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# Animal Movement in a Changing World

By

Tristan A. Nuñez

A dissertation submitted in partial satisfaction of the
requirements for the degree of
Doctor of Philosophy
in
Environmental Science, Policy and Management
in the
Graduate Division
of the
University of California, Berkeley

Committee in charge:

Professor Justin S. Brashares, Chair
Professor Wayne M. Getz
Professor Anthony D. Barnosky

Fall 2017

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# ABSTRACT

## Animal Movement in a Changing World

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Animal movement influences ecological and biogeographical dynamics, and studying it reveals helpful insights at a time when anthropogenic activities have accelerated rates of climatic and land cover change. This dissertation addresses three fundamental questions in ecology and biogeography linked to the movement and distribution of animals. First, how do animal movements affect their environments? Second, how do the effects of land use change interact with atmospheric climate change to alter species distributions? Third, how do organisms track their climatic niches through time and space? Each question is addressed with a separate study, each generating methods and results with implications for future academic work, management, and conservation.

In the first study, I tracked the daily movements of the common hippopotamus, *Hippopotamus amphibius*, a megaherbivore that transports nutrient-rich biomass between terrestrial and aquatic ecosystems. I developed a spatially explicit biomass transfer model that relates rates of ingestion and egestion to movement behavior states derived from the movement data. The biomass transfer model revealed the process by which *H. amphibius* generates patterned landscapes of nutrient removal and deposition hotspots. In addition, the model generated maps of these nutrient transfer landscapes, making it possible to explore the spatial dynamics of nutrient transfers, and showing that the amount of biomass transferred reaches levels equivalent to rates of aboveground net primary productivity. In addition to revealing the influences of *H. amphibius* on ecosystem ecology, this study also provided metrics of home range size, habitat use, and movement behavior useful for conservation planning.

The first study provides a method for nutrient transfer mapping which could be applied to many other species, and leverages increasing quantities of high-resolution movement tracking

data to map transfers of nutrients across landscapes. This can help predict the landscape-scale ecological changes resulting from the loss of animal movements that provide nutrient transfers. The approach can also be used to map other material transport dynamics, such as animal-transported seed dispersal or the movement of persistent organic pollutants.

In the second study, I used species distribution modeling to identify the interacting effects of climate and land use change on the distribution of *H. amphibius*. Hydrologic change is likely to result from ongoing shifts from rain-fed to irrigated agriculture across much of sub-Saharan Africa, where *H. amphibius* occurs. A lack of spatial data on hydrology, especially data temporally consistent with atmospheric climate datasets, has made it difficult to build species distribution models for semiaquatic species, such as *H. amphibius,* which are physiologically dependent on surface water. I overcame this challenge by coupling a simple hydrologic model to scenarios of land use and climate change, identifying potential effects on *H. amphibius* distributions. I found that increased levels of streamflow abstraction from irrigation will lead to much greater declines in *H. amphibius* habitat suitability than arise from scenarios of climate change alone. I also contrasted predictions of *H. amphibius* distributions that incorporated only atmospheric climate variables to predictions that also incorporated hydrologic variables, and found significant improvements in model performance when hydrology was incorporated.

The second study provides support for using predictive variables with strong mechanistic links to the physiology or ecology of the focal species when building species distribution models. The study also outlines a way to generate surfaces of key hydrologic variables from the climate surfaces commonly used for species distribution modeling. These surfaces have the potential to greatly improve forecasts generated by other semiaquatic species distribution models. From a conservation perspective, the second study highlights the potential for substantial losses of *H. amphibius* habitat across Africa as a result of increases in irrigation development. Other semiaquatic species in the region, as well as those dependent on the keystone ecological role of *H. amphibius* and its nutrient-transporting movements, may be similarly affected.

In the third study, I explored the role of movement in shaping species distributions in variable climates. Climatic variability at multiple time scales causes suitable climatic conditions to shift across geographic space. Recent scholarship has proposed that two species traits, the ability to colonize suitable locations, referred to as dispersal, and the ability to continue to occupy an area with unsuitable conditions, referred to as persistence, facilitate niche tracking, the process by which species follow suitable conditions moving through geographic space. By developing a model that simulates niche tracking through historically observed patterns of temporal and spatial variability, I quantified how different dispersal and persistence abilities affect niche tracking potential. I found that both dispersal and persistence facilitate niche tracking, and that small increases in persistence ability result in surprisingly large increases in niche tracking potential.

The third study makes two main contributions to ecological niche theory and distribution modeling. The first contribution is to extend niche theory to explicitly address niche tracking, enabling the spatially and temporally explicit mapping of niche tracking dynamics on real landscapes. The second contribution is to quantify the effects on niche tracking potential of increasing persistence and dispersal abilities across real climate surfaces. The results suggest that climate adaptation actions should focus not just on the ability of species to move in response to climate change, but also on their ability to persist through periods of unsuitable conditions.

# TABLE OF CONTENTS

# ACKNOWLEDGEMENTS

I am deeply grateful to the many who have advised, guided, funded, facilitated, and otherwise supported this dissertation through contributions large and small. First, to Justin Brashares, my advisor, for his patient but determined guidance, fearless willingness to bridge disciplines and communities, and facilitation of a world-class lab group. Justin's mentoring approach, emphasizing both personal and professional growth and supporting his students as people while also preparing them as emerging scholars, has been invaluable on this journey. I would also like to acknowledge the assistance and inspiration I received from the members of my dissertation committee. Wayne Getz, for his infectious enthusiasm for movement ecology, the gift of bringing out the quantitative ecologist in us non-mathematicians, and always having an appropriate citation ready at hand. Anthony Barnosky, for encouragement that extended well before I arrived at Berkeley, and for his insightful perspective: not just his disciplinary perspective, but also for his optimistic and enthusiastic approach to doing and communicating the science of global change.

The tangled bank of ecological and environmental scientists at the University of California, Berkeley, has been a wonderful intellectual environment to work in. I thank the members of my Qualifying Exam committee, including Adina Merenlender, who has continued to keep me connected to the world of climate adaptation and conservation planning, and Rauri Bowie, for graciously introducing me to the world of phylogeography. David Ackerly has selflessly shared invaluable insights on species distribution modeling and biogeography. Sally Thompson, of Civil and Environmental Engineering, went above and beyond in connecting and walking me through relevant and tractable literature on hydrologic modeling. The members of my graduate student cohort, as well as the Brashares, Getz, Middleton, Merenlender, and Kelly labs, have all provided a community of supportive and committed friends and fellow scholars. Iryna Dronova of Landscape Architecture and Environmental Planning provided a great introduction to the world of remote sensing and guided a related project on animal trail mapping. I also wish to acknowledge the intellectual community and preparation I gained at the University of Washington' School of Environmental and Forest Sciences, where I did my master's degree. That preparation and community inspired much of my dissertation work, and I particularly owe an intellectual debt to my master's advisor Joshua Lawler and former lab mate Carrie Schloss. At UW I also benefitted enormously from working with Brad McRae of The Nature Conservancy, who sadly passed away earlier this year, but whose work, dedication, and good humor will always be a personal and professional inspiration.

The collection of the hippopotamus movement data underlying Chapter 2 was only possible as the result of much effort by many people. Foremost, Douglas McCauley at the University of California, Santa Barbara, whose logistical, fundraising and intellectual groundwork made the hippopotamus tracking work possible. Doug has mentored me academically and through organizing and running the field campaign, and in all respects was a de facto committee member. Ian Warrington and Matthew Snider both contributed many months' worth of hard work on hippopotamus tracking with keen insight, innovation, and unflagging positivity. Logistical support, advice, and permission to conduct the study also came from the Government of Kenya, the Kenya Wildlife Service, the Kenya National Commission for Science, Technology and Innovation, the Mpala Research Centre, National Museums of Kenya, Dr. Isaac Lekolool, Dr. Mathew Mutinda, Margaret Kinnaird, and Henrik Rasmussen; academic support from Rebecca Lewison, Mary Power, Todd Dawson, Adam Ford, and Kelly Caylor. Jennifer

Guyton, Tara Hetz, Lacey Hughey, Cecilia Hyland, Peter Lokeny, John Naisikie Mantas, Merrill McCauley, and Michelle Thibodeau all provided invaluable field assistance. Funding was provided by the National Science Foundation (IRFP OISE #1064649 and DEB #1146247, and through the Graduate Research Fellowship Program), the Rocca Foundation, and the National Geographic Committee for Research and Exploration.

In addition to Sally Thompson's guidance on hydrologic modeling, Chapter 3 was supported by Pete Coppolillo's sharing of background data and insights into the effects of irrigation on the hippopotamus populations of the Ruaha. Ian Games facilitated access to *H. amphibius* survey data. Camila Quintana, Avery Hardy, Iris Berger, Lynna Ohanian, Rebecca Hernandez, and Kelsey Foster all provided valuable help with literature and spatial data collection, digitization, and analysis through the Undergraduate Research Apprenticeship Program. Additional funding for completion of the dissertation came from University of California Berkeley Chancellor's and Continuing fellowships, the Department of Environmental Science, Policy, and Management, and the Oliver B. Lyman Student Endowment in Wildlife and Fisheries.

Finally, this work would not have come to be without the loving support of my family. I thank my mother for an upbringing and education that had me thinking about wild places and wild things from an early age. My sister and brother-in-law have helped me keep it all in perspective. I am continually inspired and humbled by my children, whose interest in and never-ending questions about wildlife and the outdoors bring home the importance of science and stewardship on every walk we take, and who bring immeasurable joy into my life. And above all, gratitude beyond words to my wife, Lisa Dermer; more than to any other, it is to her that I owe the completion of this dissertation. Her support of this work was present at every stage in so many forms, and ran the gamut from living on a remote Kenyan field station with our toddlers to advice and professional editing. She has all of my love, respect, and admiration.

# CHAPTER 1

## General Introduction

Across the history of our species we have been inspired and intrigued by the movements of wild animals, drawing them on cave walls and featuring them in high definition video documentaries. With good reason: the movements of animals are consequential. Animal movement plays important ecological roles that shape ecosystems and environments, the geographic distributions of species, and ultimately affect human societies and economies. Animal trails can directly leave traces on land surfaces that can persist for centuries or alter geomorphologic processes (Clayton, 1975; McCarthy *et al.*, 1998), and movement enables both the daily routines and seasonal migrations of hungry herbivores that shape plant diversity and vegetation patterns and transfer or transform stocks of biomass (Huntly, 1991; Getz, 2011). The effects of movements can also be indirect, and include the transport of nutrients, seeds, or pathogens (Polis *et al.*, 1997; Cross *et al.*, 2005; Cousens *et al.*, 2010). Movement ability also shapes the distribution of species, facilitating range shifts, invasion dynamics, and insect outbreaks (Urban *et al.*, 2013). As we enter a time of unprecedented, anthropogenically accelerated ecological and biophysical change, a better understanding of the ecological and biogeographical role of animal movement will inform management efforts intended to help societies and ecosystems adapt (Nathan, 2008; Heller & Zavaleta, 2009; Barnosky *et al.*, 2012).

Two themes provide the organizational warp and weft of this dissertation. The first theme is topical, and focuses on how animal movements and distributions interact with a dynamic and changing environment. The first study (Chapter 2) seeks to understand how animal movement affects the environment, while the second study (Chapter 3) focuses on the effects of environmental change on species distributions, and the third study (Chapter 4) addresses how animal movement mediates the effects of climate dynamics on species distributions. The second theme is the common methodological approach supporting the dissertation's chapters. Each chapter approaches fundamental ecological questions with conceptual and quantitative models linked by increased computational speeds to large datasets generated by emerging technologies. The aspiration of this work is to add to our understanding of fundamental ecological processes in order to help human societies make more informed decisions about the ways we influence the movement and distribution of wildlife, the functioning of ecosystems, and the environments we share.

A robust body of research in the field of ecosystem ecology has quantified transfers of material and energy between ecosystems by animals ranging from insects to wolves to whales, greatly improving our understanding of how ecosystems are linked to each other (Power *et al.*, 2004; Darimont *et al.*, 2009; Doughty *et al.*, 2016). Simultaneously, interest has emerged in understanding how nutrient dynamics are spatially structured across landscapes within ecosystems, both within the fields of landscape ecology and the emerging field of landscape biogeochemistry (McClain *et al.*, 2003; Turner & Gardner, 2015). Few studies have spatially mapped the distribution of animal-transported nutrients across landscapes, a prerequisite to quantifying animal-driven nutrient transfer spatial dynamics (Moe & Wegge, 2008; Gillet *et al.*, 2010). However, an explosion of animal tracking data and analysis techniques is now making it possible to map animal behavioral states derived from animal movement data (Tracey *et al.*, 2013; Kays *et al.*, 2015). In the first study (Chapter 2), I link movement behavior to ingestion and egestion rates, allowing me to spatially map nutrient transfer by the common hippopotamus, *Hippopotamus amphibius.* To do so, I collected GPS tracks of *H. amphibius* daily movements at high temporal resolutions, in the first movement tracking study of the species. This nutrient transfer modeling approach quantifies the amount and spatial configuration of *H. amphibius*-transported nutrient transfer, and explicitly links movement behavior to nutrient transfers. The GPS data also provides fundamental insights into *H. amphibius* movement behavior and habitat use.

*Hippopotamus amphibius* is a semiaquatic megaherbivore that transits daily between terrestrial feeding grounds and aquatic refuges. It ingests grasses on land from grazing lawns that it maintains by repeated grazing, and then egests elsewhere on land or in refuge pools (Eltringham, 1999). Through its movements the species transports substantial amounts of nutrients which are then incorporated in the aquatic food chain, and at times alters river geomorphology with its trails (McCarthy *et al.*, 1998; Verweij *et al.*, 2006; McCauley *et al.*, 2015; Subalusky *et al.*, 2015). *H. amphibius* is classified as vulnerable by the International Union for the Conservation of Nature, because it has experienced declining populations and a shrinking distribution in recent decades (Lewison & Oliver, 2008). Land use change, including water diversion for irrigation, is thought to be a major source of population declines (Stommel *et al.*, 2016). Africa's irrigation potential is the least developed of any continent, and increasing irrigated agriculture is a central focus of development lenders, national governments, and international investors (You *et al.*, 2011). Concerns have also been raised that climate change will threaten African mammals, although the potential effects of climate change on *H. amphibius* distributions have been difficult to model (Thuiller *et al.*, 2006).

Species distribution models are a commonly used approach to predicting how species will respond to climate change (Elith & Leathwick, 2009). Less common are species distribution models which simultaneously address the effects of climate change and land use change in predicting distributions. However, the effects of land use-driven hydrologic change resulting from irrigation development need to be addressed in projections of future distributions of *H. amphibius* to be informative. Building such a model for *H. amphibius* or other similarly vulnerable semiaquatic species faces a major challenge, in that datasets of hydrologic variables coupled to baseline or future atmospheric climate conditions are not readily available (Domisch *et al.*, 2015a). To overcome this challenge, in the second study (Chapter 3), I linked a simple hydrologic model to Worldclim, a commonly used atmospheric climate dataset (Hijmans *et al.*, 2005). Doing so provided coupled datasets of atmospheric and hydrologic variables for both baseline conditions and projections of future climates. Hydrologic variables I generated using this model included streamflow and climatic water deficit, which are proxies for the availability of water and forage for *H. amphibius*. This enabled the study's main objective, assessing future potential distributions of *H. amphibius* under scenarios of land use and climate change. Additional objectives for the study included evaluating whether incorporating hydrologic variables increased the predictive ability of the species distribution model relative to using only atmospheric variables, and understanding how hydrology-informed projections differed spatially from atmospheric-only projections.

In my third study (Chapter 4), I explored the role of dispersal movements in enabling species to track suitable habitats through time. Ecological niche theory underlies species distribution modeling, and assumes that climates are stable at interannual to interdecadal timescales (Soberón, 2007). However, climatic conditions vary at these timescales, causing the geographic distribution of suitable conditions to shift from year to year or decade to decade. The process by which species follow suitable conditions moving through geographic space is called niche tracking (Tingley *et al.*, 2009). Recent empirical and theoretical work on niche tracking has argued that two species traits, dispersal (the ability to reach suitable locations) and persistence (the ability to continue to occupy an area with unsuitable conditions), affect the ability of species to track their niches (Schurr *et al.*, 2007; Jackson *et al.*, 2009; Early & Sax, 2011). However, the effects of different dispersal and persistence abilities on niche tracking had not been quantified for real climate surfaces. The objectives of the third study, then, were to quantify the relative importance of dispersal and persistence abilities in facilitating niche tracking, and to evaluate whether the effects of dispersal and persistence on niche tracking differ among climates. I extended an existing set-theory based conceptual model of species distributions to incorporate the niche tracking process and temporal variability in suitability (Soberón, 2007). I then used an extensive dataset of observed climate surfaces at high temporal and spatial resolution (annual timesteps across 85 years across the contiguous United States at a 4 km resolution) to simulate niche tracking for different species niches (Daly *et al.*, 2008). This exercise revealed the relative importance of dispersal and persistence, and provides a framework to move beyond the problematic assumptions of climatic equilibrium underlying conventional approaches to species distribution modeling.

In this introductory chapter, I highlighted organizing themes of the dissertation, how these themes are expressed in each chapter, and disciplinary context for the questions which each chapter sets out to address. In the second chapter, I used *H. amphibius* GPS tracking data to map the terrestrial and aquatic landscapes of nutrient transfer generated by their daily foraging and resting movements. In the third chapter, I coupled a simple hydrologic model to baseline and future atmospheric climate surfaces, and used resulting hydrologic and climatic surfaces with *H. amphibius* occurrences to improve predictions of present-day and future *H. amphibius* habitat suitability. In the fourth chapter, I extended niche theory to incorporate niche tracking through spatially and temporally variable climates, quantifying the effects of persistence and dispersal on the ability of species to track their niches. In the concluding chapter I addressed the general implications of my findings and avenues for future work.

# CHAPTER 2

## Hippopotamus movements produce heterogeneous nutrient landscapes

### Abstract

Flows of nutrients across and within ecosystems affect ecosystem composition, structure and functioning. Mobile organisms are important nutrient transport agents, but few studies have quantified the spatial intensity and distribution of animal-transported nutrient flows. However, advances in animal tracking technologies provide an opportunity to quantitatively assess the spatial patterns of these nutrient transfers at ecologically relevant scales. Consequently, we tracked the common hippopotamus (*Hippopotamus amphibius)*, a megaherbivore that transports nutrient-rich biomass between terrestrial and aquatic ecosystems and whose movements have never been electronically tracked. From these movement data we developed a spatially explicit biomass transfer model to reveal *H. amphibius* biomass removal and deposition hotspots. Our model also illuminates the specific behavioral processes underpinning the dynamics of biomass transfer and concentration. These first insights into how *H. amphibius* mechanistically influences ecosystem ecology may also help predict the biomass transfer dynamics of other species.

### Introduction

Research quantifying transfers of material and energy between ecosystems by mobile organisms has greatly improved our understanding of ecosystem dynamics (Polis *et al.*, 2004; Bartels *et al.*, 2012; Bauer & Hoye, 2014). Fluxes of nutrients vectored across terrestrial-aquatic boundaries influence food web structure, increase primary productivity, affect water quality, shape disease dynamics, and alter species diversity, abundance, and composition (Polis *et al.*, 1997; Lundberg & Moberg, 2003). Lateral movements of nutrients between habitat patches within ecosystems are important in similar ways (Barton *et al.*, 2013). Both cross-ecosystem and lateral flows are often highly structured spatially, which can result in spatially heterogeneous landscapes of biogeochemical and ecological processes at local to global scales (Polis *et al.*, 1997; Getz, 2013; Turner & Gardner, 2015; Doughty *et al.*, 2016).

While the importance of allochthonous nutrient transfers is becoming increasingly well understood, the mechanics by which the movement and behavior of mobile organisms controls the spatial distribution of nutrient flows remains much less explored. There is considerable variability in the spatial ecology of mobile organisms, which likely results in very different patterns of material transfer. For example, some species spread nutrient-rich biomass across the landscape, while others remove or deposit biomass in clumped or restricted locations (Willson S.M. Gende & Marston, 1998; Sanderson & Harris, 2002; Ben-David *et al.*, 2005; Hempson *et al.*, 2015). In particular, transfer hotspots (patches with disproportionately high levels of nutrient removal or deposition relative to the surrounding matrix) are crucial to understanding landscape biogeochemistry, vegetation dynamics, and patch structure (McClain *et al.*, 2003; Barton *et al.*, 2013).

Advances in tracking technologies and analytical approaches from the field of movement ecology present new opportunities to better understand animal-mediated nutrient transfers and their resultant fine-scale spatial patterns (Getz & Saltz, 2008). Specifically, these advances allow researchers to segment animal movement paths into movement behavior states (e.g. foraging, resting, travelling), and map these states spatially, allowing direct measurement of the time and space allocated to each state (McClintock *et al.*, 2013; Edelhoff *et al.*, 2015; Gurarie *et al.*, 2016). In addition, recent conceptual work has outlined ways in which different kinds of consumers shift stocks of biomass between different pools through biomass transformation webs (Getz, 2011). In this paper, we use these path segmentation approaches to develop a new spatially explicit model of biomass transfer by linking each movement state to rates of ingestion and egestion.

We apply this biomass transfer model to quantify the spatial patterns of nutrient-rich biomass transfer by the common hippopotamus (*Hippopotamus amphibius*). *H. amphibius* is a semiaquatic megaherbivore that transits daily between terrestrial feeding grounds and aquatic refuges. It ingests grasses on land, particularly from closely-cropped grazing lawns, and then egests them elsewhere on land and into adjacent river or lake ecosystems. In river systems, individuals rest for long portions of the day in social groupings in spatially-restricted daytime refuge pools, creating the possibility for high concentrations of egested biomass. As a result of this dynamic, *H. amphibius* is an important biotic nutrient vector and shapes African ecosystem ecology (Eltringham, 1999; McCauley *et al.*, 2015; Subalusky *et al.*, 2015).

*Hippopotamus amphibius* has never been electronically tracked, and little is known about the mechanisms by which these intra- and inter-ecosystem transfers are achieved. Likewise, large gaps remain in understanding the behavioral and spatial ecology of *H. amphibius*. We used high-resolution GPS tracking and accelerometer data collected from *H. amphibius* to answer four core questions: (1) Where are the source and deposition areas for biomass transferred by *H. amphibius*?; (2) What are the relative amounts of biomass movement to different areas?; (3) Does biomass become more concentrated or dispersed spatially as a result of *H. amphibius* activity?; and (4) How do differences in time and space allocated to different behaviors influence biomass redistribution? In addition, we assessed how *H. amphibius* behaviors change with time of day, and quantified nightly travel distances and foraging areas.

## Methods

**Study area.** We tracked *H. amphibius* in the Ewaso Ng'iro river in north-central Kenya, near the Mpala Research Centre (36.90 E and 0.29 N). Based upon land-based and aerial surveys of the region, we estimate the population in this 150-km$^2$ study area at 30 animals, spread along approximately 20 river-kilometers. Although regionally high, this density of animals is low compared to *H. amphibius* densities elsewhere, with censuses documenting over 100 *H. amphibius* per river-kilometer in other areas (Eltringham, 1999). The vegetation surrounding the Ewaso Ng'iro river is a mix of grazing lawns and riparian woodland, bounded by a landscape of interspersed savanna and acacia scrub.

**Study species.** Fecal and stable isotope analyses have found that *H. amphibius*' diet consists predominantly of terrestrial grasses (Eltringham, 1999; Cerling *et al.*, 2008). In particular, *H. amphibius* is noted for creating and maintaining closely-cropped grazing lawns of highly nutritious grass (Verweij *et al.*, 2006). *H. amphibius* spends daylight hours in refuge pools in rivers or in lakes, as it requires immersion to prevent thermal, UV, and water stress (Eltringham, 1999). Isotope and nutrient assays have demonstrated that by urinating and defecating in these pools, *H. amphibius* transfers terrestrial nutrients into aquatic systems, where they subsidise the aquatic food chain (McCauley *et al.*, 2015; Subalusky *et al.*, 2015). Compared to upstream areas lacking *H. amphibius*, reaches with *H. amphibius* have been estimated to have higher concentrations of organic matter, dissolved organic carbon, total nitrogen, and total phosphorus (Subalusky *et al.*, 2015). These nutrients play an important role in the productivity and functioning of aquatic ecosystems and possibly their biodiversity, but may also lead to eutrophic conditions.

**Tagging.** We tagged *H. amphibius* using tracking units capable of recording GPS positions and acceleration (e-Obs GmbH, Grünwald, Germany, adapted by Savannah Tracking Ltd. in Nairobi, Kenya). Tags were dermally affixed to *H. amphibius* via crossbow following methods used to collect spatial data from aquatic and amphibius mammals for which anesthesia poses a drowning risk (Jay *et al.*, 2006; Mate *et al.*, 2007). Thirteen animals were tagged between March 2013 and May 2015. The tracking device was programmed to record a GPS location every 10 minutes. Triaxial accelerometer readings were taken for 8 seconds at 10 Hz at 3-minute intervals from six animals. Tags were deployed across seasons, with 4 tags being deployed in months with little to no precipitation (<0.5 mm), 4 tags deployed in months with intermediate precipitation (39-51 mm), and 5 tags deployed in months with high precipitation levels (71-139 mm, Supplementary Table 1). Tagging was permitted under permissions from the University of California Animal Care and Use Committee, Kenya Wildlife Service, and the Kenya National Commission for Science, Technology and Innovation.

**Behavioral state classification.** We characterized biomass transfer spatial dynamics by using the time allocated to ingestion- and egestion-associated activities of tagged *H. amphibius* to map the transfer of biomass on land and into the river. To achieve these classifications, we first assigned a behavioral state to each GPS fix. Based on nocturnal and diurnal field observations of *H. amphibius* behavior (conducted over a four-year duration at this study site) and visual inspection of the movement data, we manually classified all fixes to one of four major movement behavioral states relevant to biomass transfer: grazing, transit, resting on land, or immersion in water. We then used this manual classification to identify movement metric thresholds for a standardized classification of all fixes. This thresholding classification approach was based on three metrics: velocity, a persistence index (the log of the ratio of velocity to the absolute turn angle), and first passage time (time it takes to cross a circle of a given radius from a focal GPS fix) (Edelhoff *et al.*, 2015). Fixes with velocities greater than 0.09 m/s were classified as transits, except if they had a persistence index less than -2.3 (indicating an tortuous, grazing-like trajectory), in which case they were labeled as grazing movements. Fixes with velocities less than or equal to 0.09 m/s were classified as grazing, unless it had a first passage time greater than 1 hour, in which case they were classified as resting. The first passage time was calculated for a radius of 20 meters, a radius chosen because it encompassed more than 98% of fixes during stationary error tests, and provided a reliable indicator of resting without movement (see Supplementary Text 1). Fixes for which one of the metrics could not be calculated, such as the velocity of the point at the start of a trajectory, were labeled as unclassified.

Missed fixes on land were extremely rare (1 miss out of 3154 fix attempts during tests) and the GPS unit did not record fixes when immersed, as water completely blocks signals from GPS satellites (see Supplementary Text 2). Therefore, periods during which two or more sequential fixes failed, and the previous and subsequent fixes were within 100m of the river, were classified as immersion.

**Activity and time allocation mapping.** Once identified, behaviors were mapped onto the study landscape. We partitioned each animal's movement trajectory into behavioral bouts, defined as sequential fixes with the same behavioral state. We mapped minimum convex polygons (MCP) around the fixes of each grazing and resting bout that lasted for three or more fixes, and calculated the area and amount of time the animal spent in the MCP. Bouts of transit fixes were by definition linear, so we did not map MCPs for transits and excluded transit points from the resulting biomass transfer maps. We also mapped the daytime refuge pools, based on field observations of use by *H. amphibius*, and calculated the amount of time spent in each pool by each tagged animal.

For every minute of the day, averaged across all tracking days, we calculated the proportion of tracks in each behavioral state. As a cross-reference for the behavioral classification, we also calculated activity index values (the mean of the standard deviations of accelerometer readings in gravitational units), for each hour of the day.

**Biomass transfer mapping.** Following activity and time allocation mapping, we proceeded to map the removal, deposition, and net change in biomass of each MCP or daytime refuge pool following use by tagged individuals. We started with the simplifying assumption that the amount of biomass removed or deposited in an MCP or pool is proportional to the amount of time spent in the MCP or pool while engaging in an ingestion- or egestion-associated behavioral state. Grazing was the only ingestion-associated state, while egestion occurred in all states.

We parameterised our removal and deposition rates from estimates developed for another semi-arid system in southern Kenya that were based on data obtained from field and zoo-based feeding studies averaged across wet and dry seasons; (Subalusky *et al.*, 2015) i.e. that a typical 1500 kg *H. amphibius* individual ingests 35.8 kg per day, and egests 17.4 kg per day (Subalusky *et al.*, 2015). All ingestion and egestion rates reported are expressed as wet mass. In other studies, modeled estimates of daily intake rates extend up to 40-50 kg per day per individual (Lewison & Carter, 2004).

To model biomass removal, we specified that removal occurred only when animals were in a grazing movement behavior state, but not while in transit, land resting, or water states. We specified a per-animal average intake rate for the population as a whole of 146 g/min while grazing, which we calculated by dividing mass daily ingestion (above) per day by the mean daily duration of grazing (4.1 +/- 0.96 h). An MCP's biomass removal is the time spent by an animal in the MCP while grazing, multiplied by the average intake rate and divided by the area of the MCP, providing a removal rate in units of g/m$^2$ per grazing event. Removal rates were summed across overlapping MCPs to create a map of removal by all tracked animals.

To model biomass deposition, we specified that egestion occurs during all movement states at identical rates (Cousens *et al.*, 2010). Thus, the time spent by an animal in an MCP or pool, multiplied by the calculated average deposition rate, represents an MCP or pool's biomass gain. By subtracting biomass removal from biomass deposition at any location used by tagged *H. amphibius*, we mapped the net transfer of biomass from tagged animals. In addition, we calculated the average amount of biomass (in kg) deposited while in each state, the spatial concentration (in g/m$^2$) of biomass deposition by state, and the distance to river of each location for each state. Because GPS measurement errors inflate distance traveled for resting and water locations, we specified a generous distance traveled of 20 m for each bout of resting fixes, and the average length of daytime refuge pools, 300 m, for water fixes. All calculations were conducted in the R environment (R Core Team, 2016).

## Results

A total of 13 *H. amphibius* were tracked for 137 km during the study (Fig. 1, Supplementary Table 1). Our GPS tracking of *H. amphibius* identified key source and deposition areas for *H. amphibius*-transferred biomass at a fine spatial grain, and revealed a high degree of heterogeneity and clumping in the spatial distribution and intensity of biomass removal and deposition (Fig. 2). Biomass removal was aggregated spatially, with removal rates highest in grazing lawns. *H. amphibius* acted to increase the spatial aggregation of transferred biomass on the landscape further, with biomass deposition more aggregated on the landscape than biomass removal (Supplementary Figure 1). Modeled rates of biomass removal were as high as 210 g/m$^2$ (all biomass measurements here and subsequently are wet biomass), while rates of deposition extended up to 110 g/m$^2$, across the 33 animal-tracking days used in the model. Net change in biomass in areas utilised by GPS-tagged *H. amphibius* ranged from losses of 190 g/m$^2$ to gains of 110 g/m$^2$.

Terrestrial-aquatic and terrestrial-terrestrial biomass transfers from *H. amphibius* can be summarised by the proportion of daily biomass deposition occurring in each state. Of the estimated 17.4 kg of biomass excreted per day by a typical individual, 3.6 ± 0.8 kg remained in grazing areas and 1.7 ± 1.5 kg were excreted during transits, leaving a net movement of 12 ± 2.5 kg of biomass away from grazing and transit areas. Of this, 11.0 ± 1.1 kg entered the aquatic ecosystem, while the remaining 1.6 ± 1.3 kg was deposited at terrestrial resting sites. Extrapolating to an estimated population of 30 *H. amphibius* in the study system egesting an estimated 522 kg of plant biomass per day, there is a daily transfer of 320 ± 34 kg per day into the river, with an additional 47 ± 39 kg per day moved into terrestrial resting sites. Because terrestrial resting sites were closer to the river than grazing areas, the effect of terrestrial-terrestrial transfers was to shift biomass toward the river (Supplementary Text 3).

The observed patterns of biomass redistribution were driven by large differences in time and space allocation between *H. amphibius* movement states (Fig. 3). Plotting behavioral states against the hour of the day revealed striking patterns in the timing of behaviors contributing to biomass removal or deposition (Fig. 4a). For grazing and transits, the highest levels of activity occurred in the evening between 2000 and 2200 hours, followed by a smaller early-morning peak between 0300 and 0500 hours. The evening peak in grazing was followed by a peak in terrestrial resting activity, occurring between 2300 and 0100 hours. In the early evening water immersion was minimal, but increased after midnight, and at dusk and dawn there were rapid shifts out of and into water, respectively, at 1900 and 0600 hours. The activity index calculated from accelerometer readings provides an independent reference that corresponded with the behavioral schedule derived from GPS fix classification (Fig. 4b).

GPS tracking provided an important supplementary view of other *H. amphibius* behavioral and movement metrics (Supplementary Table 2). The average nightly distance moved was 3100 m (range: 1300-9200; sd = 2200), the area covered by nightly movements averaged 46 ha (range: 4-230; sd = 66), and estimates of the short-term (weekly) foraging area averaged 120 ha (range: 46-250; sd = 92).

## Discussion

Our spatially explicit biomass transfer model provides a novel framework for determining the spatial distribution and the relative amount of allochthonous biomass inputs, as well as the mechanisms underlying why mobile organisms redistribute biomass across ecosystems. We consider each of these aspects below in the context of transfers by *H. amphibius.* Past studies that quantified biomass fluxes from aquatic invertebrates as a function of distance from water have greatly clarified our understanding of aquatic-terrestrial linkages (Power & Rainey, 2000). Our approach builds from these studies, enabling researchers to harness the recent increase in the availability and temporal sampling rates of GPS and accelerometer data to address transfers of biomass by larger organisms and at finer resolutions (Kays *et al.*, 2015).

Building a better understanding of the spatial patterns of biomass redistribution facilitates scholarship relating biomass transfers to landscape patterns of terrestrial vegetation, soil fertility and biogeochemistry, and the productivity of aquatic communities. Previous studies have documented changes in vegetation dynamics and patch structure as a result of biomass transfer hotspots from grazing or deposition of dung or carcasses (Payne & Moore, 2006; Moe & Wegge, 2008; Gillet *et al.*, 2010; Barton *et al.*, 2013). This research on hotspots and other spatial patterns of biomass transfer has, however, been challenging in part because of the difficulty in mapping transfers at fine spatial scales (Bardgett & Wardle, 2003; McClain *et al.*, 2003; Groffman *et al.*, 2009; Holtgrieve *et al.*, 2009). Our model helps to overcomes these issues by using fine scale animal movement data to directly map the transfer process.

For example, mapping of *H. amphibius* biomass transfers highlights the species' creation of transfer hotspots and resulting ecological dynamics. Our finding that 63 percent of biomass egested by *H. amphibius* is deposited in water, and that these aquatic depositions by *H. amphibius* are highly clumped, reinforces findings made in this same system that showed that fish and invertebrates found in *H. amphibius* daytime refuge pools exhibit tissue chemistry indicative of reliance on *H. amphibius* excreta (McCauley *et al.*, 2015). These findings overall suggest that recent declines in H. amphibius abundance (i.e. estimated between 7 and 20 % per decade) and contractions of the geographic distribution for this species are likely to have resulted in changed rates of biomass fluxes for African rivers, with potential effects on the diversity and abundance of aquatic biota (Lewison & Oliver, 2008). Although only 9 percent of biomass egested by *H. amphibius* was transferred to terrestrial resting sites, our model suggests these sites also become nutrient transfer hotspots because they are highly discrete landscape features and are used repeatedly. This raises the question of whether vegetation at *H. amphibius* terrestrial resting sites responds to these inputs with changes in productivity and species composition similar to responses observed at rest sites of other ungulates or livestock in this same region of study (Augustine *et al.*, 2003).

Understanding the relative magnitude of biomass moved by mobile organisms is also fundamental to evaluating the importance of biomass transfers. In the case of *H. amphibius*, if transfer rates modeled for our tracked animals are projected across an entire year, deposition rates are as high as 129 g (C) $yr^{-1}m^{-2}$ $individual^{-1}$ and removal rates as high as 171 g (C) $yr^{-1}m^{-2}$ $individual^{-1}$. These are significant quantities considering that observed average aboveground net primary productivity only ranges from 100 to 300 g (C) $yr^{-1}m^{-2}$ in the system (Sankaran, 2004). That *H. amphibius* transfers are comparable in magnitude to rates of net primary productivity suggests that the redistribution of nutrients by herbivores at fine spatial scales should explicitly be taken into consideration in landscape-scale studies of nutrient availability, soil fertility, or carbon cycling. Our estimates of *H. amphibius* transfer rates are not directly or quantitatively comparable to the nutrient diffusion rates modeled for megafauna in Doughty et al. (2016) (which are presented in units of square kilometers per year), but qualitatively, our results suggest that nutrient transfer by *H. amphibius* over short terms is a concentrating rather than diffusive process. Doughty et al. assume that over geologic time periods, faunal nutrient transfer is a diffusive process driven by random walk approximations of animal movement. Further theoretical and empirical work is needed to clarify whether the non-random movement behaviors revealed by the *H. amphibius* short-term GPS tracking data scale over long periods of time into diffusive processes, or if concentrating dynamics remain.

Additionally, our framework provides a better understanding of how biomass redistribution is mechanistically linked to the time and space budgets of different animal behaviors. In the case of *H. amphibius*, its allocation of time and space leads to a biomass concentrating effect, because it spends a short amount of time ingesting (30% of total time) in a larger area (86% of distance traveled), and a long time resting (70% of total time) in a more restricted area (14% of distance traveled, Fig. 3). The concentrating effect of *H. amphibius* is ecologicaly similar to the biomass-concentrating effects of many bats and seabirds, which forage over large areas but rest in restricted locations, creating guano deposits (Schmitz *et al.*, 2010). Alternately, it contrasts with the biomass-dispersing effects of bears (*Ursus arctos* and *Ursus americanus)* and wolves (*Canis lupus*), which take fish from streams and distribute them through their movements across terrestrial landscapes (Willson S.M. Gende & Marston, 1998; Darimont *et al.*, 2009). Predictions of the biomass redistributing effects of other such species could be made using movement data to derive time and space budgets similar to those that we illustrate here with *H. amphibius*.

Our biomass transfer model is sensitive to parameterisation of ingestion and egestion rates, although our approach is supported by studies of livestock relating time spent in an area to rates of nutrient deposition (Byers *et al.*, 2005; Franklin *et al.*, 2009). Improved estimates of ingestion and egestion rates can be used to make the outputs from these models more accurate and customise them to unique *H. amphibius* populations and regions. Expansion in the sample size and tagging duration will similarly enhance our understanding of how seasonal or long-term climatic changes could alter forage availability and river levels in ways that change the quantity and spatial patterns of biomass transfers. Parameters reflecting variation in egestion rates by time of day or behavioral state could easily be usefully incorporated into such models for species where they are available.

In addition to providing a spatially explicit view of the role of *H. amphibius* as nutrient vectors, our tracking data also provide a first insight into the spatial ecology of this understudied species. We determined, for example, the distance traveled and area used by our tagged animals on a nightly and weekly basis, and that animals relied heavily on areas close to the river for grazing, with grazing GPS locations averaging only 76 m from the river. These and other metrics can help conservation planners more accurately account for *H. amphibius* space needs.

In summary, our study provides a new framework for determining how mobile organisms act not only to transport, but also to concentrate allochthonous biomass inputs across and within ecosystems, with implications for ecosystem function and landscape structure. More generally, our modeling approach can be extended to describe other ecologically significant transportation by mobile fauna, such as the movement of persistent organic pollutants, the dispersal of plant seeds, or the movement of pathogens and nutrients by livestock (Franklin *et al.*, 2009; Cousens *et al.*, 2010; Peterson *et al.*, 2015). This approach requires integrating methods and insights from the separate fields of ecosystem, behavioral, landscape and movement ecology, and if applied elsewhere, has the potential to expand our understanding of the frequency and intensity with which animals are acting to link and shape ecosystems.

## Figures

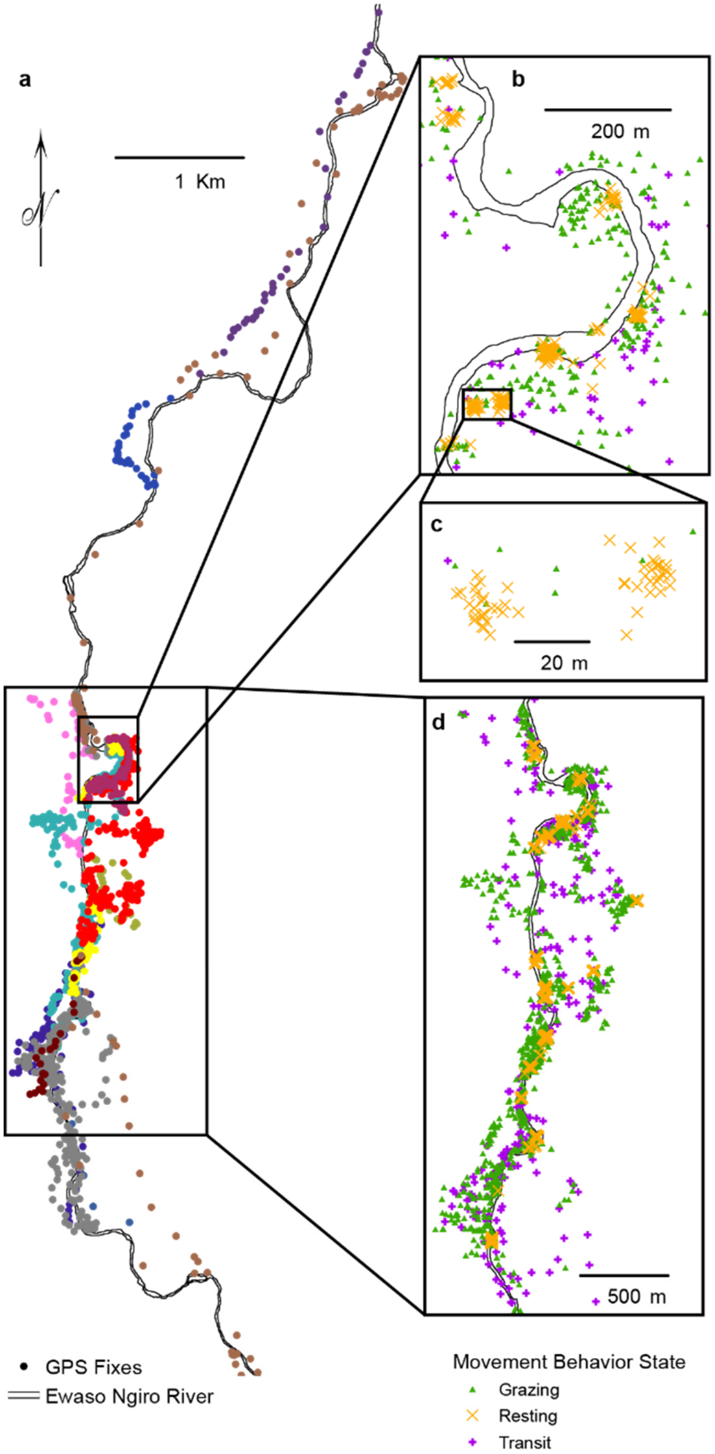


Figure 1. GPS tracks from 13 tagged *Hippopotamus amphibius* obtained over the course of this study. In a) each color represents a different individual. In b-d) colors represent grazing, resting, and transit movement states in illustrative contexts, b) shows a daytime refuge pool and adjacent grazing and terrestrial resting sites, with detail c) showing clusters of points associated with night-time resting periods on land between foraging activity, and d) showing movement states across the most heavily-used portion of the study area.

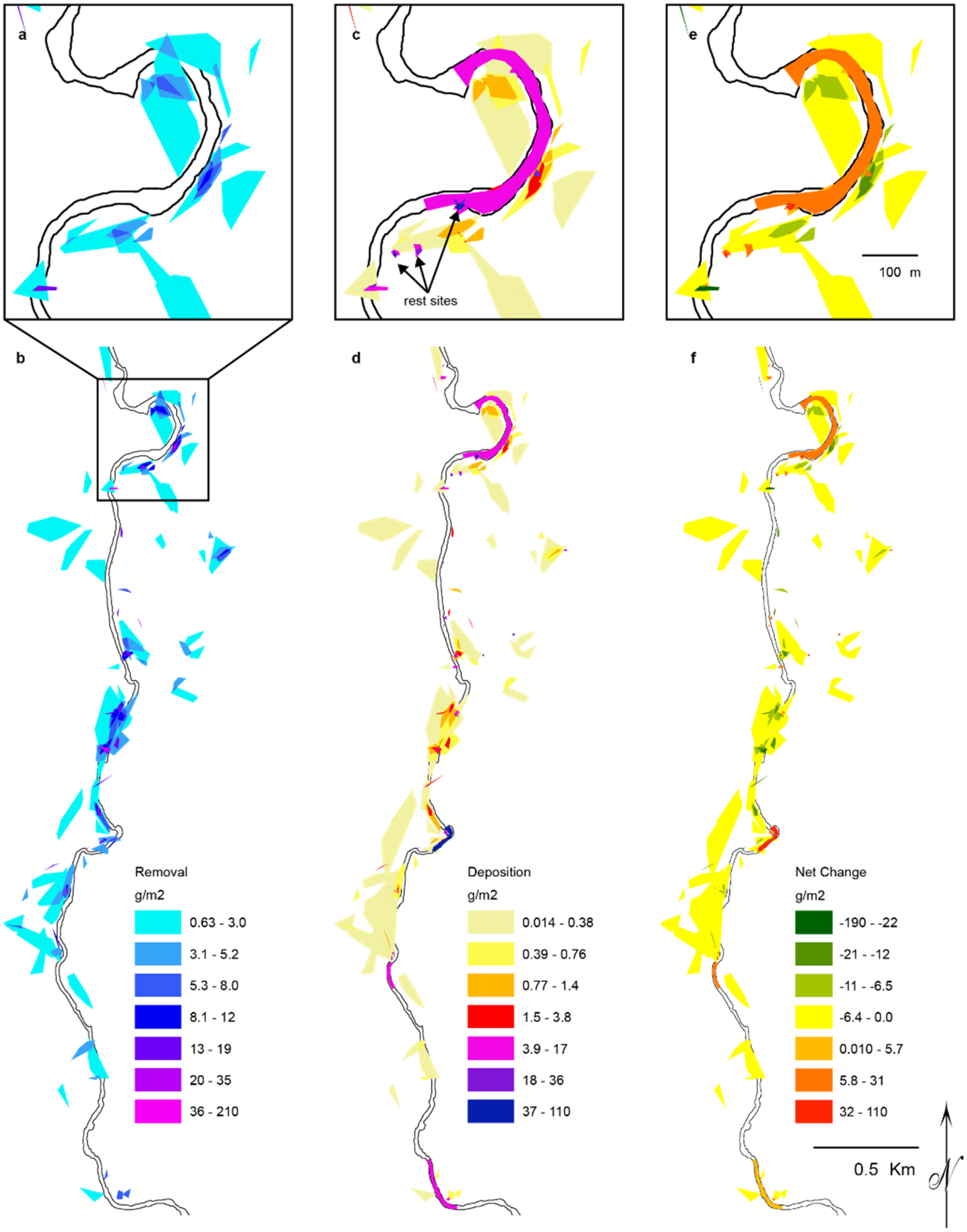


Figure 2. Landscape of biomass transfer by 13 GPS-tagged *Hippopotamus amphibius* obtained over the course of this study, at two different spatial scales along the Ewaso Ng'iro River. Biomass removal (a,b) occurs in areas where *H. amphibius* were grazing, whereas deposition (c,d) occurs in daytime-refuges in the river, resting and grazing areas. Transfer (e,f) is the difference of removal and deposition, and represents a net change of biomass across the landscape. Insets a,c,e, show an oxbow in the river used as a daytime refuge pool, with three terrestrial rest locations visible to the south of it as hotspots of biomass deposition.

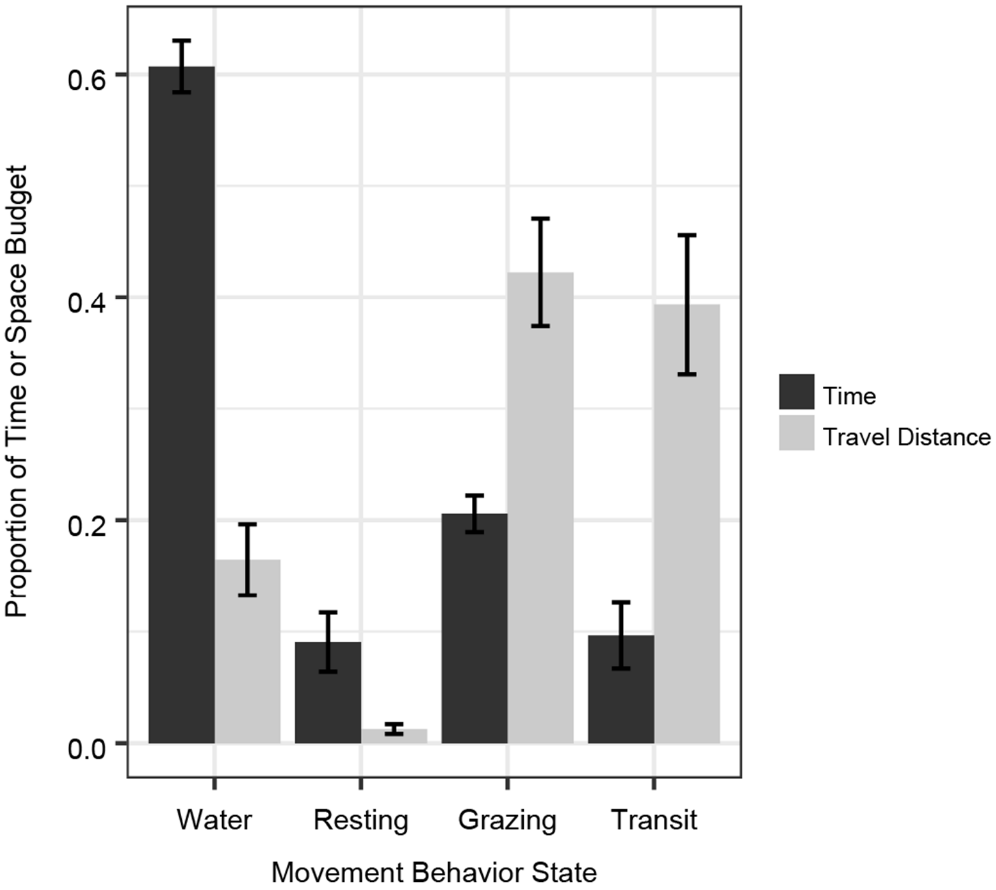


Figure 3. The mean proportion of time budget spent, and distance traveled, by *Hippopotamus amphibius* in each four core behavioral states; pooled across all tracked individuals. Error bars represent the standard error.

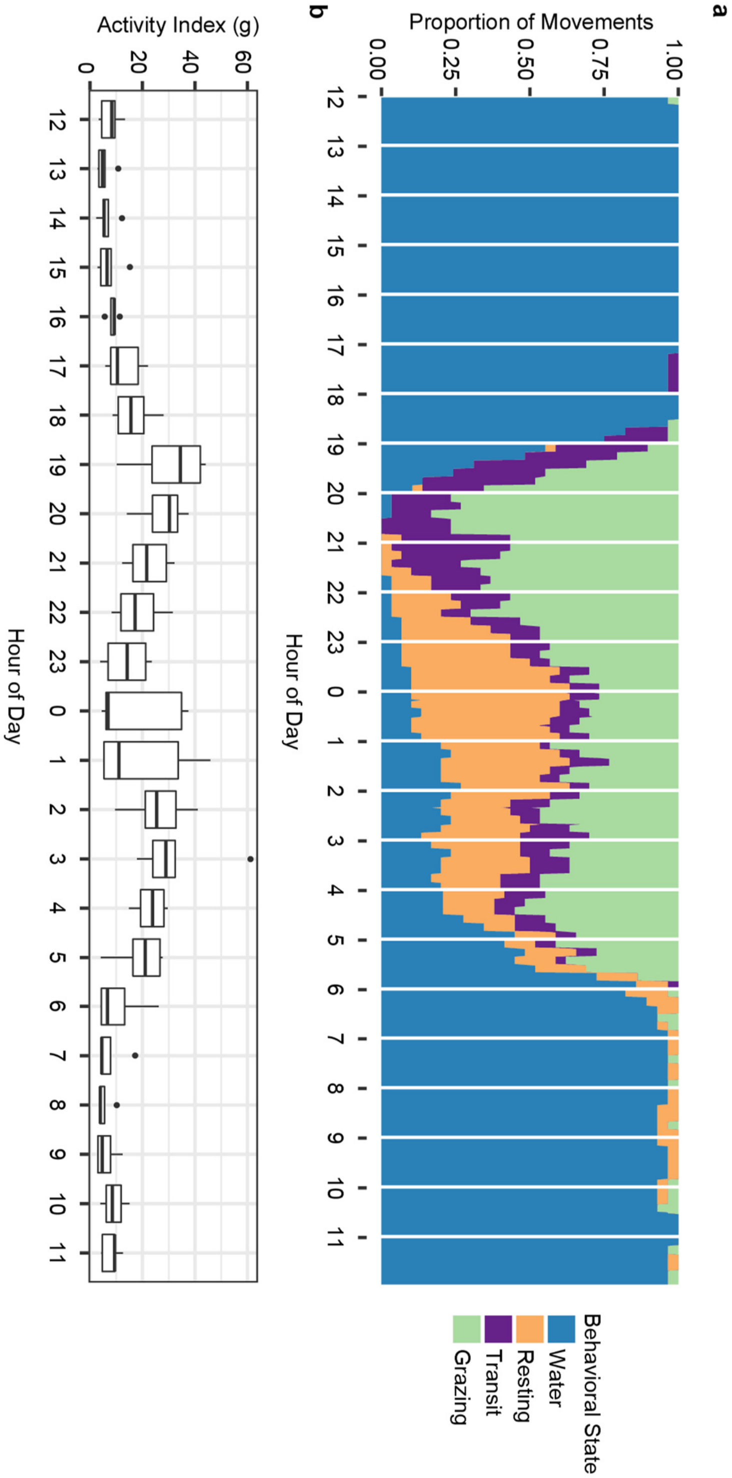


Figure 4. a) The behavioral schedule of *Hippopotamus amphibius* represents the proportion of movements in each state at a given time of day, calculated from all tracked individuals, and b) is a boxplot of the accelerometer activity index (gravitational units, g) by hour of day.

## CHAPTER 3

# Coupled effects of climate change and streamflow abstraction on semiaquatic species distributions

## Abstract

The interacting effects of climate and land use change remain a challenge for forecasts of the ecological consequences of global change. Semiaquatic species, which are evolutionarily distinct and ecologically important, are particularly likely to be affected by changes in hydrology arising both from land use and climate change. Species distribution models (SDMs) are a useful tool to predict responses of organisms to environmental change, but SDMs rarely incorporate terrestrial and hydrologic variables in ways that address the coupled effects of climate and land use-driven hydrologic change. Here we introduce an approach to building hydrology-informed SDMs that incorporates both terrestrial and aquatic drivers of habitat suitability, and allows predictions of distributions under coupled scenarios of climate and hydrologic change.

We built and evaluated hydrology-informed SDMs for the common hippopotamus (*Hippopotamus amphibius*) across Sub-Saharan Africa using five independently developed occurrence datasets. We found that hydrology-informed SDMs made more accurate predictions than atmosphere-only SDMs, and predicted suitability aligned more closely with existing range maps. We compared maps of future *H. amphibius* suitability under climate change scenarios, and found that under scenarios of no additional streamflow abstraction, the amount of suitability change predicted by atmosphere-only models was much larger than that predicted by hydrology-informed models. When we incorporated streamflow abstraction scenarios, however, our models suggested that streamflow abstraction will have a much greater effect on *H. amphibius* habitat suitability than atmospheric climate change. Our approach can be extended to other semiaquatic species to help identify extinction threats and conservation policy priorities arising from global land use and climate change.

## Introduction

Semiaquatic species both bridge and depend on the terrestrial and aquatic realms, and like their aquatic counterparts, represent evolutionarily distinct lineages and are threatened from aquatic habitat losses arising from anthropogenic land use and climate change (Gibbon *et al.*, 2000; May-Collado & Agnarsson, 2011). Semiaquatic species often play key roles in ecosystems and as cross-ecosystem linkages, either as ecosystem engineers (hippopotamuses, beavers), keystone species (otters), or nutrient vectors (hippopotamuses, waterfowl) (Moore, 2006; Post *et al.*, 2008; Schmitz *et al.*, 2010; McCauley *et al.*, 2015). Understanding their ecologies and conservation needs requires integrating insights across disciplines typically focused more on fully aquatic or terrestrial species (Strayer & Dudgeon, 2010).

In addition to their terrestrial habitat needs, semiaquatic species depend on aspects of surface hydrology, such as streamflow or water temperature, that will be affected both by global climate change (Halpin, 1997; van Vliet *et al.*, 2013a) as well as direct anthropogenic hydrologic alteration such as streamflow abstractions for irrigation (Stewart-Koster *et al.*, 2010; Poff *et al.*, 2016). Globally, streamflow abstractions for irrigation are increasing as agricultural development intensifies across the planet (Haddeland *et al.*, 2014). Species distribution models (SDMs) are a useful tool to predict responses of organisms to climate and land use change, both by identifying environmental drivers of habitat suitability and to predict future distributions (Elith & Leathwick, 2009). Semiaquatic species require an SDM approach that uses environmental covariates directly related to their unique terrestrial and aquatic requirements. In particular, these models require the incorporation of appropriate hydrologic variables.

Surface hydrology, however, requires extra effort to project to scenarios of future climates, because it is not linearly related to the atmospheric climate variables generated by general circulation models. Instead, lateral and longitudinal hydrologic connectivity spatially decouple hydrologic patterns from atmospheric ones (Domisch *et al.*, 2015a). However, hydrologic models exist that provide helpful approximations of hydrologic processes useful to the construction of SDMs for semiaquatic species, and include a range of statistical and mechanistic approaches (McMahon *et al.*, 2013; van Vliet *et al.*, 2013a). In addition to providing information on streamflow, hydrologic models can also provide information on soil moisture and vegetation processes relevant to semiaquatic species' terrestrial habitat requirements, such as climatic water deficit (Chave *et al.*, 2014).

Recent SDM studies for aquatic species have taken varying approaches to incorporating hydrology, from calculating upstream precipitation or air temperature proxies for baseline hydrologic processes (Domisch *et al.*, 2015b), to adapting the mechanistic variable infiltration capacity (VIC) hydrologic modeling framework to future climate forcing scenarios (van Vliet *et al.*, 2013b). Fortunately, for SDM purposes, it is less important for models to quantify the absolute magnitude of flows at high temporal resolutions than to consistently represent the relative spatial patterns of hydrologic variables averaged over long periods, as long as the patterns consistently reflect the underlying physical processes (Domisch *et al.*, 2015b).

We used a simple hydrologic model to provide hydrologic covariates for a model of the distribution of the common hippopotamus (*Hippopotamus amphibius)* that is driven by the atmospheric variables also used in the distribution modeling. This allowed consistent modeling of both terrestrial and aquatic variables, and allowed for projection of *H. amphibius* distributions under scenarios of future atmospheric climate and land use changes that affect hydrologic variables. *H. amphibius* is a semiaquatic megaherbivore physiologically dependent on immersion in water, making it unsurprising that past efforts at modeling *H. amphibius* using atmospheric-only SDMs have performed poorly compared with terrestrial species (Thuiller *et al.*, 2006). Compared to other semiaquatic African fauna, relatively good occurrence data for *H. amphibius* exists as it is a highly detectable and charismatic species.

We used five independent occurrence datasets to build models of *H. amphibius* occurrence under baseline conditions, and then projected *H. amphibius* habitat suitability forward under scenarios of climate change with and without additional streamflow abstractions arising from shifts from rain-fed to irrigated agricultural land use. We compared the model performance of hydrology-informed SDMs with atmospheric-only SDMs, and projected and compared spatial projections of atmospheric- and hydrology-informed SDMs of present-day habitat suitability. Using these atmospheric-only and hydrology-informed SDMs, we also projected and compared spatial projections of *H. amphibius* habitat suitability under different climate and hydrologic change scenarios.

## Methods

### *Study species, area, and resolution*

The geographical distribution of *H. amphibius* is thought to arise from its physiological and behavioral requirement of surface water for immersion, the availability of sufficient precipitation to support grass for forage, and the sufficiently low levels of persecution and land conversion by humans (Eltringham, 1999; Lewison, 2007). In particular, *H. amphibius* needs regular immersion to prevent its unique skin, which enables the highest rate of transepidermal water loss of any mammal as a thermoregulatory adaptation, from cracking (Jablonski, 2004).

Our study area was the African continent south of 20 degrees North. We excluded areas north of 20N to exclude areas north of the Sahara to reduce biases from including unoccupied but possibly suitable areas along the Mediterranean coast unavailable to *H. amphibius* due to dispersal limitations. We chose a resolution of 5 arc-minutes (approximately 9.2 km at equator) for all spatial modeling, making the side of each grid cell approximately several times longer than the typical nightly *H. amphibius* grazing movements (of 1-3 kilometers) from daytime water refuges (Eltringham, 1999).

### *Occurrence datasets*

We identified five previously published or online datasets of *H. amphibius* occurrence that consisted of point data and had country-wide or larger extents, which were assembled using different methodologies (Table 1, Figure 1).

### *Predictor datasets*

We used WorldClim (version 1.4, representative of mean climatic conditions from 1960-1990) as our source of atmospheric climate data, which were used directly and indirectly as inputs to the hydrologic model (Hijmans *et al.*, 2005). The specific variables used are listed in Table 2. We calculated a lake margin variable (the total linear distance of lake shoreline within a 5 arc-minute grid cell), from the Global Lakes and Wetlands Database (Lehner & Döll, 2004). Human population density data came from the Gridded Population of the World dataset (version 4), developed by the Center for International Earth Science Information Network, Columbia University (CIESIN 2016).

### *Hydrologic model*

We adapted a leaky-bucket hydrologic model developed and used by the U.S. National Oceanic and Atmospheric Administration's Climate Prediction Center to derive a continental-scale, first-order approximation of streamflow and climatic water deficit (Huang *et al.*, 1996). We used gridded monthly precipitation, minimum temperature, and maximum temperature from the WorldClim dataset in the model. The maximum and minimum temperature grids were used to calculate potential evapotranspiration in the EcoHydRology R package using the Priestly-Taylor equation (Fuka *et al.*, 2014), and WorldClim monthly precipitation was used without modification in the hydrologic model. Actual evapotranspiration was then calculated as a function of soil moisture and potential evapotranspiration, using Equation 3 from Huang et al. 1996.

The hydrologic model is a ‘leaky bucket’ implementation of the water balance equation,

$$\frac{dW(t)}{dt} = P(t) - E(t) - R(t) - G(t),$$

where W is soil moisture, P is precipitation, E is actual evapotranspiration, R is surface runoff, and G is sub-surface flow. By integrating soil moisture forward over time, and using precipitation and potential evapotranspiration values derived from the WorldClim data, calculation of combined surface and sub-surface flow values is possible. Details of implementation are described in Huang et al. (1996) and Fan & van den Dool (2004). We used the flow accumulation tool in ArcGIS to calculate streamflow accumulation, using monthly runoff grids generated by the hydrologic model as weights, and a 5 arc-minute flow direction grid coarsened from the HydroSHEDS 30 arc-second flow direction grid (Lehner *et al.*, 2006).

Through this process we generated grids of streamflow (annual mean, minimum, maximum, standard deviation, and range based on monthly averages), climatic water deficit (the annual sum of PET – AET in months when PET exceeds AET) (Chave *et al.*, 2014), monthly soil moisture, actual evapotranspiration, and irrigation need (Haddeland *et al.*, 2006, 2014). Estimates of baseline incremental evapotranspiration due to irrigation from the GlobWat hydrologic model was used to represent reductions to surface flow due to irrigation from existing irrigated agriculture (Hoogeveen *et al.*, 2015).

### *Candidate models*

We developed candidate models a priori that identified mechanistically plausible climatic and hydrologic controls on *H. amphibius* distribution with varying complexity (Table 3). Mechanisms included are thermoregulation (affected by air temperature and surface water availability for immersion), forage availability (air temperature, precipitation, climatic water deficit), and anthropogenic exclusion. Variables were only included in the same a priori candidate model if their pairwise Pearson’s p correlation values were less than 0.7. Most streamflow variables in particular were highly correlated with each other, so we only included minimum streamflow and the annual range of streamflow, which were not.

### *Fitted candidate models using Maxent*

We fit each of the candidate models to location data from the five occurrence datasets using the Maxent modeling framework. We used the presence-only Maxent modeling framework to construct the *H. amphibius* distribution models because our datasets were presence-only datasets (Phillips & Dudík, 2008). Rather than use debated transformations of Maxent’s raw relative occurrence rate outputs to presence-absence maps, we interpret these outputs throughout this paper as an index of habitat suitability (Merow *et al.*, 2013).

### *Model performance*

To compare atmospheric-only and hydrology-informed model performance, we used a leave-one-out cross-validation by dataset approach. Each of our occurrence datasets were assembled using different methodologies, at different time periods, and in different regions. The leave-one-out cross-validation approach involved iteratively 1) withholding one occurrence dataset, 2) building the distribution model using the remainder of the occurrence datasets, 3) using the distribution model to predict suitability in the geographical area of the withheld dataset, and 4) using the withheld occurrence dataset to calculate AUC and Maximum Kappa scores. This provided a conservative assessment of model performance, enabling explicit assessment of sensitivity to the source and methodology of each dataset.

### *Suitability mapping using baseline (1960-1990) conditions*

From the results of the leave-one-out cross-validation, we selected two models from which to compare spatial projections of suitability, the "Atmospheric Core and Protected Area Category" model and the "Streamflow Core, Lake Margin, and Climatic Water Deficit and Protected Area Category" model. We chose these as each had the highest minimum AUC score of the atmospheric-only and hydrology-informed models, respectively. Here forth we refer to these as the "atmospheric-only" and "hydrology-informed" models, although both models also incorporated protected area locations and categories. We mapped suitability geographically using these two models using the same grids used to build the models (i.e., the 1960-1990 WorldClim-derived atmospheric and hydrologic variables, and the GLWD-derived lake margin grid).

### *Assessing modeled baseline suitability with IUCN range map*

The IUCN range map was initially developed from questionnaires sent to knowledgeable country-level experts as well as published literature, as part of *H. amphibius'* initial IUCN assessment (Eltringham, 1993) (Figure S1). It consists of mostly disjunct polygons centered on river or wetland areas that supported *H. amphibius* populations at the time. Although the best available assessment of *H. amphibius* distribution, many of the polygons appear generous in their boundaries relative to the major *H. amphibius*-supporting river or lake features they typically encompass (Lewison & Oliver, 2008). We calculated the percentage of IUCN range map polygons with a maximum suitability value over 0.5 for the atmospheric-only and hydrology-informed suitability projections as an external measure of predictive accuracy of the two models.

### *Mapping suitability in 2070 under RCP 8.5 climate scenario without streamflow abstraction increases*

We first mapped future suitability under a climate change scenario without streamflow abstraction increases. To do this we calculated an ensemble of suitability maps generated from 16 different general circulation models for which projected conditions were available in 2070 (average for 2061-2080) for the business-as-usual relative concentration pathway (RCP 8.5, Supporting Text). We used future climate conditions from the WorldClim 1.4 CMIP5 dataset (Hijmans *et al.*, 2005), hydrologic variables derived from the future climate conditions using the leaky bucket model, and baseline lake margin layers. We also calculate the change in suitability for each year compared to projections using baseline (1960-1990) climates.

### *Mapping suitability in 2070 under coupled RCP 8.5 climate scenario and streamflow abstraction increases*

To address the effects of streamflow abstractions arising from land use change on hydrologic variables important to *H. amphibius* distributions, we modeled future suitability under four conservative scenarios of streamflow abstractions to address irrigation needs. As before, we used the future climate conditions from the WorldClim 1.4 CMIP5 dataset (Hijmans *et al.*, 2005), and baseline lake margin layers, but also accounted for increases in streamflow abstraction when calculating streamflow variables.

We first generated four streamflow abstraction scenarios by subtracting a fixed percentage (0.5, 1, 2, and 4%) of the "irrigation need" from upstream agricultural lands from surface streamflow. We did this using a monthly time step in the leaky-bucket hydrologic model. Irrigation need is defined as the difference between monthly potential evapotranspiration and monthly actual evapotranspiration, which is a generalization of an irrigation need formula used to predict the agricultural demand of specific crops (Doll & Siebert, 2002). We used the FAO's Major Agricultural Systems of the World map to identify cultivated grid cells (FAO, 2011), and only simulated the removal of water from grid cells in cultivated lands, and only if there was water coming into the cell from upstream as streamflow.

## Results

### *Model performance was much higher for hydrology-informed SDMs*

Model performance, measured both using AUC (Figure 2) and Maximum Kappa (Figure S3), was much higher for candidate models that incorporated hydrologic variables, increasing median AUC scores by over 20 percent. Incorporating variables related to human presence, in addition to hydrologic variables, provided a marginal increase in the model performance scores of the lowest-performing evaluation datasets.

### *Maps of projected suitability for baseline (1960-1990) conditions differed greatly between atmospheric-only and hydrology-informed models*

Maps of suitability under baseline conditions (1960-1990) made using the atmospheric-only and hydrology-informed SDMs have similar broad-scale patterns: suitability is high in tropical savannah regions of Western and Eastern Africa and the southern half of Central Africa (Figure 3). Suitability is low in arid Southern Africa and the rainforest areas of the northern half of Central Africa and the westernmost areas of Western Africa. However, the atmospheric-only and hydrology-informed suitability maps differed in key ways: patterns of suitability are much coarser-grained in the atmospheric-only map, and finer-grained in the hydrology-informed map, reflecting differences in the scales of spatial autocorrelation of atmospheric and streamflow variables. In addition, the hydrology-informed model predicted high levels of suitability in areas not identified in the atmospheric-only model, particularly along the Niger and Benou rivers, the rivers of Angola, the Nile and tributaries in Southern Sudan, and the Orange river and tributaries in South Africa.

The hydrology-informed model did a better job of predicting the distribution of the IUCN range map polygons for *H. amphibius*. The atmosphere-only model predicted maximum suitability values of 0.5 or greater in 64% of the IUCN range map polygons, whereas the hydrology-informed model predicted maximum suitability values of 0.5 or greater in 89% of IUCN polygons.

### *Atmospheric-only and hydrology-informed models differed in patterns of suitability projected in 2070 under RCP 8.5 climate scenario without streamflow abstraction increases*

Suitability maps made using the atmospheric-only and hydrology-informed models under RCP 8.5 climate scenario conditions in 2070 also differ in important ways (Figure 4). The atmospheric-only model projects that much of the study area will see substantial changes in suitability, with both increases and decreases. The absolute value of change in suitability at a continental scale, a measure of geographic shifts in suitability, averaged 10% (+/- 11%) under the atmospheric-only model, with some regions seeing suitability increases or decreases of 50% or more. The hydrology-informed model shows much lower overall levels of change in suitability, with the absolute value of change in suitability at a continental scale averaging 4% (+/- 4%). The atmospheric-only model shows general increase in suitability in Western Africa, in the Congo Basin and most of the Sahel, and heterogenous changes in northern portions of Central and East Africa, and decreases in southern East Africa and the Okavango delta region. The hydrology-informed model also projects decreases in the Okavango, in contrast, it predicts decreases in suitability across the Sahel, the Sudd, and northern East Africa.

### *Coupling streamflow abstractions with climate change scenarios dramatically decreasd suitability in 2070*

The four streamflow abstraction scenarios (abstraction increases of 0.5, 1, 2, and 4% of irrigation need on cultivated lands) all resulted in widespread decreases in suitability for *H. amphibius* in future climates compared to projections without abstraction increases (Figure 5). As the amount of streamflow abstraction increased, the extent of suitability decreases also increased.

## Discussion

### *Including hydrologic variables in semiaquatic species distribution models improves predictive ability.*

By including hydrologic variables such as streamflow, we increased the performance of our model of *H. amphibius* distribution by over 20% when testing across occurrence datasets, as well as when assessed against the IUCN range map. This substantial improvement in model performance reflects the incorporation of hydrologic variables that relate directly to physiological and behavioral *H. amphibius* habitat needs. Indeed, in a previous distribution modeling study of African mammals, the model for *H. amphibius* was the worst-performing, which the authors attributed to the lack of hydrologic variables in the study (Thuiller *et al.*, 2006). This suggests that distribution models for other semiaquatic species could be similarly improved by systematically incorporating relevant hydrologic variables. It also suggests treating the predictions of semiaquatic SDMs that do not incorporate hydrologic variables with caution.

### *Coupling hydrologic variables to atmospheric climate variables allows prediction of suitability under scenarios of climate change and streamflow abstraction*

SDMs for terrestrial species have either used static water features such as the presence, density of, or distance from rivers, lakes, and wetlands (Stensgaard *et al.*, 2006; Kirk & Zielinski, 2009; Rondinini *et al.*, 2011; Angelieri *et al.*, 2016), remote sensing proxies for water or moisture (Stensgaard *et al.*, 2006; Griffin, 2010; Matawa *et al.*, 2013), or topographic indices such as the topographic wetness index (Platts *et al.*, 2008; Wearne *et al.*, 2013). These are useful approaches, but do not address how these water features might change with hydrologic or climate change, because these variables are only available for baseline conditions, preventing the SDMs from incorporating scenarios of changes to those variables.

By coupling key hydrologic variables, such as streamflow and climate water deficit, to their primary climatic drivers, our approach makes it possible to dynamically and consistently model the responses of semiaquatic species to coupled changes in atmospheric climate and hydrology as a result of global climate change. Further, our approach allows for the simulation of increased streamflow abstraction in proportion to the amount of upstream agriculture. The conversion of rainfed agriculture to irrigated agriculture is a major ongoing form of land use conversion across Africa (Burney *et al.*, 2013). Our approach provides a simple but robust way of incorporating these increases in irrigation levels in species distribution models.

*Including hydrologic variables in semiaquatic species distribution models changes predictions of habitat suitability in the future.*

Hydrology-informed projections of changes in suitability under climate change show much less change than atmospheric-only projections, highlighting the non-linear coupling between atmospheric climate and hydrology. That hydrology-informed projections show less change than atmospheric-only projections is a counterintuitive result, given that aquatic systems generally are considered to be highly sensitive to the effects of climate change. *H. amphibius*, presumably dependent primarily on water for immersion, is projected to be less affected when hydrology is included, because relatively large changes in temperature and precipitation result in much smaller changes in surface water availability. Although on the surface encouraging for the fate of *H. amphibius* in a changing climate, the much smaller amount of suitable area identified by the hydrology-informed model greatly restricts the amount and distribution of suitable habitat for *H. amphibius.*

*Small increases in streamflow abstraction to meet irrigation needs lead to sharp declines in suitable habitat for H. amphibius*

One surprising result of this study is how sensitive suitability is to the removal of surface flow to irrigation. The diversion of streamflows to meet just 1% of potential irrigation need on cultivated lands reduced the area with suitability scores greater than 0.5 in 2070 by 37%, and diverting 4% of potential irrigation need reduced the suitable area by 68%. This suggests that areas seeing irrigation development are going to be particularly likely to see accelerating declines of *H. amphibius* populations. Much of Africa is likely to see streamflow abstraction far in excess of the 1-4% of potential irrigation need scenarios modeled in this study. The African Development Bank, World Bank, and other multilateral institutions are actively promoting both large and small-scale irrigation development projects across the continent.

Unfortunately, we are not aware of continental-scale, spatially explicit forecasts of the distribution and rates of conversion of rainfed agriculture to irrigation. In the absence of detailed models of irrigation development, our approach to modeling the effects of streamflow diversions provides insights at the scale of major river basins regarding the potential ecological effects of irrigation development. Irrigation projects could incorporate water management strategies that act to maintain key hydrologic functions (such as maintaining minimum flows most important to *H. amphibius*), similar to those enacted in other water-stressed basins (Poff *et al.*, 2016). Our model does not address ground water pumping for irrigation, which could reduce base flows important to maintaining water availability during low-flow periods.

*Model limitations and next steps*

Our use of a mechanistic leaky-bucket model allowed forward projection and the integration of scenarios of stream abstraction. However, this approach ignores important lower-order processes (soils, aspect, vegetation, etc.) that can be influential at the scale of individual watersheds (McMahon *et al.*, 2013). The direct integration of continental-scale VIC models with baseline and future climate datasets (such as WorldClim) would be a highly valuable development for semiaquatic species distribution modeling. Existing global models are both coarse in resolution and rely on older generations of IPCC climate scenarios (van Vliet *et al.*, 2013a) or do not include forward projections (Hoogeveen *et al.*, 2015). Coupling of more sophisticated hydrologic models like VIC with commonly used atmospheric climate datasets using consistent temporal and spatial resolutions, projection years, and scenarios used, would greatly facilitate more realistic SDMs.

One recent approach to the modeling of aquatic species distributions is to use flow accumulation of upstream precipitation as a proxy for streamflow (Domisch *et al.*, 2015b). This approach is valuable, but can be problematic when projected into future climates and/or across geographic regions where relative patterns of variability in precipitation and potential evapotranspiration changes (McMahon *et al.*, 2013). In particular, using metrics of upstream precipitation does not account for geographic variation in evapotranspiration rates and the degree of seasonal synchrony of evapotranspiration and precipitation in relation to each other, which are important aspects of water balance that determine streamflow.

A methodological insight arising from our use of multiple occurrence datasets is that the resolution of occurrence data of semiaquatic species should match that of the hydrologic data, particularly since the scale of spatial autocorrelation of streamflow variables are both much shorter and directional compared to atmospheric variables (Domisch *et al.*, 2015a). Occurrences in the GBIF and iNaturalist datasets were less coupled to hydrologic networks than the literature-based and aerial census datasets, likely reflecting citizen science contributions that used locations associated with national park infrastructure rather than actual *H. amphibius* locations. As a result, the AUC scores associated with the GBIF and iNaturalist datasets differed little between the atmospheric-only and hydrology-informed models, whereas the other datasets saw large differences.

Relatedly, during the evaluation of candidate models, the differences among the hydrology-informed models that incorporated different sets of variables related to human exclusion, lakes, or moisture deficit were minimal. We focused on the "Streamflow Core, Lake Margin, and Climatic Water Deficit and Protected Area Category" model in part because it included mechanisms established in the literature as important to *H. amphibius* presence, but the other hydrology-informed models with similar AUC scores are likely to be of similar validity. Although the incorporation of protected area category improved model performance overall, it is likely less important in remote regions.

### *Relevance for management and conservation*

Hydrology-informed SDMs have the potential to greatly improve our understanding of where semiaquatic species are distributed in the present, and how they may be affected by climate- and land-use driven hydrological change in the future. By consistently coupling scenarios of land-use driven streamflow abstractions with the hydrologic changes arising from climate change, these models provide a more robust picture of the interacting challenges faced by semiaquatic species.

Of these challenges, the effects of increases in streamflow abstraction are particularly concerning for *H. amphibius* populations and other semiaquatic species in Africa. The changes in habitat suitability arising from anthropogenic climate change alone, even using the business-as-usual RCP 8.5 scenario, are small compared to the widespread decreases in suitability arising when small increases in streamflow abstraction rates are included. Already *H. amphibius* populations have been negatively affected by dry-season streamflow abstraction for irrigation in the Greater Ruaha and the Limpopo river systems (Jacobsen & Kleynhans, 1993; Stommel *et al.*, 2016). Systematic studies identifying thresholds at which flow reductions lead to extirpation are needed, and could help inform mitigation actions such as limits on abstractions during low-flow periods, and the maintenance of natural or artificial pools to support stressed populations (Jacobsen & Kleynhans, 1993). Importantly, the ecological effects of streamflow abstraction may occur far downstream of extraction sites, because semiaquatic species such as *H. amphibius* rely on streamflow accumulated through the longitudinal connectivity of river networks. In this way, the cumulative effects of distributed irrigation systems, proposed as an agroecological alternative to centralized irrigation projects, may still have significant ecological consequences (Burney *et al.*, 2013).

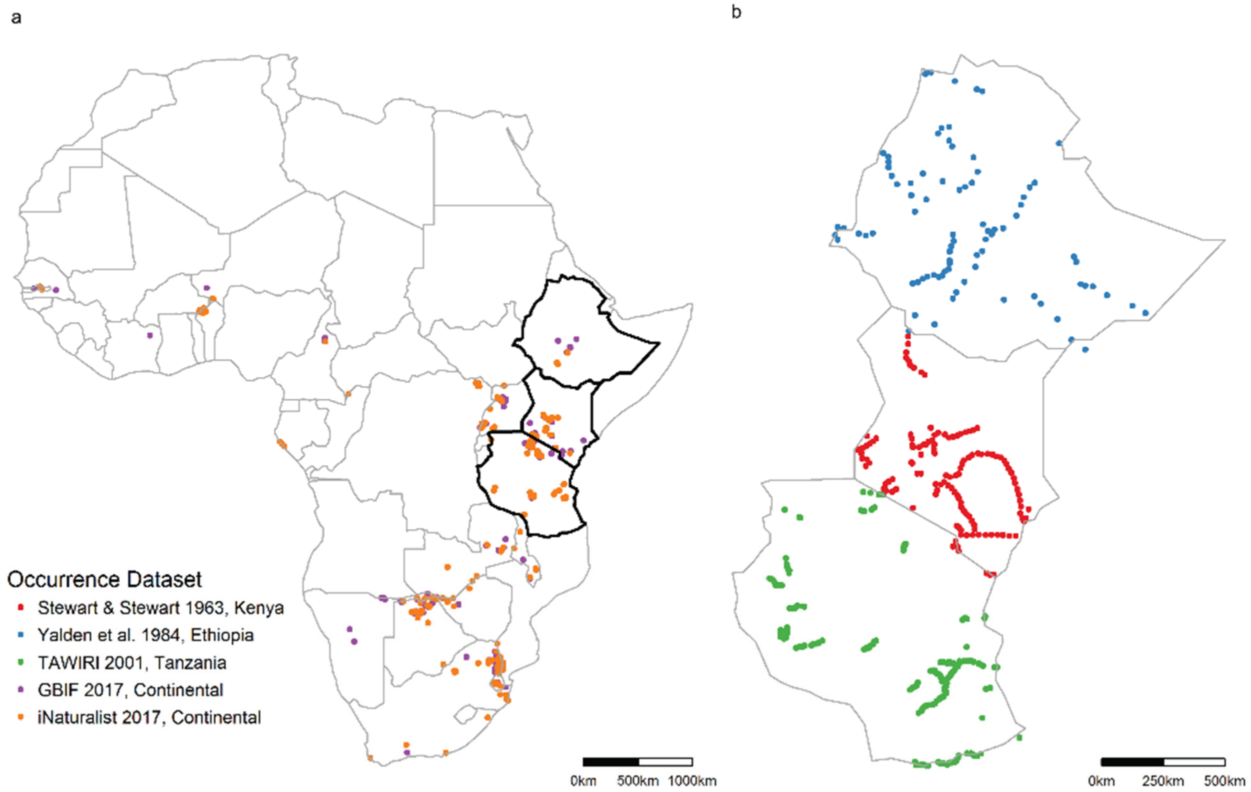


Figure 1. Occurrence datasets used in developing *H. amphibius* species distribution models a) at a continental extent, and b) in Kenya, Tanzania, and Ethiopia (country outlines highlighted in black in panel a).

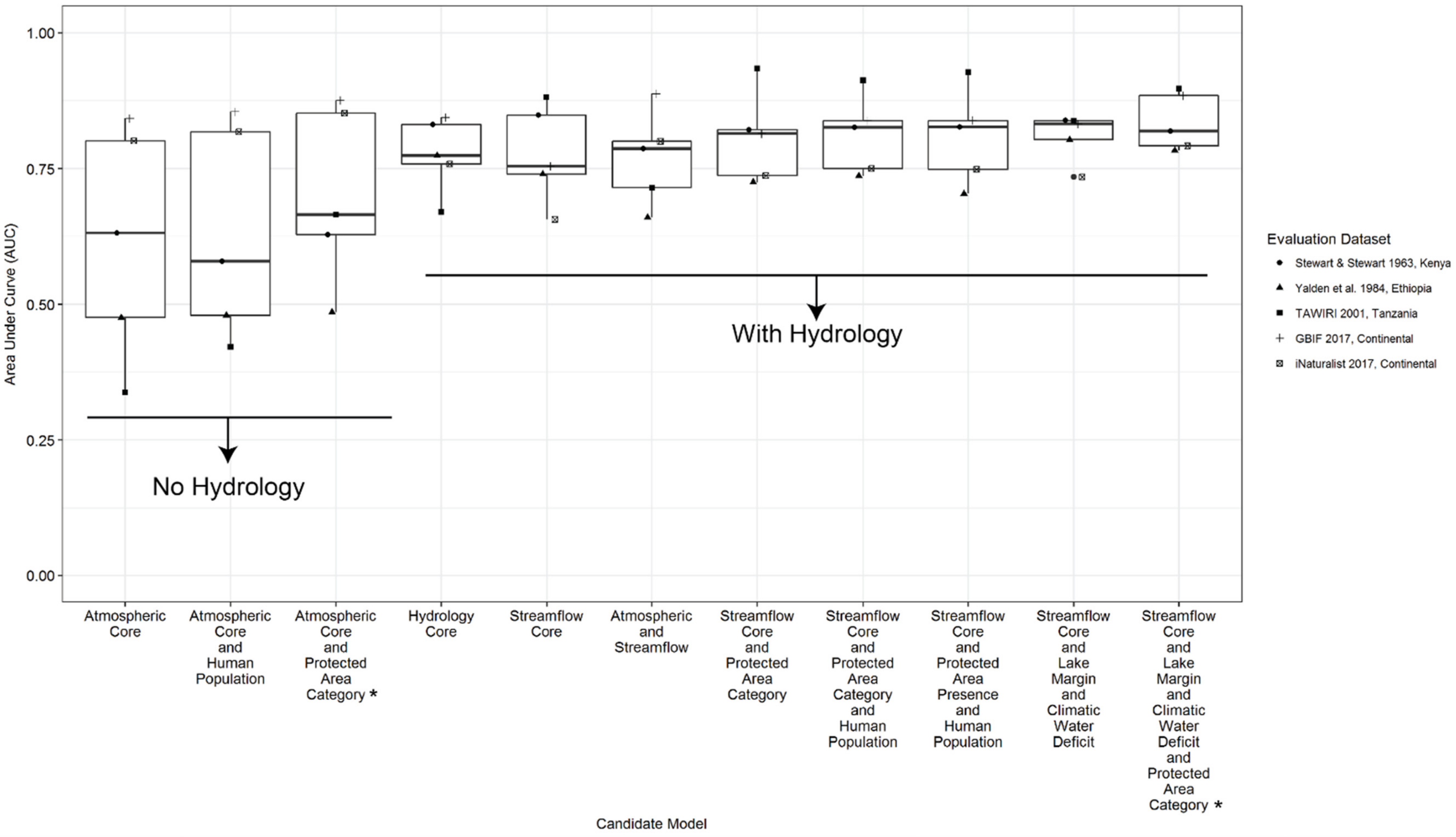


Figure 2. Model performance, measured by Area Under Curve, for candidate models using a leave-one-out cross-validation approach. The “Atmospheric Core and Protected Area Category” model and the “Streamflow Core, Lake Margin, and Climatic Water Deficit and Protected Area Category” models, labeled with asterisks, were selected for subsequent spatial projections of baseline and future distributions, as each had the highest minimum AUC score of the atmospheric-only and hydrology-informed models, respectively.

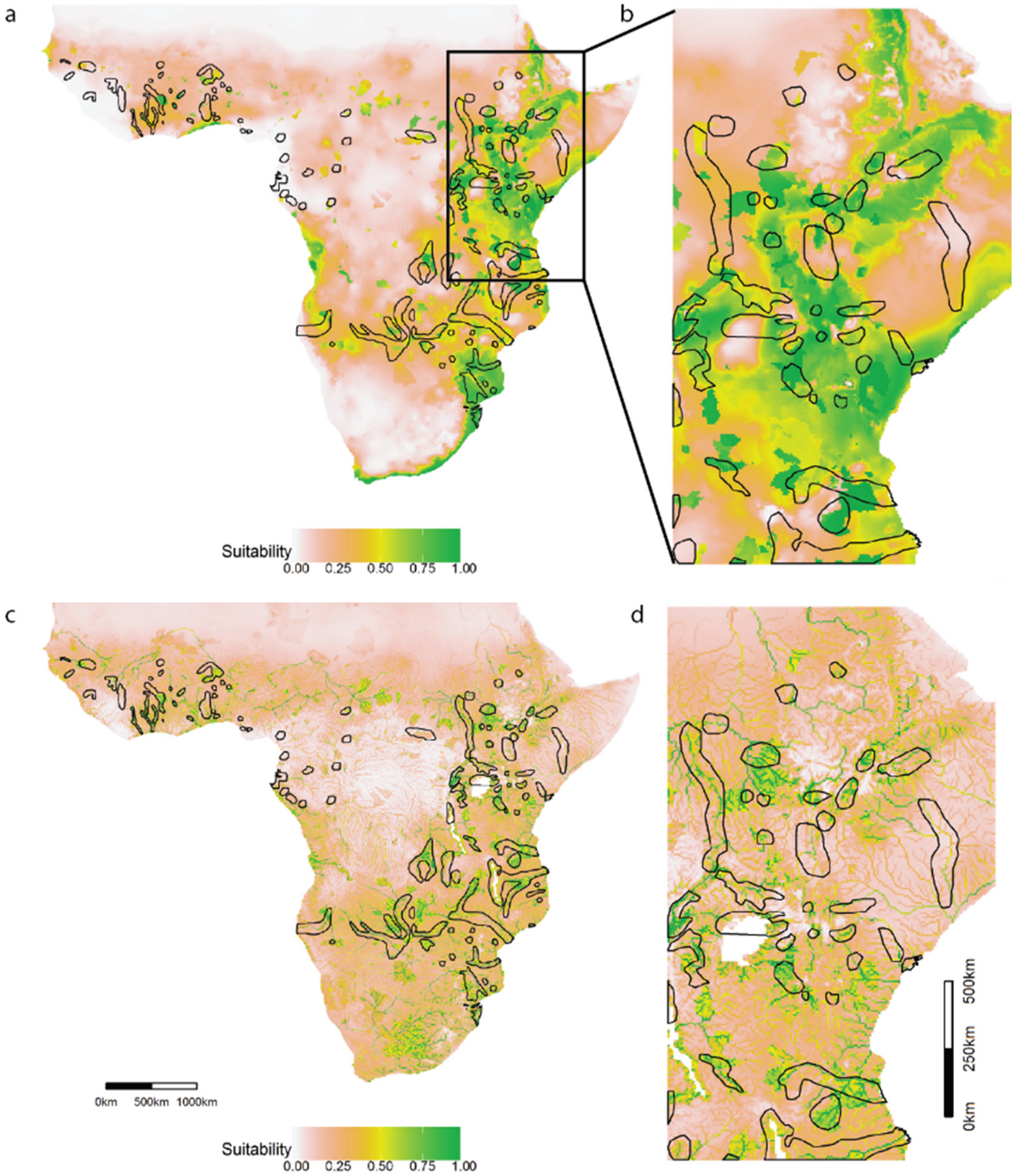


Figure 3. Suitability mapped using baseline (1960-1990) climate conditions, with either the atmospheric-only models across a) continental and b) East-African extents, or the hydrology-informed models across c) continental and d) East-African extents. Black polygons show the IUCN range map for *H. amphibius*.

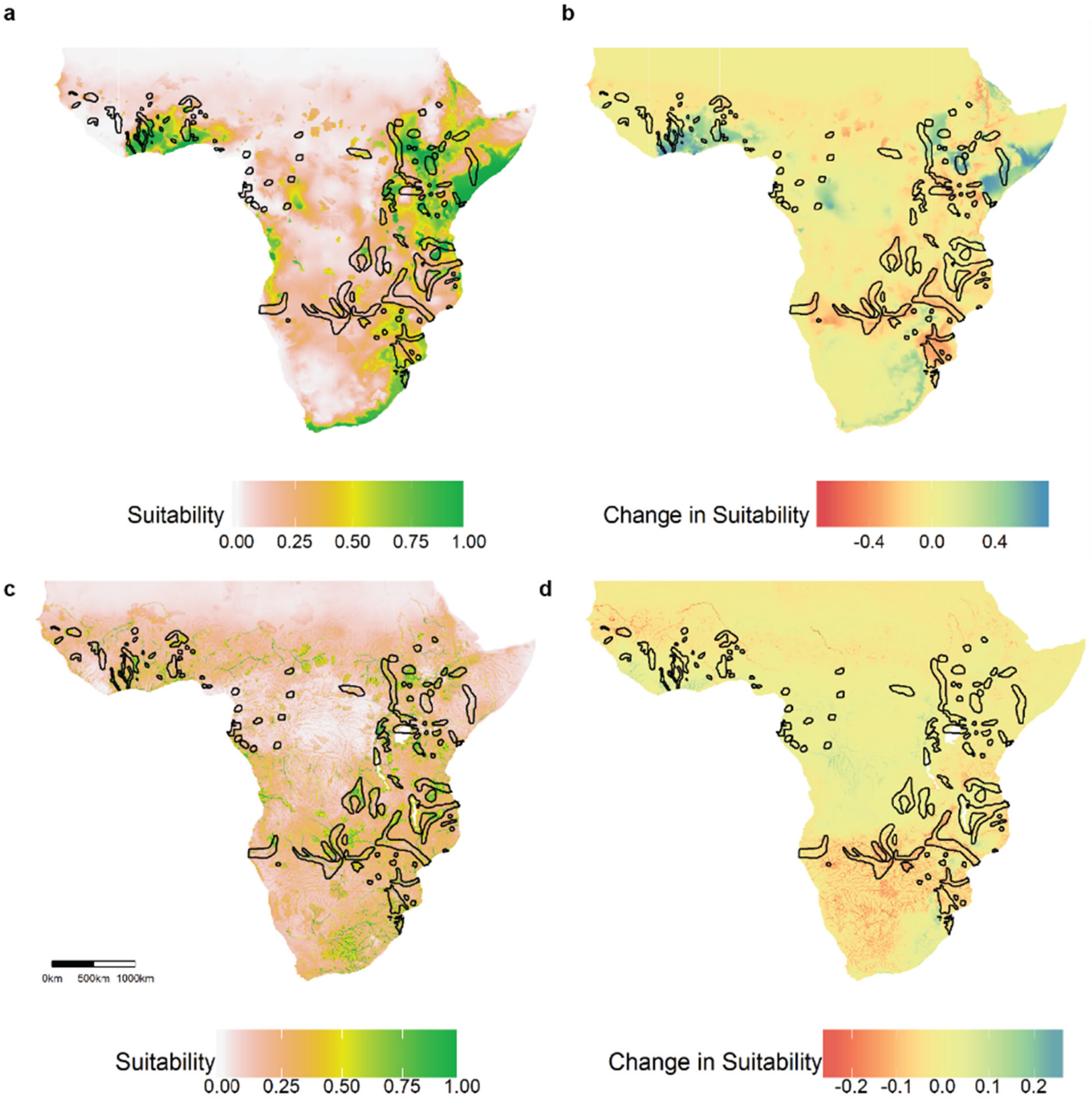


Figure 4. a) Suitability under future (2070) climate conditions and b) change in suitability between baseline (1960-1990) and 2070 conditions, as predicted by the atmospheric-only model, and c) suitability under future (2070) climate conditions and d) change in suitability between baseline (1960-1990) and 2070 conditions, as predicted by the hydrology-informed model. Note the difference in color scales of b and d, with the atmospheric-only model exhibiting greater amounts of change than the hydrology-informed model.

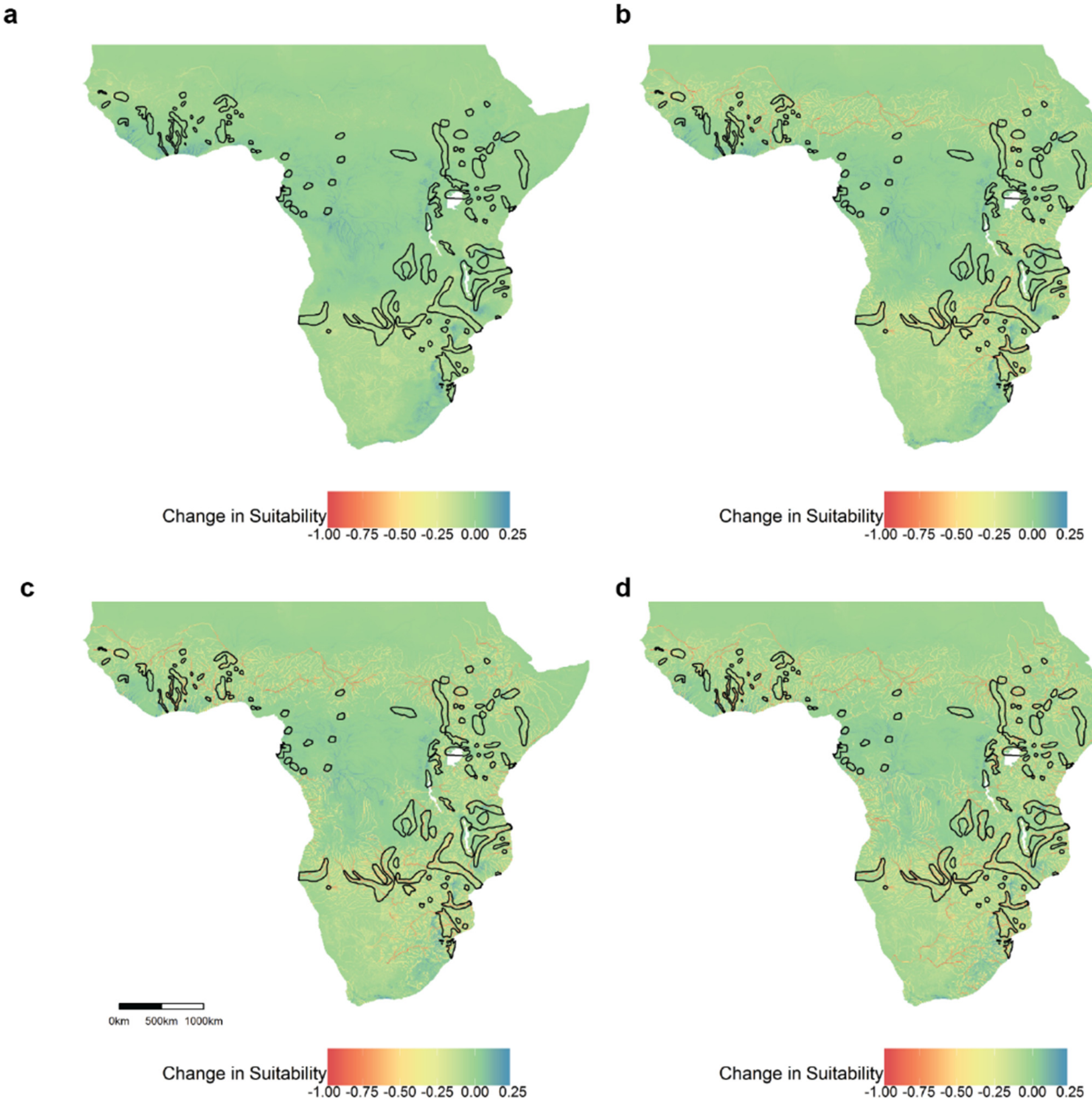


Figure 5. Change in suitability between baseline (1960-1990) conditions and future (2070, RCP 8.5) conditions under the business-as-usual relative concentration pathway (RCP 8.5) for a) the hydrology-informed model with no streamflow abstraction, and b) 0.5%, c) 2%, and d) 4% of potential irrigation need in agricultural lands met by streamflow abstraction.

Table 1: Range-wide and regional occurrence datasets available for *H. amphibius*

| **Name and reference** | **Year of study or publication** | **Extent** | **Method of Development** | **Year(s) of observations** | **Number of locations** |
|---|---|---|---|---|---|
| Tanzania (Tanzania Wildlife Research Institute, 2001) | 2001 | Tanzania | Country-wide aerial census | 2001 | 724 |
| Kenya (Stewart & Stewart, 1963) | 1963 | Kenya | Literature survey | Pre-1963 | 127 |
| Ethiopia (Yalden *et al.*, 1984) | 1984 | Ethiopia | Literature survey | Pre-1984 | 84 |
| iNaturalist (Ueda *et al.*, 2017) | 2017 | Continental | Crowdsourced images with expert validation | 1982-2017 | 243 |
| GBIF (GBIF.org, 2017) | 2017 | Continental | Literature surveys, crowdsourced images with expert validation, others | 1973-2016 | 296 |

Table 2: Atmospheric, hydrologic, and land cover variables, data sources, and methodologies.

| **Type** | **Dynamic or Static** | **Description** | **Source** | **Physiological relevance** |
|---|---|---|---|---|
| Atmospheric | Dynamic | Minimum Temp Coldest Month | WorldClim | Lower thermal limit |
| Atmospheric | Dynamic | Maximum Temp Warmest Month | WorldClim | Upper thermal limit |
| Atmospheric | Dynamic | Annual Precipitation | WorldClim | Moisture for grass and/or grass-excluding vegetation |
| Atmospheric | Dynamic | Precipitation of Driest Quarter | WorldClim | Moisture for grass and/or grass-excluding vegetation |
| Hydrologic | Static | Shore length | Derived from Global Lakes and Wetlands Database (Lehner & Döll, 2004) | Immersion |
| Hydrologic | Dynamic | Minimum streamflow<br>Standard deviation of streamflow | Derived from WorldClim using bucket model (Huang *et al.*, 1996) and HydroSHEDS streamflow routing (Lehner *et al.*, 2008). | Immersion |
| Hydrologic | Dynamic | Climatic water deficit | Derived from WorldClim using bucket model (Huang et al., 1996) | Moisture for grass and/or grass-excluding vegetation |
| Hydrologic | Static | Base flow index (% of streamflow from groundwater) | Beck et al. 2013 | Immersion during dry season |
| Human | Static | Human population | CIESIN | Human conflict, persecution, exclusion |
| Human | Static | IUCN protected area database category | World Database of Protected Areas | Human conflict, persecution, exclusion |

Table 3. A priori candidate models

| **Name** | **Variables** | **nVars** | **Type** | **Mechanisms** |
|---|---|---|---|---|
| Atmospheric Core | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter | 4 | Atmospheric | Thermoregulation, grass availability, immersion (through precipitation) |
| Atmospheric Core and Human Population | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Human Population | 5 | Atmospheric | Thermoregulation, grass availability, immersion (through precipitation), anthropogenic exclusion |
| Atmospheric Core and Protected Area Category | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Protected Area Category | 5 | Atmospheric | Thermoregulation, grass availability, immersion (through precipitation), anthropogenic exclusion |
| Hydrology Core | Climatic Water Deficit, Runoff, Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow Index | 5 | Hydrology-informed | Grass availability, immersion (through streamflow) |
| Streamflow Core | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index | 3 | Hydrology-informed | Immersion (through streamflow) |
| Atmospheric and Streamflow | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index | 7 | Hydrology-informed | Thermoregulation, grass availability, immersion (through streamflow) |
| Streamflow Core and Protected Area Category | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Category | 4 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |

|  |  |  |  |  |
|---|---|---|---|---|
| Streamflow Core and Protected Area Category and Human Population | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Category | 5 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Protected Area Presence and Human Population | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Presence | 5 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Lake Margin and Climatic Water Deficit | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit | 4 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability |
| Streamflow Core and Lake Margin and Climatic Water Deficit and Protected Area Category | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit, Protected Area Category | 5 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability, anthropogenic exclusion |

## CHAPTER 4

# Species persistence and dispersal traits limit niche tracking in variable climates

## Abstract

Species distribution models are a commonly used tool to predict the changes of species distributions in response to climate change. Conventionally, they rely on statistical relationships between multi-decadal climatic averages and species occurrences to describe species' Grinnellian niches. Recent scholarship has highlighted the importance of interannual and interdecadal variability in shaping species distributions. This work has proposed that two species traits, dispersal (the ability to reach suitable locations) and persistence (the ability to continue to occupy an area with unsuitable conditions), facilitate niche tracking, the process by which species follow suitable conditions moving through geographic space. In theory, increasing dispersal and persistence abilities should lead to increasing niche tracking abilities, but the effects of these traits on niche tracking have not been quantified. We quantify the niche tracking potential of climatic niches for a range of dispersal and persistence traits. We do so by developing a niche tracking model that models niche tracking through historically observed patterns of temporal and spatial climatic variability. We used Holdridge life zones, delineations of temperature-precipitation climate space corresponding to major vegetation types, to define climatic niches. We then used the PRISM dataset of climatic conditions in the contiguous U.S. to map the life zones spatially at an annual time step from 1895 – 1980. Using our niche tracking model, we quantify how different dispersal and persistence abilities affect niche tracking potential for different life zones. We found that both persistence and dispersal increase niche tracking ability, and that initial increases in persistence provide a much greater increase in niche tracking ability than similar increases in dispersal. We also found that dynamically mapping potential occurrences at annual timesteps resulted in spatial patterns of suitability that differed from projections developed using the standard approach of multi-decadal climatic means. Our findings suggest that species distribution models will benefit from explicitly incorporating dynamic range tracking processes arising from interannual variability and dispersal and persistence constraints. Our findings also suggest that conservation actions should provide for both persistence and dispersal while species move their distributions in response to long-term climatic change.

## Introduction

A predominant approach to understanding the effects of climate change on species distributions is species distribution modeling (Elith & Leathwick, 2009). In their most common implementation, species distribution models seek to describe a species' Grinnellian niche by relating observations of species occurrences to abiotic environmental conditions at broad spatial scales; characterization of these abiotic environmental conditions then allow geographic projections of species distributions under climate change scenarios. The Grinnellian niche is the set of abiotic conditions which enable the intrinsic growth rate of a population to be positive, within a time period of interest (Pulliam, 2000; Soberón, 2007; Araújo & Peterson, 2012). Underlying this formulation is an assumption that within the focal time period the abiotic environmental conditions are stable, so that the presence of the species reflects that the growth rate in that location is positive (Early & Sax, 2011; Schurr *et al.*, 2012). In practice, this assumption is operationalized within the species distribution modeling framework by statistically relating the locations of species occurrences to time-averaged climate variables at those locations. The period over which climate variable means are calculated is typically 30 years, reflecting the format provided in frequently used datasets of climatic averages, including WorldClim and PRISM (Hijmans *et al.*, 2005; Daly *et al.*, 2008), although occasionally shorter time periods are used.

However, climatic conditions vary at multiple time scales, including at interannual and interdecadal scales shorter than 30 years (Jackson *et al.*, 2009). Biogeographers have long been interested in the effects of climatic variability at multiple temporal scales on species range sizes and configurations (Janzen, 1967; Brown *et al.*, 1996), and this continues to be an active area of scholarship (Quintero & Wiens, 2013; Chan *et al.*, 2016). General circulation models project that climatic variability is likely to increase as a result of anthropogenic climate forcing, suggesting that a better understanding of the effects of climatic variability is needed to understand changes to species distributions under scenarios of climate change (Intergovernmental Panel on Climate Change, 2013). The implications of interannual and interdecadal variability for species distribution modeling remain largely unaddressed by the literature, although this variability is problematic for the underlying assumption that species occurrence locations represent a population-level equilibrium with their climatic conditions.

Recent scholarship has developed or highlighted three related concepts to describe species distribution responses to climatic variability. The first idea, niche tracking, is the process where species occurrences geographically track suitable conditions when those suitable conditions move elsewhere as the result of climatic change or variability (Tingley *et al.*, 2009). The second idea is that species occurrences follow 'climate paths' through space and time as they shift dynamically to track their niches, mediated by their dispersal and persistence abilities, and that gaps in climate paths can restrict the capacity of a species to successfully shift its distribution (Early & Sax, 2011). Closely related is the concept of the ecological ratchet, whereby shorter-term climate variability coupled with long-term climatic change causes suitable conditions to move back and forth across space, and that species track those suitable conditions only as their dispersal, recruitment, and persistence abilities allow (Jackson *et al.*, 2009).

Taken together, this work has raised the importance of species traits, particularly persistence and dispersal abilities, in determining how species distributions respond to spatial and temporal climatic variability. These traits, in turn, may help determine individual species' vulnerability to climate change (Nadeau *et al.*, 2017). Persistence, defined in relation to the Grinnellian niche, is the period of time during which a species continues to occur in a location despite abiotic conditions being unsuitable (i.e., they would cause the intrinsic rate of population growth to be negative; adapting from Early & Sax 2011 and Soberón 2007). Persistence through unsuitable conditions could, for example, take the form of declining local populations that do not become extirpated, or the form of bet-hedging strategies such as variable times to germination in soil seed banks (Nadeau *et al.*, 2017). Persistence of piñon pine (*Pinus edulis*) populations through periods of unsuitable conditions have helped shape its present-day distribution (Gray *et al.*, 2006). The ability to persist through unsuitable conditions arising from interdecadal climate variability increased the range shift capacity of amphibian species in projections of future distributions under climate change (Early & Sax, 2011).

The role of dispersal ability in shaping range boundaries and in limiting range shifts under scenarios of climate change has received significantly more attention than persistence (Brooker *et al.*, 2007; Corlett & Westcott, 2013). By limiting the geographic area accessible to a species, dispersal ability places measurable geographical constraints on niche tracking. For example, up to 40% of mammals are projected to be unable to keep pace with their climatic conditions under climate change scenarios (Schloss *et al.*, 2012). In the context of climatic variability, increased dispersal ability has been hypothesized to increase range sizes by facilitating recolonization of areas that fluctuate between suitable and unsuitable conditions (Brown *et al.*, 1996).

The magnitudes of the effects of different dispersal and persistence abilities on niche tracking in variable climates are unquantified, as is the importance of each trait relative to the other. In addition, because different regions of the world differ in their levels of spatial and temporal climatic variability, the degree to which dispersal and persistence enable niche tracking may vary geographically as well (Nadeau *et al.*, 2017). In order to quantify the effects of dispersal and persistence abilities on niche tracking, we begin our analysis by developing a conceptual model and metrics of niche tracking capacity.

We adapt the set theory approach outlined by Soberón (2007) to discrete time steps to explicitly incorporate the roles of dispersal, persistence, and spatial and temporal variability in climate. In Soberón's formulation, species occurrences can be classified according to three overlapping sets of geographic locations: locations where abiotic conditions create the potential for the intrinsic growth rate to be positive (the geographical translation of the Grinnellian niche), locations where biotic interactions allow the intrinsic growth rate to be positive, and locations that are geographically accessible to the species for colonization.

Here, we adapt Soberón's set theory approach, but focus only on the intersection of the set of locations with abiotic suitability and the set of locations providing geographical accessibility (leaving the effects of biotic interactions for future work), and add a temporal dimension to describe how these sets of locations evolve through time as the result of spatial and climatic variability and the historical and geographical path dependence of the niche tracking process. For conceptual clarity we also restrict ourselves to only climatic variables in determining abiotic suitability.

Our conceptual diagram (Figure 1) illustrates our approach to modeling how persistence and dispersal abilities affect niche tracking in dynamic climates. At the beginning of a year y, the set of locations with potential occurrences from the previous year, $O_{y-1}$, determines the locations of origin of propagules or dispersers. The set of locations within dispersal ability *d* (a distance) of $O_{y-1}$ is $A_y$, which is the set of locations geographically accessible to propagules or dispersers. The intersection of the accessible locations with the climatically suitable locations, $I_y = A_y \cap S_y$, determines the locations in which the species can track its niche by establishing or maintaining populations there (due to the positive intrinsic growth rates there). This set of accessible and suitable locations from the current year, $I_y$, is then unioned with accessible and suitable locations from previous years, extending back to year y-*p*, where *p* is the persistence ability, to generate the set of potential occurrences for the current year, $O_y$. For example, for a species with a persistence ability of four years, the set of the species' potential occurrences in 1980 would include accessible and suitable locations in 1980, but also include all locations that the species was able to colonize in 1979, 1978, 1977, and 1976.

Two metrics can be quantified with each time step to evaluate the effects of persistence and dispersal abilities on niche tracking. The first is the niche tracking potential, defined as the ratio of the amount of area that is suitable and accessible to the amount of area that is suitable, or Area($I_y$)/Area($S_y$). The second is the occurrence potential, which is the ratio of the amount of area occupied (irrespective of suitability) to the amount of area that is suitable, or Area($O_y$)/ Area($S_y$).

Building from this conceptual diagram, we implemented a spatially explicit niche tracking model that tracks different climatic niches (bounded areas of climate space) through observed climate surfaces from 1895 to 1980 at an annual time step across the contiguous United States, for a range of different dispersal and persistence abilities. At each time step the niche tracking potential and occurrence potential are quantified. We ask the following questions using our model, which was implemented in the R software environment (R Core Team, 2016):

1. How are niche tracking potential and occurrence potential dependent on persistence?
2. How are niche tracking potential and occurrence potential dependent on dispersal?
3. How do the effects of persistence and dispersal compare?
4. How do the effects of persistence and dispersal vary by climatic niche (life zone), and how is this related to the geographic stability of each life zone?
5. How do projections of potential occurrence from the niche tracking model differ from locations of suitable area predicted using the standard time-averaged approach (30-year climatic means)?

## Methods

Climate data: We used the Parameter-elevation Regressions on Independent Slopes Model (PRISM) annual climate dataset for the contiguous United States as our source of atmospheric climate surfaces (Daly *et al.*, 2008). We used PRISM's monthly temperature and monthly precipitation surfaces, available continuously from 1895-1980, to calculate annual biotemperature (the mean of the set of average monthly temperatures with values between 0 and 30 degrees C, Lugo *et al.* 1999) and total annual precipitation surfaces. These surfaces were at a 4-km resolution. The PRISM surfaces were developed by spatially interpolating historical observations of climate to a gridded surface, incorporating the influences of elevation, coastal, rain shadow, and other physiographic influences on climate (Daly *et al.*, 2008).

Holdridge Life Zones: Holdridge developed a system of classifying climate space into climatic niches or "life zones" corresponding to broad plant formations (such as deserts, forests, or grasslands) (Holdridge, 1967). Holdridge defined climate space as a triangular 2-d lattice using logarithmic axes of annual biotemperature, annual precipitation, and potential evapotranspiration. The core of the Holdridge system is the life zone chart representing this lattice, depicting the boundaries between different life zones in two-dimensional climate space (Figure 2). The Holdridge system provides a useful heuristic for the climatic niches of species for the purposes of understanding niche tracking dynamics, as it captures biogeographical patterns driven by moisture and temperature, but is simple to implement and independent of non-climatic variables (such as soils or spatial arrangement) used in other ecological classification schemes (e.g., ecoregions) (Lugo *et al.*, 1999). Its generality is also a strength in developing insights for coarse-filter conservation strategies for climate adaptation, as the range-scale spatial dynamics at play for a particular life zone are likely to be relevant for any particular species associated with that life zone (Hunter *et al.*, 1988). It is worth noting that the Holdridge life zones represent an area of climate space rather than a specific vegetation association, even though the life zones are labeled with the vegetation types they are most often associated with.

Following Lugo et al. (1999), we calculated annual precipitation and annual biotemperature from the PRISM climate surfaces for each year. We then classified each pixel of the contiguous U.S. according to the corresponding hexagon in the Holdridge life chart, applying this approach at an annual time step rather than using 30-year means. We pooled the classifications for hexagons by their life zone type (e.g. desert, scrub), and did not separate out latitudinal regions or altitudinal belts in order to use the most generous niche delineation within the Holdridge system. For our analyses we focused on the desert, scrub, and wet forest hexagons, because they represented large, distinct regions of the contiguous U.S. The boundaries of the climate spaces of these focal life zone types are illustrated by the orange, green, and blue outlines in Figure 1. We used the Holdridge life zone classifications and the PRISM-derived biotemperature and total annual precipitation surfaces to generate maps of the distribution of the desert, scrub, and wet forest life zones at an annual time step from 1895 to 1980, for the contiguous U.S. (Figure 3).

Niche location turnover: For each life zone type, we calculated the turnover rate of locations of the life zone from year to year. We calculated year-to-year turnover for each consecutive pair of years as the ratio of the area of the symmetric difference of the sets of locations from the two years to the area of the union of the two years' locations.

Niche tracking model: We operationalized the niche tracking model outlined in Figure 1 and in the introduction as follows. Dispersal ability was modeled in intervals of 4 km or greater due to the cell size of the underlying PRISM climate data. At a dispersal distance of 4 km we used a queen's neighborhood around cells belonging to $O_{y-1}$ to identify accessibility for colonization, and otherwise we classified cells as available for colonization if the cell centroid fell within the dispersal distance from the centroid of the nearest cell belonging to $O_{y-1}$. The dispersal distance values ranged from 4 to 40 km, at 4 km increments. Importantly, both suitable and unsuitable cells were capable of generating dispersers if they belonged to the set of potential occurrences from the previous year.

We quantified persistence ability as the number of years a species could continue to occur in a cell with unsuitable conditions, following Early and Sax (2011), but at an annual time step (Figure 4). For example, if a cell were suitable and occupied in 1895, but then became unsuitable for each of the next 3 years, then a species with a persistence of 2 years would continue to occupy the cell in 1896 and 1897, but would not occupy the cell in 1898. Persistence values used were 1, 2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 years.

To reduce sensitivity to initial conditions, we specified that occurrences in 1894, $O_{1894}$, the year previous to the start of the simulation in 1895, were all cells in which conditions were suitable for a total of 10 or more consecutive or non-consecutive years in the period from 1895 to 1980. This provided a generous initial distribution of the species, ensuring that there were source cells located near areas of repeated suitability at the start of the simulation. In quantifying niche tracking potential and occurrence potential, we discarded values from the first 20 years of the simulation (1895-1914) to allow for model spin-up and exclude effects of the initial conditions.

Comparison with time-averaged approach: We compared the niche tracking model's predictions of potential occurrence locations to the standard approach of using a 30-year mean of climatic variables to map the Grinnellian niche. We did this by first calculating the 30-year mean of biotemperature and total annual precipitation from the 30-year period ending in the focal year. For example, to calculate the 30-year mean climate corresponding to 1924, we calculated the mean climate from annual climate surfaces from 1895 through 1924. We then classified the 30-year mean climate surfaces into Holdridge life zones using the same approach as the annual life zone classification. We then calculated commission and omission error rates of the 30-year mean classification when evaluated against the occurrence outputs of the niche tracking model ($O_y$), across all years and for each persistence and dispersal combination. The commission and omission rates provide a measure of difference between predictions of the niche tracking model and the standard approach of using a 30-year mean climate.

## Results

*How are niche tracking potential and occurrence potential dependent on persistence?* Greater persistence ability increased the niche tracking potential (Figure 5), as well as the occurrence potential (Figure 6), across life zone types. Increases in persistence ability from 1 to 6 years resulted in the greatest increases in niche tracking, while beyond 6 years niche tracking increases diminished, with only minimal increases beyond persistence values of 14 years. At persistence levels of 4 years or less, 20% or more of the suitable area remained untracked across life zones (at low dispersal levels). The same pattern of increasing persistence abilities resulting in initially large but then diminishing returns held true for changes in occurrence potential, although increases diminished more slowly.

*How is niche tracking potential affected by dispersal?* Generally, increases in dispersal ability resulted in gradual increases in niche tracking and occurrence potentials (Figure 5, Figure 6), with rates of increase in occurrence potential differing substantially by life zone. Increases in dispersal ability resulted in the greatest increases in niche tracking potential at low persistence levels, and had the least effect at high persistence levels, showing similar diminishing returns as persistence increases. Across persistence levels, increases in dispersal ability also resulted in gradual increases in occurrence potential for the scrub and wet forest life zones. For the desert life zone, increasing dispersal ability at higher persistence levels increased occurrence potential more than it did at low persistence levels.

*How do the effects of persistence and dispersal compare?* Initial increases in persistence ability provided much greater increases in niche tracking than initial increases in dispersal ability. For example, for the desert life zone, a doubling of persistence ability from 2 to 4 years increased niche tracking potential by almost 25%, which would have required a 5-fold increase in dispersal ability from 4 km/year to 20 km/year. Initial increases in persistence similarly provided greater increases in occurrence potential than modeled increases in dispersal ability. Incremental increases in persistence beyond 10 years, however, resulted in smaller increases in niche tracking potential.

*How do the effects of persistence and dispersal vary by climatic niche (life zone)?* The positive relationships between dispersal, persistence and niche tracking and occurrence potentials were consistent across the desert, scrub, and wet forest life zone types. However, the degree to which increased dispersal and persistence increased niche tracking varied substantially by life zone type. All showed large jumps in niche tracking potential from initial increases in persistence ability, followed by diminishing returns, along with gradual increases from increased dispersal ability. At low (1-4 years) persistence abilities, niche tracking potential levels for the wet forest life zone were much higher than for the desert and scrub life zones. Life zones differed in turnover rates of locations of suitable conditions at annual time steps, with desert and scrub life zones having much higher turnover rates than the wet forest life zone (Figure 7).

*How do projections of potential occurrence from the niche tracking model differ from locations of suitable area predicted using 30-year climatic means?* Locations classified as suitable from 30-year climatic means differed systematically from the locations of potential occurrences identified using the niche tracking model, with the differences depending on the persistence and dispersal values used in the niche tracking model (Figure 8). Commission errors represent the rate at which 30-year climatic mean projections classified pixels as suitable that were not classified as potential occurrence locations by the niche tracking model. Omission errors represent the rate at which 30-year climatic mean projections failed to classify pixels as suitable that were identified as potential occurrence locations by the niche tracking model. There were generally few commission errors for the persistence and dispersal values modeled, except for persistence values below 4 years, and commission errors decreased as persistence and dispersal abilities increased (Figure 8). Omission errors were present for all persistence and dispersal values, and were positively associated with increases in persistence and dispersal values.

## Discussion

The magnitude of the effect on niche tracking of initial increases in persistence is surprisingly large, particularly for life zones with high year-to-year location turnover. Scholarship on species distribution modeling, range shift projections, and climate adaptation has focused on the roles of dispersal ability and climatic refugia in determining species future distributions under climate change scenarios (Keppel *et al.*, 2012; Schloss *et al.*, 2012; Urban, 2015), but relatively little attention has been paid to persistence through periods of low suitability. Our analysis provides quantitative support to previous works that have argued for the importance of persistence (Jackson *et al.*, 2009; Early & Sax, 2011). Based on our simulations, persistence appears to increase niche tracking through two mechanisms. The first is that it allows species to remain present in locations during periods of unsuitable climate either until they become suitable again. The other is that persisting populations are a source of propagules or dispersers that could colonize any suitable locations within dispersal distance the persisting population, enlarging the set of accessible locations, similar to the effect of dispersal ability on range size proposed by Brown et al. (1996).

Particularly interesting is that the largest gains in niche tracking potential come from increases in persistence ability of between 1 to 6 years. This temporal range encompasses the variability in time to germination for many plant seed banks, a bet-hedging strategy enabling plants in variable climates to increase chances of growing during a suitable year (Nadeau *et al.*, 2017). Persistence during unsuitability is more difficult to operationalize for animal populations, but could be explicitly linked to rates of local population declines during unsuitable periods. More work is needed to theoretically link persistence ability to metapopulation dynamics which account for the effects of climatic variability in shifting the population dynamics and spatial arrangement of source and sink populations (Pulliam, 2000; Soberón, 2007; Schurr *et al.*, 2012).

An implication of this result for climate adaptation is that providing for persistence may be an effective management strategy. Examples might include providing water during droughts, limiting anthropogenic disturbance during unsuitable periods arising from interannual variability, or identifying remaining microsites that provide suitable climatic conditions for protection during unsuitable periods. In particular, our results suggest that it may be valuable to identify those species with restricted persistence and dispersal abilities for monitoring during unsuitable periods.

Our results confirm that dispersal ability facilitates niche tracking, particularly for species with low persistence abilities and life zones with higher locational turnover. These results support management efforts to maintain and improve connectivity as a climate adaptation measure. However, they suggest that dispersal alone may not be sufficient to maximize niche tracking ability, particularly in areas with more variable climates, and that providing for persistence may provide larger gains in niche tracking ability. Alternately, because we did not account for anthropogenic and non-climatic barriers to dispersal, our results may underrepresent the importance of dispersal to niche tracking in landscapes fragmented by human land use, hydrology, or topography (McGuire *et al.*, 2016). More theoretically, our results support the proposition that greater dispersal abilities result in larger range sizes because greater dispersal allows species to better track climate variability through time and space (Brown *et al.*, 1996).

Niche tracking responds differently to dispersal and persistence increases in different life zones. A likely reason for different responses among life zones is that they differ in year-to-year turnover in locations of suitable conditions. The desert and scrub life zones had higher levels of turnover, and needed greater increases persistence and dispersal to reach the same level of niche tracking potential as the more stable wet forest life zone. Interestingly, the desert life zone saw occurrence potential increases two to three times those of the scrub life zone, despite similar levels of year-to-year location turnover. One explanation is that with increasing persistence and dispersal abilities, a desert species is able to occur in locations with intermittent, spatially isolated desert conditions that cover a much larger geographical area than the suitable area of a typical year. In contrast, the amount of area with intermittent and isolated scrub or wet forest conditions are smaller relative to areas suitable for scrub or wet forest life zones in a typical year. This suggests that the spatial and temporal arrangement (e.g., spatial isolation and temporal frequency of suitability) of a climatic niche plays a role in determining the effects of dispersal and persistence ability on occurrence potential. Species in different life zones are likely to have faced differing evolutionary pressures on traits related to persistence or dispersal, which may affect their vulnerability to climate change (Nadeau *et al.*, 2017). Our results suggest that climate adaptation actions may need to be tailored to the geography of the climatic niche of concern and the levels of variability that historically shaped species traits and trait variation.

Locations identified using time-averaged mapping of suitable conditions (using 30-year climatic means) differ systematically from locations of potential occurrence identified using the niche tracking model. The time-averaged projections both over- and underpredict occurrences, depending on dispersal and persistence abilities. These results indicate that projections of distributions using time-averaged climates are likely to differ substantially from the projections of the niche tracking model. These results reinforce past warnings that patterns of geographic occurrence may greatly exceed the geographic distribution of suitable conditions (Pulliam, 2000), and suggest caution about the frequent assumption that geographic distributions are equivalent to the geographical realization of the Grinnellian niche (Tingley *et al.*, 2009).

Our niche tracking model is a heuristic device meant to explore the interacting effects of interannual variability, persistence, and dispersal on the potential distributions of species, and results should be interpreted in that light. Using continental-scale climate surfaces of the contiguous U.S., the model quantifies general relationships between niche tracking, occurrence potential, and species traits. However, further analyses are needed before extending our results to specific species or regions.

One area of caution centers on the use of Holdridge life zones as proxies for species' climatic niches. We intentionally grouped the Holdridge life zones by life zone type in order to provide large (in climate space) delineations of potential species' climatic niches. Larger climate niche spaces have lower location turnover rates, resulting in more conservative assessments of the effects of dispersal and persistence on niche tracking. Real species niches are likely smaller in climate space, and are likely to be driven by additional climatic variables other than biotemperature and annual precipitation, such as minimum temperatures, or growing-season rainfall. Adding climatic variables and reducing the climate space of the niche would act to increase the effects of dispersal and persistence on niche tracking. A promising area of further analysis would be to relate climatic niche size (in climatic space) to niche tracking dynamics.

Another area of caution relates to the spatial and temporal extent and grain of the analysis. Spatially, we were limited to a 4-km grain by available climatic data, which masks microclimate heterogeneity likely to be present within each grid cell (Ackerly *et al.*, 2010). Persistence during unsuitable conditions could take the form of species relying on microclimatic conditions at finer spatial scales, suggesting that persistence may depend not only on species traits, but fine-scale climatic heterogeneity. We were also restricted to the borders of the contiguous U.S., and artificial edge effects of political borders likely reduced niche tracking near border regions. Temporally, we focused on annual time steps because many species have a generation time of 1 year (Quintero & Wiens, 2013; Nadeau *et al.*, 2017). Other temporal resolutions and durations may be more appropriate for some species, however, and could easily be accommodated by the model.

The niche tracking model is dichotomous (suitable / unsuitable, accessible / inaccessible, persisting / absent) in its approach to modeling niche processes, whereas these processes are at least in part continuous and probabilistic (Pulliam, 2000). In this light, the model acts to identify geographic boundaries or constraints on potential occurrences, whereas a probabilistic approach would be needed to measure probabilities of occurrence in space or time. Relatedly, the model assumes that all locations of potential occurrence (including where a population persists through unsuitable conditions) generate propagules or dispersers with the same dispersal ability. This reflects the general finding that sink populations within a metapopulation still generate dispersers capable of colonizing other locations (Howe *et al.*, 1991). However, persistence and dispersal ability could be modeled as continuous functions of climatic conditions.

Our conceptual model is sufficiently flexible to allow for extensions to address other key ecological and biogeographical processes. For example, the effects of biotic interactions on suitability could be brought back into the model as an additional geographic constraint on suitability. Alternately, a lag time to colonization could be added to reflect the amount of time needed for biotic habitat characteristics to become suitable to a species. For animals dependent on vegetation structures, conditions likely wouldn't be suitable until after a shift in climate that lasted long enough for corresponding vegetation to develop. For example, browsing animals might not move into a grassland area in which climatic conditions have shifted toward scrub conditions until after woody vegetation has established. The effect on niche tracking dynamics of human land use could be evaluated by weighting dispersal abilities with cost-distance models that limit the ability of species to move across landscapes (Schloss *et al.*, 2012).

An informative extension of this analysis would be to use the niche tracking model to project each life zone's niche tracking potential to future conditions (e.g. end of 21st Century) using annual climate surfaces that include climate change scenarios. Relative to expected levels of climatic change at the end of the 21st Century, the 1895-1980 time period used in this analysis has relatively lower levels of climatic change. The niche tracking potential of a species under consistently changing trends in the mean (e.g., increasing long-term mean temperatures) would likely change as a result of altered spatial and temporal configurations of suitable conditions.

Another extension of this model could explore the effects of different levels of interannual variability on niche tracking. General circulation models generally predict increases in interannual variability as a result of climate change, and increases in variability alone may affect niche tracking processes. Interannual climate variability could substantially increase the rate at which organisms would need to move to track their climates. Understanding niche tracking processes in climates with both changing trends as well as changing levels of variability will provide guidance for analyses that support conservation planning, such as climate connectivity and climate velocity (Dobrowski & Parks, 2016; McGuire *et al.*, 2016).

The niche tracking modeling approach we present here provides a flexible framework with which to quantify species distribution dynamics in variable and changing climates as a function of species traits such as dispersal and persistence. It can accommodate different spatial and temporal scales of variability, can be extended to biotic and non-climatic abiotic variables, and is grounded in existing niche theory. Advances in the availability and temporal extent and resolution of spatially explicit climate data, as well as increased processing speeds, make it possible to address the implications of climatic variability for niche tracking. Future development of species distribution models will benefit from explicitly incorporating dynamic niche tracking processes while accounting dispersal and persistence constraints.

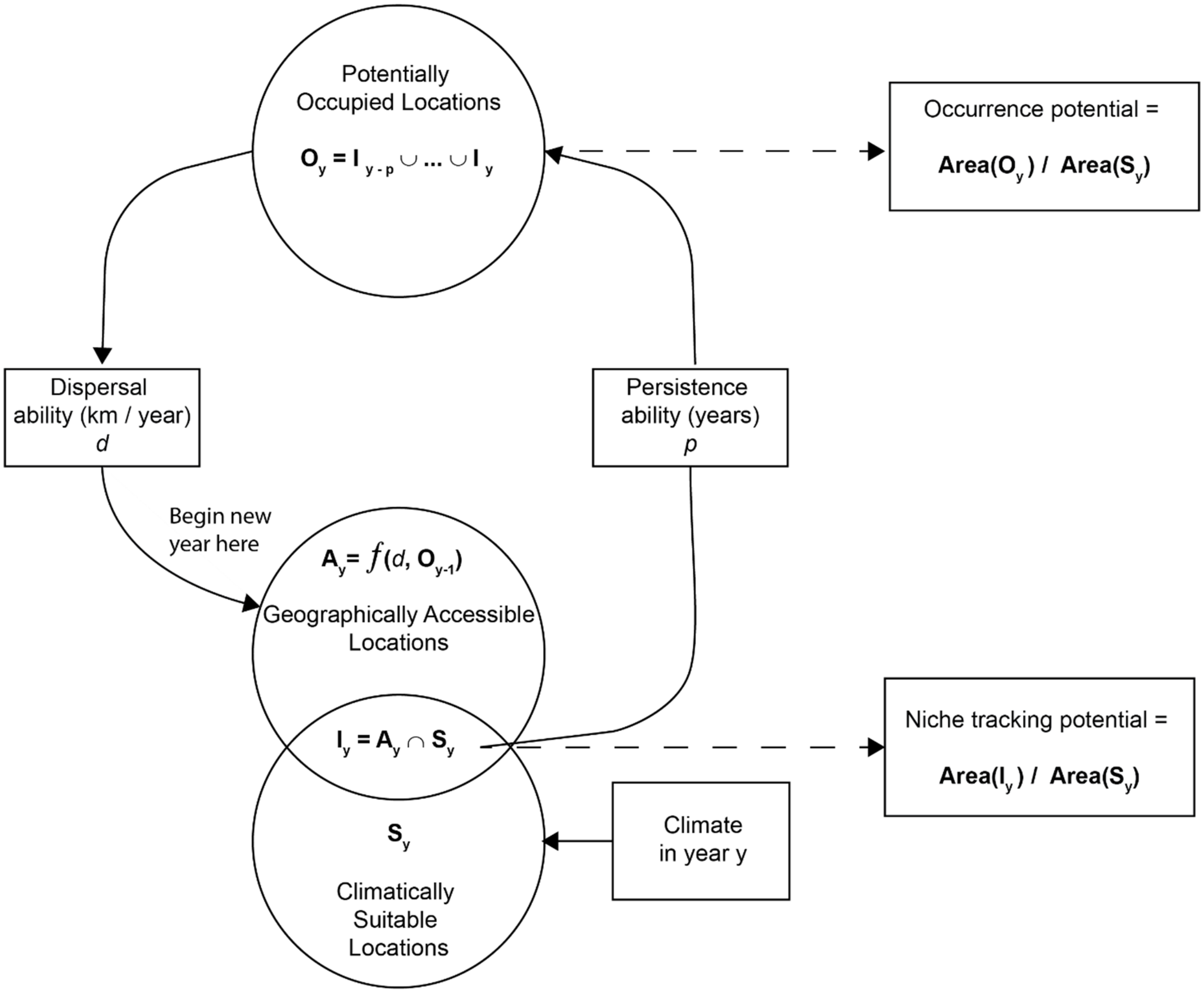


Figure 1. Conceptual diagram of the mechanisms through which dispersal ability and persistence affect the geographic distribution of species through time at annual time steps, accommodating both variable and changing climatic conditions.

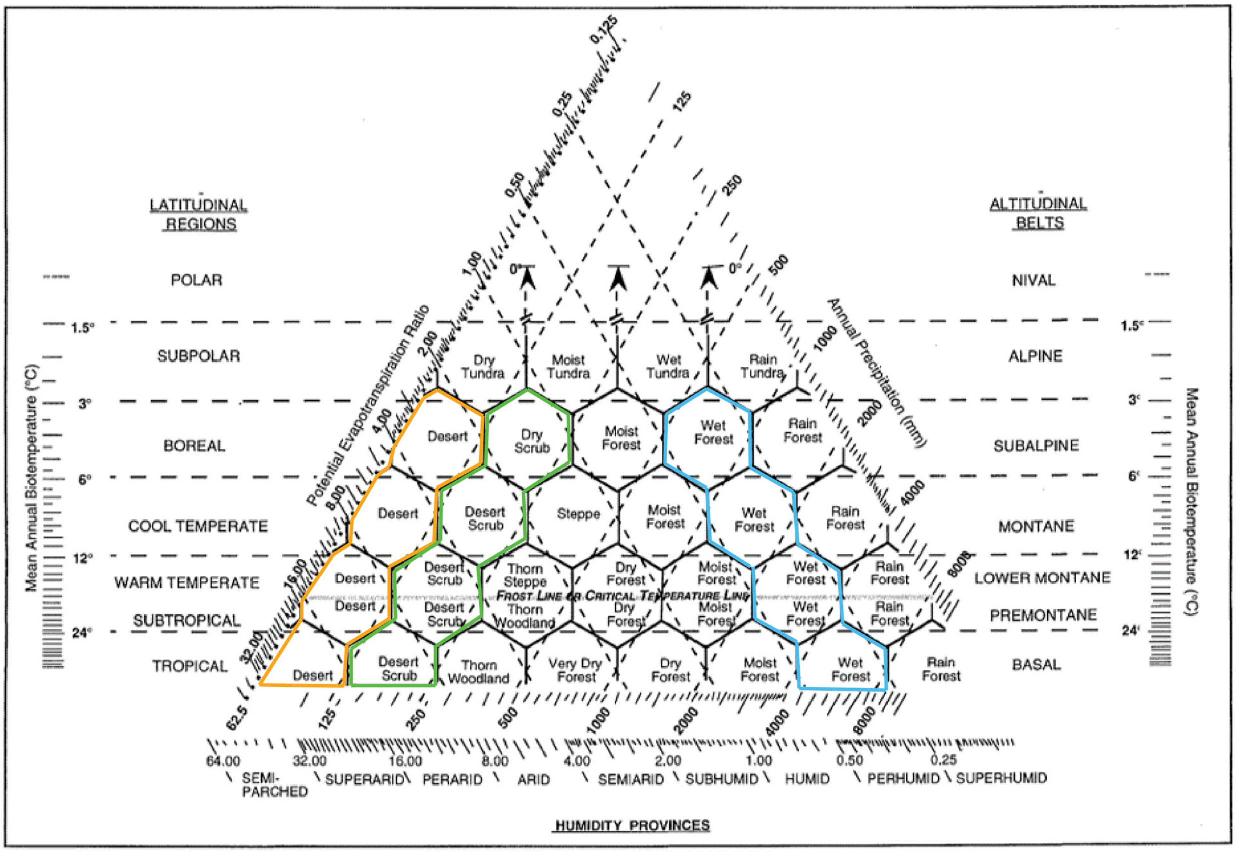
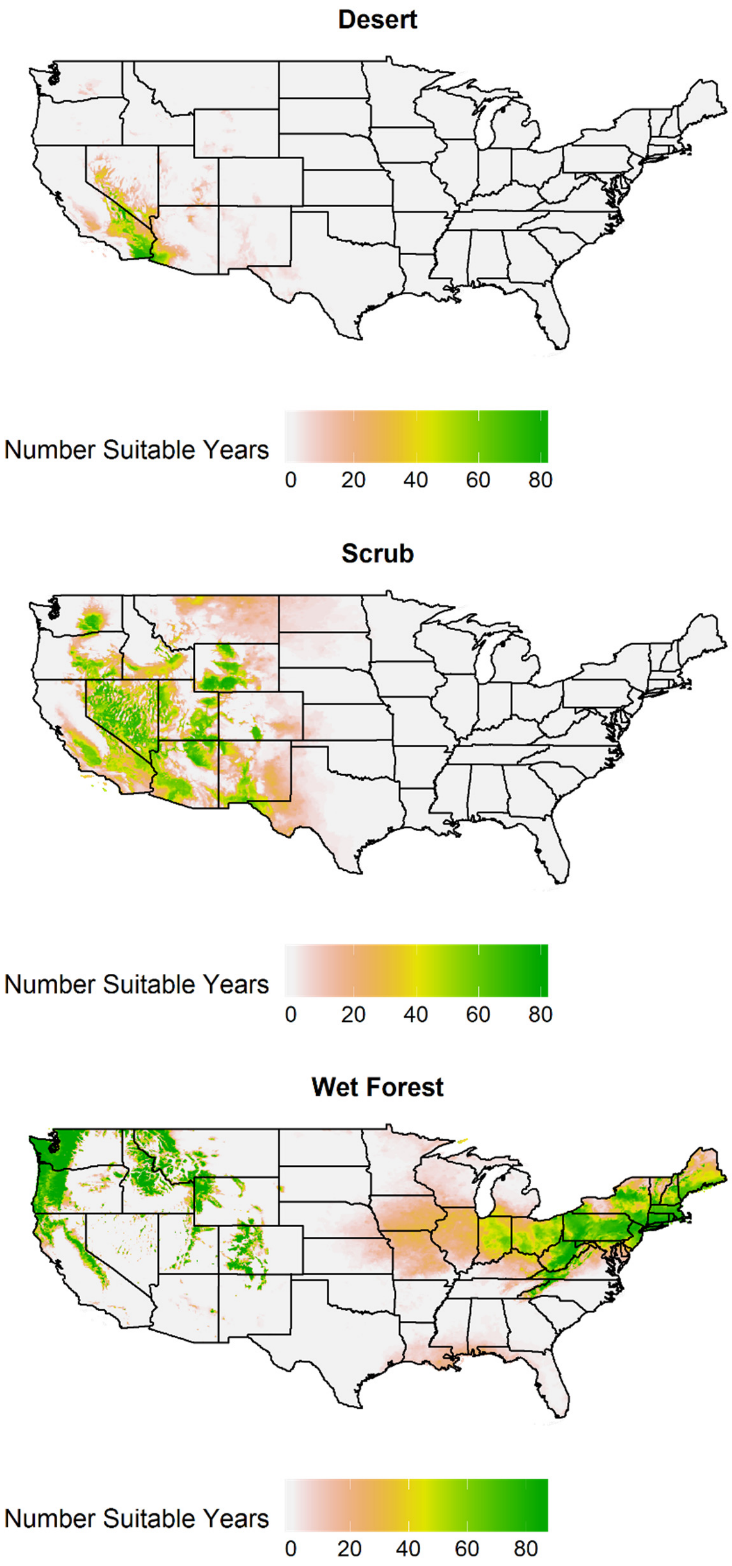


Figure 2. Holdridge life zone chart from Holdridge (1967), transformed from Lugo et al. (1999) to quantify the desert (orange), scrub (green), and wet forest (light blue) life zone types used as climatic niches in this analysis.


Desert

Scrub

Wet Forest

Figure 3. Number of years a given cell was classified as belonging to the desert, scrub, or wet forest life zone type on an annual basis between 1895 and 1980.

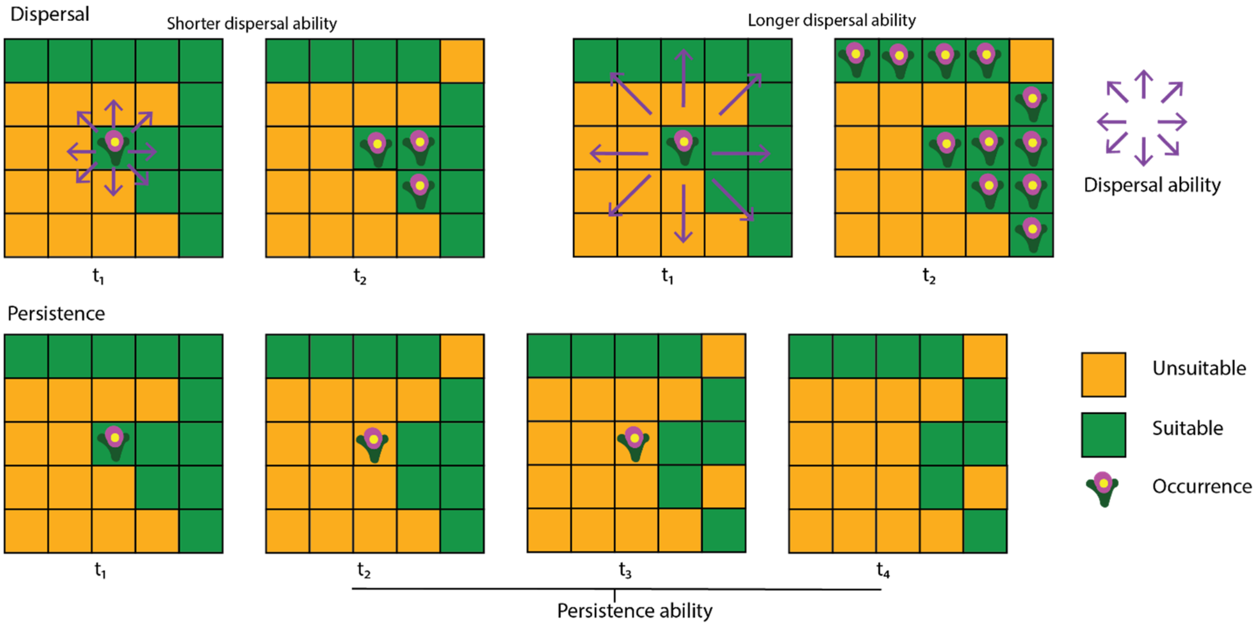


Figure 4. Dispersal and persistence processes as implemented in the niche tracking model.

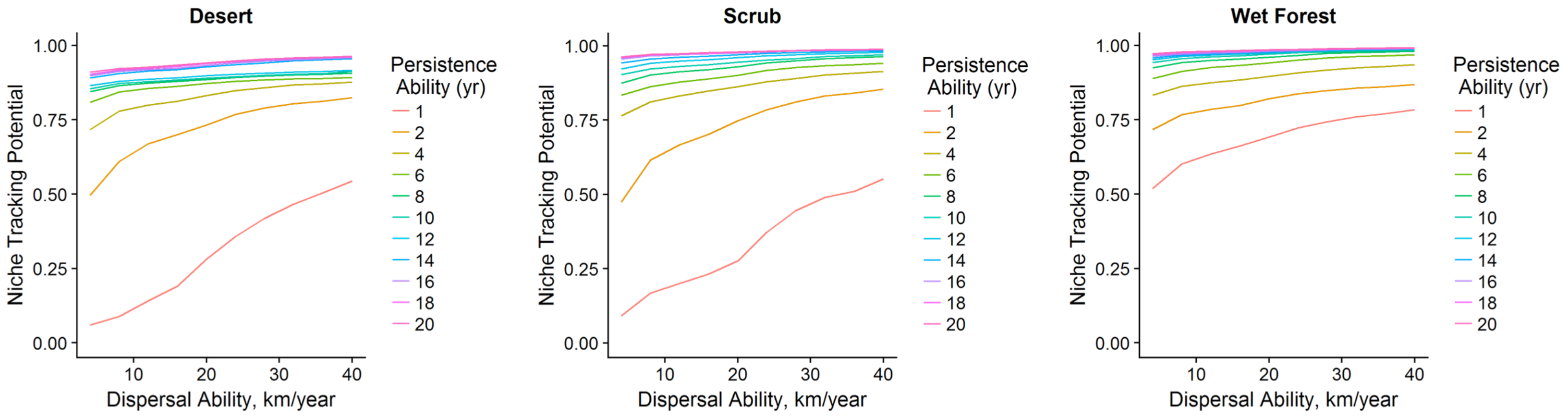


Figure 5. Niche tracking potential (ratio of accessible and suitable area to total suitable area, y-axis) of the desert, scrub, and wet forest life zones for different dispersal (x-axis) and persistence abilities.

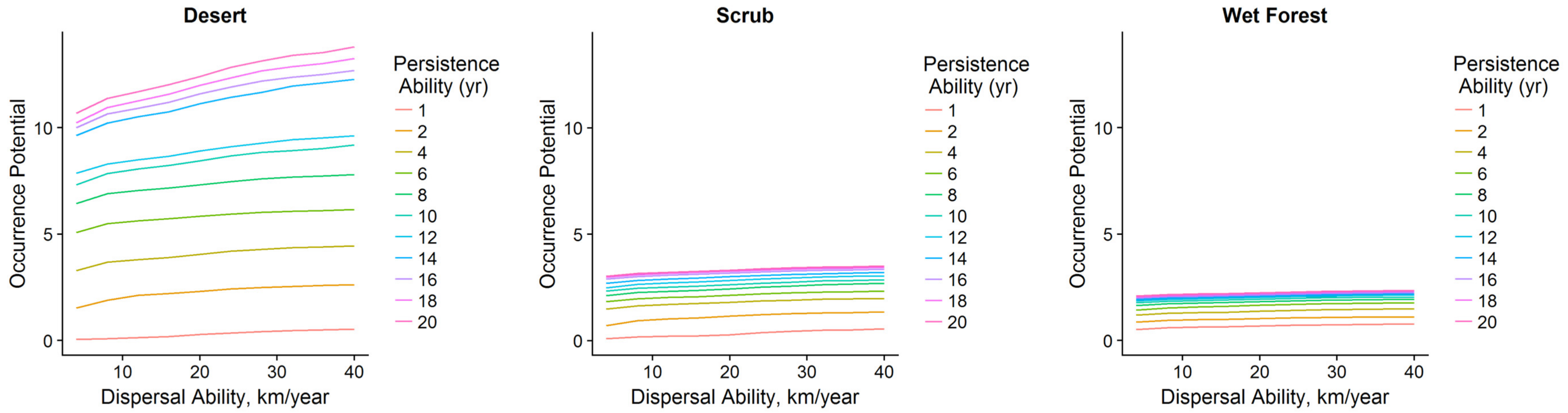


Figure 6. Occurrence potential (ratio of potentially occupied area to total suitable area, y-axis) of the desert, scrub, and wet forest life zones for different dispersal (x-axis) and persistence abilities. Y-axis values can be larger than 1 because persistence leads to potential occurrences in unsuitable areas, so that occupied area can be larger than suitable area.

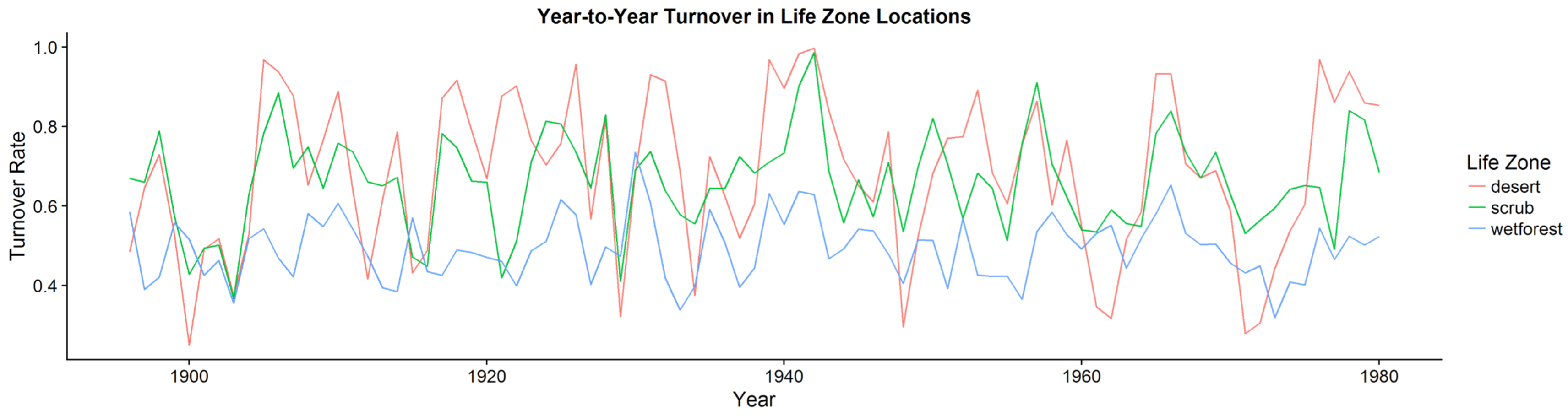


Figure 7. Year-to-year turnover in the locations for each life zone type.

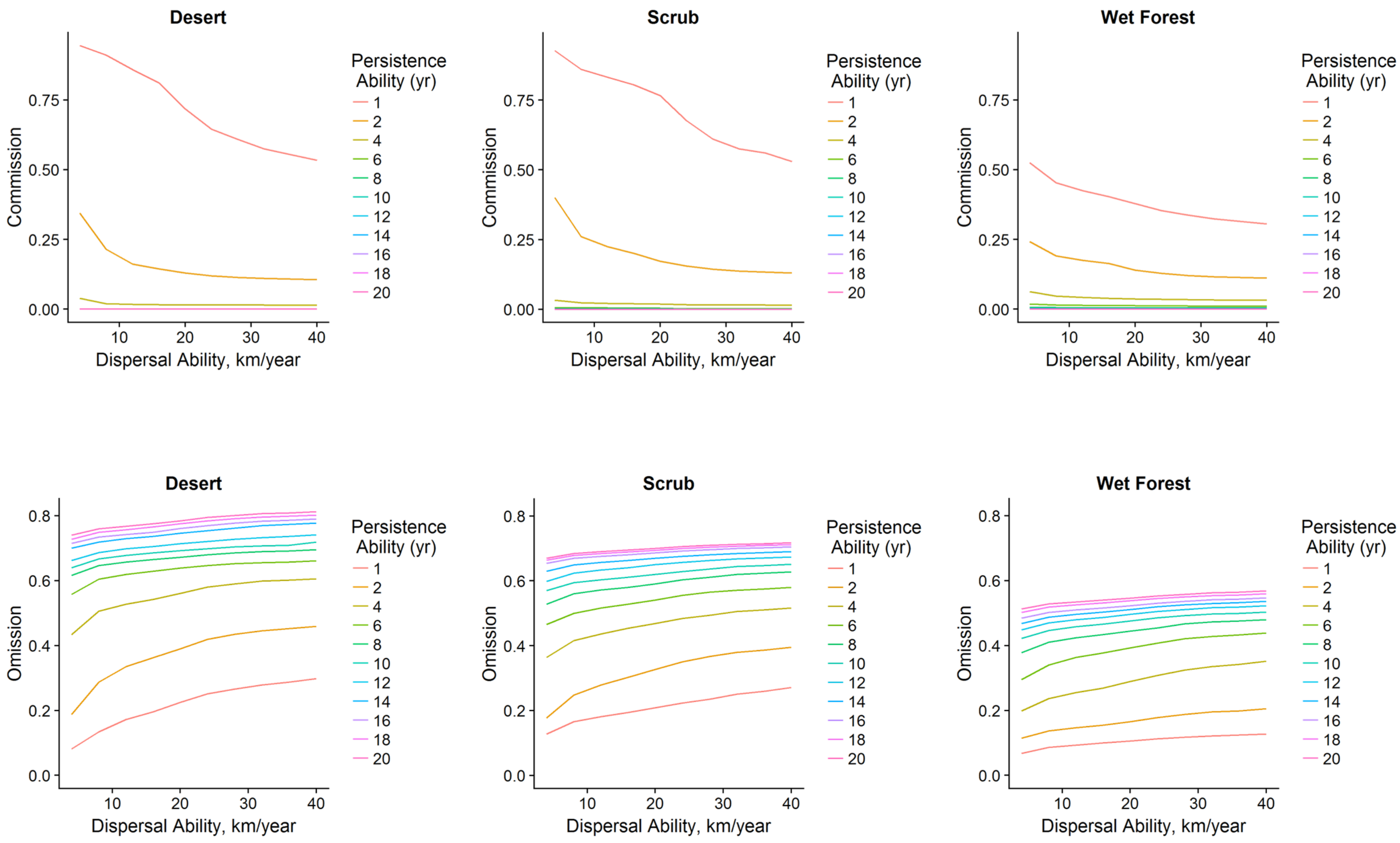


Figure 8. Errors of commission (top row) and omission (bottom row) of suitable locations classified using the standard time-averaged approach (using 30-year climatic means) when evaluated against locations of potential occurrence generated by the niche tracking model.

# CHAPTER 5

## General Conclusions

The analyses of the preceding chapters illuminate ways in which animal movement affects and is affected by ecological and biogeographical dynamics, at scales ranging from the daily movements of individual animals to the evolution of species distributions over decades. The first study (Chapter 2) showed that *H. amphibius* movements generate hotspots of nutrient transfer at concentrations comparable to net primary productivity, likely influencing the spatial dynamics of both aquatic and terrestrial systems. The second study (Chapter 3) showed that the distribution of suitable habitat for *H. amphibius* will likely shrink and shift in response to environmental change arising from the interacting effects of land use, hydrologic, and climate change. The third study (Chapter 4) had a surprise twist. Movement – in the form of dispersal – does increase niche tracking ability, but persistence, which has received much less academic attention, often has a much larger effect on niche tracking. These studies all connect large, recently available datasets of movement or environmental conditions with conceptual and quantitative models reflecting underlying spatial or ecological processes. Each of these studies has implications for the body of scholarship in which it is nested, provides analytical tools that can be extended to other species or systems, and suggests directions for future work.

### *Summary of central findings*

In the first study, the biomass transfer model revealed the process by which *H. amphibius* movement behavior generates patterned landscapes of nutrient removal and deposition hotspots. In addition, the model enabled me to generate maps of these nutrient transfer landscapes, making it possible to explore the spatial dynamics of nutrient transfers, and showing that the amount of biomass concentrated spatially reaches levels equivalent to rates of aboveground net primary productivity. In addition to revealing the influences of *H. amphibius* on ecosystem ecology, the study also provided metrics of *H. amphibius* behavioral budget, home range size, habitat use, and movement behavior useful for conservation planning.

In the second study, I used hydrology-informed species distribution modeling to identify the interacting effects of climate and land use change on the distribution of *H. amphibius*. I found that scenarios of increased streamflow abstraction for irrigated agriculture will lead to much greater declines in *H. amphibius* habitat suitability than scenarios of climate change alone. In addition, I contrasted predictions of *H. amphibius* distributions generated using only atmospheric climate variables with predictions that incorporated hydrologic variables, and found significant improvements in model performance when hydrology was incorporated.

In the third study, I explored the role of movement in shaping species distributions in variable climates. By developing a model that simulates niche tracking through historically observed patterns of temporal and spatial variability, I quantified effects of different dispersal and persistence abilities on niche tracking potential. I found that both dispersal and persistence facilitate niche tracking, and that small increases in persistence ability can greatly increase niche tracking potential relative to similarly scaled increases in movement ability.

### *Implications and directions for future work*

The movement-driven nutrient transfer model from the first study provides a novel approach to map transfers of biomass or other quantities from movement data. This model could be applied to the biomass transfers of other species of animals. Particularly rewarding would be studies of species where dung transects or soil samples could test the predictions of the nutrient transfer model. Alternately, the transport of other kinds of materials or quantities could be modeled, including animal-transported seed dispersal or persistent organic pollutants, or even waste, energy or financial flows in human societies. The finding that the movements of *H. amphibius* generate hotspots of nutrient removal and deposition challenges assumptions underlying macro-scale simulations of nutrient transfers, which assume that animals simply diffuse nutrients across nutrient gradients (e.g. Doughty *et al.*, 2016). Further work is needed to understand how the nutrient concentrating effect of *H. amphibius* daily movements scales over long time periods. One promising avenue of future work would predict and test different species' different roles as as nutrient concentrators or diffusers based on differences in patterns of space and time allocation.

The hydrology-informed species distribution modeling approach presented in the second study opens the door to more accurate predictive modeling for semiaquatic species generally. Addressing the coupled terrestrial-aquatic habitat needs of semiaquatic species has been difficult, but the linking of hydrologic and atmospheric variables for baseline and future conditions makes it possible to more accurately describe their environmental niches and future distributions. Identifying and incorporating a key physiological mechanism (dependence on surface water) into the species distribution modeling framework greatly improved predictive accuracy, supporting literature arguing for a mechanistic focus in variable selection for species distribution models (Kearney & Porter, 2009). Incorporating hydrologic variables in distribution modeling is likely to provide increased predictive accuracy not just for semiaquatic species, but for the many species dependent on riparian vegetation or other water-linked habitat features.

The niche tracking model presented in the third study is a novel effort to address temporal and spatial environmental variability in ecological niche modeling. The niche tracking model provides a way to explicitly account for environmental variability as well as dispersal and persistence traits when developing species distribution models. Several extensions of this approach are likely to be fruitful. One is to use the model to predict geographic bottlenecks of suitability under scenarios of climatic change, allowing identification of areas for conservation that, if accessible to a species, greatly increase the species' niche tracking potential. Another extension is to use the model to guide management during unsuitable climatic periods that could result in extirpations, such as extended droughts (Deguines *et al.*, 2017). A necessary next step will be to parameterize the model using the climatic niches of specific, well-studies species with known dispersal or persistence abilities. This model will also help illuminate how species access and occupy climate refugia.

The scientific community, and society at large, is faced with the enormous challenge of anticipating the ecological consequences of climate change – climate change which is occurring at rates that are evolutionarily unprecedented, and that will raise global temperatures to levels not experienced for millions of years (IPCC, 2007). Meeting this challenge will require bridging disciplinary divides and drawing from many sources of inference, including the exponentially increasing amounts of environmental and ecological data provided by technologies such as remote sensing and GPS tracking, without losing sight of the fundamental ecological processes at play.

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# APPENDICES

## Chapter 2 Appendix

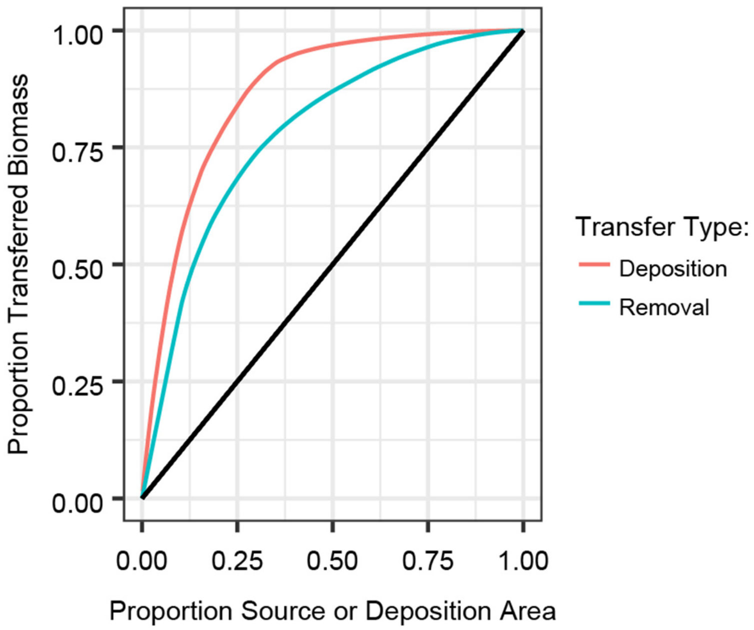
Supplementary Table 1: Deployment duration and characteristics of tagged *Hippopotamus amphibius*. Rainfall is derived over the month in which the animal was tagged. Sex was not determined for subadults.

| Animal ID | Deployment date | Tag retention (days) | Number of GPS fixes | Accelerometer recording duration (days) | Age/Sex | Calf | Rainfall (mm) |
|---|---|---|---|---|---|---|---|
| D1 | Mar-13 | 0.5 | 38 | - | Male | - | 71 |
| D2 | Mar-13 | 1.2 | 43 | - | Female | - | 71 |
| D3 | Mar-13 | 2.2 | 117 | - | Female | - | 71 |
| D4 | Jan-14 | 7.9 | 512 | - | Female | - | 0.5 |
| D5 | Nov-14 | 0.9 | 61 | - | Female | Med | 39 |
| D6 | Nov-14 | 0.1 | 6 | - | Female | Large | 39 |
| D7 | Dec-14 | 7.2 | 395 | 5.8 | Female | Large | 51 |
| D8 | Dec-14 | 5.4 | 245 | 4.2 | Female | Small | 51 |
| D9 | Jan-15 | 0.2 | 21 | 0.3 | Female | Med | 0 |
| D10 | Jan-15 | 0.9 | 57 | 0.8 | Subadult | - | 0 |
| D11 | Jan-15 | 3.3 | 143 | 3.3 | Male | - | 0 |
| D12 | Apr-15 | 6.5 | 378 | 6.5 | Female | Large | 139 |
| D13 | May-15 | 2.7 | 166 | - | Subadult | - | 126 |

Supplementary Table 2: Space use metrics. Metrics are within-individual means of the distances or areas traversed each night an individual was tracked.

| Metric | N | Mean (±SD) | Min | Max |
|---|---|---|---|---|
| Nightly movement MCP area (ha) | 11 | 46 (±66) | 4 | 230 |
| Short-term foraging area projected from nightly MCPs (ha) | 4 | 120 (±92) | 46 | 250 |
| Nightly distance moved (m) | 11 | 3100 (±2200) | 1300 | 9200 |
| Maximum velocity (m/s) | 11 | 0.46 (±0.14) | 0.22 | 0.74 |
| Velocity (m/s) | 11 | 0.0870 (±0.053) | 0.039 | 0.19 |
| Maximum distance from river (m) | 11 | 350 (±140) | 60 | 560 |
| Distance from river (m) | 11 | 88 (±58) | 9.5 | 170 |

Supplementary Figure 1: Biomass-area accumulation curve, which plots the proportion of total biomass transferred against the proportion of the area it is transferred from or onto. The black line with slope of 1 indicates evenly dispersed biomass transfer, and curves further from the black line indicate increasing levels of biomass concentration.



## Supplementary Text 1: Fix rate and spatial accuracy of GPS tracking devices

We measured the accuracy of GPS fixes using three tracking devices left in a stationary location at our study site, at a 10-minute fix rate. We first took more than three days of fixes with each device's GPS antenna oriented horizontally, and then three days of fixes with the antenna oriented vertically. We calculated mean deviation and circular error probability for each orientation and tag.

Out of 3154 fix attempts by the three test units, only one fix attempt failed to calculate a location. The mean deviation was 3.4 m (sd=0.61) for tags on a horizontal plane and 4.5 m (sd=0.39) for tags on a vertical plane. For horizontal fixes, 96% (sd=0.02) of fixes were within 10 m of the mean location, and 80% (sd=0.08) were within 5 m; for vertical fixes, 93% (sd=0.02) of fixes were within 10 m and 70% (sd=0.04) were within 5 m.

## Supplementary Text 2: Water movements

For any period in which the GPS unit failed to record two or more successive fixes (with each fix attempt spaced 10 minutes apart), we classified the movement between the previous and subsequent successful GPS fixes as occurring in water. While this approach may overestimate water use (the hippopotamus can emerge from water and travel on land for up to 8 minutes before a GPS fix is attempted), it may also underestimate it by requiring two successive failed GPS fixes. In our field tests (above), only 1 of 3154 fix attempts failed while on land. In order to exclude missed GPS fixes not due to immersion, we excluded movements where either the beginning or the end of the movement segment was more than 150 meters from the river.

## Supplementary Text 3: Distance from river

Mean distance of grazing fixes from the river was 76 ± 110 m, and terrestrial resting sites were 54 ± 120 m from the river.

## Chapter 3 Appendix

Table S1: All candidate models used in exploratory analysis.

| **Name** | **Variables** | **nVars** | **Type** | **Mechanisms** |
|---|---|---|---|---|
| Atmospheric Core | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter | 4 | Atmospheric | Thermoregulation, grass availability, immersion (through precipitation) |
| Atmospheric Core and Human Population | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Human Population | 5 | Atmospheric | Thermoregulation, grass availability, immersion (through precipitation), anthropogenic exclusion |
| Atmospheric Core and Human Population and Protected Area Category | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Human Population | 6 | Atmospheric | Thermoregulation, grass availability, immersion (through precipitation), anthropogenic exclusion |
| Hydrology Core | Climatic Water Deficit, Runoff, Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow Index | 5 | Hydrology-informed | Grass availability, immersion (through streamflow) |
| Streamflow Core | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index | 3 | Hydrology-informed | Immersion (through streamflow) |
| Atmospheric and Streamflow | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index | 7 | Hydrology-informed | Thermoregulation, grass availability, immersion (through streamflow) |
| Atmospheric and Streamflow and Human Population | Max Temperature of the Warmest Month, Min Temperature of the Coldest Month, Annual Precipitation, Precipitation of the Driest Quarter, Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Human Population | 8 | Hydrology-informed | Thermoregulation, grass availability, immersion (through streamflow), anthropogenic exclusion |

| | | | | |
|---|---|---|---|---|
| Streamflow Core and Human Population | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Human Population | 4 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Protected Area Category | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Category | 4 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Protected Area Presence | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Presence | 4 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Protected Area Category and Human Population | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Category | 5 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Protected Area Presence and Human Population | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Base-flow index, Protected Area Presence | 5 | Hydrology-informed | Immersion (through streamflow), anthropogenic exclusion |
| Streamflow Core and Lake Margin and Climatic Water Deficit | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit | 4 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability |
| Streamflow Core and Lake Margin and Climatic Water Deficit and Human Population | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit, Human Population | 5 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability, anthropogenic exclusion |
| Streamflow Core and Lake Margin and Climatic Water Deficit and Protected Area Category | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit, Protected Area Category | 5 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability, anthropogenic exclusion |
| Streamflow Core and Lake Margin and Climatic Water Deficit and Human Population and Protected Area Category | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit, Human Population | 6 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability, anthropogenic exclusion |

| | | | | |
|---|---|---|---|---|
| Streamflow Core and Lake Margin and Climatic Water Deficit and Human Population and Protected Area Presence | Streamflow Lowest Flow Month, Streamflow Standard Deviation, Lake Margin, Climatic Water Deficit, Human Population | 6 | Hydrology-informed | Immersion (through streamflow and lake margin), grass availability, anthropogenic exclusion |
| Lowflow and Climatic Water Deficit | Streamflow Lowest Flow Month, Climatic Water Deficit | 2 | Hydrology-informed | Immersion (through streamflow), grass availability |
| Lowflow and Lake Margin | Streamflow Lowest Flow Month, Lake Margin | 2 | Hydrology-informed | Immersion (through streamflow and lake margin) |

Figure S1: International Union for the Conservation of Nature range map of *H. amphibius* (Lewison & Oliver, 2008).

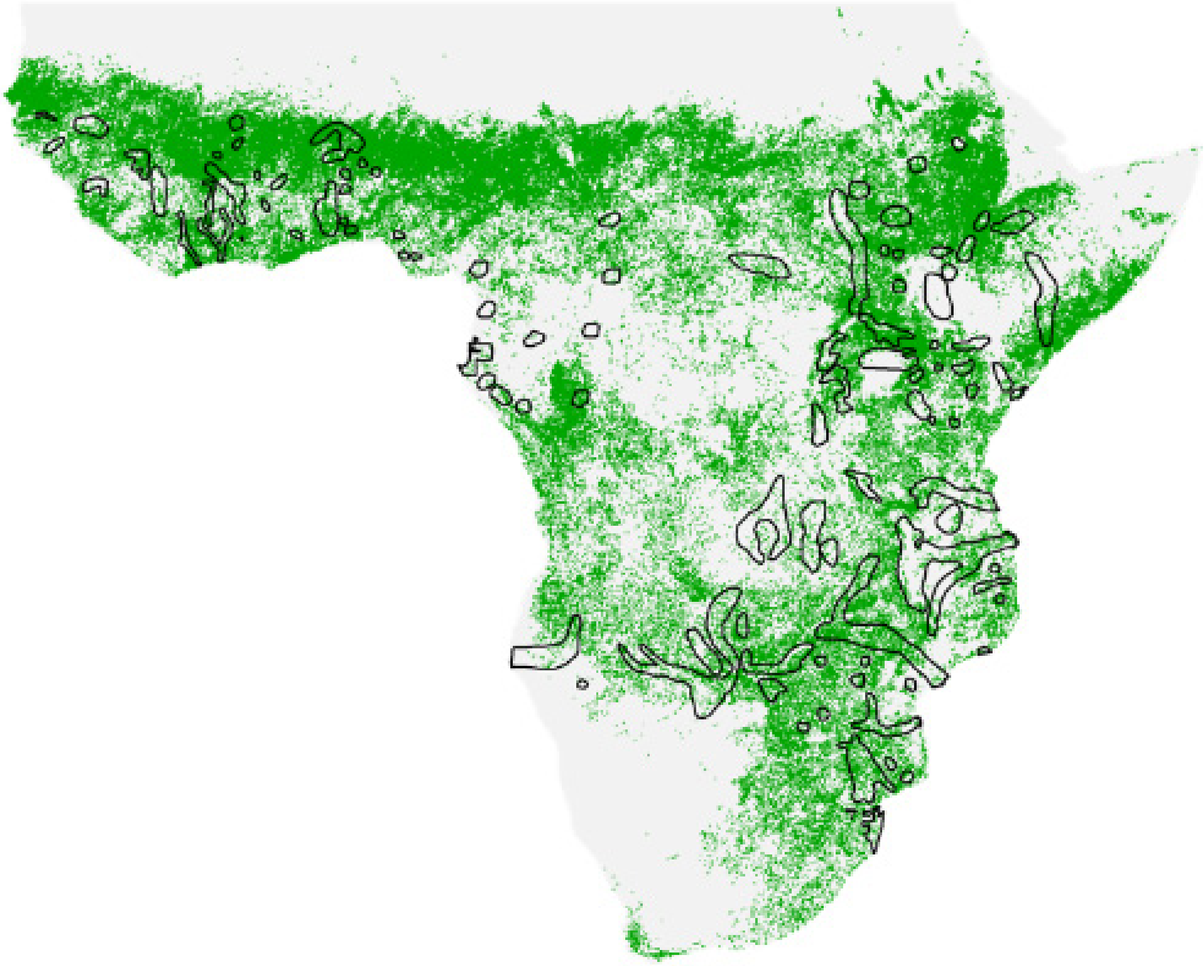


Figure S2. Cultivated lands of Africa (FAO, 2011), with the IUCN *H. amphibius* range map outlined in black.

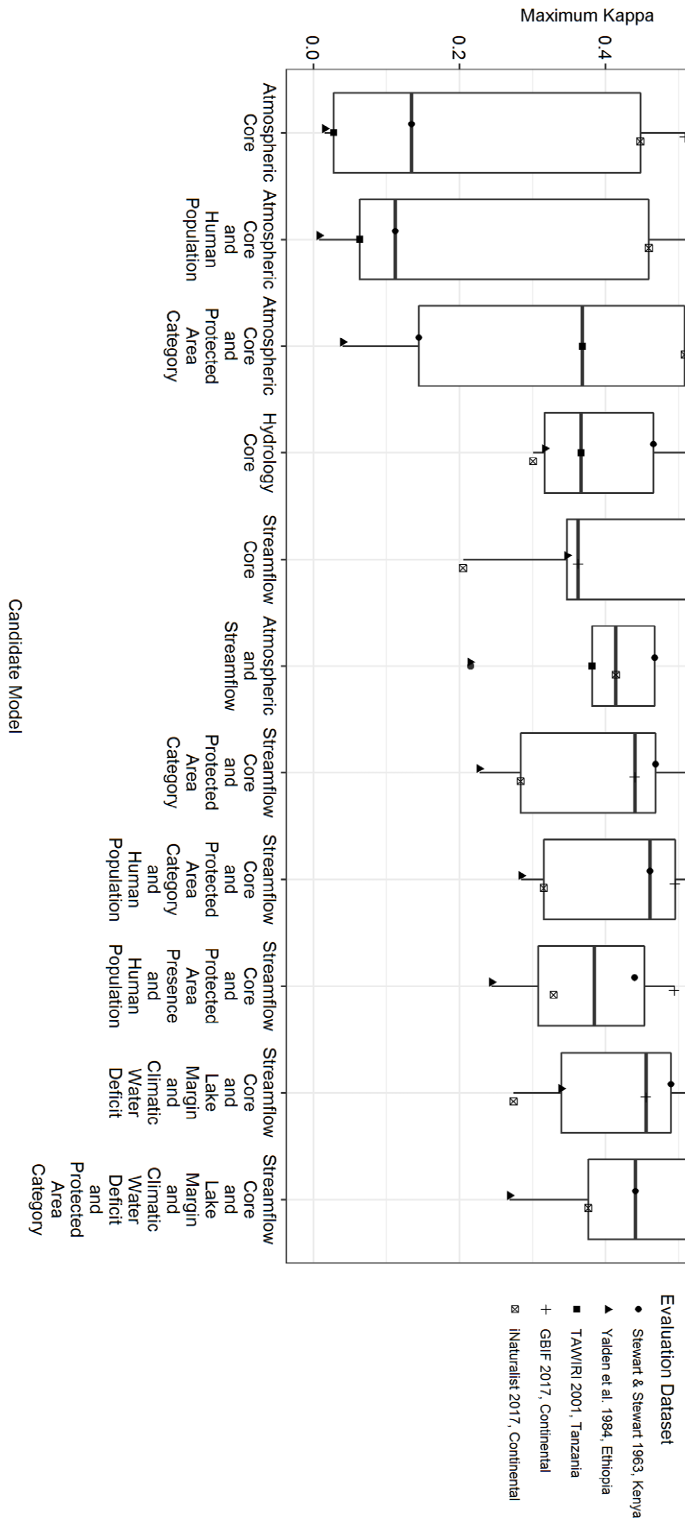


Figure S3. Model performance, measured by Maximum Kappa, for candidate models using a leave-one-out cross-validation approach.

Supporting Text:

<u>CMIP5 General Circulation Models used in future climate scenarios:</u> ACCESS1-0, BCC-CSM1-1, CCSM4, CNRM-CM5, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-ES, INMCM4, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3, NorESM1-M