periodically in arid tree island systems because nearly constant dry conditions allow lightning strikes to readily ignite fires if fuel loads are sufficient. However, infrequent thunderstorms and thus, lightning, limit how often fires occur. The frequency at which fires occur appears to be the most important aspect of the fire regime, as frequent fires continually disrupt and inhibit tree island formational processes. When fires burn arid tree islands, vegetation can be substantially reduced or die completely, thereby increasing the erodibility of tree island soils, which will be distributed more homogenously across the landscape via aeolian or hydrologic transport (Ravi & D’Odorico, 2009).

Post-fire dispersion of tree island soils concomitantly affects soil nutrient distribution. A 58-year fire exclusion experiment in the Satara region of South Africa, a savanna-tree island ecosystem, found that sites with more frequent fires had a nearly 8-fold reduction of C, N, and P concentrations in tree biomass. Similar but slightly weaker effects on C, N, and P concentrations of grasses, and soil C and N were observed. This experiment also recorded differences in tree island plant community structures that were the result of different fire frequencies. Tree abundance, biomass, and canopy cover were significantly lower in plots with shorter fire return intervals (Pellegrini *et al.*, 2015). As plants resprout or recolonize the burned landscape, soil and nutrient redistribution mechanisms will begin to reform or enhance the degraded tree islands. However, if tree island self-organization processes cannot outpace the damages incurred by frequent fires, the landscape will be converted to an arid grassland (Ridolfi *et al.*, 2008; Ravi & D’Odorico, 2009).

1.7. Vegetation

The extremely diverse assortment of environmental conditions in which tree islands exist (e.g., equatorial to subpolar, coastal to alpine, rainforest to desert), results in global tree island ecosystems having vastly different plant communities. Even tree islands within the same tree island complex can have drastically different plant communities because they are of different ages or stages of development (Wetzel, 2002). In general, older tree islands are more developed because soil building and nutrient accumulation processes have been operating for longer periods of time, increasing their size and elevation (barring erosional disturbances), thereby making older islands more conducive for trees and other late-successional plants to grow (Holtmeier, 2009).

Development and succession of tree island plant communities becomes complicated when multiple pathways of tree island formation arise from different mechanisms of nucleation and growth, as well as different topographic features, substrates, and soils within the same tree island complex. The most studied example of this comes from the Florida Everglades, where various formation pathways create multiple tree island morphologies with distinct substrates and plant communities (fixed tree islands on topographically high limestone outcrops or peat-filled limestone depressions, coastal tree islands where breaks in impervious marl sediment allow fresh groundwater upwellings, strand tree islands that developed on sawgrass ridges, and pop-up/ battery tree islands on floating mats of peat and vegetation) (Brandt et al., 2006; Willard *et al.*, 2006; Peay et al., 2007; Ross et al., 2014; Ross et al., 2021).

Tree island size also has a direct influence on plant community composition because as patch size increases, generally so does seed rain, seedling density, and plant and fungal species richness (Peay et al., 2007; Cole, 2009; Ross et al., 2016). The edge to interior ratio, a function of island size, also affects plant communities. Small tree islands have a higher edge to interior ratio, meaning a larger proportion of the island will experience edge effects that will limit the growth of some species while encouraging growth of others, especially early successional and invasive species (Carroll, 2009; Ross et al., 2016; Zemp *et al.*, 2019). Large islands, having lower edge to interior ratios, will generally have plant communities dominated by late-successional species that are adapted for sheltered, interior conditions (Albersten *et al.*, 2014).

Tree island size also mediates the effect of disturbances that primarily impact tree island edges, such as fire, inundation, and wind damage. Small tree islands and portions of tree islands with greater edge to interior ratios are susceptible to experiencing stronger impacts from these disturbances. This phenomenon has been documented in the Everglades, where subtropical hardwood trees are restricted to interior, elevated portions of tree islands that experience little to no flooding disturbance (Sah *et al.*, 2018). Similarly, in the Rocky Mountains, *Ribes montigenum* and *Vaccinium myrtillus* grow almost exclusively at the leeward side of montane tree islands because they are better insulated from extreme cold and sheltered from wind abrasion (Holtmeier, 2009).

Woody species capable of clonal reproduction (i.e., produce genets) often make tree islands more resilient to disturbances. If a disturbance kills the base of a tree such that it cannot resprout, surviving ramets will utilize nutrients released from the decaying portion of the tree, improving its growth, and stabilizing the microsite (Magyar *et al.*, 2004). This is commonly observed in high-mountain subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) tree islands of North America, where extreme wind and cold temperatures are the primary sources of tree mortality. These stresses are more extreme at the windward side of montane tree islands, so parent trees are often damaged or killed, and ramets must grow prostrate along the ground to escape the stress before erecting themselves downwind of the parent tree (Bekker & Malanson, 2008; Holtmeier, 2009; Williamson, 2020). Clonal tree species are also a major component of the plant community in arid and wetland tree islands, like rock alder (*Canthium mundianum*) in South Africa and Carolina willow (*Salix caroliniana*) in the Everglades (Mourik *et al.*, 2007). However, clonal reproduction appears to be more common in montane tree islands, likely because the extreme stressors and high mortality in montane tree islands severely limit successful recruitment from seed, giving species capable of clonal propagation a strong advantage (Kašpar, *et al.*, 2017).

Additionally, clonal species serve as important pioneer species because the presence of even a single parent tree will form positive feedbacks of soil stabilization, accumulation, and island expansion as ramets emerge from the parent tree (Bader *et al.*, 2021). This type of facilitation is a key process contributing to tree island self-organization and plant community assembly because edaphic microsite conditions become improved and stimulate additional tree growth after the initial colonization. Facilitation thereby reinforces growth and accelerates development of tree islands (Maher *et al.*, 2005; Resler & Stine, 2009; Mikola *et* al., 2018; Christmann *et al.*, 2021).

The interaction between parent trees ameliorating leeward growing conditions for clonal ramets is one of the many facilitative interactions present in montane tree islands. An experiment in the Snowy Range of Wyoming revealed neighboring herbs and trees also facilitate tree seedling survivorship in tree islands by increasing soil water availability and decreasing temperature stress and photoinhibition from overexposure to solar radiation (Maher *et* al., 2005). Similarly, a study in the Cranberry Glades of West Virginia proposed that neighboring plants facilitated the growth of young trees on tree islands by buffering them from damaging winds, temperature stress, and overexposure to solar radiation (Resler & Stine, 2009). A long record of field studies further supports that intra- and interspecific facilitative interactions are common across tree islands and are crucial to their persistence and growth (Brooke *et al.*, 1970; Buckner, 1977; Holtmeier & Broll, 1992). Although the bulk of the literature on facilitation comes from subalpine montane tree islands ecosystems, facilitation does not appear to be any less common nor important in the other tree island types; it has just been studied more intensively in montane systems. Stoffella et al. (2022) pointed out that facilitation is especially understudied in the Everglades and addressed this data gap by tracking planted tree survival and growth under experimental tree density and water level (i.e., stress) treatments on constructed tree islands. Species exhibited various responses to the treatments but in general, trees subject to flooded conditions experienced increased survival and growth when planted at higher densities (up to 1m apart) because neighbors facilitatively reduced abiotic stress (assumedly by aerating soil, accumulating soil, or increasing nutrient availability).

The facilitative interactions documented across tree island ecosystems may differ mechanistically from one another, but there is universality in that tree islands must rely on facilitation and other positive feedbacks to overcome disturbances and stressors characteristic of the matrix habitats. Harsh exogenous conditions restrict the species pool of plants that can survive and regenerate on tree islands. The intrinsic patchiness and isolation of tree islands further constrains plant community composition via dispersal limitation. As a result, tree island plant communities are subsets of the regional species pool, with diversity decreasing as environmental stress and dispersal limitation increase. Krummholz tree islands provide a clear example of this because even among large islands, extreme stresses often limit tree composition to a single species (Resler & Fonstad, 2009).

Strong constraints on tree island community composition may make it more difficult and unlikely for rare plants to successfully integrate into tree island communities. Wetzel (2002) noted that no endemic nor rare plants were known to inhabit any of the wetland tree islands across the globe. Since the publication of Wetzel's review and the other chapters of Tree Islands of the Everglades, an uptick in tree island vegetation studies have revealed that there are rare plant species (referring to state or federally listed species, or those on the IUCN red list) inhabiting tree islands but still, no plants endemic to tree islands have been recorded. Tree islands in the Florida Everglades host several state-listed trees like the Florida royal palm *(Roystonea regia*) and satinleaf (*Chrysophyllum oliviforme*) (Ross et al., 2005). The IUCN also lists red bay (*Persea borbonia*) as globally endangered, but in Florida the trees are not listed because their populations are large enough to not warrant immediate conservation concern, despite outbreaks of laurel wilt that are greatly reducing some local populations (Snyder, 2014). The only other tree island ecosystem where rare plants have been documented is in the Caribbean; several species of rare orchids, including a new species, were recently discovered in western Cuba and another orchid, endemic to Grand Cayman, was found in buttonwood (*Conocarpus erectus*) tree islands (Diochon et al., 2003; Sauleda, 2018a, 2018b).

WILDLIFE

This updated review of the tree island literature revealed a global paucity of information on tree island fauna. This knowledge gap was first highlighted in Sklar & van der Valk's (2002) *Tree Islands of the Everglades*. Since its publication, researchers have repeatedly pointed out that wildlife is poorly researched in the tree island ecosystems they are discussing and more research effort is required to advance this aspect of tree island research (Eckles, 2013; Ferreira Neto et al., 2021).

Studying wildlife is not only important for improved management and conservation of the faunal communities inhabiting tree islands, but also for the tree islands themselves, and the greater ecosystem within which tree islands occur. Although the literature only mentions this in passing, tree island fauna have a pronounced effect on their environment because they heavily influence ecosystem processes that maintain and moderate growth of tree islands. The fauna-tree island-ecosystem relationships of essentially all tree island systems are characterized by a high degree of interconnectedness that appears to stem from the regular transport of nutrients and material, and dispersal of wildlife. Reciprocal interactions emerge from the spatiotemporal movement of biota, nutrients, material, and energy across the landscape, giving the fauna-tree island-ecosystem hierarchy its interdependent nature.

1.8. Tree Islands as Habitat

Tree island ecosystems are intrinsically patchy and heterogenous at the landscape-level because they are spatially discrete, separated by matrix habitat. Matrix habitats are accompanied by exogenous disturbances and stressors that incur harsh conditions on wildlife inhabiting the tree islands. Tree islands offer refuge from these environmental stressors while also providing increased cover and high-quality food sources (Daley, 2009). For these reasons, most species of wildlife preferentially inhabit and spend more time in tree islands than the matrix. A capture-mark-recapture study of small mammals in the Okavango Delta, Botswana found that most species disperse to and preferentially use tree islands at least during the rainy season because water levels in the grassland matrix increase and restrict dry ground availability (Plasvic, 2015). Similarly, in the harsh sub-alpine regions of North America, many species of wildlife escape the extreme conditions by taking refuge in tree islands. Most species inhabiting these islands are small mammals, like the mountain pika, hoary marmot, golden-mantled ground squirrel, and pocket gopher, which spend most of their time foraging within tree island patches (Walker, 2021).

Whereas subalpine tree islands typically have low faunal diversity, other tree island systems are more diverse and support dissimilar taxa. Tree island diversity is limited by the richness of the regional species pool, as the species that occupy tree islands are a subset of those in the surrounding environment. For instance, fluvial tree islands in the Rio Negro of the Brazilian Amazon host very diverse faunal communities, as would be expected, considering the exceptionally speciose faunal community of the Amazon (Ferreira Neto et al., 2021). Eleven species of mammals from diverse and dissimilar lineages and life histories were detected during a narrow sampling window of 60 days. Species included red brocket deer (*Mazama americana*), coati (*Nasua nasua*), four-eyed opossum (*Philander opossum*), jaguar (*Panthera onca*), lesser anteater (*Tamandua tetradactyla*), and more; other species were known to occur in the immediate region and may use the tree islands but were not detected on trail cameras nor during spoor surveys. Perhaps the most interesting finding of Ferreira Neto et al.'s (2021) work was that faunal community composition and richness between fluvial tree island patches was attributed to soil fertility; islands with increased fertility had more diverse communities and higher species richness.

Interestingly, tree island or patch area and distance to mainland, two tenets of the generally accepted and widely tested island biogeography, metapopulation, and metacommunity theories (MacArthur & Wilson, 1967; Wilson, 1992; Hanski & Gilpin, 1991; Leibold et al., 2004), could not explain faunal community characteristics of fluvial tree islands in the Rio Negro. However, contradictory results are prevalent among studies based on these theories, as other research does support the notion that patch size and isolation (i.e., distance to mainland or neighboring patches) are important factors influencing faunal community traits (Simberloff, 1976; Artz & Waddington, 2006; Peay et al., 2007; Zarnetske et al., 2017; Hamer et al., 2021). In Leibold & Chase's (2017) review of metacommunity ecology, they explain that patch isolation typically does affect species richness and deviations from this generality are often explained by the presence of species that disproportionately impact the community. However, this conclusion may be too community-focused, overemphasizing the role of species composition on metacommunity patterns while underestimating the role of habitat quality, heterogeneity, and landscape factors. Differing results among studies that assessed how tree island size, isolation, habitat quality, and other relevant environmental characteristics affected wildlife supports the idea that the effect any particular tree island characteristic has on the constituent faunal community may be specific to that tree island ecosystem. Although the most influential tree island characteristics may differ from one ecosystem to the next, it is clear that tree islands strongly affect and shape the faunal patterns of behavior, community composition, and structure.

1.9. Effects of Wildlife on Tree Islands

1.9.1. Nutrient Input

Reciprocally, wildlife affect and shape the tree islands they utilize through various patterns of habitat use, resource consumption, and other behaviors that alter their physical and chemical environments. Increased nutrient concentrations is one of the strongest effects wildlife have on tree islands. Wildlife can be major importers of nutrients to tree islands by uptaking nutrients from the surrounding matrix and redistributing them onto tree islands (Blackmore et al., 1990, Coultas *et al*., 2008; Piercey-Normore, 2008; Desbiez *et al*., 2009). Each species' contribution to nutrient redistribution is a function of species' abundance, individuals' nutrient load, movement and behavior, proportion of matrix-derived food sources, and strength of tree island selection (Kitchell et al., 1999; Albeke, 2010).

Prayag et al., (2020) measured the amount and effects of nutrient input by the sociable weaver (*Philetairus socius*), a passerine, on islands of fertility in the Kalahari savanna of South Africa. These islands are often composed of individual camel thorn trees (*Vachellia erioloba*), which facilitate the growth of a modest understory. The trees are also utilized by the sociable weaver to support their large communal nests. A single nest can be occupied by several hundred birds and colonies are known to occupy nests for decades. Prayag et al.'s experiment found that sociable weaver colonies were associated with a fourfold increase in tree island soil N and P. Soil $\delta^{15}N$ values indicated that these nutrients were faunally derived. A replication of the experiment was conducted using nest and control poles instead of trees to isolate sociable weavers' nutrient input from other species of wildlife. Ratios of nest versus control nutrient concentrations and $\delta^{15}N$ values were very similar between island and pole experiments. The results demonstrated that fauna, primarily sociable weavers, are major vectors of nutrient redistribution to Kalahari fertility islands.

In the Everglades, phosphorus (the limiting nutrient) and other nutrients accumulate on tree islands partly because most species of wildlife select for tree island habitat and spend more time on tree islands than in the matrix habitats, increasing the likelihood that when animals defecate or die, those nutrients will be deposited on and incorporated into the tree island (Wetzel *et al*., 2017). However, wading birds have been recognized as disproportionately important vectors of nutrient redistribution. They are the leading faunal importer of phosphorus and other nutrients because they will forage in the marsh matrix but will roost in colonies and defecate on tree islands, redistributing large amounts of marsh-derived nutrients onto tree islands. Wading bird guano from a large colony reportedly contributed 20 times as much P as all other sources, and larger colonies may input 3000 times more P than aeolian deposition, another major source of P on Everglades tree islands (Wetzel *et al*., 2005). Wading birds in the Everglades do not distribute nutrients homogenously across tree islands within a landscape. Consequently, tree island P levels can vary drastically, and are largely dependent on whether the island is an active rookery, has a legacy or was recently used as a rookery (50 years ago or less), and how large the roosting colony is or was (Wetzel *et al*., 2005). Non-wading bird wildlife, like whitetail deer, are also known to forage in the marsh but otherwise select for tree islands, making them potentially important vectors of nutrient redistribution in the Everglades (Labisky et al., 2003). However, the relative contribution of these species to tree island nutrient input has never been directly studied (Lago, 2009).

Faunal redistribution of nutrients is presumed to be a universally important process controlling localized nutrient loads. But aside from the above examples, it is seldom studied in the context of tree island systems. Even in otherwise well-studied tree island ecosystems, like the Okavango Delta, there have been no efforts to quantify faunal nutrient inputs despite a theorized mechanism of nutrient redistribution and an abundance of megafauna that utilize these tree islands. (Gondwe et al., 2021).

1.9.2. Seed Dispersal

The discontinuity of tree island landscapes functions as an environmental filter that limits plant community composition according to species' dispersal ability (Jonatar Alves da Cruz et al., 2013; Suganuma & Durigan, 2022). Plants solely capable of short-distance dispersal tend to be filtered out of tree island communities because interisland dispersal is not possible unless tree islands are very closely aggregated (Hanan *et al*., 2010). Consequently, the regional subset of plants that inhabit tree islands consists primarily of species capable of long-distance seed dispersal (Hovestadt et al., 1999; Fragoso et al., 2003; Ross et al., 2016). Of the various modes of long-distance seed dispersal (e.g., *anemochory* (dispersal by wind), *hydrochory* (dispersal by water), *zoochory* (dispersal via animals)), zoochory more strongly shapes plant community assembly patterns in tree island landscapes (Van Leeuwen, 2018).

The success of zoochory as a mode of seed dispersal is partially attributable to it being able to disperse seeds over greater distances (+1000 km) than anemochory. However, zoochory and hydrochory operate over similar spatial extents (Cain et al., 2000). However, unlike anemochory and hydrochory, zoochory also has the advantage of diaspores following a nonrandom trajectory to suitable microsites (i.e., tree islands) (Holtmeier & Broll, 2010). This nonrandom trajectory is referred to as "directed dispersal" and in this context, it is facilitated by regular movement of fauna between tree islands and faunal selection of tree islands as habitat.

Faunal selection of tree islands increases the time wildlife spend on tree islands relative to matrix habitats, increasing the likelihood that seeds are deposited on tree islands (Blackmore et al., 1990; Cole et al., 2010). However, certain tree islands will be selected for more strongly than others and receive relatively more faunally dispersed seeds, thereby adding heterogeneity to the floral metacommunity composition. The degree of selection for a particular island is a function of faunal life history, behavior, environmental requirements, and preferences, as well as landscape and tree island characteristics, such as patch size, which is often emphasized as an important factor in the ecology of metacommunities and patchy habitats (Gaines et al., 2002; Leibold et al., 2004; Zarnetske et al., 2017).

Cole et al., (2010) conducted seed dispersal experiment near Las Cruces Biological Station in Costa Rica that controlled for tree island size, among other variables, to observe what effects these variables had on zoochorous dispersal. Three tree islands of various sizes (4x4 m, 8x8 m, and 12x12 m) were planted within 50x50 m plots that were replicated across seven sites. Seed rain data over 18 months indicated that tree island size had a strong influence on zoochorous seed dispersal. Medium and large islands received twice as many tree seeds per unit area as small islands, and the large islands received seeds from more than twice as many tree species than the small islands did. It is important to point out that in the context of natural tree island habitats, even the “large” experimentally planted tree islands (12x12 m) would generally be considered very small. An improved understanding of how zoochory is affected by island size and other landscape characteristics could be achieved through additional experimentation or observational studies at larger spatial scales that more closely resemble naturally occurring tree islands. Cross-ecosystem analyses would also make important contributions towards understanding how zoochory varies between ecosystems or tree island types (e.g., peatland tree islands versus riverine, subalpine, arid, etc.).

The prevalence of zoochory over alternative modes of seed dispersal in tree islands was thoroughly discussed in Langstroth’s (1996) dissertation on tree islands of La Chacra, a savanna in the Llanos de Moxos region of Bolivia. Hydrochorous trees were less prevalent than the author expected, given that this landscape experiences prolonged seasonal inundations. Langstroth postulated that limited water flow in La Chacra hindered long-distance dispersal of hydrochorous species, reducing the relative abundance of these trees. Anemochorous trees were common and important constituents of the nearby gallery forests and murundus, tree islands originating from termite mounds. However, their seeds typically do not disperse more than 100 m, which explains why anemochorous trees were nearly absent from the tree islands of La Chacra; these islands are typically spread further apart than 100 m. Langstroth states that zoochory is the most effective mode of seed dispersal for trees in La Chacra's tree islands, and this is reflected in their tree communities being almost exclusively composed of zoochorous species. More specifically, the majority of these zoochorous trees are dispersed via *endozoochory* (animal ingests and excretes diaspore); small seeds being primarily dispersed by birds and bats, and large seeds primarily by medium-sized rodents and cattle. Faunal selection of edible diaspores shifts tree assemblages towards being increasingly composed of endozoochorous species. Other modes of zoochorous seed dispersal (i.e., *synzoochory* (animal intentionally transports diaspore without ingesting) and *epizoochory*/ *ectozoochory* (animal unintentionally transports diaspore on the outside of its body)) shape tree assemblages too, but their effects are likely weaker in tree islands; the effect each dispersal syndrome has on tree assemblages is related to its prevalence in the seed dispersal network (Vild et al., 2017).

Ross et al. (2016) reported similar findings from South Florida's hardwood hammocks. This study found that the majority (>75%) of trees in South Florida's hardwood hammocks produced endozoochoric fruit. However, species that employ alternative modes of seed dispersal (i.e., anemochory, barochory, hydrochory) were nearly absent from hammocks in tree islands of the interior Everglades peatland. The larger proportion of endozoochoric species in tree island hammocks (~100%) was related to spatial isolation and smaller hammock area. It is inferred from their metacommunity analyses that zoochory is the most advantageous means of inter-island dispersal among hardwood hammock trees in the Everglades. However, cocoplum (*Chrysobalanus icaco*) and pond apple (*Annona glabra*) are the main components of the wetter non-hammock portion of tree islands and can disperse via hydrochory, in addition to endozoochory. The coastal plain willow (*Salix caroliniana*) is another common tree that is found along the outskirts of tree islands, and it primarily disperses via anemochory but hydrochory and epizoochory are also possible (Mossman, 2009).

Although zoochorous seed dispersal has community-wide effects on forest composition and species distributions, it does not affect the constituent tree species equally. Some trees rely more heavily on zoochorous dispersal than others (i.e., some have multiple dispersal mechanisms, like cocoplum and pond apple) and some species rely on a single species of faunal disperser. For example, in the Maracá Island Ecological Reserve of Brazil, diaspores of the palm *Maximiliana maripa* are handled or consumed by many species of wildlife. However, the manner in which *M. maripa* diaspores are handled or consumed and excreted typically renders them susceptible to infestation by parasitic bruchid beetles (73-100% infestation rate), inducing seedling mortality. Brazilian or lowland tapirs appear to be the only effective agent of long-distance seed dispersal for *M. maripa* in this system. Tapirs disperse seeds far from parent trees, which have high beetle populations, reducing the likelihood of density-dependent seed parasitism. Additionally, tapirs' fecal matter is unique in that it creates a protective barrier that prevents beetles from accessing and parasitizing the seeds (Fragoso et al., 2003).

A similar case occurs in the western United States, where whitebark pine (*Pinus albicaulis*) is the pioneer and major component of montane tree islands. Whitebark pine is also a keystone species because it disproportionately increases floral and faunal biodiversity, is the primary means of shelter, and its seeds are a highly nutritious food source for wildlife such as grizzly bears, black bears, deer, elk, ground squirrels, other rodents, and birds (Wood, 2015; Wagner, 2017; Degrassi *et al.*, 2019). Although many species of wildlife consume whitebark pine seeds, the seeds are dispersed exclusively by the Clark's nutcracker (*Nucifraga columbiana*) (Resler & Stine, 2009). Clark's nutcracker cache thousands of seeds in preparation for food shortages throughout the winter and spring, but nearly half of the seeds are never retrieved and if environmental and microsite conditions are suitable, they will germinate (Maier, 2012).

A study in the Hudson Bay Lowlands of Manitoba, Canada also revealed that wolves (*Canus lupus*) and other wildlife were dispersers of lichen-forming fungi but the relative importance of epizoochory versus other modes of dispersal were not evaluated (Piercey-Normore, 2008). Nevertheless, without faunal dispersers, many species of fungi may struggle to disperse from one tree island to another and the functional relationship of fungi as habitat for invertebrates, food for wildlife, decomposers, nutrient cyclers, and symbionts for healthy forest development would be reduced (Piercey-Normore, 2008; Almeida et al., 2020).

1.9.3. Herbivory

Seed dispersing fauna are not the only agents that disproportionately shape plant community structure; herbivorous fauna also strongly affect plant communities. Herbivores are known to alter plant communities in a multitude of ways, some of which are unexpectedly beneficial. In South Africa, ungulate herbivores graze across a savanna-broadleaf mosaic, but they are attracted to the high-quality understory forage in acacia-dominated tree islands. These herbivores spend more time in acacia patches than expected relative to tree island patch size and availability (i.e., habitat selection). Selection for acacia tree islands concentrates excreta deposition, delivering an inward nutrient flux that outweighs nutrient losses from erosion, leaching into groundwater, and dispersion by fires (all of which would otherwise result in gradual degradation and loss of acacia tree islands). Thus, ungulate herbivory indirectly maintains these acacia tree islands by focusing nutrient redistribution within acacia patches (Blackmore, 1990).

However, an experiment, also in South Africa, showed that ungulate herbivores browse heavily on tree seedlings growing along the edges of tree islands. Damage from browsing decreased seedling growth rates, limiting recruitment and expansion of tree islands. The negative effects of browsing were also found to be more severe when islands were impacted by fire, presumably because browsers are increasingly attracted to post-fire regrowth (Mourik et al., 2007).

More often than not, herbivory is conceptualized as a biological disturbance that damages and limits growth of the affected plant communities. Whether herbivory has a net-positive or -negative influence is dependent on the intensity of grazing/browsing pressure, how herbivores alter nutrient cycles, and whether plants can escape herbivory once they reach a certain size or developmental stage. One example of this comes from montane and krummholz islands of North America, where several species are known to browse on seedlings. Black grouse (*Lyrurus tetrix*) and ptarmigan (*Lagopus mutus, Lagopus lagopus, Lagopus leucurus*) stunt the growth of young trees by consuming buds and terminal shoots, which make up nearly all of their winter diet (Holtmeier, 2009). Jackrabbits (*Lepus spp.*) also restrict seedling growth by repeatedly consuming seedlings' tips. Once seedlings grow tall enough such that the edible portions exceed the accessible range of grouse, ptarmigan, and jackrabbits, seedlings escape their browsing pressure. However, these taller, more mature plants still receive browsing pressure from mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*), thereby limiting tree island growth during all stages of tree development (Walker, 2021).

Fossorial and semi-fossorial animals, like rodents (Family *Cricetidae*) are also regular inhabitants of and have a very influential role in montane tree islands. Rodents are capable of substantially restricting seedling establishment and reducing tree growth by regularly predating on seeds and seedlings (Bekker & Malanson, 2008; Munier et al., 2010). Pocket gophers (*Thomomys bottae*) are noted as particularly impactful because in addition to seed and seedling predation, they girdle seedlings, clip roots, and uproot trees as they excavate subterranean tunnels (Bekker & Malanson, 2008). Thus, tree islands attract a broad range of herbivores with different foraging behaviors that limit tree growth through multiple pathways, making it a major restrictive force on tree island development.

1.9.4. Bioturbation

Pocket gophers and other fossorial species can also exert indirect stresses on trees downwind of them. When fossorial animals burrow, soil is brought up to the surface and loose particles are readily carried by the wind. The airborne sediment abrades the windward side of downwind tree islands, damaging the most exposed individuals and hampering upwind growth of tree islands (Holtmeier, 2009).

On the other hand, aeolian sedimentation from burrowing animals can positively affect tree island growth. In the Mojave Desert, rodent burrowing activity contributes to the aeolian sediment load, from which dust deposits and accumulates around impediments to air flow, such as rocks, plants, and irregular terrain. The impediments progressively form mounds of sediment that may function as points of formation for fertility islands or expand existing islands (Pietrasiak, 2012).

Burrowing activity by vertebrates and invertebrates also contributes to fertility island development and expansion in the immediate vicinity of faunal burrows because soil mixing alters soil structure and chemistry in ways that tend to promote tree growth (Daryanto & Eldridge, 2012). Gabet et al. (2005) found that upheaval of deeper soils to the surface via pocket gophers burrowing is the primary mechanism for soil and nutrient input in the soil creep process (i.e., downslope movement of soil and nutrients) of California’s semi-arid grasslands. Bioturbation by soil dwelling and fossorial fauna can also reduce the bulk density of soil, thereby increasing water infiltration rates. In Brazil, ant mound- and tunnel-building was found to generally increase soil aeration and infiltration (Leite et al., 2018).

These changes in soil structure form microtopographic mounds because fauna locally increase sediment, reduce bulk density, or induce soil-swelling from increased infiltration. All of these effects serve to improve growing conditions for plants and could lead to fertility island development if the effects of bioturbation are localized and strong enough (Mora & Lázaro, 2013).

Bioturbation can also influence tree island development by altering the soil nutrient profile. Fertility islands originating from termite or ant mounds are common in semi-arid and arid environments across the world, largely because bioturbation of soils, off-mound foraging, and within nest food storage concentrates nutrients in and around mounds (Araujo, 2013; Müller, 2013; Kitivo et al., 2015; Cramer et al., 2016). Smith (2014) found that granivorous ants increased soil C and N pools by 14% through harvesting and transporting seeds to their belowground nests. Smith also found that when native semi-fossorial mammals were reintroduced to fertility islands in New South Wales, Australia, soil organic carbon increased because these species create "foraging pits" that trap and facilitate the downward transport of nutrients into the soil.

Surficial foraging pits (a.k.a digs or excavations) and the associated localized increase in soil nutrients has also been studied in Glacier National Park. In this system, grizzly bears often dig in subalpine meadows surrounding tree islands of subalpine fir (*Abies lasiocarpa*) and white bark pine (*Pinus albicaulis*) to forage on plant roots, insects, and small mammals. Experimental and observational data revealed grizzly bear dig sites significantly increased mineral nitrogen (NH_4^+-N and NO_3^--N) in soils which contributed to increased plant growth and seed production (Tardiff & Stanford, 1998).

Black bears in non-tree island habitats of South Florida have been reported to excavate for belowground food sources, namely alligator eggs and invertebrate species (Maehr & Brady, 1984; Maehr, 1997). Although not yet reported in the literature, black bears have been observed digging for reptilian eggs on tree islands, and fecal samples indicate they also dig for belowground insects on tree islands. Bioturbation in Everglades tree island soils is common among black bears and other species that forage for belowground food sources (e.g., feral hogs, vultures, crows) and species that conceal eggs in shallow excavations (e.g., turtles and snakes) (observation, 2022). Bioturbation by burrowing animals and insects is also expected to occur on Everglades tree islands, but the prevalence and effects of this process remain unstudied (Coultas et al., 2008).

CONCLUSION

The range and abundance of tree island ecosystems across the world is vast. The ubiquity of tree islands is attributed to the interaction between landscape heterogeneity, positive feedbacks of self-organization, and strong exogenous stressors. These three ecological facets must be balanced for tree islands to develop and persist. If self-organizing feedbacks outweigh stressors, islands will coalesce into contiguous forest, and if stressors outweigh self-organizing feedbacks, islands will degrade into the matrix habitat; landscape heterogeneity moderates the distribution and prevalence of potential tree island sites within a system. Landscape heterogeneity, feedbacks, and stressors exist under all environmental conditions and are embodiments of the surrounding environment. Consequently, tree islands can differ drastically across tree island systems and even within the same system, with variation in geomorphic shapes and sizes, climatic conditions, hydrologic regimes, fire regimes, nutrient regimes, flora, and fauna. Among these fundamental components of tree island ecosystems, fauna is generally studied the least and, in many systems, there has been no direct effort to study the wildlife. However, the amalgamation of findings to date has revealed wildlife is heavily reliant on tree islands for habitat and resources. Reciprocally, tree islands are profoundly affected by wildlife. Echoing the words of many previous researchers, research effort and knowledge on tree islands has advanced substantially since the previous literature review by Wetzel (2002) but there is still a dearth of information (especially regarding tree island-fauna relationships) that must be addressed to improve conservation, management, and restoration of tree islands globally.

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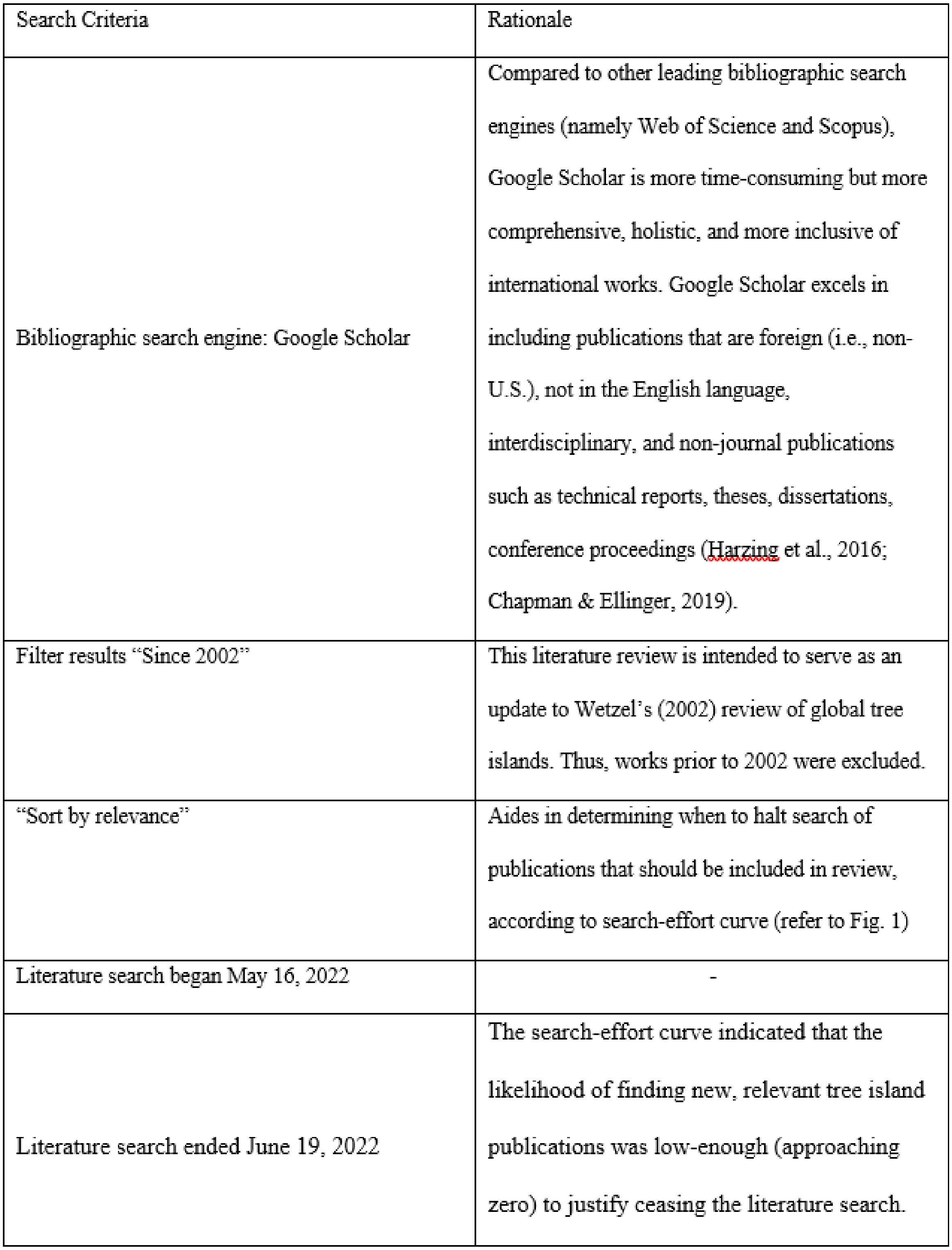
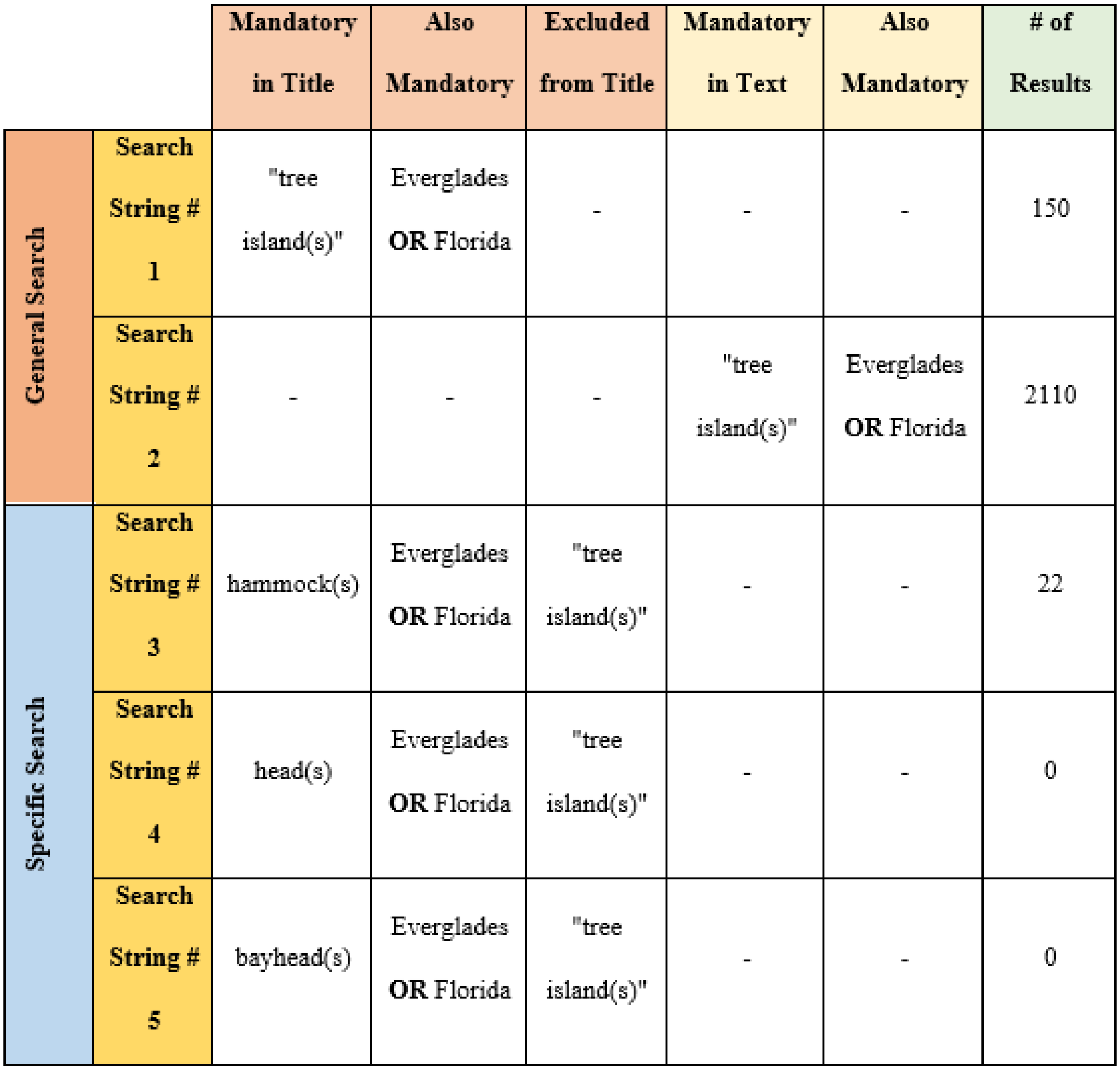
APPENDIX

Table 1. Search Criteria of Literature Review



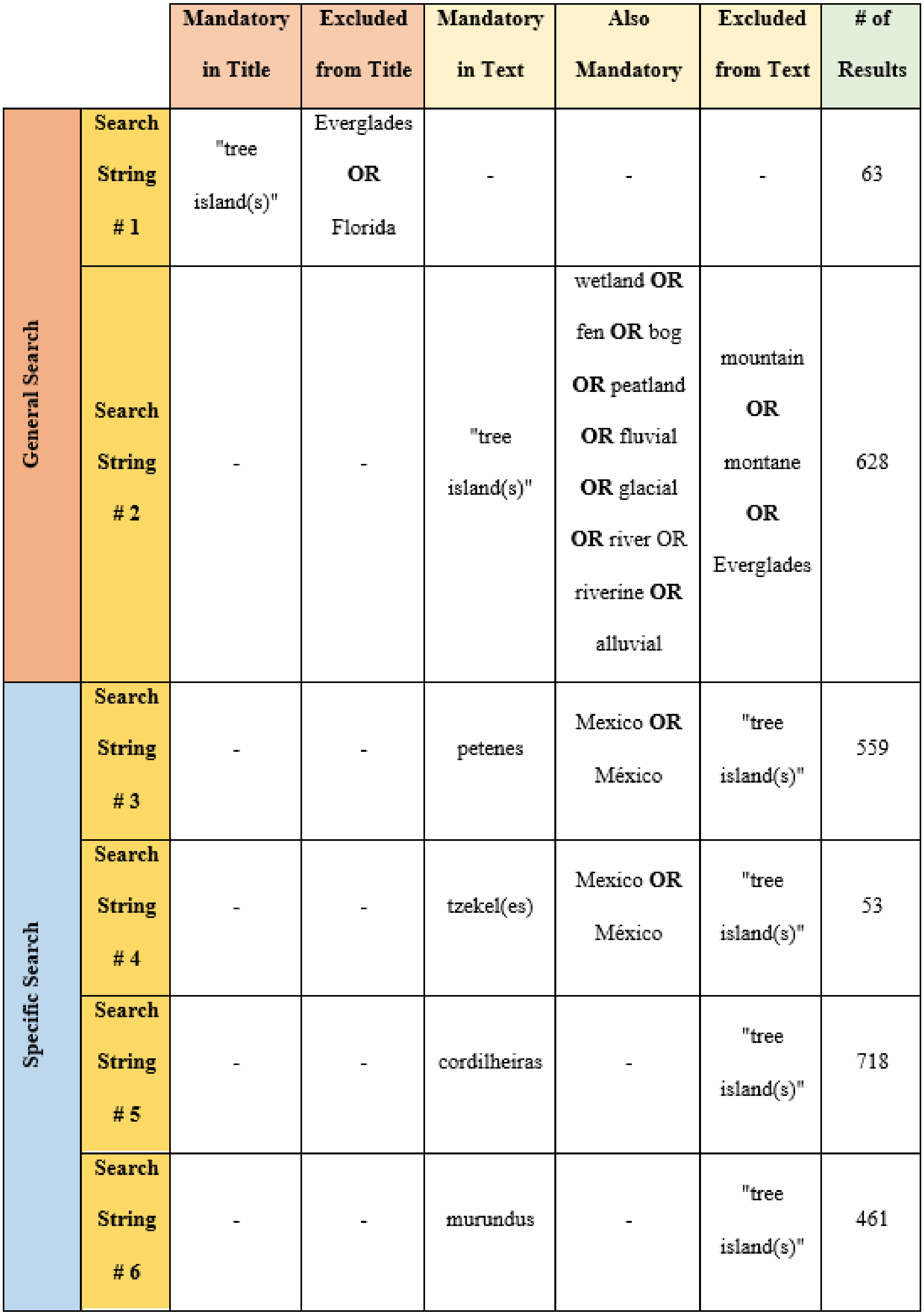
Search Criteria	Rationale
Bibliographic search engine: Google Scholar	Compared to other leading bibliographic search engines (namely Web of Science and Scopus), Google Scholar is more time-consuming but more comprehensive, holistic, and more inclusive of international works. Google Scholar excels in including publications that are foreign (i.e., non-U.S.), not in the English language, interdisciplinary, and non-journal publications such as technical reports, theses, dissertations, conference proceedings (Harzing et al., 2016; Chapman & Ellinger, 2019).
Filter results "Since 2002"	This literature review is intended to serve as an update to Wetzel's (2002) review of global tree islands. Thus, works prior to 2002 were excluded.
"Sort by relevance"	Aides in determining when to halt search of publications that should be included in review, according to search-effort curve (refer to Fig. 1)
Literature search began May 16, 2022	-
Literature search ended June 19, 2022	The search-effort curve indicated that the likelihood of finding new, relevant tree island publications was low-enough (approaching zero) to justify ceasing the literature search.

Table 2. Search Terms for Florida Everglades Tree Islands



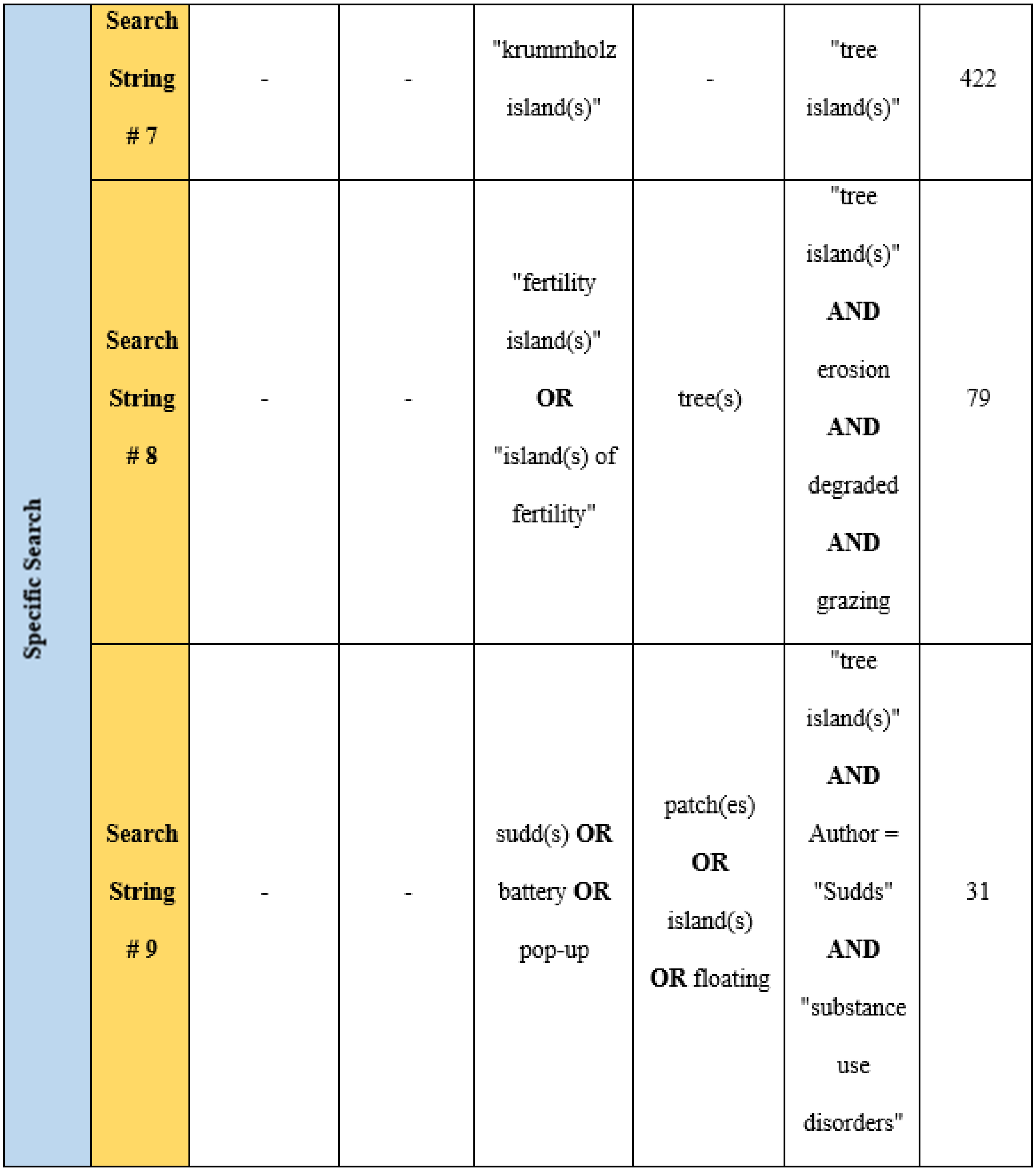
		Mandatory in Title	Also Mandatory	Excluded from Title	Mandatory in Text	Also Mandatory	# of Results
General Search	**Search String # 1**	"tree island(s)"	Everglades **OR** Florida	-	-	-	150
	Search String # 2	-	-	-	"tree island(s)"	Everglades **OR** Florida	2110
Specific Search	**Search String # 3**	hammock(s)	Everglades **OR** Florida	"tree island(s)"	-	-	22
	Search String # 4	head(s)	Everglades **OR** Florida	"tree island(s)"	-	-	0
	Search String # 5	bayhead(s)	Everglades **OR** Florida	"tree island(s)"	-	-	0

Table 3. Search Terms for Non-Everglades Tree Islands



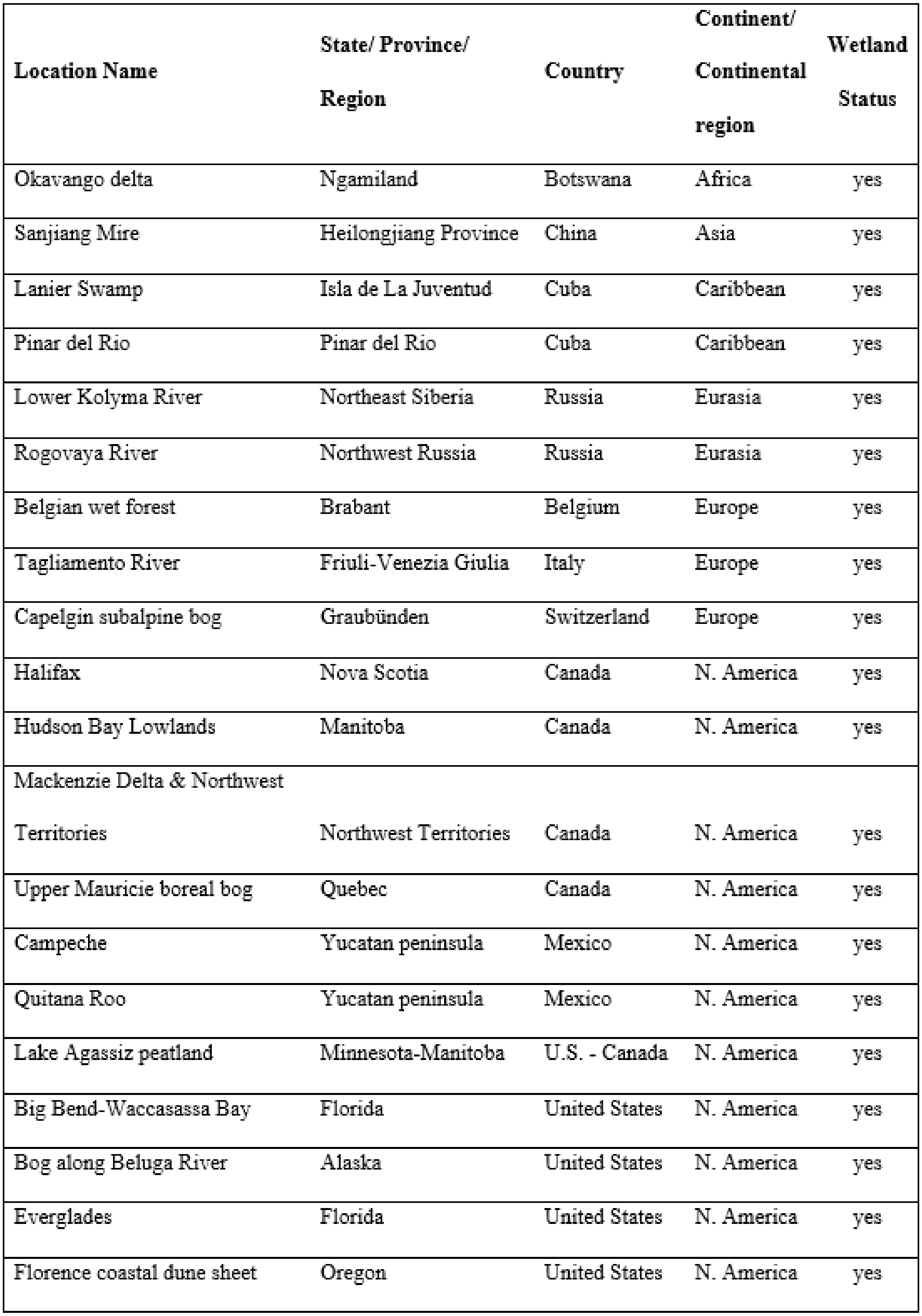
		Mandatory in Title	**Excluded from Title**	**Mandatory in Text**	**Also Mandatory**	**Excluded from Text**	**# of Results**
General Search	**Search String # 1**	"tree island(s)"	Everglades **OR** Florida	-	-	-	63
	Search String # 2	-	-	"tree island(s)"	wetland **OR** fen **OR** bog **OR** peatland **OR** fluvial **OR** glacial **OR** river OR riverine **OR** alluvial	mountain **OR** montane **OR** Everglades	628
Specific Search	**Search String # 3**	-	-	petenes	Mexico **OR** México	"tree island(s)"	559
	Search String # 4	-	-	tzekel(es)	Mexico **OR** México	"tree island(s)"	53
	Search String # 5	-	-	cordilheiras	-	"tree island(s)"	718
	Search String # 6	-	-	murundus	-	"tree island(s)"	461

Table 3. Search Terms for Non-Everglades Tree Islands (Continued)



Specific Search	**Search String # 7**	-	-	"krummholz island(s)"	-	"tree island(s)"	422
	Search String # 8	-	-	"fertility island(s)" **OR** "island(s) of fertility"	tree(s)	"tree island(s)" **AND** erosion **AND** degraded **AND** grazing	79
	Search String # 9	-	-	sudd(s) **OR** battery **OR** pop-up	patch(es) **OR** island(s) **OR** floating	"tree island(s)" **AND** Author = "Sudds" **AND** "substance use disorders"	31

Table 4. Tree Island Systems Identified During Literature Searches

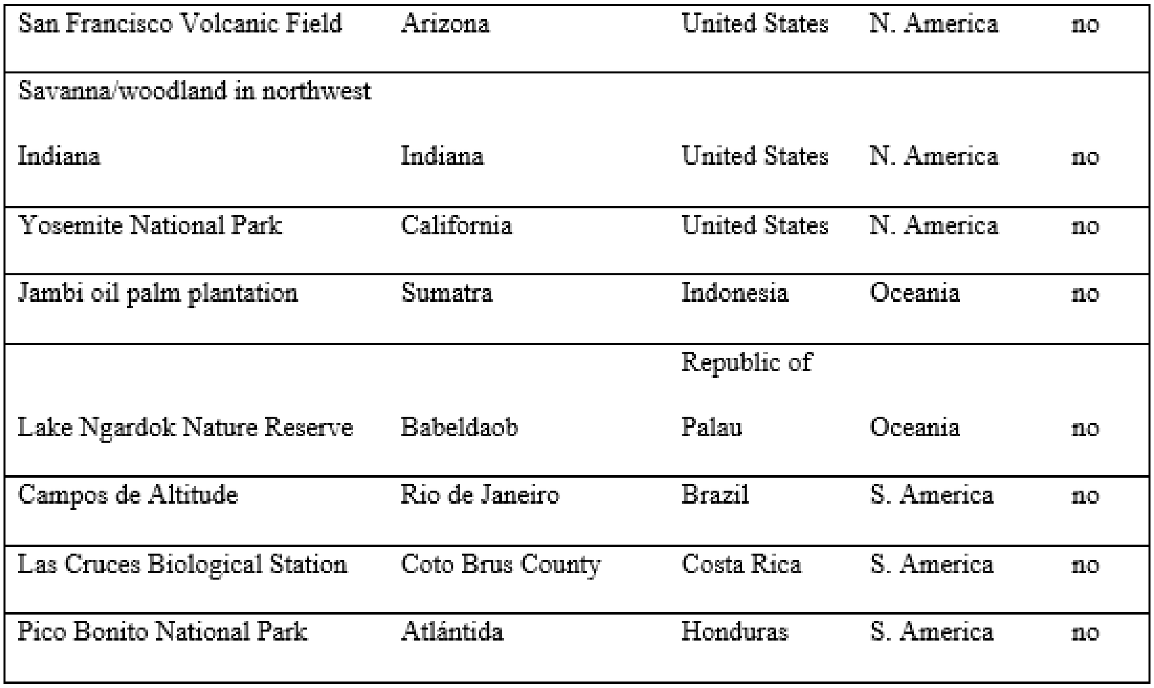


Location Name	**State/ Province/ Region**	**Country**	**Continent/ Continental region**	**Wetland Status**
Okavango delta	Ngamiland	Botswana	Africa	yes
Sanjiang Mire	Heilongjiang Province	China	Asia	yes
Lanier Swamp	Isla de La Juventud	Cuba	Caribbean	yes
Pinar del Rio	Pinar del Rio	Cuba	Caribbean	yes
Lower Kolyma River	Northeast Siberia	Russia	Eurasia	yes
Rogovaya River	Northwest Russia	Russia	Eurasia	yes
Belgian wet forest	Brabant	Belgium	Europe	yes
Tagliamento River	Friuli-Venezia Giulia	Italy	Europe	yes
Capelgin subalpine bog	Graubünden	Switzerland	Europe	yes
Halifax	Nova Scotia	Canada	N. America	yes
Hudson Bay Lowlands	Manitoba	Canada	N. America	yes
Mackenzie Delta & Northwest Territories	Northwest Territories	Canada	N. America	yes
Upper Mauricie boreal bog	Quebec	Canada	N. America	yes
Campeche	Yucatan peninsula	Mexico	N. America	yes
Quitana Roo	Yucatan peninsula	Mexico	N. America	yes
Lake Agassiz peatland	Minnesota-Manitoba	U.S. - Canada	N. America	yes
Big Bend-Waccasassa Bay	Florida	United States	N. America	yes
Bog along Beluga River	Alaska	United States	N. America	yes
Everglades	Florida	United States	N. America	yes
Florence coastal dune sheet	Oregon	United States	N. America	yes

Table 4. Tree Island Systems Identified During Literature Searches (Continued)

Smith Island	Maryland	United States	N. America	yes
Savannah River	Georgia	United States	N. America	yes
Seney patterned fen	Michigan	United States	N. America	yes
Waccamaw River	South Carolina	United States	N. America	yes
Cerrado ecoregion	Mato Grosso do Sul	Brazil	S. America	yes
Maraca Island Ecological Reserve	Roraima	Brazil	S. America	yes
Pantanal	Mato Grosso do Sul	Brazil	S. America	yes
Llanos Orientales	Central Colombia	Colombia	S. America	yes
El Cajas National Park	Andes Mountains	Ecuador	S. America	yes
Changbai Mountains	Northeast China	China	Asia	no
Guangdong subtropical shrubland	Guangdong	China	Asia	no
Stift Heiligenkreuz forest estate	Austrian Alps	Austria	Europe	no
Queyras-Mount Viso area	French-Italian Alps	France-Italy	Europe	no
Jasper National Park	Alberta	Canada	N. America	no
Archbold Biological Station	Florida	United States	N. America	no
Charleston Peak	Nevada	United States	N. America	no
Glacier National Park	Montana	United States	N. America	no
Great Basin Desert	Utah	United States	N. America	no
Guánica Dry Forest	Puerto Rico	United States	N. America	no
Niwot Ridge	Colorado	United States	N. America	no
North Cascade Range	Washington	United States	N. America	no
Point Reyes National Seashore	California	United States	N. America	no

Table 4. Tree Island Systems Identified During Literature Searches (Continued)



San Francisco Volcanic Field	Arizona	United States	N. America	no
Savanna/woodland in northwest Indiana	Indiana	United States	N. America	no
Yosemite National Park	California	United States	N. America	no
Jambi oil palm plantation	Sumatra	Indonesia	Oceania	no
Lake Ngardok Nature Reserve	Babeldaob	Republic of Palau	Oceania	no
Campos de Altitude	Rio de Janeiro	Brazil	S. America	no
Las Cruces Biological Station	Coto Brus County	Costa Rica	S. America	no
Pico Bonito National Park	Atlántida	Honduras	S. America	no

CHAPTER II. ENVIRONMENTAL DRIVERS OF MAMMAL DIVERSITY AND METACOMMUNITY STRUCTURE ON EVERGLADES TREE ISLANDS

INTRODUCTION

A metacommunity is a network of non-contiguous local communities that are ecologically linked through the dispersal of their constituent species (Leibold & Chase, 2017). Metacommunity theory provides a robust framework to analyze how community composition and spatiotemporal species distributions are controlled by local and regional processes, environmental heterogeneity, species' interactions, and dispersal. Thus, metacommunity theory is ideal for investigating ecological patterns and dynamics in spatially disjunct or patchily distributed ecosystems. Patchiness often results from human alterations to the landscape, but naturally fragmented, patchy ecosystems are common as well.

Many concepts from habitat loss and fragmentation studies have carried over to metacommunity theory because continuously increasing human influence across the world has significantly altered and augmented fragmentation in naturally patchy systems like the Florida Everglades, United States (Tilman et al., 1994; Kupfer, 1995; Gonzalez et al., 2011). The Everglades is comprised of several interconnected habitat types that exist as a mosaic. In the interior or central Everglades, sawgrass marsh and deeper sloughs cover most of the area, forming an herbaceous wetland matrix with dense sawgrass ridges and tree islands scattered throughout the landscape (Heisler et al., 2002; Bernhardt, 2011). Tree islands are groups of trees and woody vegetation, usually associated with soil mounds elevated above the surrounding matrix. The relatively well-drained condition of tree islands allows their characteristic trees and upland flora to exist as inclusions in a landscape that otherwise experiences too much inundation for their survival.

The discontinuous distribution of Everglades tree islands subdivides this ecosystem into spatially and environmentally distinct patches. Despite the discreteness of tree islands, they share similar abiotic characteristics, ecosystem processes, and communities of flora and fauna that are functionally connected to one another through dispersal. Thus, the ecological similarity and connectivity between tree islands forms a metacommunity at the regional scale (Leibold & Chase, 2017). However, the natural structure and distribution of species across the tree island metacommunity has been complicated by anthropogenic influences on the Everglades ecosystem.

Changes to the physical structure and hydrology of the landscape began circa 1880 with the construction of a system of canals and levees that drained South Florida to make the land more conducive for agriculture and urban development (Light & Dineen, 1994). Drainage efforts accelerated in the mid-1900s, with the focus shifted towards water control and flood prevention in developed areas. The sprawling canal and levee system fragmented the Everglades into disjunct “compartments” that disrupted the natural sheet flow. Compartmentalization also resulted in extreme high- and low-water levels, unnatural hydroperiods, and hydrologically mediated changes to fire regimes (Sklar & van der Valk, 2002).

Altered hydrology and soil consuming muck fires have been the most deleterious anthropogenic factors affecting Everglades tree islands, but increased nutrient and pollutant concentrations, as well as the expansion of invasive plants have also contributed to tree island degradation (Zaffke, 1983; Pemberton & Ferriter, 1998; Sklar & van der Valk, 2002; Gu et al., 2013; Rodgers et al., 2018). Currently, fewer than half of all pre-drainage tree islands remain in the landscape and their total area has dwindled down to a little more than 30% of their original extent (Patterson and Finck, 1999). These changes reduced patch size and increased distance between patches, altering the landscape structure and increasing effects of habitat fragmentation. The habitat quality of remnant tree island patches also degraded from elevational loss, shifts in plant community structure, and loss of floral diversity as fire and flood events reduced terrestrial refugia for the tree islands' upland plant communities (Wetzel et al., 2008; Aich et al., 2014).

In addition to providing terrestrial refugia for flood-intolerant flora, tree islands are also considered habitats of critical importance to the survival and well-being of native wildlife (Sklar & van der Valk, 2002). Therefore, the degraded condition of tree islands is a major problem for Everglades fauna because these forests provide them with essential food sources, dry refugia, and breeding and nesting sites (Labisky, 2003; Eckles, 2013; Buckman, 2021). Mammals are presumed to be the taxa most reliant on tree islands because mammals require dry land for most, or all, of their habitat and life history requirements and tree islands provide the only dry refuge in the central Everglades. Even semi-aquatic mammals that spend much of their time in the water, like the river otter (*Lotra canadensis*), require dry ground to socialize, rest, mate, rear offspring, and consume large prey (Hamilton, 2014). The availability of suitable habitat, ecosystem functions, and resources that tree islands provide have already diminished with the degradation and loss of tree islands, the ramifications of which have been observed through the decline of mammalian diversity, abundance, and distributions since the pre-drainage era (Schemnitz, 1974; Smith & Bass, 1994; USACE, 1999; Dorcas *at* al., 2012; Margenau, 2021).

Despite consensus among ecologists and management agencies that the relationships between tree islands and the mammalian metacommunity are crucial for successful wildlife management and ecosystem-wide restoration in the Everglades, research in this field has been limited (Smith & Vrieze, 1979; Gaines et al., 2002; McDonald & Labisky, 2005; Eckles, 2013). Most studies to date have investigated the response of rodents or whitetail deer (*Odocoileus virginianus*) to punctuated flood events, omitting other mammals. Also, these studies focused on hydrology as the ecological driver for mammalian habitat use and movement but excluded other potentially influential factors such as landscape connectivity, patch size, habitat quality, vegetative characteristics, breeding seasons, and other phenological changes.

The paucity of research has left several fundamental research questions uninvestigated. The following research questions and hypotheses were developed to begin filling in this knowledge gap.

- Q_1

How does severity of matrix-derived stress (i.e., deep and prolonged flooding in matrix surrounding tree islands, and inundation of tree islands) affect species diversity at several scales in the mammal metacommunity?

- H_1

Increased matrix-derived stress will decrease alpha (α), mean alpha ($\bar{\alpha}$), and gamma (γ) diversity, while increasing “true” beta diversity ($\beta = \gamma / \bar{\alpha}$) because species’ hydrologic tolerances exist along a gradient, and as hydrologic stress increases across tree islands, the number of species whose hydrologic tolerances exceed the hydrologic stress becomes reduced. Increased matrix-derived stress will also increase compositional beta diversity (dissimilarity between sites’ community compositions) because the flooded matrix will hamper dispersal, so species will be arranged on patches whose environmental conditions are best suited for that species' prolonged or indefinite persistence on the island.

- *Q_2*

How does tree island landscape structure (i.e., patch size, connectivity to neighboring patches, and proximity to sources) affect mammalian alpha diversity?

- *H_2*

Reduced tree island patch size and connectivity to neighboring tree islands and source populations will reduce mammalian alpha diversity. Alpha diversity of a patch is subject to the effects of patch size, as this controls the total available habitat and influences the number of conspecific and heterospecific individuals that can coexist on a patch (Simberloff, 1974). Mammalian alpha diversity on tree islands will also be influenced by connectivity between neighboring tree islands (i.e., the number and/or areal cover of neighboring patches) because these mammals must disperse between multiple tree island patches, even in the same day, to satisfy all their habitat and resource requirements. Similarly, a tree island's alpha diversity will be affected by its proximity to a source population, because sources provide a steady supply of migrants from various species and the closer a tree island is to the source, the more likely it will be colonized by migrants (MacArthur & Wilson, 1967). Thus, tree islands of smaller patch sizes will not be able to support as many species as larger patches. Also, reduced connectivity between patches and to a source population will decrease the likelihood of species successfully dispersing to those patches, further reducing alpha diversity.

- *Q_3*

How does spatial variation in matrix-derived stress factors affect metacommunity structure?

- *H_3*

The severity of matrix-derived stress will markedly affect the three aspects of metacommunity structure – coherence, range turnover, and boundary clumping.

  - Coherence is the measure of how filled species' ranges are when the metacommunity is fit to a single environmental gradient (Leibold & Mikkelson, 2002). The study system is characterized by moderate to high levels of matrix-derived stress and limited patches of suitable habitat. Thus, it is hypothesized that environmental filtering will be a stronger controlling force than competition or other biotic relationships, so the metacommunities will exhibit positive coherence. Relative to high-stress systems, moderate levels of matrix-derived stress will have higher coherence because species' dispersal capability to suitable habitat patches will be higher. Meanwhile, high matrix stress will limit dispersal and decrease metapopulation size, so coherence will remain positive but will be relatively low as fewer individuals occupy available patches.
  - Turnover is the number of replacements between species along the environmental gradient (Leibold & Mikkelson, 2002). Turnover will increase with stress because dispersal limitation will isolate assemblages on patches for extended periods of time, increasing intrapatch competition pressure between conflicting and mutually exclusive species combinations. The caveat is if stressors are high, but population densities are very low, such that mutually exclusive species rarely encounter each other, then turnover may be negative.
  - Boundary clumping describes how species ranges are distributed along the environmental gradient (Leibold & Mikkelson, 2002). Boundary clumping will

increase with matrix stress because intensified mutual exclusivity and limited dispersal among assemblages will force more species combinations to replace each other across their distributional ranges than in a less pressured system, where species can disperse to mitigate these pressures.

Considering these metacommunity aspects and the hypothesized dynamics in this study system, three potential metacommunity structures emerge and are dependent on the level of matrix-derived stress and population densities (Fig. 1). In the first scenario, a metacommunity experiences high levels of stress but has sufficiently high populations for species interactions to engender mutual exclusion at local patches; under these conditions, the metacommunity will follow the positive coherence, turnover, and boundary clumping pathway to produce a ‘Clementsian’ structure. In the second scenario, high stress has reduced population densities such that conflicting species interactions are minimal and mutual exclusion does not occur; in which case the metacommunity will follow the positive coherence, negative turnover, and positive boundary clumping pathway, to produce a ‘nested clumped’ structure. In the third scenario, matrix-derived stress is low enough to facilitate regular dispersal; regardless of population densities, the metacommunity will follow the positive coherence, negative turnover, and negative boundary clumping pathway, to produce a ‘nested hyperdispersed’ structure (Fig. 1).

boundary clumping pathway, to produce a ‘nested hyperdispersed’ structure (Fig. 1).

- Q_4

What ecological factors drive mammalian distributions and habitat use across habitat patches.

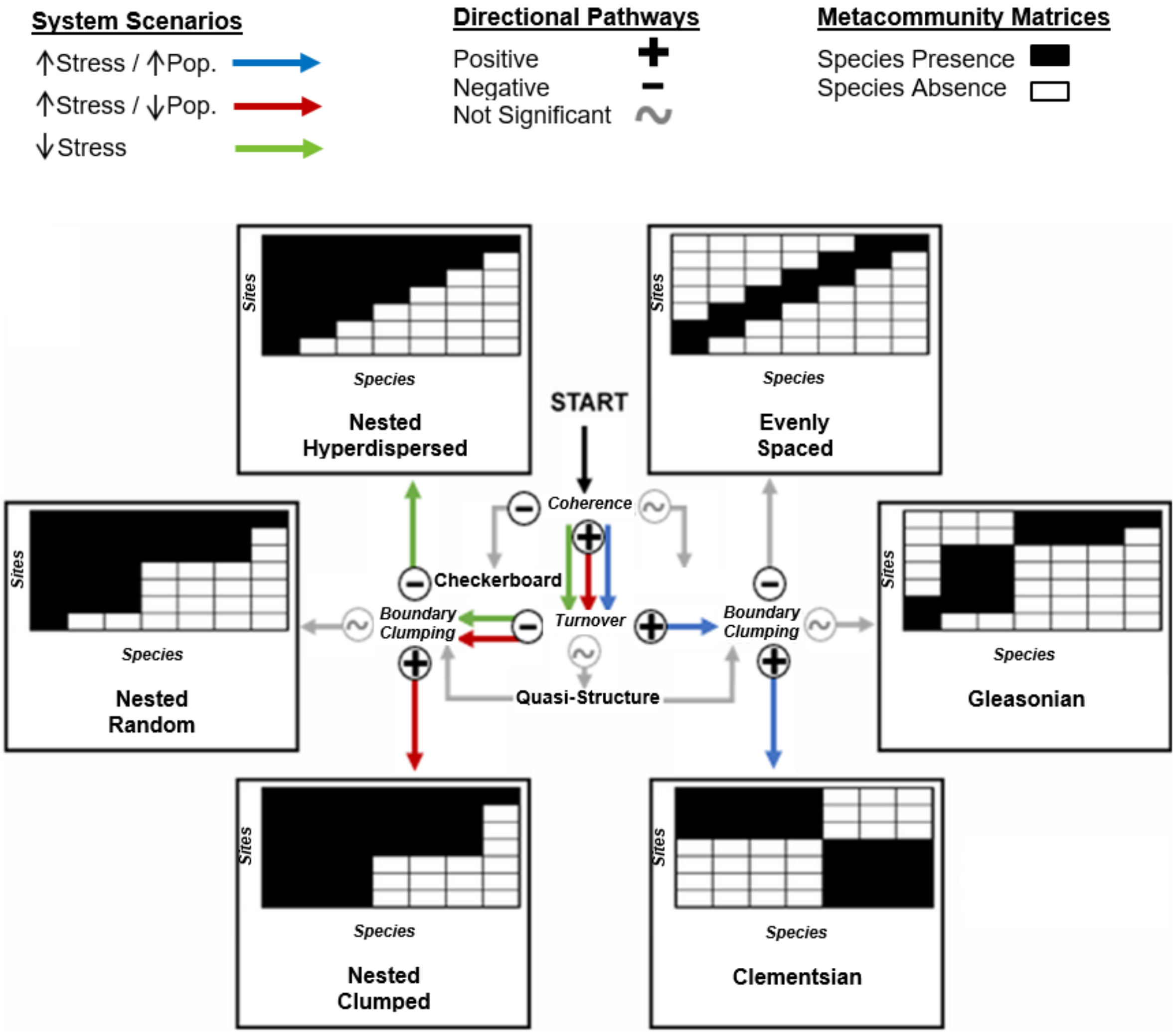


Figure 1. Conceptual pathway showing how metacommunity patterns are determined by different aspects of metacommunity structure. Colored arrows represent the three ecological scenarios discussed in hypothesis 3 and their predicted pathways; grey arrows are other potential pathways that the scenarios are not hypothesized to follow. The blue arrow represents a metacommunity with a high population but high matrix-derived stress that severely limits dispersal (first scenario, as described above). The red arrow represents a metacommunity with high matrix-derived stress, severely limiting dispersal, and whose population densities are low-enough such that exclusionary species interactions are negligible (second scenario, as described above). The green arrow represents a metacommunity with matrix-derived stress that is low enough to facilitate regular dispersal, regardless of population densities (third scenario, as described above). Modified from Eden et al. (2022).

❖ H_4

Mammalian distributions and habitat use will be primarily controlled by local effects of matrix-derived stress (i.e., marsh depth, relative water levels, and hydroperiod of tree islands). Although many environmental variables likely shape habitat quality, as perceived by mammals on tree islands, high levels of matrix-derived stress will ultimately limit which tree islands are accessible or habitable, thereby controlling species' distributions. Similarly, if the level of stress is below a species' tolerance threshold but sufficiently high to reduce habitat quality, then the species' habitat use will be lower relative to islands characterized by less matrix-derived stress.

To test the above hypotheses, remote monitoring data were collected on the mammalian communities of tree islands across distinct subregions of the Everglades. Patterns of mammalian metacommunity structure were assessed following the Elements of Metacommunity Structure (EMS) framework. Then, local water levels and hydroperiod were used to explain species' distributions and spatiotemporal habitat use, while controlling for other biotic and abiotic factors at regional and local (i.e., individual patch) scales.

METHODS

2.1. Site Selection

Selection of study sites was limited to "fixed" tree islands, whose nucleation is generally associated with topographic high points in the limestone bedrock and develop into a teardrop shape that tapers and slopes downward from the upstream, higher elevation head to the tail (Sklar & van der Valk, 2002). Fixed tree islands are by far the most common type of tree island across the central Everglades and exclusion of other tree island types (e.g., floating tree islands) ensures comparability of study sites because their abiotic characteristics and biogeochemical processes are similar. The study was conducted along a North—South transect, longitudinally positioned to intercept the Miccosukee Indian Reservation at its northern extent and span across four adjoining compartmentalized areas of the central Everglades: Water Conservation Area 3A North (3AN), Miccosukee Water Conservation Area 3A South (3AS), the Triangle (TRI), and Everglades National Park (ENP). A total of 40 tree islands were studied: ten in 3AN, 24 in 3AS, three in TRI, and three in ENP. Selecting tree islands across these four different study areas allows for analyses of metacommunity structure, species' distributions, relative abundances, habitat use, and environmental drivers at multiple spatial scales.

The study areas vary hydrologically, independent of their latitudinal positioning. 3AN is the northernmost and has the driest hydrologic regime; on average, the matrix dries down for several months each year. 3AS lies immediately to the south and has the wettest hydrologic regime. Also, ground elevation in 3AS slopes downward from North to South, so study islands are intrinsically aligned along a gradient of water depth, which aids in isolating hydrologic effects (Light & Dineen, 1994). The TRI is entirely within the boundaries of the Miccosukee Indian Reservation and positioned in the northwest corner of 3AS, but its hydrologic regime is drier than the rest of 3AS because compartmentalizing canals and levees restrict hydrologic inflows. The southernmost study area is ENP, which has experienced unnaturally dry conditions for decades. The variation in regional hydrology captured by this study design means that if matrix-derived stress is an influential driver of metacommunity structure, diversity, and species' habitat use (as hypothesized), it should be reflected in mammals' distributions and relative abundances across study region.

Initially, 34 study tree islands were selected randomly along the transect in 3AS and 3AN. The initial sample sites were visually inspected to assess whether they covered the full range of tree island environmental characteristics (e.g., island size, elevation, habitat, matrix water depth) in these study areas. Additional tree islands were incrementally added to the study following a stratified systematic approach: upon assessment of initial tree island characteristics, islands were added that filled gaps in trait combinations. The 3 islands in TRI were added because they are similar in size, habitat, in close proximity, and parallel in latitude to 3 islands in 3AS. An additional 3 tree islands were selected in ENP (Gumbo Limbo, Black Hammock, and Satinleaf) because these islands have been monitored for decades and extensive datasets on island elevation, hydrology, and vegetation were available. Also, these islands are distinct from the other study islands in that the highest areas on the islands have not been inundated in more than 20 years and support tropical hardwood hammocks.

2.2. Camera Trapping

Camera trapping began in December of 2017 on 4 study tree islands in 3AS. By January 2019, camera trapping included 18 tree islands in 3AS and 3 in the TRI. The 3AN islands were added in September 2019, and by August 2021, all 40 study tree islands were being monitored. Trail cameras were used to monitor mammals on the study tree islands because the cameras are a minimally invasive passive monitoring tool that can continuously and contemporaneously survey multiple sites, record large amounts of data with minimal effort, and diminish observer bias, thereby outperforming most aspects of other mammalian survey techniques (Dertien et al., 2019; Zwerts et al., 2021). The study tree islands were reached via airboat and the head was accessed by foot. Tree island heads were explored to identify the optimal location to set up a trail camera. Optimal locations include natural openings, game trails, or other areas that provided a clear range of view, so if an animal passes in front of the camera, it would be detected and clearly identifiable, free from obstructions like tree trunks, branches, etc.

One trail camera (Bushnell Trophy Cam HD Aggressor No Glow 20 mp) was deployed in the head of each tree island. Nylon straps were used to mount cameras to tree trunks or branches 0.5 m above the ground and at a ~10° downward angle; camera height varied slightly depending on microsite conditions (e.g., obstructions, understory cover, canopy height, suitable trunks to mount camera). Cameras were programmed to high-sensitivity, taking a single photo when motion was detected, followed by a 10-second interval between photos. Trail cameras were revisited at 5-to-6-week intervals to exchange batteries, download photos, and replace cameras if needed. This aided trail cameras to run without interruption, minimizing data gaps from wildlife- and weather-caused damage to the camera, or other functional issues.

All downloaded photos were manually sorted and photos with wildlife were labeled by species or the narrowest taxonomic rank. Important behavioral information was also included in the photo label to aid interpreting results of species' temporal habitat use. For instance, it would be valuable to note that a bear repeatedly visited a particular tree island in the month of May to forage on turtle eggs, as this might affect the number of monthly occurrences. Similarly, demographic data were included if determinable. For instance, whitetail deer could typically be identified as fawns when spots were present on their coat and according to sex by the presence of antlers or other sexual dimorphisms. When a species was captured on camera multiple times in less than 60 minutes, it was recorded as one occurrence unless there was obviously another individual (e.g., male whitetail deer can be uniquely identified by antler structure), in which case each distinct individual would be counted as an additional occurrence. To account for variation in sampling periods and the number of days each camera was operational (i.e., trap days), occurrence data were transformed into a relative abundance index (RAI) by summing monthly and annual occurrences, then dividing by the number of camera trap days. The RAI most accurately represents species' habitat use because multiple occurrences can be recorded from the same individual, and RAI can fluctuate temporally (e.g., monthly), without fluctuations in species abundance. However, RAI can also represent relative abundance if RAI is measured across sites during the same timeframe, or across time at the same site because RAI is expected to vary proportionally to species abundance in these scenarios.

The protocol for mice and rats (hereon, collectively referred to as rats) differed slightly: the occurrence interval for rats was 30 minutes. This shorter interval was selected because rats have far higher population densities and smaller territories than other mammals observed on tree islands. Thus, multiple rat detections after 30 minutes are likely to capture multiple individuals. Note, the shorter interval inflates rat RAI relative to other species, but interspecific comparison of species relative abundances or habitat use (e.g., are there more rats than raccoons) is not of analytical interest and does not interfere with any statistical tests described in this research. Photos of rats were problematic because they were often detected at night and individuals were moving quickly, resulting in obscure photos of individuals that were rarely identifiable to the species-level (except for black rats (*Rattus rattus*), whose tails are uniquely longer than their head and body). Consequently, most photos of rats could only be labeled as "rats", lumping all potential species, i.e., cotton mouse (*Peromyscus gossypinus*), marsh rice rat (*Oryzomys palustris*), hispid cotton rat (*Sigmodon hispidus*), house mouse (*Mus musculus*), Norway rat (*Rattus norvegicus*), and black rat (*Rattus rattus*)) into a single group, despite known differences in behavior, life history, and spatiotemporal habitat use (Smith & Vrieze, 1979; Gaines et al., 1998; Gaines et al., 2002; Fernandez et al., 2008; Chapman, 2019).

2.3. Landscape Characteristics

The stressfulness of the inundated matrix, limited availability of suitable habitat patches, and high variation of patch characteristics within and across the metacommunities make it very important to account for the influence of landscape on mammalian distributions and use of tree islands. Remote sensing to digitize the study tree islands was performed through ArcGIS Pro using the orthorectified World Imagery Basemap (0.3 m resolution in continental United States), because this map provided stark contrasts in vegetation that made tree island boundaries readily distinguishable from the surrounding matrix habitats. Tree island head area and connectivity between neighboring islands were determined. Assessing landscape connectivity can be a practical quandary because the most feasible methods, such as the nearest neighbor index (Euclidean distance from one patch to the closest neighboring patch), often yield oversimplified results. Meanwhile, more sophisticated indices typically require data on species' movement or dispersal abilities, which must be obtained from the study region or a similar landscape where species' dispersal is assumed to be comparable (Kindlmann & Burel, 2008). However, the data required for these species-specific approaches to measuring connectivity do not exist, and pursuit of such data is outside the scope of this research. Instead, a concentric ring approach was developed, in which multiple "rings" were established 100 m, 250 m, 500 m, 1000 m, and 2000 m away from the perimeter of each study tree island to capture heterogeneity of landscape connectivity at multiple spatial scales, which may be related to species' inferred dispersal abilities. The smallest ring was 100 m because it is rare for neighboring tree islands to be within 100 m of one another and a smaller spatial scale would not capture sufficient data to detect any meaningful patterns. The largest ring was 2000 m, the average Euclidean distance a male black bear (the species and demographic with the greatest dispersal capability among Everglades mammals) are reported to travel in a single day (Karelus et al., 2017). The latter study was in a drier habitat of North Florida but bear movement patterns were very similar to those found by Maehr (1996) in Southwest Florida and the Miccosukee Tribe Fish and Wildlife Department (unpublished data, 2023) east of Big Cypress National Preserve. The number and total area of neighboring tree islands from each study island to each ring was calculated in ArcGIS Pro. These data were incorporated into a multiple linear regression (via dbRDA, described in Statistical Analyses) to determine which spatial scale of connectivity between tree islands was most ecologically relevant to the overall mammal metacommunity.

Matrix habitat and associated barriers to dispersal are important landscape characteristics to include in analyses because they affect species' dispersal, thereby influencing distributions (Ricketts, 2001; Kupfer et al., 2006). In the central Everglades, marsh water depth is the primary barrier to dispersal for mammals. The average marsh ground elevation was calculated for each spatial ring with the Everglades Depth Estimation Network (EDEN) xyLocator tool by extracting elevation data from each grid cell that lay within a ring's perimeter. Although EDEN marsh elevation data have been smoothed to avoid bias from 'upland' habitat such as tree islands (Liu et al., 2009), EDEN cells in which tree islands comprised ≥25% of cell area were omitted from calculations. Matrix water depth time series were calculated for each spatial ring by subtracting daily marsh water level from the average marsh elevations in the respective EDEN cells. Marsh dry downs were calculated as the greatest number of continuously dry days in Water Years 2019 – 2023 (a "Water Year" spans from May 1 – April 30 of the following year (e.g., Water Year 2019 = May 2018 – April 2019), beginning at the onset of the wet season in South Florida). The mean marsh depth was calculated by averaging daily marsh depth estimates from Water Year (May – April) 2019 – 2023. The mean high-water depth was calculated by averaging daily marsh depth estimates during the six months of each Water Year (2019 – 2023) that marsh water levels were highest. The interannual mean and maximum annual amplitude of marsh depth from Water Year 2019 – 2023 were also used as hydrologic variables. Annual marsh amplitudes were calculated for each spatial ring by subtracting the shallowest daily marsh depth from the deepest in each Water Year. Interpolated EDEN marsh data were not available in the TRI study area, but marsh water levels were estimated by adding daily water levels from L28S1, the closest water level gauge (4 km away) to the 3 TRI tree islands' field-measured elevations relative to plot water depth (discussed below). A continuous water level monitoring gauge was eventually deployed, centrally located between the 3 TRI tree islands, and confirmed that the L28S1 canal water level fluctuated synchronously and to a similar extent as marsh water levels.

The structure and distribution of species in a metacommunity can be heavily impacted by the presence and proximity of patches to a mainland or source populations (MacArthur & Wilson, 1967; Altermatt, 2013; Bogoni et al., 2018; Wehr et al., 2023). Large, contiguous tracts of forested habitat are considered source populations for mammals in this study system; however, the only such source is Big Cypress National Preserve, located to the west of 3AS. The levees that border each study area may function similarly to sources by providing a rescue effect to nearby tree islands because the levees' elevations are high enough to avoid inundation, even during extreme flood events. The shortest Euclidean distance from each study tree island to Big Cypress (only in 3AS) or the nearest levee was calculated in ArcGIS Pro.

2.4. Elevation Survey

Elevation closely interacts with water levels to determine local hydrologic conditions and vegetation type of Everglades tree islands. Thus, tree island elevation is vital for Everglades mammals because they require a dry site of suitable forest cover for reproduction, refuge, food acquisition, and other species-specific behaviors. As water levels surrounding tree islands fluctuate, dry land availability and elevation relative to the water surface fluctuate accordingly.

Extreme water levels from October 2020 – January 2021 completely inundated tree islands and provided an opportunity to survey tree island elevations in 3AN, TRI, and 3AS; elevations of tree islands in ENP had previously been surveyed by Florida International University's South Florida Terrestrial Ecology Lab (SOFTEL). ArcGIS Pro was used to plot transects along the longest axis of each tree island, from the head to the tail. Survey points were spaced every 5 m along the transect (every 10 m if the island head exceeded 200 m). Water depth was measured 3 times in a 1 m radius around each point. Surveying continued along a transect until the habitat transitioned from closed-canopy (≥50% cover) forest, characteristic of the tree island's head, to open-canopy (<50% cover) tail habitat. Elevation along the transect of each tree island's head in 3AN, TRI, and 3AS was calculated by averaging the 3 water depth values at each plot, then subtracting average plot water depth from coordinates' water level data interpolated by the EDEN xyLocator tool on the survey date. Liu et al. (2009) used similar methods in the same study area and found 95% of EDEN modeled water levels were within a 5 cm range of field-measured water levels.

2.5. Tree Island Hydrology

The calculated tree island elevation profiles were assumed to be constant throughout the study period, as no data were available for sites' rates of peat accretion or decomposition, and sediment deposition or erosion. However, these processes generally operate slowly on Everglades tree islands, so potential fluxes in soil elevation are considered negligible during the short duration of this study. Tree island elevations were plotted against water surface time series, extrapolated from the EDEN xyLocator, to get accurate and fine-scale hydrologic data on tree islands from Water Year 2019 – 2023, which encompassed the entire time that trail camera monitoring occurred. However, trail cameras were active for different time periods (due to different deployment dates and occasional data loss) and because different time periods are characterized by different hydrologic conditions that may affect species distributions, movements, and detection on tree islands, another hydrologic time series was developed that varied among tree islands, contingent upon when trail cameras were active. Both hydrologic time series were used to independently determine daily inundation status of tree islands, whether EDEN cell water levels were above or below mean and maximum head elevations, calculated from elevation transects. Daily inundation status was used to calculate annual discontinuous hydroperiod, number of days a tree island was inundated in a Water Year, and the multiannual (Water Year 2019 – 2023) average discontinuous hydroperiod. Tree islands' daily relative water levels were also calculated and averaged across annual and multiannual bases by subtracting EDEN water level from mean and maximum head elevations.

2.6. Vegetation Survey

Vegetation surveys were conducted to examine how differences in habitat type, floral diversity, and plant community structure affect mammals' spatial use of Everglades tree islands. The SOFTEL lab has repeatedly surveyed tree islands as part of a long-term monitoring program in ENP. Vegetation was surveyed along islands' North-South transects between 2001 – 2002 and have since been carried out in permanent plots representing tree island hammocks, bayheads, and bayhead swamps (Table 1). The most recent data (2022) from the ENP study islands' hammock and bayhead permanent plots were used in these vegetation analyses. Bayhead swamp plots were not included because these are lower elevation sites in the near-tail or tail portion of tree islands, which were not included in the trail camera monitoring nor other aspects of this project.

Surveys in 3AN, TRI, and 3AS were modeled after SOFTEL's methods, as described in Sah et al. (2020), so that vegetation data were comparable across all study areas. However, instead of using permanent plots in 3AN, TRI, and 3AS, transects were surveyed along the longest axis of the tree island heads, in the same locations as the elevation surveys. Nested plots were spaced every 5 m along the transect in hardwood

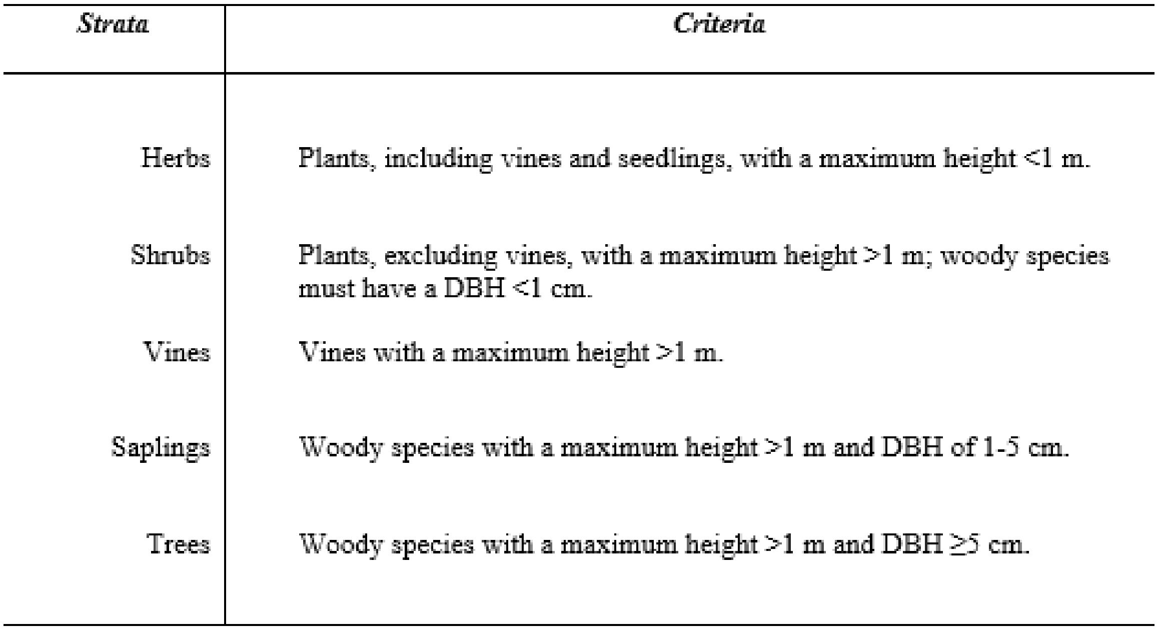
Table 1. Dominant vegetation classes with defining criteria and characteristics.

Vegetation	***Class Description***
Hardwood Hammock	Closed canopy forest (>50% cover) with individuals often exceeding 10 m. Exhibits minimal flooding stress. Presence of characteristic flood intolerant "hammock" trees (e.g., *Ficus aurea, Bursera simaruba, Sideroxylon foetidissimum*). Degraded hammocks may be mixed with non-hammock trees of higher flood tolerances.
Bayhead	Closed canopy forest (>50% cover) seldomly exceeding height of 8 m. Exhibits flooding for several months each year. Dominant trees can tolerate regular and prolonged floods: Acer rubrum, *Chrysobalanus icaco*, *Ilex cassine, Magnolia virginiana*, *Persea borbonia, Annona glabra*, *Salix caroliniana*.
Bayhead Swamp	Open canopy forest (<50% cover) with heights typically <5 m. Exhibits prolonged flooding. Dominant trees are the same as "Bayhead" but *Annona glabra* and *Salix caroliniana* are more abundant.
Cypress	Dominated by *Taxodium distichum*. Canopy may be open or closed and of variable height. Exhibits moderate to prolonged flooding.
Opening	Treeless gap in an otherwise closed canopy forest. Typically dominated by ferns. Early successional stage after a disturbance (storm, fire, or indigenous farming or settlement) has cleared a small area of trees.
Brazilian Pepper	Closed canopy forest (>50% cover) where the dominant tree species is the invasive Brazilian pepper (*Schinus terebinthifolius*). Brazilian pepper often forms a monotypic stand, outcompeting native trees and severely restricting understory growth. Brazilian pepper stands typically occur on higher elevation sites, such as former hammocks.

hammock habitat and 10 m apart throughout the rest of the head. If tree island heads were less than 50 m long, then all plots were spaced 5 m apart, regardless of habitat type. A 16 m^2 square plot was established at each transect point and the plot's vegetation was classified as hardwood hammock, bayhead, bayhead swamp, cypress, opening, or Brazilian pepper (Table 1).

Crown cover was estimated as the total space occupied by individual species or ground cover types (including interleaf gaps), as viewed from above. Species cover estimates were made for the full extent of each taxon within the plot. Due to overlapping canopies of different species the sum of all species' cover in a plot could exceed 100%. Crown cover estimates were converted to cover classes using Sah's (2004) scale: 1 = 0-1%, 2 = 1-4%, 3 = 4-16%, 4 = 16-33%, 5 = 33-66%, and 6 = >66%. Ground cover classes were estimated for total live understory (agglomerative cover of seedlings, herbs, and shrubs that does not differentiate between species or strata, thereby ignoring overlapping canopies such that cover estimates cannot exceed 100%), leaf litter, deadfall, and bare ground (exposed soil or rock). Plants were stratified into 5 categories: herbs, shrubs, vines, saplings, and trees (Table 2). A single nested subplot ($4m^2$) was established at the center of each plot to estimate cover classes for herb and shrub species. The $16m^2$ plots were used to measure stem density and to estimate canopy cover class for vines, saplings, and trees. Also, the diameter at breast height (DBH) and maximum height of each tree whose trunk originated within the plot was measured. Then, a vertical line intercept method was used to describe canopy structure along tree island transects (Sah, 2004). A height pole was positioned at the center of each plot and extended to the top of the canopy. Tree species were recorded as present in 1 m height intervals if their canopies intercepted a 30 cm radius around the height pole. A crown density profile was generated by calculating the percent occupancy for each species, at each height interval, across all plots on a tree island.

Table 2. Stratification and defining criteria of plants in vegetation surveys.



Strata	*Criteria*
Herbs	Plants, including vines and seedlings, with a maximum height <1 m.
Shrubs	Plants, excluding vines, with a maximum height >1 m; woody species must have a DBH <1 cm.
Vines	Vines with a maximum height >1 m.
Saplings	Woody species with a maximum height >1 m and DBH of 1-5 cm.
Trees	Woody species with a maximum height >1 m and DBH ≥5 cm.

2.7. Statistical Analyses

2.7.1. Species Diversity

Mammalian occurrence data were analyzed at local and regional scales. Alpha diversity (α) is defined as the diversity of a single tree island; mean alpha diversity ($\bar{\alpha}$) is defined as the arithmetic mean of islands' alpha diversities in the entire sample pool or a specified subset of sites; gamma diversity (γ) is the total regional diversity of all 40 study tree islands; and true beta diversity (β) follows the multiplicative definition of beta diversity, where $\beta = \gamma / \bar{\alpha}$. True beta diversity is practical for providing a sample-wide point estimate of heterogeneity across sites but is uninformative regarding pairwise differences between sites, and pairwise beta diversity ($\beta = \gamma / \alpha$) can be impractical for measuring and interpreting pairwise differences between many site combinations

(Gardener, 2014). Instead, compositional beta diversity or dissimilarity should be used (discussed in Metacommunity Structure, below).

Species diversity was measured using Hill diversity (a.k.a. Hill numbers, effective number of species, and true diversity), a generalized weighted mean that incorporates the number of species, relative abundances, and rarity into the equation:

$$D = \left(\sum_{i=1}^{S} p_i \, (r_i)^{\ell} \right)^{1/\ell}$$

where D is Hill diversity, S is total number of species sampled, p_i is the proportion of species i to the entire sample, r_i is the reciprocal of p_i (i.e., rarity), and the exponent ℓ determines how rarity is scaled. Researchers select the value of ℓ according to how they want rare versus common species to be leveraged. The value of ℓ can technically range infinitely, but the calculated diversity will be hypersensitive to rare species and exceed the observed species richness if $\ell > 1$, and if $\ell < -2$ then the diversity metric becomes insufficiently informative. Thus, researchers tend to constrain Hill diversity estimates with $-2 < \ell < 1$ and most commonly $\ell = 1, 0$, and/or -1. When $\ell = 1$, then D = species richness, making the measure of diversity especially sensitive to presence of rare species; when $\ell = 0$, D = Hill-Shannon diversity, which is not biased towards rare nor common species; when $\ell = -1$, D = Hill-Simpson diversity, which is most sensitive to variation among common species (Roswell et al., 2021).

Hill diversity, originally from Hill (1973), has surged in popularity since Jato (2006) reinvigorated the literature by postulating how Hill diversity was advantageous over traditional measures (e.g., Simpson, Shannon, Réyni, and Tsallis indices). One advantage of Hill diversity is that it directly measures community diversity, whereas traditional measures use probability (Simpsons indices) or entropy (other indices) as proxies for diversity (Jato, 2006). Hill diversity is also a unifying method because although the traditional raw indices have different mathematical properties that make them difficult to compare, all these indices can easily be transformed to Hill values, which share the same properties, behaviors, and interpretation (Jato, 2006; Roswell et al., 2021). Another major advantage of using Hill diversity is that it is the only known measure of diversity that satisfies all six axioms that a diversity index should satisfy: (1) *Symmetry* – diversity is a symmetric function; (2) *Continuity* – diversity is a continuous function; (3) *Evenness* – diversity is maximized for a fixed number of species when all species abundances are equal (i.e., evenness); (4) *Principle of Transfer* – transferring abundance increases diversity; (5) *Monotonicity* – introducing new species increases diversity; (6) *Replication* – if n communities have equal diversity but no shared species, their pooled diversity will be n times greater than the individual communities (Daly et al., 2018). Perhaps the greatest advantage of using Hill diversity is the ease of comparing and interpreting results, as the units are always expressed as number of species and this index responds linearly to changes in species abundance, unlike most other diversity indices (Roswell et al., 2021).

Species richness ($\ell = 1$) was included in diversity analyses because the number and identity of species present, regardless of species' rarity or detectability, is the most foundational facet of biodiversity. Hill-Shannon diversity ($\ell = 0$) was also analyzed because it integrates species' relative abundances into biodiversity estimates and is not biased towards rare or common species. Hill-Simpson diversity estimates were calculated but omitted from analyses because they were nearly identical to those of Hill-Shannon ($R^2 = 0.98$), thereby not adding any valuable insight. Furthermore, Hill-Simpson (and the classic Simpson index) is used less in ecological literature, as it is biased towards dominant species, and less representative of a community's "true diversity" (Gardener, 2014).

Species richness and Hill-Shannon diversity were calculated for all 40 tree island sites using R Statistical Software (v4.3.1; R Core Team, 2023) and the *iNEXT* R package (v3.0.0; Hsieh & Chao, 2022). 'Observed' richness and Hill-Shannon diversity were calculated from trail camera occurrence data, where occurrences separated by the appropriate time interval were fed into the iNEXT species abundance model. Use of observed diversity metrics can be misleading because sample units are often characterized by different sample sizes and effort. Rarefaction by sample size or effort has been the typical means of handling unequal samples, but the concomitant discarding of data and potential results is less than ideal. Instead, samples were standardized by coverage, as calculated by Chao and Jost (2012):

$$C = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where C is coverage, f_1 is the number of species for which only 1 individual was detected (i.e., "singletons"), f_2 is the number of species for which only 2 individuals were detected (i.e., "doubletons"), and n is the number of individuals sampled. Coverage uses species habitat use data to estimate what proportion of individuals in the community are species included in the sample. Thus, coverage is functionally an estimate of how completely a community has been sampled (e.g., a coverage estimate of 0.9 would be interpreted as 90% of individuals in the community are species present in the sample) (Roswell et al., 2021).

Like all sample standardization methods, coverage is imperfect because the true number, abundances, and detection rates of species in a community is unmeasurable in most field studies. However, coverage-based standardization is the best available method because it accounts for underlying species abundance distributions, different sample sizes, and unequal sampling effort (Roswell et al., 2021). Coverage values can be used to rarefy or extrapolate sampled diversity. Which method is optimal for a dataset is dependent on estimated values and variability of coverage across samples; extrapolation to 100% coverage, the asymptotic estimate of true community diversity, is preferred but such extrapolation would be unreasonable if samples' coverage values are low and associated error with the estimates is unacceptably high.

Generalized linear mixed models (GLMM) regress one or more predictor variables (i.e., "fixed effects") against a single response variable, like classic linear regressions. However, GLMMs are more sophisticated and flexible, such that they include random effects of samples and can model nonnormal distributions in the exponential family (e.g., binomial, gamma, gaussian, Poisson) (Bolker et al., 2009). GLMMs were constructed to determine how matrix-derived hydrologic stress affected mammal alpha diversity on tree islands across the metacommunity. The best-fit distributions of response variables, alpha species richness and Hill-Shannon diversity, were determined using the *fitdistrplus* package (Delignette-Muller & Dutang, 2015). Alpha species richness and Hill-Shannon diversity both fit lognormal distributions best, so the lognormal distribution with a log link was use to construct candidate GLMMs. Two sets of candidate GLMMS were constructed; one set modeled sites' alpha species richness as the response variable, and the other modeled alpha Hill-Shannon diversity as the response variable. Fixed effects were derived from the hydrologic explanatory variables (Appendix B), and tree island site was modeled as the random effect. First, candidate GLMMs with only one explanatory variable were constructed to model the fixed effects of each explanatory variable. Akaike Information

Criterion (AIC) was applied to the single fixed effect models to identify whether a particular variable had a disproportionate importance in explaining the response variable. Average marsh water depth in a 1000 m radius around each study tree island during Water Year 2019 – 2023 (WATR) was a disproportionally important variable to include in models according to its AIC score ($AIC_{WATR} = 151.4$; AIC of other variables were between 186 – 191). Additional candidate GLMMs were constructed by modelling all possible combinations of WATR with the other hydrologic explanatory variables, barring co-presence of variables that essentially measure the same hydrologic property (e.g., “WY.mean” and “Hydro.mean”, could not be present in the same model because they both represent tree islands’ mean hydroperiods). All GLMMs were modeled using the R package *glmmTMB* (Brooks et al., 2017); the R^2 values were calculated using the R package MuMIn (v1.47.5; Bartoń, 2023); and GLMMs were plotted using the R packages *emmeans* (v1.8.9; Lenth, 2023) and *ggplot2* (Wickham, 2017).

Generalized linear mixed models were constructed to determine how patch size (area of tree island head) and connectivity to neighboring tree islands affected mammal alpha diversity across the metacommunity. One set of lognormal GLMMs modeled alpha species richness as the response variable, and the other modeled alpha Hill-Shannon diversity as the response variable. To determine the effect of patch size on the response variables, the log area (m^2) of study tree islands’ heads were modeled as the fixed effect and tree island site was modeled as the random effect. To determine the effect of connectivity on the response variables, candidate models were constructed for each concentric ring around study tree islands (100 m, 250 m, 500 m, 1000 m, and 2000 m radius from the study tree islands’ perimeter). Candidates’ fixed effects were modeled as the distance to the nearest potential source population, number of neighboring tree islands, the percent area of neighboring tree islands, the combined effect of number and percent area of neighboring tree islands, and the interaction between number and percent area of neighboring tree islands. “Combined” connectivity models were also constructed, using patch size and the connectivity variables as the fixed effects. Models did not include fixed effects from multiple spatial scales (e.g., percent area of neighbors from 100 m and 250 m ring) to avoid overfitting models and identify at which spatial scale is alpha diversity most impacted by landscape connectivity. The most parsimonious models of connectivity’s effect on alpha species richness and Hill-Shannon diversity were selected using the lowest AIC scores. GLMMs were also constructed to assess whether there was an interaction between landscape and hydrologic fixed effects on species richness and Hill-Shannon diversity (e.g., the effect of connectivity on species richness may become increasingly important as tree island hydroperiod increases). Interaction models were constructed for all possible combinations of a single landscape variable with a single hydrologic variable (Appendix B).

2.7.2. Metacommunity Structure

Metacommunity structure was analyzed with the Elements of Metacommunity Structure (EMS) framework, as initially outlined in Leibold & Mikkelson (2002). The EMS framework ordinates a matrix of species (presence or abundance/occurrence data are acceptable) at sites by rearranging sites and species to maximize similarities between community composition and species distributions, respectively. Although various indirect gradient analyses could be used, reciprocal averaging (a.k.a., correspondence analysis) along the primary axis was selected for this study because this ordination technique is generally considered best suited for use with the EMS framework (Presley et al., 2010).

Observed species distributions along the latent environmental gradient were used to quantify the three elements of metacommunity structure (i.e., coherence, turnover, and boundary clumping). Coherence is a measure of the number of embedded absences, or how completely species fill the sites within their ranges. Turnover is the number of species replacements across sites for all species combinations. Boundary clumping is the degree to which species distributions are clumped, randomly, or evenly distributed along the latent environmental gradient. The EMS framework uses the values and levels of significance for each statistical test to determine which idealized structure (i.e., random, checkerboard, Clementsian, Gleasonian, evenly spaced, nested, or quasi-structure combinations of these original six) most closely resembles the metacommunity in question.

Ordination and analyses of the elements of mammal metacommunity structure were performed with the *metacom* R package (v1.5.3; Dallas, 2020). Occurrence data were standardized to the total number of trap days surveyed at each tree island site (i.e., RAI) to correct for differences in habitat use that arose strictly from unequal sampling effort. Metacommunity analyses compared the RAI matrix to 1000 randomly generated and re-ordinated null model simulations. Null model simulations used the default ‘r1’ method, which keeps the number of species at a site (i.e., row totals) constant and fills each species’ range across sites (i.e., columns) according to marginal probabilities (Dallas &Pulliam, 2022). The r1 method is preferred over more liberal and more conservative null models because the alternatives become increasingly prone to type I and type II errors, respectively (Presley et al., 2010). The statistical outputs would indicate positive coherence if there were fewer embedded absences in the empirical dataset than the null model simulations’ mean (also indicated by a negative z-value). Positive turnover would be indicated if there were more species replacements in the empirical dataset. Boundary clumping was assessed with the Morisita's index, where a clumped distribution was indicated if the index value was >1, random distribution if the index was ~1, and overdispersion if the index was <1. The results from testing coherence, turnover, and boundary clumping were only considered statistically significant if the corresponding p-value was ≤ 0.05.

Bray-Curtis dissimilarity was selected to measure compositional beta diversity or dissimilarity between sites' mammal communities because this index accounts for differences in species abundances, is effective at detecting underlying environmental gradients, and is not affected by the "double-zero problem" (i.e., joint species absence at sites creates misleading results for similarity/dissimilarity) (Austin, 2013; Gardener, 2014). The dissimilarity matrix was used for hierarchical clustering of tree island sites. Clusters were agglomeratively constructed, opposed to divisively, because agglomerative clustering considers all pairwise combinations of dissimilarity, are superior at clustering sites (especially in large datasets or when outliers are present), and the results are more interpretable (Roux, 2018; Sharma & Batra, 2019). The *cluster* (v2.1.4; Maechler et al., 2022), *dendextend* (Galili, 2015), and *pvclust* (v2.2-0; Suzuki et al., 2019) R packages were used to determine which agglomerative method optimally clustered sites in a way that made ecological sense and was statistically significant. Ward's criterion for assessing optimality was used for this dataset because it resulted in the highest agglomerative coefficient (0.90), clusters were clearly identifiable, within-cluster similarity was maximized, and no outliers remained. Subsequently, Mann-Whitney tests were implemented to determine if species richness, Hill-Shannon diversity, and community evenness were significantly different across clusters.

To determine whether a linear or unimodal ordination should be used on the metacommunity data, a detrended correspondence analysis (DCA) was performed to measure the length of the first axis. If the axis length is < 3, the community is homogenously distributed, and linear ordination would be selected. If the axis length is > 4, the community is heterogenous, and unimodal ordination would be selected (Lepš & Šmilauer, 2003). The first DCA axis measured 2.70 S.D. so a linear ordination was selected.

Distance-based redundancy analysis (dbRDA) is a multi-step direct gradient analysis that linearly ordinates community data to constraining environmental variables. The first step of dbRDA performs principal coordinates analysis (PCoA) on the compositional beta diversity or community dissimilarity matrix. Standard redundancy analysis (RDA) is limited to Euclidean distances, while dbRDA can use any dissimilarity measure and represent it in Euclidean space (Legendre & Anderson, 1999; Stuber et al., 2019). Bray-Curtis dissimilarity with Hellinger transformation was used to improve the linearity and reduce the effect of dominant species on site dissimilarities (Legendre & Gallagher, 2001). Then, multivariate multiple linear regressions fit the response matrix to the matrix of explanatory variables. Since this regression technique assumes linearity between the response and explanatory variables, all combinations were checked for linearity and transformations were made as necessary; tree island area was log transformed, and categorical habitat and vegetation data with *k* classes were modeled as (*k*-1) binary dummy variables (Borcard et al., 2011).

Response and explanatory variables were presumed to exhibit spatial autocorrelation. To measure and correct for effects of spatial autocorrelation, tree island sites' coordinates were converted to a distance-based Moran's eigenvector map, a matrix of Euclidean distances between sites truncated by a threshold (Borcard & Legendre, 2002). This threshold is dependent on the matrix distance values. The threshold is equal to the shortest pairwise distance between sites that still permits all sites to be spatially “linked”, meaning all sites can be connected by distance values less than or equal to the threshold. A PCoA is performed on the truncated distance matrix to create orthogonally uncorrelated linear vectors at multiple scales. The first vector (MEM1) reflects the broadest spatial scale, and the last vector (MEM*n*, when there are *n* vectors) reflects the finest spatial scale (Borcard et al., 2011). Vectors that displayed positive spatial autocorrelation (observed Moran’s index larger than the expected Moran’s index) were added to the matrix of explanatory variables used in the global dbRDA model.

Environmental variables encompassed landscape, hydrologic, and vegetative traits of tree island sites. The global model included all 45 environmental variables and 7 spatial MEM variables (Appendix B). The MEMs were treated as conditioning variables to partial out the effects of spatial autocorrelation on mammalian response and constraining environmental variables. The burdensome number of explanatory variables required a reduced model to explain dbRDA results. Traditional model selection approaches, namely AIC, are not suitable with dbRDA because constrained ordinations do not have a log-likelihood; quasi-AIC scores can be calculated and may be helpful but should not be relied on as the primary model selection criteria (Godínez-Domínguez & Freire, 2003). Multiple model building and reducing pathways were implemented and cross analyzed to ensure consistent results when selecting the most parsimonious model. Model selection was partly based on low variance inflation factors (VIFs). Explanatory variables with VIFs <4 was desired because they are considered to have little to no multicollinearity. Some multicollinearity exists if VIFs are between 4 and 10, and VIFs >10 suggest high multicollinearity and problematic variables should be removed (Gardener, 2014). Permutation tests of dbRDA models further assisted in model selection by measuring the marginal effects and statistical significance of each constraining variable on models' pseudo-F statistic (F), the ratio of constrained variance to total variance. Explanatory variables were only added to a model if their marginal effects were significant according to the permutation test. However, every additional variable in a model inevitably increases the amount of explained variance. Thus, to avoid overfitting a model, Ezekiel's adjusted R^2_{adj} of the global model was used as a cutoff criterion. That is, if a model's R^2_{adj} was higher than the global model's, it was not selected (Blanchet et al., 2008).

The dbRDA model was constructed with the *vegan* package (v2.6-4; Oksanen et al., 2022) and *capscale* function. Model outputs were projected as a triplot, an ordination of sites, Hellinger transformed species, and explanatory variables. Triplots are plotted and interpreted differently depending on which scaling method is selected. A triplot with scaling = 1 scales the eigenvectors to their unit length, accurately plotting a two-dimensional interpretation of Euclidean distances between sites (Borcard et al., 2011). This does not plot the Euclidean distances between species accurately and the angles between variables do not necessarily represent their correlations. Scaling = 2 scales each eigenvector to the square root of its eigenvalue, accurately plotting a two-dimensional interpretation of Euclidean distances between species but not sites (Borcard et al., 2011). The tips of species score vectors reflects the optimal environmental conditions of species, modeled as a function of the likelihood of species presence, and relative abundance or habitat use. The angle between species scores accurately represents how correlated they are. Smaller angles between species mean that they are more correlated; wider (~right) angles mean the species are less correlated, unless the arrows point opposite to each other, then they are negatively correlated. The angles between variables, and the angles between species and variables also measure how correlated they are (Zuur et al., 2007). A correlation triplot (i.e., scaling = 2) was selected because it improves the interpretability of how Hellinger transformed species composition differs across sites while maintaining an intuitive display of how species are correlated to explanatory variables. Then, variation partitioning was performed with the R package *rdacc.hp* (Lai et al., 2022) to quantify the unique and combined effects of each constraining variable on the Hellinger transformed community matrix.

RESULTS

Estimated coverages of mammal communities on tree islands were very high. The mean coverage of all sampled tree islands was 0.99 and the lowest was 0.84 (the next lowest was 0.96). Species richness and Hill-Shannon diversity were standardized for each tree island by extrapolating to the asymptote of species diversity curves, where coverage is approximately 1.00 or sampled to represent 100% of the community. Such high coverage estimates resulted in little extrapolation and a minor increase from observed to asymptotically estimated alpha diversity of tree island sites. Of the 40 sampled tree islands, only 6 exhibited an increase from observed to estimated alpha species richness (1 – 4 additional species) (Fig. 2). The estimated increase of alpha Hill-Shannon diversity was even less (3% increase) and not statistically significant. Twelve mammal species were detected across all 40 tree islands ($\gamma_R = 12$; Appendix A). Gamma Hill-Shannon diversity was $\gamma_H = 3.18$. Mean alpha species richness across all tree islands was $\bar{\alpha}_R = 5$. Mean alpha Hill-Shannon diversity across all tree islands was $\bar{\alpha}_H = 2.40$. True beta richness and Hill-Shannon diversity was $\beta_R = 2.40$ and $\beta_H = 1.33$, respectively.

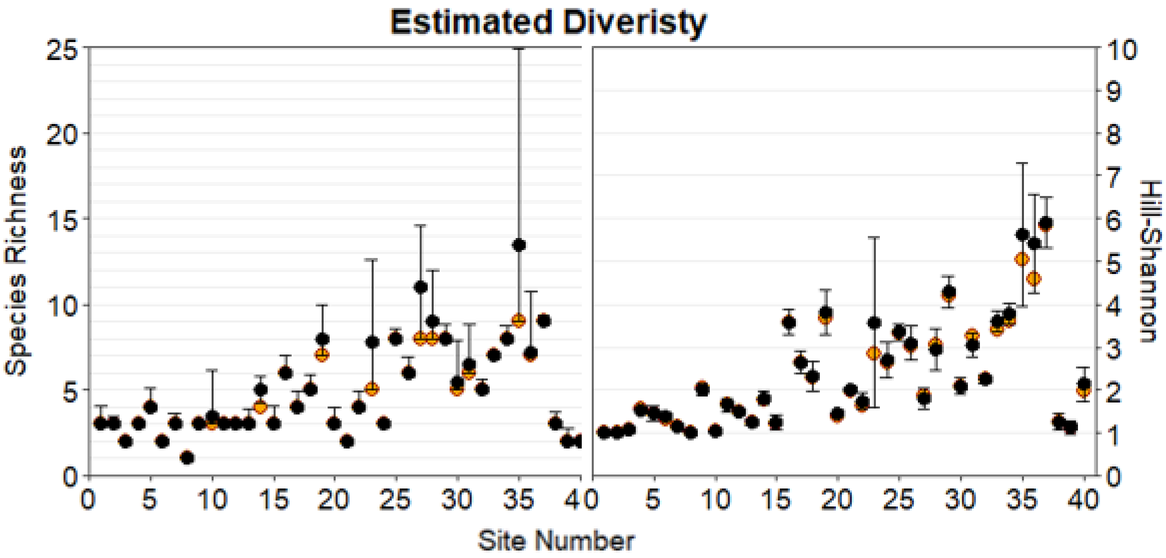


Figure 2. Species richness (left) and Hill-Shannon diversity (right) values were asymptotically estimated via coverage-based extrapolation for all 40 sampled tree islands. Orange circles represent the observed diversity, and black circles represent the asymptotically estimated diversity for each tree island site. When a site's orange circle is not visible, the observed and estimated values are identical. Error bars extend across the 95% confidence level for each asymptotic estimate. Note that confidence of asymptotic estimates decreases (wide error bars) with lower sample coverage and higher species diversity because diverse communities, especially with rare species, require more extensive sampling.

The effects of matrix-derived hydrologic stress on species richness and Hill-Shannon diversity at each tree island site were modeled using the most parsimonious GLMM models, selected by the lowest AIC scores. The most parsimonious models for alpha species richness and Hill-Shannon diversity each modeled WATR as the only fixed effect. Matrix-derived hydrologic stress had a negative logarithmic effect on species richness and Hill-Shannon diversity across the mammal metacommunity (Fig. 5). The proportion of variance explained by a model's fixed effects was calculated as the marginal R^2; the proportion of variance collectively explained by a model's fixed and random effects was calculated as the conditional R^2. The marginal and conditional R^2 for the most parsimonious species richness model were 0.34 and 0.52, respectively. The marginal and conditional R^2 for the most parsimonious Hill-Shannon diversity model were 0.49 and 0.74, respectively.

The effects of patch size on species richness and Hill-Shannon diversity at each tree island site were very low and did not fit predicted values well. The marginal and conditional R^2 for the effect of patch size on species richness were <0.01 and 0.04, respectively. The marginal and conditional R^2 for the effect of patch size on Hill-Shannon diversity were <0.01 and 0.50, respectively. The effects of connectivity (i.e., between patches and to the nearest source population) on species richness and Hill-Shannon diversity were also very low and poorly fit predicted values. The most parsimonious model for the effect of connectivity on species richness modeled the number of neighboring tree islands in the 500 m radius ring as the fixed effect. The marginal and conditional R^2 for the effect of connectivity on species richness were <0.01 and 0.01, respectively. The most parsimonious model for the effect of connectivity on Hill-Shannon diversity modeled the percent area of neighboring tree islands in the 2000 m radius ring as the fixed effect. The marginal and conditional R^2 for the effect of connectivity on Hill-Shannon diversity were 0.02 and 0.51, respectively. GLMMs were also constructed that modelled all possible combinations of interactions between pairs of landscape (i.e., proximity to source, patch size, and connectivity) and hydrologic variables; these models were not statistically significant and poorly fit predicted values.

Reciprocal averaging ordination of the mammal species by tree island site matrix revealed the primary axis to explain 46% of the total inertia (Eigenvalue = 0.35). The ordinated matrix was characterized by a nested structure, as indicated by positive coherence, negative turnover, and clumped species range boundaries when compared to the null model simulations. However, only coherence and turnover were statistically significant (Fig. 3; Table 3).

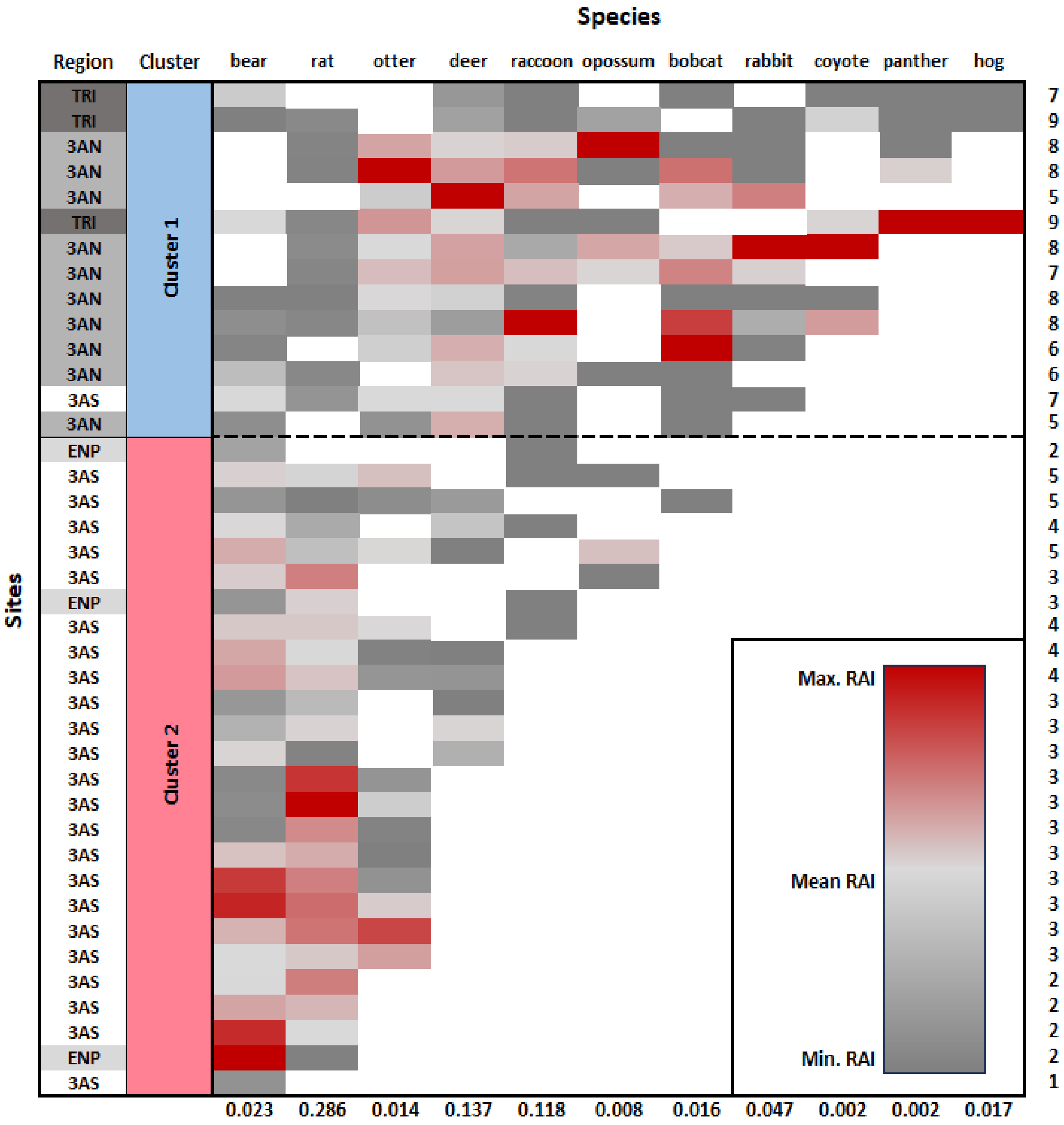


Figure 3. Ordinated sites-species matrix of all tree island sites and mammals detected during camera trapping. Sites and species' relative abundances (RAI) were organized according to their reciprocal averaging Axis-1 score. Filled cells indicate species presence and are color-coded according to each species RAI. A cell tinted red indicates the corresponding species' RAI is higher than its mean across all sites. The left y-axis displays study area (3AN = Water Conservation Area 3A North; 3AS = Miccosukee Water Conservation Area 3A South; TRI = Triangle; ENP = Everglades National Park) and cluster (described below) each tree island belongs to. The right y-axis displays row counts (i.e., number of species at each site) and the bottom x-axis displays column means (i.e., the mean RAI for each species across).

Table 3. Elements of metacommunity structure statistical analyses

Coherence			Turnover			Clumping	
EA	**x̄**	**SD**	**RE**	**x̄**	**SD**	**M**	
53	152	4	485	1747	23	1.67	
Value	**z**	***p***	**Value**	**z**	***p***	**Value**	***p***
+	- 7.24	<0.001	-	- 2.27	0.02	+	0.15

The ordinated matrix of mammals' relative abundances on tree islands and the null model simulations' mean (x̄) and standard deviation (SD) were used to calculate z-scores (z) and the statistical outputs for coherence, turnover, and range boundary clumping. Coherence, turnover, and range boundary clumping for the empirical matrix were calculated as the number of embedded absences (EA), number of species replacements (RE), and Morisita's index (M), respectively. The value (+/-) of each metacommunity element was considered statistically significant if the p-value (*p*) was ≤0.05.

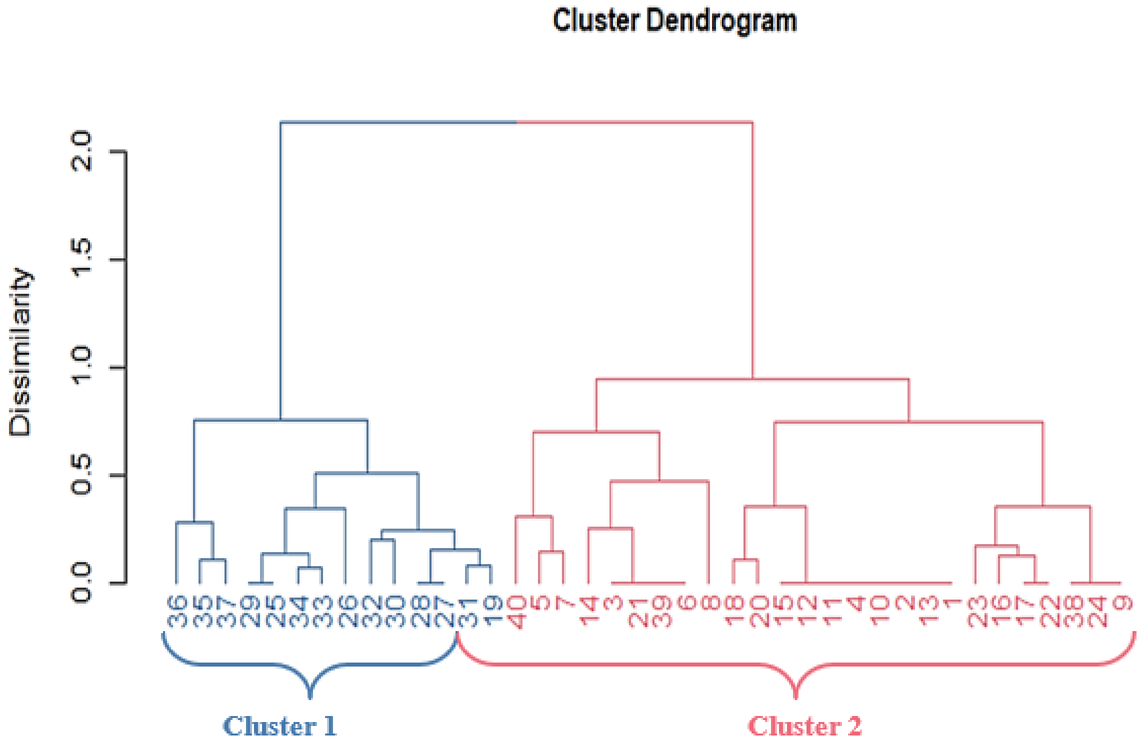


Figure 4. Dendrogram of hierarchical agglomerative clustering. Sites were clustered into 2 groups using Ward's criterion. Site numbers and dendrogram branches were color coded by cluster.

Although range boundary clumping was not statistically significant, positive clumping of the tree island metacommunity warranted further investigation into how sites were grouped along the latent environmental gradient. Two distinct clusters were identified using hierarchical agglomerative clustering (Fig. 4). Bootstrapping (1000 iterations) revealed clustering to be statistically significant ($p\text{-value} \leq 0.05$). Clusters were characterized by significant differences in gamma species diversity. Gamma species richness of Cluster 1 and 2 was $\gamma_{R1} = 11$, and $\gamma_{R2} = 8$, respectively. Gamma Hill-Shannon diversity of Cluster 1 and 2 was $\gamma_{H1} = 4.17$, and $\gamma_{H2} = 1.49$, respectively. Clusters' mean alpha diversities (mean of species richness or Hill-Shannon diversity estimates for sites within a cluster) were also significantly different (Fig. 6). Mean alpha species richness of Cluster 1 and 2 was $\bar{\alpha}_{R1} = 8$, and $\bar{\alpha}_{R2} = 3$, respectively. Cluster 1 also had higher mean alpha Hill-Shannon diversity. Mean alpha Hill-Shannon diversity of Cluster 1 and 2 was $\bar{\alpha}_{H1} = 3.81$, and $\bar{\alpha}_{H2} = 1.72$, respectively. True beta richness for Cluster 1 and 2 were $\beta_{R1} = 1.38$ and $\beta_{R2} = 1.00$, respectively. True beta Hill-Shannon diversity for Cluster 1 and 2

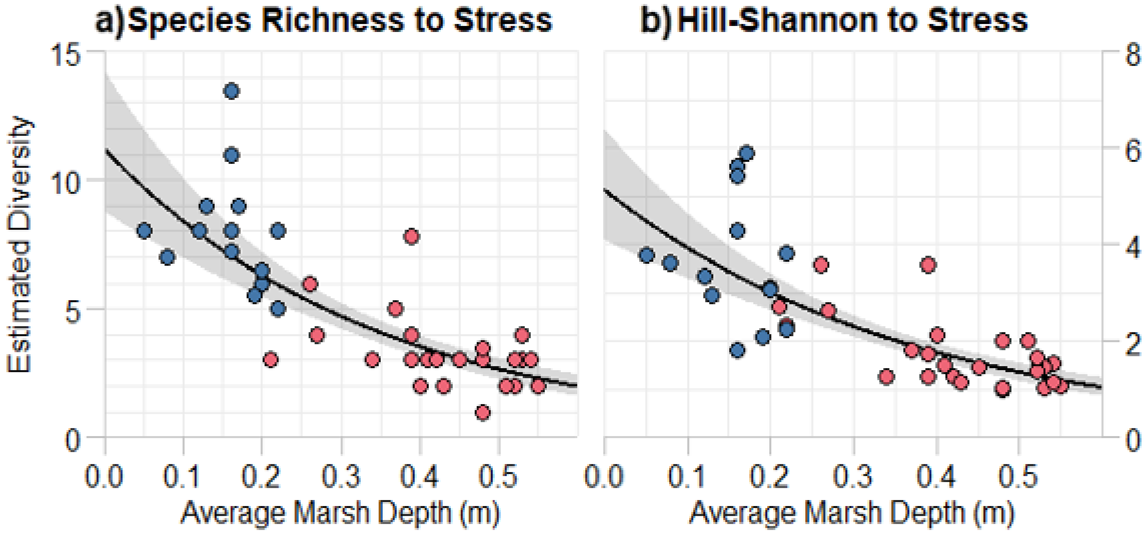


Figure 5. GLMMs of the effect of matrix-derived hydrologic stress on tree island site's estimated alpha species diversity. Species richness (a) and Hill-Shannon diversity (b) were estimated from coverage-based asymptotes for each study tree island, Tree islands were color coded by cluster (Cluster 1 is blue; Cluster 2 is pink). The solid black line depicts the predicted values of a model, and the gray band depicts the 95% confidence interval based on predicted standard errors.

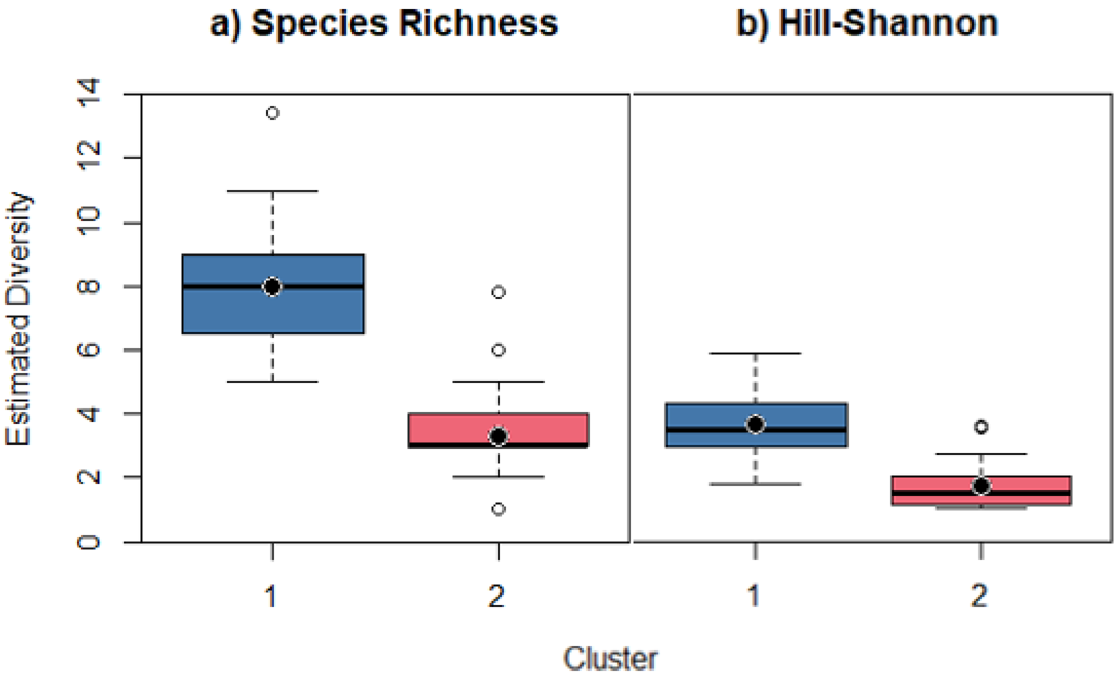


Figure 6. Boxplots of clusters' estimated alpha species diversities. Species richness (a) and Hill-Shannon diversity (b) were estimated from coverage-based asymptotes.

were $\beta_{H1} = 1.14$ and $\beta_{H2} = 0.87$, respectively. Low true beta diversity of clusters indicated that species richness and Hill-Shannon diversity are rather homogenous within each cluster (McCune & Grace, 2002).

Clusters were not characterized by significant differences in community evenness ($p = 0.66$). Indicator species analysis was also performed but failed to identify any significant indicators (squared Pearson's residual > 4) between clusters. However, whitetail deer and raccoons had the strongest positive association with Cluster 1, and rats had the strongest with Cluster 2; to a lesser degree, black bear were also positively associated with Cluster 2. All other mammals were positively associated with Cluster 1.

Numerous explanatory variables required a reduced dbRDA model that optimally explained the greatest amount of variance without overloading variables. Variable interactions (e.g., marsh depth x hydroperiod) were also tested for, but all contributed negligibly to explained variance and were statistically insignificant. Forward selection model building and reducing pathways were paired with multiple selection criteria to construct and comprehensively analyze potential models. The global model was reduced to a model with 4 constraining variables: mean marsh depth in a 1000 m radius around each study tree island during the half of the year with the highest water levels (DEEP), the mean annual amplitude of marsh water depth (maximum daily water depth – minimum daily water depth of a Water Year) in the 1000 m radius from Water years 2019 – 2023 (MRSH), the log area of study tree islands (AREA), and the percent area of neighboring tree islands in the 1000 m radius (NBR%). This model also included 3 conditioning spatial variables: MEM2, MEM3, and MEM4, which capture significant levels of spatial autocorrelation among explanatory variables at different spatial scales (Fig. 7).

The constraining variables explained 44% of the total variation in the Hellinger transformed mammalian metacommunity. The first dbRDA axis captured the bulk of the explained variation (33% of the total and 76% of the variation fitted from the constraining axes). The second axis explained a smaller portion of the variation (5% of the total and 12% of the fitted). The canonical coefficients for axis 1 are: DEEP = -0.9027, MRSH = 0.2086, NBR% = 0.0204, and AREA = -0.0118. The canonical coefficients for axis 2 are: DEEP = -0.3365, MRSH = 1.4468, NBR% = 0.0180, and AREA = -0.1656. Axis 1 was most strongly correlated with DEEP; axis 2 was most strongly correlated with MRSH but was also heavily influenced by DEEP. The vector angles among constraining variables reflected a moderately strong positive correlation between DEEP and MRSH, whereas DEEP and NBR%, and NBR% and AREA were negatively correlated. Rabbit, bobcat, deer, raccoon, opossum, and otter vectors exhibited very strong positive correlations. Hog, coyote, and panther were also positively correlated. The aforementioned species

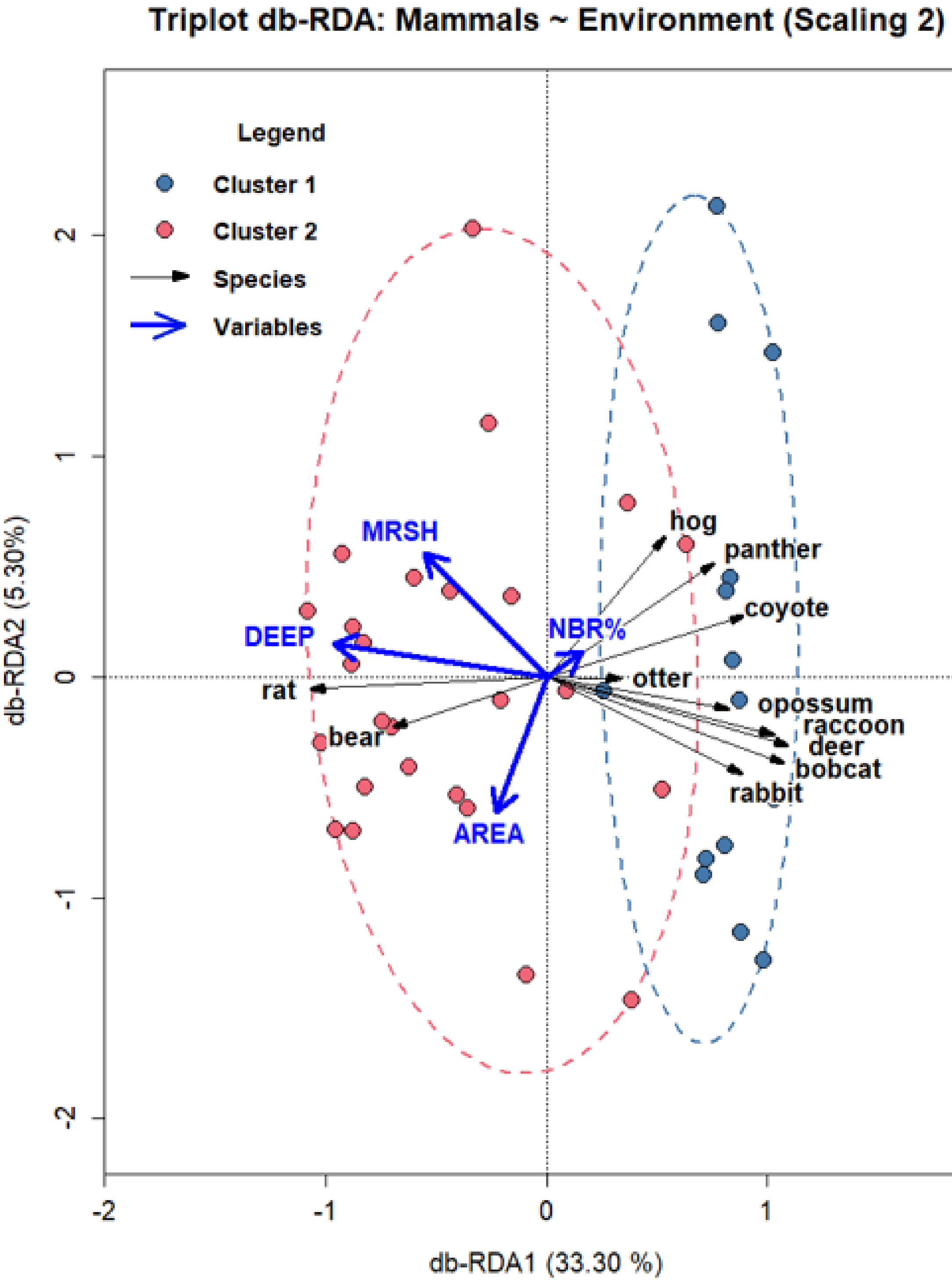


Figure 7. Distance-based redundancy analysis correlation triplot of constraining variables, Hellinger transformed species, and sites scores fitted as orthogonal linear combinations of constraining variables (*i.e.*, linear combination or “lc” scores). Ellipsoid hulls delineate the site clusters, color coded as indicated in the legend.

characterized the community composition of Cluster 1. Cluster 2 was characterized by bear and rat, which were negatively correlated with the species in Cluster 1. Species in Cluster 1 had a strong negative response to DEEP and a supplementary positive response to NBR%, with otters being the least affected, as indicated by their position closer to the origin. Rabbit, deer, bobcat, raccoon, opossum, and otter responded negatively to MRSH and did not appear correlated with AREA. Meanwhile hog, panther, and coyote responded negatively to AREA and did not appear correlated with MRSH. Rats and bears had the strongest positive responses to DEEP and AREA, respectively.

Variation partitioning of the dbRDA model revealed how variation in the Hellinger transformed mammal metacommunity was allocated among the constraining variables. Explained variation for each variable was split into “unique” and “shared” fractions. Unique variation refers to the fraction of explained variation that is attributed solely to a single variable, and shared variation refers to the fraction that is jointly explained by two

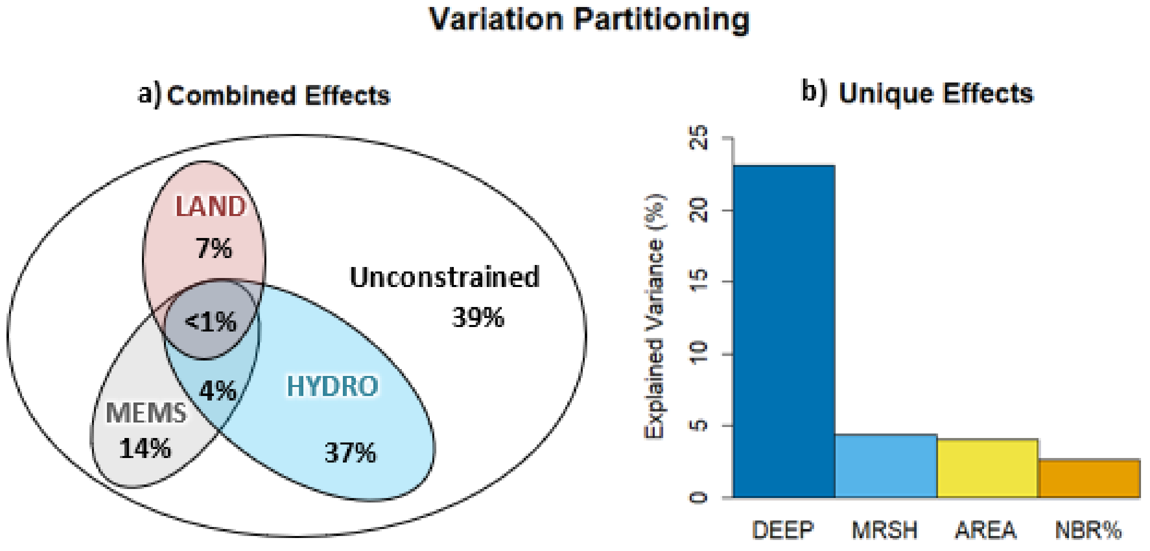


Figure 8. Variation partitioning of constraining and conditioning variables on mammal metacommunity composition. The combined effects figure (a) shows the unique and jointly explained variation of constraining variables. AREA and NBR% were combined as grouped variable “LAND”; DEEP and MRSH were combined as grouped variable “HYDRO”; the three conditional MEM variables were combined as grouped variable “MEMS”. The unique effects figure (b) shows the total explained variation unique to each constraining variable.

or more of the variables (not an interaction of the variables). The combined effects of unique and shared variation on the Hellinger transformed mammal dissimilarities are displayed in Fig. 8a, and unique effects of constraining variables are displayed in Fig. 8b.

The conditional variables, MEM2, MEM3, and MEM4 were amalgamated and partialled out as a single spatial component (“MEMS”) to account for multiple scales of spatial autocorrelation in the mammal metacommunity and constraining variables. The combined effects of MEMS explained 17% of the total variation, with 14% being unique to MEMS. The AREA and NBR% constraining variables were amalgamated and partialled out as a single landscape component (“LAND”) to depict how multiple aspects of tree island landscape characteristics impact the mammal metacommunity. LAND uniquely explained 7% of the total variation (4% of the total variation was uniquely attributed to AREA, and 3% to NBR%) and did not jointly explain a significant amount of variation with any other variables. The DEEP and MRSH constraining variables were also amalgamated and partialled out as a single hydrologic component (“HYDRO”) to depict how hydrologic characteristics impact the mammal metacommunity. The combined effects of HYDRO explained 41% of the total variation, with 37% being unique to HYDRO (23% and 4% of the total variation was uniquely attributed to DEEP and MRSH, respectively; DEEP and MRSH jointly explained 10% of the total variation).

DISCUSSION

The mammal metacommunity of central Everglades tree islands was surveyed across a wide spatial and environmental gradient. Camera trapping on the 40 study tree islands was thorough and comprehensive, as indicated by the high estimates for sample coverage (minimum = 87% and mean = 99%). Thus, samples’ observed community compositions are considered to accurately represent their true compositions. Such high coverage estimates resulted in little extrapolation from observed to asymptotically estimated species richness and Hill-Shannon diversity. Asymptotic estimates of diversity were used in all further diversity analyses because these values are standardized by sample completeness. However, asymptotic estimates of diversity are susceptible to overestimating the true diversity of a sample, especially for highly diverse samples because they require more intensive sampling to fully capture the species present and characterize the community (Roswell et al., 2021). Overestimation of alpha species richness appears to have occurred in at least one sample, where the tree island's asymptotic alpha species richness was estimated to be 13, exceeding the asymptotic gamma species richness ($\gamma_R = 12$) of all 40 sampled tree islands. The upper 95% confidence level of two other tree islands' alpha species richness estimates also exceeded 12 species, but overestimation did not appear to be a pervasive problem as most samples exhibited very slight or no increase in alpha diversity from observed to estimated values (Fig. 2). Observed and asymptotically estimated gamma species richness of all 40 sampled tree islands were equal, evidencing that the true mammal metacommunity richness on tree islands in the central Everglades is fully represented by the mammal species detected during camera trapping (Appendix A). The mean species richness of tree islands was substantially lower than the gamma diversity ($\bar{\alpha}_R = 5$), reflecting mammal species richness across tree islands to be moderately heterogenous ($\beta_R = 2.40$) (McCune & Grace, 2002). The same pattern was observed with Hill-Shannon diversity across tree islands, but diversity was lower ($\gamma_H = 3.18$; $\bar{\alpha}_H = 2.40$) and more homogenous in this regard ($\beta_H = 1.33$).

The heterogeneity among tree islands in species richness and Hill-Shannon diversity was largely attributed to matrix-derived hydrologic stress. As stress increased, alpha species richness and Hill-Shannon diversity exhibited a negative logarithmic decrease (Fig. 5). Mean marsh water depth (WATR) was the primary driver of this decrease in diversity, explaining 34% and 52% of the variation in species richness and Hill-Shannon diversity, respectively. The observed decreases in alpha diversities across the stress gradient did not follow the predicted values very smoothly; instead, a distinct shift in alpha species richness and Hill-Shannon diversity occurred near 0.25 m average marsh water depth. The shift in diversities is aligned with the transitional boundary between sites' clusters. Mean species richness and Hill-Shannon diversity of sites in Cluster 1 were more than twice as high as sites in Cluster 2. Meanwhile, differences in within-cluster diversities were very low; true beta species richness and Hill-Shannon diversities for Cluster 1 and Cluster 2 were nearly equal to 1. Thus, Hypothesis 1 was supported in that tree island alpha species richness and Hill-Shannon diversities were nearly homogenous within each cluster but mean alpha and gamma diversities decreased across clusters as matrix-derived hydrologic stress increased. Complementarily, true beta diversities (i.e., heterogeneity) increased across clusters as matrix-derived hydrologic stress increased.

Patch size and connectivity are two cornerstones of spatial ecology and related theories (i.e., island biogeography, metapopulation, metacommunity (MacArthur & Wilson, 1967; Levins, 1968; Wilson, 1992). The potential effects of patch size and connectivity on mammalian diversity in central Everglades tree islands were analyzed across an expansive trait gradient (i.e., very large to small patch sizes, and high to low connectivity). Nonetheless, there was a lack of evidence supporting Hypothesis 2, i.e., that mammal alpha diversity would decrease as patch size and connectivity among neighboring tree islands or to a source population decreases. The lack of support for this hypothesis could be because these aspects of spatial ecology genuinely do not have a profound effect on mammal diversity in this metacommunity. It is also worthwhile to consider that anthropogenically induced degradation and loss of tree islands has resulted in more than 50% and 60% loss of total tree island number and area, respectively (Patterson & Finck, 1999). Thus, it is plausible that the decreased area and heterogeneity among central Everglades tree islands reduced any effects of landscape connectivity on mammal diversity to a level that is not discernible with the methods used.

The EMS framework was implemented to analyze patterns in mammal diversity and composition across the metacommunity. Ordination of sites' community composition, based on species' RAI, revealed a strong latent environmental gradient underlying metacommunity structure (Fig. 3). Mammal metacommunity structure was nested, following the positive coherence, negative species turnover, and positive range boundary clumping pathway (Fig. 1). Although range boundary clumping was not statistically significant, hierarchical agglomerative clustering of mammals' RAI identified two distinct clusters along the latent environmental gradient (Fig. 4). The mammal metacommunity appears to be characterized by a nested clumped structure, as predicted under the second ecological scenario in Hypothesis 3: a high stress environment heavily influences metacommunity structure, and the stress limits population densities such that mutually exclusive species interactions are not the primary structural force on the metacommunity. The hypothesized mechanism for this metacommunity to achieve a nested clumped structure is supported by the strong effects of matrix-derived hydrologic stress on alpha species richness and Hill-Shannon diversity, two important components of metacommunity structure (Fig. 5) Furthermore, mammal RAIs were very low across the metacommunity. RAIs are affected by species' detection rates and most accurately represent habitat use in this study design, but RAIs are presumed to be proportional to absolute populations. Such low RAI values (median mammal RAI = 7 occurrences per year, and some species are <1 occurrence per year) likely reflects low absolute populations, which is consistent with findings from Dorcas et al. (2012) that showed an 87.5 – 99.3% decline of the Everglades' native mammal species between 1996 – 2011. Similarly, the Florida Fish and Wildlife Conservation Commission's (FWC) arial transect surveys in 3AS have shown a precipitous decline in the whitetail deer population from 2017 – 2022 (FWC, 2022).

The effects of environmental variables on mammal compositional beta diversity were determined using dbRDA ordination and variation partitioning of Hellinger transformed Bray-Curtis dissimilarities. None of the vegetative independent variables had a strong enough effect on the mammal metacommunity to be included in the parsimonious ordination model. Mammal distributions and habitat use were affected by landscape characteristics (i.e., patch size (AREA), and percent area of neighboring tree islands (NBR%), but the unique effects of these constraining variables each explained <4% of the total variation between tree islands' mammal communities. Meanwhile, local marsh hydrologic characteristics (HYDRO) explained more than 4x the total variation than landscape characteristics (LAND), and nearly 85% of all fitted variation. The effects of local marsh hydrology on the mammal metacommunity also overshadowed the effects of tree island hydrology (e.g., relative water level and hydroperiod of mean head elevation), which had clear effects on species' distributions and habitat use, but because these effects were weaker and multicollinear to the effects of marsh hydrology, they were not included in the most parsimonious dbRDA model (Fig. 7). The unique effects of marsh water depth's mean amplitude (MRSH) only contributed 4% to the total variation, but the combined effect of its unique and shared portion (with DEEP) contributed to 14% of the total variation. Mean marsh high-water depth (DEEP) uniquely explained more than 5x the total variation than any other constraining variable and more than 50% of all fitted variation (Fig. 8b). These findings support Hypothesis 4, that matrix-derived stress, represented by DEEP, is the strongest controlling force on mammal distributions and habitat use of tree islands in the central Everglades.

Mean marsh high-water depth was also the primary determinant for how mammals clustered across the metacommunity. Mammals clustered into two distinct community types. The community composition of sites in Cluster 1 were characterized by upland mammals (bobcat, coyote, deer, hog, opossum, panther, rabbit, and raccoon) and otter, while the composition of sites in Cluster 2 were characterized by bear and rat (Fig. 7). The positions and angles of species' environmental optima in the ordination space demonstrated that species in Cluster 1 were negatively affected by DEEP and positively affected by percent area of neighboring tree island patches (NBR%). These findings imply that shallower marsh water depths and higher total tree island area functionally increase landscape connectivity by relaxing matrix-derived hydrologic stress and facilitating interpatch movement, thereby increasing abundances or tree island habitat use of mammals in Cluster 1.

Contrastingly, bear and rat optima were associated with tree islands surrounded by deep marsh high-water levels and were negatively related to connectivity. The negative relationship between tree island connectivity and tree island use by bear and rats does not suggest that these species benefit from or select for tree islands with decreased interpatch connectivity. Instead, this pattern likely emerged because NBR% and DEEP are negatively correlated, and these species increasingly use tree islands surrounded by deep marsh, despite the associated decrease in connectivity. This is consistent with findings from literature that showed black bear and certain species of myomorphs (i.e., rats and mice) in Florida select for wetland forests and other mesic habitats (Calandriello, 1999; Ulrey, 2008; Garrison et al., 2012; Humm, 2017; Karelus et al., 2018; Chapman, 2019; Romanach et al., 2021). Smith & Vrieze (1979) also state that myomorphs become concentrated on Everglades tree islands when there is standing water in the surrounding marsh. Furthermore, tree islands in a deep marsh matrix tend to experience longer hydroperiods (i.e., strong positive correlation between marsh water depth and tree island hydroperiod; hydroperiod was omitted from the parsimonious dbRDA due to a high VIF), which increases the prevalence of flood-tolerant trees, namely cocoplum (*Chyrsobalanus icaco*) and pond apple (*Annona glabra*). The prolific fruiting of these trees provides abundant forage for bear and rats (evidenced by fecal samples and dental scarring on fruits, respectively). Thus, the affinity of black bear and myomorphs for mesic sites and increased availability of forage may have contributed to their increased occurrences and positioning of their environmental optima on sites characterized by deep marsh high-water levels.

Rats increased use of tree islands in Cluster 2 likely also reflects elevated populations due to a release from predation, as mammalian predators were not detected on these tree islands throughout the duration of this study (except one bobcat occurrence on tree island #23). Whereas mammalian predators occurred regularly on tree islands in Cluster 1 and their habitat use was positively correlated with the presence and increased habitat use of mammalian prey species. Florida panther and coyote are the largest predatory mammals in the Everglades and their tree island use was highest on sites where feral hogs were present. These correlations may reflect that panthers and coyote select for tree islands with high prey availability and hogs are a preferred food source because of their large size, frequent reproduction, and rapid population growth rates (Belden et al., 1988; Maehr et al., 1990; Dalrymple & Bass, 1996; Dees et al., 2001; Thornton et al., 2004). Similarly, bobcat tree island use was highly correlated with tree island use by high-quality prey species, whitetail deer and meso-mammals (Boulay, 1992; Labisky & Boulay, 1998; Thornton et al., 2004).

CONCLUSION

This is the most comprehensive study to date investigating how environmental characteristics drive patterns of mammal diversity, metacommunity structure, and habitat use across the Everglades tree island landscape. Trail camera monitoring over a +5-year sampling period detected twelve species; myomorphs were counted as 1 species but likely represent 3 native (cotton mouse, marsh rice rat, and hispid cotton rat) and one invasive species (black rat). The expansive range of environmental characteristics included in tree island sampling and the extremely high sample coverage estimates (mean = 99%) indicated that the detected species and estimated diversities fully represent the mammal metacommunity of central Everglades tree islands.

Mammal diversity varied markedly between individual tree islands, ranging from 1 – 13 species and 1 – 6 species according to coverage estimated species richness and Hill-Shannon diversity, respectively (Fig. 2). Heterogeneity between tree islands' species richness and Hill-Shannon diversity were largely explained by the interannual average of tree islands' local (within 1000 m radius) marsh water depths, a facet of matrix-derived stress for terrestrial mammals in the Everglades landscape. As matrix-derived stress increased, tree islands' mammalian alpha diversities decreased and a precipitous decline in most species' habitat use occurred near 0.25 m of average marsh water depth. Average marsh water depth does not account for temporal variation of stress and its effect on the mammal metacommunity. Hypothetically, two tree islands could experience average marsh water depths that are equal and < 0.25 m, but one island experiences drastic amplitudal change (i.e., seasonally very deep, then very shallow or dry marsh) and the other experiences very little amplitudal change (~0.25 m depth year-round). It is unclear whether 0.25 m of average marsh water depth (regardless of amplitude) will sustain a healthy and diverse mammal community, or if periodic dry downs that temporarily alleviate matrix-derived stress are needed to sustain diversity and these conditions coincidentally result in 0.25 m average marsh depth. Amplitude of marsh depth and the length of periodic drydowns were included in GLMM model selection but were not included in the most parsimonious model of matrix-derived stress on diversities (Fig. 5). The multiannual scope of this research could have blurred the effects of amplitude, periodic drydowns, and other hydrologic variables on mammal diversities. Analyses that assess intra-annual variation of hydrologic variables are needed to disentangle how various facets of matrix-derived stress affect mammal diversity on Everglades tree islands. However, the 0.25 m water depth criterion is a valuable preliminary baseline for managers to model which tree islands will support diverse mammal communities.

Tree island patch size, number and area of neighboring tree islands, and proximity to the nearest potential source population had indiscernibly weak effects on mammal alpha species richness and Hill-Shannon diversity. The potential benefits of landscape connectivity on diversity could have been too weak to detect with this observational field study design because anthropogenically induced degradation and loss of tree islands have already drastically reduced landscape connectivity such that approximately 30% of pre-drainage tree island area remains (Patterson & Finck, 1999), and the total percent area of neighboring tree islands was <5% for nearly all sampled tree islands. A difference in 2% versus 5% areal cover of neighboring tree islands may have a negligible impact on mammal diversity, but 2% versus 17% (5% of current sampled area/ 30% of pre-drainage area = 17% predicted area of pre-drainage tree islands) may have an appreciable difference. The potential effects of increased landscape connectivity on mammal diversity among tree islands in the central Everglades remains uncertain but future studies could improve our understanding if areas with higher tree island connectivity (e.g., Water Conservation Area 1 has ~14% tree island area (Brandt et al., 2000)) were included.

The weakness of the effects of total tree island availability (i.e., patch size and percent area of neighboring tree islands) and absence of vegetative characteristics on metacommunity composition emerged partly from the metacommunity-wide approach used in model selection for dbRDA and variation partitioning; selected variables parsimoniously explained the overall metacommunity variation, but not necessarily the variation for each individual species. Consequently, important effects of a variable on a species could be obscured or completely omitted depending on model selection. For instance, multiple linear regression (results not shown) revealed raccoons were most sensitive to landscape connectivity at the spatial scale of 500 m, not 1000 m as selected in the metacommunity's parsimonious model. Thus, the effect of connectivity on raccoons in the metacommunity model would be obscured. Similarly, a variable may have an important effect on a particular species but not the overall metacommunity, so the variable would be omitted from the metacommunity' s most parsimonious model and its effect go unrecognized. Despite these obfuscations, it was clear that greater percent area of neighboring tree islands significantly increased most species' tree island use. Patch size also had a clear positive effect, but only on black bear. The effects of total tree island availability and other aspects of landscape structure on mammal metacommunity composition could be further refined with the integration of telemetry data to identify the most important spatial scales of landscape connectivity and habitat availability for each species.

The Everglades mammal metacommunity has been undergoing a multi-decadal decline but has seldom been a focus of management, conservation, or restoration efforts in the Everglades. This decline has previously been attributed largely to predation by Burmese pythons (*Python molurus bivittatus*) (Dorcas et al., 2012). Pythons undoubtedly have a significant impact on mammal populations, and this study revealed that species interactions between mammalian predators and prey may also have important effects on metacommunity compositional structure. However, the metacommunity's idealized nested structure coupled with findings from the dbRDA analyses indicated that environmental filtering by matrix-derived hydrologic stress (i.e., mean marsh high-water depth (DEEP)) was the predominant force determining mammal metacommunity structure, diversity, distribution, and habitat use. Marsh and tree island hydrologic variables were highly correlated, but marsh hydrologic variables were better predictors of mammal diversity and habitat use (Fig. 5 and 7, respectively), likely because mammals require shallow matrix conditions to disperse between tree islands and frequent dispersal between islands is necessary for these mammals to acquire the resources needed to sustain themselves.

Central Everglades tree islands that exhibit low levels of matrix-derived hydrologic stress had the most speciose mammal communities and as stress increased, tree island communities reduced to smaller subsets of those found in more diverse sites. Tree islands that exhibited mean marsh high-water depths <0.4 m supported a diverse array of upland mammals, including the endangered Florida panther. In contrast, tree islands with mean marsh high-water depths >0.4 m were depauperate of most mammals, effectively only supporting black bear and myomorphs, which were ubiquitous across the central Everglades tree island landscape because of their tolerance or affinity for mesic conditions. At these depths, small- and meso-mammals are not able to walk across the marsh, although semi-aquatic species could swim. The water's depth would also make it very physically and calorically demanding for larger species to move across the matrix. Thus, as marsh-depth increases, the metacommunity's functional connectivity decreases and mammals become isolated on tree islands. Isolation limits resource availability and increases stress, thereby reducing mammals' diversity, distributions, abundances, and habitat use. These findings are mechanistically supported by prior research from Everglades tree islands and other patchy habitats across the globe that show prolonged periods of matrix-derived hydrologic stress reduce mammal diversity, abundances, and reproduction by increasing isolation, starvation, disease incidence, predation, and flood-related mortality (Sheppe & Osborne, 1971; Creekmore & Glaser, 1999; Dalecky et al., 2002; MacDonald & Labisky, 2004; MacDonald-Beyers, & Labisky, 2005; Wuczyński & Jakubiec, 2013; Abernathy et al., 2019).

To restore the tree island landscape and mammal metacommunity in areas of the Everglades where these species have been lost largely due to excessive or prolonged inundation (e.g., southern portion of 3AS), managers should prioritize reducing matrix-derived stress to a level that is tolerable for the target species and in accordance with the modeled or presumed "natural" pre-drainage hydrologic regime. Other regions of the

Everglades experience an unnaturally dry hydrologic regime (e.g., northern portion of 3AN) and managers should seek to increase matrix-derived stress to a natural level. However, this management objective is complicated by the extensive loss of tree island elevation from soil consumptive fires and oxidation. If managers increase matrix-derived stress prior to restoring tree island elevations, mammals and other fauna and flora that rely on tree islands would be extirpated as additional, irreversible tree island loss would occur. Considering the severe tree island loss that has already occurred, it is crucial that managers implement operations that conserve the condition of existing tree islands and explore novel methods of tree island restoration (e.g., nucleation of new tree islands, add biodegradable platforms or soil fill to increase tree island head elevation, and strategically plant species that accelerate soil accretion), especially if restoration involves increasing matrix-derived stress. Successful restoration of patchy landscapes, like the Florida Everglades, is contingent on researchers comprehensively investigating and identifying how patch and matrix environmental characteristics drive metacommunities' diversity and structure. Understanding how ecological drivers affect metacommunities and their constituent species will help managers and decision makers design and prioritize projects that maximize efficiency and overall impact of conservation or restoration plans.

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APPENDICES

Appendix A. List of Mammals Observed in Camera Trapping

Common Name		**Scientific Name**
Black bear		*Ursus americanus floridanus*
Bobcat		*Lynx rufus*
Coyote		*Canis latrans*
Eastern gray squirrel		*Sciurus carolinensis*
Feral hog		*Sus scrofa*
Florida panther		*Felis concolor coryi*
Marsh rabbit		*Sylvilagus palustris*
Raccoon		*Procyon lotor*
River otter		*Lutra canadensis*
Virginia opossum		*Dideplphis virginiana*
Whitetail deer		*Odocoileus virginianus seminolus*
Rat	Cotton mouse	*Peromyscus gossypinus*
	Marsh rice rat	*Oryzomys palustris*
	Hispid cotton rat	*Sigmodon hispidus*
	Norway rat	*Rattus norvegicus*
	Roof rat	*Rattus rattus*

* Multiple myomorph species were likely present but could not be consistently identified to the species level; these myomorphs were collectively named “rat” and treated as a single species in analyses.

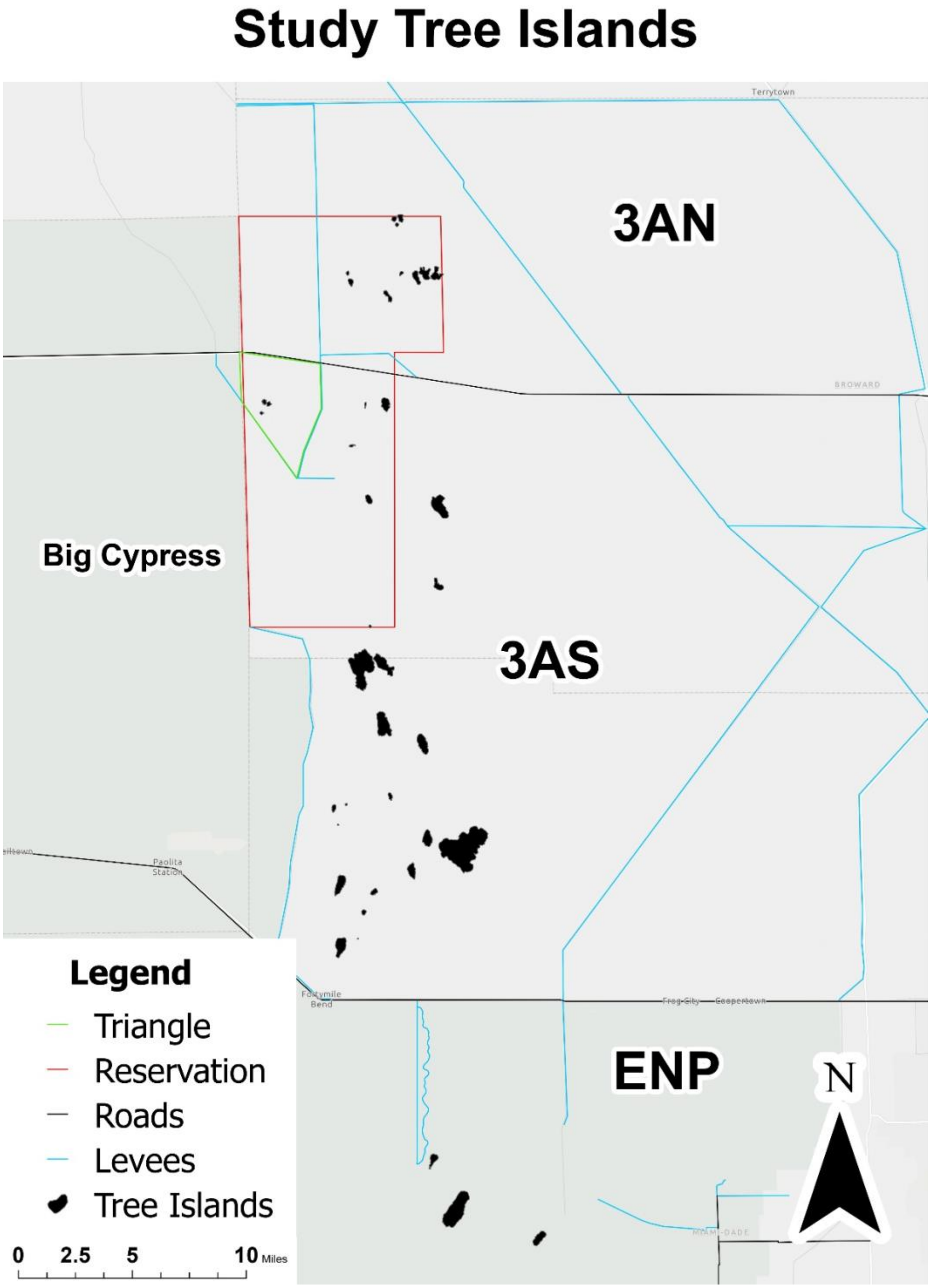
Appendix B. List of Explanatory Variables

Term	Acronym in Analyses	Type	Definition
Landscape variables			
Area	**AREA**	**Positive continuous**	**log area (m) of the study tree island's head**
Neighbor100		Positive continuous	Percent area of neighboring tree islands in a 100 m radius surrounding the study tree island
Neighbor250		Positive continuous	Percent area of neighboring tree islands in a 250 m radius surrounding the study tree island
Neighbor500		Positive continuous	Percent area of neighboring tree islands in a 500 m radius surrounding the study tree island
Neighbor1000	**NBR%**	**Positive continuous**	**Percent area of neighboring tree islands in a 1000 m radius surrounding the study tree island**
Neighbor2000		Positive continuous	Percent area of neighboring tree islands in a 2000 m radius surrounding the study tree island
no.100		Positive Integer	Number of neighboring tree islands in a 100 m radius surrounding the study tree island
no.250		Positive Integer	Number of neighboring tree islands in a 250 m radius surrounding the study tree island
no.500		Positive Integer	Number of neighboring tree islands in a 500 m radius surrounding the study tree island
no.1000		Positive Integer	Number of neighboring tree islands in a 1000 m radius surrounding the study tree island
no.2000		Positive Integer	Number of neighboring tree islands in a 2000 m radius surrounding the study tree island
Structure.Dist.		Positive continuous	Shortest Euclidean distance from the study tree island to a "source" (Big Cypress National Preserve or levee)
Hydrologic variables			
Amplitude.mean		Positive continuous	Mean annual amplitude (x2) of daily marsh water depth (from Water Years 2019 - 2023), adjusted for camera trap days
Amplitude.max		Positive continuous	Maximum annual amplitude (x2) of daily marsh water depth (from Water Years 2019 - 2023), adjusted for camera trap days
Amplitude.WY.mean		Positive continuous	Mean annual amplitude (x2) of daily marsh water depth (from Water Years 2019 - 2023)
Amplitude.WY.max	**MRSH**	**Positive continuous**	Maximum annual amplitude (x2) of daily marsh water depth (from Water Years 2019 - 2023)
Mean.Depth	**WATR**	**Positive continuous**	**Mean marsh depth (from Water Years 2019 - 2023)**
Mean.HighWater.Dep	**DEEP**	**Positive continuous**	**Mean high-water marsh depth (measured during the 6 deepest months of each Water Year (from Water Years 2019 - 2023))**
Hydro.mean		Positive Integer	Mean annual hydroperiod from Water Years 2019 -2023
Hydro.max		Positive Integer	Maximum annual hydroperiod from Water Years 2019 -2023
Hydro.mean.adj		Positive Integer	Mean annual hydroperiod from Water Years 2019 - 2023, adjusted for camera trap days
Hydro.max.adj		Positive Integer	Maximum annual hydroperiod from Water Years 2019 - 2023, adjusted for camera trap days
LongestDry.mean		Positive Integer	Mean of greatest number of continuously dry days in a Water year (from Water Years 2019 - 2023)
LongestDry.max		Positive Integer	Maximum of greatest number of continuously dry days in a Water year (from Water Years 2019 - 2023)
LongestDry.WY.mean		Positive Integer	Mean of maximum number of continuously dry days in each Water year (from Water Years 2019 - 2023)
LongestDry.WY.max	**DDRY**	**Positive Integer**	Maximum number of continuously dry days (from Water Years 2019 - 2023)
RE.mean		Positive continuous	Mean elevation of tree island plots, relative to daily water levels from Water Years 2019 - 2023
RE.max		Positive continuous	Maximum elevation of tree island plots, relative to daily water levels from Water Years 2019 - 2023
Vegetation variables			
Canopy		Positive Continuous	Average canopy cover class of vegetation plots
Ground.fern		Binary	Herb layer dominated by ferns
Ground.herb		Binary	Herb layer dominated by herbaceous plants
Ground.seedling		Binary	Herb layer dominated by tree seedlings
Hammock		Binary	Presence of hardwood hammock species
Percent.Wetland		Positive Continuous	Percent of plant species are facultative or obligate wetland species according to National Wetland Plant List (NWPL)
Shrub.fern		Binary	Shrub layer dominated by ferns
Shrub.herb		Binary	Shrub layer dominated by herbaceous plants
Tree.Richness		Positive Integer	Observed species richness of tree species
ANNGLA		Binary	Tree layer dominated by (Annona glabra)
BURSIM		Binary	Tree layer dominated by (Bursera simaruba)
CHRICA		Binary	Tree layer dominated by (Chrysobalanus icaco)
EUGAXI		Binary	Tree layer dominated by (Eugenia axillaris)

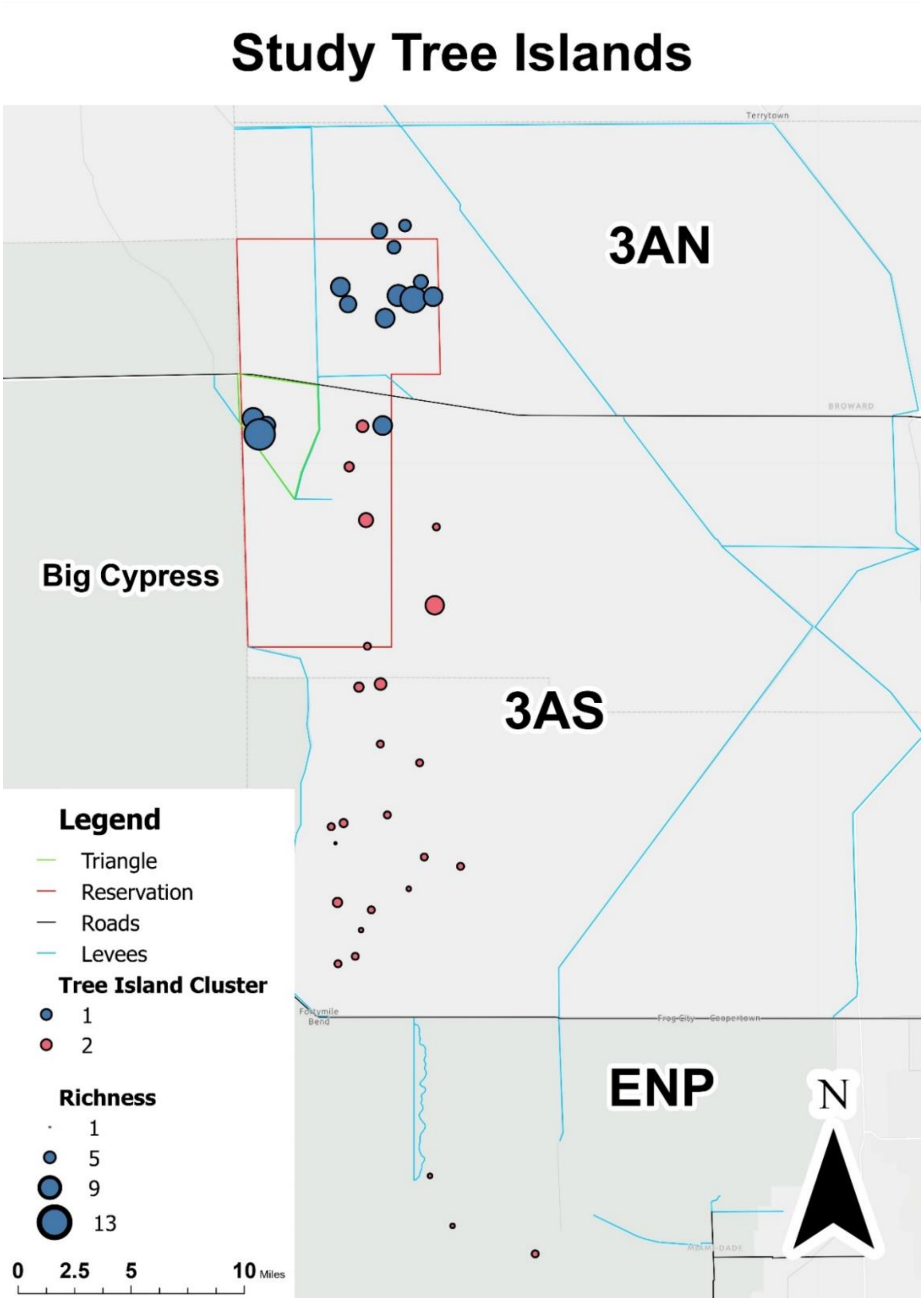
Appendix B. List of Explanatory Variables (Continued)

Term	Acronym in Analyses	Type	Definition
Vegetation variables (continued)			
FICAUR		Binary	Tree layer dominated by (Ficus aurea)
SALCAR		Binary	Tree layer dominated by (Salix caroliniana)
SCHTER		Binary	Tree layer dominated by (Schinus terebinthifolius)
TAXDIS		Binary	Tree layer dominated by (Taxodium distichum)
Spatial variables			
MEM1		Continuous	Moran's eigenvector map: eigenvector 1
MEM2	**MEM2**	**Continuous**	**Moran's eigenvector map: eigenvector 2**
MEM3	**MEM3**	**Continuous**	**Moran's eigenvector map: eigenvector 3**
MEM4	**MEM4**	**Continuous**	**Moran's eigenvector map: eigenvector 4**
MEM5		Continuous	Moran's eigenvector map: eigenvector 5
MEM6		Continuous	Moran's eigenvector map: eigenvector 6
MEM7		Continuous	Moran's eigenvector map: eigenvector 7
Variable Interactions			
Area X Neighbor100		Positive continuous	Multiplicative interaction between terms
Area X Neighbor250		Positive continuous	Multiplicative interaction between terms
Area X Neighbor500		Positive continuous	Multiplicative interaction between terms
Area X Neighbor1000		Positive continuous	Multiplicative interaction between terms
Area X Neighbor2000		Positive continuous	Multiplicative interaction between terms
Area X no.100		Positive continuous	Multiplicative interaction between terms
Area X no.250		Positive continuous	Multiplicative interaction between terms
Area X no.500		Positive continuous	Multiplicative interaction between terms
Area X no.1000		Positive continuous	Multiplicative interaction between terms
Area X no.2000		Positive continuous	Multiplicative interaction between terms
Mean.Depth X Hydro.mean		Positive Continuous	Multiplicative interaction between terms
Mean.HighWater.Depth X Hydro.max		Positive Continuous	Multiplicative interaction between terms
Mean.Depth X Hydro.mean.adj		Positive Continuous	Multiplicative interaction between terms
Mean.HighWater.Depth X Hydro.max.adj		Positive Continuous	Multiplicative interaction between terms
Mean.Depth X RE.mean		Positive Continuous	Multiplicative interaction between terms
Mean.HighWater.Depth X RE.max		Positive Continuous	Multiplicative interaction between terms

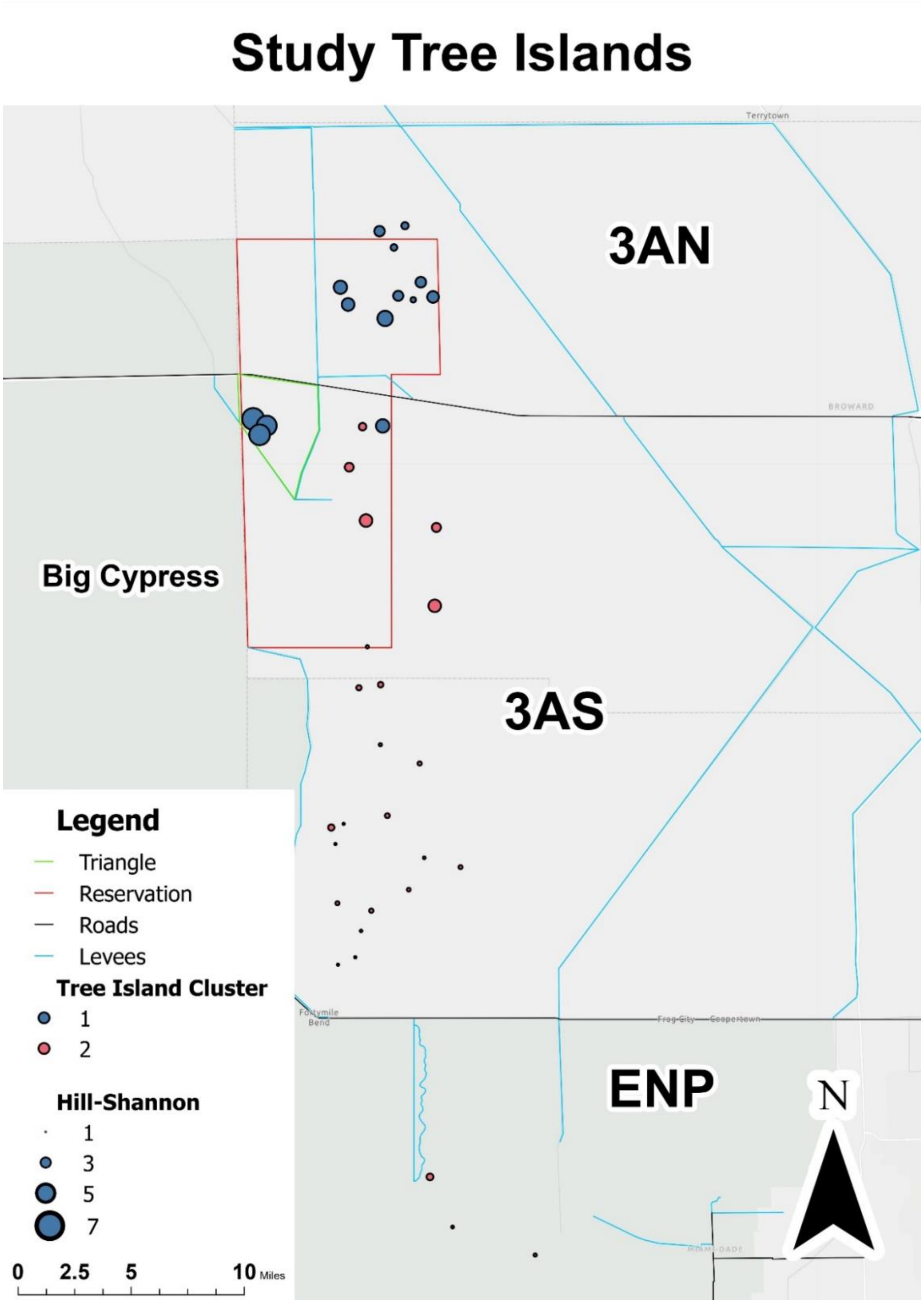
Appendix C. Maps



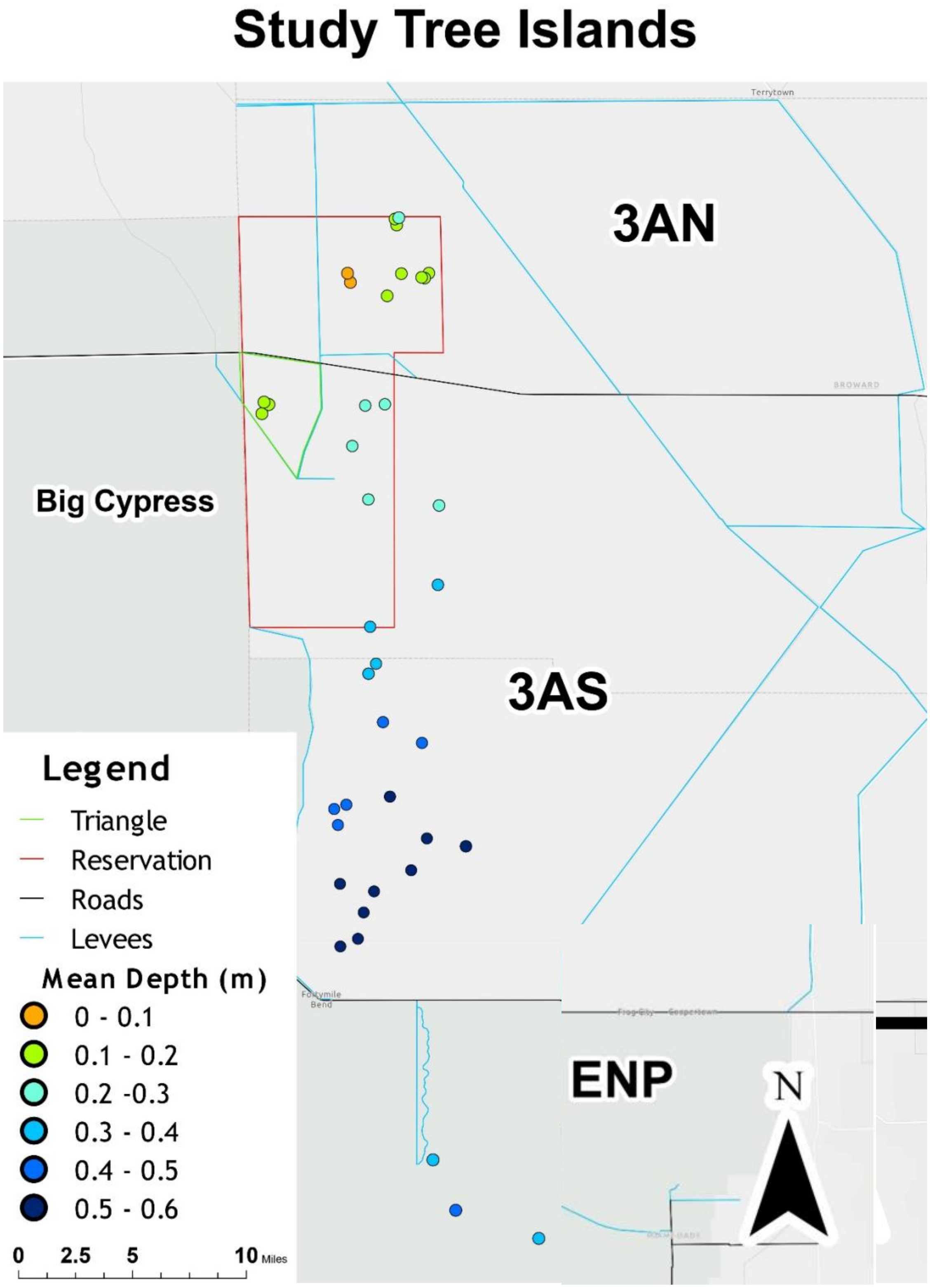
Map 1. Digitized polygons of 40 study tree island heads. Polygons reflect the true locations and shapes of tree island heads, but sizes are 5x the scale of their true areal extent (for visual aid of small tree islands).



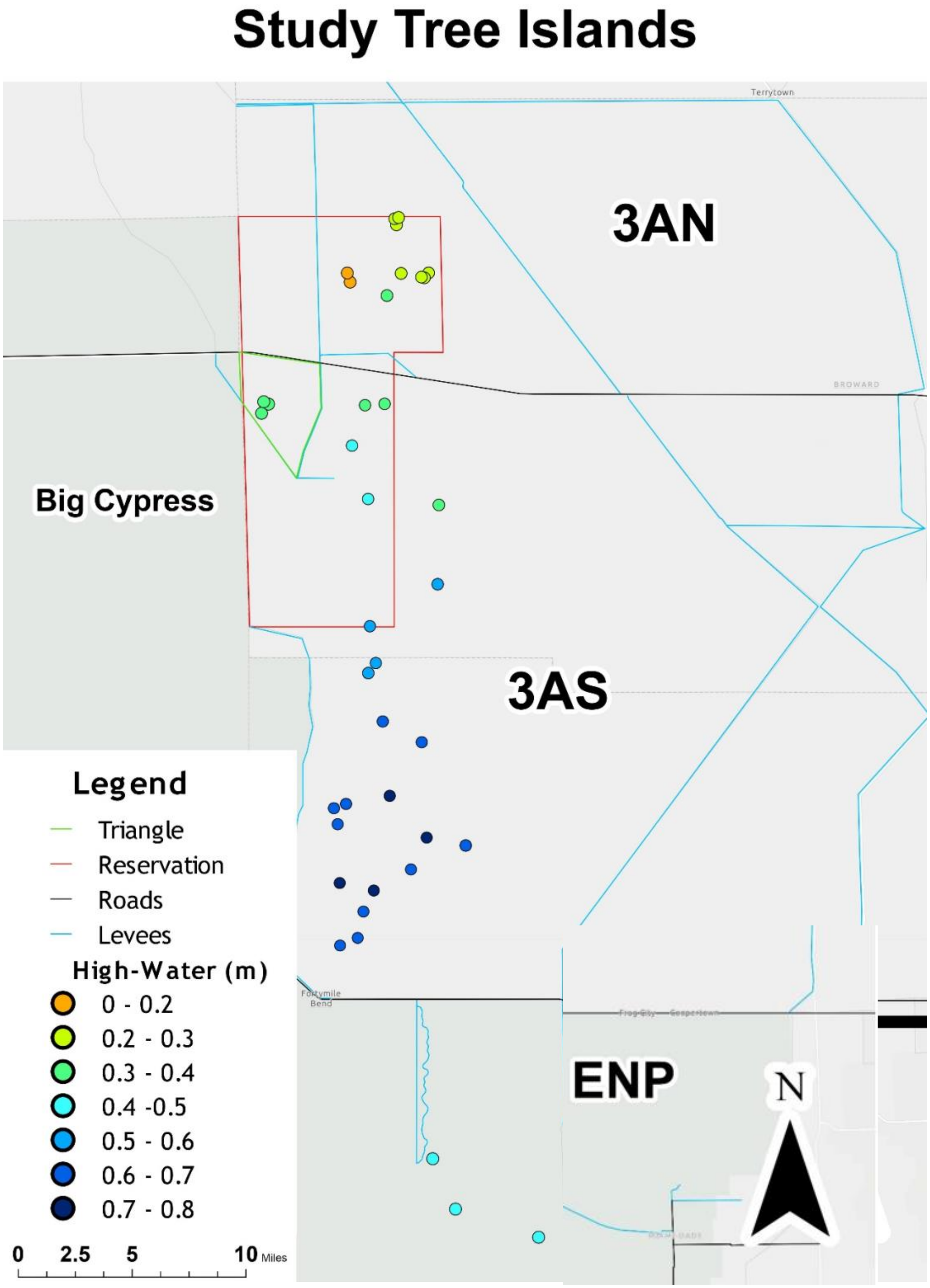
Map 2. Tree island sites' species richness, estimated from coverage-based asymptotes. Tree islands are color coded by cluster, as determined from hierarchical agglomerative clustering.



Map 3. Tree island sites' Hill-Shannon diversity, estimated from coverage-based asymptotes. Tree islands are color coded by cluster, as determined from hierarchical agglomerative clustering.



Map 4. Tree island sites' mean marsh water depth in a 1000 m radius around each study tree island during Water Year 2019 – 2023 (WATR). WATR was the variable that had the strongest effect on mammal alpha diversities according to GLMM models (Fig. 5)



Map 5. Tree island sites' mean marsh high-water depth in a 1000 m radius around each study tree island during Water Year 2019 – 2023 (DEEP). DEEP was the variable that had the strongest effect on mammal compositional beta diversity according to dbRDA (Fig. 7) and variation partitioning (Fig. 8).

Appendix D. Trail Camera Photographs

WCA 3AS


62F 17C
12-11-2022 01:17:02


Bushnell
TROPHY CAM
71°F 21°C
06-09-2021 07:01:38


Bushnell
TROPHY CAM
69°F 20°C
12-15-2021 06:33:10


Bushnell
TROPHY CAM
77°F 25°C
10-12-2021 01:13:14


Bushnell
TROPHY CAM
72°F 22°C
01-18-2021 16:22:02


84F 29C
10-26-2022 15:34:20

Triangle


Bushnell
TROPHY CAM
56 °F 14 °C
01-22-2020 15:43:44


Bushnell
TROPHY CAM
73 °F 22 °C
03-16-2023 17:25:34


Bushnell
TROPHY CAM
77 °F 25 °C
06-09-2019 12:59:35


Bushnell
TROPHY CAM
87 °F 30 °C
07-29-2020 15:59:28


Bushnell
TROPHY CAM
88 °F 31 °C
04-02-2023 15:56:45


Bushnell
TROPHY CAM
70 °F 21 °C
01-10-2023 12:03:25

WCA 3AN


Bushnell
TROPHY CAM
86°F 30°C
06-25-2022
11:57:08


Bushnell
TROPHY CAM
84°F 28°C
09-01-2020
19:52:30


Bushnell
TROPHY CAM
86°F 30°C
05-30-2020
12:18:18


Bushnell
TROPHY CAM
88°F 31°C
11-11-2021
14:50:22


Bushnell
TROPHY CAM
72°F 22°C
09-19-2019
20:22:15


Bushnell
TROPHY CAM
71°F 21°C
03-05-2020
04:26:16

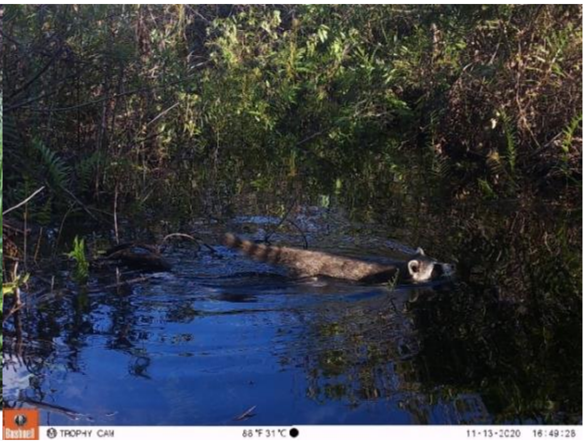

Bushnell
TROPHY CAM
82°F 27°C
10-23-2020 17:23:23


Bushnell
TROPHY CAM
86°F 30°C
09-20-2021 14:24:21


Bushnell
TROPHY CAM
97°F 36°C
05-31-2017 04:04:26


Bushnell
TROPHY CAM
76°F 24°C
11-11-2020 09:19:12


Bushnell
TROPHY CAM
78°F 25°C
01-21-2022 13:49:29


Bushnell
TROPHY CAM
88°F 31°C
11-13-2020 16:49:28

Appendix E. Tree Island Photographs

CHAPTER III. FLORIDA BLACK BEARS' SPATIOTEMPORAL USE OF EVERGLADES TREE ISLANDS

INTRODUCTION

The Florida black bear (*Ursus americanus floridanus*; hereon "bear") is widely distributed across the state and inhabits a diverse array of forested habitats, such as xeric scrub, pine flatwoods, swamps, and tropical hardwood hammocks (FWC, 2019). The adaptability of bears to a swath of environmental conditions facilitates the expansiveness of their range and resilience to ecological alterations. However, intense land clearing practices ensued post-European settlement of Florida and catalyzed a decline in the statewide bear population (FWC, 2012). The estimated statewide bear population pre-European settlement was 11,000, but with continued land clearing and development, the bear population plummeted to 300 by 1974 (97% decline), (McDaniel, 1974). The State readily responded to the diminished population by designating the Florida black bear as a threatened species; since then, the bear population has steadily increased to a present-day population exceeding 4,000 individuals (Scheick, 2023).

Due to landscape-scale variation in habitat type and continued human development sprawling into natural areas, the range and statewide population size of bears has been spatially restricted to seven subpopulations: Eglin, Apalachicola, Osceola, Ocala/St. Johns, Chassahowitzka, Highlands/Glades, and Big Cypress (Scheick et al., 2023). These subpopulations function as a metapopulation through occasional migration between subpopulations, with most migrants being subadult males (Maehr et al., 1998; Maehr, 2001; Dobey et al., 2005; Dixon et al., 2006). Considering the requisite of landscape connectivity for sustaining a healthy metapopulation and large home range of black bears in Florida (female = 23 – 98 km^2; male = 93 – 350 km^2), it is vital that large contiguous tracts of bear habitat are conserved and connected through habitat corridors or a "traversable matrix" with islands of forested habitat (FWC, 2019). Although researchers and management agencies have acknowledged forested islands as suitable bear habitat that is particularly valuable for maintaining metapopulation connectivity, very little is known about how Florida black bears use forested islands (Maehr, 1996; Dixon et al., 2006; Ulrey, 2008; FWC, 2019).

Forested islands are especially common across South Florida because elevational heterogeneity in the wetland landscape creates a mosaic of habitat types. However, a multidecadal hiatus in South Florida bear research thwarted understanding how bears use naturally fragmented forest islands. Most published studies date back to the 1980's and 1990's (Brady & Maehr, 1985; Maehr et al., 1988; Maehr, 1996), but the Florida Fish and Wildlife Conservation Commission (FWC) has ramped up bear research in recent years (Brian Scheick, personal communication, 2023). Additionally, past and ongoing studies of the Big Cypress subpopulation exclusively surveyed southwest Florida, but this subpopulation is known to range further east, into the Everglades.

The Florida Everglades is a subtropical seasonal wetland that is generally considered low-quality bear habitat because unforested herbaceous marsh and deeper channelized sloughs are the dominant habitat types, but thousands of forested islands known as "tree islands" perforate the wetland matrix (Maehr, 1996; Stone et al., 2002; Lodge, 2019). Tree islands exist as slightly elevated mounds of peat soil whose relatively short hydroperiods are conducive for growth of woody species. Tree islands offer the only terrestrial and forested refugia in the Everglades and have therefore been presumed to be foci of faunal biodiversity and habitat use by bears and other mammals in the Everglades. Although bears have been documented to use Everglades tree islands, they have never been the focus of a study and virtually nothing is known about bears in this ecosystem (Schemnits, 1974; Meshaka et al., 2002).

This will be the first study into the ecology of Florida black bears on Everglades tree islands. The overarching goal of this research is to improve the ecological understanding of how bears use spatially disjunct forested islands by answering how ecological and phenological factors affect spatial and temporal variation of bear habitat use. The following hypotheses were developed to tackle this research goal.

- It is hypothesized that bears' use of tree islands will be positively affected by increased tree island patch size and interpatch connectivity because bears search for resources over a large home range (larger than any single tree island), so bears will rely on larger tree islands that assumedly provide more resources but still require neighboring tree islands to satisfy their resource requirements.

- Increased hydrologic stress is hypothesized to limit bears' use of tree islands; longer tree island hydroperiod and deeper average marsh conditions will reduce bear habitat use on those tree islands because inundation will degrade habitat quality and restrict interpatch dispersal.

- Bears are hypothesized to increasingly use tree islands whose vegetative communities support an abundance of mast (i.e., fruit) trees because forage availability is a preeminent environmental factor affecting bear distribution, home range size, and habitat use (Moyer et al., 2007; Stratman & Pelton, 2007; Murphy et al., 2017). Also, temporal increases in mast availability will increase bear activity, as bears will be attracted to an island and will exploit the ripe fruit while it is available.

- Bears' use of tree islands will oscillate annually. It is hypothesized that tree island use will peak in the summer months because males will be searching for a mate, and mother-cub family units increase foraging activity to replenish nutrient stores from parturition and nursing as cubs transition from milk to solid foods. Seasonal fluctuations in water level will also affect tree island use such that high-water will restrict bear activity, and low-water levels will facilitate dispersal.

METHODS

3.1. Site Selection

This study was conducted in Miccosukee Water Conservation Area 3A South (3AS) of the central Everglades. This study area is eastwardly adjacent to the Big Cypress Swamp (BC), where much of the Big Cypress bear subpopulation resides. However, 3AS is disjoined from BC and other neighboring conservation lands because 3AS is a compartmentalized unit of the Everglades, bound by major roadways (I-75/ "Alligator Alley" and US-41/ "Tamiami Trail", to the north and south, respectively), canals, and levees. Compartmentalization of 3AS has resulted in an anthropogenically altered hydrologic regime, where inflows from the north typically do not drain southward into Everglades National Park fast enough, causing water levels, hydroperiod, and ponding of water to increase from North to South in 3AS. A North-South transect was established along the western portion of 3AS, extending from Tamiami Trail to Alligator Alley. Twenty-four tree islands were randomly selected as study sites along this transect (Appendix A). Tree islands were visually assessed in the field to ensure that the study sites comprehensively encapsulated the range of environmental conditions that characterize tree islands in 3AS.

3.2. Camera Trapping

Trail cameras (a.k.a. camera traps) were used to monitor bears on the study tree islands because trail cameras continuously and contemporaneously monitor species with minimal to no impact on species behavior at sites. In most circumstances, trail cameras provide the optimal means for surveying mammals because they detect and store tremendous amounts of data, minimize survey effort, and nearly eliminate observer bias (Dertien et al., 2019; Zwerts et al., 2021). Note that bias can emerge if cameras are not deployed following a consistent protocol (see protocol below) or if multiple individuals are screening and identifying species in photographs (only one individual managed photos). Four trail cameras were initially deployed in December 2017, and additional cameras were incrementally added; 19 cameras were deployed by November 2018, and the entire 24 by May 2020. Since then, cameras have been continuously operating.

A single trail camera (Bushnell Trophy Cam HD Aggressor No Glow 20 mp) was deployed in the “head” of each study tree island (i.e., the upstream, higher elevation, drier portion of the island). Because the location, size, and microtopography of heads is highly variable between tree islands, the exact location of trail cameras was determined after a thorough visual inspection of the head. Trail camera locations were selected to maximize the expected likelihood of successfully detecting wildlife, based on the presence of tracks or scat and microsite conditions (i.e., game trails, natural clearings, or area with large range of view). Trail cameras were placed approximately 0.5 m above the ground (mounted to tree trunks or branches via nylon straps) and positioned at a slight downward angle; exact camera height and angle varied slightly between sites to avoid vegetation that would otherwise obstruct the camera’s view. Trail cameras were set to the high-sensitivity motion-sense mode, taking a photo with a 0.2 second trigger speed whenever motion was detected, followed by a 10-second interval between photos. Cameras also use infrared technology during low light conditions to take photos at night without flash. Study islands were revisited once every 5 to 6 weeks to ensure that all cameras were working properly, had sufficient battery, and were still positioned properly; any necessary adjustments were made at this time and cameras were occasionally replaced when damage from severe weather or wildlife activity occurred.

Trail camera photos were downloaded upon each recurring visit to study tree islands. Photos were manually screened for bear detections and labels were added to describe important life history information or behavioral activity observed in the photos (e.g., labels often resemble “mother with 2 cubs” or “bear forages on turtle nest”). The short photo interval (10 seconds) often results in dozens of photos of the same bear in a short timespan (several minutes). To avoid inflating bear habitat use data, “occurrences” were separated by a 60-minute interval; when a bear was detected on a camera multiple times in less than 60 minutes, it was recorded as a single bear occurrence. If a bear was detected again, after the 60-minute interval, then another occurrence would be recorded. The exception is if there are multiple, clearly distinguishable bears being detected in the same 60-minute interval, an occurrence would be recorded for each individual (e.g., a photo of a large male, followed by a subadult would be recorded as 2 separate occurrences). Bear tree island habitat use was measured by converting monthly bear occurrences at a camera to a Relative Abundance Index (RAI):

$$\mathrm{RAI} = \left(\frac{\#\ of\ occurrences}{\#\ of\ trap\ days}\right) \times 100$$

RAI standardizes raw occurrence data by monthly trap days to correct for differences in sampling effort between sites (i.e., cameras were initially deployed on different dates and occasional damage to cameras would disrupt monitoring) (Jenks et al., 2011 and others). Multiplying standardized occurrences by 100 is not necessary but is helpful for interpreting very small RAI values (e.g., RAI of 3 translates to 3 bear occurrences per 100 trap days).

Differences in sites' RAI, measured during the same time span, can reflect differences in population sizes; RAI can also capture changes in population size if the survey period is long enough to capture generational changes (i.e., multiple years), and the sample sites are held constant across the survey period. Over short time spans (i.e., intra-annual), changes in RAI are interpreted as variation in habitat use because bear abundance is considered static within a "Bear Year" (BY); a BY will begin in February and end the following January because parturition typically peaks in early February (Brian Scheick, personal communication, 2023). Annual mortality rate of bears is unknown in the Everglades and could not be incorporated into RAI models, but human induced mortality (e.g., vehicle collision) is considered rare for bears in this study area, and Maehr (1996) states that natural causes of bear mortality is generally low in Florida.

3.3. Landscape Structure

The effects of landscape structure on black bear distribution, habitat use, and movement has been well established across much of North America, including Florida, but not in the Everglades (Maehr et al., 2003; Dixon et al., 2006; FWC, 2019; Wilton, 2020; Lara-Díaz et al., 2021; Lewis et al., 2022). Landscape structure may be particularly impactful to bears in the Everglades because the total areal extent of forested habitat is limited, and the structural characteristics of tree islands are highly variable. ArcGIS Pro (orthorectified World Imagery Basemap with 0.3 m resolution in continental United States) was used to digitize and measure the patch size (i.e., area) of the 24 study tree islands' heads. Heads were clearly distinguishable from the near tail, tail, and surrounding marsh because of stark contrasts in vegetation type and tree density. The heads of tree islands were used to measure patch size, instead of the entire spatial extent of tree islands (head to tail), because the near tail and tail habitat's hydric conditions, dense sawgrass (*Cladium jamaicense*) understory, and lack of overstory is considered unsuitable bear habitat.

Connectivity between tree island patches is another key component of landscape structure. Although tree islands are not literally connected to one another (for instance, by a corridor), the spatial configuration of tree islands does affect functional connectivity. Connectivity of study tree islands was measured at multiple spatial scales because it is unknown which scale is most ecologically relevant to bears in this ecosystem. Multiple concentric "rings" were delineated 100 m, 250 m, 500 m, 1000 m, and 2000 m from the digitized boundary of each study tree islands' head. Interpatch connectivity was measured between 100 – 2000 m because the nearest neighboring tree islands are rarely less than 100 m apart, so scales smaller than 100 m could not practically be measured. The upper bound for measuring connectivity (2000 m) was based on findings from telemetry studies by Maehr (1996), Karelus et al. (2017), and the Miccosukee Tribe Fish and Wildlife Department (MTFWD) (unpublished, 2023), which indicate that the average Euclidean distance male Florida black bears travel in a day is 2000 m; average daily distance travelled by males is substantially larger than that of females. ArcGIS Pro was used to digitize the heads of all neighboring tree islands within each spatial ring surrounding study tree islands. These polygons were used to calculate the number and total area (%) of tree island heads neighboring each study island.

Connectivity of study tree islands to the nearest potential source population was also measured because proximity to a source can affect species' presence and distributions

(MacArthur & Wilson, 1967). The Big Cypress National Preserve, immediately west of 3AS, is a mosaic of land cover types, but much of the preserve is contiguously forested (Appendix A, Map 2). Thus, BC may function as a “mainland” source population for bears in South Florida, from which bears disperse to tree islands in 3AS. Manmade levees surrounding 3AS may also function as a source because their elevations are several feet higher than any tree island in 3AS, providing a rescue effect via dry refugia for bears during floods that completely inundate tree islands. The connectivity of each study tree island to a potential source population was calculated in ArcGIS Pro by measuring the shortest Euclidean distance from each tree island to the edge of BC and the nearest levee.

3.4. Hydrology

Habitat type, habitat quality, primary productivity, and mammals’ ability to disperse across the Everglades are largely affected by local hydrologic conditions (Gaines et al., 2002; Childers, 2006; Todd et al., 2010; Hamilton, 2014). Hydrologic conditions of tree islands are determined by the interaction between tree islands’ elevations and local water levels. Tree island elevations were measured in December 2020, when extreme high-water inundated all study tree islands (and likely all other tree islands in 3AS). Elevation transects were established down the longest axis of each study island, typically north to south because tree islands are oriented in the direction of water flow. Surveying began at the upstream end of transects and stopped where the head transitioned into near tail or tail habitat, marked by an obvious visual decline in canopy cover, canopy height, and tree density.

Water depth was measured every 5 m along the transect if the tree island head was less than 200 m long, or every 10 m if the head exceeded 200 m. The water depth of each survey point was averaged from 3 measurements taken immediately around each survey point, thereby reducing random variation from microtopographic differences in elevation. Then, the estimated water level at each survey point, on the date the point was surveyed, was obtained from the Everglades Depth Estimation Network (EDEN) xyLocator tool; the EDEN xyLocator uses nearly 300 water gauges to generate a water surface grid (comprised of 400 m x 400 m grid cells) and interpolate the water level at the given coordinates. Elevation (according to a geodetic datum) at each survey point was calculated by subtracting the surveyed water depth from the interpolated water level data.

Since the elevation profile of tree island heads was now tied to a geodetic datum, hydrologic conditions of each tree island could be analyzed across time using EDEN's record of daily water levels. Water level data was extracted for Bear Years 2019 – 2023, but for the first 8 months of BY 2019 (BY 2019 = February 2018 – January 2019) only the initial four trail cameras were active. Different trail camera deployment dates and periodic trail camera failure (from drained batteries or damage from wildlife) resulted in variation between tree islands' survey durations and periods. Differential occurrences of bears on tree islands could merely arise from the hydrologic conditions during the survey period. Thus, two water level time series were created for each study tree island; one time series measures hydrologic variables for every day between BY 2019 – 2023, and the other time series measures hydrologic variables only for days that cameras were active. The discontinuous hydroperiod of tree island heads were calculated for each time series by determining how many days in each Bear Year the water level was above or below the mean elevation of all points surveyed along a head's transect. Hydroperiod was also calculated in reference to the maximum elevation surveyed along a head's transect; maximum elevations typically do not accurately represent the head's overall elevation but represent small microtopographical features that become increasingly important dry refugia to wildlife during flood events. Also, tree island heads' mean and maximum elevations relative to the local marsh water level (i.e., relative elevation) were measured by subtracting EDEN daily water level data from the corresponding head elevations, then averaging daily relative elevation values for each Bear Year.

The local hydrologic conditions in the marsh surrounding tree islands could be of equal or greater importance than hydrologic conditions on tree islands because marsh water depth and hydroperiod could limit interpatch dispersal of bears between tree islands. Hydrologic conditions were measured for each spatial ring (100 – 2000 m) because it is unclear which spatial scale is most ecologically relevant to bear dispersal in this ecosystem. Coordinates for all EDEN grid cells bound within a spatial ring were input to EDEN xyLocator, unless ≥25% of a grid cell was comprised of tree island; Liu et al., (2009) states that tree islands and other upland habitats were smoothed out of EDEN marsh elevation estimates, but removal of these cells served as an additional safety precaution to avoid artificially inflating marsh elevation estimates. Mean marsh ground elevation was calculated for each spatial ring by averaging grid cell marsh elevations retrieved from EDEN xyLocator. Two marsh water depth time series, from BY 2019 – 2023, were generated (for the same reasons and following the same criteria as the two tree island hydrologic time series) by subtracting EDEN grid cells' daily water level data from mean marsh ground elevation of each spatial ring. These daily water depth time series were used to calculated mean marsh water depth and mean high-water marsh depth for each Bear Year; "mean high-water marsh depth" was calculated by only averaging water depth values from the six months that water depths were greatest. Averaging marsh depth provides valuable point estimates but does not provide information on how much a tree island's local water depth fluctuates, so annual (BY) amplitudes of marsh depth were calculated by subtracting the greatest annual marsh depth by the smallest. The marsh around many tree islands will dry down intermittently during the dry season; continuous dry downs were measured as the longest number of consecutive days in a BY that water level was below the mean marsh elevation, and discontinuous marsh hydroperiods were calculated as the total number of days in a BY that water level was below the mean marsh elevation.

3.5. Vegetation

The plant community on study tree island heads was surveyed to analyze the effects of plant diversity, community composition, and structure on bears' use of tree islands. Square survey plots (16 m^2) were established at regular intervals (every 5 m if hardwood hammock habitat (or if head was less than 50 m long), and every 10 m if other habitat type) along the same transect used to measure elevation. Plant species were separated into 5 strata, based on the following criteria: (1) Herbs = maximum height <1 m; (2) Shrubs = maximum height >1 m, diameter at breast height (DBH) <1 cm, and not a vine; (3) Vines = vine with maximum height >1 m; (4) Saplings = woody species with maximum height >1 m and DBH 1 – 5 cm; (5) Trees = woody species with maximum height >1 m and DBH >5 cm.

Upon arriving to a plot, crown cover was estimated for each species whose crown extended into the plot, including individuals whose stems originated outside the plot. Crown cover was ocularly estimated as the percent of the plot's area covered by a species. Interleaf gaps in individuals' crowns were included in areal estimates, and overlapping crowns of the same species, in the same strata were agglomeratively (not additively) considered in species' crown estimates; thus, the maximum crown cover of a species was ≤100%. Crown cover was estimated for herb and shrub species within a $4m^2$ subplot, nested and centrally located within each $16m^2$ plot, but the $16\ m^2$ plot was used for the other strata. Estimated crown cover percentages were organized into 6 bins used by Sah (2004): 1 = 0-1%, 2 = 1-4%, 3 = 4-16%, 4 = 16-33%, 5 = 33-66%, and 6 = >66%. Estimated values that fell within a bin were converted to the bin's mean value (Irvine et al., 2019) Species were also categorized as non-forage, soft mast, hard mast, or vegetative forage sources according to field observations and bear dietary records (Maehr, 1996; Stratman & Pelton, 1999; Murphy et al., 2017). Mean values of species' crown cover in each forage category were summed together and used as index of forage availability on individual tree islands; the summed crown cover of all forage sources was also calculated as an index of total forage availability on each tree island.

Plant surveys also measured sapling and tree stem density (number of individuals of a species in the $16\ m^2$ plot). The DBH of trees were recorded if their trunk originated inside the plot. Trees with multiple trunks (splitting below 1 m) were treated as the same individual, but a DBH was recorded for each trunk. The DBH of trees was used to calculate basal area of tree islands. A telescopic height pole was used to measure tree height of individuals whose trunk originated within the plot.

3.6. Fruit Phenology

Bear behavior and habitat use is strongly influenced by forage availability, but because bears in South Florida have such broad diets and the plant community on tree islands is so diverse, this study could not feasibly survey all types or species of forage (Maher, 1996). This study narrowed its focus on forage availability to mast from fruit trees because these species are characteristic and particularly abundant on Everglades tree islands. Personal observation and unpublished data from MTFWD (2023) found bear scat on tree islands to be primarily comprised of seeds from cocoplum (*Chrysobalanus icaco*), pond apple (*Annona glabra*), strangler fig (*Ficus aurea*), and cabbage palm (*Sabal palmetto*). These tree species were selected to be the subjects of fruit phenology surveys.

A pilot study was conducted to calculate "minimum optimal sample size" of individual trees per species per sample site (i.e., tree island) that would be used in the fruit phenology survey. Only cocoplum was surveyed in the pilot study because in February 2021, when the pilot study occurred, none of the other species of interest were fruiting. The pilot study occurred on the L-28 Interceptor Levee, western levee of the "Triangle" (Appendix A, Map 4), because this cocoplum grows abundantly at this location, and individuals are located on the edge of the levee, allowing the surveyor to easily circumvent each tree and count the exact number of fruits on each tree; in dense forested settings, crowded or overlapping canopies would disrupt the view of the observer. The starting location of the survey was randomly selected along the L-28 Interceptor and 70 mature cocoplum (>5 cm DBH) were sampled. Standard error of the mean number of fruits per tree was being graphed in real-time; standard error declined as sampling increased and approached its asymptote around 35 samples, so surveying continued until 70 samples (double the amount required to approach the asymptote). The dataset (number of fruits per tree were) permuted 100 times and standard error curves were calculated for each permutation. The average inflection point of the standard error curves occurred at ~6 sampled trees. The number of samples for this study was deemed satisfactory after the average inflection point of the curve was reached because continued survey effort beyond this inflection point results in diminishing return (Kays et al., 2020). The sample size of the fruit phenology surveys was selected to be 10 individuals per species per sample site.

Fruit phenology was surveyed on 7 tree islands across 3AS, subsampled from the 24 study islands (Appendix A, Map 4). These tree islands were strategically selected to ensure samples possessed a sufficient number of trees to sample from, were spread across the N-S transect, and the sample pool encompassed a complete range of elevational/hydrologic conditions and patch sizes, since these tree island characteristics likely affect primary productivity and fruit phenology. Using ArcGIS Pro, 10 points were randomly generated on the head of each tree island (digitized during measurement of patch sizes). Upon the initial visit to survey each island, the observer navigated to each of the random points, and selected the nearest tree to each point, for all the species of interest. On some tree islands there were not 10 individuals of a particular species, in which case the observer tagged as many individuals of that species that were found on the island. All selected trees were tagged with nonintrusive, non-constrictive numerical identification so the same individuals were monitored upon subsequent surveys.

Fruit phenology surveys occurred monthly over a two-year span, from March 2021 – February 2023. The surveys estimated abundance of ripe fruit for the species of interest. Ripe fruit abundance was visually estimated following the protocols to calculate the Fournier Index; the amount of ripe fruit present was visually estimated as a percent of the hypothetical maximum amount the tree could produce, based on the observer’s prior knowledge and expertise (Ramos & Santos, 2005; originally from Fournier, 1974). Only one individual surveyed fruit phenology because the subjective nature of this index makes it highly susceptible to observer bias if multiple surveyors are used. The estimated percent of ripe fruit on each tree was converted to an abundance rank: 0 = 0%, 1 = 1 – 25%, 2 = 26 – 50%, 3 = 51 – 75%, and 4 = 76 – 100%. The abundance ranks for each species were used to calculate Fournier’s Index of Fruiting Intensity on each tree island:

$$Fournier\ Index\ (\%) = \frac{(\text{sum of Ranks for all individuals of a species})}{(4 * \text{number of individuals of species})} * 100$$

3.7. Statistical Analyses

Presence of spatial autocorrelation was tested for by calculating and comparing the global Moran's *I* to the expected value (-1/ (N-1)). If results from the Moran's *I* autocorrelation test fail to reject the null hypothesis that there is no spatial autocorrelation in bear RAI across tree island sites, then no further spatial autocorrelation analyses will be pursued (Zuur & Smith, 2007). If results from the Moran's *I* autocorrelation test reject the null hypothesis, then distance-based Moran's eigenvector maps (MEMs), an improved method of spatial eigenvector mapping, will be generated to measure spatial autocorrelation at multiple spatial scales across the study region (Dray et al., 2006).

If spatial autocorrelation tests reveal eigenvectors characterized by positive spatial autocorrelation, those MEMs would be included as fixed effects in generalized linear mixed models through forward selection of eigenvectors until spatial autocorrelation is reduced to be not statistically significant or the "double stopping criterion" is violated (Griffith & Peres-Neto, 2006; Dormann et al., 2007; Blanchet et al., 2008; Bauman et al., 2018). First, Blanchet et al.'s (2008) "double stopping criterion" requires preventing oversaturation and multicollinearity by removing explanatory variables with variance inflation factors (VIFs) >4 from the global model (model including all explanatory variables). Then, a test of significance using Bonferroni adjusted p-values is performed on the global model; if the global model's p-value is <0.05, then the Type I error rate (falsely rejecting null hypothesis) is not inflated by forward selection. Lastly, model overfitting is prevented by using the global model's Ezekiel's adjusted R^2 (R^2_{adj}) as a cutoff criterion (a forward selected model's R^2_{adj} can't exceed the global model's R^2_{adj}). Thus, the forward selected model will not exhibit multicollinearity, Type I error inflation, or model overfitting.

Generalized linear mixed models (GLMMs) were constructed in R Statistical Software (v4.3.1; R Core Team, 2023) using the *glmmTMB* package (Brooks et al., 2017) to determine how variation of environmental variables (i.e., landscape characteristics, hydrology, vegetation, and fruit availability) affect bears' spatial use of tree islands. The *fitdistrplus* package (Delignette-Muller & Dutang, 2015) was used to select the best-fit distribution of bear RAI, averaged across the entire survey period (BY 2019 – 2023), at each tree island. Spatial GLMMs were constructed by modelling bear RAI as the response variable, tree island site as the random effect, and environmental variables as the fixed effects (Appendix A). The *glmmLasso* package (Groll, 2023) was used to reduce data dimensionality and select the most parsimonious spatial GLMM through L1-penalized estimation of fixed effects. Three parsimonious models of spatial GLMMs would be selected: a model for (1) landscape, (2) hydrologic, and (3) vegetation/ fruit variables.

Preliminary temporal analyses revealed that bears' low monthly RAI would not yield discernible findings regarding bears' temporal use of individual tree islands. Instead, temporal changes in bears' use of tree islands were analyzed at the regional scale by averaging RAI across all study tree islands for each month (BY 2019 -2023). Presence of temporal autocorrelation was tested for by calculating the autocorrelation function of the bear RAI time series using the *acf* function in the *stats* package (R Core Team, 2023). If the temporal autocorrelation test revealed monthly bear RAI to be autocorrelated with the previous month (lag = 1), then the autocorrelation would be accounted for by including the first-order autoregressive covariance structure (*ar1* in *glmmTMB*) into GLMMs (Bolker et al., 2020).

Results from fruit phenology surveys were used to model how variation in monthly ripe fruit availability affect bears' temporal use of tree islands. Bear RAI was modelled as the response variable and random effects were modelled as month nested in BY. Monthly Fournier's Index was averaged across all sites for each species, and all possible combinations of these species were included in GLMMs (Appendix A). Then, the most parsimonious fruit phenology GLMM was selected using *glmmLasso*. The goodness of fit of GLMMs will be estimated using the trigamma R^2 with the *r.squaredGLMM* function in the *MuMIn* package because it is generally more accurate than other R^2 measures and "is recommended whenever available" for GLMMs (Barton, 2023).

Considering that fruit phenology surveys were limited to BY 2022 – 2023, these data could not be used for modelling phenological patterns of bears over the entire study period (BY 2019 – 2023). Instead, the most parsimonious fruit availability GLMM would be used to identify the most ecologically relevant fruiting species and help establish fruiting seasons. Fruiting seasons would be used as a categorical fixed effect in temporal GLMMs that consider other phenological factors. Three biological seasons were also established and included in temporal GLMMs because bears exhibit seasonal shifts in behavior. Biological seasons were defined as: denning (January – April), breeding (May – August), and hyperphagia (September – December) (Maehr 1997; Maehr et al. 2003; Ulrey, 2008). Temporal GLMMs modelled how variation of phenological variables (i.e., month, monthly hydrologic conditions, biological season, and fruiting season) affect bears' temporal use of tree islands. Bear RAI was modelled as the response variable, month nested in BY as the random effect, and phenological variables as the fixed effects (Appendix A). The most parsimonious temporal GLMM was selected using *glmmLasso*.

The same process of modelling spatial, fruit availability, and temporal GLMMs for bear RAI was replicated using RAI of bear cubs. Cubs were defined as black bears in their first year of life (Mark & Erickson, 1966). Cubs were readily distinguishable from yearlings (1-2 years old) in trail camera photos by assessing their size (estimated weight) and considering time of year. Cub, yearling, and mature bear weight are known to vary across the United States but bears <50 lbs are likely cubs (Marks & Erickson, 1966; Rogers, 1987; Auger, 2004). Bears near the ~50 lbs threshold would be difficult to categorize as cubs or yearlings, but the time of year the bear was observed will determine this categorization. For instance, cubs in Florida are typically 1 – 3 months old by April and weigh 3 – 6 lbs (Garrison, 2004); thus, if a ~50 lb bear is observed in April, it will surely be a yearling.

RESULTS

3.8. Spatial Patterns

The global Moran's *I* was used to detect whether black bear RAI across study sites was spatially autocorrelated. The observed value was $I = 0.028$, and the expected value was $E = -0.045$. However, $p = 0.25$, so I was not considered significantly higher than E, thereby failing to reject the null hypothesis that there was no spatial autocorrelation and additional steps to reduce spatial autocorrelation via adding MEMs as fixed effects in GLMMs was not deemed necessary.

Bear and cub RAI both fit gamma distributions with a log link function best and were used to construct candidate GLMMs. However, cub RAI was zero-inflated so a gamma "hurdle" distribution was used to model non-zeros and zeros through two separate processes, where zeros can be either "structural" (i.e., expected according to data and distribution) or "excess" zeros (McDowell, 2003; Kassahun et al., 2014). Explanatory variables considered in spatial GLMM model selection included study tree islands' landscape and vegetative characteristics, and hydrologic conditions of tree islands and the surrounding marsh (Appendix A).

Model selection of spatial GLMMs with landscape variables as fixed effects identified (1) tree island patch size (hereon "AREA") and (2) the number of neighboring tree islands in a 500 m radius around study islands to be the best predictors of bear RAI (hereon "N500") (Fig. 1a). The marginal trigamma R^2 (amount of variance explained solely by fixed effects) of this model = 0.75. The conditional trigamma R^2 (amount of variance explained by entire model) of this model = 0.84. The coefficients of AREA and N500 equal 1.11 and -0.12, respectively. Both variables were statistically significant ($p < 0.05$), but the absolute value of AREA's coefficient was greater than N500's, so AREA was considered this model's focal explanatory variable (Table 1).

Model selection of spatial GLMMs failed to identify any hydrologic variables across tree island sites with meaningful effects on bear RAI. All candidate models either yielded results where fixed effects were not significant, or the coefficients of hydrologic fixed effects were ≈0.

Model selection of spatial GLMMs with vegetation and fruit variables only included the mean crown cover of soft mast tree species (hereon "MAST") to be the best predictor of bear RAI (Fig. 1b). The marginal and conditional trigamma R^2 of this model were both 0.32. MAST had a significant positive effect on bear RAI (coefficient = 0.02; $p < 0.05$) (Table 1).

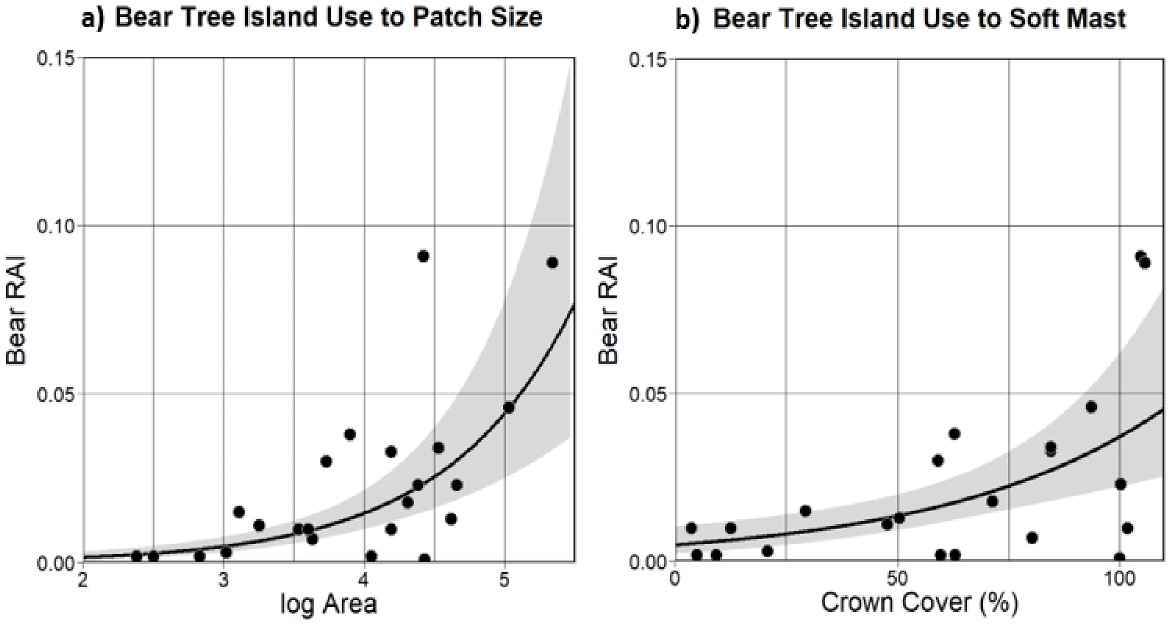


Figure 1. Fixed effects of landscape variables (a) and vegetative/fruit variables (b) on bear RAI from the parsimonious spatial GLMMs. In (a), the log area of study tree island patch size (AREA) is displayed on the x-axis because it is the model's focal explanatory variable; the mean of the non-focal variable (N500) was applied to this model but is not displayed. In (b), the summed crown of soft mast trees (MAST) was the model's only fixed effect. The solid black line depicts the predicted values of a model, and the gray band depicts the 95% confidence interval based on predicted standard errors conditioned on random effects.

Model selection of spatial GLMMs with landscape variables as fixed effects identified (1) tree island patch size (hereon "AREA") and (2) the number of neighboring tree islands in a 1000 m radius around study islands to be the best predictors of cub RAI (hereon "N1000") (Fig. 2a). The marginal and conditional trigamma R^2 of this model were 0.86. AREA had a positive effect on cub RAI (coefficient = 1.83), while $N1000_{cub}$ had a negative effect on cub RAI (coefficient = -0.10. Both variables were statistically significant ($p < 0.05$), but the absolute value of AREA's coefficient was greater than N1000's, so AREA was considered this model's focal explanatory variable (Table 1).

Model selection of spatial GLMMs with hydrologic variables identified tree island hydroperiod based on the head's mean elevation (hereon "HYDRO") to be the best predictor of cub RAI (Fig. 2b). The marginal and conditional trigamma R^2 of this model were both 0.53. HYDRO had a significant positive effect on cub RAI (coefficient = 0.44; $p < 0.05$) (Table 1).

Model selection of spatial GLMMs with vegetation and fruit variables modelled the presence of hardwood hammock trees (hereon “HAMM”) as the best predictor of cub RAI (Fig. 2c). The marginal and conditional trigamma R^2 of this model were 0.75 and 0.91, respectively. HAMM had a significant positive effect on bear RAI (coefficient = 2.17; $p < 0.05$) (Table 1).

Table 1. Spatial variables used as fixed in the parsimonious spatial GLMM models.

		Focal Variable	**Non-focal Variable**	R^2_{marg}	R^2_{cond}	*p*
Bear	**Landscape**	**AREA**	**N500**	0.75	0.84	<0.05
	Coef.	+1.11	-0.12			
	Hydrology					
	Coef.	*NA*	*NA*		*NA*	
	Vegetation	**MAST**		0.32	0.32	<0.05
	Coef.	+0.02	*NA*			
Cub	**Landscape**	**AREA**	**N1000**	0.86	0.86	<0.05
	Coef.	+1.83	-0.1			
	Hydrology	**HYDRO**		0.53	0.53	<0.05
	Coef.	-0.02	*NA*			
	Vegetation	**HAMM**		0.75	0.91	<0.05
	Coef.	2.17	*NA*			

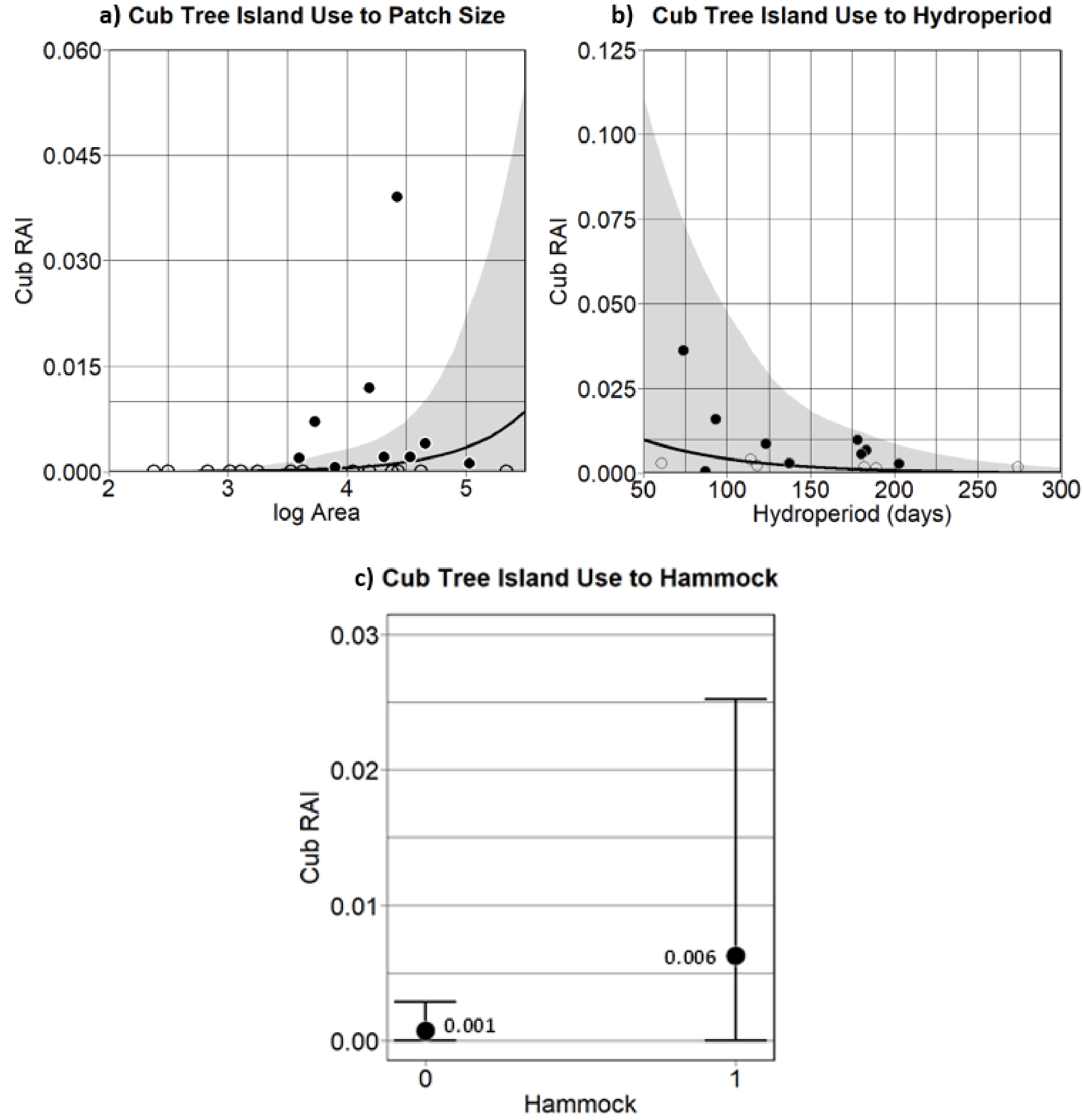


Figure 2. Fixed effects of landscape variables (a), hydrologic variables (b), and vegetative/fruit variables (c) on cub RAI from the parsimonious spatial GLMMs. In (a), the log area of study tree island patch size (AREA) is displayed on the x-axis because it is the model's focal explanatory variable; the mean of the non-focal variable (N1000) was applied to this model but is not displayed. In (b), the hydroperiod of tree island heads at their mean elevation (HYDRO) was the model's only fixed effect. The solid black lines in (a) and (b) depict the predicted values of a model, and the gray bands depict the 95% confidence interval based on predicted standard errors conditioned on random effects and zero-inflation. In (c), hammock presence (HAMM) was modeled as a binary fixed effect (0 = absent; 1 = present). Black points depict the mean predicted estimate of cub RAI when hammock species are absent or present, and the black bars depict the 95% confidence interval for each estimate based on predicted standard errors conditioned on random effects and zero-inflation.

3.9. Temporal Patterns

Autocorrelation functions (ACFs) were estimated for bear and cub RAI time series from BY 2019 – 2023. Monthly bear RAI exhibited significant positive autocorrelation at time lag 1 (coefficient = 0.59) and dropped sharply but remained significant at time lag 2 (coefficient = 0.32). Significant negative autocorrelation was detected at time lag 6 (coefficient = -0.35), then returned to significant positive autocorrelation at time lag 12 (coefficient = 0.46). The ACF oscillated around 0 with a gradually weakening signal and a periodicity of 12 time lags (months). Monthly cub RAI was characterized by a similar ACF, in which the first time lag was positively and significantly autocorrelated (coefficient = 0.15). The cub ACF oscillated around 0 but there were no significant negative autocorrelations; significant positive autocorrelations had at a periodicity of roughly 11 months (Fig. 3b). The strong positive autocorrelations of bear and cub time series at time lag 1 indicate that their RAI in any given month is significantly autocorrelated to the previous month. To mitigate the risk of misinterpreting temporal analyses, the first-order autoregression covariance structure at time lag 1 (AR1) was included as a fixed effect in temporal GLMMs.

The most parsimonious fruit phenology GLMM fit the monthly interspecies average of cocoplum, pond apple, and strangler fig Fournier Indices (hereon “FRUT”) as the only fixed effect modelling bear RAI (Fig. 4b). The marginal and conditional trigamma R^2 of this model were both 0.24. FRUT had a significant positive effect on bear RAI (coefficient = 0.18; $p < 0.05$) (Table 2). Since the FRUT was the strongest fixed effect among the fruit variables, the monthly values of FRUT were evaluated across time to establish fruiting seasons that were ecologically meaningful to bears and could be incorporated into the broader phenological GLMMs which used the entire bear time series

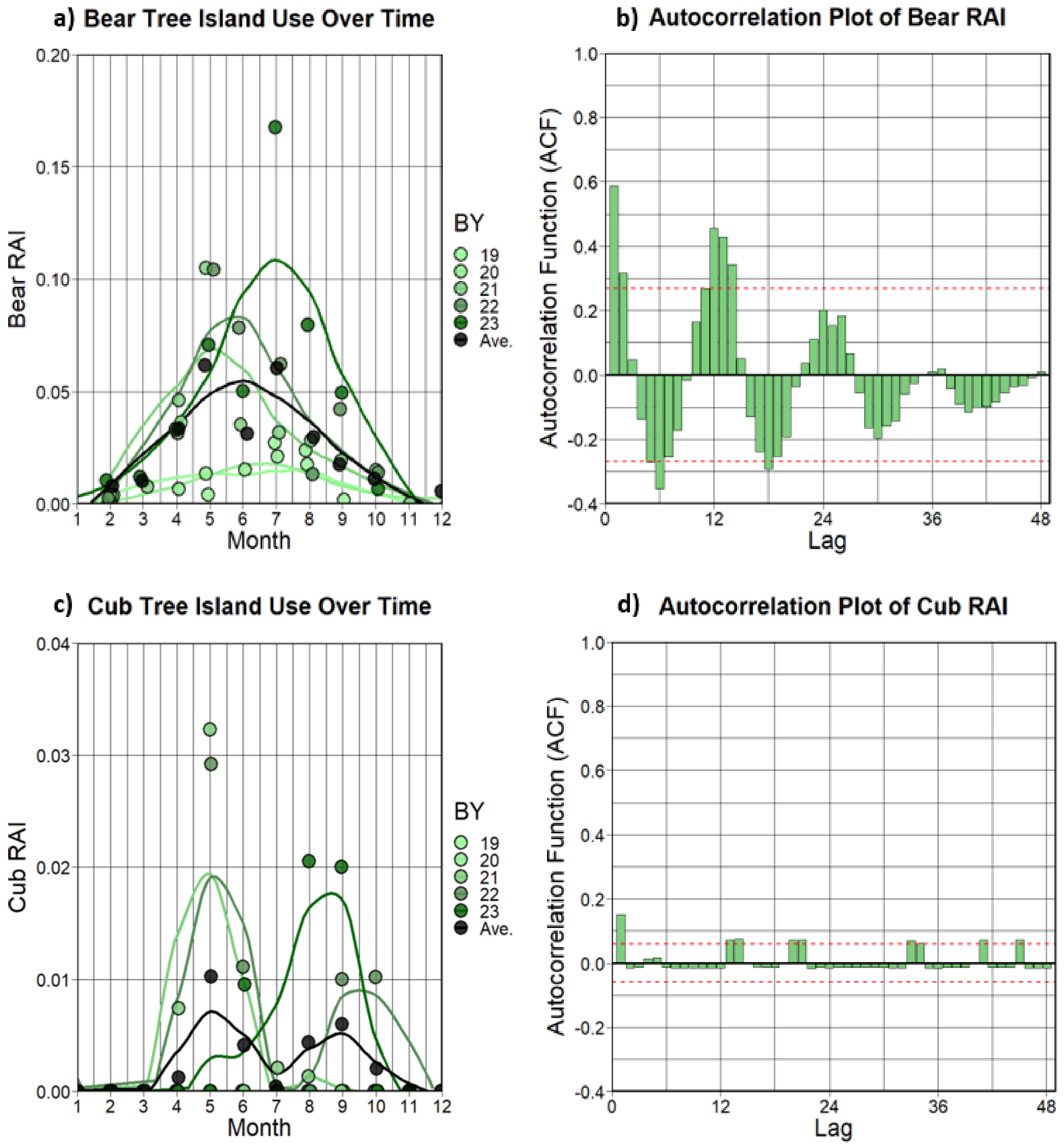


Figure 3. Scatterplot (a) depicts monthly bear RAI averaged across sites in each BY and the average for all BY. Color coded lines depict locally estimated scatterplot smoothing (loess) trendlines for each BY. The autocorrelation plot (b) depicts estimated temporal autocorrelation of bear RAI across time lags; dashed red lines represent the 95% confidence intervals. Scatterplot (c) depicts monthly cub RAI averaged across sites in each BY and the average for all BY. Color coded lines depict locally estimated scatterplot smoothing (loess) trendlines for each BY. The autocorrelation plot (d) depicts estimated temporal autocorrelation of cub RAI across time lags; dashed red lines represent the 95% confidence intervals.

as the response variable. Two distinct fruiting seasons were identifiable and categorized as “high” (June – August) and “low” = “September – May”; FRUT values during the high season were +2x greater than during the low season.

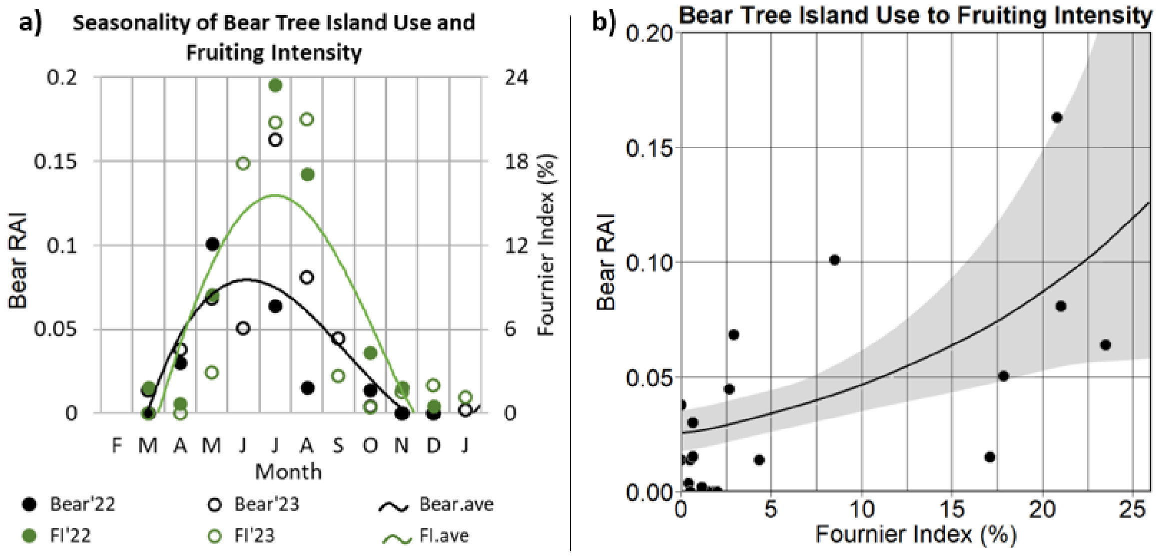


Figure 4. Scatterplot (a) depicts monthly bear RAI and the Fournier Index values of FRUT averaged across sites in BY 2022 – 2023 (period when fruit phenology was surveyed) and the average for both BY. Color coded lines depict locally estimated scatterplot smoothing (loess) trendlines for the interannual averages of bear RAI and FRUT. Temporal GLMM (b) models the fixed effects of monthly fruit availability (FRUT) on bear RAI. The solid black line depicts the predicted values of the model, and the gray band depicts the 95% confidence interval based on predicted standard errors conditioned on random effects, zero-inflation, and the autoregression covariance structure.

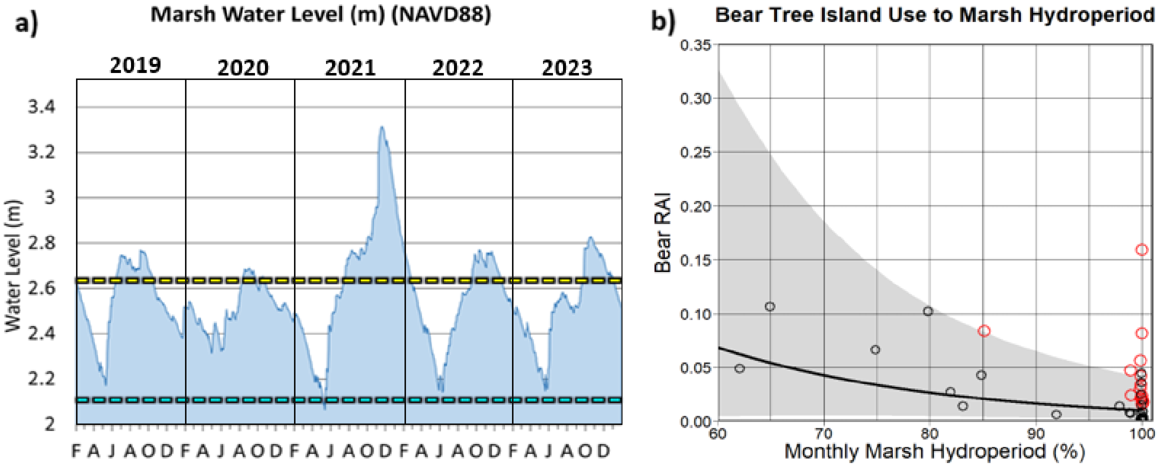


Figure 5. In (a), daily marsh water level (blue area) is displayed from BY 2019 – 2023. The dashed yellow line depicts the average mean elevation of the 24 tree island heads. The dashed blue line depicts the average marsh elevation in the 1000 m radius surrounding tree islands. Temporal GLMM (b) models the fixed effects of monthly marsh hydroperiod (MRSH) on bear RAI. Data points are grouped by fruit season (FSSN): black circles are values measured during the season of high fruit availability, and red circles are values measured during the season of low fruit availability. The solid black line depicts the predicted values of the model, and the gray band depicts the 95% confidence interval based on values of the random effects, zero-inflation, and the autoregression covariance structure.

The most parsimonious temporal GLMM with phenological variables (from BY 2019 – 2023) modelled monthly marsh hydroperiod in a 1000 m radius around study islands (hereon “MRSH”) and fruit seasons (hereon “FSSN”) as fixed effects (Fig. 5b). The marginal and conditional trigamma R^2 of this model were 0.36 and 0.78, respectively. MRSH had a significant negative effect on bear RAI (coefficient = -0.05; $p < 0.05$) (Table 2). Temporal GLMMs of cub RAI were attempted following the same procedure used to model temporal variation in bear RAI., but candidate models were either uninterpretable and not significant, or the coefficients of phenological fixed effects were ≈0.

Table 2. Temporal variables used as fixed in the parsimonious spatial GLMM models.

		Focal Variable	**Non-focal Variable**	R^2_{marg}	R^2_{cond}	*p*
Bear	**Fruit ('22-23)** Coef.	**FRUT** +0.18	*NA*	0.24	0.24	<0.05
	Phenology Coef.	**MRSH** -0.05	**SESN** -0.74	0.36	0.78	<0.05
Cub	**Fruit ('22-23)** Coef.	*NA*	*NA*		*NA*	
	Phenology Coef.	*NA*	*NA*		*NA*	

DISCUSSION

3.10. Bears

Trail cameras continuously monitored the 24 study tree island heads from February 2018 – January 2023. The number of sampled sites, wide range of environmental conditions that characterized sites, spatial scale, and duration of this study provided the requisite framework to comprehensively analyze spatial and temporal patterns of regional black bear habitat use. A total of 637 bear occurrences were recorded across the 29,374 trap days, so average monthly bear RAI = 0.025 (~1 occurrence per 40 trap days). Bears occurred on all study tree islands, but substantial variation across sites' average RAIs revealed that tree island habitat use of bears was spatially heterogenous, with bear RAI at the most intensively used islands being more than 10x higher than at the least used islands. The most parsimonious spatial GLMMs were used to identify which landscape, hydrologic, and vegetative variables best explained spatial variation in bears' use of Everglades tree islands.

The most parsimonious model for landscape variables identified the log area of tree island patch size (AREA) and the number of neighboring tree islands in a 500 m radius around the study island (N500) to be the best predictors of bear spatial habitat use (Fig. 1a; Table 1). For every unit increase in tree islands' log area, the log odds of bear RAI increased by 1.11 (Table 1). If converted to the odds scale, for every unit increase in tree island log area, there is approximately a 2-fold (200%) increase in the odds that a tree island will have higher bear habitat use. Thus, the hypothesis that bear habitat use will increase with tree island patch size was supported.

Meanwhile, bear habitat use was lower at sites with higher connectivity (N500). The estimated coefficient of N500 (-0.12 on log odds or 0.89 on odds scale) is interpreted as: for every unit increase in the number of neighboring tree islands (in a 500 m radius), there is approximately an 11% decrease in the odds that a tree island will have higher bear habitat use. These findings contradicted the hypothesis that bear habitat use would be positively affected by increased connectivity. This finding should be interpreted with caution because it does not conflict with the notion that increased habitat connectivity is beneficial for bears. The observed negative relationship between connectivity and bear habitat use may arise from a dynamic in which increased connectivity (i.e., more neighboring tree islands) means bears will utilize more tree islands within their range, thereby decreasing the amount of time spent on an individual tree island. Consider a scenario in which bear A and bear B spend an equal amount of time on tree islands (10 hours), and they divide their time spent on tree islands equally between the number of tree islands in their range. If bear A has 5 tree islands in its range and bear B has 10 tree islands in its range, then bear A will spend 2 hours on each island, while bear B spends 1 hour on each island. This simplified example likely exemplifies why bear habitat use according to RAI values was lower on tree islands with higher connectivity.

GLMM selection failed to identify hydrologic variables of tree islands or the surrounding marsh that meaningfully explained spatial variation in bear habitat use across tree islands. However, the most parsimonious temporal GLMM for bears identified monthly mean hydroperiod of the marsh within 1000 m of study islands (MRSH) as one of the predictors for bear temporal habitat use (Fig. 5b; Table 2). The marsh of all study islands is inundated for most of the year and the local marsh of some islands may remain inundated for more than a year. When marshes do dry down, bear tree island use increases as monthly marsh hydroperiod decreases. The estimated coefficient of MRSH (-0.05 on log odds or 0.95 on odds scale) is interpreted as: for every unit increase in the monthly marsh hydroperiod, there is approximately a 5% decrease in the odds that a tree island will have higher bear habitat use. Thus, the hypothesis that bear habitat use will be restricted by hydrologic stress was only partially supported because although monthly marsh hydroperiod negatively affected bear habitat use, the spatial effects of hydrology were inconclusive.

The most parsimonious model for vegetative variables identified the mean crown cover of soft mast tree species (MAST) to be the best predictor of bear spatial habitat use (Fig. 1b; Table 1). Percent crown cover of masting species functioned as an index representing how much soft mast forage was available per unit area on tree islands. The estimated coefficient of MAST (0.02 on log odds or 1.02 on odds scale) is interpreted as: for every unit increase of MAST, there is approximately a 2% increase in the odds that a tree island will have higher bear habitat use.

Fruit phenology surveys on a subset of the study tree islands (from BY 22 – 23) complemented these findings and identified the interspecies average of soft mast availability from cocoplum, pond apple, and strangler fig (FRUT) to be the best predictor of temporal patterns in bear use, when compared to other individual and combined metrics of soft mast availability (Fig. 4b; Table 2). The estimated coefficient of FRUT (0.18 on log odds or 1.20 on odds scale) is interpreted as: for every unit increase of FRUT, there is approximately a 20% increase in the odds that a tree island will have higher bear habitat use. The most parsimonious temporal GLMM for bears also identified the effect of fruiting season (FSSN) on bear temporal habitat use as a predictor (Fig. 5b; Table 2). The estimated coefficient of FSSN (-0.74 on log odds or 0.48 on odds scale) is interpreted as: there is a 48% increase in the odds that a tree island will have higher bear habitat use during the high- than the low fruit availability season. These results supported the hypothesis that bears' spatial and temporal habitat use would be higher among tree islands with greater forage availability. Parsimonious models indicated that the importance of forage availability was primarily driven by soft mast (instead of hard mast or vegetative forage) of tree species (instead of herb or shrub layers). The temporal findings also supported the hypothesis that bear habitat use would oscillate seasonally, with increased use during summer months. The peaks in bear habitat use coincided with peak in soft mast availability (Fig. 4), and with the breeding season (May – August) in which males increase activity to find mates, and mother-cub family units increase activity in search of forage as cubs are weaned.

3.11. Cubs

A total of 101 cub occurrences were recorded across the 29,374 trap days, so average monthly bear RAI = 0.003 (~1 occurrence per 290 trap days). Even though bears occurred across all study tree islands, cubs only occurred on 9 islands. Despite the cub dataset being substantially smaller than the total bear dataset, there were ample data to discern important spatial and temporal patterns of tree island habitat use. The most parsimonious spatial GLMMs were used to identify which landscape, hydrologic, and vegetative variables best explained spatial variation in cubs use of Everglades tree islands.

Results from the most parsimonious model of landscape variables to cubs' spatial habitat use were very similar to the landscape model for bears. Patch size (AREA) and the number of neighboring tree islands in a 1000 m radius around the study island (N1000) to be the best predictors of cub spatial habitat use (Fig. 2a; Table 1). The estimated coefficient of AREA (1.83 on log odds or 6.24) is interpreted as: for every unit increase in tree island log area, there is approximately a 5-fold (500%) increase in the odds that a tree island will have higher cub habitat use. Cub habitat use was lower at sites with higher connectivity (N1000). The estimated coefficient of N1000 (-0.10 on log odds or 0.90 on odds scale) is interpreted as: for every unit increase in the number of neighboring tree islands (in a 1000 m radius), there is approximately an 10% decrease in the odds that a tree island will have higher cub habitat use. These findings supported the hypothesis that habitat use will increase with tree island patch size but did not support the hypothesis that bear habitat use would be positively affected by connectivity; these findings should be interpreted the same way as discussed for the bear landscape characteristics model.

Unlike for the bear hydrologic model, a parsimonious hydrologic model was able to discern spatial effects on cub habitat use. This model identified the mean hydroperiod of tree island heads (HYDRO) as the best predictor of cub spatial habitat use (Fig. 2b; Table 1). The estimated coefficient of HYDRO (-0.02 on log odds or 0.98 on odds scale) is interpreted as: for every unit increase of HYDRO, there is approximately an 2% decrease in the odds that a tree island will have higher cub habitat use. This supported the hypothesis that higher levels of hydrologic stress would reduce spatial habitat use of bears, but specifically of cubs.

The most parsimonious model for vegetative variables identified the presence of hardwood hammock trees (HAMM) to be the best predictor of cub spatial habitat use (Fig. 2c; Table 1). Hammocks are considered potentially important habitat for bears because they support a diverse community of mast-bearing tree species that are also indicators of healthy, high-elevation (relative to the water levels) tree islands because these trees are very flood sensitive (Jones et al., 2006; Ross et al., 2016). The estimated coefficient of HAMM (2.17 on log odds or 8.76 on odds scale) is interpreted as: there is nearly a 8-fold (776%) increase in the odds that a tree island will have higher cub habitat use if hammock species are present. Although the spatial effect of hammock presence on cub habitat use is strong, it is unclear whether this finding supports the hypothesis that tree islands with an abundance of mast will have higher bear habitat use because although many masting species are associated with hammocks, this model specifically did not include any of the spatial fruit variables. The increased likelihood of cubs' spatial habitat use being higher on islands with hammocks could also stem from the low hydrologic stress and short hydroperiod associated with these sites, especially since HYDRO was already identified as the best hydrologic predictor of cubs' spatial habitat use.

Although no GLMMs explained temporal patterns in cubs' tree island use, there is a clear phenological pattern. Cubs only occurred in BY 2021 – 2023 and only 2 islands experienced cub occurrences in multiple years. The lack of cubs in BY 2019 was largely due to the limited number of sample sites; only 4 islands were monitored for most of BY 2019. However, cubs were also never detected in BY 2020, even though nearly all study islands were being monitored (including 8 of the 9 islands where cubs were eventually recorded). The lack of cubs in BY 2020 may be related to the consistently deep marsh water levels in BY 2019 - 2020 (Fig. 5a) because marsh depth negatively affected bears, restricts available habitat, likely reduces forage availability, and recruitment is heavily dependent on health and ecological conditions before and after denning (Elowe & Dodge, 1989; Garrison, 2004). Thus, if marsh water levels are consistently high in the months following cub emergence (e.g., average marsh depths >0.26 m from February – June of BY 2020), cubs cannot disperse and may not satisfy their nutrient requirements. Thus, cub mortality is expected to increase, and would be reflected by low cub RAI.

Perhaps the most important temporal aspect of cubs' tree island habitat was that the first detections of cubs occurred in April of each year and peaked in May. Based on the estimated size of these cubs and the age-size relationship, it is very likely that these cubs were born in early February. When cubs are this young (2 – 3 months), they tend to stay in the immediate vicinity of their natal den (Brian Scheick, personal communication, 2023). At this age, cubs would be too small to disperse between tree islands, especially if the marsh matrix is inundated. Thus, these early-season cub detections reveal the locations of natal dens and confirms that bears breed, den, and rear offspring on Everglades tree islands. Another intriguing finding was that cub habitat use was bimodal (Fig. 3c). Cubs' habitat use observably declined after the initial peak in May, then peaked again in August – September. The decline in cub habitat use appears to reflect when cubs are mobile and old enough (4 – 5 months) to range further from their natal den, potentially migrating from their natal tree island. The subsequent increase in cub habitat use may coincide with the same mother-cub family unit returning to the study tree island (or a new family unit colonizing the tree island) to forage and satisfy cubs' increasing caloric requirements as they grow and gradually shift from nursing on milk to consuming solid foods.

CONCLUSION

North American black bear research and management often focuses on large contiguous tracts of suitable habitat, but the notion that small and isolated forest patches can provide valuable habitat in the context of habitat fragmentation or connecting black bear subpopulations has become increasingly popular (Hellgren et al., 2005; Hiller et al., 2015; Murphy et al., 2017; Murphy et al., 2018). The Florida Everglades is a particularly useful study system to investigate how habitat use of bears and other terrestrial mammals is affected by landscape and other environmental factors because the ecological characteristics of tree islands and the wetland matrix are highly variable across the system and across time. This 5-year study also marks the very first investigation into black bear ecology in the Everglades; bears have been studied in southwest and central Florida, but the Everglades is ecologically distinct from the habitats in these surrounding areas.

Five years of continuous monitoring revealed that Florida black bear are ubiquitous across Everglades tree islands but habitat use varied greatly across tree islands. The primary spatial drivers of bears habitat use were patch size, connectivity, and availability of forage. Among these variables, patch size of tree islands had the strongest, and a positive effect on bear habitat use. Contrary to what was hypothesized, as connectivity between tree islands increased, bear habitat use appeared to decrease. This does not reflect bears selecting for sites with low connectivity but is likely a function of increased connectivity between neighboring islands facilitating regular interpatch dispersal, thereby reducing the amount of time spent on the study island. It is still considered that increased connectivity between forest patches has a positive impact on regional bear habitat quality.

Hydrologic conditions also shaped patterns of bear habitat use. Hydroperiod and water depth are considered environmental stressors to bears in this system because both spatiotemporally reduce available upland refugia, limit dispersal ability, and may reduce recruitment of offspring. Hydroperiod had a moderate negative impact on the spatial habitat of cubs but did not have a significant effect on bears overall. This may be due to cubs' size and fragility (compared to yearlings and mature bears) making them more susceptible to threats associated with hydrologic stress (e.g., predation, ephemeral habitat reduction, degraded habitat quality). However, bears' temporal use of tree islands was negatively impacted by marsh water depth, with bears seemingly selecting for tree islands with shallower (or dry) conditions in the local marsh.

Among vegetative variables, the presence of hardwood hammock had a strong positive relationship with the increased likelihood of cubs occurring on a tree island. Considering that cubs in the Everglades are born on tree islands and will spend several months on an island before being able to disperse, pregnant females may select for tree islands with hammocks as denning locations because hammocks indicate low hydrologic stress and host a diverse suite of mast bearing trees. The increased availability of soft mast (namely from cocoplum, pond apple, and strangler fig) had strong a positive effect on bears' spatiotemporal habitat use of tree islands. The abundance and high nutritional quality of these fruits is likely a strong selective force for bears. However, it is unclear how much of the temporal variation should be attributed to increased forage availability instead of biological seasons because the peak in ripe fruit abundance is synchronous with males increasing their range to mate, mothers foraging more to replenish lost energy stores from recently breeding and nursing cubs, and cubs transitioning from milk to solid foods as their growth requires an abundance of nutritional and high-calorie food sources (all of which expected to increase bear activity).

The utter absence of research on black bears in the Florida Everglades prompted the opportunity to add novel insight to existing literature of black bears habitat use by studying this species in an untrammeled research setting. Many of this study's findings were consistent with findings from black bear studies of other Florida subpopulations and of other subspecies. For instance, this study determined that there is dramatic spatial and temporal variation in ripe fruit availability, and this variation is a primary driver of bear habitat use. Maehr (1996) found very similar results in southwest Florida; his research showed that bears in southwest Florida relied more intensively on seasonal fruit sources than most other American black bear populations. The importance of landscape characteristics (namely patch size and connectivity) to bear distribution and habitat use was also a finding common to bear research in other systems (Dixon et al., 2006; Morzillo et al., 2011; Gantchoff & Belant, 2017; Ditmer et al., 2018; Hooker et al., 2021).

It is crucial to point out that nearly all studies that have investigated the effects of landscape structure on bears treat forested patches as steppingstones between large, contiguous tracts of bear habitat. Forested patches are generally considered unsuitable or unsustainable habitat. However, Everglades tree islands do not link large, contiguous habitat patches or subpopulations to one another, yet bears are ubiquitous, occupy the habitat year-round, appear in good body condition, and are reproducing successfully on tree islands. The cub survival and population growth rate are not known for bears in the Everglades, but trail camera photos revealed that family units often consist of 2 – 3 cubs and most cubs seem to survive throughout the first 1½ - 2 years (after which the family unit often disbands, and individuals become difficult to identify).

This challenges the notion that small habitat patches function as steppingstones or are low-quality habitat by default because of suboptimal landscape characteristics. Perhaps researchers and managers have underestimated or overlooked the ecological value of habitat patches for bears and other wildlife that require large spatial and resource requirements by focusing too intensively on landscape characteristics. The success of bears despite stressful hydrologic conditions, small patch sizes, and reduced connectivity (loss of tree island area exceeds 60% in this region (Patterson & Finck, 1999)) is most likely attributable to the year-round food sources and seasonal hyperabundance of high-quality forage on Everglades tree islands.

Continued effort is needed to better understand the dynamics of black bear habitat use, tease apart related or synchronous ecological drivers (e.g., fruiting abundance and biological season), and improve researchers/managers ability for determining the ecological value of habitat patches or patchy ecosystems. In the context of black bears on Everglades tree islands, camera trapping efforts should be continued to gain a better understanding of long-term population trends across the Everglades. Genetic and telemetry data of individuals is also needed to refine bear distribution, population, gene flow, survival and mortality rates, habitat use, and reproductive information. Lastly, multi-year dietary studies would be needed to comprehensively identify which food sources are most valuable to black bears and how the relative importance of different sources varies seasonally. Continuing and expanding research to include these aspects of black bear ecology will fill in key data gaps in this body of literature and allow managing agencies to maximize conservation, restoration, and management success for black bears and other wildlife that live under bears’ ecological umbrella.

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APPENDICES

Appendix A. List of Explanatory Variables

Term	Acronym in Analyses	Type	Definition
Landscape variables			
Area	**AREA**	**Positive continuous**	**log area (m) of the study tree island's head**
Dist.Source		Positive continuous	Shortest Euclidean distance from the study tree island to "source" (Big Cypress National Preserve)
Dist.Levee		Positive continuous	Shortest Euclidean distance from the study tree island to a levee
Neighbor100		Positive continuous	Percent area of neighboring tree islands in a 100 m radius surrounding the study tree island
Neighbor250		Positive continuous	Percent area of neighboring tree islands in a 250 m radius surrounding the study tree island
Neighbor500		Positive continuous	Percent area of neighboring tree islands in a 500 m radius surrounding the study tree island
Neighbor1000		Positive continuous	Percent area of neighboring tree islands in a 1000 m radius surrounding the study tree island
Neighbor2000		Positive continuous	Percent area of neighboring tree islands in a 2000 m radius surrounding the study tree island
no.100		Positive Integer	Number of neighboring tree islands in a 100 m radius surrounding the study tree island
no.250		Positive Integer	Number of neighboring tree islands in a 250 m radius surrounding the study tree island
no.500	**N500**	**Positive Integer**	**Number of neighboring tree islands in a 500 m radius surrounding the study tree island**
no.1000	**N1000**	**Positive Integer**	**Number of neighboring tree islands in a 1000 m radius surrounding the study tree island**
no.2000		Positive Integer	Number of neighboring tree islands in a 2000 m radius surrounding the study tree island
Hydrologic variables	*The hydrologic variables belwoe were calculated for 2 time series: (1) all days in BY 2019 - 2023, and (2) days in BY 2019 - 2023 when trail cameras were active		
Amplitude.mean		Positive continuous	Mean annual amplitude (x2) of daily marsh water depth (from BY 2019 - 2023)
Amplitude.max		Positive continuous	Maximum annual amplitude (x2) of daily marsh water depth (from BY 2019 - 2023)
Mean.Depth		Positive continuous	Mean marsh depth (from BY 2019 - 2023)
Mean.HighWater.Depth		Positive continuous	Mean high-water marsh depth (during the 6 deepest months of each BY (from BY 2019 - 2023))
Hydro.mean	**HYDRO**	**Positive Integer**	**Mean annual hydroperiod from BY 2019 -2023**
Hydro.max		Positive Integer	Maximum annual hydroperiod from BY 2019 -2023
LongestDry.mean		Positive Integer	Mean of greatest number of continuously dry days in a BY (from BY 2019 - 2023)
LongestDry.max		Positive Integer	Maximum of greatest number of continuously dry days in a BY (from BY 2019 - 2023)
RE.mean		Positive continuous	Mean elevation of tree island plots, relative to daily water levels from BY 2019 - 2023
RE.max		Positive continuous	Maximum elevation of tree island plots, relative to daily water levels from BY 2019 - 2023
Vegetation variables			
Canopy		Positive Continuous	Average canopy cover class of vegetation plots
Ground.fern		Binary	Herb layer dominated by ferns
Ground.herb		Binary	Herb layer dominated by herbaceous plants
Ground.seedling		Binary	Herb layer dominated by tree seedlings
Ave.Height		Positive Continuous	Average height of trees, measure to the tallest branch/leaf of individuals
Basal.Area		Positive Continuous	Basal area of tree island head,derived from DBH
Hammock	**HAMM**	**Binary**	**Presence of hardwood hammock species**
Live.Cover		Positive Continuous	Total crown cover of understory (herb and shrub cover, agglomeratively)
Forage.Under.All		Positive Continuous	Crown cover of understory species that yield forage to bears (hard mast, soft mast, and vegetative)
Forage.Under.Hard		Positive Continuous	Crown cover of understory species that yield hard mast forage to bears
Forage.Under.Soft		Positive Continuous	Crown cover of understory species that yield soft mast forage to bears
Forage.Under.Veg		Positive Continuous	Crown cover of understory species that yield vegetatitve forage to bears
Forage.Tree.All		Positive Continuous	Crown cover of tree species that yield forage to bears (hard mast, soft mast, and vegetative)
Forage.Tree.Hard		Positive Continuous	Crown cover of tree species that yield hard mast forage to bears

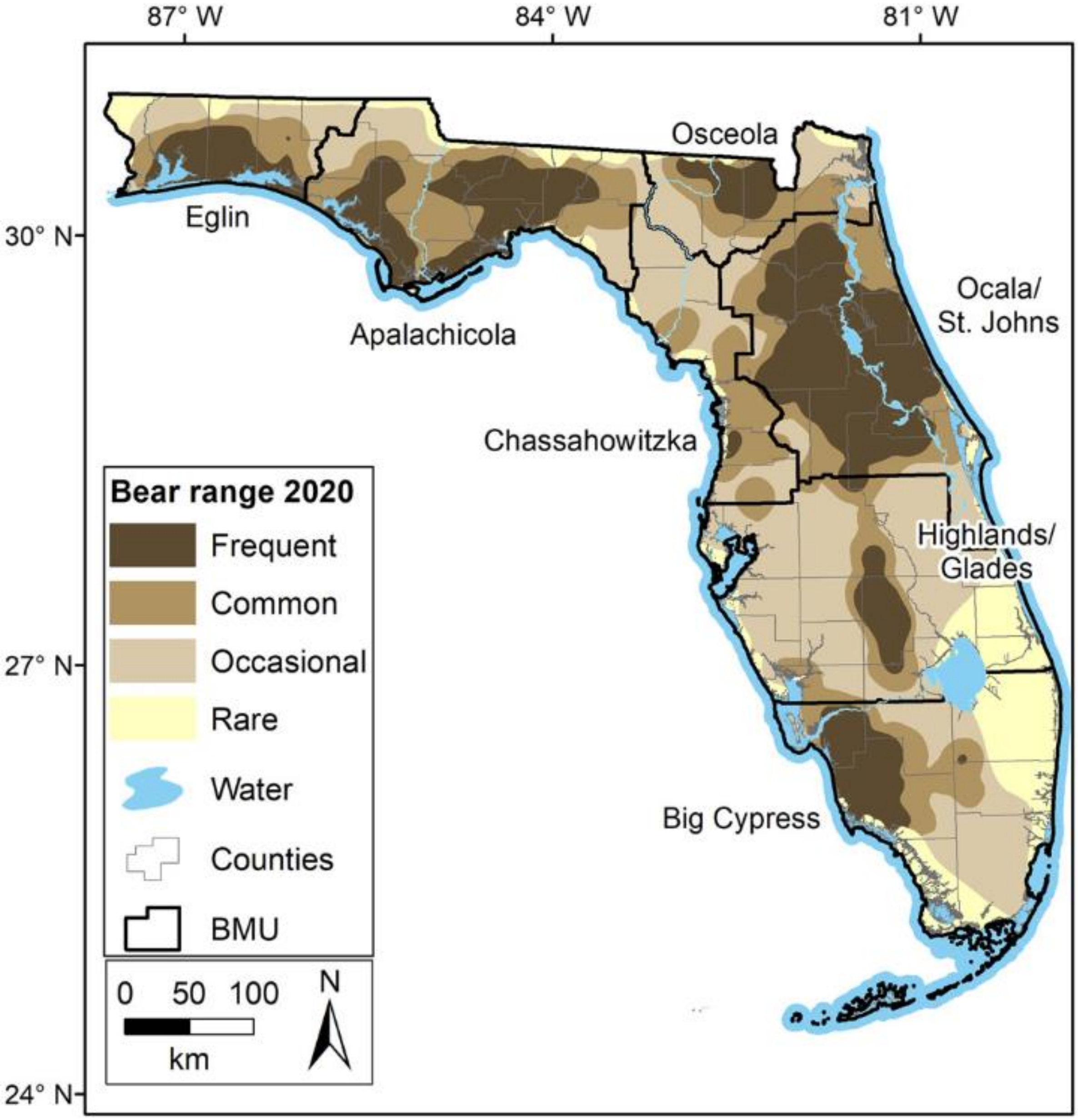
Appendix A. List of Explanatory Variables (Continued)

Term	Acronym in Analyses	Type	Definition
Landscape variables			
Forage.Tree.Soft	**MAST**	**Positive Continuous**	**Crown cover of tree species that yield soft mast forage to bears**
Forage.Tree.Veg		Positive Continuous	Crown cover of tree species that yield vegetatitve forage to bears
Shrub.fern		Binary	Shrub layer dominated by ferns
Shrub.herb		Binary	Shrub layer dominated by herbaceous plants
Stand.Density		Positive Integer	Number of trees per hectare (multi-trunk trees are treated as one individual)
Tree.Richness		Positive Integer	Observed species richness of tree species
ANNGLA		Binary	Tree layer dominated by (*Annona glabra*)
CHRICA		Binary	Tree layer dominated by (*Chrysobalanus icaco*)
FICAUR		Binary	Tree layer dominated by (*Ficus aurea*)
SALCAR		Binary	Tree layer dominated by (*Salix caroliniana*)
TAXDIS		Binary	Tree layer dominated by (*Taxodium distichum*)
Variable Interactions			
Area X Neighbor100		Positive continuous	Multiplicative interaction between terms
Area X Neighbor250		Positive continuous	Multiplicative interaction between terms
Area X Neighbor500		Positive continuous	Multiplicative interaction between terms
Area X Neighbor1000		Positive continuous	Multiplicative interaction between terms
Area X Neighbor2000		Positive continuous	Multiplicative interaction between terms
Area X no.100		Positive continuous	Multiplicative interaction between terms
Area X no.250		Positive continuous	Multiplicative interaction between terms
Area X no.500		Positive continuous	Multiplicative interaction between terms
Area X no.1000		Positive continuous	Multiplicative interaction between terms
Area X no.2000		Positive continuous	Multiplicative interaction between terms
Mean.Depth X Hydro.mean		Positive Continuous	Multiplicative interaction between terms
Mean.HighWater.Depth X Hydro.max		Positive Continuous	Multiplicative interaction between terms
Mean.Depth X RE.mean		Positive Continuous	Multiplicative interaction between terms
Mean.HighWater.Depth X RE.max		Positive Continuous	Multiplicative interaction between terms

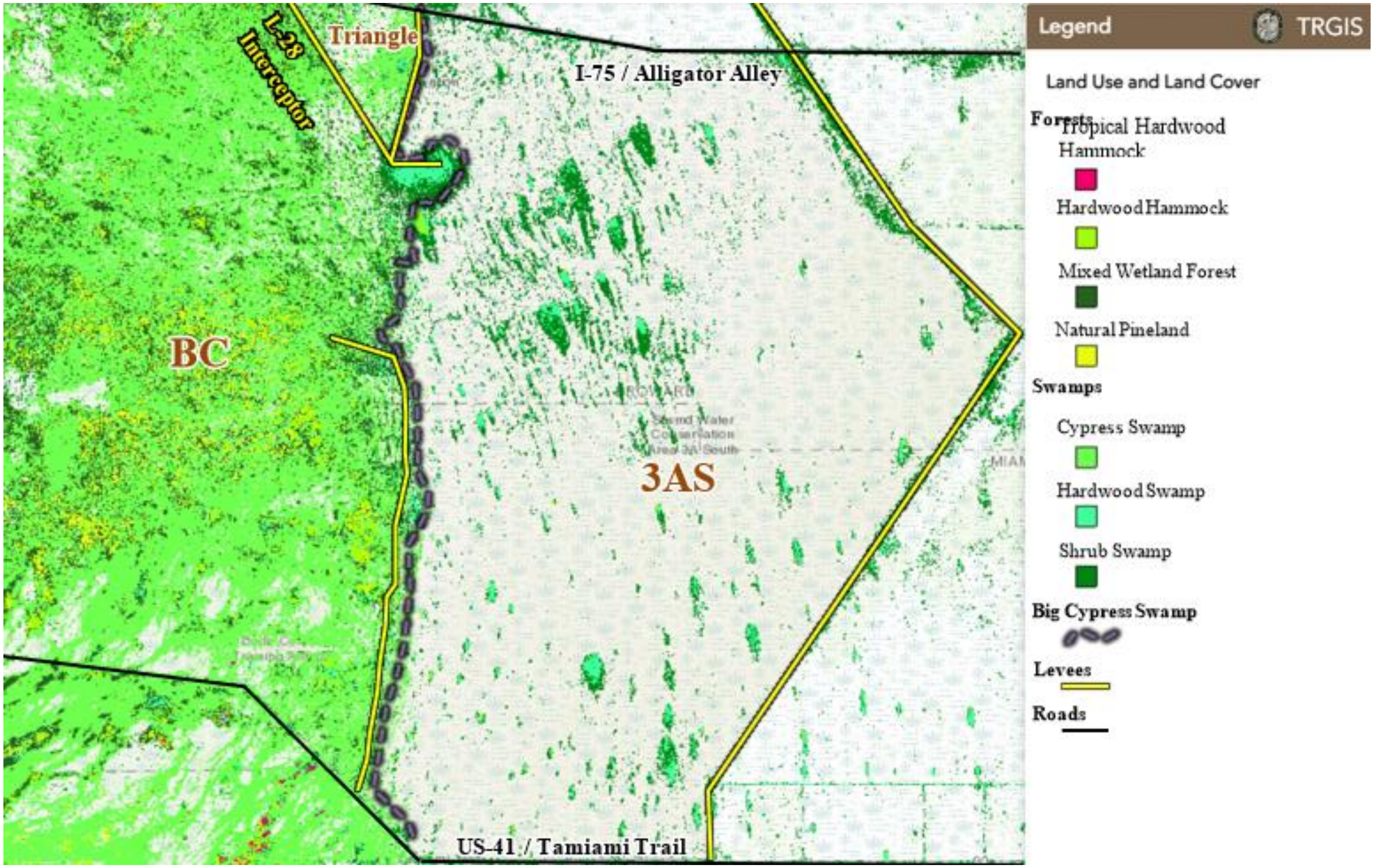
Appendix A. List of Explanatory Variables (Continued)

Term	Acronym in Analyses	Type	Definition
Phenological fruit survey variables (BY 2022 - 2023)			
ANNGLA		Positive continuous	Monthly average Fournier Index (%) of sampled *Annona glabra*
CHRICA		Positive continuous	Monthly average Fournier Index (%) of sampled *Chysobalanus icaco*
FICAUR		Positive continuous	Monthly average Fournier Index (%) of sampled FICAUR
SABPAL		Positive continuous	Monthly average Fournier Index (%) of sampled SABPAL
FI.A.C		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled ANNGLA & CHRICA
FI.A.F		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled ANNGLA & FICAUR
FI.A.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled ANNGLA & SABPAL
FI.C.F		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled CHRICA & FICAUR
FI.C.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled CHRICA & SABPAL
FI.F.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled FICAUR & SABPAL
FI.A.C.F	**FRUT**	**Positive continuous**	**Monthly interspecies average Fournier Index (%) of sampled ANNGLA & CHRICA & FICAUR**
FI.A.C.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled ANNGLA & CHRICA & SABPAL
FI.A.F.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled ANNGLA & FICAUR & SABPAL
FI.C.F.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled CHRICA & FICAUR & SABPAL
FI.A.C.F.S		Positive continuous	Monthly interspecies average Fournier Index (%) of sampled ANNGLA & CHRICA & FICAUR & SABPAL
Phenological variables (BY 2019 - 2023)			
Month		Positive Integer	Month of the year (January = month 1, and so on)
Fruit.Season	**SESN**	**Binary**	**Seasons of high or low fruit availability (based on parsimonious fruit survey variables)**
Bio.Season		Positive Integer	Bear biological season in a given month (Denning = 1, Breeding = 2, Hyperphagia = 3)
Hydro.TI		Positive continuous	Monthly tree island hydroperiod for mean head elevation
Hydro.TImax		Positive continuous	Monthly tree island hydroperiod for max head elevation
Hydro.Marsh	**MRSH**	**Positive continuous**	**Monthly marsh hydroperiod (in each spatial ring)**
No.Dry.Nbrs		Positive Integer	Number of neighboring islands (in each spatial ring) whose mean elevation is above monthly water level
RE.mean		Positive continuous	Mean elevation of tree island plots, relative to average monthly water level
RE.max		Positive continuous	Maximum elevation of tree island plots, relative to average monthly water level
RE.marsh		Positive continuous	Marsh elevation (in each spatial ring), relative to average monthly water level

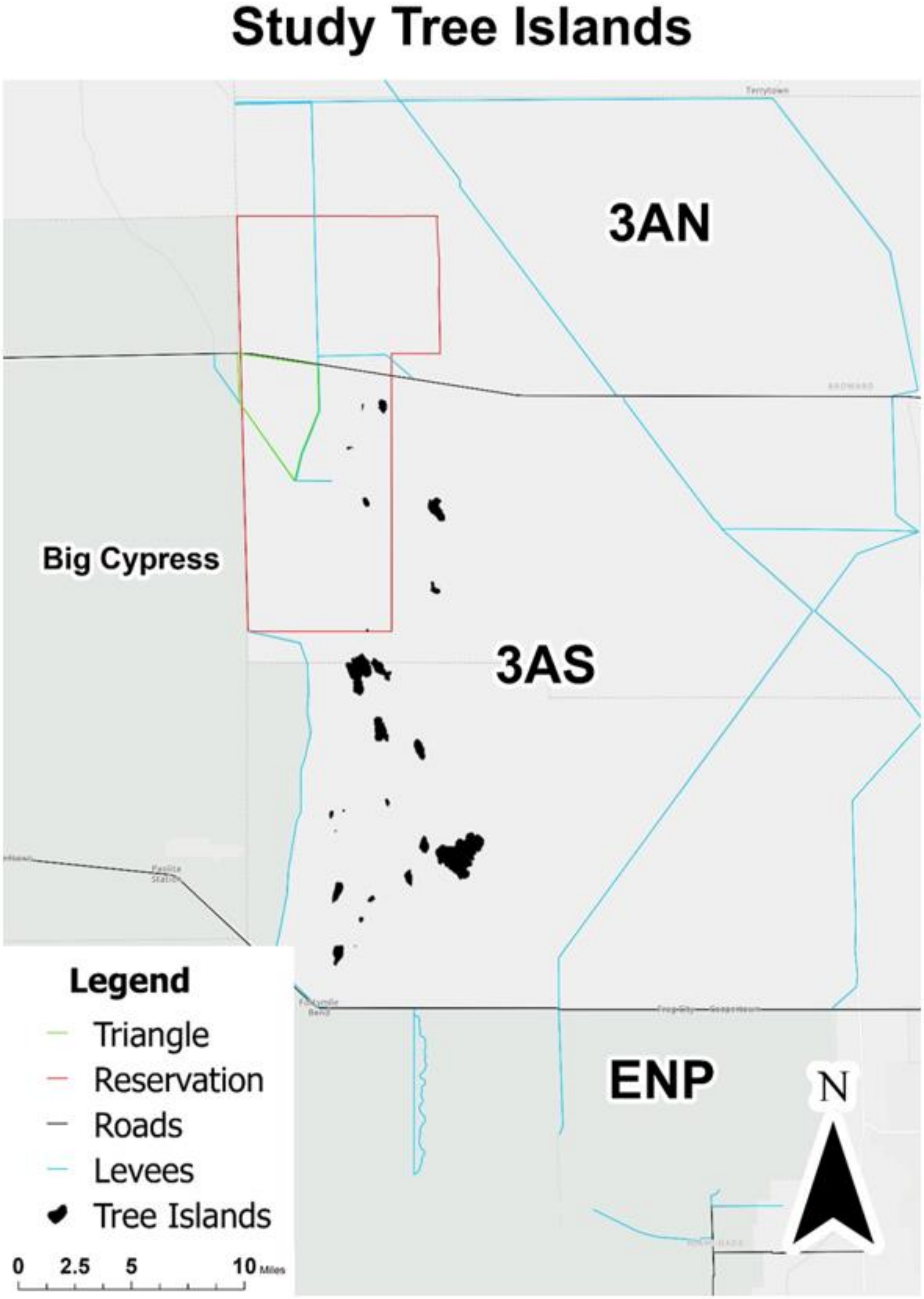
Appendix B. – Maps



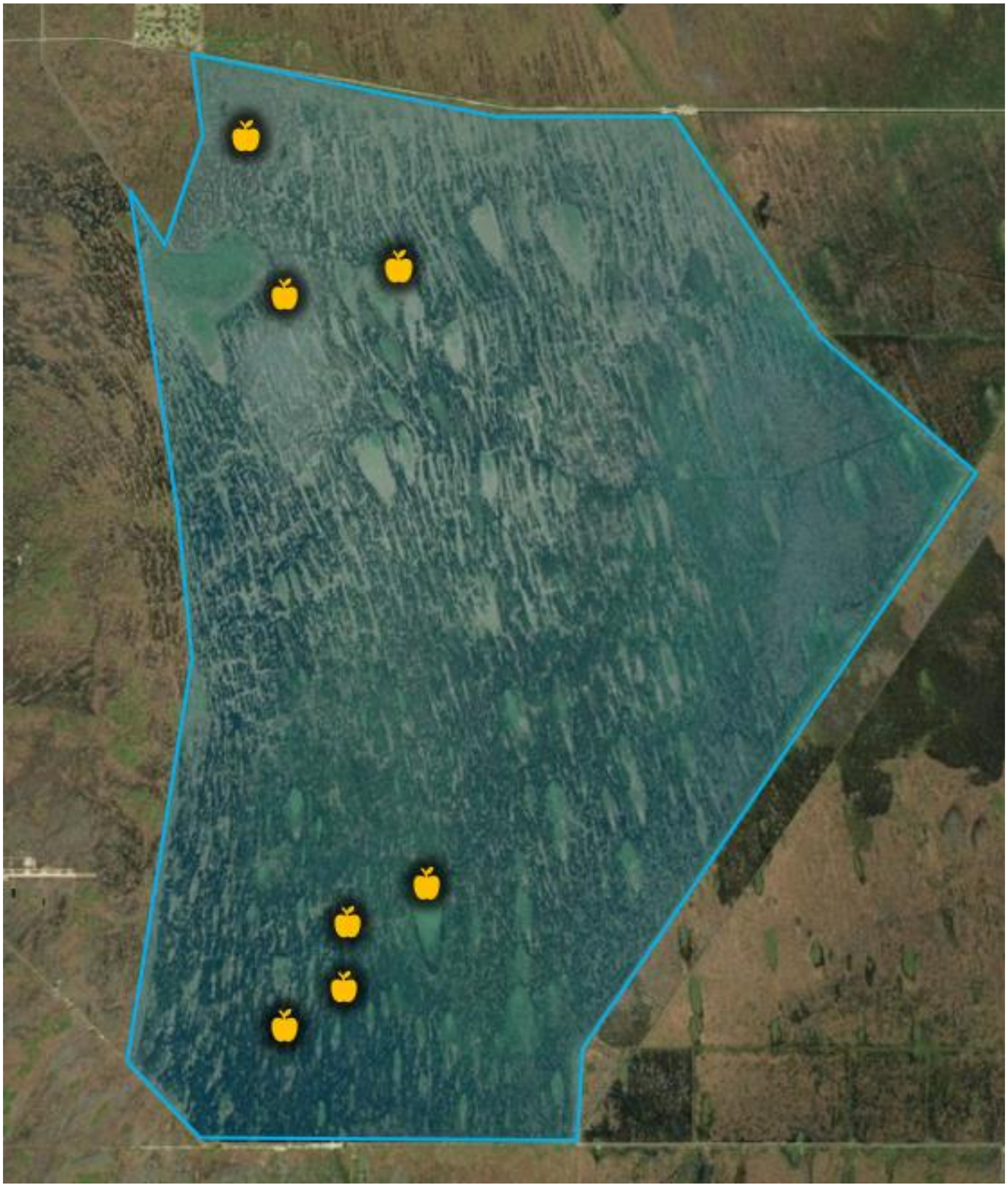
Map 1. Florida's 7 black bear subpopulations (labeled), in 2020. Frequent occurrence polygons were determined for each subpopulation based on the 90% kernel density estimation and can be generally interpreted as focal region of subpopulations. Data and map obtained from Scheick et al., (2023).



Map 2. Shows land cover classifications across study area (3AS) and the westwardly adjacent Big Cypress Swamp (BC), which is considered a mainland source population for Florida black bears in the Everglades. Levees surrounding 3AS are also displayed because they may provide a rescue effect, similar to a true source population. Map obtained and modified from FWC Terrestrial Resources Geographic Information System (TRGIS) web mapping application.



Map 3. Digitized polygons of 24 study tree island heads. Polygons reflect the true locations and shapes of tree island heads, but sizes are 5x the scale of their true areal extent (for visual aid of small tree islands).



Map 4. The above map shows locations of 7 tree islands in 3AS where fruit phenology was surveyed (orange fruit icons depict the location of each study tree island). These islands were selected for study because of their array of landscape conditions (high vs low elevation, and large vs small areal extent), abundance of native fruit trees, and logistical ease to access.

Appendix C. – Photos

Photo 1. Black bear foraging from cocoplum tree.

Photo 2. Black bear mother and cub dig up softshell turtle nest to eat eggs.

Photo 3. Yearling black bear foraging from cocoplum tree.

Photo 4. Black bear marks cabbage palm trunk with claws.

Photo 5. Black bear scat composed almost entirely of Brazilian pepper flesh and seeds.

Photo 6. Black bear scat composed mostly of pond apple seeds with some turtle shells.

Photo 7. Black bear scat composed mostly of cabbage palm seeds, but other unidentifiable seeds also present.

Photo 8. Black bear tracks leading from one tree island to another during a dry down in 3AS when water levels receded below the marsh surface.

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