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From Pet to Pest? The Potential Global Range and Food Web Effects of a Generalist Carnivore

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FROM PET TO PEST? THE POTENTIAL GLOBAL RANGE AND FOOD WEB EFFECTS OF A GENERALIST CARNIVORE

by

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ABSTRACT

The Nile monitor lizard [*Varanus niloticus* (Linnaeus, 1766)] is a generalist carnivore, native to Sub-Saharan Africa and the Nile River but now established in North America as a result of the pet trade. Once introduced, they are a potential invasive threat to native wildlife. Here, I create ensemble species distribution models (SDMs) to predict the global distribution of this generalist carnivore given current and future climate conditions. I then quantify the monitor's potential effects on 85 food webs representing >900 different species within the projected regions based on stomach content data. Climate, vegetation, and elevation data are used for 507 georeferenced observation points from the Nile monitor's native range to produce current and future (2070) ensemble SDMs. Explanatory variables are evaluated as ten alternative models organized in three subsets according to model assumptions. The true skill statistic (TSS), sensitivity, and specificity were used to assess model performance, and the best subset was averaged to represent an ensemble model. Food web impacts after the generalist predator's addition are determined by changes in nine metrics of food web structure. The most predictive (TSS scores ≥0.87) ensemble SDM was based on the MARS and FDA algorithms using elevation and climate for current and future conditions. This model shows that, if introduced, Nile monitors will likely spread into many regions in the Americas, the Caribbean, Madagascar, Southeast Asia, and Australia. Assuming unabated carbon emissions by 2070, climate change will enhance that potential range. Adding Nile monitors to food webs generally increases overall trophic links, connectance, link density, and fraction of intermediate taxa, with decreases in the

fraction of top and basal taxa. These results are consistent with a generalist predator that affects many species and is likely to affect food web stability. The potential Nile monitor range is vast and encompasses multiple biodiversity hotspots. Given many strong food web interactions by this generalist predator, vulnerable regions should actively prohibit/regulate Nile monitors as pets, enforce those restrictions, and promote exotic pet amnesty programs. Southern US states should especially act soon to prevent spread of the Nile monitor to the Neotropics from its current introduced population in Florida and as released pets.

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CHAPTER ONE: INTRODUCTION

Successful vertebrate invaders possess some or all of the following traits: close association with humans, abundance in a wide native range, competitive nature, large size, broad diet, and a high tolerance to various physical conditions (Ehrlich 1989; Sakai et al. 2001). Africa's Nile monitor, *Varanus niloticus* (Linnaeus, 1766), represents all of these traits and *may* become invasive where it is introduced. This Old World monitor is established in urban areas across southern Florida, starting in 1990 as a result of the exotic pet industry (Enge et al. 2004; Campbell 2005; Engemen et al. 2011). The Nile monitor has the largest geographic distribution of the African varanids where it reaches substantial population densities (40-60/km^2) and can grow to 2.4m with a body mass of ≤7.3kg (Edroma and Ssali 1983; Bayless 2002; de Buffrenil and Hemery 2002; Enge et al. 2004; Campbell 2005). The Nile monitor is a generalist carnivore and scavenger that consumes a wide range of both invertebrate and vertebrate prey, and can thrive in various environments (e.g. grasslands, lowland forests, swamps, seashores, and semi-deserts), especially with a permanent water body nearby. Though it is poikilothermic, the Nile monitor extends its occupied thermal range beyond organismal limits by burrowing underground (Edroma and Ssali 1983; Losos and Greene 1988; Luiselli 1999; Faust 2001; Bennett 2002; Enge et al. 2004; Campbell 2005). In addition, the Nile monitor reaches sexual maturity in two years, has a clutch size of 50-60 eggs per year, and uses ~300m activity area around its burrow and ≤5ha to forage (Edroma and Ssali 1983; de Buffrenil and Hemery 2002; Campbell 2005; Ciliberti et al. 2012).

But *how* invasive might the Nile monitor be? An invasive species is one that (a) spreads, and (b) causes ecological and or economic harm after it is established in a new geographic location (Doody et al. 2009; Sakai et al. 2001; Hardin 2007). The purpose of this work was to address (a) above – the potential spread of the Nile monitor, assuming introduction as occurred in Florida, and (b) above- the potential ecological effects of the Nile monitor in introduced regions based on diet and ecological network analyses. The Nile monitor is a popular commodity, exported in great quantities each year from places such as Benin, Ghana, Nigeria, Tanzania, and Togo into Europe and the United States (Faust 2001). Also, the Nile monitor is: bred in introduced regions for the pet trade; one of the most commonly sold African monitor species in the US; and available for sale in multiple countries (Faust 2001; Enge et al. 2004). A Google search (10 July 2016) for the phrase "Nile monitor for sale" and restricted to the past year obtained 20 distinct websites. The same search unrestricted in time obtained ~1,450 web hits; clearly this predator is widely sold, typically as juveniles.

The successful establishment in Florida by this large predator may portend the future of other global regions, as a result of ongoing global pet trade and economic development. It is crucial to predict where this generalist predator may spread and the resulting ecological implications so that regions at risk may act to prevent similar introductions (Sakai et al. 2001). Therefore, I projected the current and future (2070) global distribution of the Nile monitor using alternative ensemble species distribution models (SDMs) based on climate, vegetation, and elevation.

Once I accurately predicted the regions at risk of Nile monitor spread across the globe, published food webs from those regions were analyzed before and after Nile monitor addition for changes in food web network structure. Contrary to popular food web practices, my analyses were based solely on species *addition* to the network rather than species loss in order to avoid assumptions about secondary extinction (Strong and Leroux 2014). This will also lead to novel interactions amongst species that may in turn result in novel effects on the food web metrics (Strong and Leroux 2014). Based on changes in native food web metrics, I was able to estimate the potential for this non-native predator to enact such novel effects on native food web structure.

This thesis presents the first global ensemble SDMs (both current and future) for the Nile monitor. This is also the first study that estimates ecological changes in food web structure as a result of Nile monitor introduction, again on a global scale. These are two unique endeavors and therefore warrant the two separate chapters that follow. Chapters 3 and 4 document my thorough research to answer the two most basic questions that can be asked for any introduced species: 1) where will it go? and 2) what can it do if it gets there? (respectively).

CHAPTER TWO: NILE MONITOR ENSEMBLE SPECIES DISTRIBUTION MODELING

Background

Successful vertebrate invaders possess some or all of the following traits: close association with humans, abundance in a wide native range, competitive nature, large size, broad diet, and a high tolerance to various physical conditions (Ehrlich 1989; Sakai et al. 2001). Africa's Nile monitor, *Varanus niloticus* (Linnaeus, 1766), represents all of these traits. This Old World monitor is established in urban areas across southern Florida, starting in 1990 as a result of the exotic pet industry (Enge et al. 2004; Campbell 2005; Engemen et al. 2011). The Nile monitor has the largest geographic distribution of the African varanids where it reaches substantial population densities (40-60/km^2) and can grow to 2.4m with a body mass of ≤7.3kg (Edroma and Ssali 1983; Bayless 2002; de Buffrenil and Hemery 2002; Enge et al. 2004; Campbell 2005). The Nile monitor is a generalist carnivore and scavenger that consumes a wide range of both invertebrate and vertebrate prey, and can thrive in various environments (e.g. grasslands, lowland forests, swamps, seashores, and semi-deserts), especially with a permanent water body nearby. Though it is poikilothermic, the Nile monitor extends its occupied thermal range beyond organismal limits by burrowing underground (Edroma and Ssali 1983; Losos and Greene 1988; Luiselli 1999; Faust 2001; Bennett 2002; Enge et al. 2004; Campbell 2005). In addition, the Nile monitor reaches sexual maturity in two years, has a clutch size of 50-60 eggs

per year, and uses ~300m activity area around its burrow and ≤5ha to forage, (Edroma and Ssali 1983; de Buffrenil and Hemery 2002; Campbell 2005; Ciliberti et al. 2012).

But where might the Nile monitor spread? The purpose of this work was to project the potential global range of the Nile monitor, assuming introductions occur (as in Florida). The Nile monitor is a popular commodity, exported in great quantities each year from places such as Benin, Ghana, Nigeria, Tanzania, and Togo into Europe and the United States (Faust 2001). Also, the Nile monitor is: bred in introduced regions for the pet trade; one of the most commonly sold African monitor species in the US; and available for sale in multiple countries (Faust 2001; Enge et al. 2004). A Google search (10 July 2016) for the phrase "Nile monitor for sale" and restricted to the past year obtained 20 distinct websites. The same search unrestricted in time obtained ~1,450 web hits; clearly this predator is widely sold, typically as juveniles.

The successful establishment in Florida by this large predator may portend the future of other global regions, given ongoing global pet trade and economic development. It is crucial to predict where this generalist predator may spread and the resulting ecological implications in order to identify in advance the regions at risk so that they may act to prevent similar introductions (Sakai et al. 2001). Therefore, I projected the current and future (2070) global distribution of the Nile monitor using alternative ensemble species distribution models (SDMs) based on climate, vegetation, and elevation. Climate variables are typically used for SDMs (Guisan and Zimmermann 2000), whereas vegetation reflects climate and other factors (e.g., edaphic conditions, biotic interactions), and elevation is related to both climatic and topographic

conditions. Thus, work here advances SDM research by evaluating alternative SDMs alone and in combination, to more closely represent strong inference and model selection (Chamberlin 1890; Platt 1964; Burnham and Anderson 2002).

This work was not based on genetic subpopulations of the Nile monitor (e.g., Dowell et al. 2016) because (a) that would assume genetic subsets will be introduced only to certain regions (e.g., only W. African animals will appear in the Americas; Dowell et al. 2016) whereas global trade actually exists and can be expected to continue; and (b) climate tolerances have not been experimentally demonstrated to differ among genetic populations of Nile monitors. It is possible that genetic subsets may have more narrow potential ranges than those projected here, but that possibly is an answer to a different question than the one addressed here.

Methods

I geo-referenced 507 unique point locations of 800 Nile monitor observations documented in the primary literature (de Buffrenil and Francillon-Viellot 2001; Bayless 2002; Berny et al. 2006; Ciliberti et al. 2011), using Google Maps (Google 2013; Appendix A). These coordinates served as native range reference points for climate, vegetation, and elevation data.

Global predictor data were collected with a 30 arc-second ($1km^2$) resolution: current and future (2070) bioclimatic variables (WorldClim), mean annual net primary productivity (NPP) based on Moderate Resolution Imaging Spectroradiometer (MODIS), and elevation [Shuttle Radar Topography Mission (SRTM); WorldClim] (Hijmans et al. 2005, Zhoa et al. 2015).

Elevation and NPP variables had similar projections but different extents; the 'raster' package in R was used to merge the layers and project them as one (Hijmans et al. 2015).

Seven hypothesized models [i.e., each predictor variable (climate, NPP, elevation) and all combinations] were computed and compared to determine which variables (or combinations) most accurately predict potential Nile monitor range. This approach was intended to be analogous to model selection based on information theoretic criteria (Burnham and Anderson 2002). The criterion to evaluate alternative models was the true skill statistic (TSS), which is insensitive to prevalence or size of the specific data set used, and can account for both omission and commission errors. As a result, TSS is preferred to the kappa statistic and area under the curve (AUC; Allouche et al. 2006; Lobo et al. 2008). The TSS scales from -1 to 1 and measures the rates of true positives (sensitivity) and true negatives (specificity) that result from random guesses; +1 indicates perfect agreement (i.e., always distinguishes between suitable and unsuitable habitat) and values ≤ 0 indicate a performance no better than random (Allouche et al. 2006). To permit all possible models to be reported and compared, a low quality threshold was set (0.4), but TSS scores were then compared among models, where those with greater scores were identified as more accurate.

All models were projected as ensemble SDMs with the 'Biomod2' package in R with 80% data split to calibrate and evaluate the models and equal weight given to both presences and absences (prevalence=0.5) (Thuiller et al. 2009; Thuiller et al. 2014). The ensemble framework of Biomod2 reduces predictive uncertainty by combining individual modeling algorithms to find

a central trend amongst them, rather than individual predictions that can vary among SDMs (Marmion et al. 2009; Barbet-Massin et al. 2012). Biomod2 includes ten modeling algorithms (Table 1; Thuiller 2014).

Biomod2 enables the creation of pseudo-absences (PAs) to produce binomial data when only true presences are provided, as in the case of Nile monitor data. A PA is generated by choosing a cell from the initial background (everything that isn't a "presence" value) to produce artificial absence data with a chosen strategy (Barbet- Massin et al. 2012; Thuiller et al. 2014). Either "true" absences or pseudo-absences are required by all of the SDMs used by Biommod2 to compare with presence data and differentiate environmental conditions that predict species ranges [MaxEnt is commonly referred to as a "presence-only model," but this is misleading since it still requires background data to run (Barbet-Massin et al. 2012)] (Phillips et al. 2009; Thuiller et al. 2014). All PAs were generated here by the 'random' algorithm strategy in Biomod2 (where all cells of initial background are candidates and chosen randomly) with three PA repetitions each time (Barbet-Massin et al. 2012). However, the number of PAs chosen affects the outcomes of alternative models in Biomod2; models should be evaluated in PA-based subsets that optimize the use of PAs and increase predictive accuracy (Barbet-Massin et al. 2012; Brown and Yoder 2015). Therefore, alternative modeling algorithms listed above were organized into three groups (A, B, and C; Table 2) based on PA selection abundance.

Table 1: 10 modeling algorithms used in Biomod2 for ensemble SDM.

Algorithm	Description
Generalized Linear Model (GLM)	Statistically relates together the systematic elements in a model with the random ones
Boosted Regression Tree (BRT)	Also known as General Boosted Model (GBM; Brown and Yoder 2015); improves the performance of a single model by fitting many models and combining them for prediction
Generalized Additive Model (GAM)	Uses nonparametric, data-defined smoothers to fit nonlinear functions
Classification Tree Analysis (CTA)	Classifies remotely sensed and ancillary data in support of land cover mapping and analysis
Artificial Neural Network (ANN)	Identifies complex non-linear relationships between input and output data sets
Surface Range Envelope (SRE)	Analysis of within which range of each variable the data is recorded and renders predictions

Algorithm	Description
Flexible Discriminant Analysis (FDA)	Uses adaptive, nonparametric regression models to allow nonlinear decision boundaries
Multiple Additive Regression Splines (MARS)	Provides an alternative regression-based technique for fitting nonlinear responses
Random Forest (RF)	Classifier consisting of a collection of tree-structured classifiers; each tree casts a unit vote for the most popular class
Maximum Entropy (MAXENT)	Estimates a probability distribution from incomplete information by finding the distribution of maximum entropy among all distributions satisfying specific constraints

Table 2: PA selection groups and associated modeling algorithms.

Group	Modeling Algorithm	Number of PAs
A	GAM, GLM, SRE, MaxEnt, ANN	1,000 with minimum of 10 runs
B	MARS, FDA	100 with minimum of 10 runs
C	CTA, BRT, RF	= presences with 10 runs (when <1,000 presences)

The result was three ensemble models (for groups A, B, and C) for each of the seven hypotheses, for a total of 21 ensemble models for current climate conditions that could be compared using TSS in a model-selection framework. This approach represents a technically important advance beyond prior SDMs that used a single modeling algorithm (e.g., MaxEnt) without comparison to organized alternatives and/or did not use TSS (Dowell et al. 2016).

The above procedure was repeated for future climate models but using only climate and elevation variable sets (future NPP data do not exist). Future (2070) climate data were based on the National Center for Atmospheric Research (NCAR) assumptions of greenhouse gas (GHG) emissions for Representative Concentration Pathways (RCPs). We compared two climate models to bracket potential future climate scenarios: the most optimistic model 2.6 assumes annual GHG emissions peak 2010-2020 and then decline substantially. In contrast, the most pessimistic model 8.5 assumes annual GHG emissions continue to rise throughout the 21st century (Hijmans et al. 2005). Current elevation data (SRTM; WorldClim) were used in future distribution models on the assumption that elevations would not change substantially by 2070. In summary, I modeled two possible future GHG projections for climate or climate + elevation models and each of the

three PA-based subsets (12 total). Combined with current climate models, 33 total ensemble models were computed.

All model comparisons were based on TSS score and its components, sensitivity and specificity. I ranked models simply, where a model was judged to be most predictive if it: had the highest TSS score; was most parsimonious (i.e., used the fewest explanatory variables); and produced the highest sensitivity and specificity values. If needed, sensitivity (true positives) was valued as more important than specificity (true negatives) because the goal was to predict where the Nile monitor may inhabit, rather than where it may not.

Results

Current Climate: Performance

Among models based on individual predictors, the Bioclim variable set produced greater TSS scores ($0.78 \leq TSS \leq 0.87$) than mean NPP ($0.46 \leq TSS \leq 0.53$) or elevation ($0.22 \leq TSS \leq 0.56$; Table 3). Therefore, climate alone was more important than vegetation or elevation when predicting potential Nile monitor distributions. However, including elevation or NPP improved climate-based models. The combination of Elevation+Bioclim produced TSS scores ($0.81 \leq TSS \leq 0.88$) that were slightly greater than the more complex Elevation+NPP+Bioclim ($0.80 \leq TSS \leq 0.88$) or NPP+Bioclim ($0.79 \leq TSS \leq 0.88$), and certainly more predictive than Elevation+NPP ($0.28 \leq TSS \leq 0.62$; Table 3). Bioclim was again important to every leading model, but Elevation and NPP in combination with Bioclim slightly improved TSS relative to Bioclim alone.

Table 3: TSS scores for current mean consensus models projected in Biomod2 for each PA Group (A, B, C). A includes GAM, GLM, SRE, MaxEnt, and ANN; B includes MARS and FDA; C includes CTA, BRT, and RF.

	TSS			Sensitivity			Specificity		
Hypothesis	A	B	C	A	B	C	A	B	C
Bioclim	0.78	0.87	0.86	0.95	0.96	0.90	0.83	0.91	0.97
Elevation	0.56	0.22	0.56	0.77	0.62	0.77	0.80	0.60	0.80
NPP	0.46	0.46	0.53	0.69	0.69	0.62	0.77	0.77	0.91
NPP+Bioclim	0.79	0.81	0.88	0.97	0.96	0.95	0.82	0.85	0.93
Elevation+NPP	0.28	0.31	0.62	0.59	0.59	0.98	0.69	0.71	0.65
Elevation+Bioclim	0.81	0.88	0.86	0.98	0.97	0.92	0.83	0.91	0.94
Elevation+NPP+Bioclim	0.80	0.85	0.88	0.97	0.92	0.92	0.83	0.93	0.95

The Elevation+Bioclim model had the highest TSS score in every PA Group (A, B, and C). Importantly, PA Group B (MARS and FDA) had the highest TSS score, as well as high sensitivity and specificity scores (0.88, 0.97, and 0.91 respectively). Similar high scores were found in PA Group C (CTA, GBM, and RF) for the NPP+Bioclim model (0.88, 0.95, and 0.93), and Group C for the Elevation+NPP+Bioclim model (0.88, 0.92, and 0.95), but the Group B Elevation+Bioclim model was more parsimonious and had greater sensitivity (Table 3). The high TSS scores indicate that the Elevation+Bioclim SDM for PA Group B was very predictive. High sensitivity and specificity scores for that model indicated that it was very likely to correctly identify species occurrence probabilities. I chose to rely on the Elevation+Bioclim SDM for PA Group B (MARS and FDA algorithms) to project potential global Nile monitor distribution.

Current Climate: Projections

Based on my conclusion, the potential Nile monitor range can be confidently projected if it is introduced and permitted to spread. In current climate conditions, suitable habitat for the Nile monitor exists on five continents: North America, South America, Africa, Asia and Indopacific, and Australia [Figure 1(a-f)]. It is worth remembering that Nile monitors (and other varanids) are not currently in the Americas, other than the established population in Florida or current pets in unknown but numerous locations.

In North America's current climate, the established population in Florida appears to be constrained to the subtropical portion of that peninsula, with limited potential to spread northward on the Florida peninsula [Figure 1(b)]. However, should the lizard be released and become established in the southwestern US (e.g., Phoenix, Tucson, El Paso) or coastal California, it could spread southward into large areas of Mexico, Central America, and South America. In that case, the Nile monitor is likely to inhabit much of tropical and subtropical Neotropics [Figure 1(b-c)]. In addition, if introduced the Nile monitor should be able to successfully inhabit the Caribbean islands and could spread into the Baja California peninsula from San Diego/Tijuana. Potential southern limits to the Nile monitor's range extend to southern Chile and Argentina [Figure 1(c)]; clearly the South American range could be extensive, comparable to its native African range.

Beyond the Americas, the Nile monitor could spread into the majority of Madagascar if released there [Figure 1(d)]. To the east of Africa, the Arabian Peninsula is climatically suitable, though mesic/riparian habitats often used by Nile monitors are sparse there.

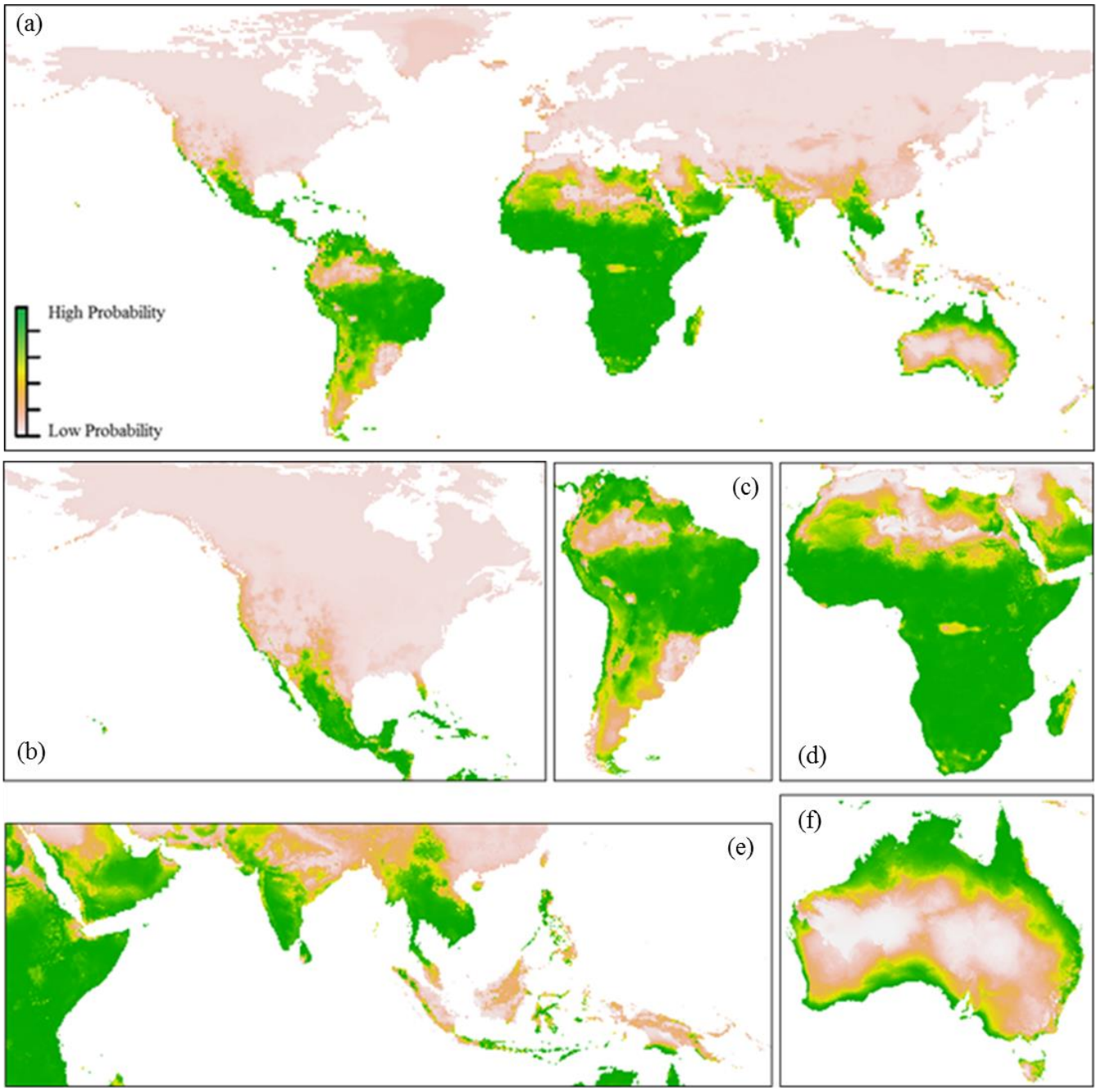

Figure 1(a-f): Mean current Elevation+Bioclim consensus model with PA Group B; (a)World, (b)North America, (c)South America, (d)Africa, (e)Asia, and (f)Australia

More likely are invasions in much of Southeast Asia, including southern and western India, Sri Lanka, the Indochina Peninsula, Northern Philippines, and parts of Indonesia [Figure 1(e)]. Interestingly, relatively high topographic relief in parts of the Malay Peninsula, Borneo, and New Guinea may exclude the Nile monitor, though it could inhabit southern lowlands on Borneo and various Indonesian islands. In Australia, the Nile monitor could inhabit much of the continent's coastal habitat, especially in northern tropical and subtropical regions [Figure 1(f)]. It is also likely to inhabit portions of northern Tasmania, but is not likely to succeed in New Zealand [Figure 1(a)].

Future Climate (2070): Performance

Both the optimistic future climate model (2.6 RCP) and the pessimistic future climate model (8.5 RCP) produced high TSS scores ($0.79 \leq TSS \leq 0.87$ and $0.78 \leq TSS \leq 0.88$, respectively; Table 4 and 5). Results of elevation alone were the same as in the current climate models because elevation did not change. The Elevation+Bioclim 2.6 RCP model produced TSS scores ($0.79 \leq TSS \leq 0.87$) that were very similar to Bioclim alone and to the 8.5 RCP model ($0.79 \leq TSS \leq 0.88$).

Table 4: TSS scores for future mean consensus models projected in Biomod2 with RCP 2.6 for each PA Group (A, B, C). A includes GAM, GLM, SRE, MaxEnt, and ANN; B includes MARS and FDA; C includes CTA, BRT, and RF.

	TSS			Sensitivity			Specificity		
Hypothesis	A	B	C	A	B	C	A	B	C
Bioclim 2.6	0.79	0.82	0.87	0.95	0.96	0.90	0.83	0.91	0.97
Elevation+Bioclim 2.6	0.79	0.87	0.87	0.97	0.97	0.94	0.82	0.90	0.93

Table 5: TSS scores for future mean consensus models projected in Biomod2 with RCP 8.5 for each PA Group (A, B, C). A includes GAM, GLM, SRE, MaxEnt, and ANN; B includes MARS and FDA; C includes CTA, BRT, and RF.

	TSS			Sensitivity			Specificity		
Hypothesis	A	B	C	A	B	C	A	B	C
Bioclim 8.5	0.78	0.87	0.88	0.98	0.98	0.90	0.80	0.90	0.97
Elevation+Bioclim 8.5	0.79	0.88	0.87	0.98	0.98	0.91	0.81	0.89	0.96

Similar to projections for current climate conditions, PA Group B was the most accurate model for future 2.6 RCP and 8.5 RCP projections. Scores for PA Group C differed only slightly, but Group B had higher sensitivity scores. Based on high TSS scores with sensitivity and specificity scores both >0.80, I considered future projections based on PA Group B (i.e. an ensemble model based on MARS and FDA algorithms) to confidently indicate the Nile monitor's future distribution. Elevation+Bioclim 8.5 RCP Group B was projected due to its high TSS scores, marked climatic difference from current conditions, and the fact that carbon emissions still have not reduced in 2016 according to the 2010-2020 goals of the 2.6 RCP model [Figure 2(a-f)].

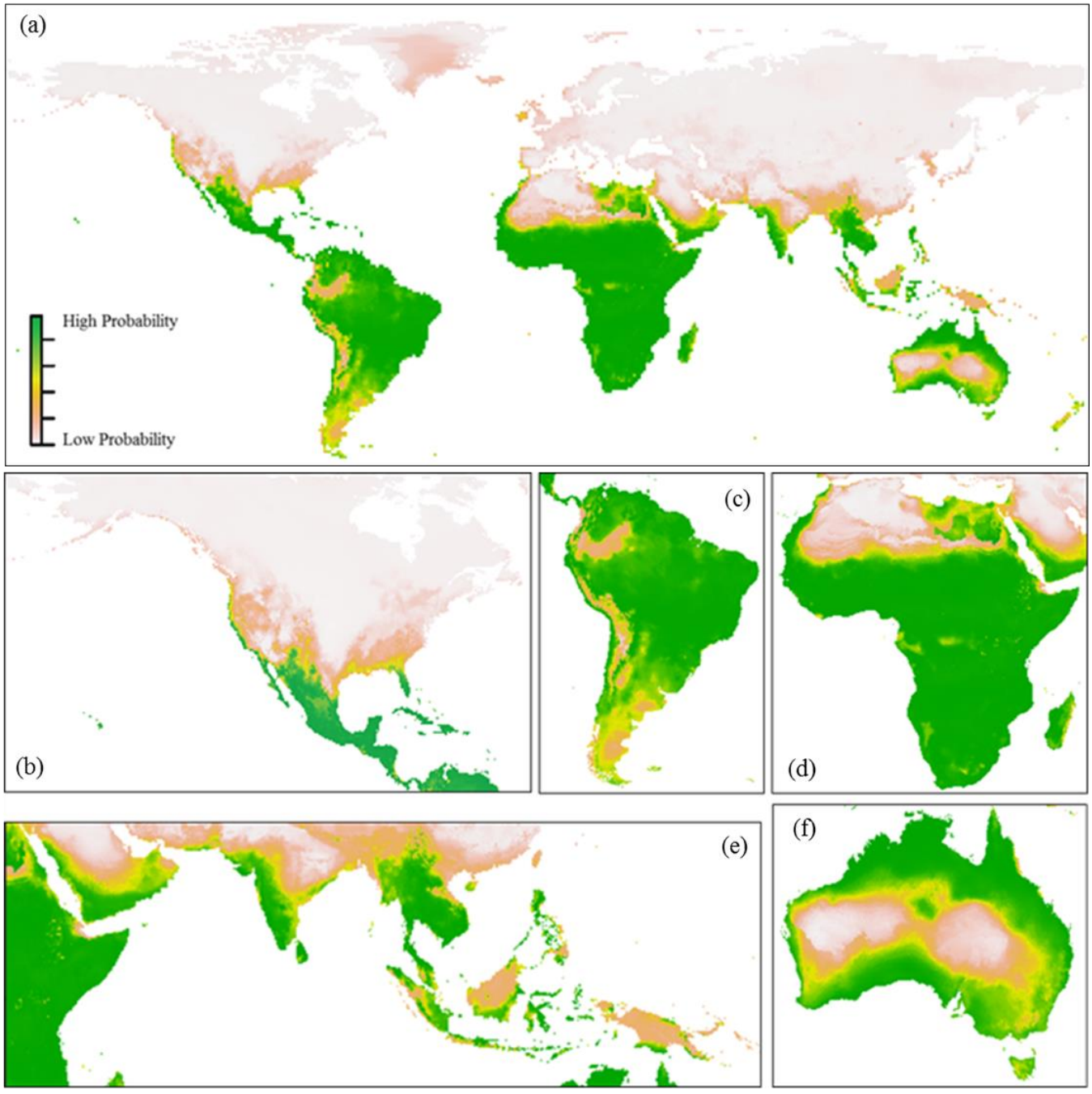

Figure 2(a-f): Mean 2070 Elevation+Bioclim consensus model with PA Group B; (a)World, (b)North America, (c)South America, (d)Africa, (e)Asia, and (f)Australia

Future Climate (2070): Projections

Potential Nile monitor range margins should shift substantially from current limits in multiple regions if GHG emissions increase according to "business-as-usual" projections [Figure 2(a-f)]. In North America, the Florida range extends northward to include the entire peninsula and parts of the Florida panhandle, as well as habitats along the Gulf coast [e.g., Houston; Figure 2(a-b)]. This greater range makes it more possible that Nile monitors could extend out of their current Florida range to enter Mexico and then extend to Central and South America. It is also more likely given future climate that the potential range on the West Coast of the US would extend northward to include coastal Oregon and southward to more fully connect into Mexico and beyond [Figure 2(b)]. Thus, if the Nile monitor establishes wild populations in coastal California and the business-as-usual climate scenario unfolds, Nile monitors could extend their range around the northern coast of the Gulf of California into Mexico, Central, and South America. More expeditious would be release and establishment in southwestern cities in Arizona and New Mexico [Figure 2(b)]. For South America, future climate projections indicate further spread into the Amazon rainforest and Uruguay but some retraction in the Andes Mountains [Figure 2(c)].

Elsewhere, the Nile monitor may contract its range in the Arabian Peninsula relative to projections based on current climate but extend further in Madagascar (if introduced there) to occupy all but its eastern coast [Figure 2(d)]. In Southeast Asia, the potential range is contracted in India, consolidated in the Indochina Peninsula, and increased in Indonesia to extend to the Malay Peninsula and Borneo [Figure 2(e)]. On the Australian continent, the Nile monitor could

occupy the entire coast and substantial areas inland, including much of tropical and subtropical Northern Territory and Queensland [Figure 2(f)]. It could also occupy most of Tasmania and shows increased (but still limited) success in New Zealand [Figure 2(a)].

Discussion

The carefully-selected and well-supported ensemble SDMs predict that, if introduced, the Nile monitor will invade many tropical, subtropical, and warm temperate regions, consistent with its wide African range. The potential range includes numerous biodiversity hotspots in Central and South America, the Caribbean, Madagascar, Southeast Asia, and southwest Australia (Myers et al. 2000). By 2070, the ensemble SDM predicts further spread, including expansion from its current North American range on the Florida peninsula to other Gulf states in the US and potentially then into Central and South America. Though not yet introduced in the southwestern US (e.g., California, Arizona), future climate conditions should enable Nile monitors to spread from there to Central and South America. Nile monitors that are released from captivity or escape are likely to impact many populations of multiple species that are naïve to this large, generalist predator. The invasive potential of the Nile monitor should be a concern to multiple regions worldwide. Policies and regulations to prevent that spread will be wiser than responses after Nile monitors have invaded.

Multiple alternative ensemble SDMs were generated and compared. This approach was consistent with the use of multiple working hypotheses and model selection, though I used TSS to select models rather than information theoretic criteria (Chamberlin 1890; Burnham and Anderson 2002**).** The use of TSS (and its components, specificity and sensitivity) is more robust

than ROC curve computations (Allouche et al. 2006; Lobo et al. 2008). Species distribution models have often been evaluated using a single set of predictors (e.g., Bioclim) and a single set of modeling algorithms (e.g., MaxEnt; Dowell et al. 2016). The Biomod2 package in R (Thuiller et al. 2014) advances SDM research by enabling evaluation of multiple predictors for ensembles of SDMs. In addition, we organized ensembles as subsets among the ten possible modeling algorithms, where subsets were based on pseudo-absence optima of models (Barbet-Massin et al. 2012). Analyses organized in three PA Groups was an important step, as Groups differed in TSS scores. Overall, Group C had the greatest TSS scores for four of the seven hypotheses, followed by Group B (two of the seven), then Group A (one of the seven) (Table 3). Based on results here, groups of SDMs based on PAs followed by TSS-based model selection should be preferable to an *a priori* choice of one Group or SDM. Overall, we considered this multiple ensemble and model selection approach to be valuable and a potential advancement in SDM research relative to single-model approaches.

The TSS, sensitivity, and specificity scores of the most parsimonious ensemble model exceeded those of most published SDMs. This ensemble SDM was based on the MARS and FDA models, used elevation and climate variables as predictors, and was computed with 100 PAs and at least ten runs. A more complex ensemble model that also included MODIS-based estimates of primary production had a slightly lower TSS; both parsimony and TSS scores supported the selection of the elevation + climate model (hereafter "best ensemble SDM").

The best ensemble SDM predicted a Nile monitor distribution that was consistent with my *a priori* understanding of its native range and habitat preferences (de Buffrenil and

Francillon-Viellot 2001; Bayless 2002; Berny et al. 2006; Ciliberti et al. 2011) and was both highly specific and sensitive (i.e., had high proportions of true presences and absences, respectively). The Nile monitor range projected by that best ensemble SDM is roughly consistent with the latitudinal extent of its African native range. The predicted range includes many regions inhabited by potential prey species that are evolutionarily naïve to any of the 53 *Varanus* species; introduction and establishment of Nile monitors in those regions would add an entirely new predator to those ecosystems. Because potential Nile monitor range is so inclusive, many biodiverse regions are potentially vulnerable to its invasion.

The best SDM overlaps substantially with numerous biodiversity hotspots (Myers et al. 2000), indicating that many endemic species may be vulnerable to Nile monitor predation if it is introduced to those regions. Moreover, this generalist predator is long-lived and opportunistic in its habitat and prey choices; Nile monitors should have general effects relative to more stenotypic predators (Luiselli 1999; Faust 2001; Bennett 2002; Enge et al. 2004; Campbell 2005). This potential for broad and strong impacts should be of great concern, worthy of far greater attention than has been afforded to Nile monitors among the many invasive species.

Africa, Asia, Southeast Asia, and Australia already have indigenous species of monitors (Pianka et al. 2004), and native species may be expected to have evolved with those predators. However, potential prey species and even native varanids may not be immune to the negative effects of a new congener. Varanids are diverse, comprised of different body sizes, habitats, and diets that fill different niches (Pianka et al. 2004). If introduced, the Nile monitor may prey on and/or compete with native monitors, or bring a slightly different niche space to a region

inhabited by other varanids. In that case, Nile monitors that are introduced and establish where congeners are native may also impact fauna, though probably less so than where native congeners do not exist.

Future climatic conditions should expand the potential invasive range of the Nile monitor. By 2070, the currently established population in South Florida may expand to include much of the Florida peninsula and extend westward into other states. This predominantly coastal range expansion may increase chances of expansion through Texas into Mexico. If Nile monitors can pass through that narrow and patchy geographic arc to reach Mexico, then they should be able to establish a large population throughout much of tropical and subtropical Central and South America.

An alternative scenario, and potentially more threatening scenario, depends on release or escape from captivity in coastal California or the southwestern US states. Given that introduction, monitors are very likely to spread unimpeded into Mexico, then much of the rest of Central and South America. Thus, two possibilities (one from current Florida populations, another from potential released/escaped animals in the southwestern US) could initiate wide invasion of the Neotropics, and that invasion is more likely with climate change. Invasions of other regions may be less widespread and require multiple introductions because suitable habitats are more geographically fragmented (e.g., Indonesian islands, Indian subcontinent, Indochina peninsula). In addition, many of these other regions are already inhabited by Nile monitor congeners (e.g., *V. salvator*); native, endemic species there may be less naïve to monitor predatory effects.

Nile monitors (and congeners) are readily available as pets via direct and online sales, including multiple vendors located in the US regions discussed above. Nile monitors were apparently introduced to Florida ~1990; legal restrictions on sales and ownership began ~20 years late, in 2010 (Enge et al. 2004; Campbell 2005; Engemen et al. 2011). In the intervening two decades, Nile monitors established substantial populations in multiple locations. If legal restrictions are to prevent the spread of this large, generalist predator and consequent impacts in biodiverse regions, those restrictions must be pre-emptive rather than post-hoc. I recommend that the countries and states that include high-probability regions depicted in Figure 1(a-f) and 2(a-f) where Nile monitors are not native should ban the import, sales, and ownership of Nile monitors (and potentially other *Varanus* species) *before* they are introduced. In parallel, exotic pet amnesty programs to voluntarily relinquish captive exotic species are increasingly successful. Such a program in Florida has yielded 2,530 exotic pets surrendered in ten years; some of those animals may have been released otherwise (FFWCC 2015). Similar programs should be well-supported to prevent release of Nile monitors (and potentially other *Varanus* species).

Without greater and more consistent trade restrictions, Nile monitors are likely to establish, spread, and inhabit extensive, vulnerable regions of the world. The well-supported projections described here are only prevented now by voluntary actions of thousands of monitor owners, many of whom fully understand the predatory capabilities of their pets. However, the vast numbers of Nile monitors in the pet trade mean that chance events (e.g., escapes) and intentional releases (e.g., of large, aggressive adults) are possible. As observed in Florida, Nile monitors can soon establish large populations once they are introduced to the wild (Enge et al.

2004; Campbell 2005; Engemen et al. 2011). The added effects of a 2m, 7kg, semi-arboreal, semi-aquatic, generalist carnivore into tropical and subtropical ecosystems of the world should be sufficient to warrant strong trade restrictions, daunting penalties for release, and enhanced exotic pet amnesty programs.

CHAPTER THREE: NILE MONITOR FOOD WEB EFFECTS

Background

It is impossible to fully understand the role of any organism in its ecosystem until its interactions with surrounding biota are examined. This is a fundamental goal of analyzing food webs as complex ecological networks; to learn to predict the impacts a particular species may have on the ecosystem and potentially mitigate negative effects. For example, understanding impacts of an introduced species could substantially alter conservation efforts to protect against this prominent, environmental perturbation (Ings et al. 2009). Food web analyses can reveal elements of biodiversity, species interactions, and ecosystem structure (Dunne et al. 2002a), and may be useful to quantify the potential effects of such a threat. The Nile monitor (*Varanus niloticus;* Linnaeus, 1766) is an example of a current threat that requires more understanding in these areas, and therefore a thorough analysis of its potential food web effects as an exotic predator.

The Nile monitor is a generalist, semi-aquatic predator native to Sub-Saharan Africa that has been introduced to the U.S. (established in southern Florida) as a result of the pet trade industry. Its impressive size (2.4m), body mass (≤7.3kg), and substantial population densities (40-60/km^2) compound the threat of the Nile monitor's eclectic diet where it is known to prey upon many vertebrate and invertebrate species (both in its native and introduced ranges) (Edroma and Ssali 1983; Losos and Greene 1988; Luiselli 1999; Faust 2001; Bayless 2002; Bennett 2002; de Buffrenil and Hemery 2002; Enge et al. 2004; Campbell 2005; Engemen et al.

2011). Furthermore, concern for the exotic species is augmented in light of new research predicting the potential extent of the monitor across the globe if released (Chapter 2).

An ensemble species distribution model (SDM) for current climatic conditions shows that the Nile monitor has the potential to spread (if introduced) to many tropical, subtropical, and warm temperate regions across five major continents: North America, South America, Africa, Asia, and Australia (including numerous biodiversity hotspots in Central and South America, the Caribbean, Madagascar, Southeast Asia, and southwest Australia) [Figure 1(a-f); Myers et al. 2000]. An ensemble SDM for the year 2070 predicts further potential spread (if introduced) plus expansions in Madagascar and New Zealand [Figure 2(a-f)]. With the Nile monitor's popularity in the global pet trade—a Google search (10 July 2016) for the phrase "Nile monitor for sale" and restricted to the past year obtained 20 distinct websites and ~1,450 unrestricted web hits—the possibility of the monitor being released in any of these predicted regions does not require much stretch of the imagination.

While there is now a greater understanding of the potential spread of this introduced predator, little is known about the Nile monitor's potential ecological impacts in these regions if the monitor were to be established. Knowledge of the Nile monitor's effects on native fauna is crucial as it would provide much-needed insight into the predator's capabilities as an introduced species, and help to justify and inform warnings and mitigation work in regions at risk (Sakai et al. 2001). Therefore, the purpose of this work was to determine the potential ecological effects of the Nile monitor in introduced regions based on diet data and ecological network analyses of food webs.

Food web data from the monitor's predicted regions of dispersal [Figure 1(a-f) and 2(a-f)] were selected and analyzed before and after Nile monitor addition with advanced ecological network software, producing nine metrics from the binary, predator-prey matrices. Changes in these food web metrics were used to quantify ecological impacts of the exotic predator on native food web structures at global and regional spatial scales.

I anticipated some food web metrics to be more affected and meaningful than others. Species richness would trivially increase by one with addition of the Nile monitor to the food webs (extinctions were not predicted without more specific information per food web). Accordingly, I expected the number of taxa in basal, intermediate, and top levels would change only slightly. Knowing that Nile monitors are generalist predators, I expected that the number of trophic links, and thus connectance and link density would increase most, and indicate the breadth of potential Nile monitor food web effects (Dunne et al. 2002a). From a biogeographical perspective, I expected that the Nile monitor would have larger effects on regions where *Varanus* species are not native (North America, South America, and New Zealand). Finally, I note that food web analyses cannot indicate potential demographic effects (e.g., on threatened species); those effects must be evaluated by more specific approaches than possible for this global analysis.

Methods

Published food web data were collected from the GlobalWeb database (Thompson et al. 2012), which includes 358 food web matrices. Other databases and literature were explored (e.g. EcoWeb; Cohen 2012), but represented redundant data. Eighty-five food webs,

representing >900 different species, were selected because they were located within the projected global range [Figure 2(a-f); mean 2070 Elevation+Bioclim consensus model with PA Group B] and in habitats known to be preferred by Nile monitors (Appendix B). It is important to note that no food webs already included *Varanus* species; thus native/non-native regional comparisons were not due to the "equalization" of food web membership. All of the species listed were determined to either have a high or low probability of being consumed by the Nile monitor, based on literature reviews (Losos and Greene 1988; Luiselli et al. 1999; Bennett 2002; Campbell 2005) and comparisons to data on >300 Nile monitor stomach contents from the introduced Florida population (Campbell, unpublished data), based on body size, habits (e.g., ground-dwelling vs. arboreal), and taxonomy.

Each symmetrical, binary (0 or 1 values) food web matrix was quantified by the 'foodweb' package in R (Perdomo 2014) before and after Nile monitor invasion as a top predator in each matrix. Thus analyses were based on species *addition* to the network rather than species loss (as is more common in food web analyses). No species were assumed to be driven to extinction by introduction of the Nile monitor (Strong and Leroux 2014). For matrices representing food webs invaded by Nile monitors, low-probability prey taxa for Nile monitors were assigned "0" in the Nile monitor column, whereas high-probability prey taxa were assigned "1."

Each food web (pre- and post-invasion by Nile monitors) was evaluated using nine metrics, and differences between pre- and post-invasion were calculated (Table 6; Hildrew et al. 2007; Thompson et al. 2012; Perdomo 2014).

Table 6: Food web metrics used to analyze changes in network structure with Nile monitor introduction.

Metric	Description
Species Richness (S)	Number of "trophic species," where a trophic species may be more inclusive than taxonomic species (e.g., "beetles" = one trophic species)
Number of Trophic Links (L)	Directed feeding links between taxa
Connectance ($C= L/S^2$)	Proportion of potential links that actually occur; a standard measure of web complexity (typically 0.05-0.30)
Link Density (L/S)	Mean number of links per taxon
Fraction of Basal Taxa (b)	Number of taxa which do not consume other taxa
Fraction of Intermediate Taxa (i)	Number of taxa which both consume and are consumed by other taxa
Fraction of Top Taxa (t)	Number of taxa not consumed by others
Trophic Levels	Position occupied in a food chain
Prey:Predator Ratio (b+i)/(t+i)	Measure of food web shape (high values indicate more triangular food webs, indicating greater complexity, connections, and stability, whereas lower values indicate food webs

Metric	Description
	that are more square and indicate potential trophic cascades with more biomass as top predators)

Connectance and link density metrics are commonly reported when studying changes in food network structure, based on the premise that heavily linked species strongly affect food webs and their robustness to species loss (Dunne et al. 2002a; Strong and Leroux 2014). However, the importance of different food web metrics has been actively debated (Martinez 1992; Dunne et al. 2002b; Thompson et al. 2012). For example, the addition of a top predator to a stream food web resulted in noticeably increased connectance even though the invader had little impact on prey abundance (for which the opposite would be assumed; Woodward and Hildrew 2001). Therefore, changes in all nine metrics above were used to understand potential changes to food webs with the addition of the Nile monitor. Metrics were reported as mean values among analyzed food webs with $\pm$ 95% confidence intervals; significant change to food webs was inferred if one confidence interval did not include its opposite mean. Percent change between mean values was also calculated.

Results

Of the 85 food webs, 15 were in North America (United States and Central America), 8 in South America, 11 in Africa, 4 in Asia (Southeast Asia), 17 in Australia, and 30 in New Zealand. Food webs were unevenly distributed among terrestrial (5/85; e.g. forest, sand beach) and aquatic (80/85; e.g. estuary, marsh, swamp, lake, pond, stream, reservoir, river, wetland) food webs, reflecting a bias in the literature that could not be circumvented. Despite this bias, about 66% of the potential prey items listed in the 85 food webs were classified as having a high probability of being consumed by the Nile monitor, consistent with its general diet.

Most food web metrics (species richness, trophic links, connectance, link density, fraction of intermediate taxa, and trophic positions) increased with the addition of Nile monitors, whereas three decreased (fractions of basal taxa, top taxa, and prey:predator ratio; Table 7).

Table 7: Food webs before and after Nile monitor addition (N=85 binary, predator-prey matrices from the global projected future Nile monitor range). Mean values are reported with 95% confidence intervals along with % mean change. Metrics are listed in Table 6.

	Range		Mean		
Metric	Before	After	Before	After	% Mean Change
S	7-117	8-118	47(±6.1)	48(±6.1)	2.1
L	10-966	14-988	164(±40)	179(±40)	9.2
C	0.02-0.31	0.02-0.27	0.08(±0.01)	0.09(±0.01)	13
L/S	1-9	1.3-9.1	2.9(±0.34)	3.2(±0.34)	10
b	0.08-0.93	0-0.9	0.34(±0.05)	0.33(±0.05)	-2.9
i	0.24-0.88	0.25-1	0.63(±0.03)	0.66(±0.03)	4.8*
t	0.01-0.52	0-0.22	**0.08(±0.02)**	**0.05(±0.01)**	**-38**
Levels	2-9	1-9	4.7(±0.36)	5.5(±0.34)	17
(b+i)/(t+i)	0.79-13.5	0.88-9.7	1.9(±0.42)	1.8(±0.33)	-5.3

** Represents 79 food webs; 6 had initial values = 0, which made % change calculation moot.*

As expected, species richness increased due to Nile monitor addition (2.1%; Table 7). More importantly, the number of trophic links (9.2%), connectance (13%), and link density

(10%) all increased substantially, though not significantly given the range of food webs analyzed (Table 7). The fraction of intermediate species increased (4.8%) and the number of trophic positions generally increased by ~1 (17%), consistent with Nile monitors often comprising a new top predator in modeled food webs.

In terms of decreased metrics, the fraction of basal species decreased (-2.9%), the fraction of top species decreased significantly (-38%), and the prey:predator ratio decreased (-5.3%) (Table 7). In summary, the Nile monitor had a high probability of consuming the original top species in the food web, forcing them to become new intermediate species by definition while the Nile monitor became a new top predator in the web. This effectively decreased the fraction of top taxa while increasing the fraction of intermediate taxa (Table 7). Since each trophic layer relies on those species in the one below it for energy, an increase in intermediate species results in an increased reliance on the basal taxa, therefore reducing the fraction of basal taxa available in the web (Table 7).

Biogeographic Food Web Patterns

Food webs were compared among different regions for potential patterns in Nile monitor effects (Table 8). Food web data were not evenly distributed across the six reported regions, which may interfere with inference.

Table 8: Food webs before and after Nile monitor addition represented by region (N=85 binary, predator-prey matrices from the global projected future Nile monitor range). Mean values are reported with 95% confidence intervals along with % mean change. Metrics are listed in Table 6.

	S	L	C	L/S	b	i	t	Levels	(b+i)/(t+i)
NORTH AMERICA									
Before	21(±6.4)	57(±35)	0.12(±0.03)	2.2(±0.61)	0.18(±0.05)	0.70(±0.05)	0.12(±0.03)	5.5(±0.85)	1.1(±0.09)
After	22(±6.4)	70(±39)	0.14(±0.03)	2.6(±0.61)	0.17(±0.04)	0.74(±0.04)	0.10(±0.03)	6.1(±0.74)	1.1(±0.09)
% Change	4.8	23	17	19	-5.6	5.7	-17	11	0
SOUTH AMERICA									
Before	35(±6.9)	163(±54)	0.14(±0.03)	4.5(±1.1)	0.14(±0.05)	0.79(±0.07)	0.07(±0.03)	7.1(±1.3)	1.1(±0.05)
After	36(±6.9)	188(±59)	0.15(±0.03)	5.0(±1.2)	0.13(±0.05)	0.81(±0.05)	0.06(±0.02)	7.6(±1.1)	1.1(±0.07)
% Change	2.9	15	7.1	11	-7.1	2.5	-14	7.0	0
AFRICA									
Before	23(±5.3)	44(±14)	0.10(±0.02)	**1.9(±0.32)**	0.16(±0.03)	0.75(±0.04)	0.09(±0.04)	**5.0(±0.46)**	1.1(±0.08)

	S	L	C	L/S	b	i	t	Levels	(b+i)/(t+i)
After	24(±5.3)	57(±18)	0.11(±0.02)	**2.3(±0.35)**	0.15(±0.03)	0.79(±0.04)	0.06(±0.02)	**5.8(±0.44)**	1.1(±0.04)
% Change	4.4	30	10	**21**	-6.3	5.3	-33	**16**	0
ASIA									
Before	42(±50)	107(±134)	0.14(±0.11)	2.5(±0.75)	0.22(±0.06)	0.68(±0.10)	0.09(±0.06)	6.0(±1.4)	1.2(±0.07)
After	43(±50)	125(±146)	0.15(±0.11)	2.9(±0.59)	0.14(±0.09)	0.79(±0.17)	0.07(±0.09)	5.3(±3.2)	1.1(±0.10)
% Change	2.4	17	7.1	16	-36	16	-22	-12	-8.3
AUSTRALIA									
Before	39(±7.2)	85(±24)	0.06(±0.01)	2.1(±0.31)	0.45(±0.14)	**0.65(±0.04)**	**0.13(±0.05)**	**2.9(±0.37)**	3.4(±1.9)
After	40(±7.2)	100(±27)	0.07(±0.01)	2.4(±0.31)	0.44(±0.14)	**0.72(±0.04)**	**0.03(±0.01)**	**3.8(±0.36)**	3.1(±1.4)
% Change	2.6	18	17	14	-2.2	**11**	**-77**	**31**	-8.8

	S	L	C	L/S	b	i	t	Levels	(b+i)/(t+i)
NEW ZEALAND									
Before	76(±6.5)	314(±83)	0.05(±0.00)	3.7(±0.66)	0.49(±0.03)	0.49(±0.03)	0.02(±0.01)	**4.5(±0.40)**	2.0(±0.17)
After	77(±6.5)	329(±84)	0.05(±0.00)	3.9(±0.65)	0.48(±0.03)	0.50(±0.03)	0.01(±0.00)	**5.4(±0.35)**	2.0(±0.16)
% Change	1.3	4.8	0	5.4	-2.0	2.0	-50	**20**	0

Overall, biogeographic regions were consistent with increases in species richness, trophic links, connectance, link density, fraction of intermediate taxa, and trophic levels (with minor exceptions—0% change in connectance for New Zealand and a 12% decrease in trophic levels for Asia; Table 8). Consistent decreases were also found in the fraction of basal taxa, top taxa, and prey:predator ratio (with minor exceptions—0% change in prey:predator ratio for North and South America, Africa, and New Zealand; Table 8). Furthermore, several regions exhibited significant changes due to Nile monitor addition: link density (21% increase in Africa), number of trophic levels (16% increase in Africa, 31% in Australia, and 20% in New Zealand), fraction of intermediate taxa (11% increase in Australia), and fraction of top taxa (77% decrease in Australia) (Table 8; in bold).

Overall, regional results (Table 8) are consistent with global results (Table 7), with increased interactions from the generalist predator (increased trophic links, connectance, and link density). In general, results indicate that the Nile monitor will displace top predators and make them become intermediate predators.

Among regions, North America exhibited the highest percent of change in species richness (4.8%), trophic links (23%), connectance (17%), and link density (19%) due to Nile monitor addition (aside from Africa where they are natively found; Table 8). Though not significant, these results reflect an overall stronger effect on the North American terrestrial and aquatic food webs compared to other nonnative regions. Conversely, New Zealand generally had the lowest percent of change in species richness (1.3%), trophic links (4.8%), connectance (0%), link density (5.4%), fraction of basal species (-2%), and fraction of intermediate taxa (2%), with

only a significant change in increase for fraction of trophic levels (20%; Table 8). South America fell within the middle in terms of metrics changes, with no significant changes throughout (Table 8).

Discussion

Multiple regions across the globe are suitable habitats for the Nile monitor because they are generally similar to its native range in Africa [Figure 1(a-f) and 2(a-f)]. With sustained popularity in the exotic pet trade industry worldwide, Nile monitors remain likely to be released and potentially affect native fauna in those regions. The threat of this potential spread is not confined to already-regulated pets based on past trade (Dowell et al. 2016), but includes potential future legal and illegal trade as well. This potential spread implies a risk for native animals that face a novel, generalist predator that may have little competition. Africa, Asia, Southeast Asia, and Australia already have indigenous *Varanus* species, but native species in those regions are not necessarily immune to the potential effects of the Nile monitor, given the genus' diversity in anatomy and niche utilization (Pianka et al. 2004).

The fact that the Nile monitor is a generalist predator is a cause for concern because of the breadth of potential interactions/trophic links and potential impact on resident community structure (Dunne et al. 2002a; Russo et al. 2014). The global increases in food web trophic links (9.2%), link density (10%), and connectance (13%) due to Nile monitors are consistent with a generalist species and a cause for concern that network stability will decrease in "at risk" regions (Dunne et al. 2002a).

To make matters worse, the Nile monitor is likely to assume the position of "top predator" (ignoring humans) in many published food webs, as was analyzed here. Little is known about what preys on the Nile monitor, so further analyses are needed when more information becomes available in the future. This top position in the food network is especially threatening, since the trophic position occupied by a nonnative species is the main factor contributing to its impacts on food web structure (Strong and Leroux 2014). While certain metrics are relied on more heavily to reveal impacts occurring on food network structure (e.g. connectance, commonly interpreted as increased web robustness/complexity; Dunne et al. 2002a), it is still just as important to remember the quality of the species being introduced, including the trophic position that it assumes. Metric results are meaningless without context in the species' biology.

Overall, my results show a general trend of increased species richness, trophic links, connectance, link density, fraction of intermediate taxa, and trophic levels, leading to increased interactions by Nile monitors with many species. Decreases were found in the fraction of basal taxa, prey:predator ratio, and a significant decrease in top taxa (-38%; Table 7). Strong and Leroux (2014) found similar results in their terrestrial mammal food web study of nonnative mammal addition. With sequential addition of nonnative species, their number of links, connectance, link density, and fraction of intermediate species steadily increased, whereas their prey:predator ratio, fraction of basal taxa, and fraction of top taxa steadily decreased; the same pattern shown in my results (Strong and Leroux 2014).

On a regional level across the globe (North America, South America, Africa, Asia, and Australia), food web analyses revealed similar metric results among continents (and New

Zealand). General increases occurred for species richness, trophic links, connectance, link density, trophic positions (except in Asia), and fraction of intermediate taxa. Decreases in the fraction of basal taxa, top taxa, and prey:predator ratio also occurred. Once again, increases in trophic links, link density, and connectance across all of these "at risk" regions reveal high interconnectivity amongst the Nile monitor and native species in these regions, consistent with its known role as a generalist predator.

While food web metrics in all six regions changed, North America revealed the most changes in food web metrics within the nonnative regions overall after Nile monitor addition (though they were not significant); this suggests that the increases in species richness, trophic links, connectance, and link density are warnings of a highly effectual predator (Table 8). New Zealand resulted in the lowest percent of changes in the food web metrics (Table 8), likely due to the fact that all of the food web data for New Zealand were aquatic (streams) and not representative of the full breadth of the semi-aquatic predator's diet. South America showed medial change in metrics across the board; less than North America but still offering a higher effect than New Zealand. These results indicate that the Nile monitor may not have strong effects as would be assumed for fauna that have not evolved with *Varanus* species. However, results here should be considered tentative until additional food webs become available for South America (and all of the regions for that matter), to help reduce the high amounts of variation present within the available food web dataset. Also, one must remember that food web effects differ greatly from potential effects on particular species of concern (e.g., kiwis in New Zealand). Overall, my original expectation to see larger effects (greatest changes in food web metrics) on

regions where the species is not natively found (North America, South America, and New Zealand) was only supported for North America. Again, bias in the quality/type of food webs used (unequal ratio of terrestrial:aquatic) is a likely contributing factor to such differences across the regions, but this study could only be done with the published food webs made available through the databases. Future works may include less bias among habitats and continents after more food webs become available in these regions.

Nevertheless, the abundant changes in food web metrics in North America are still important to consider. In the United States alone, there are 707 listed (endangered, threatened, emergency listing, similarity of appearance endangered and threatened) animal species (USFWS 2016). In Florida (the state where the Nile monitor already has an established breeding population), there are 64 listed animal species (USFWS 2016). With so many listed species, the results of this regional food web study should raise an alarm for the conservation of vulnerable species. Food web results here were based on the Nile monitor as a generalist predator and thus are consistent with its high propensity to prey on many animal species. I recommend that all regions including high-probability areas of spread [Figure 1(a-f) and 2(a-f)] should actively ban import, sales, and ownership of the Nile monitors *before* they are introduced. Given its established population in Florida and potential range and food web effects, North America (primarily the United States and Central America) warrants special attention.

Minimizing the presence of Nile monitors in the global pet trade is an important step that needs to become a reality in the near future if there is to be any hope of mitigating against this generalist predator's effects (especially for listed species and those in biodiversity hotspots;

Myers et al. 2000; USFWS 2016). However, there is more that can be done at a *local* level to aid in these efforts as well. Irresponsible pet ownership is a major ailment that affects many introduced species populations each year across the globe. The logical/effective solution to this obstacle is to make sure such potentially harmful species are in the hands of experienced and responsible pet owners *only*. Exotic pet amnesty programs can be important for this purpose, allowing for inexperienced pet owners to voluntarily relinquish their exotic species to someone who can properly prevent the potential spread of the species into the wild. Florida, for example, has yielded >2,530 exotic pets over the past ten years, and should serve as a positive example to other regions and promote similar programs (FFWCC 2015).

The Nile monitor has already made its way from Africa to North America due to the exotic pet trade industry. With the expediency of transport and booming economy that are evident in 2016, there is currently little standing in the way of delivering the Nile monitor to any region of the globe; this is where the dangers of potential release, spread, and ecological effects of this generalist carnivore can be realized on such a large scale. There are now well-supported studies indicating the potential spread of the Nile monitor (with high probabilities) across the globe [Table 3, 4, and 5; Figure 1(a-f) and 2(a-f)] and evidence showing altered food web structure in those same areas if the predator were to be released (Table 7 and 8). These results answer two pressing questions about the introduced species: 1) where can the Nile monitor go? and 2) what can it do if it gets there? Now, the only question that remains is this: when will we finally realize and enforce the need for stricter import, export, and ownership laws in regards to

the exotic pet trade industry? This is a question that needs to be answered sooner rather than later, or the Nile monitor may very well be coming to a town near you.

CHAPTER 4: CONCLUSIONS

This thesis has made the following contributions to the field of ecology:

- advanced ensemble SDM practices by evaluating alternative SDMs alone and in combination, to more closely represent strong inference and model selection (Chamberlin 1890; Platt 1964; Burnham and Anderson 2002);
- produced the first world-wide projection maps (current and future) for the Nile monitor [Figure 1(a-f) and 2(a-f)] with high accuracy (Table 3, 4, and 5);
- conducted the first world-wide food web analysis to predict the ecological impacts of potential Nile monitor spread (Table 7 and 8);
- advanced food web analysis by focusing on species *addition* rather than removal from secondary extinction (Strong and Leroux 2014) and compared the resulting metrics with ±95% confidence intervals;
- stressed the importance of both local and global solutions for Nile monitor mitigation (or exotic species in general) such as supporting pet amnesty programs, experienced exotic pet ownership, and enforcing stricter regulations on the pet trade industry.

This paper did not explicitly set out to answer the classic question of the Nile monitor's classification as an "invasive species;" to do so would require that it already invade and exert ecological and economic effects. Instead, this thesis was meant to provide insight on the monitor's *potential* effects should it sustain its popularity in the pet trade (with the seemingly lax monitoring that accompanies the industry). If current practices continue, this work shows that the Nile monitor is likely to spread (global ensemble SDMs) and have ecological effects (changes in

food web structure) that match the definition of an invasive species, though it has yet to become established in the regions at risk aside from Florida (Sakai et al. 2001; Enge et al. 2004; Campbell 2005; Doody et al. 2009; Hardin 2007; Engemen et al. 2011). I believe that the Nile monitor does not belong outside the realms of its native (and extensive) range in Africa, and that national and international efforts should prevent that from happening.

Ultimately, it is my hope that my thesis will advance the understanding of introduced species' effects by promoting a more thorough technique to produce and analyze ensemble SDMs as well as encourage the holistic analysis of food web metrics (rather than only focusing on one or two). With the well-supported results of my current and future (2070) ensemble SDMs (Table 3, 4, and 5) and extensive food web analyses (Table 7 and 8) for the Nile monitor, there is ample evidence to demand closer monitoring and stricter policies regarding the monitor (*Varanus* species) trade industry. While large-scale policies undoubtedly take time to go into effect (if at all), there are still more options that can be supported at a local level to aid in the mitigation efforts of introduced species, such as the exotic pet amnesty program [a successful endeavor as evidenced by the Florida Fish and Wildlife Conservation Commission (2015)] and increases in responsible/more experienced exotic pet ownership gained through increased awareness.

The Nile monitor is a 2m, 7kg, semi-arboreal, semi-aquatic, generalist carnivore with the potential to be introduced into tropical and subtropical ecosystems of the world and interact with many species found in those native food webs. We need to do all that we can to prevent this

potential from becoming a reality, and the above description of the Nile monitor warrants immediate action to accomplish this goal.

APPENDIX A: GEO-REFERENCED NILE MONITOR LOCATIONS

Appendix A: 507 Unique, geo-referenced Nile monitor point locations documented in primary literature (de Buffrenil and Francillon-Viellot 2001; Bayless 2002; Berny et al. 2006; Ciliberti et al. 2011).

Latitude	Longitude
-17.436944	14.721111
-17.3660286	14.7645042
-17.3660286	14.7645042
-17.270929	14.71554
-17.033333	14.616667
-16.9270066	14.3385236
-16.9	14.766667
-16.8119382	14.9526715
-16.7087216	13.4070057
-16.695	13.184722
-16.6525	13.3913889
-16.5319444	12.6008333
-16.4818167	16.0326307
-16.2345633	12.8050911
-16.194292	15.873363
-16.0757749	14.1652083
-15.833333	11.283333
-15.683333	16.466667
-15.6177942	11.8816553
-15.5870081	11.8620441
-15.577094	13.438927
-15.55	14.116667
-15.5034785	16.5105628
-15.5034785	16.5105628
-15.4800382	11.5770712
-15.35799	14.176162
-15.2769034	12.8629191
-15.180413	11.803749
-15.119167	15.395278
-14.6587821	17.8664964
-13.665759	9.5600812
-13.2731283	8.4464697
-13.234444	8.484444
-13.22106	13.13907
-12.8486076	15.5121868
-12.3839	8.160027
-12.38333	12.51667
-12.3549785	12.8481657
-12.324937	12.384069
-12.233333	9.666667
-12.183333	12.55
-12.0918248	8.0386295
-11.967619	7.6538679
-11.8749152	12.8252941
-11.718056	7.350556
-11.616667	12.616667
-11.5731242	9.7619129
-11.4452717	14.4367876
-11.3533333	6.7233333
-11.333333	7.95
-10.8479688	7.9877141
-10.801389	6.313333
-10.7617521	6.2794565

Appendix A.

-10.7274007	6.4217344
-10.5296115	6.5525815
-9.7232673	8.1911184
-9.4728244	7.0024321
-8.981389	7.2375
-8.884141	14.463091
-8.4666667	7.4333333
-8.000504	12.6645871
-7.9143486	12.6632451
-7.637	7.454
-7.469444	14.473611
-5.976305	14.252429
-5.933333	6.133333
-5.75	6.983333
-5.666667	11.316667
-5.616667	9.416667
-5.2902242	6.829215
-5.018889	14.138889
-4.198611	14.495833
-4.133465	5.3408557
-4.033333	5.316667
-4.033333	5.316667
-3.0025615	16.7665887
-2.2771971	8.2360711
-2	9.5
-1.978864	9.4372793
-1.5208624	6.7470436
-0.4714694	10.9662089
-0.3442449	16.9562322
-0.2466709	5.5355933
-0.2185196	5.6235
-0.2	5.55
-0.1884286	5.6493797
-0.1729106	5.8511836
-0.0886948	5.9779631
-0.046345	7.830422
-0.0139908	6.1049957
0.0613889	5.9083333
0.1752525	10.6562119
0.1869644	7.1359001
0.291356	5.8656458
0.4101619	6.5701645
0.475556	10.355556
0.8675134	5.9402949
1.5	6.583333
1.6760691	12.2497072
1.7417143	6.2639324
2.104869	13.505513
2.433333	6.366667
2.5597215	12.399372
3.366667	6.45
3.3792057	6.5243793
3.4346913	6.4548115

Appendix A.

4.8261424	9.1192516
5.0546643	9.2928248
5.2037671	7.9931026
5.506625	8.219267
6.016667	9.083333
6.797592	8.6492838
7.4615627	9.0570696
7.483333	5.533333
8.325	4.95
8.333333	6.083333
8.516667	12
8.536111	7.730556
8.7481167	3.6198322
8.8362755	7.3508259
8.9	4.966667
9.1938889	3.9966667
9.3208412	4.8004575
9.324308	-1.657532
9.844167	10.315833
9.91	2.935
9.933333	9.933333
10.0166667	3.7
10.04	12.45
10.35	12.283333
10.4101587	3.0776334
10.6562606	-3.4426092
11.1617356	-2.8821033
11.866362	-4.7691623
11.883333	2.966667
11.8891721	-4.1428413
12.0318456	9.4535964
12.19	-5.56
12.2547919	-3.18427
12.3893488	-5.9871641
12.62078	13.3091
12.866667	0.566667
13.263843	2.6759012
13.3	8.9833
13.416501	-12.5905158
13.6479521	8.2595632
13.8666667	-17.3333333
13.914399	-5.2365685
14.1001326	13.330266
14.1001326	13.330266
14.318101	9.6624261
14.366667	4.433333
14.373372	-9.6031493
14.65	13.5
14.766667	-9.133333
15.0674317	-13.7351702
15.2136302	2.0462273
15.291944	-4.267778
15.313889	-4.331667

Appendix A.

15.316667	11.15
15.3885806	-4.4145016
15.87	4.94
16.1580937	-16.2802221
16.2522143	-14.1868497
16.3293197	-18.8555909
16.85	-6.283333
16.958792	10.4582889
17.1514061	-26.5090889
17.307631	7.169832
17.4558555	12.8306085
17.5	-9.066667
17.95	-25.466667
18.33564	0.041662
18.65427	-34.050383
18.655936	-33.8446999
18.6792115	-33.9767174
18.683501	-33.820537
18.7274748	-34.0189342
19.08527	5.726189
20.1569444	-31.8302778
20.216667	10.9
20.3333333	-28.6
20.3333333	-28.6
20.958309	-6.479166
21.785231	2.575454
21.845833	-18.369167
22.183333	-18.75
22.448833	-5.897
22.6779684	-14.9931607
22.833333	-2.116667
22.932782	-9.700122
23.2587992	-14.4076036
24.2687687	-11.2372581
24.3122184	-11.2326441
24.41482	-28.47277
24.439722	-31.068333
24.5094141	-20.4707726
24.6979651	-28.5184086
24.733333	2.8
24.766667	-34.033333
24.849722	-28.111389
25.0563889	-31.7108333
25.2	0.516667
25.2067011	-10.5201555
25.2659777	-29.5123509
25.4	-33.766667
25.534544	-33.900735
25.5396	-33.89738
25.5414623	-33.8789427
25.6	-33.958056
25.6	-33.958056
25.602369	-4.405519

Appendix A.

25.6805868	-25.2076148
25.680587	-25.207615
25.833333	-17.933333
25.833333	-17.933333
25.912222	-24.658056
25.916667	-27.833333
25.919609	-24.673549
26.0384335	-10.312413
26.0714	-8.90042
26.083333	-32.683333
26.083333	-25.533333
26.133333	-9.266667
26.208139	-10.30594
26.3352799	-28.9625
26.3987323	1.8445973
26.4	-29.033333
26.4	-24.633333
26.40206	-24.637199
26.4252906	-8.1988056
26.438009	2.42024
26.51173	-8.654946
26.6	-8.266667
26.6111137	-29.2892118
26.69286	-9.241506
26.783333	3.133333
26.833333	2.933333
26.883333	-33.6
26.9970153	-16.8054223
27.0970475	-26.7145297
27.1216667	-18.9105556
27.1216667	-18.9105556
27.2323367	-28.307254
27.25	-15.9166667
27.3028803	2.3893071
27.479444	-11.664722
27.5437144	1.3185114
27.54471	-10.51164
27.6933496	-26.3236413
27.7063889	-25.7680556
27.7490656	-15.861252
27.7978333	-25.64931
27.8591824	-25.7400652
27.866667	-32.983333
27.89506	3.692196
27.958697	-25.9934479
27.9717606	-16.9556508
28.0156811	-7.3246877
28.0613	-7.385832
28.0666667	-17.4330556
28.1010948	-12.8467404
28.1080468	-25.9173515
28.14543	-26.38497
28.188056	-25.746111

Appendix A.

28.188056	-25.746111
28.221	-25.746
28.224885	-25.7311808
28.2558391	-25.7929901
28.2672801	-25.4120326
28.283333	-15.416667
28.331671	3.546253
28.334	-9.286
28.35	-16.816667
28.406111	-24.7
28.4352948	-20.5065248
28.4389535	-26.3525092
28.5	-20.5
28.53747	-16.87705
28.557914	-31.1856293
28.576994	1.070314
28.626479	-20.1325066
28.6498144	-12.9906407
28.7036111	-20.2325
28.80398	-31.5985
28.9202672	-28.7036714
28.983333	-27.65
29.0099435	-24.1855443
29.1448793	-3.3728836
29.1855785	-2.0448431
29.1913918	-5.9127393
29.2531439	4.3667333
29.2727539	-0.5949593
29.3	-25.4333333
29.366667	-3.383333
29.3947135	-29.0887033
29.433333	-3.966667
29.45	-1.183333
29.45	0.49
29.464359	-3.5090144
29.5107708	-6.2555679
29.5107708	-6.2555679
29.5107708	-0.0649884
29.5169444	-28.6488889
29.536146	-30.1566232
29.5369	-31.6288
29.6035495	-30.030286
29.6738889	-29.3927778
29.683333	-4.9
29.6962677	-0.3256071
29.70997	3.73503
29.7454995	-7.271896
29.766147	-7.03982
29.8352303	-31.5191085
30	-22.216667
30.00348	-28.85882
30.0202964	-0.1618829
30.08021	-24.39752

Appendix A.

30.0958333	10.6155556
30.133333	-0.033333
30.1345038	-0.8342004
30.1675902	-28.7401997
30.2801166	-30.8175858
30.29252	-30.69104
30.2974199	-30.4848267
30.366667	-30.85
30.3794118	-29.6006068
30.379722	10.636389
30.4191985	-15.6274633
30.45	-30.75
30.474894	19.169825
30.5711111	-1.6177778
30.583333	-29.066667
30.59433	-30.27351
30.6020104	-7.4430244
30.655	-1.7322222
30.666667	-30.316667
30.7982029	-17.9033054
30.8	-17.9
30.883333	-30.05
30.9015642	-30.0216412
30.9388678	-29.9050873
30.9654	-17.8548091
30.9694163	-25.4752984
30.98	2.3
30.9933114	-29.7423114
30.9962356	-26.5380011
31.0218404	-29.8586804
31.033333	-25.7
31.0449768	-29.5723246
31.05	-29.65
31.053056	-25.786111
31.066667	-25.65
31.0851019	-24.6006166
31.091415	-26.2340472
31.1338071	-25.1829033
31.136111	-8.458333
31.136111	-8.458333
31.1581523	-28.7517133
31.162408	29.990056
31.166667	-26.4
31.2088526	30.0130557
31.316667	-26.516667
31.3198491	-14.2412572
31.3713164	21.7991419
31.3713164	21.7991419
31.4241897	-29.2116108
31.4456179	-27.8872252
31.4513314	-11.8280231
31.4698984	-24.6012388
31.4858333	2.7291667

Appendix A.

31.4998161	10.0977537
31.5172613	30.5909933
31.5547402	-23.9883848
31.591944	-24.995833
31.6	4.85
31.625799	22.3372319
31.666667	4.9
31.6810647	-25.4397991
31.683333	-26.683333
31.7195459	-21.8051615
31.75	-19.066667
31.7651362	22.5173453
31.8111111	2.1461111
31.8135556	-26.043518
31.816667	-1.333333
31.933333	-26.816667
31.95	-26.45
31.95	-25.433333
31.9906978	-26.3217316
32	-8
32.033333	-27.616667
32.0797222	-27.6241667
32.1286261	1.9536213
32.183333	-28.416667
32.2427	-0.4287222
32.25	-26.8666667
32.2675	-28.018889
32.46	0.05
32.4833333	-28.1833333
32.5	-28
32.516667	15.566667
32.5742215	4.4071306
32.579	-27.5
32.617859	-8.115491
32.633333	-18.966667
32.6396357	25.6872431
32.6673018	-27.5564587
32.8733117	-19.8032402
32.8998293	24.088938
32.9	-2.516667
32.9437667	1.5047051
32.9508094	-21.5468633
33.0096245	7.7992265
33.0338767	-2.0298925
33.15	24.516667
33.204167	0.424444
33.3205544	19.5356379
33.423056	-3.661944
33.438353	-0.7557754
33.438353	-0.7557754
33.4488637	-11.6772852
33.5672045	13.567469
33.6	-16.166667

Appendix A.

33.933333	-9.933333
34.108601	-10.60657
34.1643201	-0.4115968
34.2949409	-11.6085556
34.399276	11.80538
34.458641	-13.7795533
34.483333	0.333333
34.6155676	0.220292
34.6856509	-11.6701147
34.7561246	-13.9897893
34.801	-16.035
34.8444805	0.1255761
34.85	-19.833333
34.85	-14.016667
34.916667	-14.083333
35	-10.941111
35.027222	-17.441667
35.14418	-16.551901
35.1469189	-17.332581
35.2368246	-14.6436038
35.253304	-14.4861733
35.266667	-16.916667
35.316667	-22
35.333333	-15.383333
35.3411388	-17.8176872
35.6969984	-15.2608259
35.8001626	0.8322602
35.8061779	-3.6190593
36.0023225	3.6268222
36.0675952	0.6242788
36.333333	-10.283333
36.6944136	-3.372301
36.7820334	-0.3406224
36.8266604	-1.2872167
36.8333333	-1.3666667
36.887222	-17.876389
36.8976626	-7.8590278
36.983333	-6.833333
36.983333	-6.833333
37	5
37.516667	-5.533333
37.5321341	0.6124547
37.666667	-6.816667
37.7783333	-7.0291667
37.806568	-7.377925
37.82	-2.275
37.8512309	6.3346153
38.2941721	-5.7852349
38.4166667	-2.1833333
38.5	-4.75
38.7368187	-0.1750904
38.7577605	7.5931759
38.9	-6.433333

Appendix A.

38.9876741	-8.0086976
39.100278	-5.035
39.1023228	-5.0888751
39.283333	-6.8
39.29208	8.5644743
39.333333	-0.15
39.3621196	-6.1357295
39.3804134	-4.6471628
39.45	-4.166667
39.55	-3.966667
39.6285874	-3.8148404
39.630556	-4.026111
39.6449084	-4.0430411
39.6682065	-4.0434771
39.7549511	-7.869895
39.8784831	-3.3300563
39.8784831	-3.3300563
40.009838	-1.205366
40.111389	-10.28
40.666389	-15.010556
40.75	-14.966667
40.7833333	-1.2
40.7988889	-2.3386111
40.9006408	-2.2695575
41.8824233	5.3392084
42.283333	2.333333
42.55	3.816667
42.5515731	6.29398
42.7727	0.1659
44.0274519	6.9745714

APPENDIX B: GLOBALWEB FOOD WEB DATA

Appendix B: Suitable food web data used from GlobalWeb database (Thompson et al. 2012).

Food Web #	Location	Habitat
1	India	Estuary
2	South Africa	Estuary
4	U.S.A.(California)	Salt marsh
6	U.S.A.(California)	Estuary - marine
14	Hawaii	Mangrove swamp
15	Hawaii	Mangrove swamp
33	Malawi	Lake
36	Hawaii	Mangrove swamp
38	Malawi	Lake
39	Malawi	Lake
46	Texas	Lake
47	U.S.A.(Florida)	Swamp
50	U.S.A.(California)	Sand beach
60	U.S.A.(Arizona)	Forest
70	U.S.A.	Estuary
74	South Africa	Sand beach
77	Ethiopia	Lake
78	Uganda	Lake
85	Malaysia	Swamp
114	Zimbabwe	Lake
115	Peru	Sand beach
116	U.S.A.	Pond
117	Panama	Lake
120	Uganda	Lake
130	U.S.A.(Everglades)	Estuary
204	Africa	Lake
218	New Zealand	Stream
219	New Zealand	Stream
220	New Zealand	Stream
221	New Zealand	Stream
222	New Zealand	Stream
223	New Zealand	Stream
224	New Zealand	Stream
225	New Zealand	Stream
226	New Zealand	Stream
227	New Zealand	Stream
228	New Zealand	Stream
229	New Zealand	Stream
230	New Zealand	Stream
231	New Zealand	Stream
232	New Zealand	Stream
233	New Zealand	Stream
234	New Zealand	Stream
235	New Zealand	Stream
236	New Zealand	Stream
237	New Zealand	Stream
238	New Zealand	Stream
239	New Zealand	Stream
240	New Zealand	Stream
241	New Zealand	Stream
242	New Zealand	Stream
243	New Zealand	Stream
244	New Zealand	Stream
245	New Zealand	Stream

246	New Zealand	Stream
247	New Zealand	Stream
249	Brazil	River
250	Brazil	Reservoir
251	Brazil	Reservoir
252	Brazil	River
254	Brazil	River
255	Brazil	River
256	Brazil	River
288	U.S.A.	Estuary-marine
289	Ethiopia	Lake
295	U.S.A.	Pond
298	Australia	Stream
299	Australia	Stream
300	Australia	Stream
301	Australia	Stream
302	Australia	Stream
303	Australia	Stream
304	Australia	Stream
305	Australia	Stream
306	Australia	Stream
307	Australia	Stream
308	Australia	Stream
310	India	Reservoir
326	Belize	Forest
327	Australia	Wetland
328	Australia	Wetland
329	Australia	Wetland
330	Australia	Wetland
331	Australia	Wetland
346	Australia	Stream
347	Brazil	Stream
354	Caribbean	Terrestrial

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