METAPOPULATION DYNAMICS OF GOPHER FROGS (*RANA CAPITO*) IN GEORGIA

by

EVA KERR

(Under the Direction of John C. Maerz)

ABSTRACT

Anthropogenic threats like habitat loss and degradation lead to the breakdown of spatial population dynamics and population extirpation. The Gopher Frog (*Rana capito*) is a species of greatest conservation need in Georgia and pending evaluation for listing under the U.S. Endangered Species Act. Managers in Georgia are actively restoring landscapes that currently support or could potentially support Gopher Frog populations, and one objective is to increase the occupancy and abundance of Gopher Frog populations on those landscapes to improve the species resilience. However, we know little about how Gopher Frog population dynamics function in large landscapes. There are now only two sites in Georgia that are logistically feasible to study Gopher Frog metapopulation dynamics: Ceylon Wildlife Management Area and the Jones Center at Ichauway. We integrated occupancy and genetic data along with an individual-based model to understand Gopher Frog population processes in these landscapes and inform management priorities.

INDEX WORDS: landscape ecology; landscape genetics; metapopulation dynamics; Gopher Frog; management

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DEDICATION

I would like to dedicate this thesis to my dad, Chris Kerr, and my partner, Jonathan Campbell. My dad fostered my love of the outdoors and later encouraged my love for amphibians and reptiles. Jon has supported me every step of the way, including keeping me fed and helping me debug challenging code. Thank you both.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The biggest threat to the persistence of most species is – by far – habitat loss and degradation (Brooks et al., 2002; Cushman, 2006; Hanski, 2011). Beyond the direct loss of populations, habitat loss and degradation affect the resilience of populations in remaining habitat fragments. Our understanding of the ways that habitat loss and degradation affect population and species persistence is rooted in the principles of landscape ecology and metapopulation theory. A complete understanding of metapopulation processes, including demographic and evolutionary processes affected by habitat loss, is essential to effectively diagnose threats and develop management actions to increase population or species persistence. This thesis lays a foundation to better understand the landscape ecology and evolutionary dynamics of a high priority, threatened amphibian species to guide management decisions to meet local, state, and range-wide goals for the species.

Landscape Ecology

Most populations are inherently patchy across the landscape, with individuals unevenly distributed within populations. Hall et al. (1997) defined habitats as the resources and conditions in an area that allow a species to occupy a patch. Landscapes are – by definition – heterogeneous (Turner & Gardner, 2015), composed of patches of habitat embedded within a surrounding "matrix" of non-habitat (Forman, 1995). The composition and structure of the landscape drive regional population dynamics by determining both patch occupancy and the movement of individuals between patches, referred to as functional connectivity (Cushman et al., 2015). Functional connectivity is shaped by the distance between patches, the resistance of the matrix, the dispersal ability of the organism, and the characteristics of habitat patches that influence source–sink dynamics (Crawford et al., 2016; Murphy et al., 2010; Taylor et al., 2006). Within each patch, local population dynamics are governed by demographic processes, such as birth and death rates which vary with habitat patch quality (Pulliam, 1988). These dynamics result in some habitat patches that consistently produce a surplus of individuals, “source patches”, while other populations experience more deaths than births and persist only through immigration, “sink patches” (Pulliam, 1988). Several frameworks have been developed to represent population structure in landscapes, with metapopulation theory being one of the most widely applied.

In the narrowest sense, metapopulations are defined by four criteria: habitat patches have resident breeding populations, individual populations should not be large enough to be self-sustaining, populations should be connected through recolonization, and their dynamics must be asynchronous to prevent simultaneous extinction (Hanski et al., 1995). Broadly, metapopulations are sets of independent populations connected by “relatively rare” dispersal events. Isolated populations can act as a refuge from disease and promote local adaptation that increases adaptive diversity across a metapopulation. At the same time, occasional connectivity between these isolated populations can support demographic or genetic rescue through rare dispersal events (Cushman, 2006; Hanski et al., 1995; Hanski, 2011; Marsh & Trenham, 2001). This dynamic increases persistence probabilities of small populations and reduces the likelihood of extinction.

Habitat Loss and Fragmentation

Habitat loss occurs both through the complete conversion of habitat or through subtle changes that lead to the reduction of resources or conditions such that a patch can no longer sustain occupancy by a species. The latter is recognized as habitat degradation, but without intervention, will eventually be functional habitat loss. In addition to directly reducing the amount of habitat to support species, habitat loss disrupts key processes that drive both population dynamics and extinction risk (Haddad et al., 2015; Hanski, 2011). Habitat loss leads to decreased size and increased isolation of suitable habitat patches (Fahrig, 1997, 2019). This process generally leads to fragmented landscapes where remnant habitat patches exist within a matrix of varying levels of resistance. In these landscapes, restricted movement reduces gene flow, which can increase local adaptation but more often leads to loss of genetic diversity (Dixo et al., 2009; Lino et al., 2019). The chronic winnowing of genetic diversity within isolated populations diminishes a population's ability to respond to environmental change, leads to inbreeding depression, and can ultimately result in local extinction (Stockwell et al., 2003). There is a threshold at which local extinction rates exceed colonization rates, resulting in the collapse and extinction of the metapopulation (Bulman et al., 2007). Consequently, some have questioned whether true metapopulations are phases of what are better described as "mainland – island" populations now on the precipice of extinction (Fronhofer et al., 2012). Whether one believes or doubts whether most natural populations function according to classic metapopulation theory (Baguette, 2004; Fronhofer et al., 2012; Hanski, 2004), all agree that dispersal and connectivity are important for maximizing species distributions and persistence on landscapes, and that functional connectivity is declining for many species including most taxa of conservation concern. Landscapes that still support remnant, but disconnected populations present opportunities for restoration and management aimed at reestablishing connectivity and the associated population dynamics to improve long-term species persistence (Armstrong, 2005; Fahrig & Grez, 1996).

Metapopulation models can, when used appropriately, also guide conservation (Drechsler et al., 2003; Fronhofer et al., 2012; Hanski, 2004, 2011; Harrison & Fahrig, 1995). If not explicitly, metapopulation theory is often implicitly embedded within most conservation practices (Hanski, 2011). For example, common actions used to complement habitat restoration and conservation include the creation of movement corridors, population supplementation, translocations and repatriations, and the creation of assurance colonies and captive breeding programs. These actions address the loss of stable core populations, and the importance of natural dispersal in sustaining populations. Therefore, understanding processes like functional connectivity that drive local population and metapopulation dynamics can identify effective management strategies (Wendt et al., 2021).

Amphibians as a Metapopulation Model

While there has been disagreement on the applicability of metapopulation theory to amphibians, metapopulation theory is generally recognized as a useful framework for amphibian conservation because it appears to fit well with their use of patchy, aquatic breeding habitats, high apparent natal philopatry and breeding site fidelity, and regular barriers or resistance to dispersal (Billerman et al., 2019; Cushman, 2006; Marsh & Trenham, 2001; Smith & Green, 2005). Many amphibian populations are comprised of subpopulations which may be represented by a single breeding site or clusters of proximate, potentially "source-sink" or "patchy-population breeding sites." These populations are often isolated by larger distances between breeding sites due to the loss of some breeding sites and barriers to dispersal such as large rivers or – increasingly – human modified landscapes where much of the terrestrial matrix is unsuitable for dispersal. The metapopulation framework has proven readily adaptable to comparing management scenarios for threatened amphibians; for example, guiding decisions on habitat restoration and reintroductions to increase breeding site and metapopulation persistence (Chandler et al., 2015; Wendt et al., 2021).

Amphibian Functional Connectivity

When studying metapopulation dynamics of pond-breeding amphibians, ponds act as patches in a landscape with varying levels of resistance and create a natural system for understanding functional connectivity (Marsh & Trenham, 2001; Murphy et al., 2010). Migrating adults or dispersing juveniles allow for potential recolonization between breeding sites and are facilitated or restricted depending on the resistance of the terrestrial landscape (Cushman, 2006; Roznik et al., 2009; Semlitsch, 2008). Landscape resistance depends on land cover type and condition, geographic barriers like elevation, or anthropogenic features like large roads (Cushman, 2006; Gibbs, 1998; Murphy et al., 2010; Roznik et al., 2009). While landscape resistance influences movement of individuals, demographic characteristics like species density and patch characteristics like habitat quality influence patch occupancy and whether the patch acts as a source or sink population (Murphy et al., 2010; Pulliam, 1988). Source patches typically have high quality breeding habitat, sufficient hydroperiods, and resources to support larval recruitment and juvenile dispersal into the landscape (Semlitsch, 2008; Semlitsch et al., 2015). Within sink patches, intrinsic recruitment does not outweigh mortality, and the site is dependent on subsidies of immigrants to persist (Pulliam, 1988).

Landscape genetics provides a framework for understanding functional connectivity in amphibians by revealing patterns of gene flow in relation to landscape composition and structure (Crawford et al., 2016; Murphy et al., 2010; Watts et al., 2015). A landscape genetic study of

Columbia spotted frogs (*Rana luteiventris*) found that gene flow decreased with greater distance and topographic complexity between sites and with the presence of predatory fish, and increased with higher site productivity and longer growing seasons (Murphy et al., 2010). Understanding the functional connectivity of pond-breeding amphibians using genetic information can lead to more effective management decisions. Results can be used to identify locations where habitat restoration would be optimal and determine where population supplementation or reintroduction by translocations might be most effective (Cushman, 2006; Wendt et al., 2021). The degree of functional connectivity across a landscape can vary among species because of differences in movement ability [vagility] and because of specific microhabitat or other needs that make it possible for a species to persist during movement. Thus, there is a clear need for functional connectivity studies of conservation priority species, but opportunities for such studies can be limited for rare species if there are few landscapes that can support metapopulation structure and processes.

Simulations as a Management Tool

Models are an important tool in wildlife management, because they can provide a proxy to represent real-world systems and help predict potential outcomes. Simulation models mimic these systems while allowing researchers to control processes and parameters, providing an alternative or complement to field studies and helping to overcome the constraints of working with rare species (Landguth et al., 2015). Importantly, repeated simulations under a variety of parameters can lead to more confident inferences than empirical data, where the range of conditions or values that can be tested is much more limited (Landguth et al., 2015). Additionally, varying parameters across simulations allows for predicting how sensitive systems may be to environmental change or management actions (Landguth et al., 2015). One particularly powerful type of simulation model is the individual-based model (IBM) (Fahrig, 1997; Grimm & Railsback, 2013; Railsback & Grimm, 2012). In these models, individuals are represented as entities that can interact with each other and with their environment (Railsback & Grimm, 2012). This approach permits modeling known biological processes at the individual level and then observing how larger-scale patterns emerge over space and time. Ideally, these emergent patterns are confronted with real observations as part of model validation. IBMs have been applied across a wide range of contexts including modeling microhabitat selection (Burrow, 2021), evaluating invasion scenarios (Asper, 2015), identifying priorities for future field studies (Burton et al., 2012), and testing management actions such as reintroductions (Thesing, 2023) or habitat restoration (Dick & Ayllón, 2017).

Empirical data from landscape genetic studies provide insight into the processes that create observed patterns. However, these studies generally do not evaluate the demographic mechanisms behind genetic patterns. Spatially explicit IBMs provide a framework to determine landscape and demographic mechanisms driving genetic patterns and gene flow (DeAngelis & Grimm, 2014; Hearn et al., 2019; Landguth et al., 2010; Landguth & Cushman, 2010). Individuals within a landscape are assigned attributes like genotypes and specific behaviors such as breeding and dispersal. When IBMs are combined with empirical genetic data from landscape genetics they allow for “improved rigor” in determining how landscape features influence population dynamics and movement of individuals among breeding sites and within metapopulations (Shirk et al., 2012). Understanding the demographic and behavioral mechanisms behind genetic patterns is essential in generating robust hypotheses about how individuals likely interact with landscape features, which is fundamental to deciding on effective management actions.

Gopher Frogs

Gopher Frogs (*Rana capito*) are a conservation priority species endemic to the U.S. Southeastern Coastal Plain. They are tightly associated with the Longleaf pine (*Pinus palustris*) ecosystem that once covered nearly 90 million acres (Harrington et al., 2013). Specifically, Gopher Frogs depend on isolated, seasonal wetlands with dense emergent herbaceous vegetation for breeding, and open, frequently burned pine uplands with abundant Gopher tortoise (*Gopherus polyphemus*) burrows, small mammal burrows (Blihovde 2006), or stump holes (Roznik et al., 2009). Only approximately five percent of the longleaf pine ecosystem remains or has been restored (Harrington et al., 2013; Kirkman & Jack, 2017; McIntyre et al., 2018; Winger., 2022). Gopher Frog populations have declined extensively across the species' range except for peninsular Florida (Enge et al., 2023) likely due to habitat loss and degradation (i.e. land use changes and fire suppression) of longleaf pine uplands and breeding wetlands (Crawford et al., 2020; Enge et al., 2014), and other stressors (e.g. climate change; Binita et al., 2015; Crawford et al., 2022). Today, Gopher Frogs are listed as a Species of Greatest Conservation Need in all states within their range (NC, SC, GA, AL, and FL) and are currently under review for listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 2015). Gopher Frog life history and behavior suggest the species likely evolved in landscapes with high densities of isolated, seasonal wetlands (Crawford, Maerz, et al., 2022). Their dependence on seasonal wetlands likely means their populations relied on periodic breeding booms to persist (Crawford, Farmer, et al., 2022). Gopher Frog subpopulations likely experienced local extinctions and recolonization through mainland-island or metapopulation dynamics. However, this is very different than many of the landscapes where Gopher Frogs are managed today. Though most Gopher Frogs remain within 0.5-1 km of a breeding site, individual frogs have been documented migrating ~ 4 km between their terrestrial refugia and a breeding site (Humphries & Sisson, 2012; Marshall et al., 2023; Smith et al., 2021). Therefore, it is presumed that Gopher Frogs are capable of relatively long-distance dispersal that might be important in their metapopulation dynamics. Little is known about how Gopher Frogs migrate or ultimately disperse through different landscape matrix environments. Studies suggest a bias among juvenile and adult Gopher Frogs to move through more open canopy, pine-grassland habitat types with more abundant animal burrows (Neufeldt, 2004; Roznik & Johnson, 2009) and that fire-suppressed or closed canopy habitats may present more resistance to movement by juvenile Gopher Frogs because of reduced refugia availability (Roznik et al., 2009). Studies also suggest that juvenile Gopher Frogs may move along small dirt roads when present (Roznik & Johnson, 2009; Ruppert, 2025). However, these studies are limited to breeding movements of adult Gopher Frogs and emigration of recently metamorphosed juvenile Gopher Frogs. To our knowledge, there is no documentation of dispersal movements of Gopher Frogs.

In Georgia, most extant Gopher Frog populations are located on relatively small parcels of managed lands (i.e., conserved properties with active management) with only one to three known breeding wetlands and likely no functioning metapopulation structure (B. A. Crawford, Farmer, et al., 2022). Gopher Frogs on these small managed lands are isolated from other populations by distance and resistance caused by large areas of land developed for agriculture, silviculture, or other purposes. There are only three known landscapes in Georgia that have the potential to support robust Gopher Frog metapopulations: Ceylon Wildlife Management Area

(WMA) and the adjacent Cabin Bluff Conservation Easement (hereafter Ceylon), Fort Stewart, and the Jones Center at Ichauway (hereafter Ichauway). A fourth site, Alapaha River Wildlife Management Area (ARWMA), has the potential to support a metapopulation with multiple segregated breeding sites identified; however, Gopher Frog abundance on the site appears very low such that the population(s) on ARWMA may be at risk of extinction without intervention. Ceylon is in southeast GA supports one the largest populations of Gopher Frogs on state-managed public lands with what we hypothesize may be four to nine distinct populations separated by high resistance maritime forests and tidally influenced drains and creeks. Ichauway is in southwest GA and also supports multiple Gopher Frog breeding wetlands that may compose three distinct populations separated by paved and dirt roads, a creek, large distances and some landcover types assumed to be unsuitable for Gopher Frogs including hardwood forests, wildlife food plots, and off-site large scale irrigated agricultural fields. The status of Gopher Frog populations across Fort Stewart is poorly known because military operations make access and study very difficult. Therefore, Ceylon and Ichauway represent the only landscapes in Georgia at this time, where it is still logistically feasible to study Gopher Frog metapopulation processes.

Almost nothing is known about the local status and fine scale genetic structure of Gopher Frog populations. There has been a range-wide phylogeographic study of Gopher Frogs (Devitt et al., 2023), but there has only been one study of Gopher Frog fine scale genetic structure in North Carolina (Arbogast et al., 2022). However, that study focused on isolation by distance rather than isolation by resistance, which assumes that geographic distance alone drives genetic patterns. This may not be biologically meaningful if landscape features such as large creeks or highways play a stronger role in structuring populations. Within Georgia, there has been a study of Southern leopard frog (*Rana sphenocephala*) landscape genetics on Ichauway that found evidence of a weak spatial genetic structure, mostly defined by an outlier site (McKee et al., 2017). Leopard Frogs are primarily generalists in their use of breeding habitats and have larval life histories that differ from those of Gopher Frogs, which are more specialized in their breeding habitat use. Thus, there remains a gap in understanding the fine-scale landscape genetic structure of Gopher Frogs.

Thesis Objectives

Ceylon and Ichauway provide a unique opportunity to examine connections among presumed distinct Gopher Frog breeding populations across landscapes with multiple breeding sites and different matrices of terrestrial habitat between breeding sites. The two landscapes could allow us to identify factors important to the persistence of Gopher Frog breeding populations and the natural and anthropogenic factors that facilitate or impede dispersal. Therefore, the objectives of this thesis were to (1) determine Gopher Frog breeding occupancy in wetlands on Ceylon and Ichauway, (2) evaluate Gopher Frog genetic structure on these sites, (3) estimate genetic diversity within wetlands and genetic differentiation between wetlands, (4) identify natural and anthropogenic landscape features that appear to facilitate or act as barriers to dispersal and connectivity among Gopher Frog breeding sites, and (5) use an individual-based model to simulate local and landscape demography consistent with current patterns of breeding occupancy. This thesis is divided into five chapters (including this introduction) with chapters 2-4 written as manuscripts to be submitted for publication. Chapter 2 examines Gopher Frog breeding wetland occupancy at Ceylon and Ichauway using an integrated, multi-season, hierarchical Bayesian occupancy model. This chapter is dovetailed with master's research by Jade Samples evaluating wetland restoration effects on priority amphibian and plant species.

Chapter 3 presents a population and landscape genetic study of Gopher Frogs on Ceylon and Ichauway using 10 microsatellite loci. I estimate population structure with Structure, genetic diversity within sites, genetic differentiation between sites, and landscape resistance with *ResistanceGA*. Chapter 4 describes a spatially explicit individual-based model in Netlogo that simulates the annual life cycle of Gopher Frogs within the Ceylon landscape. The model is parameterized by demographic and movement studies of Gopher Frogs and other closely related species of Nenirana. I use the model to predict Gopher Frog occupancy and genetic structure, validate which landscape features facilitate or act as barriers to connectivity, and test different management strategies across Ceylon. Chapter 5 summarizes the finding of this thesis and discusses the applications to Gopher Frog and amphibian conservation as a whole.

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CHAPTER 2

ESTIMATING GOPHER FROG (*RANA CAPITO*) OCCUPANCY WITHIN TWO SOUTHEASTERN LANDSCAPES[1]

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Abstract

Gopher Frogs (*Rana capito*) are a Species of Greatest Conservation Need due to extensive population declines across the species' range. They now exist primarily in small, highly isolated populations with few sites large enough to support more than one or two breeding wetlands. Ceylon WMA and The Jones Center at Ichauway currently represent the only landscapes in Georgia where it is still logistically feasible to study Gopher Frog landscape processes. The objectives of this study were to document and estimate Gopher Frog occupancy of potential breeding wetlands and estimate the influence of site features on occupancy patterns in landscapes that may support metapopulation dynamics. We predicted that Ceylon WMA would have lower rates of Gopher Frog occupancy than Ichauway due to Ichauway's management history, larger areas of habitat, and relatively less heterogeneous landscape. We used a combination of acoustic recording unit, egg mass, dipnet, and tortoise burrow surveys to detect Gopher Frogs. In addition, we collected site- and wetland level-data through a combination of site visits and GIS delineation. We analyzed the collected data in an Integrated Bayesian Occupancy Model in JAGs to estimate the effect of site and wetland level covariates on occupancy. The estimated mean occupancy for the 13 focal wetlands at Ichauway was 0.734 (95% CI: 0.590–1.000), whereas the mean occupancy for the 14 focal wetlands at Ceylon was 0.264 (95% CI: 0.120–0.476). We found evidence for a negative relationship between canopy cover and mean estimated occupancy probability. Additionally, we found a positive relationship between wetland hydroperiod and mean estimated occupancy probability. The higher overall occupancy at Ichauway likely reflects greater wetland suitability for Gopher Frogs and, we hypothesize, a landscape that better facilitates dispersal among breeding sites. In contrast, the high canopy cover of wetlands and the larger areas of unsuitable "matrix" habitat at Ceylon likely reduce wetland suitability and connectivity across the landscape. Our results suggest that

Ceylon would benefit from actions to improve wetland suitability and terrestrial dispersal for Gopher Frogs to increase occupancy and population and species resilience on that landscape.

Introduction

Gopher Frogs (*Rana capito*) are a conservation priority species endemic to the Southeastern Coastal Plain. They are tightly associated with the Longleaf pine (*Pinus palustris*) ecosystem. Gopher Frogs depend on isolated, seasonal wetlands with dense emergent herbaceous vegetation for breeding, and open, frequently burned pine uplands with abundant Gopher tortoise (*Gopherus polyphemus*) burrows, small mammal burrows (Blihovde 2006), or stump holes to support juvenile and adult growth and survival outside of the breeding season (Roznik et al., 2009). Only approximately five percent of the longleaf pine ecosystem remains or has been restored (Harrington et al., 2013; Kirkman & Jack, 2017; McIntyre et al., 2018; Winger., 2022). Gopher Frog populations have declined extensively across the species' range except for peninsular Florida (Enge et al., 2023) likely due to habitat loss and degradation (i.e. land use changes and fire suppression) of longleaf pine uplands and breeding wetlands (Crawford et al., 2020; Enge et al., 2014), and other stressors (e.g. climate change; Binita et al., 2015; Crawford et al., 2022). Today, Gopher Frogs are listed as a Species of Greatest Conservation Need in all states within their range (NC, SC, GA, AL, and FL) and are currently under review for listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 2015). Gopher Frog life history and behavior suggest the species likely evolved for landscapes with high densities of isolated, seasonal wetlands (Crawford, Maerz, et al., 2022). Their dependence on seasonal wetlands likely means their populations relied on periodic breeding booms to persist (Crawford, Farmer, et al., 2022). Gopher Frog populations likely experienced local extinctions and recolonization through mainland-island or metapopulation dynamics. However, this is very different than many of the landscapes (Dahl, 1990; Lane et al., 2023) where Gopher Frogs persist today.

In Georgia, most extant Gopher Frog populations are located on relatively small parcels of managed lands (i.e., conserved properties with active management) with only one to three known breeding wetlands and likely no functioning metapopulation structure (B. A. Crawford, Farmer, et al., 2022). Most of these populations are isolated from other known populations by distance and resistance caused by large areas of land developed for agriculture, silviculture, or other purposes. There are only three known landscapes in Georgia that currently are known to support potential Gopher Frog metapopulations: Ceylon Wildlife Management Area and the adjacent Cabin Bluff conservation easement (hereafter Ceylon), Fort Stewart, and the Jones Center at Ichauway (hereafter Ichauway; Fig 2.1; J.C. Maerz personal communication, 2023). The status of Gopher Frog populations across Fort Stewart is poorly known because military operations make access and study very difficult. Therefore, Ceylon and Ichauway represent the only landscapes in Georgia where it is still logistically feasible to study Gopher Frog landscape processes.

The objectives of this study were to document and estimate Gopher Frog occupancy of potential breeding wetlands and estimate the influence of site features on Gopher Frog occupancy patterns on the Ceylon and Ichauway landscapes. We predicted that Ceylon WMA would have lower rates of occupancy than Ichauway due to Ceylon's shorter history of conducive wetland and upland management and its more heterogeneous landscape with larger areas of presumably unsuitable habitat. Our sampling efforts were integrated with the collection of tissue samples for a landscape genetic analysis to further inform the metapopulation dynamics on these sites (Kerr, Chapter 3). Together, these studies will be used to validate an individual-based model (IBM) that simulates the annual life cycle of Gopher Frogs within the Ceylon landscape (Kerr, Chapter 4). We conducted this study as part of a larger multi-site project evaluating wetland management effects on priority amphibian and plant species (Maerz et al., 2025; Samples, 2025).

Methods

Study Landscapes

Ichauway – The Jones Center at Ichauway is an 11,740-ha research site that focuses on natural resource management research, education, and conservation (*About Us - Jones Center*; Smith et al., 2006). Ichauway is located on the Dougherty Plain, in Baker County, Georgia. The site is dominated by a second-growth longleaf pine matrix with wiregrass (*Aristida stricta*) understory that is managed with bi-annual prescribed fire and currently supports 80–100 year old trees (*About Us - Jones Center*; Smith et al., 2006). Longleaf pine was harvested across most of the site in the 1920s and existing trees were naturally regenerated. Within the property, there are more than 90 seasonal wetlands (Fig. 2.2), Ichawaynochaway Creek, and the Flint River (*About Us - Jones Center*; Smith et al., 2006). Ichauway supports a very high diversity of flora and fauna including 31 species of amphibians and a large, stable gopher tortoise population (Smith et al., 2006). Ichauway also contains multiple known Gopher Frog breeding wetlands. However, these wetlands are separated by paved and dirt roads, a creek, large distances and some landcover types assumed to be unsuitable for Gopher Frogs including hardwood forests, wildlife food plots, and off-site large scale irrigated agricultural fields. Therefore, it is unknown if there are multiple, but isolated Gopher Frog populations or a single widely dispersed population on the property. Gopher Frog breeding has been monitored on site since 1994 with records of robust breeding years (2013, 15 wetlands) and poor breeding years (2018, 1 wetland) (L. Smith, personal communication). Since 2017 Georgia has undergone a multi-year drought (*Historical Data and Conditions | Drought.Gov*) resulting in the detection of Gopher Frog breeding in only three wetlands on the property and leaving the current state of Gopher Frog on the property uncertain (L. Smith, personal communication).

Ceylon Wildlife Management Area – Ceylon WMA is a 10,970-ha property located on Floyd's Neck south of the Satilla River in Camden County, Georgia just east of I-95. The landscape once held large areas of open longleaf pine savanna with a high density of isolated wetlands (Fig. 2.3), dense areas of maritime hardwood forest, and tidal river marsh and salt marsh. After the Civil War, the longleaf pine was harvested, leaving approximately 1,619 ha of longleaf wiregrass habitat across the property with some trees as old as 145 years (Lee, 2020). For most of the 20th Century, until the state opened the property as a public WMA in 2021, Ceylon was held privately and used primarily for timber extraction and hunting. Landowners managed the landscape with prescribed fire and "low impact" timber harvest, which is credited with allowing the persistence of soils and sections of habitats in reasonably good condition (i.e. open canopy pine savanna with herbaceous ground cover). At the time the site was acquired by Georgia DNR, the property contained thousands of Gopher Tortoises as well as populations of Gopher Frogs, and other priority species (Lee, 2020; M. Elliot, personal communication). Nonetheless, many of the wetlands had been encroached by pines, and pine forests surrounding wetlands had high basal area, both of which likely contributed to shorter wetland hydroperiods (Golladay et al., 2021), and several wetlands on the property were modified by ditching or digging pits in the basins to concentrate water and reduce wetland surface areas. Landowners created several borrow pits on the property, which now function as relatively permanent sources of freshwater in a landscape that is otherwise composed predominantly of ephemeral wetlands, tidal creeks, and forest drains.

Surveys of Ceylon for Gopher Frogs and other priority amphibians have occurred episodically since 2008. Not all the information from that work is publicly available and its effort did not focus systematically on the property. Three known and one potential Gopher Frog breeding site were identified prior to 2012. In 2020, a sample of Gopher tortoise populations on the property by GDNR identified several clusters of Gopher Frogs in tortoise burrows across the property including recently metamorphosed juveniles in burrows a few meters from wetlands (Marshall et al., 2023). Beginning in 2021, the Maerz Herpetology Lab at the University of Georgia began visiting many of the wetlands on the property and conducting opportunistic acoustic surveys and scoping tortoise burrows to capture Gopher Frogs for radio telemetry (Maerz et al., 2025; Maerz, 2022). The efforts since 2020 have expanded the known distribution of Gopher Frogs on Ceylon and called into question the assumption that there were only three potential breeding sites on the property. One emerging pattern was that Gopher Frogs are likely distributed in distinct units associated with each sandhill and clusters of tortoise burrows. These sandhills are separated from each other by low maritime forest that includes streams, some of which are tidally influenced. These maritime forests and streams likely create resistance for movement of Gopher Frogs on the property. Further, the westernmost portion of the property appears to lack Gopher Frogs despite apparently suitable terrestrial habitat and an abundance of tortoises, potentially because the wetlands in that area are all currently unsuitable due to past land activities.

Data Collection

For some sites we had existing monitoring data from 2022 (see below). Beginning in late 2023 through the winter and summer of 2024, large rain events filled the basins of study wetlands on both Ceylon and Ichauway, providing the best conditions for Gopher Frog breeding since 2020 (Past Weather | National Centers for Environmental Information (NCEI)). Therefore, we used this opportunity for intensive monitoring to identify where Gopher Frog breeding wetlands in 2024.

We initially identified all wetlands on both properties using previously delineated wetland boundaries and then selected survey sites based on wetland type, historic and recent Gopher Frog status, and an assessment of current wetland conditions (Fig. 2.2; Fig. 2.3). Ichauway had more consistent historic records of Gopher Frog occurrences than at Ceylon, where surveys had been sporadic and less thorough. As a result, it is possible that some potential Gopher Frog wetlands at Ceylon had been overlooked; however, based on the known ecological requirements of Gopher Frogs (Enge et al., 2014; Kirkman et al. 1999) and the current state of many Ceylon wetlands, we believe this is unlikely. Forested wetlands were presumed unsuitable and not considered for monitoring in this study. Among the remaining wetlands, we used a combination of acoustic recording units (ARU; SongMeter Minis and Micros, Wildlife Acoustics, Inc.), egg mass, dipnet, and tortoise burrow surveys to detect Gopher Frogs at study wetlands.

We deployed ARUs on trees or fence posts within each wetland from approximately October 2023-July 2024, but we removed them if a wetland dried before July. At Ceylon, we had ARUs deployed at six wetlands in the 2022 and 12 wetlands in 2023 - 2024. At Ichauway, we had ARUs at ten historic Gopher Frog wetlands and three potential wetlands from 2022 - 2024.

The ARUs recorded for five minutes on the hour from 1800 h to 0200 h daily. We randomly selected only two or three 5-minute call files from within 48 hours of a rain event with > 0.25 mm of precipitation (Cork, 2019). Trained individuals listened, identified, and assigned the calls a calling intensity score using the North American Amphibian Monitoring Program (NAAMP) index (Weir & Mossman, 2005).

We also completed monthly dipnet surveys in 14 wetlands at Ceylon in 2024 and 12 wetlands at Ichauway in 2023 and 2024. We visited each wetland from January to July and recorded wetland characteristics including maximum water depth and the percent of the wetland area ponded. Dipnet sampling only took place if the wetland held water. In 2023, multiple trained observers completed dipnet surveys totaling one-person-hour per wetland. For each amphibian species x life stage (e.g.. egg, larvae, juvenile, adult, or calling adult) detected, observers recorded the total number of individuals detected by dipnet, seen visibly, or heard calling. In 2024, the sampling protocol was modified. Instead of recording the total number of a species observed, we recorded the number of sweeps-to-first-detection for each species x life stage observed.

At Ichauway, we surveyed up to 12 wetlands for egg masses in 2023 and 2024, though our effort focused most consistently on nine wetlands known to be historic breeding sites or believed to be most suitable for Gopher Frog breeding (i.e., grass-sedge marshes or cypress savannas; Kirkman et al. 1999). Surveys took place approximately bi-weekly from January to July in 2023 and April in 2024 if the wetlands had water. Multiple observers walked transects parallel to the shore across the wetland searching for egg masses until observers covered the wetland or until 30 minutes had passed. Each observer recorded species of amphibian egg masses, the number of egg masses, and wetland characteristics such as water depth at the egg mass.

At Ceylon, we also scoped Gopher Tortoise burrows using a burrow camera (Environmental Management Systems) in areas surrounding known historic or potential Gopher Frog breeding wetlands (within approximately 600 m of those wetlands) and in areas where Gopher Frogs were detected during Gopher Tortoise surveys in 2020. We combined our data with the 2020 survey data and with additional Gopher Frog records on Ceylon dating back to 2008. This created a database with every known Gopher Frog location on Ceylon. Using this database for each wetland, we used GIS to measure the distance to the nearest terrestrial Gopher Frog location. We then measured for each wetland the distance to the nearest known Gopher Tortoise burrow location from the 2020 Gopher Tortoise surveys.

For each wetland, we used GIS and satellite imagery to estimate canopy cover. Trained personnel used 2024 World Imagery from ERSI (https://services.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer) in QGIS to digitize the tree canopy within the wetland and if possible, identified trees as cypress or pine. We calculated percent canopy cover by dividing canopied area by the total wetland area available from previously digitized wetland boundaries (Table 2.1.). In addition, we visited wetlands to ground truth digitized estimates of canopy cover and composition.

Data Analysis

We used an Integrated Bayesian Occupancy Model in JAGs to estimate Gopher Frog occupancy and the influence of site features on occupancy at study wetlands on Ceylon and Ichauway. This framework allowed us to incorporate multiple sampling methods and account for imperfect detection with method-specific detection estimates. We chose a static model over a dynamic model because we did not have enough years of data to meaningfully determine extinction and colonization rates.

True occupancy was $z_{j,w,t}$ such that if Gopher Frogs occupied site *j* at wetland *w* in calendar year *t* $z_{j,w,t} = 1$ otherwise; $z_{j,w,t} = 0$. We modeled occupancy as a Bernoulli random variable $z_{j,w,t} \sim Bern(\psi_{j,w,t})$ where $\psi_{j,w,t}$ is the probability that a Gopher Frog occupies site *j* at wetland *w* in year *t*. We modeled Gopher Frog occupancy probability ($\psi_{j,w}$) on the logit scale as a linear function of site- and wetland-level covariates:

$$logit(\psi_{j,w}) = \alpha_0 + \alpha_1 * Landscape_j + \alpha_2 * Canopy_{j,w} + \alpha_3 * Hydroperiod_{j,w} + \alpha_4 * NearbyWetlands_{j,w} + \alpha_5 * Terrestrial_{j,w} * TerrestrialEffort_{j,w}$$

We included an effect of landscape on occupancy to account for variation between Ceylon and Ichauway as the sites have different management histories. The canopy cover covariate was the percent canopy cover calculated using GIS. We defined the hydroperiod covariate as the ratio of visits during which the wetland held water to the total number of survey visits (Table 2.1.). The nearby wetlands covariate was the number of wetlands within a 500 m buffer of the wetland (Table 2.1.). The terrestrial covariate for each wetland was the distance to the nearest terrestrial Gopher Frog divided by the distance to the nearest Gopher tortoise burrow. This covariate included an effort scaler because it only took place at Ceylon, and the scaler allowed us to mask this covariate for Ichauway. We included terrestrial sampling as a covariate rather than a detection method because many terrestrial detections occurred near multiple wetlands, making it unclear which wetland the frogs originated from. In future analyses, we plan to incorporate terrestrial detections that fall within a small buffer around wetlands (e.g., ≤100 m). We centered and scaled each continuous covariate.

We modeled detection as three separate Bernoulli random variables to incorporate the three different methodologies: ARU call files, dipnetting, and egg mass surveys. The detection models were conditional on the latent state occupancy (z). For call surveys,

$$y.call_{j,w,m,t} \sim Bern(z_{j,w,t} * p.call_{j,w,m,t} * effort.call_{j,w,m,t}),$$

with detection probability defined as

$$logit(p.call_{j,w,m,t}) = \beta_{call.0} + u^{month}[month]_m + year_t.$$

For dipnetting,

$$y.dip_{j,w,m,t} \sim Bern(z_{j,w,t} * p.dip_{j,w,m,t} * effort.dip_{j,w,m,t}),$$

$$logit(p.dip_{j,w,m,t}) = \beta_{dip.0} + u^{month}[month]_m + year_t.$$

And for egg mass surveys,

$$y.egg_{j,w,m,t} \sim Bern(z_{j,w,t} * p.egg_{j,w,m,t} * effort.egg_{j,w,m,t}),$$

$$logit(p.egg_{j,w,m,t}) = \beta_{egg.0} + u^{month}[month]_m + year_t.$$

We constructed effort arrays for each sampling method to indicate whether a wetland was or was not sampled, to account for variation in sampling effort and methods across sites, wetlands, months, and years. We included a random effect of month ($u^{month}[month]_m$) and a fixed effect of detection for each method to account for the variation between months and years. For example, 2024 was a year with high precipitation, whereas 2023 had markedly low precipitation. Month specific random effects were drawn from normal distributions with precisions τ_{mon}, with hyperpriors placed on the precisions, $\tau_{\text{mon}} \sim \text{Exponential}(1)$. All priors and hyperpriors in both the occupancy and detection model were uninformative.

We fit the model using JAGs (Plummer, 2003) within R (v 4.5.1)(R Core Team, 2025) through the *jagsUI* (Kellner, 2015) package. We used Markov Chain Monte Carlo (MCMC) sampling to generate posterior distributions. We ran three Markov chains for 70,000 iterations, removed the first 15,000 iterations as burn-in, and thinned the remaining by a factor of five to produce a total of 33,000 samples. We used these samples to calculate posterior means and 95% Bayesian credible intervals for each parameter. We assessed model convergence with the Gelman-Rubin diagnostic and found that for nearly all modeled parameters, the Gelman–Rubin diagnostic was ≤ 1.02.

Results

We initially identified 91 wetlands on Ichauway. By filtering wetlands based on their conditions, we identified 12 historic and one potentially suitable wetland for Gopher Frogs for sampling. Some of the historic wetlands had recent Gopher Frog detections prior to 2023, but some had only a single detection in 1998. Two historic Gopher Frog wetlands were not included in our monitoring because each of those wetlands had a single historic detection more than ten years ago. At Ceylon, we identified 145 wetlands, 4 of which were historic Gopher Frog detection locations with breeding confirmed at only one, 5 were considered likely based on current conditions and proximity to historic Gopher Frog records, 10 were considered potential based on current conditions, 82 were considered unsuitable. There were 44 that we did not have the opportunity to classify current conditions for, but nearly all were far from historic Gopher Frog records. We sampled all 4 historic and all 5 likely wetlands, and 5 of the 10 potential wetlands that seemed most suitable and proximate to historic Gopher Frog records.

Among the 26 wetlands we sampled with ARUs, dipnetting, and egg mass searches, we detected Gopher Frogs 79 times. We had 55 detections among 10 wetlands on Ichauway (naïve occupancy = 0.769) and 9 detections across 3 wetlands on Ceylon (naïve occupancy = 0.214; Table 2.2). We had 40 detections by call on ARUs, 16 detections by dipnet survey, and 8 detections by egg mass surveys. We did not detect Gopher Frogs in 2022, detected them only on Ichauway in 2023, and at both sites in 2024 (Table 2.3). We detected Gopher Frogs from January to June at Ichauway and March to June at Ceylon (Table 2.3). We detected 49 Gopher Frogs during terrestrial surveys of tortoise burrows at Ceylon in 2024 (Table 2.4).

The estimated mean detection probabilities were 0.177 (95% CI; 0.057, 0.369) for egg mass surveys, 0.176 (95% CI; 0.067, 0.368) for dipnet surveys, and 0.248 (95% CI; 0.179, 0.336) for call files. Both month and year had uncertain effects on detection by ARU, dipnet survey, or egg mass survey (Table 2.5; Fig. 2.4; Fig 2.5). However, detection using ARU varied seasonally, with lower detection in early winter (October–December) and higher detection in late winter to spring (January–May). Dipnet surveys showed a slight non-monotonic trend, with detection probabilities higher in April and lower in February and July (Table 2.6; Fig. 2.6). Similarly, egg mass surveys showed higher detection in February, and lower detection in January and April (Table 2.6; Fig. 2.6). Detection by ARU was lower in 2022 while detection by dipnet or egg mass survey was lower in 2023 (Table 2.6; Fig 2.7).

The estimated mean occupancy among the focal wetlands was 0.734 (95% CI; 0.590, 1.000) for Ichauway and 0.264 (95% CI; 0.120, 0.476) for Ceylon (Fig. 2.8; Fig. 2.9; Fig. 2.10). Ten wetlands on Ichauway and three wetlands on Ceylon had a mean predicted occupancy probability over 0.5 (Fig. 2.8; Fig. 2.9; Fig. 2.10). We found evidence for a negative relationship between canopy cover and mean estimated occupancy probability. Though the 95% CI overlapped zero (Table 2.7; Fig. 2.11), in 95.5% of simulations the estimated occupancy probability was negatively correlated with canopy cover. In 90.4% of simulations the estimated occupancy probability was positively correlated with hydroperiod (Table 2.7; Fig. 2.11). We found no evidence that the number of nearby wetlands was correlated with estimated occupancy probability (Table 2.7; Fig. 2.11). At Ceylon, which was the only site where we examined this parameter, we found evidence that the proximity to the nearest known Gopher Tortoise burrow, which was expressed as the ratio of the distance to the nearest terrestrial Gopher Frog compared to the nearest Gopher Tortoise burrow, had a positive relationship with mean estimated occupancy of a wetland. In 86% of simulations, occupancy probability was positively correlated with the ratio of the nearest Gopher Frog detection to the nearest known Gopher Tortoise burrow (Table 2.7; Fig 2.11).

Discussion

Our objective was to document and estimate Gopher Frog occupancy of historic and potential breeding wetlands and estimate the influence of site features on occupancy patterns on Ichauway and Ceylon. At Ichauway, we detected Gopher Frogs at 9 of the 12 historic wetlands sampled and at one new wetland we had identified as potentially suitable. These results indicated relatively consistent occupancy across the Ichauway landscape. At Ceylon, we detected Gopher Frogs at two of the four historic wetlands but only one of the five wetlands we identified as likely suitable. While we did not detect breeding at two historic wetlands and the other wetlands we identified as likely or potentially suitable at Ceylon, we believe breeding did occur at four of those wetlands due to the high number of recently metamorphosed Gopher Frogs detected in tortoise burrows immediately surrounding those wetlands (Table 2.4).

Through our surveys, we found that detecting Gopher Frogs using dipnet and egg mass surveys had low success on Ceylon compared to Ichauway. We hypothesize this may reflect small population sizes on Ceylon making detections of calling males or egg masses difficult.

Often at Ceylon ARUs recorded only a single calling male, suggesting breeding population sizes were small. In contrast, we did detect choruses of multiple Gopher Frogs calling concurrently in some Ichauway wetlands and egg masses and tadpoles were easier to detect on that landscape. In a case like Ceylon, terrestrial surveys targeting recently metamorphosed Gopher Frogs in tortoise burrows nearest to wetlands were more effective for confirming occupancy and successful recruitment from a wetland. Because we sampled in a particularly high precipitation year, it is possible that Gopher Frogs bred in habitat that is not usually available, such as the pine flatwoods at Ceylon that remained flooded for the majority of 2024. We assumed that wetlands not included in our study were unoccupied, but this could not be confirmed without substantially greater resources supporting a more extensive survey of the property. As a note, detections in wetlands can be lower in larger and deeper wetlands (Curtis & Paton, 2010). Although area and depth vary across sites, wetlands at Ichauway are generally larger but shallower (mean area = 48,661.65 m^2; mean depth = 70.755 cm) than those at Ceylon (mean area = 11,076.22 m^2; mean depth = 80.550 cm).

Our results were inconsistent with some previous studies that found the proximity of other wetlands has positive effects on amphibian occupancy (Semlitsch, 2000). This result may reflect the fact that many nearby wetlands – particularly on Ceylon – were currently unsuitable for Gopher Frogs. Focusing on the number of nearby wetlands occupied by or suitable for Gopher Frogs could be a better metric for habitat connectivity.

Though Gopher Frogs are generally associated with geographically isolated wetlands that dry regularly if not annually (Enge et al., 2014), we found evidence of a positive relationship between hydroperiod and mean estimated probability of Gopher Frog occupancy (Table 2.7; Fig. 2.11). All the wetlands in our study were geographically isolated, so it is possible that, among isolated wetlands, those with longer hydroperiods support Gopher Frog reproduction in more years and therefore are more likely to remain occupied. We note that it had been four years since any of the wetlands at Ceylon held sufficient water for Gopher Frog or other amphibian breeding. Because of the protracted dry period, it might be that only the wetlands with the longest hydroperiods had breeding populations large enough to persist. The positive relationship between hydroperiod and occupancy probability also likely was affected by Gopher Frog use of borrow pits as breeding sites at Ceylon. Gopher Frogs have been documented breeding in borrow pits on other sites in Georgia (Neufeldt, 2004). Borrow pits likely represent relatively reliable breeding habitats during periods when natural wetlands fail to fill or hold sufficient water for breeding. Borrow pits may be increasingly important for sustaining Gopher Frogs on landscapes experiencing increasing frequency and intensity of drought (Binita et al., 2015; Crawford, Maerz, et al., 2022). However, borrow pits might also act as sinks if they support more abundant or persistent predator communities, support disease reservoirs (e.g. ranavirus and amphibian chytrid fungus; Petranka et al., 2007; Richter et al., 2013), or if tadpoles experience stronger negative density dependence effects due to the relatively small size of borrow pits. We also caution that our measure of hydroperiod was calculated for a single year, 2024, when most study wetlands remained filled due to heavy rainfall. As a result, there was relatively uniformly long hydroperiods across wetlands on both landscapes, which likely limits our measure of potential long-term variation in hydroperiod among wetlands. Data on long-term hydroperiod dynamics of wetlands on Ceylon might improve our estimates and understanding of how hydroperiod currently shapes Gopher Frog wetland occupancy on large landscapes.

Our findings support the prediction that Ceylon had lower rates of occupancy than Ichauway. This “landscape” effect is likely due to differences in land use and management history between the two sites. Although both are large properties, Ichauway has been managed toward a desired state (open canopy pine woodlands; McIntyre et al. 2019) for nearly half a century. Ichauway had a disproportionate number of the more open canopied wetlands (Fig 2.12), likely reflecting the longer history and more concerted efforts at wetland vegetation management and highlighting the need for targeted canopy thinning in wetlands at Ceylon. In addition, the uplands on Ichauway are managed with biannual prescribed fire, resulting in open-canopy pine uplands across much of the property. In contrast, Ceylon is a recent state acquisition with terrestrial habitat management just beginning. For this reason and due to natural variation in soils, topography, and hydrology, Ceylon represents a more heterogeneous landscape, with larger areas of presumably unsuitable habitat, only a portion of which has been subject to habitat management. Studies suggest that juvenile and adult Gopher Frogs most often move through open canopied, pine-grassland systems with more abundant animal burrows (Neufeldt, 2004; Roznik & Johnson, 2009) and that fire-suppressed or closed canopied systems may present more resistance to movement by juvenile Gopher Frogs because of reduced refugia availability (Roznik et al., 2009). Though most Gopher Frogs remain within 0.5-1 km of a breeding site, individual frogs have been documented migrating ~ 4 km between their terrestrial refugia and breeding sites (Humphries & Sisson, 2012; Marshall et al., 2023; Smith et al., 2021). Therefore, it is presumed that Gopher Frogs are capable of relatively long-distance dispersal that facilitate recolonization though this phenomenon has not been directly observed. The structural differences between Ichauway and Ceylon likely affect how Gopher Frogs move between terrestrial refugia and wetlands and disperse across the two landscapes and resulting in different patterns of wetland occupancy. The higher overall occupancy observed at Ichauway likely reflects both greater wetland suitability and lower upland resistance between wetlands, allowing recolonization events. In contrast, at Ceylon, the lower wetland suitability and more heterogeneous landscape may limit dispersal between wetlands, increasing the likelihood that local extinctions may not be recolonized.

Although Ceylon has maintained a few Gopher Frog breeding strongholds, limited dispersal between wetlands at this site may reduce demographic rescue effect and gene flow, which can lead to smaller population sizes and more frequent local extinction among habitat patches (Dixo et al., 2009; Lino et al., 2019). Thus, management actions should focus on targeted habitat restoration to maximize connectivity among Ceylon breeding populations. Though not likely as acute an issue on Ichauway, management to maintain or improve Gopher Frog connectivity among wetlands and populations on the landscape is likely to further increase occupancy and species persistence.

When current conditions for dispersal or small population sizes limit the potential for natural recolonization in the near term, population supplementation or reintroduction through translocation or captive rearing will likely be necessary to complement habitat management. In the future, a genetic study on Ceylon and Ichauway could inform management actions including identifying natural and anthropogenic landscape features that currently act as barriers to connectivity and prioritizing wetlands for restoration and translocation to increase the number of occupied breeding sites, the size of breeding populations, and ultimately the resilience of Gopher Frogs on these landscapes.

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Tables and Figures

Table 2.1. Covariates in the Integrated Bayesian Occupancy Model, where Gopher Frog occupancy probability was modeled on the logit scale as a linear function of these covariates. Values include landscape (Ceylon or Ichauway), wetland ID, 2024 hydroperiod (% of sampling visits when the wetland held water), canopy cover (percent of wetland area with tree canopy), the ratio of distance to the nearest terrestrial Gopher Frog to the nearest Gopher Tortoise burrow (Ceylon only), and the # of wetlands within 500 m.

Site / Landscape	Wetland ID	Hydroperiod 2024	Canopy Cover	Terrestrial	# of Nearby Wetlands
Ceylon	22	1	51.17	0.3875	7
Ceylon	37	0.8	82.24	0.986	16
Ceylon	41	1	96.25	0.595	10
Ceylon	54	1	77.9	0.1326	9
Ceylon	55	0.8333	23.27	0.9338	5
Ceylon	59	1	45.9	1	5
Ceylon	60	1	46.31	0.4261	3
Ceylon	62	1	82.83	0.5063	4
Ceylon	69	1	65.88	0.2326	3
Ceylon	109	1	36.6	0.5158	3
Ceylon	127	1	62.55	0.2611	7
Ceylon	109b	1	72.9	0.1362	3
Ceylon	41b	1	4.91	0.2018	1
Ceylon	69b	1	63.54	0.1475	2
Ichauway	15	0.8571	25.07	NA	2
Ichauway	21	0.75	6.03	NA	5
Ichauway	37	1	25.94	NA	16
Ichauway	39	0	43.58	NA	16
Ichauway	40	1	74.68	NA	15
Ichauway	41	1	62.22	NA	10
Ichauway	42	1	15.68	NA	11
Ichauway	46	1	9.88	NA	8
Ichauway	49	1	9.54	NA	7
Ichauway	50	1	2.39	NA	5
Ichauway	51	1	3.08	NA	1
Ichauway	53	1	4.5	NA	3
Ichauway	55	1	4.26	NA	5

Table 2.2. Gopher Frog wetland detections at Ceylon and Ichauway by sampling method (dipnet surveys, call files, and egg mass surveys at Ichauway only). Wetlands with at least one detection are shown for each site. We detected Gopher Frogs at three wetlands on Ceylon and at ten wetlands on Ichauway.

Site	Dipnet Surveys	Call Files	Egg Mass Surveys	Total Detections	Wetlands with Detections
Ceylon	3	6	NA	9	41, 41B, 59
Ichauway	13	34	8	55	15, 21, 37, 42, 46, 49, 50, 51, 53, 55

Table 2.3. Gopher Frog wetland detections at Ceylon and Ichauway by year and month for by sampling method (dipnet surveys, call files, and egg mass surveys at Ichauway only). At Ceylon, Gopher Frogs were detected in wetlands only during 2024, with detections from March through June. At Ichauway, Gopher Frogs were detected in wetlands in both 2023 and 2024, with detections from January through June.

Site	Method	Years with Detections	Months with Detections
Ceylon	Call Files	2024	March, May, June
Ceylon	Dipnet Surveys	2024	March, April
Ichauway	Call Files	2023,2024	January, February, March, April, May
Ichauway	Dipnet Surveys	2024	March, April, May, June
Ichauway	Egg Mass Surveys	2024	February, March

Table 2.4. The number of terrestrial Gopher Frogs located using a tortoise burrow camera or during road cruising in 2024 for the 14 focal wetlands on Ceylon. Distances were calculated from each terrestrial Gopher Frog point to all wetlands, and the three nearest wetlands were identified for each point. The number of terrestrial records is shown for the nearest wetland, ranging from 0 to 13 detections (49 total).

Wetland ID	Number of Terrestrial Records
37	13
55	12
59	11
41	6
41B	3
109	1
109B	1
127	1
54	1
22	0
60	0
62	0
69	0
69B	0
Total	**49**

Table 2.5. Posterior summaries of month (random effect, pooled) and year (fixed effect, pooled) on detection probability for each sampling method from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Values represent posterior means, 95% credible intervals, and Bayesian p-values (the proportion of posterior simulations with the same sign as the mean estimate). Estimates in bold indicate parameters that had a Bayesian p-value > 0.80.

Method	Variable (pooled)	Mean	95% CI		Bayesian p-value
Call Files	u^{month}	-0.411	-2.183	0.800	0.710
Call Files	$year_t$	-0.506	-1.952	0.931	0.754
Dipnet Surveys	u^{month}	-0.130	-1.050	0.546	0.620
Dipnet Surveys	$year_t$	-0.591	-2.033	0.847	0.790
Egg Mass Surveys	u^{month}	-0.313	-2.052	0.638	0.682
Egg Mass Surveys	$\boldsymbol{year_t}$	**-0.634**	**-2.085**	**0.841**	**0.802**

Table 2.6. Posterior summaries of month (random effect) and year (fixed effect) on detection probability for each sampling method from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Values represent posterior means, 95% credible intervals, and Bayesian p-values (the proportion of posterior simulations with the same sign as the mean estimate). Estimates in bold indicate parameters that had a Bayesian p-value >0.80.

Method	Variable	Definition	Mean	95% CI		Bayesian p-value
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: October**	**-2.8**	**-7.561**	**0.073**	**0.971**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: November**	**-2.815**	**-7.49**	**0.03**	**0.973**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: December**	**-3.169**	**-7.829**	**-0.445**	**0.992**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: January**	**1.026**	**-0.762**	**2.994**	**0.872**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: February**	**1.442**	**-0.363**	**3.468**	**0.941**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: March**	**1.113**	**-0.654**	**3.017**	**0.895**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: April**	**1.109**	**-0.659**	**3.012**	**0.896**
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: May**	**2.187**	**0.158**	**4.425**	**0.983**
Call Files	u^{month}	Month Effect: June	0.194	-2.392	2.64	0.576
Call Files	u^{month}	Month Effect: July	-1.467	-6.263	1.489	0.792
Call Files	u^{month}	Month Effect: August	-0.016	-5.187	5.168	0.505
Call Files	$\boldsymbol{u^{month}}$	**Month Effect: September**	**-1.737**	**-6.888**	**2.487**	**0.804**
Call Files	$\boldsymbol{u^{year}}$	**Year Effect: 2022**	**-2.359**	**-4.412**	**-0.41**	**0.992**
Call Files	$\boldsymbol{u^{year}}$	**Year Effect: 2023**	**1.924**	**0.291**	**3.592**	**0.989**
Call Files	$\boldsymbol{u^{year}}$	**Year Effect: 2024**	**-1.083**	**-2.758**	**0.584**	**0.899**
Dipnet Surveys	u^{month}	Month Effect: October	-0.003	-2.684	2.736	0.5
Dipnet Surveys	u^{month}	Month Effect: November	0.002	-2.759	2.751	0.5
Dipnet Surveys	u^{month}	Month Effect: December	0.01	-2.704	2.74	0.504
Dipnet Surveys	u^{month}	Month Effect: January	-0.795	-3.6	1.03	0.764

Dipnet Surveys	u^{month}	**Month Effect: February**	**-1.022**	**-3.817**	**0.73**	**0.846**
Dipnet Surveys	u^{month}	Month Effect: March	0.262	-1.245	1.774	0.645
Dipnet Surveys	u^{month}	**Month Effect: April**	**1.134**	**-0.186**	**2.681**	**0.953**
Dipnet Surveys	u^{month}	Month Effect: May	0.328	-1.1	1.791	0.682
Dipnet Surveys	u^{month}	Month Effect: June	-0.235	-1.866	1.233	0.618
Dipnet Surveys	u^{month}	**Month Effect: July**	**-1.258**	**-4.025**	**0.441**	**0.91**
Dipnet Surveys	u^{month}	Month Effect: August	0.019	-2.731	2.801	0.507
Dipnet Surveys	u^{month}	Month Effect: September	0.002	-2.733	2.72	0.499
Dipnet Surveys	u^{year}	Year Effect: 2022	-0.001	-2.771	2.743	0.499
Dipnet Surveys	u^{year}	**Year Effect: 2023**	**-2.204**	**-4.26**	**-0.237**	**0.987**
Dipnet Surveys	u^{year}	Year Effect: 2024	0.431	-1.331	2.22	0.683
Egg Mass Surveys	u^{month}	Month Effect: October	-0.021	-4.214	4.155	0.503
Egg Mass Surveys	u^{month}	Month Effect: November	-0.017	-4.141	4.069	0.502
Egg Mass Surveys	u^{month}	Month Effect: December	-0.021	-4.197	4.213	0.506
Egg Mass Surveys	u^{month}	**Month Effect: January**	**-1.744**	**-6.294**	**0.616**	**0.904**
Egg Mass Surveys	u^{month}	**Month Effect: February**	**1.536**	**-0.309**	**3.562**	**0.953**
Egg Mass Surveys	u^{month}	Month Effect: March	-0.076	-2.275	1.935	0.52
Egg Mass Surveys	u^{month}	**Month Effect: April**	**-1.805**	**-6.372**	**0.542**	**0.917**
Egg Mass Surveys	u^{month}	Month Effect: May	-0.572	-4.91	2.248	0.603
Egg Mass Surveys	u^{month}	Month Effect: June	-0.574	-5.029	2.257	0.602
Egg Mass Surveys	u^{month}	Month Effect: July	-0.506	-4.907	2.494	0.584
Egg Mass Surveys	u^{month}	Month Effect: August	0.044	-4.066	4.204	0.505
Egg Mass Surveys	u^{month}	Month Effect: September	-0.004	-4.224	4.183	0.501
Egg Mass Surveys	u^{year}	Year Effect: 2022	0.01	-2.762	2.779	0.503
Egg Mass Surveys	u^{year}	**Year Effect: 2023**	**-2.531**	**-4.596**	**-0.537**	**0.994**
Egg Mass Surveys	u^{year}	Year Effect: 2024	0.618	-1.28	2.578	0.735

Table 2.7. Posterior summaries of covariate effects on occupancy probability from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Values represent posterior means, 95% credible intervals, and Bayesian p-values (the proportion of posterior simulations with the same sign as the mean estimate). Estimates in bold indicate parameters that had a Bayesian p-value > 0.80.

Variable	Definition	Mean	95% CI	Bayesian p-value

$\boldsymbol{\alpha_1}$	**Landscape**	**2.279**	**0.659**	**3.934**	**0.997**
$\boldsymbol{\alpha_2}$	**Canopy Cover**	**-1.020**	**-2.257**	**0.179**	**0.955**
$\boldsymbol{\alpha_3}$	**Hydroperiod**	**1.083**	**-0.721**	**2.795**	**0.904**
$\boldsymbol{\alpha_4}$	# Of Nearby (≤500) Wetlands	-0.150	-1.421	1.111	0.593
$\boldsymbol{\alpha_5}$	**Terrestrial**	**0.878**	**-0.638**	**2.649**	**0.859**

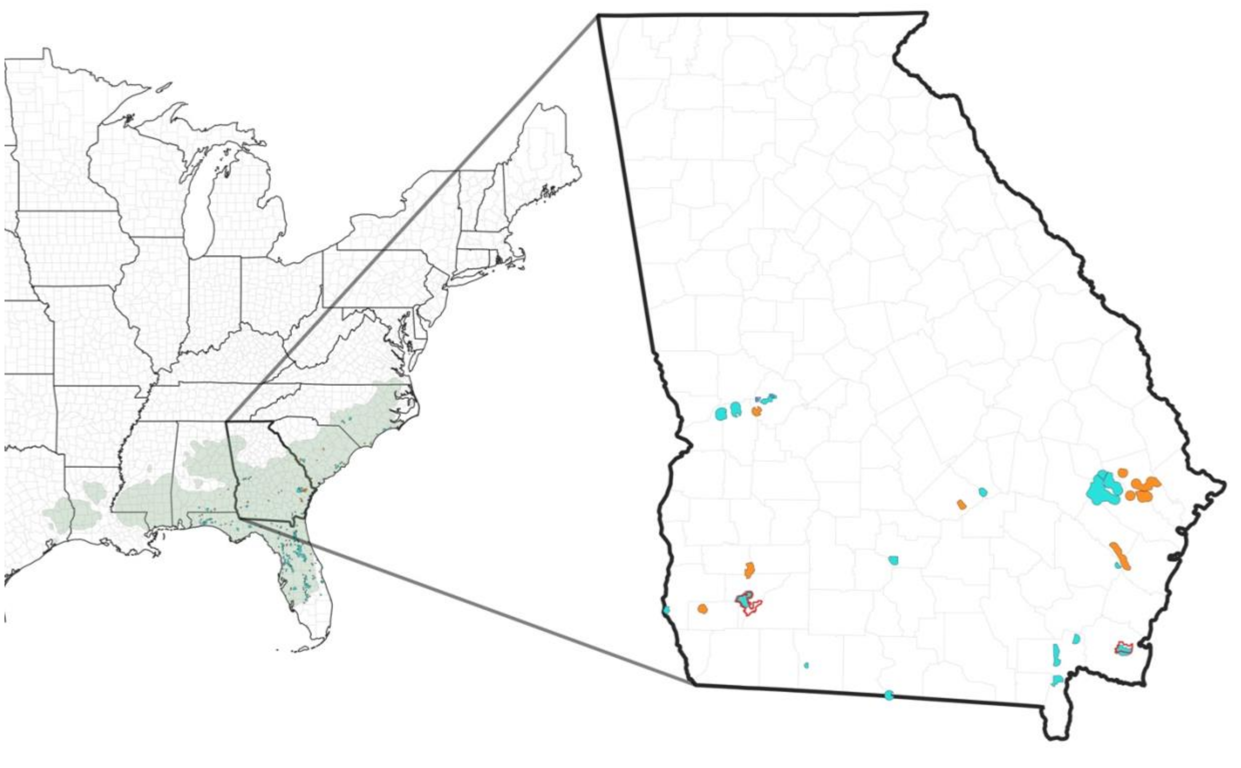

Figure 2.1. Map of Eastern US with light green shading representing the historic range of longleaf pine. Georgia, USA is emphasized and locations of known and predicted extant Gopher Frog populations are shown in blue, whereas populations predicted to be extinct are in orange (Crawford & Maerz, 2021). Study sites, Ichauway in Baker County and Ceylon Wildlife Management Area in Camden County, are highlighted in red.

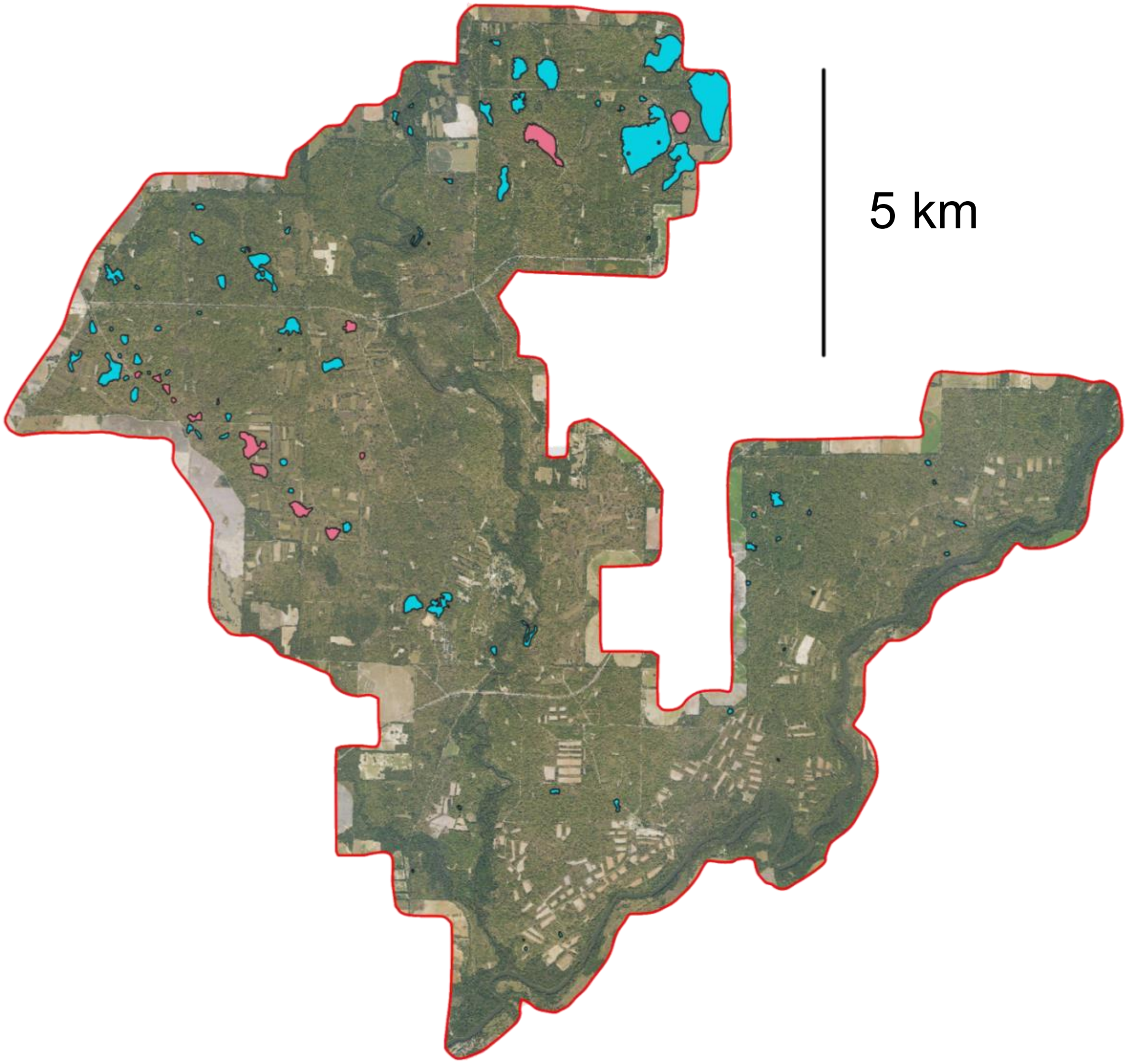

Figure 2.2. Map of Ichauway located in Baker County, Georgia, showing the 13 study wetlands sampled for Gopher Frogs, colored pink. Wetlands deemed unsuitable for Gopher Frogs and not included in the study are colored light blue.

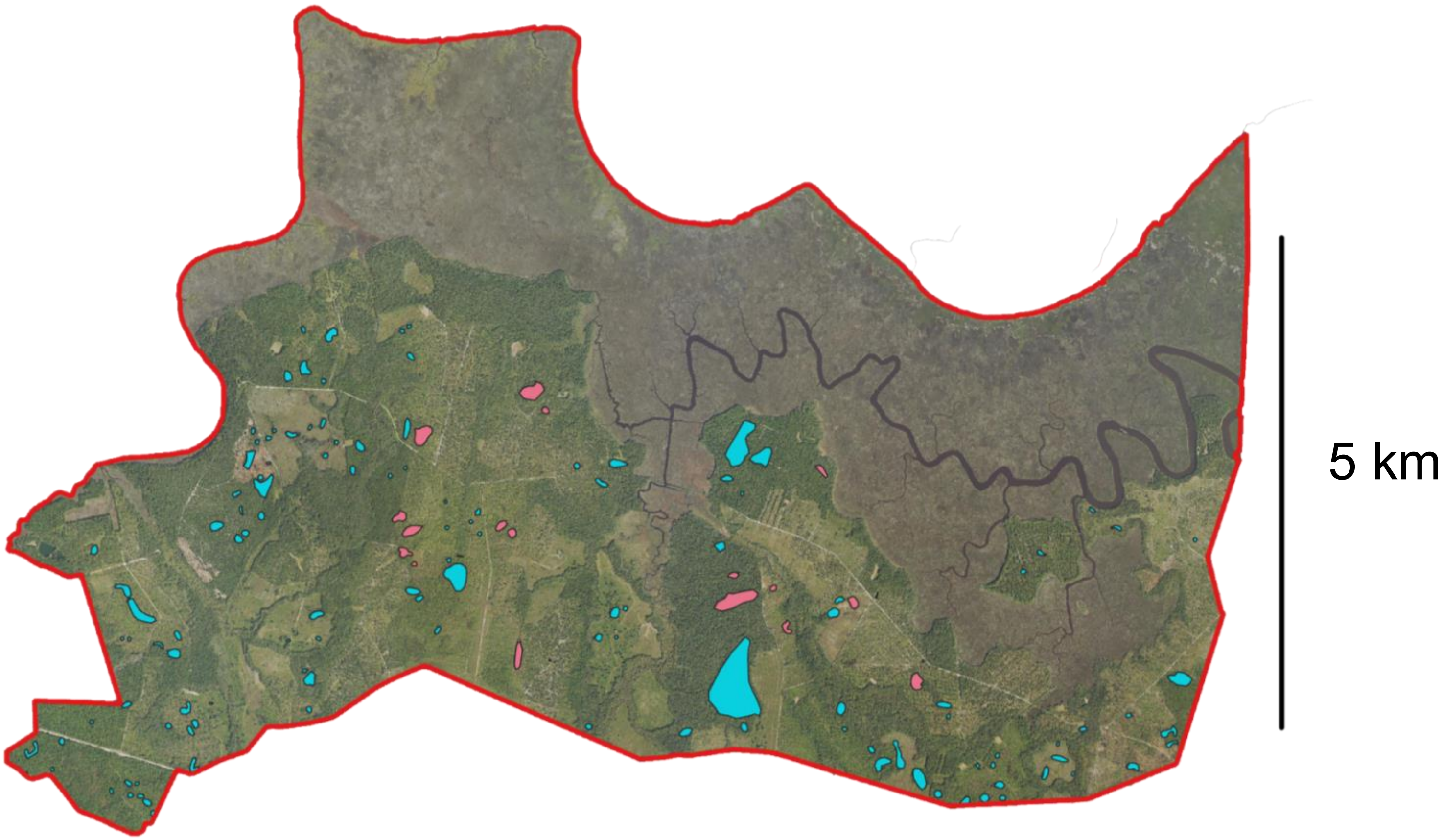

Figure 2.3. Map of Ceylon located in Camden County, Georgia, showing the 14 study wetlands sampled for Gopher Frogs, colored pink. Wetlands deemed unsuitable or unknown for Gopher Frogs and not included in the study are colored light blue.

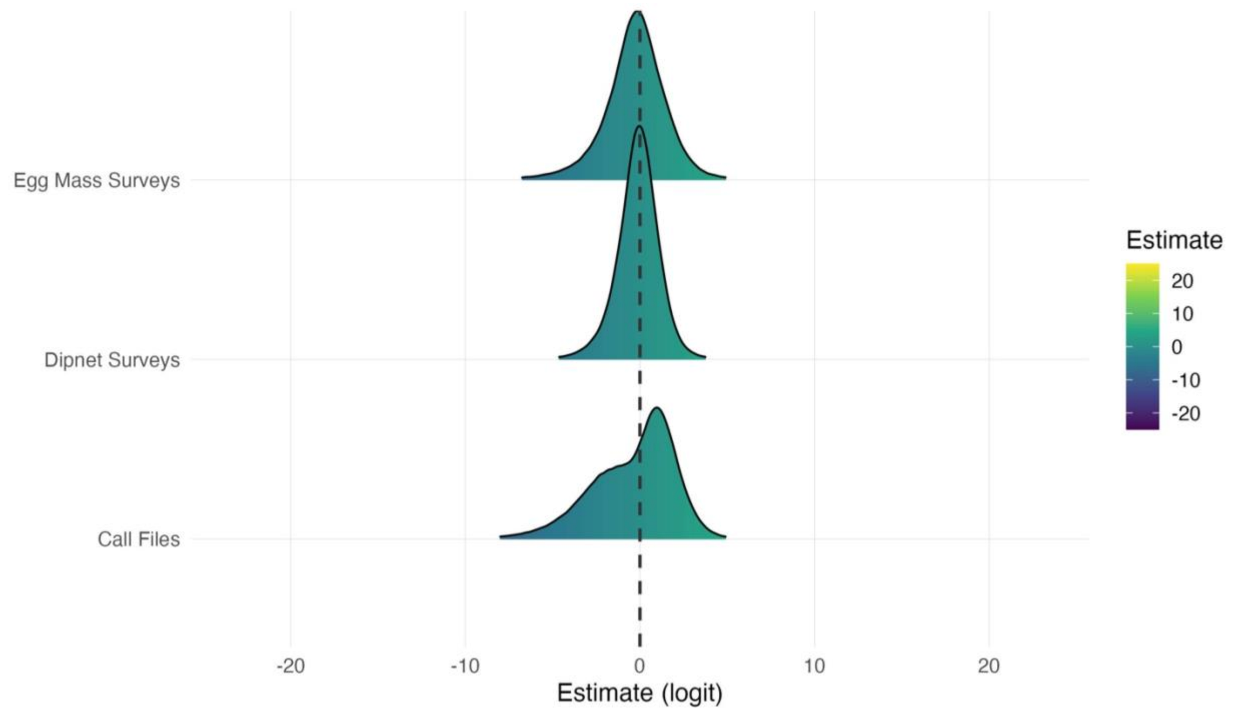

Figure 2.4. Posterior distribution of month as a random effect on detection for each sampling method (egg mass surveys, dipnet surveys, and call files) from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Estimates are on the logit scale.

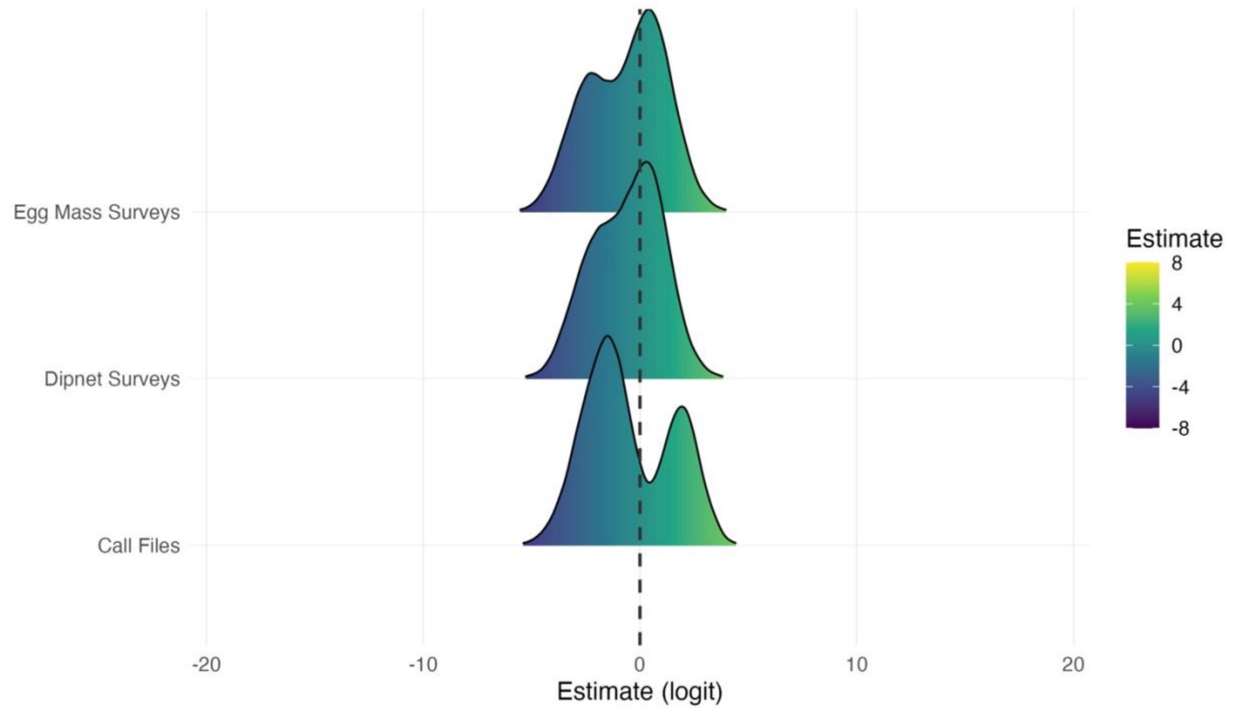

Figure 2.5. Posterior distribution of the effect of year on detection for each sampling method (egg mass surveys, dipnet surveys, and call files) from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Estimates are on the logit scale.

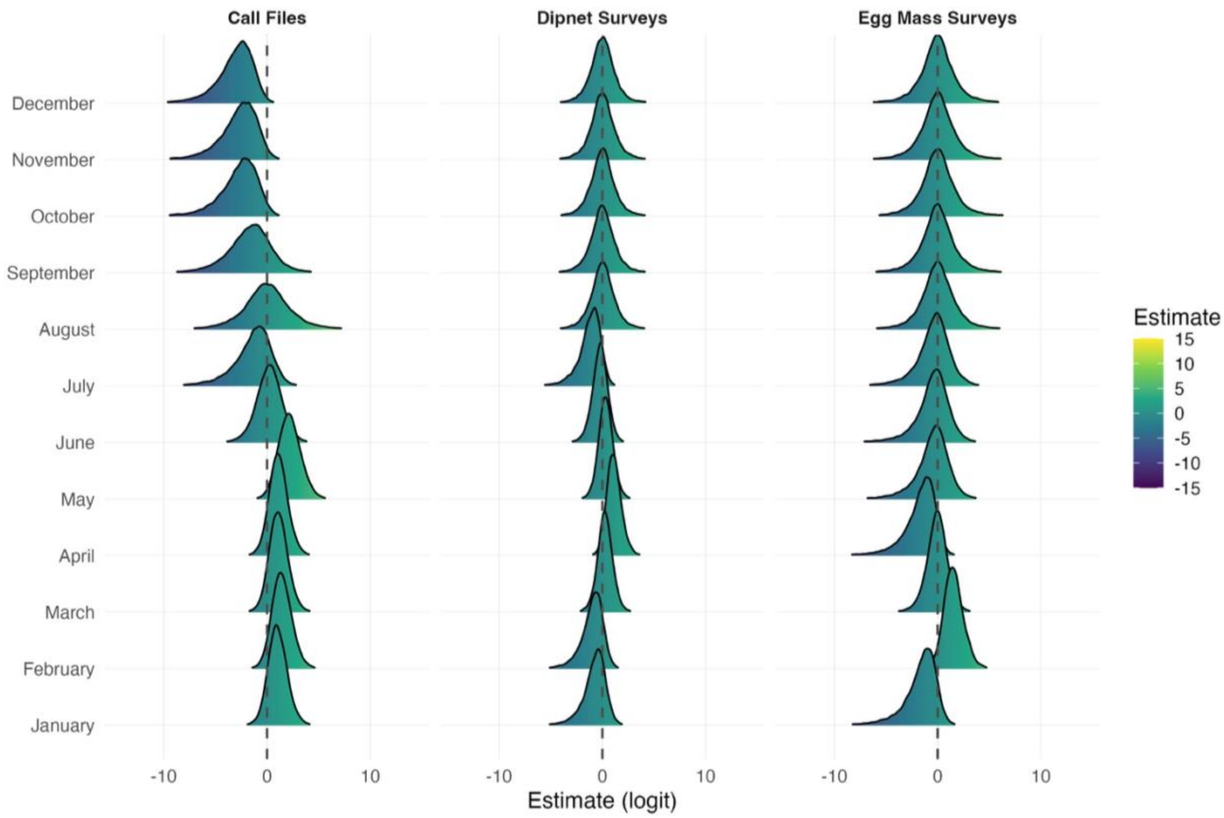

Figure 2.6. Posterior distribution of month as a random effect on detection for each sampling method (egg mass surveys, dipnet surveys, and call files) and month from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Estimates are on the logit scale.

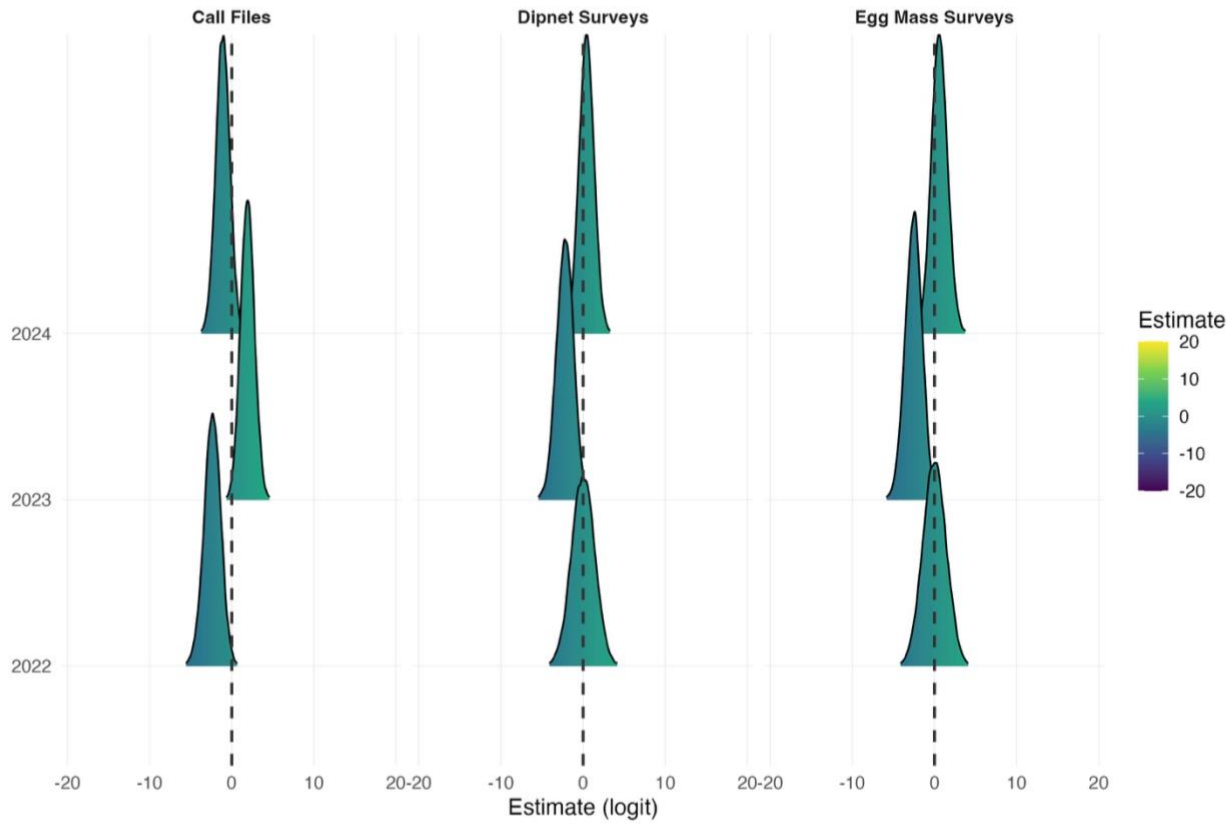

Figure 2.7. Posterior distribution of the effect of year on detection for each sampling method (egg mass surveys, dipnet surveys, and call files) and year (2022 – 2024) from the Integrated Bayesian Occupancy Model estimating Gopher Frog occupancy on Ceylon and Ichauway. Estimates are on the logit scale.

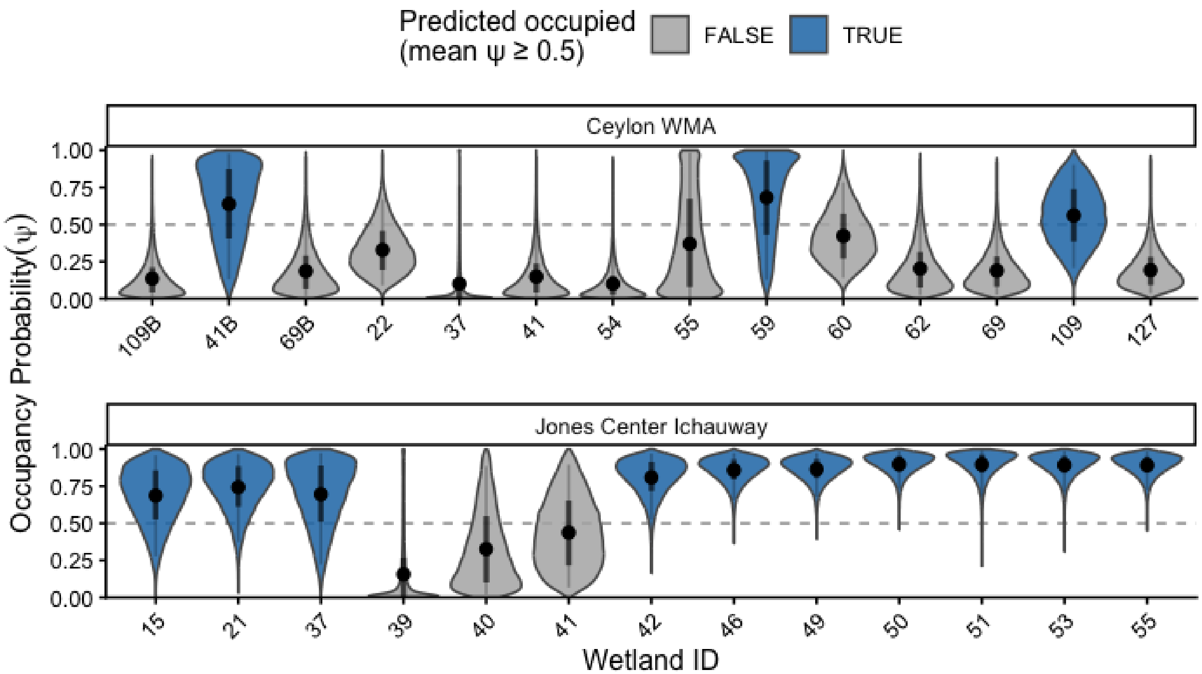

Figure 2.8. Predicted occupancy probability of Gopher Frogs from the Integrated Bayesian Occupancy Model by wetland at Ceylon and Ichauway. Points represent posterior mean ψ, with thick bars indicating 80% credible intervals and thin bars 95% credible intervals. The dashed line denotes occupancy probability of 0.5 with fill indicating if wetlands were classified as "predicted occupied" (overall posterior mean denotes occupancy probability ≥ 0.5).

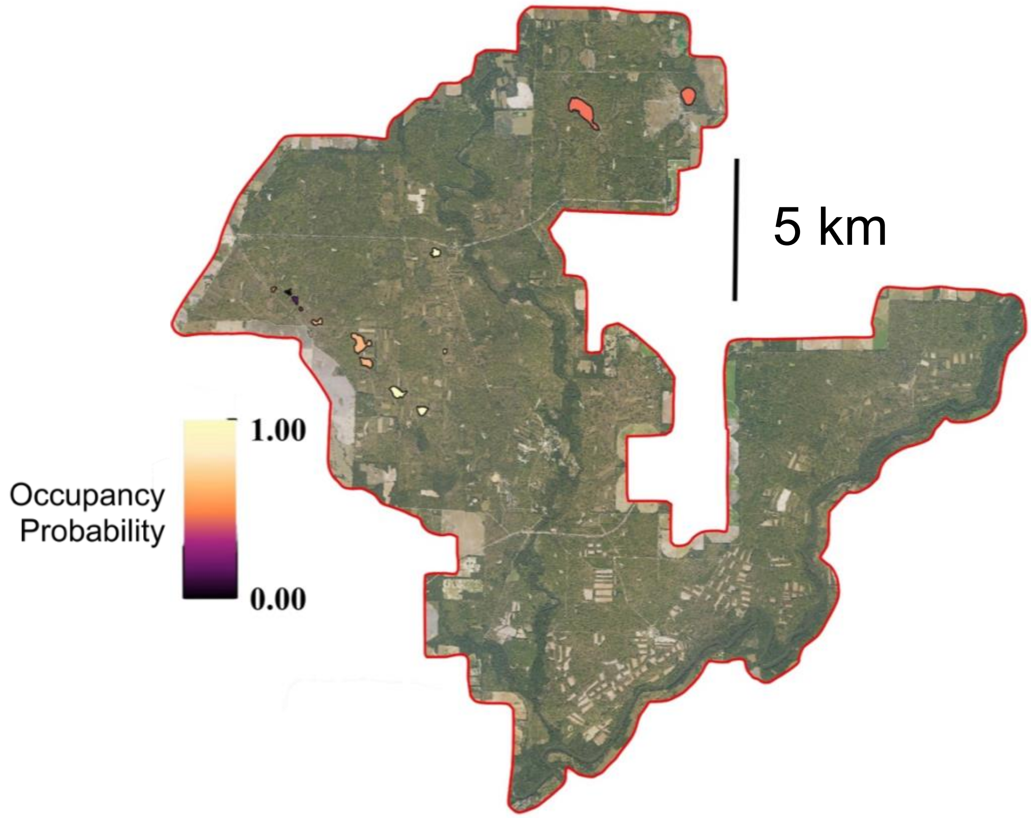

Figure 2.9. Map of Ichauway located in Baker County, Georgia with study wetlands colored by their predicted occupancy probability of Gopher Frogs from the Integrated Bayesian Occupancy Model. Black represents a predicted occupancy probability of zero while pale yellow represents a predicted occupancy probability of one.

Figure 2.10. Map of Ceylon located in Camden County, Georgia with study wetlands colored by their predicted occupancy probability of Gopher Frogs from the Integrated Bayesian Occupancy Model. Black represents a predicted occupancy probability of zero while pale yellow represents a predicted occupancy probability of one. The visual of the occupancy probability of borrow pits such as 41B may be disrupted by their small size.

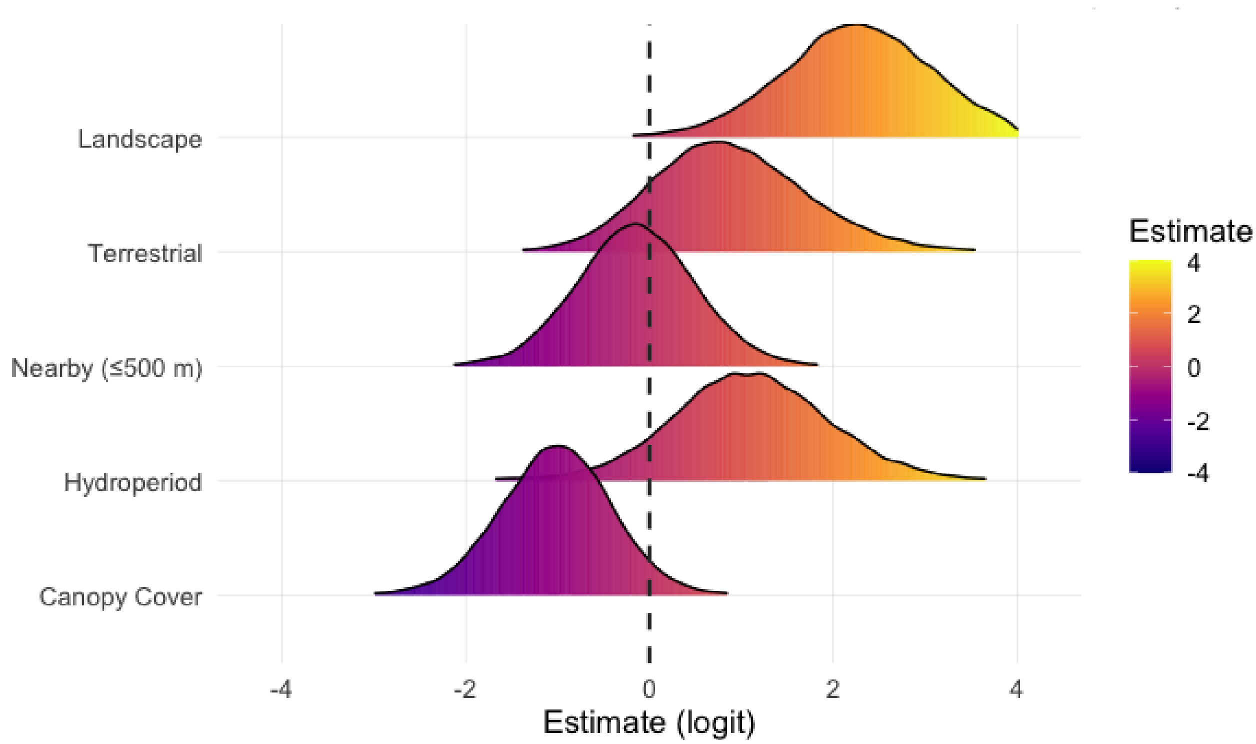

Figure 2.11. Posterior distribution of effect of covariates (landscape, terrestrial, the number of nearby wetlands, hydroperiod, and canopy cover) on Gopher Frog occupancy at Ceylon and Ichauway from the Integrated Bayesian Occupancy Model. Estimates are on the logit scale.

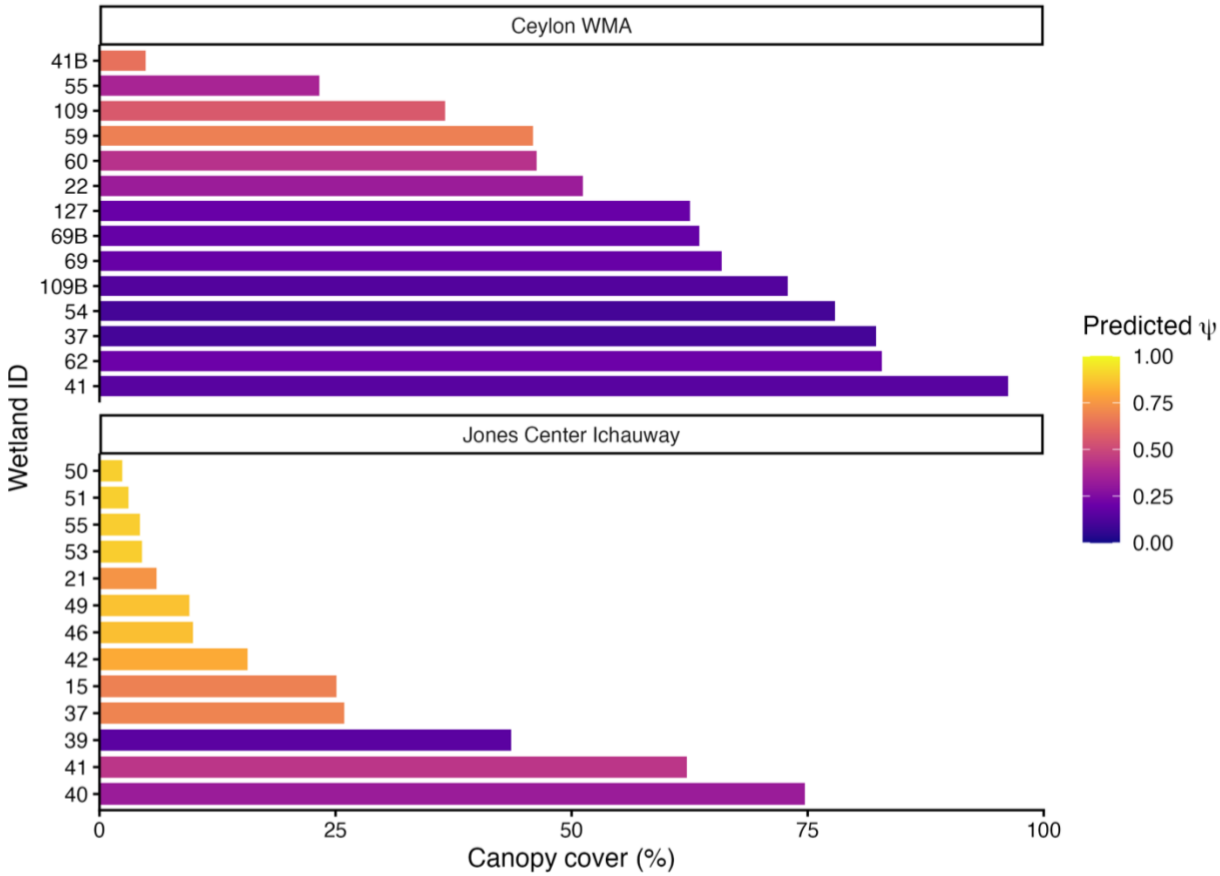

Figure 2.12. Percent canopy cover by wetland at Ceylon and Ichauway, calculated by digitizing tree canopy within each wetland in QGIS and dividing the canopied area by the total wetland area. Bar lengths represent percent canopy cover, and colors correspond to the mean predicted occupancy probability of Gopher Frogs from the Integrated Bayesian Occupancy Model.

CHAPTER 3

USING LANDSCAPE GENETICS TO ESTIMATE POPULATION STRUCTURE AND FUNCTIONAL CONNECTIVITY OF GOPHER FROGS (*RANA CAPITO*) IN TWO LANDSCAPES[2]

[2] Kerr, E.O., Shamblin, B.M., Bothwell, H.M., Samples, J.A., Smith, L.L., Maerz, J.C. To be submitted to a peer-reviewed journal.

Abstract

Anthropogenic threats like habitat loss and degradation disrupt functional connectivity, which determines population or metapopulation resilience within a landscape. Some management actions are aimed at increasing connectivity to improve demographic and genetic rescue among isolated populations, which requires knowledge of which landscape features facilitate or act as barriers to connectivity. Landscape genetics provides a framework for understanding functional connectivity by revealing patterns of gene flow in relation to landscape composition and structure. Gopher Frogs are a high priority species of greatest conservation need in all states within their range, and very little is known about what fine-scale landscape features impact Gopher Frog landscape ecology. We estimated genetic diversity and genetic structure for Gopher Frogs in two landscapes in Georgia currently characterized as supporting robust Gopher Frog populations. For the larger landscape which had more breeding sites and fewer areas of presumably unsuitable terrestrial matrix, we found evidence of 3 genetic clusters with spatial structure between the northeastern and southwestern portions of the property. These clusters were separated by distance, Ichawaynochaway Creek, and a major road. The limited structure and high heterozygosity within populations and across the landscape suggested high breeding site connectivity across the landscape; however, estimated allelic richness was low compared to published estimates for another large landscape with reported high connectivity. In contrast, the smaller landscape with more matrix habitat had high spatial genetic structure indicative of low functional connectivity. In addition, we found relatively low allelic richness and low heterozygosity consistent with historic bottlenecks and small effective population sizes. The low allelic richness in both landscapes leads us to hypothesize that Gopher Frog populations in both landscapes have experienced genetic bottlenecks, potentially due to repeated cycles of drought or

short hydroperiods. We also hypothesize that the low connectivity and low heterozygosity in the smaller landscape are the result of poor wetland vegetation condition supporting small population sizes or higher amounts of matrix limiting connections among populations. Our results are useful to ongoing management of both landscapes, because we have found evidence of low genetic diversity in two landscapes previously characterized as "robust" based on commonness of Gopher Frogs. We recommend that managers prioritize wetland restoration concurrent with ongoing terrestrial management and consider translocations to improve the genetic status of populations in both landscapes. Our results are also important because they demonstrate that distance between breeding sites is likely less important than local wetland features and the intervening terrestrial matrix in structuring Gopher Frog populations.

Introduction

Alterations to the landscape affect biotic population dynamics, because it is the composition and structure of landscapes that determine both habitat patch occupancy and the movement of individuals between patches. Landscapes are – by definition – heterogeneous (Turner & Gardner, 2015); composed of patches of suitable habitat embedded within a surrounding "matrix" of non-suitable habitat (Forman, 1995). The extent to which landscape composition and structure affect the movement of individuals between patches is referred to as functional connectivity (Cushman et al., 2015). In altered landscapes, restricted functional connectivity reduces gene flow (Cushman et al., 2015; Hanski, 2011). Reduced gene flow can increase local adaptation but most often leads to the loss of local genetic diversity (Dixo et al., 2009; Lino et al., 2019). The chronic winnowing of genetic diversity within isolated populations can diminish a population's ability to respond to environmental change and lead to inbreeding depression that can ultimately result in local extinction even when habitat quality is maintained

(Stockwell et al., 2003). For this reason, understanding how landscapes affect functional connectivity is important for identifying threats to populations and guiding effective habitat management actions to improve species persistence in managed landscapes (i.e., conserved properties with active management; Armstrong, 2005; Fahrig & Grez, 1996).

Functional connectivity is shaped by the distance between patches, the resistance of the matrix (i.e., the degree to which landscape features constrain movement), the dispersal ability of the organism, and the characteristics of habitat patches that influence source–sink dynamics (J. A. Crawford et al., 2016; Murphy et al., 2010; Taylor et al., 2006). The degree of functional connectivity across a landscape can vary among species because of differences in microhabitat requirements and movement ability [vagility]. Amphibians can be useful organisms for understanding functional connectivity within landscapes because of their frequent use of patchy, aquatic breeding habitats, high apparent natal philopatry and breeding site fidelity, and susceptibility to barriers or resistance to dispersal (Billerman et al., 2019; Cushman, 2006; Marsh & Trenham, 2001; M. A. Smith & Green, 2005). Many amphibian populations are comprised of subpopulations which may be represented by a single breeding site or clusters of proximate, potentially “source-sink” or “patchy-population” breeding sites. These populations are often isolated by larger distances between breeding sites and barriers to dispersal. Migrating adults and dispersing juveniles connect these subpopulations by colonizing or recolonizing breeding sites, but their movement is facilitated or restricted by the resistance of the terrestrial landscape (Cushman, 2006; Roznik et al., 2009; Semlitsch, 2008). Landscape resistance depends on land cover, geographic barriers like elevation, or anthropogenic features like large roads or expanses of high resistance matrix such as agriculture or urban land cover (Cushman, 2006; Gibbs, 1998; Murphy et al., 2010; Roznik et al., 2009). While landscape resistance shapes movement between patches, patch-level characteristics such as species density and habitat quality influence site occupancy and whether a site functions as a potential source or sink population (Murphy et al., 2010; Pulliam, 1988; Semlitsch, 2008; Semlitsch et al., 2015). Habitats that support small populations and are more vulnerable to stochastic loss of genetic diversity can become demographically isolated if they produce too few individuals to disperse to other populations (Baguette & Schtickzelle, 2003; Frankham, 1996; Jackson & Fahrig, 2016; Murphy et al., 2010). If conditions support low abundances across a metapopulation, insufficient recruitment can constrain dispersal across the landscape.

Landscape genetics provides a framework for understanding functional connectivity by revealing patterns of gene flow in relation to landscape composition and structure (J. A. Crawford et al., 2016; Murphy et al., 2010; Watts et al., 2015). For example, a landscape genetic study of Columbia spotted frogs (*Rana luteiventris*) found that gene flow decreased with greater distance and topographic complexity between sites and with the presence of predatory fish, and gene flow increased with higher site productivity and longer growing seasons (Murphy et al., 2010). Understanding functional connectivity of rare species can identify actions for conservation-dependent populations such as the optimum locations for breeding sites or habitat corridors or where to source and release translocated individuals to supplement or establish new populations (Cushman, 2006; Wendt et al., 2021). Thus, there is a clear need for studies of functional connectivity studies for amphibians, but opportunities for such studies can be limited for rare species if there are few landscapes that still support multiple populations connected through dispersal or metapopulation dynamics.

Gopher Frogs (*Rana capito*) are a conservation priority species endemic to the Southeastern Coastal Plain. They are tightly associated with the Longleaf pine (*Pinus palustris*) ecosystem that once covered most of the southeastern coastal plains of North America (Harrington et al., 2013). Gopher Frogs depend on isolated, seasonal wetlands with dense emergent herbaceous vegetation for breeding, and open, frequently burned pine uplands with abundant Gopher Tortoise (*Gopherus polyphemus*) burrows, small mammal burrows (Blihovde 2006), or stump holes (Roznik et al., 2009). Only approximately five percent of the longleaf pine ecosystem remains or has been restored (Harrington et al., 2013; Kirkman & Jack, 2017; McIntyre et al., 2018; Winger., 2022). Gopher Frog populations have declined extensively across the species' range except for peninsular Florida (Enge et al., 2023) likely due to habitat loss and degradation (i.e. land use changes and fire suppression) of longleaf pine uplands and breeding wetlands (Crawford et al., 2020; Enge et al., 2014), and other stressors (e.g. climate change; Binita et al., 2015; Crawford et al., 2022). Today, Gopher Frogs are listed as a Species of Greatest Conservation Need (SGCN) in all states within their range (NC, SC, GA, AL, and FL) and are currently under review for listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 2015). Gopher Frog life history and behavior suggest the species likely evolved for landscapes with high densities of isolated, seasonal wetlands (B. A. Crawford, Maerz, et al., 2022). Their dependence on seasonal wetlands likely means their populations relied on periodic breeding booms to persist and subpopulations likely experienced local extinctions and recolonization through mainland-island or metapopulation dynamics (B. A. Crawford, Farmer, et al., 2022). This is very different than most landscapes where Gopher Frogs are managed today.

It is widely presumed that Gopher Frogs are capable of relatively long-distance dispersal; however, little is actually known about how Gopher Frogs disperse through different landscape matrices. Studies of adult Gopher Frog movements during breeding migrations have shown that some individuals migrate over 4 km between terrestrial and breeding habitats; however, most individuals likely remain within 500 m of a breeding site (Humphries & Sisson, 2012; Marshall et al., 2023; L. L. Smith et al., 2021). Studies suggest a bias among juvenile Gopher Frogs first emigrating from their natal wetlands and migrating adult Gopher Frogs to move through more open canopy, pine-grassland habitat types with more abundant animal burrows (Neufeldt, 2004; Roznik & Johnson, 2009). Fire-suppressed or closed canopy systems may also present more resistance to movement by emigrating juvenile Gopher Frogs because of reduced refugia availability (Roznik et al., 2009). Studies also suggest that juvenile Gopher Frogs may move along small dirt roads (Roznik & Johnson, 2009; Ruppert, 2025). However, these studies are limited to breeding movements of adult Gopher Frogs and emigration of recently metamorphosed juvenile Gopher Frogs. To our knowledge, there is no documentation of dispersal movements of Gopher Frogs between populations.

In Georgia, most extant Gopher Frog populations are located on relatively small parcels of managed lands with only one to three known breeding wetlands and likely no functioning metapopulation structure (B. A. Crawford, Farmer, et al., 2022). Each of these populations is isolated from other populations by large distances across land developed for agriculture, silviculture, or other purposes. There are only three known landscapes in Georgia that are believed to currently support robust Gopher Frog metapopulations: Ceylon Wildlife Management Area and the adjacent Cabin Bluff conservation easement (hereafter Ceylon), Fort Stewart, and the Jones Center at Ichauway (hereafter Ichauway; J.C. Maerz personal communication, 2023). Ceylon is in southeast GA supports one the largest populations of Gopher Frogs on state-managed public lands with what we hypothesize may be four to nine distinct populations separated by high resistance Maritime forests and tidally influenced drains and creeks (Maerz et al., 2025; Maerz, 2022). Ichauway is in southwest GA and supports multiple Gopher Frog breeding sites that may compose three distinct populations separated by a highway, a large creek, and a matrix of land cover types including agriculture. The status of Gopher Frog populations across Fort Stewart is poorly understood because military operations make access and monitoring difficult. Therefore, Ceylon and Ichauway represent the only landscapes in Georgia where it is currently logistically feasible to study factors that affect Gopher Frog functional connectivity (Fig 3.1).

Ceylon and Ichauway provide a unique opportunity to examine connections among presumably distinct Gopher Frog breeding populations within landscapes with multiple breeding wetlands and different matrices of terrestrial habitat between wetlands. The landscapes could allow us to identify factors important to the persistence of Gopher Frog breeding populations and the natural and anthropogenic factors that facilitate or impede dispersal. Therefore, the objectives were to (1) evaluate Gopher Frog genetic structure within the two landscapes, (2) estimate genetic diversity within populations and genetic differentiation between populations, and (3) identify natural and anthropogenic landscape features that facilitate or act as barriers to dispersal and connectivity among Gopher Frog breeding sites.

Methods

Study Landscapes

Ichauway – The Jones Center at Ichauway is an 11,740-ha research site that focuses on natural resource management research, education, and conservation (*About Us - Jones Center*; Smith et al., 2006). Ichauway is located on the Dougherty Plain, in Baker County, Georgia. The site is dominated by a second-growth longleaf pine matrix with wiregrass (*Aristida stricta*) understory that is managed with bi-annual prescribed fire and currently supports 80–100 year old trees (*About Us - Jones Center*; Smith et al., 2006). Longleaf pine was harvested across most of the site in the 1920s and existing trees were naturally regenerated. Within the property, there are more than 90 seasonal wetlands (Fig. 2.2), Ichawaynochaway Creek, and the Flint River (*About Us - Jones Center*; Smith et al., 2006). Ichauway supports a very high diversity of flora and fauna including 31 species of amphibians and a large, stable gopher tortoise population (Smith et al., 2006). Ichauway also contains multiple known Gopher Frog breeding wetlands. However, these wetlands are separated by paved and dirt roads, a creek, large distances and some landcover types assumed to be unsuitable for Gopher Frogs including hardwood forests, wildlife food plots, and off-site large scale irrigated agricultural fields. Therefore, it is unknown if there are multiple, but isolated Gopher Frog populations or a single widely dispersed population on the property. Gopher Frog breeding has been monitored on site since 1994 with records of robust breeding years (2013, 15 wetlands) and poor breeding years (2018, 1 wetland) (L. Smith, personal communication). Since 2017 Georgia has undergone a multi-year drought (*Historical Data and Conditions | Drought.Gov*) resulting in the detection of Gopher Frog breeding in only three wetlands on the property and leaving the current state of Gopher Frog on the property uncertain (L. Smith, personal communication).

Ceylon – Ceylon is a 10,970-ha property that once held large areas of open longleaf pine savanna with a high density of isolated wetlands, dense areas of maritime hardwood forest, and tidal river marsh and salt marsh. For most of the 20th century, until the state opened the property as a public WMA in 2021, Ceylon was held privately and used primarily for timber and hunting. Landowners managed the landscape with prescribed fire and "low impact" timber harvest, which is credited with allowing the persistence of soils and sections of habitats in reasonably good condition (i.e. open canopy pine savanna with herbaceous ground cover). The landscape includes approximately 1,619 ha of longleaf–wiregrass habitat with trees up to 145 years old, dense maritime hardwood forests, tidal river marshes and salt marshes, and a network of seasonal wetlands (Lee, 2020; Fig 3.3). Nonetheless, many of the wetlands had become degraded from pine succession into the basins, pine forests surrounding wetlands were dense and likely contributed to shorter hydroperiods (Golladay et al., 2021), and several wetlands on the property were modified by ditching or digging pits in the basins to concentrate water and reduce wetland surface areas. Borrow pits distributed across the property now provide relatively permanent freshwater sources within a landscape otherwise dominated by ephemeral wetlands, tidal creeks, and forest drains. Surveys of the property for Gopher Frogs and other priority amphibians and reptiles have occurred episodically since 2008. The surveys found that the property contained thousands of Gopher Tortoises as well as populations of Gopher Frogs, and other priority species (Lee, 2020; M. Elliot, personal communication). Early surveys of the property revealed three known and one potential Gopher Frog breeding sites. Survey efforts since 2020 have expanded the known distribution of Gopher Frogs on Ceylon and called into question the assumption that there were only three potential breeding sites on the property (Maerz et al., 2025; Maerz, 2022; Marshall et al., 2023). One pattern that has emerged is that Gopher Frogs are likely distributed in distinct units associated with each sandhill and areas of dense tortoise burrows. These sandhills are separated from each other by low maritime forest that includes streams, some of which are tidally influenced. These maritime forest habitats or streams may create resistance for movement of Gopher Frogs on the property.

Sample Collection and Genotyping

At Ichauway and Ceylon, we collected genetic samples when an observer found any Gopher Frog egg mass, tadpole, juvenile, and adults during surveys from January to September

2024 (Kerr Chapter 2, Samples 2025). We employed multiple capture methods as Gopher Frogs are a rare and cryptic species. We conducted monthly dipnet surveys in 14 wetlands at Ceylon 12 wetlands at Ichauway, bi-weekly egg mass surveys at 12 wetlands at Ichauway, and scoped Gopher tortoise burrows surrounding historic Gopher Frog wetlands and used funnel traps to capture them. Samples sizes were uneven between sites and wetlands due to variation in sampling effort and habitat quality (Chapter 2). We were most successful with dipnet and egg mass surveys at Ichauway and funnel trapping juvenile frogs at Ceylon. We collected 5–10 eggs, adult toe clips, or tadpole tail clips and preserved all samples in 95% ethanol. Gopher Frogs were handled under Georgia DNR Permit #1000602439 and tissue sampling was approved by the University of Georgia Institutional Animal Care and Use Committee (IACUC Protocol #A2023 11-003-Y1-A0). We extracted the DNA with Qiagen DNeasy blood and tissue kits and genotyped samples at 10 microsatellite loci (Devitt et al., 2023; Nunziata et al., 2012) which were analyzed on a 3730xl DNA analyzer at the Cornell Institute of Biotechnology. We manually called alleles using GeneMapper™ (v 5.1) (Chatterji & Pachter, 2006) and discarded samples that were Southern leopard frogs based on failed loci (eg. Lica 25, Lica 41) and non-overlapping alleles (eg. Lica7, Lica 14, Lica 41). In addition, we used COLONY to detect full siblings and kept only one sibling in the final dataset. Including full siblings can lead to false population structure and biased population genetic parameters (Anderson & Dunham, 2008; Goldberg & Waits, 2010).

Genetic Structure, Diversity, and Differentiation

We used the program STRUCTURE (Pritchard et al., 2000) (v 2.3.4) to determine genetic structure of Gopher Frogs at Ceylon and Ichauway. STRUCTURE (Pritchard et al.,

2000) uses Bayesian clustering to probabilistically assign individuals to *K* populations based on their genotype. We analyzed Ceylon and Ichauway samples separately under the admixture model. We ran 11 replicate runs for each *K* from 1 to 5, each with a burn-in of 50,000 followed by 100,000 MCMC iterations. We determined the most supported *K* using STRUCTURESELECTOR (Li & Liu, 2018), a web-based software that reports the commonly used Ln Pr(X|K) (Pritchard & Wen) and ΔK (Evanno et al., 2005) statistics along with four newer statistics (Puechmaille, 2016) and runs CLUMPAK (Kopelman et al., 2015) for graphical representations. We calculated genetic diversity and differentiation separately for Ceylon and Ichauway both before and after STRUCTURE (Pritchard et al., 2000) analysis to understand genetic diversity and differentiation between populations defined by space and by genetic structure analysis. Before the genetic structure analyses, we assigned individuals to populations based on their location in the landscape. While this is best practice, our Ceylon samples were spread across the site, so a priori populations were more difficult to define than on Ichauway, where samples were clustered around wetlands. Thus, after the STRUCTURE (Pritchard et al., 2000) analyses, we assigned individuals to populations based on their highest membership coefficient (Q) and assigned individuals with $Q < 0.8$ as admixed. We calculated genetic diversity with observed (H_O), and expected (H_E) heterozygosity, allelic richness (A_r rarefied to the smallest sample size), and F_{IS} (inbreeding statistic) using the R package, *hierfstat* (Goudet, 2005). For global genetic differentiation, we calculated F_{st} (Goudet, 2005) and Hedrick's standardized G'_{st} (Hedrick, 2005) using the R package *mmod* (Winter, 2012) which standardized G_{st} to account for differences in heterozygosity between loci. In addition, we calculated Weir and Cockerham's (1984) (Weir & Cockerham, 1984) F_{IS} per locus and population using

Genepop (v 4.8.4) (Rousset, 2008), and tested deviations from Hardy–Weinberg equilibrium for each locus.

Landscape Resistance

To determine which landscape features influence gene flow, we used the *ResistanceGA* R package (Peterman, 2018) that applies a genetic algorithm (GA) to optimize categorical and continuous resistance surfaces based on genetic and effective distances. We ran *ResistanceGA* separately for Ceylon and Ichauway to assess fine-scale landscape effects. *ResistanceGA* requires sample locations, raster layers, and a genetic distance matrix. For Ceylon, we included one continuous raster (Gopher Tortoise soil suitability index) and two categorical layers (land cover and wetlands; Fig 3.3). We included the tortoise soil suitability layer to test the idea that sandhills and dense areas of tortoise burrows are driving the population structure of Gopher Frogs across Ceylon. The Gopher Tortoise soil suitability index was developed by NRCS (Natural Resources Conservation Service) at 10 m resolution. The land cover layer comprised 10 land cover types, while wetlands were treated as binary. To create the land cover layer in 2020, GADNR hand-digitized photos and LiDAR at about a 1m resolution and ground-truthed with site visits. We combined similar landcover features, reducing the original 26 classes to 10, because AIC within *ResistanceGA* penalizes models with many parameters. We included land cover as categorized as to understand the fine scale land cover effects like how maritime forest, tidal creeks, or sand roads influence structure on the site. We included wetlands to understand if they are used during dispersal but left them as binary as to not make the model overly complex. For Ichauway, we used the same continuous raster as Ceylon (Gopher Tortoise soil suitability index) and three categorical layers (land cover, wetlands, and roads; Fig 3.2). Land cover and roads contained multiple categories, 10 and three respectively, and wetlands were again binary. The categorical layers were delineated over time on Ichauway using a combination of digitizing aerial photography and ground classification at a resolution of about 20 m. Ichauway updated the land cover data in 2022 following Hurricane Michael and again we reduced the original 33 classes to 10. We included roads for Ichauway but not for Ceylon because Ceylon's land cover dataset already includes roads, and the property only has sandy, low-traffic roads. Ichauway, on the other hand, has a range of road types, from sandy low-traffic roads and firebreaks to paved highways, which likely influence Gopher Frog movement quite differently. Since the raster layers varied in resolution, we standardized them to the coarsest layer, 10 m for Ceylon and 20 m for Ichauway.

We calculated pairwise genetic distance, how genetically similar two individuals are to each other, using a multi-axis principal components analysis (PCA), which has been shown to perform better than other metrics when sample size and genetic structure are low (Shirk et al., 2017). We used the R package *adegnet* (Jombart, 2008) to create a multiple contingency table and run the PCA. We then calculated Euclidean distances based on the first 30 PCs between individuals and created the genetic distance matrix.

After we developed our inputs, we ran *ResistanceGA* for Ceylon and Ichauway. *ResistanceGA* randomly assigned resistance values to categorical layers. For continuous layers, we applied inverse monomolecular transformations, and *ResistanceGA* then optimized transformation parameters like the shape of the transformation and the maximum resistance value. Then *ResistanceGA* used Circuitscape (McRae et al., 2008), a program that uses circuit theory to calculate pairwise effective distances. Effective distances are measures of distance between sampling locations that account for the resistance of the intervening landscape.

ResistanceGA then fit a linear mixed effects model with Maximum Likelihood Population Effects (MLPE) to compare effective distances with pairwise genetic distances. Using log-likelihood as the objective function, the algorithm iteratively updates resistance values and transformation parameters to identify the combination that best explains genetic patterns. For this thesis we only ran the single surface model due to time constraints but will expand to include the multi surface model in the future.

Results

Genetic Structure, Diversity, and Differentiation

We genotyped 65 Gopher Frog samples from Ichauway, but after removing full siblings, we were left with 43 samples (see Table 3.1 for the spatial distribution of samples and Table 3.2 for the total number of samples by method and number of full-sibling samples). STRUCTURESELECTOR (Li & Liu, 2018) found that the most supported K was 4 (Fig. 3.4.A). However, we believe K = 3 is the most biologically realistic clustering for Ichauway. The fourth cluster in K = 4 does not include any individuals with assignment proportions greater than approximately 0.5 and does not align well with our knowledge of the landscape, suggesting this cluster represents model over-partitioning rather than a true genetic cluster. In contrast, K= 3 aligns well with landscape structure and composition and contains multiple individuals with Q greater than 0.8 for each cluster. Thus, the rest of the results and discussion will follow K= 3. We found evidence of spatial structure across the landscape with a high number of admixed individuals distributed throughout the property (Fig 3.5; Fig. 3.6.A). Among those admixed individuals, there was a tendency for higher proportions of cluster 1 and 2 assignments toward the northeastern portion of the landscape, although there was no clear spatial separation between these two clusters Fig 3.5; Fig. 3.6.A). Individuals with high proportions of cluster 3 were located primarily on the western portion of the property Fig 3.5; Fig. 3.6.A).

We quantified within- and among-population genetic variation for both a priori populations and genetically inferred clusters. For a priori populations, observed heterozygosity (H_O) ranged from 0.650 - 0.833, expected heterozygosity (H_E) from 0.654 - 0.784, inbreeding coefficient (F_{IS}) from -0.123 - 0.093, and allelic richness (A_r) from 1.653 - 1.783 (Table 3.3). We found similar estimates from genetically inferred clusters, with values ranging from H_O= 0.654 - 0.772, H_E = 0.661 - 0.795, and F_{IS} = -0.036 - 0.134, except for A_r, which ranged from 3.900 – 5.344 (Table 3.5). At the site scale, we found global measures of variation estimates from a priori populations with H_O= 0.720, H_E = 0.749, F_{ST} = 0.064, and G'_{ST} = 0.304 (Table 3.4) and similar estimates from genetically inferred clusters with H_O= 0.712, H_E = 0.727, F_{ST} = 0.073, and G'_{ST} = 0.354 (Table 3.6).

For Ceylon, we genotyped 53 Gopher Frog samples but were left with 38 samples after removing full siblings (see Table 3.1 for the spatial distribution of samples and Table 3.2 for the total number of samples by method and number of full-sibling samples). STRUCTURESELECTOR (Li & Liu, 2018) found that the most supported K was 3 (Fig. 3.4.B) with clear evidence of spatial structure (Fig 3.6.B; Fig. 3.7). We also found evidence suggesting a recent dispersal event from Population 1 to Population 2 (Fig. 3.6.B; Fig. 3.7). We found slightly lower genetic diversity estimates than those for Ichauway for both a priori populations and genetically inferred clusters. We found genetic diversity estimates from a priori populations with values ranging from H_O= 0.400 - 0.669, H_E = 0.597 - 0.701, F_{IS} = -0.003 – 0.038, and A_r= 1.400 - 1.699 (Table 3.3). We found similar estimates from genetically inferred clusters, with values ranging from H_O= 0.564 - 0.750, H_E = 0.588 - 0.694, and F_{IS} = -0.022 - 0.020, except for

A_r, that ranged from 2.320 – 2.510 and was slightly lower than that of Ichauway (Table 3.5). In addition, we found global differentiation that showed lower heterozygosity and stronger structure than Ichauway, with estimates from a priori populations with H_O= 0.566, H_E = 0.641, F_{ST} = 0.134, and G'_{ST} = 0.462 (Table 3.4) and similar estimates from genetically inferred clusters with H_O= 0.651, H_E = 0.644, F_{ST} = 0.107, and G'_{ST} = 0.398 (Table 3.6).

Landscape Resistance

ResistanceGA bootstrap analyses identified Euclidean distance followed by wetland as the most consistent predictors of gene flow on Ichauway. Distance was selected as the top model in 64% of bootstrap replicates, and wetland was selected in 36% of bootstrap replicates (Table 3.7). In contrast, on Ceylon, the wetland was the top model in 56% of bootstrap replicates, while Euclidean distance was top in 44% (Table 3.7). Model predictions indicated that on Ichauway, non-wetland areas were assigned higher resistance values (3) than wetlands (1; Table 3.8), whereas on Ceylon, wetlands had slightly higher resistance (2) than non-wetlands (1; Table 3.10). Tortoise soil suitability index ranked third at both sites but was not identified as the top model in any bootstrap replicate (Table 3.7; Table 3.9; Figure 3.8).

Discussion

We were successful in meeting our first two objectives to evaluate Gopher Frog genetic structure within the two landscapes and estimate genetic diversity within populations and genetic differentiation between populations. Ichauway had three estimated genetic clusters but a high number of admixed individuals suggesting spatial connectivity. However, there is spatial structure between the northeastern portion of the property, dominated by clusters one and two, and the western portion of the property, primarily composed of cluster three. These sections of the property are separated by about 4.5 km and two vicariant features: a major paved road and

Ichawaynochaway Creek. Previous studies on pond-breeding amphibians have found roads and creeks to act as barriers to movement depending on road traffic, species vagility, and swimming abilities (Carr & Fahrig, 2001; Cayuela et al., 2020; Cushman, 2006) and is further supported by our evidence of Gopher Frog genetic isolation by distance (IBD) across Ichauway. Within the northeastern portion of the property, however, there does not appear to be spatial distinction between clusters one and two, so we do not know what is driving the genetic clustering.

Despite this spatial structure, the lower values of F_{ST} and G'_{ST} at Ichauway reflected higher gene flow among populations despite the much larger landscape size and distances between populations (Holsinger & Weir, 2009). This was surprising given the size of the Ichauway landscape and the distance among breeding wetlands. Distances between Gopher Frog breeding wetlands on Ichauway range from 0.25 to 9.40 km. Despite some breeding wetlands being 2.2 km from the next closest known breeding wetland, most genetic clusters were represented across the landscape in small proportions and admixture was common. Our results are similar to an earlier study of Southern Leopard Frog (*Rana sphenocephala*) landscape genetics on Ichauway that found evidence of weak spatial genetic structure, mostly defined by a single outlier site (McKee et al., 2017). McKee et al. (2017) also found evidence that roads were negatively associated with genetic diversity. Together these studies suggest that conditions on Ichauway are conducive to maintaining high connectivity for amphibians with high vagility, though roads and Ichawaynochaway Creek may limit dispersal between the northeastern and western portions of the property. The conditions that are likely supporting high connectivity include a high density of geographically isolated wetlands and extensive suitable upland habitat with limited high resistance matrix.

We hypothesize that Gopher Frog populations at Ichauway have experienced a recent genetic bottleneck. A study on Gopher Frogs in Florida on a site with high connectivity found similar measures of genetic diversity as we observed on Ichauway except for allelic richness (Richter et al., 2009). Allelic richness was lower on Ichauway compared to the Florida landscape. Allelic richness is more sensitive to recent losses of genetic diversity than other metrics (Broquet et al., 2010; Nei et al., 1975; Spencer et al., 2000). We hypothesize that there has been a recent loss of genetic diversity on Ichauway due to recent frequent and prolonged droughts. Crawford et al. (2022) found Gopher Frog populations are resilient to periodic droughts (up to four years per decade), but if drought frequency increases, populations may face significant declines or local extinctions (Binita et al., 2015). Since 2007, Georgia has undergone several multi-year droughts in addition to non-drought years when wetland hydroperiods were still too short to support Gopher Frog breeding or larval development (*Historical Data and Conditions | Drought.Gov*). Since 2017, the Herpetology Lab at Ichauway detected regular Gopher Frog breeding at only three wetlands on the property (though we detected Gopher Frog breeding occurred at 10 wetlands during a very wet year in 2024, Kerr Chapter 2; Samples 2025).

Though a relatively smaller landscape, Ceylon had three genetic clusters that were clearly spatially distinct and likely represent relatively independent populations. We note that despite high sampling effort in the area around 109/109B, we were only able to find two frogs in that area. It is possible with more samples from the area around 109/109B and from other likely breeding sites near 59 (Kerr, Chapter 2), that this single population might be discriminated as two populations, one centered around wetlands 59, 60, 62, and 112 and another centered around 109/109B. However, the distances between the occupied and potentially suitable wetlands between 59 and 109B are all < 1.1 km, which is well within the documented migration distances of Gopher Frogs (Marshal et al. 2022). Overall, the population clusters on Ceylon appear to be driven by the high coverage of unsuitable habitat that separates areas with dense tortoise populations. Based on the observed genetic structuring, these areas of tortoise soils seem to function as islands or peninsulas of Gopher Frog habitat. In contrast, Ichauway has suitable tortoise soils and open pine–grassland across most of the landscape, which we expect supports high functional connectivity.

Like Ichauway, Ceylon had low levels of allelic richness compared to the Florida population (Richter et al., 2009); however, Ceylon also had lower heterozygosity locally (within populations) and at the landscape scale. Ceylon has also undergone several recent cycles of multi-year failure of wetlands to fill and hold water sufficient for Gopher Frog breeding, including no water in any wetlands between breeding events in 2020 to 2024. Furthermore, low allelic richness and low heterozygosity combined are consistent with smaller population sizes or lower functional connectivity. Within Ceylon, the lowest heterozygosity and allelic richness occurred within the population that encompassed wetlands 59, 109, and 109B. This result was unexpected, as this population is situated within a cluster of occupied and potentially suitable wetlands. In contrast, the population centered around wetland 41 and a nearby small borrow pit 41B had higher allelic richness and heterozygosity. Reduced diversity in the population around 59, 109, and 109B could be indicative of a smaller population size in that part of the landscape. As we noted previously, we only found two Gopher Frogs around 109/109B despite extensive sampling effort. Though the Gopher Frog populations at Ceylon had low allelic richness and heterozygosity, the F_{IS} was around 0, indicating there is no evidence of inbreeding or outbreeding depression at this time (Holsinger & Weir, 2009).

The evidence of low allelic richness among Gopher Frogs on Ichauway and Ceylon suggests populations on both landscapes have recently undergone bottlenecks. These apparent bottlenecks appear unrelated or only partially related to habitat conditions. A recent study found that metapopulations that function with periodic booms driven by resource availability, such as large rainfall events that fill wetlands followed by busts where wetlands do not fill, show variation in genetic diversity depending on fragmentation and gene flow (Hill et al., 2023). Metapopulations with a few large subpopulations and frequent gene flow tend to have lower allelic richness but higher heterozygosity than landscapes with many small, isolated subpopulations and infrequent gene flow (Hill et al., 2023). These genetic patterns are consistent with patterns we observed between our two landscapes and further support the inference that local population sizes and connectivity interact with stochastic events such as weather to affect patterns of genetic diversity. Moore and Mims (2024) and Meléndez-Cal-y-Mayor (2025) both report ongoing declines in allelic richness within amphibian metapopulations. Additional analyses could be conducted using programs such as BOTTLENECK (Cristescu et al., 2010; Piry et al., 1999), along with continued genetic sampling of the sites over time (i.e. every four to five years to capture multiple generations) to determine if there is ongoing genetic erosion in the Gopher Frog populations within these managed landscapes.

We were relatively unsuccessful in meeting our third objective of estimating which landscape features facilitate or act as barriers to dispersal. We found evidence for IBD on both Ichauway and Ceylon (Table 3.7). A recent study in North Carolina also found evidence of IBD within Gopher Frog populations, which they attributed to local breeding philopatry (Arbogast et al., 2022). A recent review of amphibian dispersal reported that IBD was present in 85% (63/74) of landscape genetic studies on pond breeding amphibians (Cayuela et al., 2020). We expected to see evidence that certain soils, landcover types, or roads had increased resistance; however, our results were inconsistent, and we are reluctant to trust these findings. The land cover layers for both sites contained 10 categorical levels, and AIC penalizes models with many parameters. Modeling landscapes with fewer land cover parameters might improve sensitivity to detecting land cover resistance. In addition, studies have found that using a higher number of markers (i.e. SNPs) increases the power of landscape genetic inferences compared to using a smaller number of loci, such as the 10 microsatellites used here (Landguth et al., 2012). We also believe that the difference in the estimated resistance of wetlands for Ichauway and Ceylon was most likely a result of sampling bias. Most samples at Ichauway were collected within wetlands, whereas most samples at Ceylon were collected in the surrounding terrestrial matrix (Table 3.11). Because *ResistanceGA* relates resistance distance to genetic distance, the distribution of sample locations influences which habitats are inferred to facilitate movement. As a result, only the data from Ceylon were likely well suited to estimating resistance of terrestrial land cover.

Considering only the results for Ceylon, wetland was the top model in 56% of bootstrap replicates and had higher resistance than non-wetland land cover (Table 3.10). Euclidean distance was the top model in 46% of replicates (Table 3.7). We did not expect this result. We expected that terrestrial conditions would have higher resistance. However, at Ceylon, wetland conditions appear to function as a larger barrier to functional connectivity than terrestrial conditions. The biological relationship to these two land cover categories is important when trying to interpret this result. Terrestrial habitats would reduce connectivity by impeding movement or reducing survival of individuals using that habitat. While it is possible that wetlands also affect Gopher Frogs by impeding movement or reducing survival, this is not biologically intuitive. We cannot think of a reason why moving through wetlands would reduce survival of Gopher Frogs. We note that numerous telemetry studies of Gopher Frogs have not reported migrating animals moving through or avoiding wetlands but rather moving through uplands (Hunt, 2019; Roznik et al., 2009; Ruppert, 2025; Thesing, 2023). We hypothesize that the resistance of wetlands occurs through local wetland effects on breeding success and population size. Many wetlands on Ceylon are currently unsuitable for Gopher Frogs (high pine or hardwood canopy cover, low emergent vegetation, Samples, 2025). These conditions create lower survival of Gopher Frog tadpoles and smaller juvenile frogs that should have lower terrestrial survival (Burrow and Maerz, 2021). If many of the wetlands on Ceylon currently function as population sinks, they would create demographic resistance to genetic connectivity. Poor wetland conditions would support smaller populations, leading to more limited opportunity for dispersal among suitable wetlands. This result does not mean that terrestrial resistance is not also important in currently limiting genetic connectivity on Ceylon. The high coverage of matrix may be discouraging the movement or limiting the survival of dispersing Gopher Frogs on, but at present, this effect may be secondary to the effect of wetland conditions. In the future, we plan to further test the effect of wetland conditions on gene flow by including wetlands with categorical levels of suitability for Gopher Frog breeding rather than treating wetlands as a binary feature.

Together, our results suggest that two of the largest landscapes still supporting Gopher Frog populations in Georgia show signs of reduced allelic richness consistent with recent bottlenecks. Gopher Frogs on Ceylon also show reduced levels of heterozygosity and increased isolation of populations consistent with small population sizes limited by breeding habitat quality and high amounts of unsuitable terrestrial matrix. Reduced allelic richness and heterozygosity can lower adaptive potential and increase extinction risk from stochastic events (Allentoft & O’Brien, 2010) and increase the potential for inbreeding and outbreeding depression, which can lead to an extinction vortex despite efforts to improve habitat quality (Hanski, 2011). The risk of inbreeding and associated reductions in fitness is likely higher at Ceylon. It would be beneficial for future research to test the relationship between genetic diversity and fitness in Gopher Frogs to determine the point at which reductions in genetic diversity will lead to measurable fitness consequences such as reduced embryonic or larval survival (Allentoft & O'Brien, 2010; Pröhl & Rodríguez, 2023). In addition, additional analyses such as calculating effective population size (N_e) would reveal how much of a population is governing evolutionary processes. Actions aimed at improving gene flow in landscapes like Ceylon should be a management consideration. Ceylon is undergoing aggressive upland restoration through thinning and prescribed fire. Our results suggest that, for the Gopher Frog populations on Ceylon, terrestrial management must be complemented with wetland restoration and the potential translocation of individuals among populations within the landscape. Improving the number and quality of wetlands at Ceylon should help buffer the populations against extinction by potentially increasing both population size and connectivity. In the meantime, we would recommend initially considering moving individuals among adjacent populations – potentially using larval captive rearing to produce large numbers of juveniles. Moving animals between adjacent populations would emulate likely dispersal patterns on the landscape. At Ichauway, we recommend continued wetland and upland management, along with long-term genetic monitoring and potential population supplementation to maintain heterozygosity and increase allelic richness. We emphasize that any of these actions should be planned carefully and incorporate adaptive management principles including an associated learning loop to know what genetic management actions are effective and improve future management decisions (Waples & Drake, 2004; Williams & Brown, 2012).

Our results raise concerns for many of the remaining Gopher Frog populations in Georgia that are restricted to smaller landscapes with only one or two breeding wetlands. Our study landscapes supported multiple breeding wetlands and Gopher Frogs were relatively common. However, both landscapes still showed signs of potentially recent genetic loss. If increasing drought cycles and shorter wetland hydroperiods are responsible for losses of allelic richness at Ichauway and Ceylon, then we would expect the populations in smaller landscapes with one or two wetlands to also have lost significant allelic richness and have very low levels of heterozygosity. We are aware of work by a collaborator that confirms low levels of allelic richness and heterozygosity and high estimates of inbreeding depression for some of these smaller Gopher Frog populations in Georgia (A. Krohn, personal communication). Awareness of this issue is particularly important given that some of those populations in smaller landscapes serve as donor populations for captive-rearing programs. Therefore, continued monitoring of genetic diversity and inbreeding depression and potential translocation efforts may be necessary for the populations in smaller landscapes. However, the deciding on the ideal source for translocations to these smaller landscapes and captive-rearing programs may be complicated by potentially distinct genetic lineages across the state of Georgia (Devitt et al., 2023) and the evidence of low levels of diversity we found at Ichauway and Ceylon.

Our study illustrates the potential value of conducting landscape genetic studies in multiple landscapes. Management decisions based on inferences from a single site may not apply to other locations with different landscape features (Wade et al., 2025). Incorporating data from multiple sites can reduce this uncertainty and improve the effectiveness of management decisions across the species' range. Limitations to the inferences we could make in this current study can be addressed through future research using other types of genetic data (e.g. SNPs).

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Tables and Figures

Table 3.1. Number of Gopher Frog samples collected at wetlands and terrestrial locations at Ceylon and Ichauway, with nearest wetland site indicated for terrestrial captures.

Site	Sample Location	Nearest Wetland	# of samples
Ceylon	Wetland	41B	13
Ceylon	Wetland	59	6
Ceylon	Terrestrial	37	8
Ceylon	Terrestrial	54/55	10
Ceylon	Terrestrial	41/41B	4
Ceylon	Terrestrial	59	10
Ceylon	Terrestrial	109/109B	2
Ichauway	Wetland	15	30
Ichauway	Wetland	21	11
Ichauway	Wetland	42	3
Ichauway	Wetland	49	1
Ichauway	Wetland	51	9
Ichauway	Wetland	53	8
Ichauway	Terrestrial	Holt Pond	3

Table 3.2. Number of Gopher Frog samples by sample type (egg mass, tail clip, or toe clip), shown as total samples and as the number of individual samples identified as full siblings by COLONY for both Ceylon and Ichauway.

Site	Summary Type	Egg Mass	Tail Clip (Larvae)	Toe Clip (Adult or Juvenile)
Ceylon	Total	2	8	43
Ceylon	Full sib	1	3	14
Ichauway	Total	5	31	3
Ichauway	Full sib	1	13	0

Table 3.3. Within population genetic variation for spatially defined populations on Ichauway and Ceylon. Values represent observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), and allelic richness rarefied to the smallest sample size (A_r).

Site	Population	H_O	H_E	F_{IS}	A_r
Ichauway	1	0.700	0.778	0.093	1.767
Ichauway	2	0.727	0.784	0.072	1.783
Ichauway	3	0.833	0.775	-0.123	1.787
Ichauway	4	0.683	0.700	0.003	1.695
Ichauway	5	0.650	0.654	-0.010	1.653
Ichauway	6	0.750	0.750	-0.033	1.750
Ichauway	7	0.700	Na	Na	1.700
Ceylon	1	0.669	0.701	0.038	1.699
Ceylon	2	0.614	0.624	0.003	1.624
Ceylon	3	0.580	0.597	-0.003	1.597
Ceylon	4	0.400	Na	Na	1.400

Table 3.4. Global genetic variation for spatially defined populations on Ichauway and Ceylon. Values represent observed heterozygosity (H_O), expected heterozygosity (H_E), fixation statistic (F_{ST}), and Hedrick's genetic differentiation statistic standardized (G'_{ST}).

Site	H_O	H_E	F_{ST}	G'_{ST}
Ichauway	0.720	0.739	0.064	0.304
Ceylon	0.566	0.641	0.134	0.462

Table 3.5. Within population genetic variation for genetically inferred clusters on Ichauway and Ceylon. Values represent observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), and allelic richness rarefied to the smallest sample size (A_r).

Site	Population	$\boldsymbol{H_O}$	$\boldsymbol{H_E}$	$\boldsymbol{F_{IS}}$	$\boldsymbol{A_r}$
Ichauway	1	0.772	0.745	-0.035	4.855
Ichauway	2	0.736	0.709	-0.036	4.315
Ichauway	3	0.654	0.661	-0.020	3.900
Ichauway	Admixed	0.686	0.795	0.134	5.344
Ceylon	1	0.625	0.617	-0.022	2.377
Ceylon	2	0.664	0.682	0.020	2.510
Ceylon	3	0.564	0.588	0.006	2.320
Ceylon	Admixed	0.750	0.694	-0.111	3.000

Table 3.6. Global genetic variation for genetically inferred clusters on Ichauway and Ceylon. Values represent observed heterozygosity (H_O), expected heterozygosity (H_E), fixation statistic (F_{ST}), and Hedrick's genetic differentiation statistic standardized (G'_{ST}).

Site	$\boldsymbol{H_O}$	$\boldsymbol{H_E}$	$\boldsymbol{F_{ST}}$	$\boldsymbol{G'_{ST}}$
Ichauway	0.712	0.727	0.073	0.354
Ceylon	0.651	0.644	0.107	0.398

Table 3.7. The best model results Gopher Frog (*Rana capito*) populations after bootstrapping in ResistanceGA for Ichauway and Ceylon. Values represent the surface type, number of parameters (k, equal to the number of categories plus one), average log-likelihood (LL), average Akaike Information Criterion (AIC and AICc), the difference from the best model (Delta AICc), the marginal R^2 (R^2_m), root mean square error (RMSE), and the percentage of bootstrap replicates in which each surface was selected as the top model. R^2_m indicates how much of the variation in genetic distance is explained by the fixed effects, and RMSE represents the average deviation between the model-predicted resistance distances and the observed genetic distances.

Site	Surface	k	LL	AIC	AICc	Delta AICc	R2m	RMSE	Top
Ichauway	Euclidean distance	2	-334.818	673.636	674.267	0.000	0.116	0.833	63
Ichauway	Wetlands	3	-333.967	673.933	675.267	1.000	0.151	0.830	37
Ichauway	Soil	4	-334.819	677.638	679.990	5.723	0.116	0.833	0
Ichauway	Roads	5	-334.459	678.918	682.668	8.401	0.127	0.833	0
Ichauway	Landcover	12	-333.272	690.544	725.211	50.944	0.146	0.828	0
Ichauway	Stacked (all layers)	21	-333.884	709.768	1633.768	959.501	0.139	0.830	0
Ceylon	Wetlands	3	-311.379	628.758	630.170	0.000	0.258	0.852	56
Ceylon	Euclidean distance	2	-312.787	629.573	630.240	0.070	0.207	0.855	44
Ceylon	Soil	4	-311.271	630.541	633.041	2.871	0.220	0.848	0
Ceylon	Landcover	12	-307.026	638.053	677.053	46.883	0.292	0.831	0
Ceylon	Stacked (all layers)	17	-309.431	652.861	856.861	226.691	0.252	0.842	0

Table 3.8. Resistance values assigned to each categorical surface, land cover, road, and wetland, categories from the ResistanceGA on Ichauway. Values represent the surface type, feature name, and the resistance values assigned to that feature using Circuitscape. The highest resistance value possible for Ichauway was 3.

Surface	Feature Name	Resistance Value
Landcover	Agricultural/Opening	3.000
Landcover	Conifer Pine	1.517
Landcover	Hardwood Mix	1.000
Landcover	Longleaf/And/Hardwood	1.003
Landcover	Nonpine Conifer	1.005
Landcover	Pond	1.001
Landcover	River	2.986
Landcover	Shrub/Scrub	3.000
Landcover	Stream/Creek	1.301
Landcover	Urban/Built-Up	2.868
Roads	Firebreak	1.023
Roads	Road	2.608
Roads	Sandy Road	3.000
Wetlands	Wetland	1
Wetlands	Non- Wetland	3

Table 3.9. Results from the ResistanceGA optimization of the continuous surface, the tortoise soil suitability index, on Ichauway and Ceylon for Gopher Frogs. We applied a reverse monomolecular transformation, and the model found that resistance decreased as soil suitability increased.

Site	Surface	Transformation	Shape	Maximum
Ichauway	Tortoise Soil Suitability	Reverse Monomolecular	2.955	0.001
Ceylon	Tortoise Soil Suitability	Reverse Monomolecular	8.402	1

Table 3.10. Resistance values for Gopher Frogs assigned to each categorical surface, land cover and wetland, feature from the ResistanceGA optimization on Ceylon. Values represent the surface type, feature name, and the resistance values assigned to that feature using Circuitscape. The highest resistance value possible for Ceylon was 2.

Surface	Feature Name	Resistance Value
Landcover	Atlantic Coastal Plain Upland Longleaf Pine Woodland	1.988
Landcover	Drain	1.992
Landcover	Estuarine water & Tidal Wooded swamp	1.997
Landcover	Maritime	1.927
Landcover	Open Field	1.401
Landcover	Open Water & Pondshore	1.022
Landcover	Pine Plantation	1.000
Landcover	Southern Atlantic Coastal Plain Wet Pine Savanna and Flatwoods	1.012
Landcover	Successional	1.897
Landcover	Transportation	1.018
Wetlands	Wetland	2
Wetlands	Non- Wetland	1

Table 3.11. Habitat type of Gopher Frog sample locations on Ceylon and Ichauway. Values include the percentage of samples collected in wetlands and in the upland matrix. Because ResistanceGA analyzes pairwise distances, the table also shows the percentage of sample pairs where both samples were collected in the matrix, both in wetlands, and one in each habitat type.

Site	% of Samples Taken in Wetlands	% of Samples Taken in Upland Matrix	% Matrix-Matrix Pairs	% Matrix-Wetland Pairs	% Wetland-Wetland Pairs
Ceylon	14.3	85.7	73.0	25.4	1.6
Ichauway	83.3	16.7	2.3	28.7	69

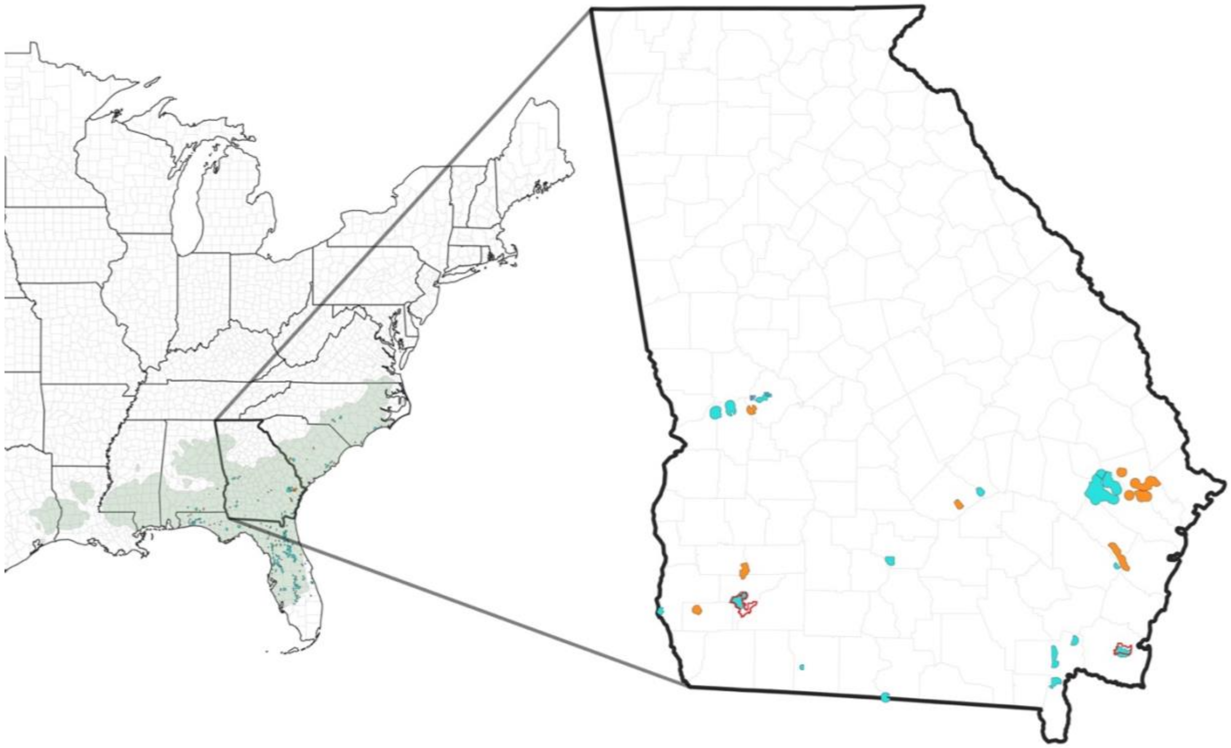

Figure 3.1. Map of Eastern US with light green shading representing the historic range of longleaf pine. Georgia, USA is emphasized and shows locations of Gopher Frog populations. Blue polygons represent known or predicted extant populations, while orange polygons indicate populations predicted to be extinct (Crawford & Maerz, 2021). Study sites, Ichauway in Baker County and Ceylon WMA in Camden County, are highlighted in red.

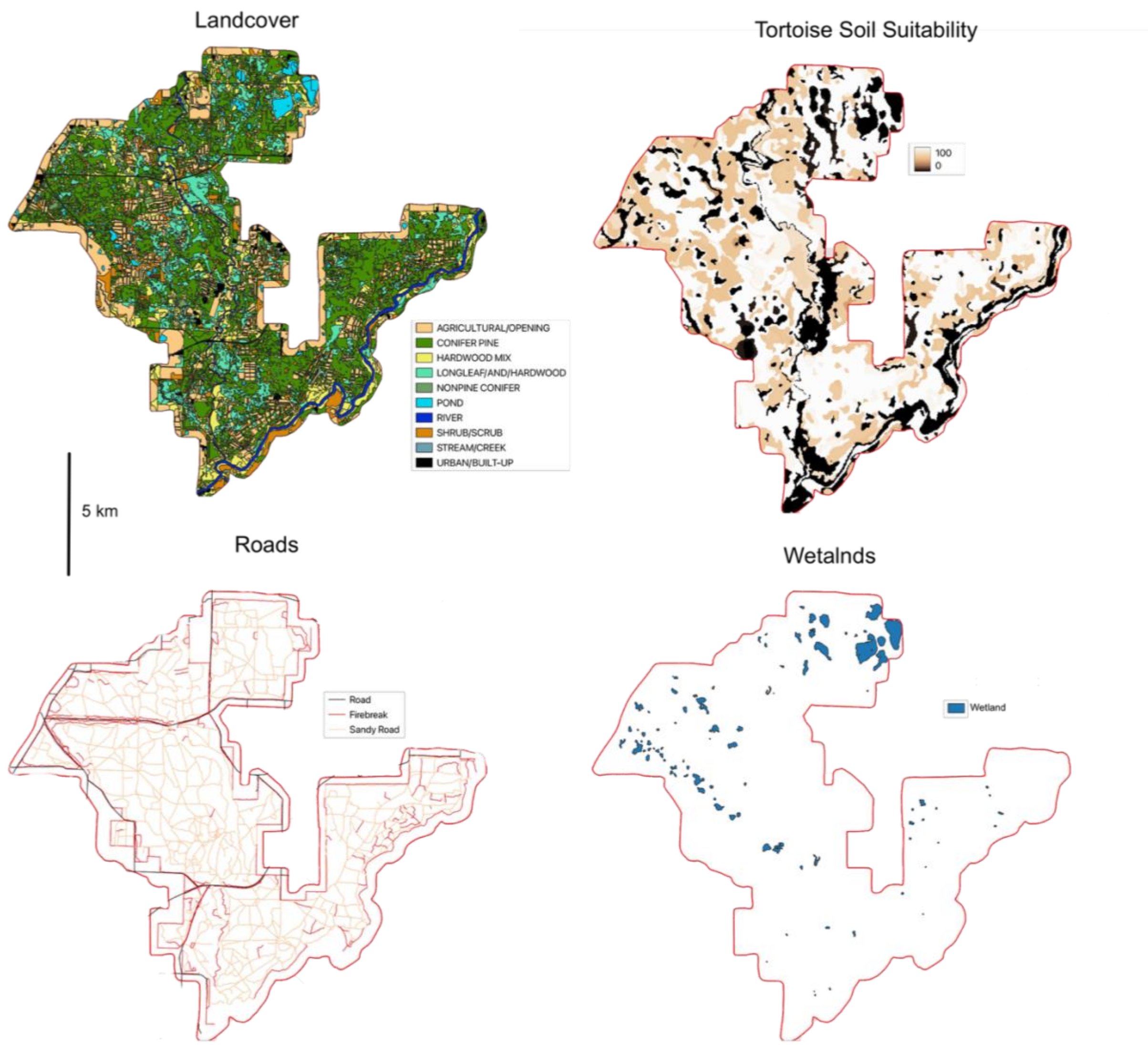

Figure 3.2. ResistaneGA raster layer inputs for Ichauway. We included one continuous raster (Gopher Tortoise soil suitability) and three categorical layers (land cover with 12 levels, roads with 3 levels and wetlands as binary).

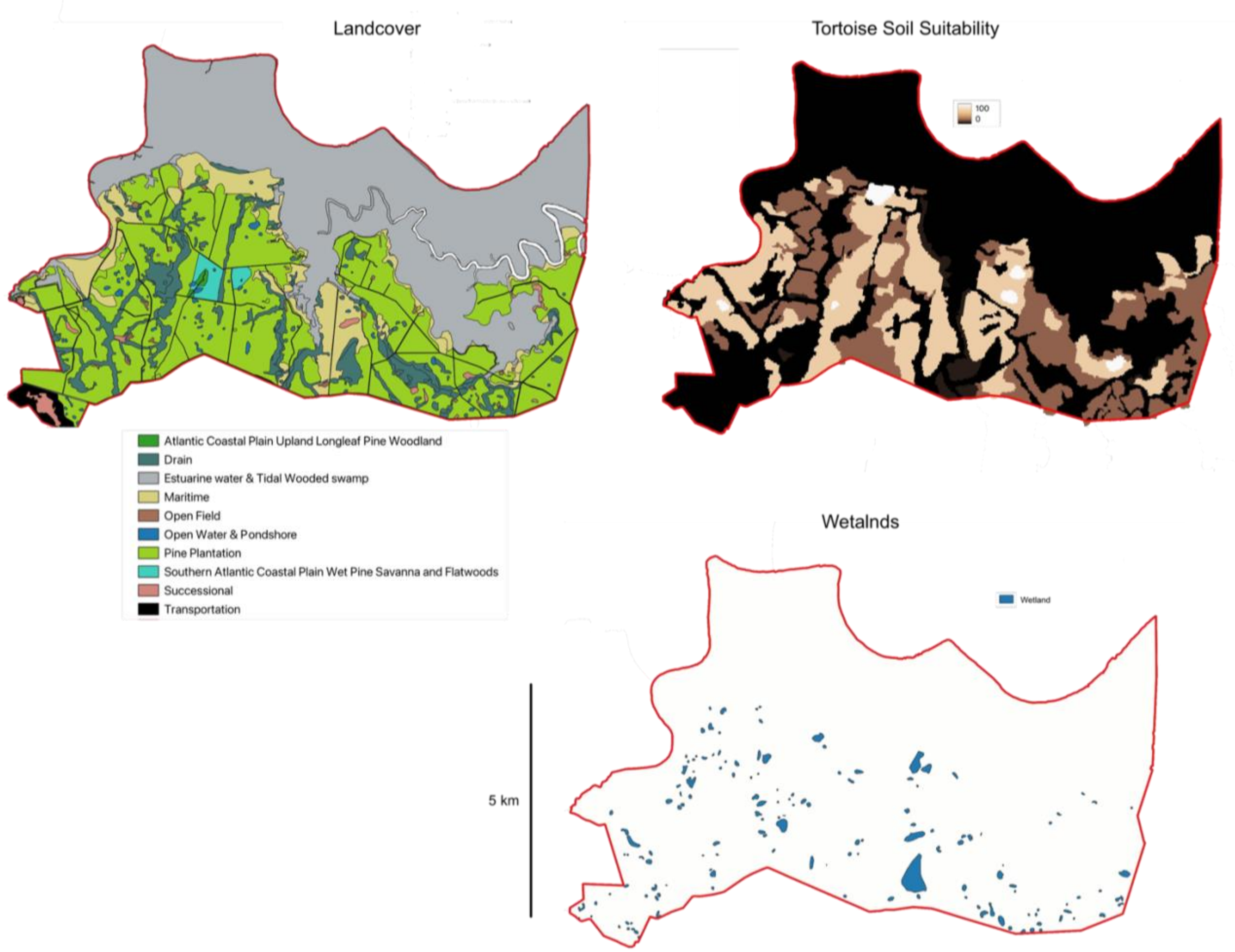

Figure 3.3. ResistaneGA raster layer inputs for Ceylon. We included one continuous raster (Gopher Tortoise soil suitability) and two categorical layers (land cover with 10 levels and wetlands as binary)

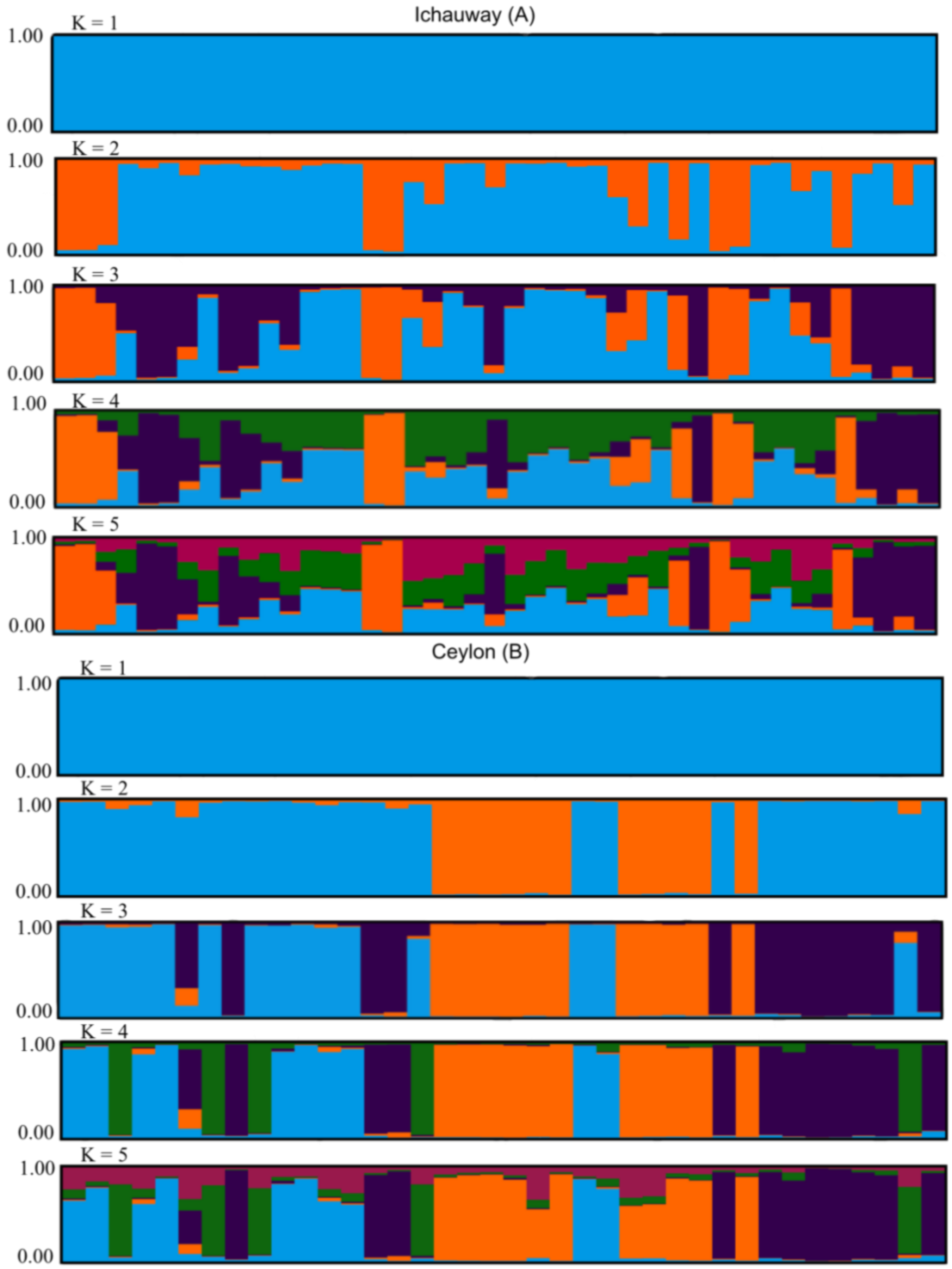

Figure 3.4. CLUMPAK structure plots showing genetic clusters of Gopher Frogs K 1- 5 identified by Structure Selector for Ichauway and Ceylon. Each vertical bar represents an individual, and the colors indicate the proportion of their genetic ancestry from each cluster. Structure Selector identified K = 4 as the most supported value for Ichauway (A) and K = 3 for Ceylon (B). However, K = 3 is likely the most biologically supported cluster for Ichauway.

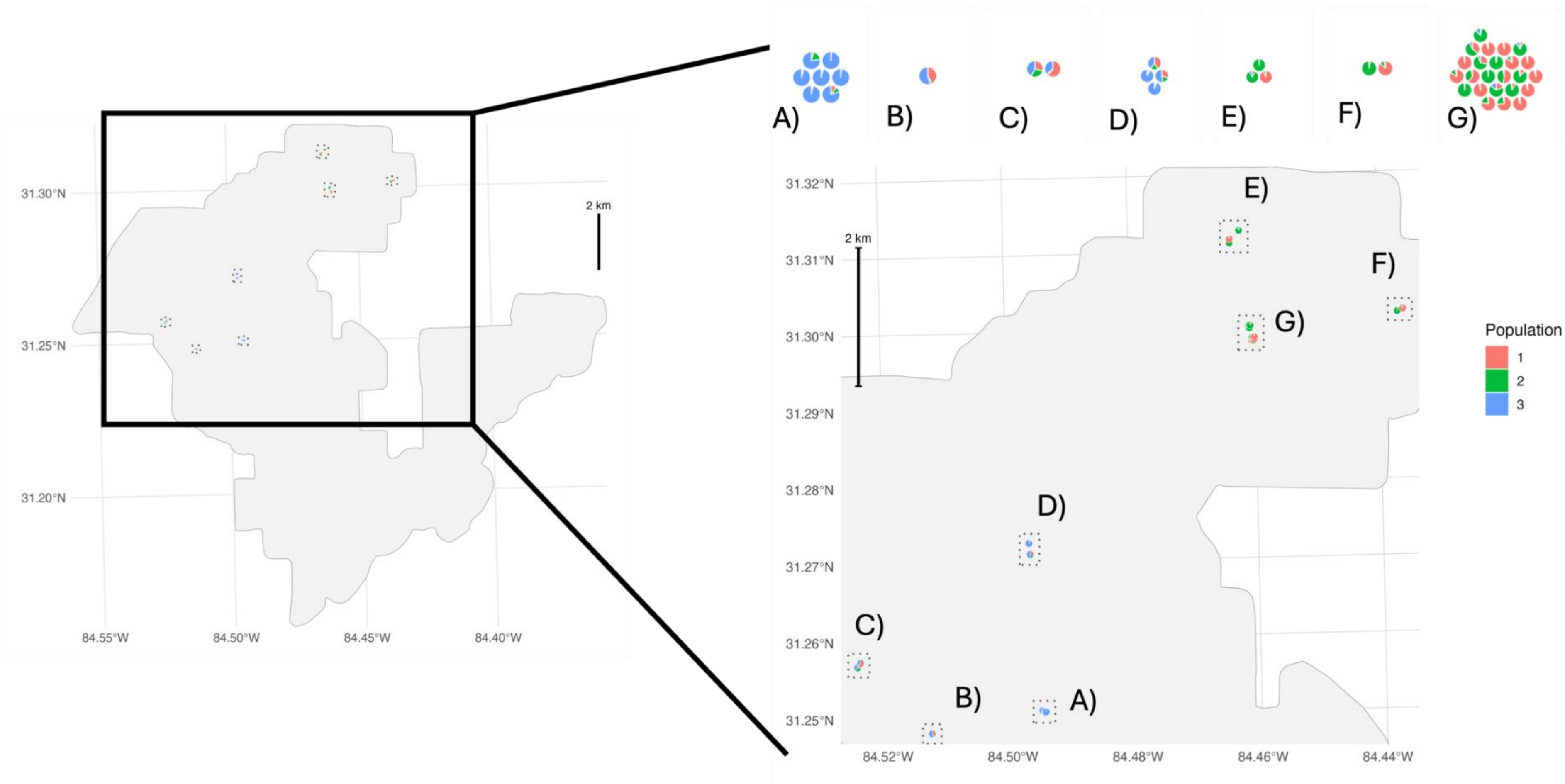

Figure 3.5. Map of Ichauway with pies representing Gopher Frog individual assignment probabilities based on STRUCTURE analysis at K= 3. Each pie represents an individual frog, with the proportion of each color corresponding to membership in one of the genetic clusters.

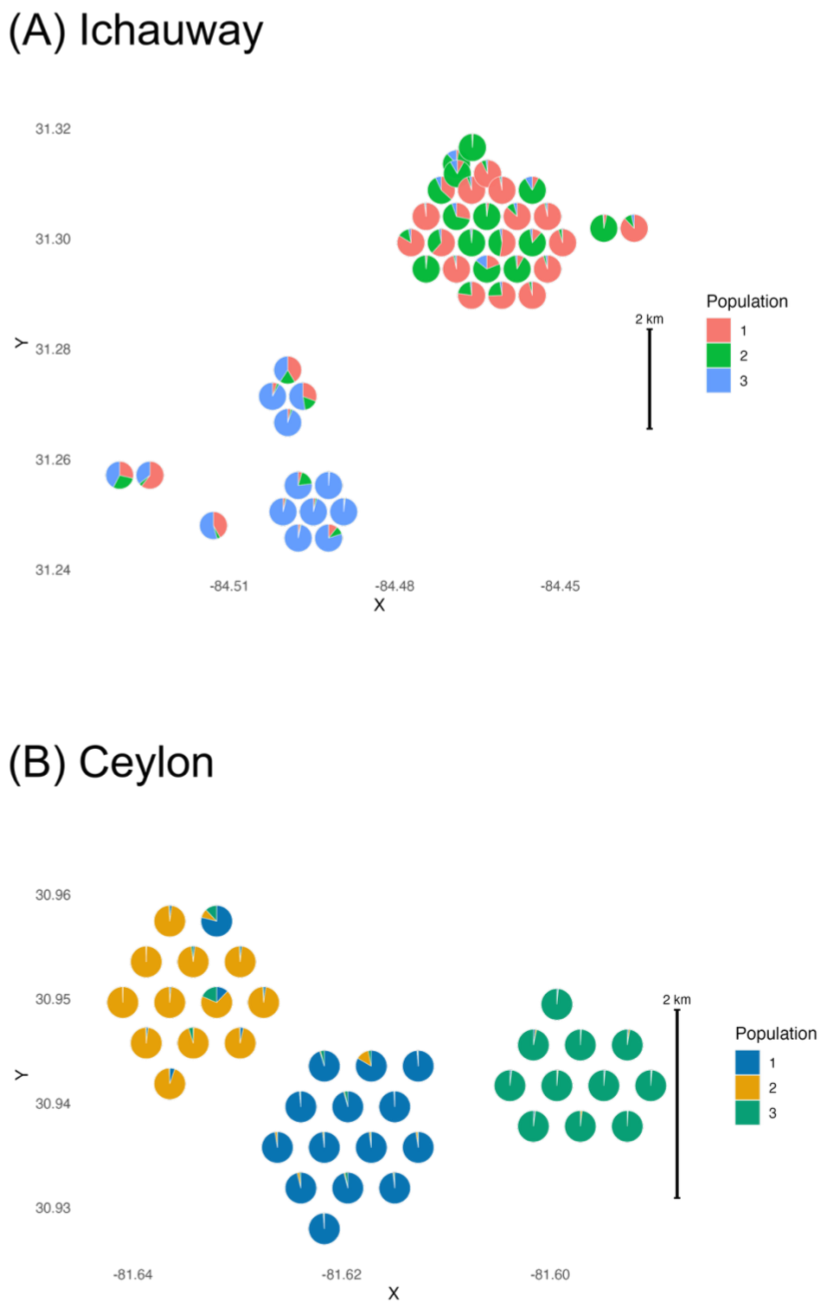

Figure 3.6. Individual assignment probabilities at Ichauway (A) and Ceylon (B) based on STRUCTURE analysis at K = 3 for both properties. Each pie represents an individual frog, with the proportion of each color corresponding to membership in one of the genetic clusters. Pies are positioned in general space but spread out so there is no overlap.

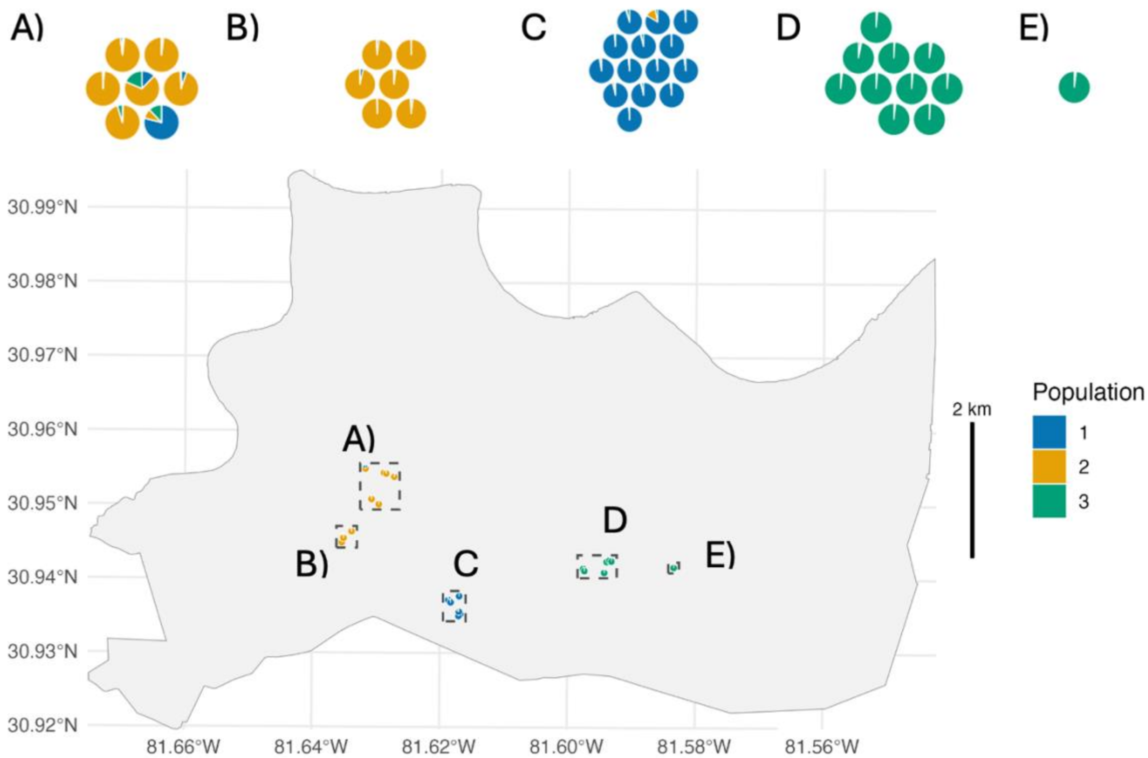

Figure 3.7. Map of Ceylon with pies representing Gopher Frog idividual assignment probabilities based on STRUCTURE analysis at K= 3. Each pie represents an individual frog, with the proportion of each color corresponding to membership in one of the genetic clusters.

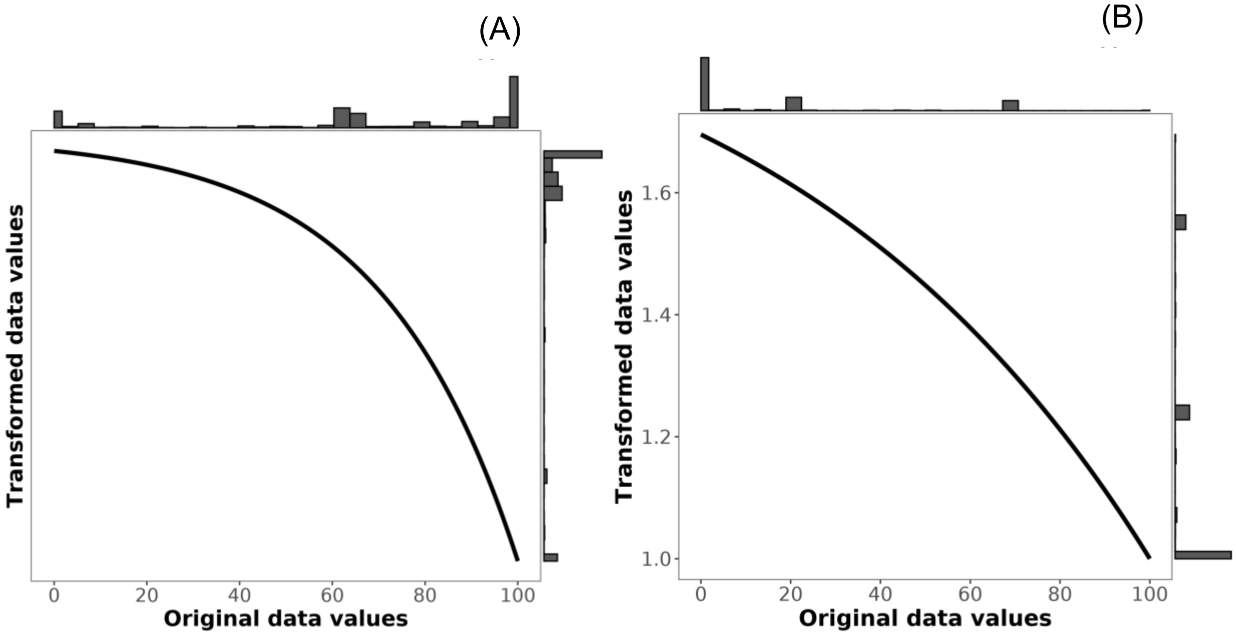

Figure 3.8. Results from the ResistanceGA optimization of the continuous surface, the tortoise soil suitability index, on Ichauway (A) and Ceylon (B) for Gopher Frogs. We applied a reverse monomolecular transformation, and the model found that resistance decreased as soil suitability increased.

CHAPTER 4

SIMULATING THE INFLUENCE OF HABITAT CONDITIONS ON A GOPHER FROG (*RANA CAPITO*) METAPOPULATION USING AN INDIVIDUAL-BASED MODEL[3]

[3] Kerr, E.O., Maerz, J.C. To be submitted to a peer-reviewed journal.

Abstract

The composition and structure of landscapes drive population dynamics by determining both patch occupancy and the movement of individuals between patches. There is a great need to understand these processes in rare or threatened species to inform strategies that enhance their persistence within managed landscapes. In Georgia, Gopher Frog (*Rana capito*) populations now exist on relatively small, isolated landscapes with only one or two breeding wetlands. As a result, little is known about how landscapes affect Gopher Frog metapopulation dynamics. We used an Individual-Based Model (IBM) to simulate how terrestrial landscape and wetland features influence the patterns of breeding site occupancy and genetic structure of Gopher Frog populations on one of the few remaining landscapes that support multiple breeding wetlands in Georgia. We ran a total of 45 simulations, including 15 runs for each of two canopy cover scenarios and 30 runs for different landscape resistance scenarios: 10 varying maritime forest resistance, 10 varying forest drain resistance, and 10 varying planted pine forest resistance. Each simulation was run for 15 years. Our simulations indicate that canopy cover in wetlands is a stronger driver of wetland occupancy than the influence of upland landscape resistance on potential migrants. In addition, we found evidence that Gopher Frog "metapopulations" are functioning with mainland-island or source-sink dynamics where one or more breeding sites act as sources for the colonization of nearby wetlands. This IBM model can be used to aid management agency decisions to increase the distribution and resilience of Gopher Frogs on this and other landscapes in Georgia.

Introduction

Understanding metapopulation processes and how they are affected by landscape alteration is important to effectively manage population or species' persistence. Landscapes are – by definition – heterogeneous (Turner & Gardner, 2015); composed of patches of suitable habitat embedded within a surrounding "matrix" of non-suitable habitat (Forman, 1995). The composition and structure of the landscape drive population dynamics by determining both patch occupancy and the movement of individuals between patches, referred to as functional connectivity (Cushman et al., 2015). Functional connectivity is shaped by the distance between patches, the resistance of the matrix, the dispersal ability of the organism, and the characteristics of habitat patches that influence local source–sink dynamics (J. A. Crawford et al., 2016; Murphy et al., 2010; Taylor et al., 2006). Within each patch, local population dynamics are governed by demographic processes, such as birth and death rates which vary spatially with habitat patch quality (Pulliam, 1988). These dynamics form some habitat patches that consistently produce a surplus of individuals, "source patches", while other populations experience more deaths than births and persist only through immigration, "sink patches" (Pulliam, 1988). Several frameworks have been developed to represent population dynamics in complex landscapes such as mainland–island theory, a version of source-sink dynamics in which large, persistent population acts as a source to nearby small populations (Heard et al., 2012; MacArthur & Wilson, 2001), and metapopulation theory (Cushman, 2006; Hanski, 2011; Hanski et al., 1995; Hanski & Gyllenberg, 1993; Marsh & Trenham, 2001).

While it is debated, we hypothesize that metapopulation theory is the best framework for amphibian conservation, because it appears to fit well with their use of patchy, aquatic breeding habitats, high apparent natal philopatry and breeding site fidelity, and regular barriers or resistance to dispersal (Billerman et al., 2019; Cushman, 2006; Marsh & Trenham, 2001; M. A. Smith & Green, 2005). Metapopulations are defined by four criteria: habitat patches have resident breeding populations, populations should not be large enough to be self-sustaining without occasional immigration, populations should be connected through recolonization, and population dynamics must be sufficiently independent [asynchronous] to prevent simultaneous extinction (Hanski et al., 1995). Isolation can provide refuge from disease and promote local adaptation that increases adaptive diversity across a metapopulation, while dispersal events between isolated populations may be infrequent, dispersal supports demographic or genetic rescue that increases persistence of small populations and leads to recolonization of unoccupied patches (Cushman, 2006; Hanski, 2011; Hanski et al., 1995; Marsh & Trenham, 2001). Consistent with this framework, many amphibian populations are comprised of subpopulations represented by a single breeding site or clusters of proximate, potentially "source-sink" or "patchy-population breeding sites." These subpopulations are often isolated by large distances between breeding sites due to natural barriers, matrix resistance, or human activities that lead to the loss of some intermediate breeding sites when the terrestrial matrix is unsuitable for dispersal. The metapopulation framework has proven readily adaptable to comparing management scenarios for threatened amphibians, for example, guiding decisions on habitat restoration and reintroductions to increase breeding site and metapopulation persistence (Chandler et al., 2015; Wendt et al., 2021).

Models are an important tool in wildlife management, because they can provide a proxy to understand and represent real-world systems and predict outcomes of management actions. Simulation models mimic these systems while allowing researchers to control processes and parameters, providing an alternative or complement to field studies and helping to overcome the constraints of working with rare species (Landguth et al., 2015). Importantly, repeated simulations under a variety of parameters can lead to more confident inferences than empirical data, where the range of conditions or number of replicates is much more limited (Landguth et al., 2015). By varying parameters across simulations, managers can evaluate the sensitivity and uncertainty of system responses to environmental change or management actions (Landguth et al., 2015). Individual-based models [or agent-based models] (IBMs) are a particularly powerful type of simulation model (Fahrig, 1997; Grimm & Railsback, 2013; Railsback & Grimm, 2012). In these models, individual organisms are represented as entities that can interact with each other and with their environment (Railsback & Grimm, 2012). This approach permits modeling known biological processes at the individual level and then observing how larger-scale patterns emerge over space and time. Ideally, these emergent patterns are confronted with real observations as part of model validation. IBMs for pond-breeding amphibians have been applied across a wide range of contexts including modeling microhabitat selection (Burrow, 2021), evaluating invasion scenarios (Asper, 2015), identifying priorities for future field studies (Burton et al., 2012), and testing management actions such as reintroductions (Thesing, 2023) or habitat restoration (Dick & Ayllón, 2017).

Spatially explicit IBMs provide a framework to determine how landscape and demographic mechanisms drive metapopulation structure and gene flow (DeAngelis & Grimm, 2014; Hearn et al., 2019; Landguth et al., 2010; Landguth & Cushman, 2010). While empirical data from landscape genetic studies provide insight into the processes that create observed patterns, they generally do not evaluate the behavioral or demographic mechanisms behind genetic patterns. When IBMs are combined with empirical data from landscape genetic studies they allow for "improved rigor" in determining how landscape features influence population dynamics and movement of individuals among breeding sites and within metapopulations (Shirk et al., 2012). Understanding the demographic and behavioral mechanisms behind genetic patterns is essential in generating robust hypotheses about how individuals likely interact with landscape features, which is fundamental to deciding on effective management actions.

Gopher Frogs (*Rana capito*) are a conservation priority species endemic to the Southeastern Coastal Plain and are tightly associated with the Longleaf pine- (*Pinus palustris*) Wiregrass (*Aristida stricta)* ecosystem. Gopher Frogs depend on isolated, seasonal wetlands with dense emergent herbaceous vegetation and low canopy cover for breeding (Kerr, Chapter 2), and open, frequently burned uplands with abundant Gopher tortoise (*Gopherus polyphemus*) burrows, small mammal burrows (Blihovde 2006), or stump holes (Roznik et al., 2009a). Only approximately five percent of the longleaf pine ecosystem remains or has been restored (Harrington et al., 2013; Kirkman & Jack, 2017; McIntyre et al., 2018; Winger., 2022). Gopher Frog populations have declined extensively across the species' range except for peninsular Florida (Enge et al., 2023) likely due to habitat loss and degradation (i.e. land use changes and fire suppression) of longleaf pine uplands and breeding wetlands (Crawford et al., 2020; Enge et al., 2014), and other stressors (e.g. climate change; Binita et al., 2015; Crawford et al., 2022). Today, Gopher Frogs are listed as a Species of Greatest Conservation Need in all states within their range (NC, SC, GA, AL, and FL) and are currently under review for federal listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 2015).

Gopher Frog life history and behavior suggest the species likely evolved for landscapes with high densities of isolated, seasonal wetlands (B. A. Crawford, Maerz, et al., 2022). Their dependence on seasonal wetlands likely means their populations relied on periodic breeding booms to persist (B. A. Crawford, Farmer, et al., 2022). Gopher Frog populations likely experienced local extinctions and recolonization through mainland-island or metapopulation dynamics. However, this is very different from many of the landscapes where Gopher Frogs are managed today. Though most Gopher Frogs are known to remain within 0.5-1 km of a breeding site, individual Frogs have been documented migrating as far as ~ 4 km between their terrestrial refugia and a breeding site (Humphries & Sisson, 2012; Marshall et al., 2023; L. L. Smith et al., 2021). Therefore, it is presumed that Gopher Frogs are capable of relatively long-distance dispersal that might be important in their metapopulation dynamics. Little is known about how Gopher Frogs migrate or ultimately disperse through different landscape matrix environments. Studies suggest a bias among juvenile and adult Gopher Frogs to move through more open canopy, pine-grassland habitat types with more abundant animal burrows (Neufeldt, 2004; Roznik & Johnson, 2009) and that fire-suppressed pine forests or other closed canopy landcover types may present more resistance to movement by juvenile Gopher Frogs because of reduced refugia availability (Roznik et al., 2009b). Studies also suggest that juvenile Gopher Frogs may move along small dirt roads when present (Roznik & Johnson, 2009; Ruppert, 2025). However, these studies are limited to breeding movements of adult Gopher Frogs and emigration of recently metamorphosed juvenile Gopher Frogs. To our knowledge, there is no documentation of dispersal movements of Gopher Frogs between subpopulations.

In Georgia (GA), most extant Gopher Frog populations are located on relatively small parcels of managed lands (i.e., conserved properties with active management) with only one to three known breeding wetlands and likely no functioning metapopulation structure (B. A. Crawford, Farmer, et al., 2022). Each of these populations are isolated from other populations by distance and resistance caused by large areas of land developed for agriculture, silviculture, or other purposes. Ceylon Wildlife Management Area, hereafter Ceylon, is an exception. Ceylon supports a large metapopulation composed of at least three distinct populations of Gopher Frogs with at least 6 breeding wetlands (Kerr, Chapter 3). However, the findings from that study are correlative. Thus, the objectives of this study were to use an Individual-Based Model (IBM) to simulate how landscape and wetland features influence the patterns of breeding site occupancy and the genetic structure of Gopher Frog populations on Ceylon. We expect the model to produce patterns of breeding wetland occupancy, terrestrial occupancy, and landscape genetic structure similar to observed patterns (Kerr, Chapters 2 & 3). If sufficiently validated, the model can then be used to evaluate management scenarios, including spatially explicit habitat management and translocation decisions to maximize Gopher Frog persistence on Ceylon and other managed landscapes.

Methods

Focal Landscape

Ceylon Wildlife Management Area is a 10,970-ha property that once held large areas of open longleaf pine savanna with a high density of isolated wetlands, dense areas of maritime hardwood forest, and tidal river marsh and salt marsh (Fig 4.1). For most of the 20th Century, until the state opened the property as a public WMA in 2021, Ceylon was held privately and used primarily for timber and hunting. Landowners managed the landscape with prescribed fire and "low impact" timber harvest, which is credited with allowing the persistence of soils and sections of habitats in reasonably good condition (i.e. open canopy pine savanna with herbaceous ground cover). The landscape includes approximately 1,619 ha of longleaf–wiregrass habitat with trees up to 145 years old, dense maritime hardwood forests, tidal river marshes and salt marshes, and a network of seasonal wetlands (Lee, 2020). Nonetheless, many of the wetlands had become degraded from pine encroachment into the basins, pine forests surrounding wetlands were dense and likely contributed to shorter hydroperiods (Golladay et al., 2021), and several wetlands on the property were modified by ditching or digging pits in the basins to concentrate water and reduce wetland surface areas. Borrow pits distributed across the property now provide relatively permanent freshwater sources within a landscape otherwise dominated by ephemeral wetlands, tidal creeks, and forest drains. Surveys of the property for Gopher Frogs and other priority amphibians and reptiles have occurred episodically since 2008. The surveys found that the property contained thousands of Gopher Tortoises as well as populations of Gopher Frogs and other priority species (Lee, 2020; M. Elliot, personal communication). Early surveys of the property revealed two known (41B and 109B) and one potential (59) Gopher Frog breeding site (M. Elliot, personal communication). The survey efforts since 2020 have expanded the known distribution of Gopher Frogs on Ceylon and called into question the assumption that there were only three potential breeding sites on the property (Maerz et al., 2025; Maerz, 2022; Marshall et al., 2023; Fig 4.1). We completed wetland and terrestrial surveys in 2024 (Kerr, Chapter 2) and detected Gopher Frogs at two of the three historic wetlands but at only one of the wetlands we identified as likely suitable. While we did not detect breeding at one historic wetland and the other wetlands we identified as likely or potentially suitable, we suspect breeding occurred at wetlands four of those wetlands due to the large number of recently metamorphosed Gopher Frogs detected in tortoise burrows immediately surrounding those wetlands. One emerging pattern is that Gopher Frogs are likely distributed in distinct units associated with each sandhill and high tortoise burrow densities. These sandhills are separated by low maritime forest that includes streams, some of which are tidally influenced. These maritime forest habitats or streams may create resistance for movement of Gopher Frogs on the property.

Model overview

Due to the complicated nature of IBMs, we followed best practices by providing detailed methods and sub model descriptions in a standard Overview, Design Concepts, and Details (ODD) protocol (Appendix A). A basic summary of the model is as follows. The model simulates the annual life cycle of Gopher Frogs and includes key biological processes such as immigration, mating, oviposition, larval survival, juvenile emigration and habitat selection, juvenile and adult terrestrial mortality, and dispersal modeled at the level of individual frogs. Each of these processes are parameterized by field studies from our lab and published studies. We used NetLogo (Version 6.4.0) to simulate these processes in a spatially explicit representation of Ceylon. By simulating individual performance and behaviors of frogs within a landscape, the model allows for understanding local population dynamics and larger-scale patterns, like changes in population size and distribution, to emerge over time. We then used the model to simulate how landscape features influence the patterns of breeding site occupancy and the genetic structure of Gopher Frog on Ceylon.

Model Initialization

The spatial scale of the model is Ceylon, and the temporal scale is annual, with each "tick" representing one year. Before running the model, we initialized the landscape and created frogs in that landscape. We built the model landscape using landcover (Fig 4.1), wetland, and tortoise burrow GIS layers from the Georgia Department of Natural Resources (GADNR). To create the land cover layer in 2020, GADNR hand-digitized photos and LiDAR at about a 1m resolution and ground-truthed with site visits. We assigned each landcover type a resistance value between 0 and 10 based on expert opinion, with values of 10 representing impassable barriers and lower values reducing movement speeds proportionally. The wetland layer includes every wetland on the property. We assigned each wetland a hydroperiod, canopy class, area, initial occupancy status, and a wetland-specific genetic string (Table A4.1). Canopy cover data were obtained in two ways. First, categorical canopy classes were available from a previous GA DNR project in which a trained expert manually digitized canopy cover from 2020 aerial photographs (M. Elliot personal communication, 2025). Second, for 14 wetlands previously identified as potentially suitable for Gopher Frogs (Kerr, Chapter 2), we manually digitized canopy polygons using 2024 World Imagery in QGIS. Trained personnel delineated canopy cover within each wetland and, where possible, identified dominant tree types (cypress or pine). Canopy cover percentage was calculated by dividing the canopy polygon area by the total wetland area. Because the DNR canopy data were categorical, we converted the continuous canopy cover estimates to categorical classes as follows: 0–30% = open, 30–60% = semi open, and 60–100% = closed. For the rest of the wetlands, we used the DNR canopy cover classes. In both methods, wetlands dominated by cypress were classified as closed-canopy wetlands. Because canopy cover influences larval survival (Burrow & Maerz, 2021), the model could be potentially sensitive to how we assigned canopy cover values. Therefore, we subsequently tested the different canopy cover methods.

Before running the model, we initialized the first generation of frogs in the landscape. We used the 14 potentially suitable wetlands and an additional 6 wetlands that we had surveyed to determine where frogs were initialized (Fig 4.1, Kerr, Chapter 2). For each frog, we assigned age, sex, natal wetland, and genotype based on the natal wetland's genetic string, and we placed individuals at random burrows within 300 m of that natal wetland. We initialized genotypes from natal wetlands so that as frogs dispersed between wetlands, we could track genetic mixing. We used 10 loci for the simulated genotypes to match the population genetic dataset from Ceylon (Kerr, Chapter 3).

Model Process

Once we initialized the landscape and created frogs, each tick followed the annual life cycle of Gopher Frogs, including immigration, mating, oviposition, larval survival, adult and juvenile emigration, adult and juvenile terrestrial survival, and dispersal modeled at the level of individual frogs (Figure A4.1). Each tick begins by determining the weather for that year. The model draws annual weather from historical precipitation data, which determines which wetlands hold water. In dry years, only permanent wetlands hold water; in average years, permanent and semi-permanent wetlands hold water; and in wet years, all hydroperiod types hold water. On the first tick, the model forces the weather classification to wet. On subsequent ticks, it randomly selects one record from a list of October–July precipitation years from 1980 to 2023, classified as dry, average, or wet. This period reflects the Gopher Frog breeding season, which can extend from late fall through summer.

After determining weather, adult frogs (males ≥ 2 years, females ≥ 3 years) (Terrell et al., 2023) move to wetlands with water to breed, except in dry years when the model skips breeding. Males return to their natal wetland or move to the nearest wet wetland. Females select the wetland with the loudest chorus within 1,000 m (Marshall et al., 2023), and if they do not detect a chorus, they move to their natal or nearest wetland. Juveniles survive with probability 0.46 (Table A4.3), then attempt a secondary dispersal and settle in tortoise burrows if they find one within a 500 m search radius. Researchers have not directly observed this secondary dispersal in Gopher Frogs, but adults often occur farther from wetlands (Marshall et al., 2023) than recently metamorphosed juveniles have been observed to emigrate (Hunt, 2019; Thesing, 2023), suggesting that there may be a secondary dispersal after initial juvenile emigration.

Adult females in wetlands with males present select mates at random and produce larvae. The model calculates larval survival in each wetland based on female density (Terrell et al., 2023), canopy cover (Burrow & Maerz, 2021), and hydroperiod (Table A4.4). Each offspring inherits a genotype by sampling alleles from both parents across 10 loci. After breeding, adults undergo a survival draw and either die or re-settle in burrows. Adults that had just bred for the first time survived with probability 0.390, while those that had bred before survived with probability 0.639 (Terrell et al., 2023). Offspring disperse for up to seven days, with a daily survival probability of 0.822 (Table A4.3) and movement distances drawn from observed daily dispersal movements or radio-tracked, recently metamorphosed, emigrating frogs (Hunt, 2019; Thesing, 2023). Juveniles settle if they encounter a burrow. After dispersal, all surviving offspring have 0.46 probability of surviving the remainder of the year (Table A4.3).

The model scales all movement by the landscape resistance. Patches with a resistance value of 10 act as barriers that frogs cannot cross, and patches with lower resistance slow movement proportionally to their resistance value.

Simulations

We ran multiple simulations and varied conditions to explore the effects of different canopy cover classification methods and landscape resistance values on model results. We ran 10 simulations, 15 ticks [years] each, using the GADNR canopy cover classes and held landscape resistance constant. We ran an additional 5 simulations, 15 ticks each, using manually digitized canopy cover and again held resistance constant. In these canopy cover simulations, we used resistance values set by expert opinion for all landcover types (Table A4.2). For example, pine plantation had a base value of 2, Southern Atlantic Coastal Plain Maritime Forest had a base value of 3, Southern Atlantic Coastal Nonriverine Swamp and Wet Hardwood had a base value of 4, and Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall had a base value of 3. We then used the GADNR canopy cover classes and varied the resistance values for these four landcover types to assess their influence on population and genetic structure (Table A4.2). For pine plantation, we ran five simulations with resistance set to 0 and five simulations with resistance set to 4. For Southern Atlantic Coastal Plain Maritime Forest, we ran five simulations with resistance set to 0 and five simulations with resistance set to 6. Because Southern Atlantic Coastal Nonriverine Swamp and Wet Hardwood and Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall together make up the drain features on the property, we varied their resistance values simultaneously. We ran five simulations with both features set to 0, and another five simulations with Southern Atlantic Coastal Nonriverine Swamp and Wet Hardwood set to 8 and Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall set to 6. Each simulation produced a CSV file summarizing wetland breeding, including the number of breeding females, total number of male and female offspring, and total larval survival for each wetland and year. In addition, each simulation created a separate CSV with information on individual frogs including ID, age, natal wetland, genotype, breeding wetland, and burrow coordinates collected every 5 ticks.

Analysis

Each unique combination of canopy cover data and resistance values constituted a distinct scenario, resulting in eight scenarios in total. To analyze the outputs from these scenarios, we calculated summary statistics such as average percentage of wetlands occupied across all ticks, number of wetlands occupied in more than 50 percent of final ticks, average number of wetlands occupied at least once, and the five most commonly occupied wetlands at the final tick. To assess genetic mixing, we calculated the allelic composition of each wetland in the final year by pooling all individual genotypes by natal wetland and calculating the proportion of each allele. We used the summary statistics and allelic composition to understand how population and genetic structure varied between each scenario and decide which model best reflects our field observations.

After identifying the model that best reflects our field studies, we conducted additional analyses to understand if Gopher Frogs dynamics at Ceylon are consistent with metapopulation dynamics. We pooled all simulations to summarize how far frogs traveled to breed from their natal wetland. We averaged results to identify wetlands where frogs bred at their natal site and, for those that dispersed, the wetlands they moved to, allowing us to identify potential source populations. To determine colonization and extinction dynamics, we defined colonization as breeding at a non-natal wetland that had no occupancy or breeding during the preceding three years. We categorized recolonization as when a previously active wetland was inactive for more than five years before being recolonized. We used a three-year window for colonization to capture dispersal events while minimizing the likelihood of counting temporary absences caused by skipped breeding during short dry periods. In contrast, recolonization was evaluated using a longer, five-year window to ensure that these events represented re-establishment following local extinction rather than temporary absences caused by skipped breeding during short dry periods. Finally, we depicted the number of wetlands occupied for dry, average, and wet years to determine the role weather might have on Gopher Frog population dynamics on Ceylon.

Results

Although wetland-level occupancy patterns and genetic structure differed somewhat between model predictions and field surveys, we believe that the simulations that used the GADNR canopy scenario produced results that were most consistent with our field studies based on wetland occupancy, the terrestrial distribution of frogs, and spatial genetic structure.

All scenarios that used the GADNR canopy cover consistently predicted occupancy at wetlands 54, 127, 109B, 69 and 69B regardless of resistance scenarios, while simulations run with the manually digitized canopy cover layer only consistently predicted occupancy at 109 (Table 4.1; Table 4.2). With the exception of 127, we suspected that these wetlands might be breeding sites. Of these six wetlands, our 2024 field study detected evidence of breeding at wetlands 54 and 109/109B (Kerr, Chapter 2). There were also historic breeding records for Gopher Frogs in 54 and 109B. In addition, we detected evidence of breeding at wetlands 37, 41, 41B, 59, and 109, and there were historic records of breeding or likely breeding in 59 and 41B. We never detected breeding in 69 or 69B though there is a terrestrial record of a Gopher Frog ~870 m from 69 or 69B. The second closest suitable wetland was ~1,700 m from that terrestrial record. Across simulations using the GADNR canopy layer, historic and confirmed breeding wetlands were occupied for at least one year in 40% to 100% of simulations, and potential wetlands were occupied in 10% to 100% of simulations (Table 4.2). Only one confirmed and one potential wetland were unoccupied in the final year of all simulations. In contrast, simulations using the manually digitized canopy cover showed lower occupancy overall. Two historic and confirmed wetlands were never occupied, and only one historic and confirmed, one confirmed, and two potential wetlands remained occupied in the final year.

Simulations using the GADNR canopy layer produced three major genetic clusters from west to east: wetlands 54, 55, 37, and 127 formed a western most cluster; wetland 41 and borrow pit 41B formed a central cluster; and wetlands 59, 109, borrow pit 109B, 69, and borrow pit 69B, formed an eastern cluster (Fig. 4.3.A). These clusters mirrored the genetic structure we documented on Ceylon though we lacked genetic data from the area around 69 and 69B (Kerr, Chapter 3). Simulations using the manually digitized canopy layer also produced three or four general clusters but lacked the distinct structure seen with the GADNR canopy simulations (Fig. 4.3.B).

Finally, scenarios using the GADNR canopy data also produced terrestrial occupancy patterns that aligned more closely with field results (Fig. 4.2A), while simulations using the manually digitized canopy cover lacked a major cluster of animals on the western side of the property where we documented many frogs during field sampling (Fig. 4.2B). Thus, we believe the simulations using the GADNR canopy cover produced emergent patterns more consistent with field observation. Therefore, we only used the GADNR canopy cover model to further investigate the metapopulation dynamics of Gopher Frogs on Ceylon.

Most frogs bred at their natal wetland, but those that dispersed mostly bred at a wetland within 1 km of their natal wetland (Fig. 4.4). There were some individuals in some simulations that dispersed as far as 4 km from their natal wetland (Fig. 4.4), which was an emergent result that was highly consistent with field observation from several studies (Marshall et al., 2023 and references therein). We observed very little dispersal occurring between the east and west sides of the property (Fig. 4.6). Only 1.3% of dispersal events crossed between genetically identified populations, and ~98% of those individuals bred at the borrow pit 41B. Wetlands 54, 127, and 69 were major sources of dispersers (Table 4.3; Fig. 4.5; Fig. 4.6). There was higher allelic diversity in the western cluster than the other cluster. Further, wetlands experienced both colonization and extinction and, in some cases, subsequent recolonization events, but those that were recolonized were typically near a large source population (Table 4.5; Table 4.5). Finally, we saw on average a higher number of occupied wetlands in wet years compared to average or dry years (Fig. 4.7) showing that occupancy tends to expand during breeding booms associated with wet years and contracts back to core source populations during average or dry years.

Discussion

We believe that our IBM produced sufficiently realistic results to examine metapopulation dynamics on Ceylon. The simulations resulted in emergent patterns of wetland and terrestrial occupancy and genetic structure that closely matched field observations, providing confidence that they accurately reflect Gopher Frog dynamics across the landscape. We hypothesize that Gopher Frogs at Ceylon function broadly as metapopulations with populations connected by dispersal events, as evidenced by gene flow between populations and by extinction and colonization events. However, we believe that dynamics within population clusters were more consistent with mainland–island or source-sink dynamics where one or more populations act as consistent sources for the colonization of other proximate wetlands. Some of those proximate sink wetlands can function as sources during some years but also experience regular extinction during average to dry years. Thus, occupancy across wetlands tends to expand and contract between wet boom years and average or dry years. This finding agrees with the literature, which suggests that true metapopulations are rare in nature (Baguette, 2004; Fronhofer et al., 2012) and that we should not assume all amphibians function as true metapopulations (M. A. Smith & Green, 2005), although spatially structured populations do often occur.

As previously discussed, the GADNR canopy cover simulations produced occupancy and genetic structure more consistent with field observations than the manual canopy scenario, which was based on more recent data. This discrepancy may reflect that current occupancy is better predicted by habitat characterization from several years ago compared to present. If true, this suggests that wetland conditions at Ceylon have degraded since the initial characterization by GDNR and that Gopher Frog populations at Ceylon have incurred an extinction debt. This would mean that Gopher Frogs on Ceylon are currently persisting in habitat that will not support them long term. Extinction debt has been implicated in the enigmatic declines of other southeastern amphibian species in large landscapes (Semlitsch et al., 2017). Extinction debts can accrue through subtle changes that lead to the reduction of resources or conditions such that a patch can no longer sustain occupancy by a species without intervention. Most wetlands on Ceylon have been degraded by pine and hardwood succession into wetland basins reducing canopy openness and litter quality (Burrow and Maerz, 2021). It is also likely that high pine basal area in the uplands has shortened wetland hydroperiods (Jones et al., 2018). Collectively, it is likely these changes have been increasingly limiting the amount of suitable breeding habitat for Gopher Frogs on the property. However, extinction debts also present an opportunity. The lag between habitat degradation and extinction creates a window for intervention before a population or species is lost. Current upland thinning at Ceylon should be paired with wetland restoration to reverse declining habitat quality for Gopher Frogs [and likely other amphibians].

We believe that – currently – wetland occupancy at Ceylon is driven by local wetland-level characteristics with limited evidence of strong metapopulation dynamics across the wider landscape. In true metapopulations, each patch is equally likely to experience an extinction event due to stochastic process, but stochastic extinction is not synchronous. Our model suggests that extinction on Ceylon is likely driven by deterministic processes related to wetland conditions interacting with weather events. Our model predicted landscape scale synchronous extinction of wetlands during average or dry years. This is consistent with other studies predicting that Gopher Frog population dynamics likely involve periodic breeding booms (B. A. Crawford, Farmer, et al., 2022) to drive population growth and colonization. Other deterministic processes that we did not integrate into our model include the periodic colonization of wetlands by fish during high rain years or in sites more proximate to streams or permanent freshwater sources. Fish colonization of wetlands is well known to affect amphibian breeding success and extinction risk among wetlands (Gregoire & Gunzburger, 2008; Murphy et al., 2010). Understanding the relative importance of wetland level factors versus broader landscape processes is important when determining the appropriate scale of management actions (Marsh & Trenham, 2001). Currently, our results suggest that wetland conditions are likely the factor most affecting Gopher Frogs within populations and at the landscape scale on Ceylon. In the future, with a larger number of wetlands restored to suitable conditions, Gopher Frogs dynamics on Ceylon may function more like a stable metapopulation. Our model results predicted greater connectivity and, consequently, higher genetic diversity within the populations that occupied numerous wetlands compared to the population clusters with only a few isolated wetlands or borrow pits.

An interesting feature in the Ceylon landscape is borrow pits proximate to confirmed or potential Gopher Frog breeding wetlands. Borrow pits 41B and 109B are both confirmed Gopher Frog breeding sites on Ceylon (Kerr, Chapters 2 & 3), and our model predicted that borrow pit 69B is a potential breeding site. The borrow pits on Ceylon have permanent hydroperiods or longer hydroperiods than many of the adjacent wetlands. It is likely that these human-made features are important for sustaining Gopher Frogs near natural wetlands in portions of the landscape. Our model also predicted that borrow pit 41B was the most likely breeding site to receive successful immigrants from other populations, serving as a genetic bridge across the landscape. However, we caution against concluding that borrow pits or other human-made small, permanent water bodies are a solution to broader demographic and spatial limits on Gopher Frog populations. As our model demonstrated, negative density dependence on tadpole performance limits the potential productivity of small borrow pits relative to much larger natural wetlands. We hypothesize this negative density dependence is occurring at borrow pit 41B and 109B. Borrow pit 41B was excavated in 2006 and serves as reliable breeding habitat during extended drought periods. In 2022 during a multi-year dry period, we observed two adult Gopher Frogs being tracked with radio telemetry migrate to borrow pit 41B to attempt to breed (Maerz, unpublished data). However, our model predicts that, because of negative density dependence, 41B functions only as a small breeding reservoir rather than a primary source for Gopher Frogs in that area of Ceylon. Similar to 41B, borrow pit 109B was excavated between 2007 and 2009 and has regular detections of low numbers of Gopher Frogs nearby. Thus, borrow pits or other human-made waterbodies may be useful as a management tool for sustaining Gopher Frogs near isolated natural wetlands under increasing drought frequency and intensity (Binita et al., 2015), but they would not compensate for the need to increase large, natural breeding habitats on the landscape. Our IBM could be used to evaluate the utility of constructing borrow pits in specific locations to improve Gopher Frog persistence and functional connectivity.

Finally, we noted that among all our simulations, we never had colonization of wetlands on the western most portion of Ceylon. The farthest west we observed dispersal was to wetland 114, which was ~650 m from the cluster of wetlands 54, 55, and 127. There are two areas of open canopy forest on tortoise soils with multiple wetlands ~1.5 and 2.5 km west of wetlands 54, 55, and 127. The farther area also has an exceptionally high density of tortoise burrows. These areas are within the known movement distances of Gopher Frogs and distances we observed frogs dispersing in our simulations. The failure to predict any colonization of any wetland in that area likely reflects that all the wetlands in that area of Ceylon are currently unsuitable. Most are heavily encroached by pines and hardwoods, and some have been modified to alter their hydrology. In addition, there are no suitable wetlands between wetlands 54, 55, 127, or 37 and the western most areas of potential habitat that might serve as bridges to colonization. We believe there is opportunity to create an additional population of Gopher Frogs in the western most part of Ceylon, but this will likely require substantial restoration of the wetlands in those areas combined with the translocation of Gopher Frogs, potentially through captive-rearing, to that part of the property. Our model predicts that natural recolonization is unlikely, but this is a scenario that would need formal evaluation.

Our work is another example of how models play an important role in adaptive management (Lyons et al., 2008). Models like ours allow managers to predict how a landscape currently determines species persistence and evaluate the effects of different management actions. In this regard, models designed to explicitly aid in management are critical during the planning phase for any project (Williams & Brown, 2012). Models allow managers to carefully plan and evaluate alternatives for restoration projects before deciding how to invest limited time and resources. In addition, models can also expose implicit assumptions about systems, forcing those assumptions to be explicit and identifying additional research needs. For example, while building this model, we realized we do not yet know how annual survival differs between adults who migrate to breed and adults who skip years between breeding. We would presume that animals that don't undergo the risks of migration or the energetic expense of breeding would have higher annual survival, but we don't know this. We recognize that this information gap affects our estimates of terrestrial persistence of frogs and extinction rates at breeding sites. We believe answering this question should be a future priority in order to improve our model and further reduce uncertainty related to management decisions.

For this project, we made our model sufficiently complex to be useful for testing management strategies for Gopher Frogs in Georgia and for understanding how Gopher Frogs function across a large landscape. We do recognize that our IBM was parameterized – in part – by *in situ* studies of Gopher Frogs or closely related species in other landscapes and *ex situ* mesocosm experiments on Gopher Frogs in Georgia. Ideally our model will be improved by studies of key processes in the focal managed landscapes we hope our model will help manage. Nonetheless, the performance of our current model demonstrates it can be used to reduce uncertainty when making management decisions for the Gopher Frog, and the model will continue to improve as more species- or landscape-specific data become available. Landscapes like Ceylon that still support remnant, but disconnected populations present opportunities for restoration and management aimed at reestablishing connectivity and the associated population dynamics to improve long-term species persistence (Armstrong, 2005; Fahrig & Grez, 1996). This IBM provides an evaluation step prior to decision making and irrevocable allocation of resources by creating a framework to experiment with restoration or population supplementation actions.

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Tables and Figures

Table 4.1. Summary statistics for each simulation scenario showing Gopher Frog occupancy on Ceylon. Values represent the number of runs, mean percentage of wetlands occupied across all ticks, number of wetlands occupied in more than 50 percent of final ticks, average number of wetlands occupied at least once, and the top five wetlands occupied at the final tick with the percentage of runs in which each was occupied.

Scenario	Runs	Mean % Occupied Wetlands Over All Ticks	# Of Wetlands Occupied In ≥50% Of Final Tick	Average # Of Wetlands Occupied At Least Once	Top 5 Wetlands Occupied At Final Tick (% Of Runs Occupied)
Canopy: GADNR	10	4.1	5	32.4	127 (100%); 54 (100%); 69 (100%); 109B (90%); 69B (90%)
Canopy: Manual	5	1.9	1	22.2	109 (60%); 109B (20%); 110 (20%); 111 (20%); 112 (20%)
Drains 0/0	5	2.8	5	23.5	109B (80%); 127 (80%); 54 (80%); 69 (80%); 69B (80%)
Drains 8/6	5	4.0	5	32.2	127 (80%); 54 (80%); 69 (80%); 109B (60%); 69B (60%)
Maritime 0	5	4.5	5	34.8	54 (100%); 109B (80%); 127 (80%); 69 (80%); 69B (80%)
Maritime 6	5	3.1	0	23.4	109B (40%); 127 (40%); 54 (40%); 69 (40%); 69B (40%)
Pine 0	5	3.0	5	26.2	127 (80%); 54 (80%); 69 (80%); 109B (60%); 69B (60%)
Pine 4	5	2.8	5	21.6	127 (100%); 54 (100%); 69 (100%); 109B (80%); 69B (80%)

Table 4.2. Gopher Frog wetland occupancy for focal wetlands on Ceylon in simulations using the GADNR canopy cover. Values represent wetland id, the percent of runs in which the wetland was occupied in at least one year (excluding tick 0), the average number of years occupied (excluding tick 0), and the percent of runs in which the wetland was occupied in tick 15.

		GADNR Canopy Cover Layer			Manually Digitized Canopy Layer		
		Percent of simulations occupied			Percent of simulations occupied		
Wetland ID	Status	≥ 1 year	final year	Mean no. years occupied	≥ 1 year	final year	Mean no. years occupied
37	Historic, Confirmed	40	20	0.5	0	0	0
55	Confirmed	90	40	1.5	20	0	0.6
54	Historic, Confirmed	100	100	10.7	0	0	0
127	Potential	100	100	9.8	40	0	0.6
41	Confirmed	30	0	0.3	20	0	0.8
41B	Historic, Confirmed	60	40	2.5	80	0	1
59	Historic, Confirmed	40	20	0.4	40	0	1.2
60	Potential	10	0	0.1	20	0	0.0
112	Potential	60	30	1.6	60	0	1.4
109B	Historic, Confirmed	100	90	5.7	40	20	0.6
109	Confirmed	70	40	1.2	100	60	10.2
69	Potential	100	100	10.2	40	20	1
69B	Potential	100	90	6.2	40	20	1

Table 4.3. Wetlands colonized by Gopher Frogs from potential source populations in simulations on Ceylon using the GADNR canopy cover. We defined colonization as breeding at a non-natal wetland that had no occupancy or breeding during the preceding three years. Values represent the simulation run, the natal wetland, the number of frogs that acted as colonizers from that natal wetland, the number of wetlands colonized by those frogs, and the IDs of the colonized wetlands.

Simulation Run	Natal Wetland	Total colonizer frogs	Unique colonized wetlands	Colonized List
1	54	122	14	114, 23, 25, 26, 27, 28, 29, 38, 39, 49, 49FB, 50, 55, 55B
8	54	262	14	114, 21, 22, 23, 24, 26, 27, 29, 37, 38, 49, 50, 55, 55B
1	127	100	13	114, 23, 25, 26, 27, 28, 29, 38, 39, 49, 50, 55, 55B
8	127	116	13	114, 22, 23, 24, 26, 27, 29, 37, 38, 49, 50, 55, 55B
1	69	55	7	109, 111, 63, 66, 67, 69B, 70
5	69	63	6	109, 62, 63, 67, 70, 71
5	127	11	5	26, 27, 49, 55, 55B
8	69	54	5	109, 63, 67, 70, 71
5	54	14	4	26, 49, 55, 55B
5	69B	8	4	111, 63, 70, 71

Table 4.4. Wetlands colonized by Gopher Frogs from potential source populations in simulations on Ceylon using the manually digitized canopy layer. We defined colonization as breeding at a non-natal wetland that had no occupancy or breeding during the preceding three years. Values represent the simulation run, the natal wetland, the number of frogs that acted as colonizers from that natal wetland, the number of wetlands colonized by those frogs, and the IDs of the colonized wetlands.

Simulation Run	Natal Wetland	Total colonizer frogs	Unique colonized wetlands	Colonized list
2	109	123	11	109B, 110, 111, 112, 57, 59, 60, 62, 63, 69, 69B
3	109	402	8	109B, 110, 111, 112, 57, 62, 69, 69B
2	59	9	3	41B, 57, 60
2	60	6	3	57, 59, 62
2	110	1	1	59
2	112	1	1	62
2	22	1	1	21
2	55B	1	1	22
5	59	1	1	41B

Table 4.5. Wetlands in simulations on Ceylon using the GADNR canopy cover in which Gopher Frogs went extinct and were subsequently recolonized. We defined recolonization when a previously active wetland was inactive for more than five years before being recolonized. Values represent the simulation run, the wetland ID, and what year that wetland went extinct and was subsequently recolonized.

Simulation Run	Wetland ID	Extinct After	Recolonized At
1	109	0	15
1	55	0	10
1	55B	0	10
1	69B	0	10
2	109	0	9
2	22	0	9
2	55	0	9
2	55B	0	9
3	109	0	13
3	37	0	13
3	41	0	14
3	55B	0	13
4	109	0	12
4	109B	4	11
4	112	1	12
4	37	0	12
4	55	0	12
4	55B	0	12
4	59	0	15
4	62	0	15
4	69B	0	6
5	109	0	10
5	55	0	10
5	55B	0	10
5	62	0	10
6	41B	6	15
6	69B	0	6
7	112	1	7
7	21	0	7

7	28	7	15
7	55	0	7
7	55B	0	7
7	59	0	15
7	62	0	7
7	69B	1	8
8	109	0	15
8	109B	0	13
8	112	3	9
8	112	9	15
8	114	9	15
8	21	3	9
8	21	9	15
8	22	9	15
8	37	0	15
8	38	9	15
8	49	9	15
8	55	0	9
8	55	9	15
8	55B	0	15
8	63	9	15
8	67	9	15
8	69B	1	8
8	70	9	15
8	71	9	15
9	109B	0	10
9	112	3	12
9	41B	0	6
9	55	0	12
10	22	0	9
10	55B	0	9

Table 4.6. Wetlands in simulations on Ceylon using the manually digitized canopy layer in which Gopher Frogs went extinct and were subsequently recolonized. We defined recolonization when a previously active wetland was inactive for more than five years before being recolonized. Values represent the simulation run, the wetland ID, and what year that wetland went extinct and was subsequently recolonized.

Sim	Wetland ID	Extinct After	Recolonized At
2	109B	0	10
2	112	0	6
2	22	3	10
2	55	6	12
2	62	0	10
2	69B	0	10
3	110	9	15
3	111	9	15
3	112	0	9
3	112	9	15
3	62	0	9
3	62	9	15
3	69	0	9
3	69	9	15
3	69B	0	15
5	112	0	6
5	127	0	6
5	21	0	6
5	41B	0	10
5	59	0	6
5	62	0	6

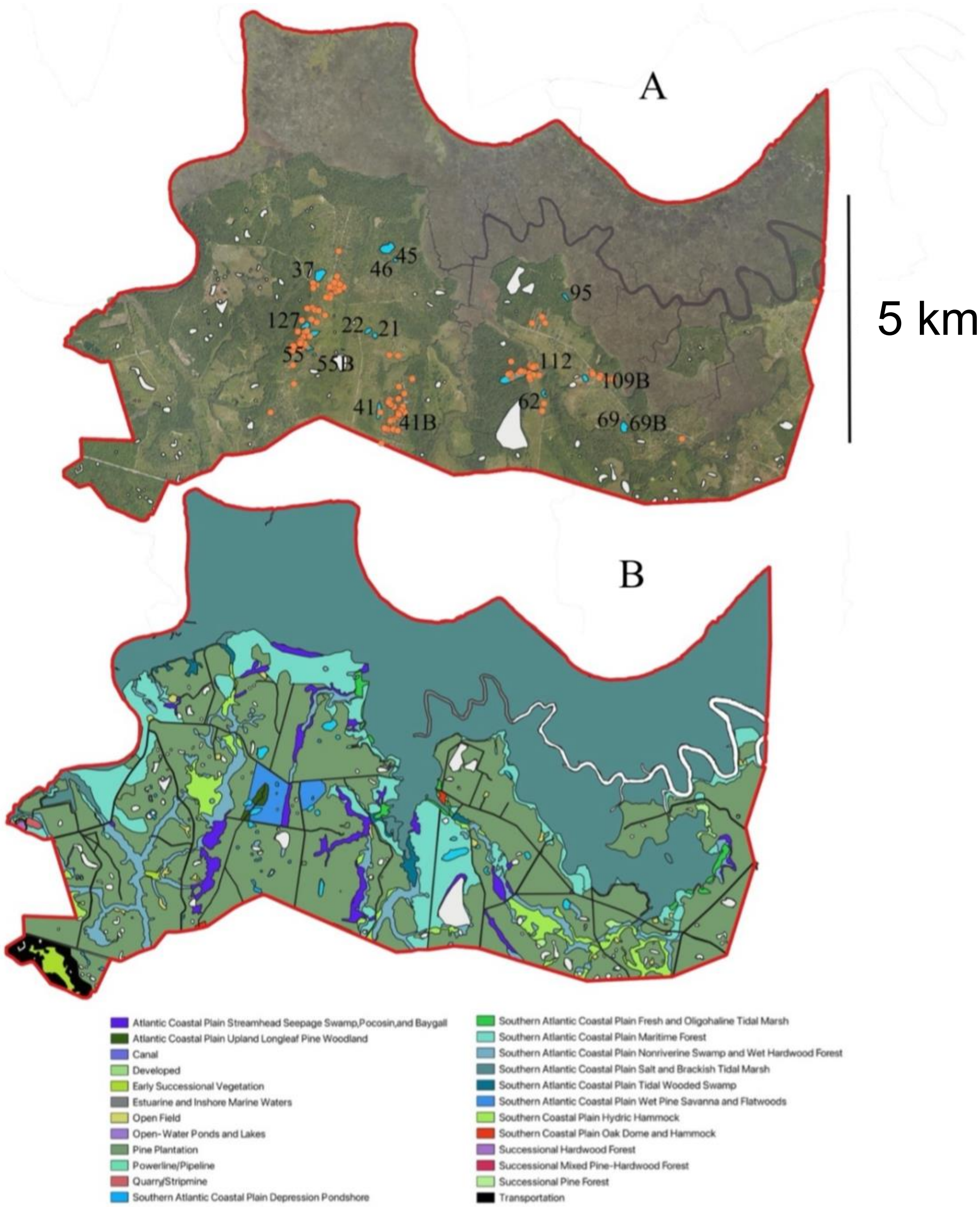

Figure 4.1. (A) Map of Ceylon located in Camden County, Georgia showing historic Gopher Frog detections in orange and wetlands where Gopher Frogs were initialized in the model, labeled by wetland ID and colored light blue; all other wetlands are shown in light gray. (B) Map of Ceylon displaying landcover types, with wetlands colored by initial status as above.

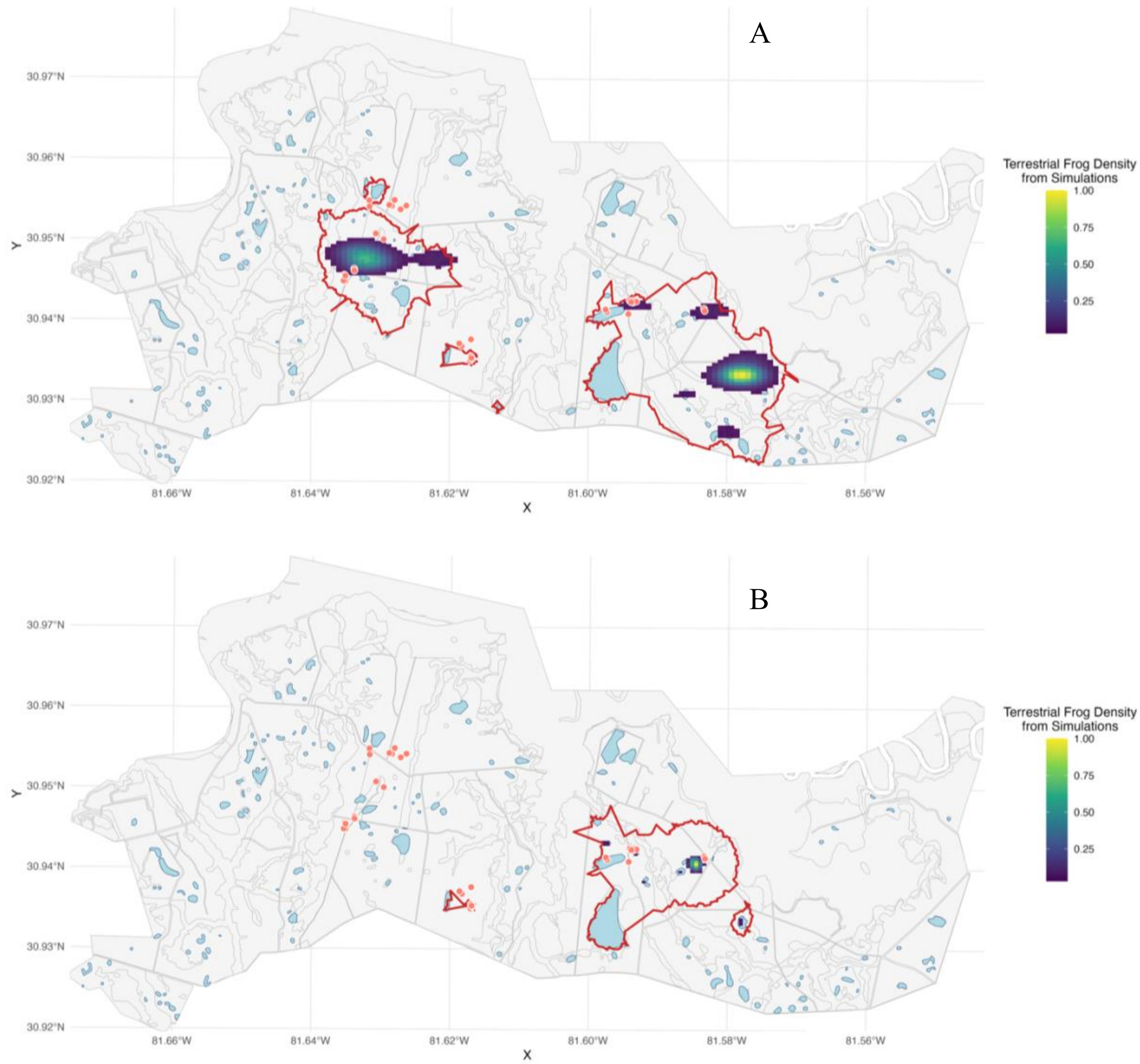

Figure 4.2. A map of Ceylon depicting historic Gopher Frog locations (salmon) and the density and outlines of terrestrial Gopher Frog locations from pooled simulations using the GADNR canopy cover (A) and the manually digitized canopy layer (B) to compare simulated terrestrial locations with known field observations

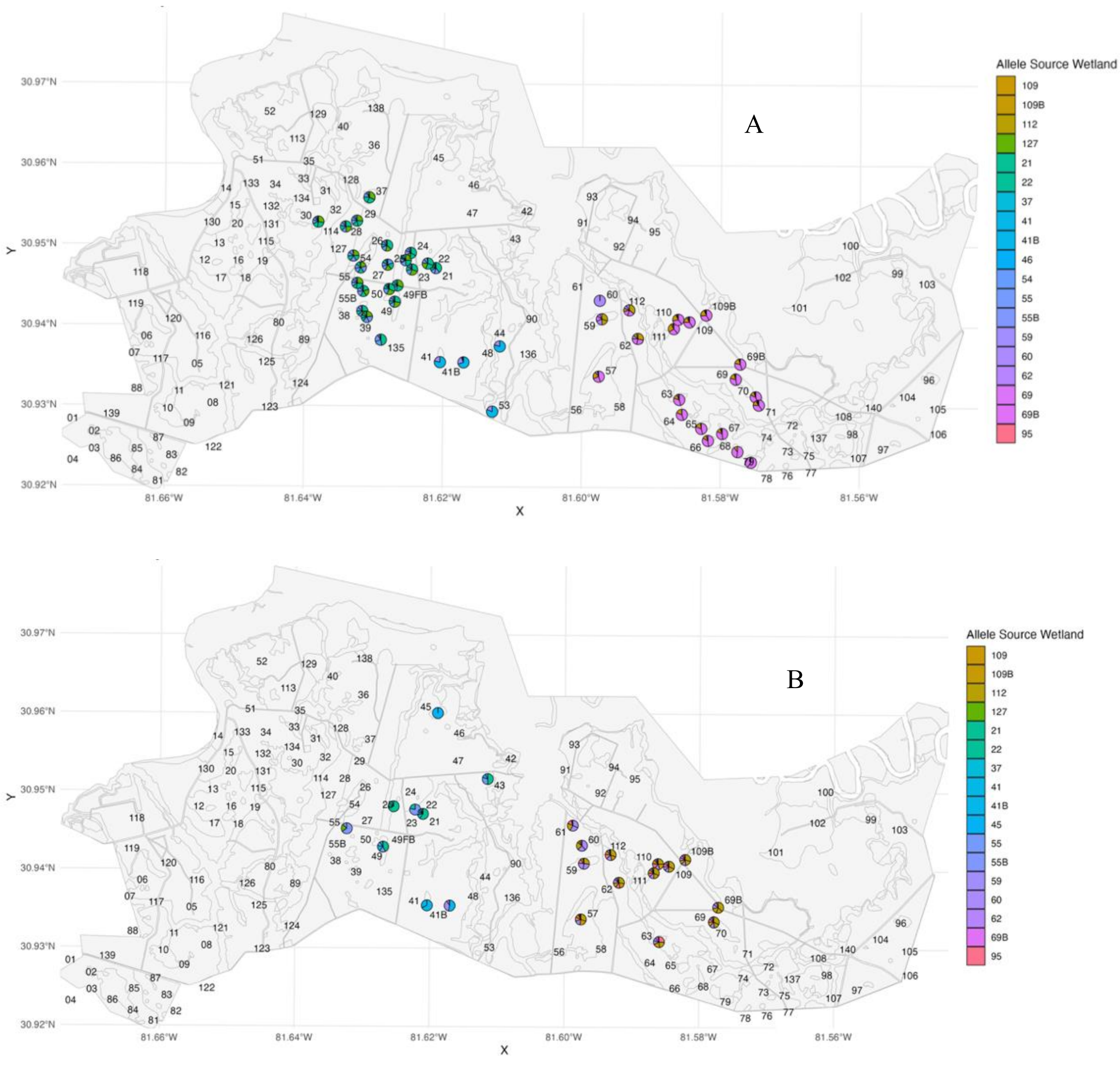

Figure 4.3. A map of Ceylon depicting the allelic composition of Gopher Frogs from simulations for each wetland in the final year. Allelic composition was determined by pooling all individual genotypes by natal wetland and calculating the proportion of each allele for simulations using the GADNR canopy cover (A) and the manually digitized canopy layer (B). Pie charts are colored by the allele source wetland.

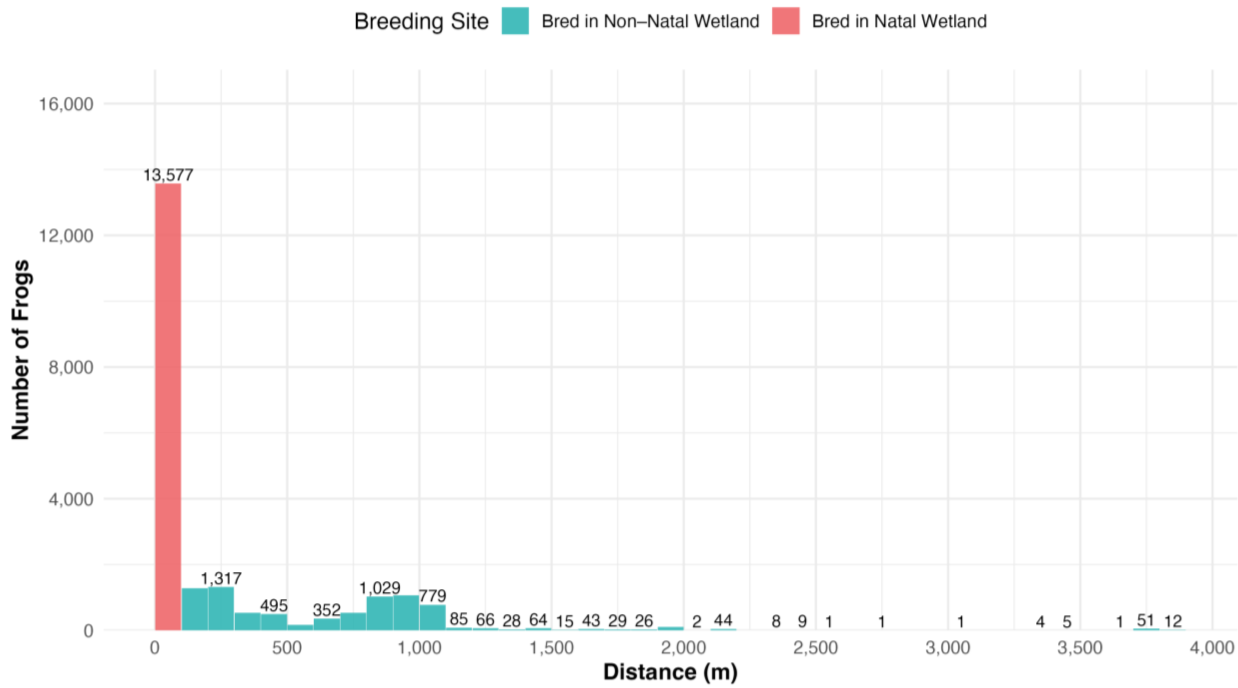

Figure 4.4. Histogram showing the distance Gopher Frogs traveled to breed from their natal wetland in simulations on Ceylon, with all simulations using the GADNR canopy cover pooled.

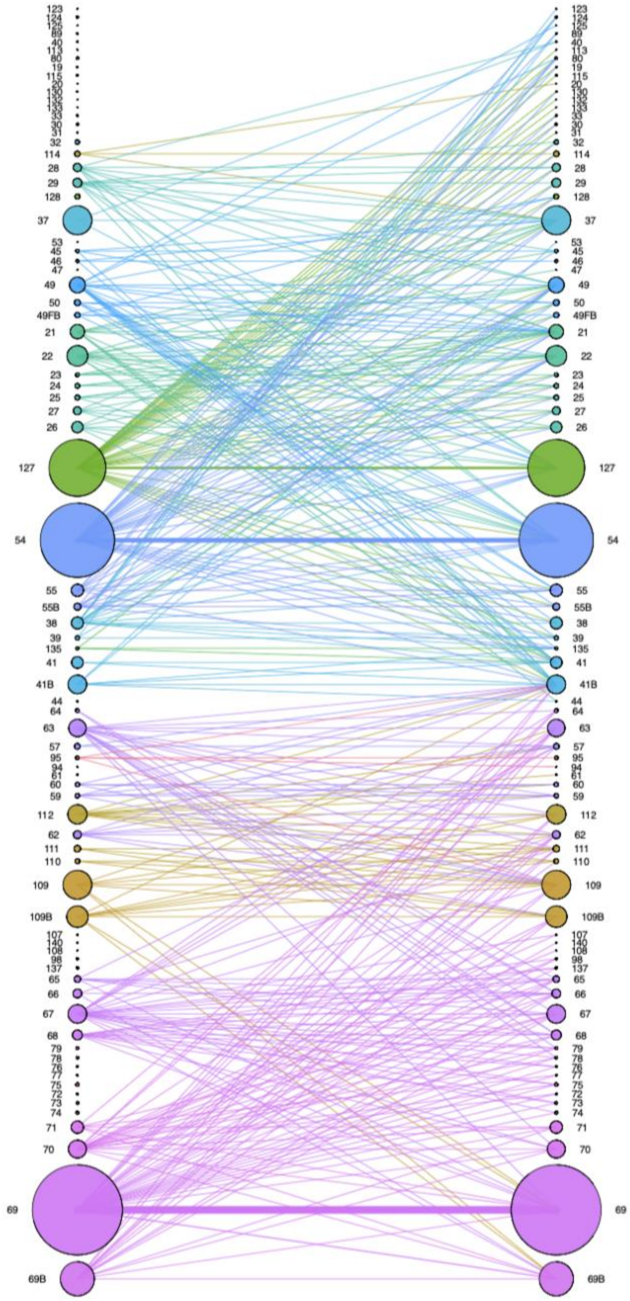

Figure 4.5. All simulations using the GADNR canopy cover were pooled and averaged to assess whether Gopher Frogs bred at their natal wetland or dispersed at Ceylon. Circles are scaled by the average number of frogs that both returned to breed at and dispersed from each wetland and colored by a unique color based on wetland ID, while the lines represent the average number of frogs moving between natal and breeding wetlands.

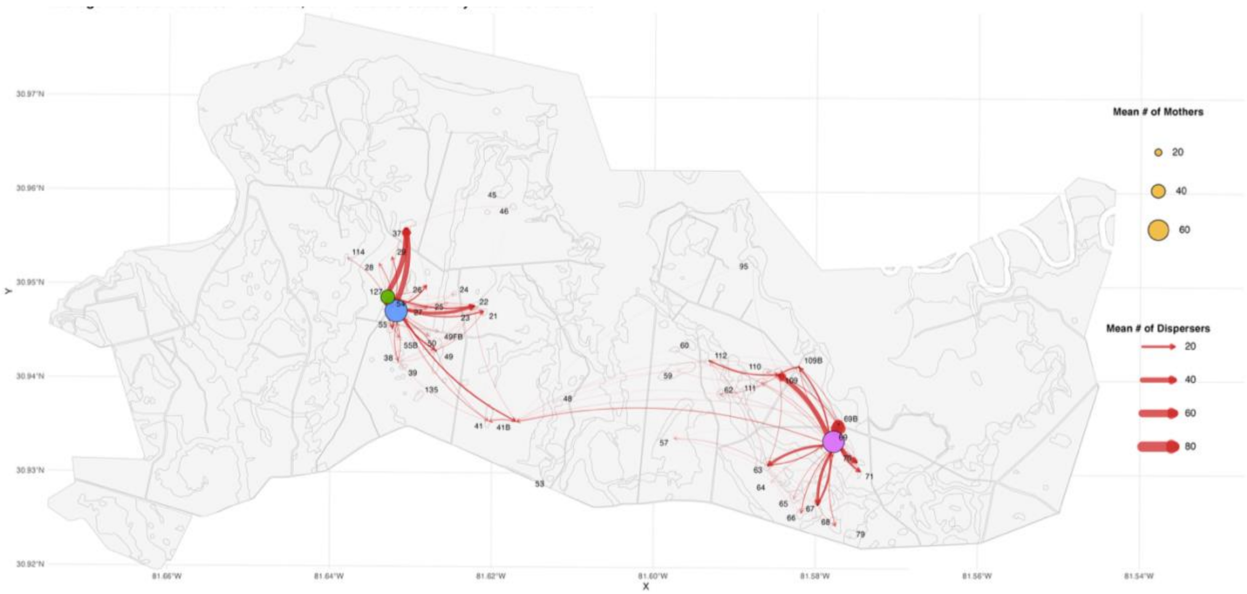

Figure 4.6. A map of Ceylon depicting the average movement of Gopher Frogs between wetlands with all simulations using the GADNR canopy cover pooled then averaged. Arrows depict the mean number of dispersers with circles scaled by the mean number of mothers at that wetland and colored by a unique color based on wetland ID

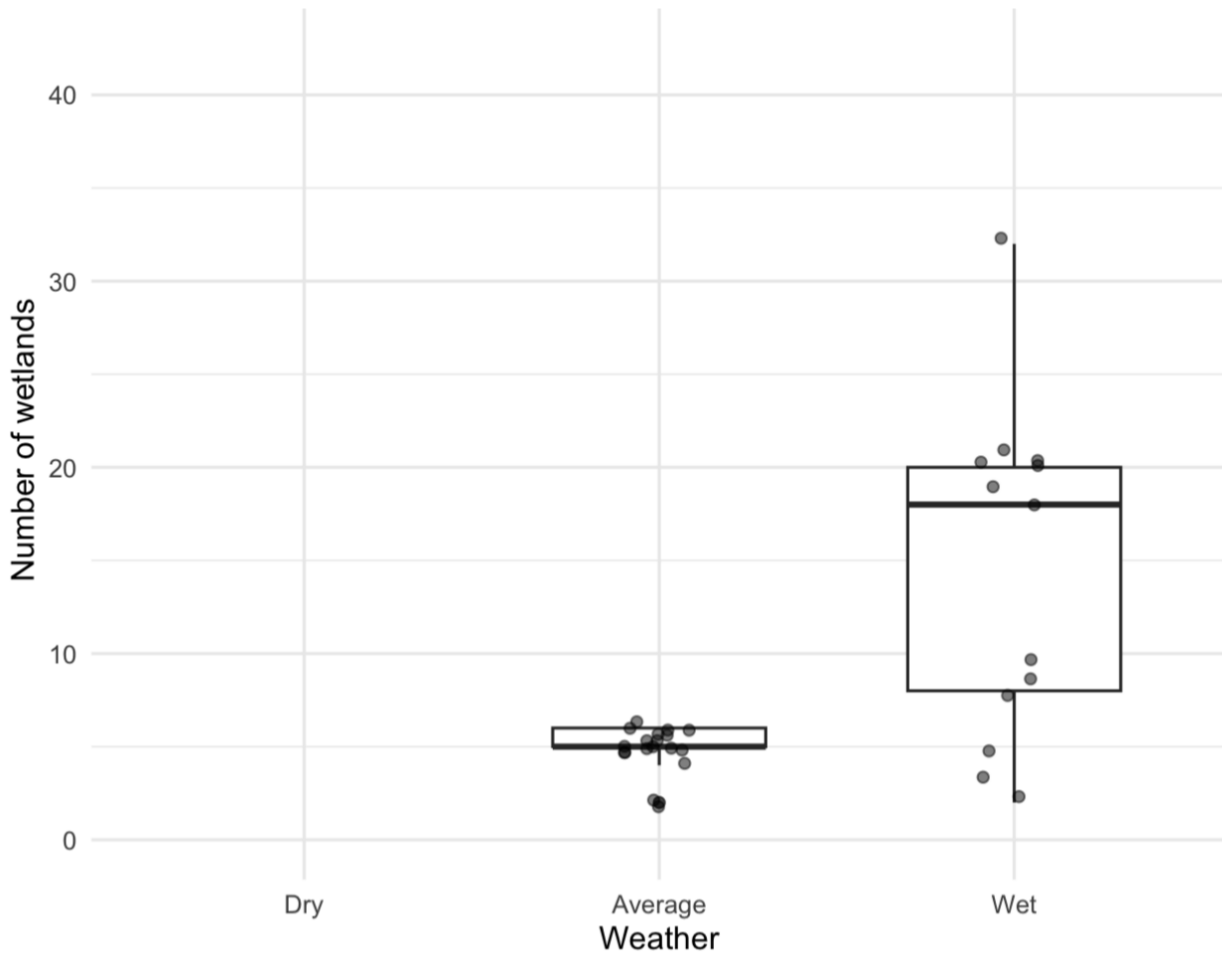

Figure 4.7. The number of wetlands occupied by Gopher Frogs in simulations on Ceylon for weather classes to show how weather impacted wetland occupancy. Boxplots summarize the distribution of the number of wetlands where at least one female successfully bred under Dry, Average, and Wet simulated weather years. Each point represents one simulation tick (year) across five simulations using the GADNR canopy cover. The upper and lower bounds of each box represent the quartile range, the central line denotes the median, and whiskers show the range of non-outlier.

CHAPTER 5

CONCLUSION

The overarching goal of this thesis was to understand what we believed were Gopher Frog metapopulation dynamics on Ichauway and Ceylon to inform management on those landscapes and the restoration of Gopher Frogs on other managed landscapes where populations are barely persisting or have gone extinct.

Our objective for chapter 2 was to document and estimate Gopher Frog occupancy of historic and potential breeding wetlands and estimate the influence of site features on occupancy patterns on Ichauway and Ceylon. At Ichauway, we detected Gopher Frogs at 9 of the 12 historic wetlands we sampled and at one new wetland we had identified as potentially suitable. At Ceylon, we detected Gopher Frogs at two of the four historic wetlands but only one of the wetlands we identified as likely suitable. Our findings support the prediction that Ceylon has lower rates of occupancy than Ichauway. We hypothesize that these differences in wetland occupancy are the result of differences in land use and management history between the two landscapes. Although both are large relatively landscapes, Ichauway is larger and has been managed in a desired state for nearly half a century. Ichauway had a disproportionate number of more open canopy wetlands characteristic of Gopher Frog breeding sites. This likely reflects the longer history and more concerted efforts at wetland vegetation management and highlights the need for targeted canopy removal and vegetation management of wetlands on Ceylon [and other landscapes]. The higher overall occupancy observed at Ichauway also likely reflects lower upland resistance and greater functional connectivity between wetlands. Higher functional connectivity supports demographic rescue and recolonization thereby sustaining higher occupancy rates. In contrast, at Ceylon, the lower wetland suitability and more heterogeneous landscape appear to be limiting dispersal between wetlands, decreasing the likelihood of demographic rescue or recolonization following local extinctions.

To further investigate the potential for dispersal and recolonization events, in chapter 3, we evaluated (1) Gopher Frog genetic structure on the sites, (2) estimated genetic diversity within populations and genetic differentiation between populations, and (3) identified natural and anthropogenic landscape features that facilitate or act as barriers to dispersal and connectivity among Gopher Frog breeding sites. We accomplished objectives one and two. Consistent with occupancy patterns, functional connectivity on Ichauway appeared to be high. We found evidence that larger vicariant features such as Ichawaynochaway Creek and a major paved road are impeding connectivity among Gopher Frog breeding wetlands on Ichauway, but absent those features, connectivity appears to be high. In contrast, we found clear evidence of genetic spatial structuring and limited functional connectivity among Gopher Frog breeding sites across Ceylon. We again found evidence of large vicariant features – in this salt marsh and tidally inundated wetlands – likely isolating Gopher Frog breeding sites. However, we also found evidence that degraded wetland conditions (closed canopies) on Ceylon are likely restricting functional connectivity on the landscape, likely by limiting recruitment from breeding wetlands and increasing the distance between suitable wetlands. The evidence of low allelic richness among Gopher Frogs on both landscapes also suggests populations on both landscapes have undergone bottlenecks, although without additional analyses we cannot determine when the bottlenecks occurred. Collectively, our results suggest that two of the most robust Gopher Frog populations in Georgia both show reasons to be concerned about their long-term resilience. Low Gopher Frog genetic diversity in both landscapes suggests the potential for a broader driver of genetic diversity loss among Gopher Frog populations. We hypothesize this could be attributable to more frequent and prolonged droughts and declining hydroperiods increasing population bottleneck events. Ceylon in particularly may not be as resilient as is assumed based on the relative commonness of Gopher Frog encounters on the landscape (Maerz, 2022). For populations like those on Ceylon, with reduced levels of heterozygosity and low functional connectivity, the risk of inbreeding depression and associated reductions in fitness is higher (Allentoft & O'Brien, 2010). Reduced genetic diversity can also lower adaptive potential and increase extinction risk from stochastic events (Allentoft & O'Brien, 2010).

At Ichauway, we recommend continued wetland and upland management to maintain currently high levels of occupancy and functional connectivity. We also recommend Ichauway further validate our diagnosis of low allelic richness. It is possible that primers developed for eastern Gopher Frog lineages are less effective at diagnosing allelic richness in western lineages. If our results are confirmed, managers of Ichauway should consider actions such as translocations from other sites, to increase Gopher Frog allelic richness and reduce the risk of inbreeding depression. It may be prudent for Ichauway to evaluate whether there is already inbreeding depression occurring within the landscape. We also recommend that the managers of Ichauway commit to long-term, periodic genetic monitoring of populations. We recommend collecting opportunistic samples during high-rainfall years when Gopher Frog breeding "booms" are most likely to occur. Annual sampling is not advised because it does not allow enough generational turnover to capture meaningful changes in allelic richness and requires lots of time and resources. This type of temporal monitoring would also permit testing of the hypothesis that drought events are associated with losses of genetic diversity. Collecting opportunistic terrestrial samples would also facilitate better analysis of whether landscape conditions are influencing gene flow. To tease apart the relative effects of the creek and road that separate the northeastern and western portions of the property, future sampling should prioritize wetlands located north of the road but west of the creek. With the current spatial distribution of samples, it is not possible to determine whether the creek, the road, or both features are driving the observed genetic structure. With long-term genetic monitoring, managers of Ichauway could determine whether translocations between the northeastern and western portions of the property are needed to maintain heterozygosity and preserve allelic richness.

For Ceylon, our results suggest the need to prioritize wetland restoration alongside other actions to increase Gopher Frog occupancy and functional connectivity. Ceylon is inherently more heterogeneous than Ichauway, but it also has a higher proportion of unsuitable wetlands and – until very recently – high basal area of planted pine in the uplands. These conditions may limiting population sizes and connectivity across the landscape, leading to the erosion of genetic diversity and increasing isolation of remaining breeding sites. Since 2020, Ceylon is undergoing aggressive upland restoration through thinning and prescribed fire. Our results suggest that, for the Gopher Frog populations on Ceylon, terrestrial management must be complemented with wetland restoration and the potential translocation of individuals among populations within the landscape. Improving the number and quality of wetlands at Ceylon should help buffer the population against extinction by potentially increasing both population size and connectivity. In the meantime, we would recommend evaluating the translocation of individuals among adjacent populations through captive rearing to emulate likely dispersal patterns on the landscape. Translocation strategies could be evaluated using models such as the individual based model developed in this thesis. We also recommend periodic genetic monitoring of Gopher Frogs on Ceylon to determine if there is ongoing erosion of genetic diversity or if recent and future management actions are improving effective population sizes, heterozygosity, and functional connectivity.

Our results for two of the three landscapes supporting more robust Gopher Frog populations raises concerns for many of the smaller remaining Gopher Frog populations in Georgia. Most of those populations are restricted to smaller landscapes with one or two breeding wetlands. We hypothesize that those populations likely exhibit low allelic richness and heterozygosity and high inbreeding depression that makes them prone to extinction regardless of habitat management. Awareness of this issue is particularly important given that some of those populations in smaller landscapes serve as donor populations for captive-rearing programs. Therefore, continued monitoring of genetic diversity and inbreeding depression and potential translocation efforts may be necessary for the populations in smaller landscapes. However, deciding on the ideal source populations for translocations to these smaller landscapes may be complicated by low levels of allelic diversity such as we found on Ichauway and Ceylon. However, deciding on the ideal source populations for translocations to these smaller landscapes may be complicated by low levels of allelic diversity such as we found on Ichauway and Ceylon and possibility of distinct Gopher Frog lineages across Georgia (Devitt et al., 2023). Divergence between populations increases the risks of outbreeding depression, which could inadvertently decrease rather than increase population resilience (Byrne & Silla, 2020; Edmands, 2007; Sagvik et al., 2005). Decisions to translocate Gopher Frogs between landscapes should be made with care and evaluation of outbreeding depression risks.

A key accomplishment of this thesis was the development of an Individual-Based Model (IBM) to simulate how landscape and wetland features influence the patterns of breeding site occupancy and the genetic structure of a hypothesized Gopher Frog metapopulation. We believe that our IBM and simulations produced sufficiently realistic results to examine metapopulation dynamics on Ceylon. The simulations captured patterns of wetland and terrestrial occupancy and genetic structure that closely matched field observations. We hypothesize that Gopher Frogs at Ceylon function as metapopulations in the broadest sense with populations connected by limited dispersal events. However, our model predicted that Gopher Frog populations within Ceylon function as a weak metapopulation at the landscape scale with relatively independent population dynamics functioning like mainland–island or source-sink models. A strength of the IBM was that we were able to incorporate terrestrial dynamics and test how different landscape resistance values affected wetland occupancy and genetic structure. Our IBM model predictions also added support to our conclusions from our occupancy and genetic studies that, currently, degraded wetland conditions are the factor most affecting Gopher Frog population status on Ceylon.

We do recognize that our IBM was parameterized – in part – by *in situ* studies of Gopher Frogs or closely related species in other landscapes and *ex situ* mesocosm experiments on Gopher Frogs in Georgia. Ideally our model will be improved by studies of key processes in the focal managed landscapes we hope our model will help manage. Nonetheless, the performance of our current model demonstrates it can be used to reduce uncertainty when making management decisions for the Gopher Frog, and the model will continue to improve as more species- or landscape-specific data become available.

Both Ichauway and Ceylon provide valuable opportunities to learn more about Gopher Frogs in managed landscapes that can lead to better models and management support tools. For example, our current model makes no distinction between the annual survival rates of frogs that migrate to breed versus those that do not migrate to breed. This seems unlikely and may be underestimating terrestrial survival and breeding population persistence. Telemetry or capture–mark–recapture studies using traditional methods or advances in genetic tagging could improve survival estimates for breeding and non-breeding Gopher Frogs in Georgia. Additionally, landscapes like Ichauway where we detected high numbers of egg masses could be used to study and estimate larval density dependence. These kinds of demographic estimates would ultimately improve our confidence in the model as a management tool.

Collectively, this thesis demonstrates how multiple complementary methods can be used to understand how populations of a threatened amphibian functions under contrasting landscape conditions, one representing a more ideal and well-managed system and the other a more degraded landscape with populations likely declining but with the opportunity to intervene. This thesis provided a comprehensive overview of two of the more robust Gopher Frog populations in Georgia by examining wetland occupancy, genetic structure and diversity, and the habitat features influencing gene flow through both field studies and an IBM. Our results revealed how Gopher Frog populations at Ichauway and Ceylon function differently due to variation in wetland and terrestrial conditions. All chapters underscored the need for continued wetland management at Ceylon and raised concerns about the genetic status of all Gopher Frog populations in Georgia. We emphasize that all wetland and Gopher Frog population management should use demographic and genetic data including models to evaluate potential actions and evaluate their risks and benefits in order to reduce uncertainty about outcomes. Actions should also incorporate adaptive management principles, including a learning loop to improve future decisions (Williams & Brown, 2012).

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APPENDIX 4.1.

ODD (OVERVIEW, DESIGN CONCEPTS, AND DETAILS; Grimm et al., 2006, 2010)

Overview

Purpose:

The purpose of this model is to predict the population and genetic structure of Gopher Frogs (*Rana capito*) on one of the few remaining landscapes that support multiple breeding wetlands in Georgia, Ceylon Wildlife Management Area, hereafter Ceylon, We used the model to simulate how landscape features influence the patterns of breeding site occupancy and the genetic structure of Gopher Frog on the site. A previous population and landscape genetic study (Chapter 3) on the site found three distinct populations and gene flow driven by isolation by distance and wetland location. However, the findings from that study are correlative in nature. Thus, we varied the resistance values for four land cover types to assess their influence on population and genetic structure (Table A4.2). For pine plantation, we ran five simulations with resistance set to 0 and five simulations with resistance set to 4. For Southern Atlantic Coastal Plain Maritime Forest, we ran five simulations with resistance set to 0 and five simulations with resistance set to 6. Because Southern Atlantic Coastal Nonriverine Swamp and Wet Hardwood and Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall together make up the drain features on the property, we varied their resistance values simultaneously. We ran five simulations with both features set to 0, and another five simulations with Southern Atlantic Coastal Nonriverine Swamp and Wet Hardwood set to 8 and Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, and Baygall set to 6.

Entities, State Variables, and Scales:

1. Entities and State Variables
    a. Frogs
        i. State Variables:

1. genetics (genetics of individual, 10 microsatellites with 2 alleles determined by parents)
2. sex (sex of individual)
3. age (age of individual)
4. natal-wetland (wetland the individual was born in)
5. home-x home-y (assigned burrow/home coordinates; used for “home-first” settlement)
6. has-bred? (has the individual bred in this tick?)
7. times-bred (how many times has this individual bred?)
8. settled? (has this juvenile (age: 0- 2 or 3) settled in a tortoise burrow?)
9. breed-location (wetland ID where the individual bred this year)
10. mate-genetics (stores male partner genotype for offspring sampling)

b. Land Patches

i. State Variables:

1. patch-has-burrow? (tortoise burrow presence)
2. land cover-type (land cover type determined by GA DNR)
3. resistance (landscape resistance, values 0 to 10)
4. wetland-id (numerical id for each wetland. Determined by GA DNR)
5. wetland-status (whether the wetland has been occupied or unoccupied by Gopher Frogs)

6. wetland-hydro (hydroperiod for each wetland; Semi, Ephemeral, Permanent)
7. wetland-canopy (canopy cover for each wetland; Semiopen, Open, Closed)
8. wetland-micro (each wetland is assigned a unique genetic string that assigns genetics to the initial frogs)
9. wetland-area (wetland area in meters squared for each wetland)

c. Global Variables

i. State Variables:

1. wetlands (GIS wetland polygons)
2. wetlandfeatures (GIS and CSV-merged list of wetland data)
3. land cover (GIS land cover shapes that are turned into patches)
4. land cover-to-color-map (CSV-driven mapping of land cover to resistance value (used in movement) and display color)
5. yearly-weather (List of actual weather data from Ceylon WMA from 1980-2023 categorized into Wet, Dry, Average)
6. current-gf-year (Year selected for this tick. Years are broken into "Gopher Frog years" from October to July)
7. current-weather (Weather category this year; Wet, Dry, Average)
8. burrow-polygons (GIS shapes of tortoise burrows. Each tortoise burrow is buffered by 10 m)
9. output-file-name, wetland-output-file-name (naming output CSVs)

10. max-burrow-search-distance (local search radius for burrow settlement (patch units; default 50 ≈ 500 m)
11. burrow-patches-all (cached agentset of patches intersecting burrow polygons)
12. emig_num_settled, emig_num_movement_deaths, emig_num_post_movement_deaths, emig_num_gave_up (emigration counters)

2. Scale
   a. The spatial scale of the model is Ceylon using a real landscape from ArcGIS. World grid is auto-sized to ~≤10 m per patch via enforce-10m-patches, with the GIS envelope bound to the NetLogo world.
   b. Temporal scale is 1 tick = 1 year.

Process overview and scheduling:

On each tick (one year) the following will occur in this order (Figure A4.1):

Age:

In this sub-model all frogs age 1 year.

- All frogs increase their age by one year. Males that reach age 2 and females that reach age 3 are reclassified as adults and updated to adult size.

Determine Weather:

In this sub-model weather for the current tick is determined.

- On the first tick (tick=0), weather is forced to Wet. On subsequent ticks, a year is randomly selected from historical precipitation records (Dry, Average, Wet). Wetland hydroperiod types are then checked against this classification to determine which wetlands hold water.

Immigrate:

In this sub-model adult frogs move to wetlands for breeding and juvenile frogs have their second dispersal.

- Adult frogs move to wetlands to breed. Males either return to their natal wetland or the nearest wet wetland. Females choose the loudest chorus within 100 patches (~1000 m) or fall back to natal/nearest options. Juveniles first face a survival filter, then attempt a second dispersal and settle in tortoise burrows if found within a 500 m search radius.

Breed:

In this sub-model, adult frogs reproduce in a wetland.

- In non-Dry years, adult females in wetlands with water select a mate at random from males present, set their breeding flag, and store his genotype for offspring creation.

Lay Eggs:

In this sub-model, age zero frogs are created.

- Wetlands with breeding females produce age zero frogs. Offspring numbers are determined by female density, wetland canopy cover, and hydroperiod, with a maximum of 35% survival. Each offspring inherits a genotype formed by sampling alleles from both parents across 10 loci.

Emigrate:

In this sub-model, adult frogs settle back into burrows after breeding and juveniles disperse.

- Post-breeding adults draw a survival outcome and either die or re-settle in burrows. Juveniles disperse for up to seven days. On each day they draw a survival outcome and a movement distance, settling if an available burrow is encountered. After the movement phase, all surviving juveniles undergo a final survival check.

Design concepts

Basic Principles

This model examines whether Gopher Frogs at Ceylon WMA function under metapopulation dynamics and examines the wetland and landscape features that influence occupancy and connectivity among wetlands.

Emergence

The model showed that that Gopher Frogs at Ceylon function as metapopulations in the broadest sense with populations connected by dispersal events as evidenced by gene flow between populations and by extinction and colonization events. However, we believe it is more likely they are functioning with mainland–island or source-sink dynamics where one or more populations act as sources for the colonization of nearby wetlands with potentially separate dynamics between the east and west sides of the property. While we did not see big differences in population structure from our resistance scenarios, a strength of this IBM is that we were able to incorporate terrestrial dynamics and test how different landscape resistance values affect wetland occupancy. The GADNR canopy cover simulations produced occupancy and genetic structure more consistent with field observations than the manual canopy scenario, which was based on more recent data. This discrepancy may reflect that populations at Ceylon are experiencing an extinction debt, meaning they are persisting in habitat that can no longer support a population long term, likely due to wetland degradation.

Adaptation

Individuals follow state-dependent behavioral rules rather than learning.

- Adults:
    - Immigration: Males return to natal wetlands if wet; otherwise, select the nearest wet wetland. Females move toward the wetland with the highest chorus intensity scaled by distance, or fallback to natal/nearest sites.
    - Post-breeding: Adults experience state-dependent survival (0.39 for first-time breeders, 0.639 otherwise). Survivors attempt to return to their home burrow; if unavailable, they search locally.
- Juveniles (age = males <2, females <3):
    - Before dispersal, subadults face a fixed survival probability of 0.46. Survivors then search locally for burrows and settle if space is available.
- Juveniles (age 0):
    - Disperse for seven days with gamma-distributed daily steps. Each day they face 0.822 survival probability; survivors settle upon finding a burrow with space. After dispersal, an additional 0.46 survival probability is applied.

Objectives

Individuals follow rules that are designed to approximate life-history strategies.

- Adults:
    - Reach a suitable wetland with water.
    - Females secure a mate at that wetland.
    - Survive and return to a burrow after breeding.

- Juveniles (age = 0; males <2, females <3)
    - Survive dispersal and settle on an available burrow patch (emigration).
    - Survive second dispersal phase and settle on an available burrow patch (immigration).
-

Learning

There is no learning in this model.

Prediction

The model does not include prediction.

Sensing

Individuals do not actively gather information through explicit sensing. Instead, they are assumed to have knowledge of internal, environmental, and social variables.

- Internal: Age, sex, and breeding history determine which behavioral rules.
- Environmental: Individuals sense local patch resistance for movement, whether nearby wetlands hold water (based on annual weather and hydroperiod), and distance and direction to potential targets. During settlement, they detect burrow presence and occupancy.
- Social: Females perceive male abundance at wetlands through an inverse-square sound decay function, which determines the perceived chorus intensity used to select a breeding wetland.

Interaction

- Direct interaction: Reproduction (one male per breeding female in a wet wetland)

- Indirect interaction: Competition for burrow space (capacity rule), and density-dependent larval survival.

Stochasticity

Stochasticity represents environmental and demographic variability.

- Environmental: Random annual selection of weather years (Dry, Average, Wet).
- Demographic: Poisson-distributed initial ages; Bernoulli survival draws (adult post-breeding, subadult pre-dispersal, juvenile daily and post-dispersal); sex determination; mate selection.
- Behavioral: Random movement headings; gamma-distributed juvenile step lengths.
- Genetic: Random allele sampling at each locus.

Collectives

- The only collective is the male chorus, an emergent group of males at a wetland whose aggregate calling intensity influences female breeding movements.
- Wetlands and burrows are fixed environmental features, not collectives.

Observation

Outputs are recorded annually and include:

- **Frog-level CSVs** with individual ID, age, natal wetland, genotype, breeding wetland, and burrow coordinates (every 5 ticks, up to 25 ticks).
- **Wetland-level CSVs** summarizing breeding females, offspring numbers, sex ratios, and total larval survival per wetland per year.
- Spatial distributions of frog agents can also be visualized directly on the NetLogo interface to observe population structure over time.

Details

Initialization

Landscape

- The model is initialized with the Ceylon WMA landscape.
- Every patch is assigned a land cover type from a GA DNR GIS layer and joined attributes from resistance-values.csv (Table A4.2.) To create the land cover layer in 2020, GADNR hand-digitized photos and LiDAR at about a 1m resolution and ground-truthed with site visits. Each land cover type is assigned a resistance from 1 to 10 based on my opinion. Patches with resistance = 10 are treated as barriers (impassable) while 1–9 allow movement with penalties.
- Wetland patches are created from a GA DNR GIS layer and joined with attributes from wetland-type.csv, including ID, hydroperiod, canopy, initial status, genetic string, and area (Table A4.1.) The GIS layer includes every wetland on Ceylon, including those that we did not visit during site surveys.
    - We consistently surveyed 20 wetlands and were able to estimate their hydroperiods. Wetlands that were not visited were labeled as having "unknown" hydroperiods and were treated as ephemeral in the model. Only the 20 visited wetlands were used to initialize frogs.
    - Canopy cover data were obtained in two ways. First, categorical canopy classes were available from a previous GA DNR survey. Second, we manually digitized canopy polygons using 2024 World Imagery in QGIS, but only for the 14 wetlands that were included in Chapter 2. Trained personnel delineated canopy within each wetland and, where possible, identified dominant tree types (cypress

or pine). Canopy cover percentage was calculated by dividing the canopy polygon area by the total wetland area.

  - o Because the DNR canopy data were categorical, we converted the continuous canopy cover estimates to categorical classes as follows: 0–30% = open, 30–60% = semiopen, and 60–100% = closed. For the rest of the wetlands not consistently visited, we used the DNR canopy cover classes. After multiple simulations, we found that using the DNR canopy data produced population structures that matched observed patterns from field surveys. However, because the DNR survey was conducted a few years earlier, while the GIS data were from 2024, this discrepancy may reflect an extinction lag. This point is discussed further in the Discussion. In both methods, wetlands dominated by cypress were classified as closed-canopy wetlands.

- Burrow polygons are loaded from a GA DNR GIS layer of 10 m buffers around tortoise burrows. Patches intersecting these polygons are flagged as containing burrows. A 10 m buffer was used because frogs failed to encounter burrows at smaller buffer sizes.
- Weather is forced to Wet on tick 0; subsequent years draw from weather_by_gf_year.csv (1980–2023).

Frog Creation

- For each wetland whose initialize = 1, n adult frogs are created, where n is chosen by the interface slider frog-count.
- Sex ratio is 1:1 (rounded for odd numbers).
- Frogs are placed at random burrows within 300 m of their natal wetland. Burrow locations are identified by intersecting the burrow GIS layer with a 300 m buffer around

the wetland. We selected 300 m because this was the smallest buffer that ensured all wetlands had at least one available burrow.

- Each frog is initialized with:
  - Age: Drawn from a Poisson distribution with mean = 4, to reflect a mostly adult population with realistic age variation.
  - Genetics: A 20-character microsatellite string from wetland-type CSV.
  - Natal wetland: The wetland where created.
  - Home coordinates: The assigned burrow location.
  - has-bred?: Set to false.
  - times-bred: Set to 0
  - Size:
    - Male, age ≥ 2 - size 3 (adult).
    - Male, age < 2 - size 1 (juvenile).
    - Female, age ≥ 3 - size 3 (adult).
    - Female, age < 3 - size 1 (juvenile).
  - Breed-location: Left blank until breeding occurs.

Input Data

- Land cover GIS: GA DNR dataset.
- Resistance CSV: Land cover types, resistance values, colors (Table A4.2.)
- Wetland GIS + CSV: GA DNR dataset
- Wetland CSV: Attributes for hydroperiod, canopy, area, genetics, and initial status (Table A4.1)
- Burrow GIS: Polygons of tortoise burrows buffered by 10 m.

- Weather CSV: Precipitation-based classification of years as Wet, Average, or Dry.

Submodels

Frogs age 1 year:

- All frogs increase their age by one year. Males that reach age 2 and females that reach age 3 are reclassified as adults and updated to adult size. These age-at-maturity thresholds were chosen based on a study of Crawfish Frogs (Terrell et al., 2023).

Determine Weather:

- Weather for each simulation tick is determined from precipitation data. On the first tick, the model labels the current Gopher Frog year as Initial and forces the weather classification to Wet. On subsequent ticks, it randomly selects one record from a list of Gopher Frog years, which contains October–July precipitation data for Ceylon WMA from 1980 through 2023, classified as Dry, Average, or Wet.
- October–July was chosen to reflect the Gopher Frog breeding season, which can extend from late fall through summer. The selected year label and its weather category are stored internally and printed to the log for tracking. A reporter then checks each wetland's hydroperiod type against the stored weather category and returns true only if that hydroperiod retains water under the current conditions. In Dry years, only permanent wetlands hold water; in Average years, permanent and semi-permanent wetlands hold water; in Wet years, all hydroperiod types hold water (Table A4.1).

Frog Immigration:

- When immigrate runs, it first identifies which wetlands have water. On the first year (tick 0), every adult frog simply attempts to return to its natal wetland, using a resistance-aware stepwise movement procedure described below.

- After year zero, in non-dry years, all breeding-age adults (males ≥2, females ≥3) make immigration decisions. Each adult draws a random threshold natal_prob from 0–1, then makes a second random draw that must be less than the first threshold to return to the natal wetland. This two-draw setup yields a natal probability of ~50%, which we chose since the true philopatry rate of Gopher Frogs is unknown. Then males either go back to their home wetland with probability natal_prob or to the closest water-filled wetland. Females scan all wetlands with water within 100 patches (~1000 m) for the loudest chorus. This radius reflects the finding that 90% of Gopher Frog observations are within 1019 m of the nearest wetland (Marshall et al., 2023). Chorus intensity is calculated with three sound-based reporters: base-sound-intensity counts the number of calling males on a wetland patch, scaled-sound-intensity applies an inverse-square decay by distance (Marten & Marler, 1977), and scaled-noise-level wraps those two to report the chorus intensity at a female's location. Females choose the wetland with the highest intensity in this radius and only fall back to natal or nearest options if no loud site is detected.
- Adults move to the chosen wetland using move-to-target-stepwise. Movement is evaluated one step at a time. If the next patch has resistance ≥ 10, it is treated as a barrier; the frog retries up to 10 random headings to find a passable neighbor. If none is found, movement halts. For passable patches (resistance 1–9), speed is reduced linearly by resistance: step-scale = 1 / (1 + 0.2 × resistance) with a floor of 0.02 patch-units per micro-step. The procedure continues, up to max-steps = 200, until the frog reaches the target (within one patch) or exhausts steps.
- Finally, all juveniles (males < 2, females < 3) attempt a secondary dispersal. Each first passes a 0.46 (Table A4.3) survival probability check, and those that survive begin a local

burrow search using find-burrow-resistance-aware. This secondary dispersal phase has never been observed directly in Gopher Frogs; however, adult frogs are typically found farther from wetlands than researchers have ever observed metamorphic Gopher Frogs emigrate, suggesting the possibility of post-metamorphic dispersal beyond the initial emigration. During this search, juveniles move step by step in random headings, and each step follows the same resistance-aware movement rule used by adults: patches with resistance = 10 are treated as barriers, triggering up to 10 random re-headings, while movement through passable patches is slowed linearly according to resistance (step-scale = 1 / (1 + 0.2 × resistance)), with a minimum of 0.02 patch units per step. This procedure continues until either a burrow patch is encountered or the maximum search radius is reached (max-burrow-search-distance, default 50 patches ≈ 500 m). We chose 500 m because metamorphic emigration is capped at 500 m, so this secondary dispersal phase allows juveniles to reflect the observation that 90% of Gopher Frogs occur within 1000 m of the nearest wetland (Marshall et al., 2023). Juveniles settle immediately if the burrow patch has capacity (< 5 occupants); if the patch is full, the search continues. We selected a capacity of < 5 for two reasons: (1) the burrow layer uses a 10 m buffer, so a single "burrow patch" likely contains multiple physical burrows; and (2) 5 was the lowest number of occupants that allowed agents to consistently find available burrows. If no suitable burrow is found within the search radius, the juvenile remains unsettled at its final location.

Breed:

- When a breeding season begins (and only if it isn't a dry year), each adult female frog standing in a water-filled wetland identifies all mature males in that same wetland patch.

If at least one male is present, she selects one mate at random, sets has-bred? = true, and stores the male's genotype in mate-genetics.

Lay Eggs:

- At the start of each year's egg-laying, any leftover age-0 frogs from a previous run are removed to avoid double-counting. However, there should not be any leftover age-0 frogs since the first procedure in a tick is to age a year. The procedure then steps through every wetland in the landscape, pulling its ID, hydroperiod, canopy type, and area (Table A4.1.) For each wetland, it identifies all adult females that have has-bred? = true and counts them as mothers. If there are no mothers, the wetland produces no recruits that year.
- When mothers are present, the model calculates tadpole survival (Table A4.4) and the total number of offspring (Table A4.4). That number is randomly split into male and female juveniles. The density dependence equation comes from a study on Crawfish frogs (*Rana areolata*), a very closely related species to Gopher Frogs (Terrell et al., 2023). That study used data from a five-year study at two focal breeding wetlands to estimate embryonic, larval, juvenile, and adult survival, age at first reproduction, fecundity, and temporary immigration and emigration. Since their density dependence equation focused on a small, open canopy, ephemeral wetland, we scaled the equation by wetland area and canopy cover. The canopy cover scalers come from another study that used mesocosms to test the effects of detritus and shade on the growth, development, and survival of Gopher Frogs (Burrow & Maerz, 2021).
- Each offspring is assigned a full 10-locus microsatellite genotype using the stored parental genotypes. We chose 10 loci because we conducted a population genetic study on Ceylon using 10 loci (Chapter 3). We initialized genotypes from natal wetlands so that

as frogs dispersed between wetlands, we could track genetic mixing. For every locus, one allele is drawn at random from the mother and one from her stored mate's genotype, then sorted so "10" and "01" are represented consistently. The 10 pairs are concatenated into a 20-character genetic string that becomes the offspring's genetics. Juveniles are then created on patches within their natal wetland, assigned sex, age = 0, size = 1.5, and colored light green. Their natal-wetland is recorded and has-bred? is reset to false. Wetland-level results, including number of mothers, number of female and male offspring, and the final survival rate, are appended to the output CSV each year.

Emigrate:

- For adults (males ≥2, females ≥3), the procedure first applies a survival draw. Adults that have never bred survive with probability 0.390, while those that have bred before survive with probability 0.639 (from Crawfish frog estimates)(Terrell et al., 2023). Survivors attempt home-first settlement: if home-x, home-y indicate a valid patch, they move there using the same resistance-aware stepwise rule as above (barrier at 10; linear slow-down with k = 0.2; floor 0.02; up to 200 steps). If the home burrow patch has capacity (<5), they stay. If home is invalid or full, they perform a local resistance-aware burrow search within 50 patches (~500 m) using the same find-burrow-resistance-aware logic; if still unsuccessful, they retain their current patch center as their new home. Survivors then set has-bred? ← false and increment times-bred. Adults failing the initial survival draw die.
- Juveniles (age 0) undergo a multi-day dispersal from the wetland to an overwintering location. Each day, they must pass an 82.2% (Table A4.3) daily survival check or die immediately. If they survive the day, they draw a total daily step length from a Gamma distribution with decreasing mean values (100 m on day 1 tapering to 8 m on day 7,

capped at 500 m) (Hunt, 2019; Thesing, 2023). These values were derived from two telemetry studies on metamorphic Gopher Frogs but were adjusted to reflect 7 days instead of 4 days (Hunt, 2019; Thesing, 2023). The drawn distance is converted into patch units using the realized meters-per-patch and then broken into many mini-steps. Each mini-step follows the same resistance-aware movement rule used elsewhere in the model: patches with resistance = 10 are treated as barriers, triggering up to 10 random re-headings, while movement through passable patches is slowed linearly according to resistance (step-scale = 1 / (1 + 0.2 × resistance)) with a minimum of 0.02 patch units per step. If the frog enters a patch flagged as a burrow and the burrow has capacity (<5 occupants), it immediately settles, marks itself as settled, and stops moving.

- After seven days, any juveniles still alive face a final 0.46 (Table A4.3) survival probability check. Those that die are logged as post-movement deaths. Survivors that never located a burrow are logged as "gave up" and simply record their final patch coordinates as their home-x and home-y. Counters for each outcome (settled, died during movement, died after movement, gave up) are updated and summarized each year.

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Tables and Figures

Table A4.1. Wetlands included in the model, with their corresponding ID, hydroperiod, canopy cover, initial status, genetic string, and area.

Wetland Id	Hydroperiod	Canopy Cover	Genetics	Area (m^2)	Initialize
37	Semi	Closed	AAAAAAAAAAAAAAAAAAAA	25206	1
54	Semi	Semiopen	BBBBBBBBBBBBBBBBBBBB	14819	1
55	Ephemeral	Closed	CCCCCCCCCCCCCCCCCCCC	8824	1
127	Semi	Semiopen	DDDDDDDDDDDDDDDDDDDD	10492	1
55B	Ephemeral	Closed	EEEEEEEEEEEEEEEEEEEE	1880	1
41	Semi	Closed	FFFFFFFFFFFFFFFFFFFF	15648	1
41B	Permanent	Open	GGGGGGGGGGGGGGGGGGGG	212	1
22	Ephemeral	Semiopen	HHHHHHHHHHHHHHHHHHHH	7410	1
21	Ephemeral	Semiopen	IIIIIIIIIIIIIIIIIIII	6105	1
45	Ephemeral	Closed	JJJJJJJJJJJJJJJJJJJJ	29142	1
46	Ephemeral	Closed	KKKKKKKKKKKKKKKKKKKK	3832	1
59	Ephemeral	Open	LLLLLLLLLLLLLLLLLLLL	50623	1
60	Ephemeral	Open	MMMMMMMMMMMMMMMMMMMM	4723	1
112	Ephemeral	Semiopen	NNNNNNNNNNNNNNNNNNNN	3213	1
62	Ephemeral	Semiopen	OOOOOOOOOOOOOOOOOOOO	7150	1
109	Semi	Closed	PPPPPPPPPPPPPPPPPPPP	8692	1
109B	Semi	Open	QQQQQQQQQQQQQQQQQQQQ	654	1
69	Semi	Semiopen	RRRRRRRRRRRRRRRRRRRR	15893	1
69B	Semi	Open	SSSSSSSSSSSSSSSSSSSS	472	1
95	Ephemeral	Semiopen	TTTTTTTTTTTTTTTTTTTT	6693	1
01	Unknown	Semiopen	NA	8804	0
02	Unknown	Semiopen	NA	2908	0
03	Unknown	Open	NA	1037	0
04	Unknown	Semiopen	NA	595	0
05	Unknown	Closed	NA	9737	0
06	Unknown	Open	NA	1041	0
07	Unknown	Open	NA	900	0
08	Unknown	Closed	NA	4125	0
09	Unknown	Semiopen	NA	4144	0
10	Unknown	Open	NA	2565	0
11	Unknown	Closed	NA	8013	0
12	Unknown	Semiopen	NA	9585	0
13	Unknown	Closed	NA	3240	0
14	Unknown	Closed	NA	1748	0
15	Unknown	Closed	NA	1489	0

16	Unknown	Closed	NA	1963	0
17	Unknown	Closed	NA	5234	0
18	Unknown	Closed	NA	3812	0
19	Unknown	Closed	NA	4251	0
20	Unknown	Closed	NA	2214	0
23	Unknown	Semiopen	NA	1237	0
24	Unknown	Closed	NA	2611	0
25	Unknown	Closed	NA	1100	0
26	Unknown	Semiopen	NA	665	0
27	Unknown	Semiopen	NA	1104	0
28	Unknown	Semiopen	NA	1467	0
29	Unknown	Open	NA	958	0
30	Unknown	Open	NA	2106	0
31	Unknown	Open	NA	1379	0
32	Unknown	Closed	NA	6889	0
33	Unknown	Semiopen	NA	3555	0
34	Unknown	Semiopen	NA	1335	0
35	Unknown	Closed	NA	1748	0
36	Unknown	Closed	NA	3717	0
38	Unknown	Semiopen	NA	8196	0
39	Unknown	Semiopen	NA	3230	0
40	Unknown	Closed	NA	1582	0
42	Unknown	Closed	NA	10872	0
43	Unknown	Open	NA	5637	0
44	Unknown	Closed	NA	7957	0
47	Unknown	Closed	NA	2985	0
48	Unknown	Closed	NA	4032	0
49	Unknown	Closed	NA	45446	0
50	Unknown	Closed	NA	1614	0
51	Unknown	Closed	NA	6565	0
52	Unknown	Semiopen	NA	1981	0
53	Unknown	Closed	NA	2860	0
56	Unknown	Semiopen	NA	7712	0
57	Unknown	Closed	NA	251921	0
58	Unknown	Closed	NA	4823	0
61	Unknown	Semiopen	NA	7223	0
63	Unknown	Semiopen	NA	9066	0
64	Unknown	Semiopen	NA	1584	0
65	Unknown	Closed	NA	3375	0
66	Unknown	Closed	NA	13250	0

67	Unknown	Semiopen	NA	15294	0
68	Unknown	Closed	NA	19773	0
70	Unknown	Closed	NA	6916	0
71	Unknown	Closed	NA	1280	0
72	Unknown	Closed	NA	1751	0
73	Unknown	Closed	NA	2168	0
74	Unknown	Open	NA	1410	0
75	Unknown	Closed	NA	5415	0
76	Unknown	Closed	NA	6030	0
77	Unknown	Semiopen	NA	2513	0
78	Unknown	Semiopen	NA	5510	0
79	Unknown	Closed	NA	4443	0
80	Unknown	Closed	NA	7721	0
81	Unknown	Closed	NA	3277	0
82	Unknown	Closed	NA	4577	0
83	Unknown	Closed	NA	2325	0
84	Unknown	Closed	NA	2091	0
85	Unknown	Closed	NA	2945	0
86	Unknown	Semiopen	NA	1601	0
87	Unknown	Closed	NA	1269	0
88	Unknown	Closed	NA	3947	0
89	Unknown	Closed	NA	1477	0
90	Unknown	Closed	NA	1907	0
91	Unknown	Semiopen	NA	5297	0
92	Unknown	Closed	NA	1264	0
93	Unknown	Closed	NA	71289	0
94	Unknown	Closed	NA	25715	0
96	Unknown	Closed	NA	22737	0
97	Unknown	Semiopen	NA	6960	0
98	Unknown	Closed	NA	6957	0
99	Unknown	Semiopen	NA	2992	0
100	Unknown	Open	NA	1963	0
101	Unknown	Open	NA	2233	0
102	Unknown	Semiopen	NA	2719	0
103	Unknown	Closed	NA	1272	0
104	Unknown	Semiopen	NA	2045	0
105	Unknown	Semiopen	NA	9145	0
106	Unknown	Semiopen	NA	3963	0
107	Unknown	Closed	NA	1104	0
108	Unknown	Closed	NA	1009	0

110	Unknown	Closed	NA	3925	0
111	Unknown	Closed	NA	8891	0
113	Unknown	Closed	NA	10296	0
114	Unknown	Closed	NA	3851	0
115	Unknown	Closed	NA	23209	0
116	Unknown	Closed	NA	4343	0
117	Unknown	Closed	NA	2924	0
118	Unknown	Closed	NA	4949	0
119	Unknown	Closed	NA	10353	0
120	Unknown	Closed	NA	26010	0
121	Unknown	Semiopen	NA	576	0
122	Unknown	Closed	NA	7326	0
123	Unknown	Semiopen	NA	2619	0
124	Unknown	Closed	NA	11769	0
125	Unknown	Closed	NA	1367	0
126	Unknown	Open	NA	750	0
128	Unknown	Closed	NA	9421	0
129	Unknown	Closed	NA	10495	0
130	Unknown	Closed	NA	11968	0
131	Unknown	Closed	NA	787	0
132	Unknown	Closed	NA	1870	0
133	Unknown	Closed	NA	1074	0
134	Unknown	Closed	NA	4498	0
135	Unknown	Semiopen	NA	2864	0
136	Unknown	Semiopen	NA	937	0
137	Unknown	Closed	NA	5614	0
138	Unknown	Semiopen	NA	1413	0
139	Unknown	Closed	NA	1087	0
140	Unknown	Semiopen	NA	2695	0
49FB	Unknown	Open	NA	466	0

Table A4.2 Land cover types included in the model, with their corresponding resistance values and the values used when resistance was varied during simulations.

Land cover	Resistance	Upper, Lower Simulation Value
Pine Plantation	2	0,4
Successional Hardwood Forest	5	
Southern Atlantic Coastal Plain Salt And Brackish Tidal Marsh	10	
Atlantic Coastal Plain Streamhead Seepage Swamp, Pocosin, And Baygall	3	0,6
Open Field	1	
Southern Atlantic Coastal Plain Nonriverine Swamp And Wet Hardwood Forest	4	0,8
Quarry/Stripmine	10	
Southern Atlantic Coastal Plain Maritime Forest	3	0,6
Successional Mixed Pine-Hardwood Forest	3	
Southern Coastal Plain Hydric Hammock	3	
Southern Atlantic Coastal Plain Depression Pondshore	1	
Early Successional Vegetation	5	
Southern Atlantic Coastal Plain Wet Pine Savanna And Flatwoods	0	
Estuarine And Inshore Marine Waters	10	
Developed	10	
Southern Atlantic Coastal Plain Tidal Wooded Swamp	8	
Successional Pine Forest	4	
Canal	8	
Southern Coastal Plain Oak Dome And Hammock	1	
Atlantic Coastal Plain Upland Longleaf Pine Woodland	0	
Transportation	1	
Southern Atlantic Coastal Plain Fresh And Oligohaline Tidal Marsh	10	
Open-Water Ponds And Lakes	0	

Table A4.3. Steps used to calculate daily survival during the first 7 days, and the annual survival used until a frog matures.

Step	Description	Equation	Result
1	Compute total survival across 2.75 years, because age 3 is the typical age at maturation. The 2.75 years represents 7 days of early juvenile survival plus 2.5 years of post-juvenile survival leading up to age 3.	$.298^{2.75}$	= 0.036
2	Use an empirically derived 7-day survival of 0.25, based on two telemetry studies (Hunt, 2019; Thesing, 2023) that reported 20–25 % survival during the first week post-emergence. Solve for the annual survival probability during the remaining 2.5 years so that total survival to age 3 matches the annual survival of 0.298.	$0.25 * x^{2.5} = 0.036$	x = 0.4606
3	Back-calculate daily survival during first 7 days	$x^7 = 0.25$	x = 0.822

Table A4.4. Steps used to calculate the total larval survival, and the number of age = 0 juveniles produced.

Component	Equation / Value	Notes
Scaled Female Density	$N = \frac{F}{A} \times 1644$	(F) = Number Of Breeding Females; (A) = Wetland Area (M^2); Scaled To Reference Area 1644 M^2
Density-Dependent Survival (Terrell et al., 2023)	$S_{dens}(N) = 0.0346/(1 + e^{0.085*(N-27)} + \varepsilon)$	Logistic Function; Declines With Higher Density With E Modeled As A Gaussian Function With A = 0.008, B= 25, And C= 9.
Wetland Multiplier (W) (Burrow & Maerz, 2021)	Closed Canopy, Wet Year = 0.25 Semi Open Canopy, Wet Year = 0.75 Open Canopy, Wet Year = 0.90 Closed Canopy, Other Years = 0.00 Semi Open Canopy, Other Years = 0.75 Open Canopy, Other Years = 0.90	Accounts For Weather × Canopy Condition
Total Larval Survival	$S = S_{dens(N)} * W$	Bounded Between 0 And 0.35
Offspring Produced	$offspring = round\ (F * 2000 * S)$	Each Female Lays 2,000 Eggs; Survival Fraction Determines Recruits

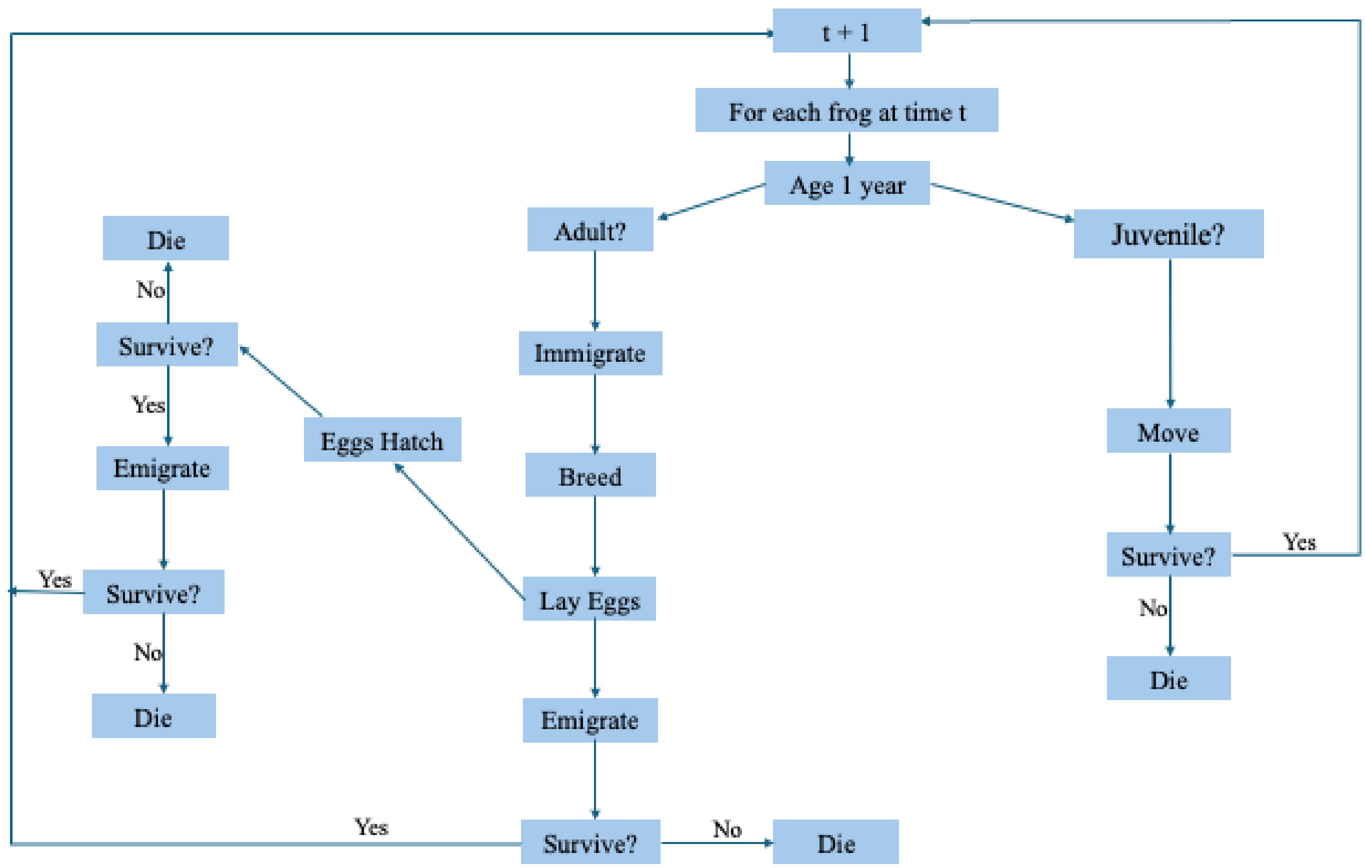

Figure A4.1. For each frog at time t, the above flow chart is followed.