

How sweet is the land?
Modeling caloric landscapes for tropical hummingbirds

by

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Abstract Approved:

Adam S. Hadley

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Pollination is a critical ecosystem function for sustaining biodiversity. However, pollinators and the services they provide are threatened by landscape-altering anthropogenic activities across the globe. Habitat loss and fragmentation, introduction of invasive species, chemical use, and urbanization have been shown to impact pollination. Pollinator foraging behavior is thought to be largely a function of available floral rewards, therefore, understanding the role of resource distributions in pollinator abundance and behavior within disturbed landscapes is a key piece of information for conservation. Fine scale information on floral resource distribution across disturbed landscapes is lacking in most systems. Here we demonstrate how existing presence-only species distribution modeling techniques (i.e., Maximum entropy modeling [MaxEnt]) can be combined with widely available environmental information to create resource landscapes for both pollinator communities and specific pollinators of interest. This model is the first of its kind, making possible simultaneous visualization of fine-scale resource configuration and quantity across broad spatial extent. We tested this method to build caloric landscapes using tropical hummingbird-plant system in Costa Rica. We found that our MaxEnt models performed well on independent data for all 13 flower species we examined. Our landscape-scale caloric map showed that available calories within each 35m² pixel ranged from 0 to greater than 30,000 across our study region. Our model provides the possibility of predicting pollinator movement and abundance based upon resource supply. As its parameters are flexible, it is broad in its potential applications. The flexibility in calibration to desired resource landscapes permits applying the model to other pollinator-plant systems. We hope that this model will complement the current ecologist's toolbox, aiding in ensuring the continuation and health of pollinator systems.

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Bachelor of Arts in International Studies in Biology thesis of Christina Nozomi Birkett presented on November 25, 2014.

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I understand that my thesis will become part of the collection of Oregon State University. My signature below authorizes release of my thesis to any reader upon request. I also affirm that the work represented in this thesis is my own work.

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CONTRIBUTION OF AUTHORS

Dr. Adam S. Hadley and Dr. Matthew G. Betts aided in the formulation of this thesis and participated in data collection. Dr. Hadley and Dr. Betts both provided insights on modeling methods and written organization. Dr. Hadley especially aided in translating study concepts into working models.

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1 GENERAL INTRODUCTION

1.1 POLLINATION: A GLOBAL PERSPECTIVE

Animal pollination is an essential service that majority of the world's plant species depend on for reproduction. Nearly 90% of all angiosperms¹ are believed to be animal pollinated (Marsh and Kaufman, 2012; Ollerton *et al.*, 2011) and between 130,000 and 300,000 animal species visit flowers regularly for nectar, actively dispersing pollen throughout the landscape (Buchmann and Nabhan, 1996; Willmer, 2011). Anthropocentrically, humans rely on pollinators and their services for sustenance and economic income (Aizen *et al.*, 2009; Bedard, 2014). The production of over 75% of domestic agricultural crops is contingent upon pollination (Dixon, 2009; Rosalind and Pitts-Singer, 2008; Roubik, 1995), with an estimated 35% of crop value attributed to pollinator services (Dixon, 2009). Remarkably, the majority of human dietary nutrition relies on pollinated crops (Chaplin-Kramer *et al.*, 2014). In the face of an increasing global populace, these services become more crucial in meeting commercial demands for food. Clearly, the human benefit of pollinator services worldwide is immense.

Recent studies reveal widespread parallel declines in pollinators and their plant resources (Biesmeijer *et al.*, 2006; Fründ *et al.*, 2010; Weiner *et al.*, 2014). Although nations worldwide manage their resources disparately, there is global consensus of a pollination crisis (Aizen and Harder, 2009; Buchmann and Nabhan, 1996; Holden, 2006; Kinver, 2014). A large portion of these alarming trends is thought to be the consequence of anthropogenic landscape alterations (Buchmann and Nabhan, 1996; Kearns, 1998; Kremen *et al.*, 2002; Montero-Castaño, 2012; Vanbergen, 2013; Willig, 2007). Approximately 60% of the world's landscapes are disturbed by deforestation, invasive species introduction, urbanization, and excessive chemical use (Bright, 1999; Clavero, 2005; Cresswell, 2011; Didham, 2007; Dixon, 2009; Gao and Liu, 2012; Gill *et al.*, 2012; Halme *et al.*, 2013; Kleijn and Raemakers, 2008; Lewanzik and Voigt, 2014; Mooney and Cleland, 2001; Priess *et al.*, 2007; Scott-Dupree *et al.*, 2009; Tan *et al.*, 2012; Torchin *et al.*, 2002; Vanbergen, 2013; Willmer, 2011). Alarmingly, the rate of anthropogenic landscape alterations is accelerating (NRC, 2003). These global threats to pollination have repercussions for not just the plants and their pollinators, but for all organisms either directly or indirectly

¹ Flowering plants. 89.4% of global terrestrial plant species are angiosperms (Crepet and Niklas, 2009).

dependent on them (Fleming, 1988; Belovsky and Slade, 2000). Thus, there is a growing international concern for pollinator system health and management (IPI, 2009).

The relationship between pollinators and their plant resources is tightly coupled, with the abundance and fitness of one strongly affecting the other (Biesmeijer *et al.*, 2006; Hadley and Betts, 2012; Tepedino and Stanton, 1981). Pollinators not only increase the quantity of plant yield, but also the quality of these fruits and seeds (Bommarco *et al.*, 2012; Garibaldi *et al.*, 2013; Hadley *et al.*, 2014; Heinrich and Raven, 1972; Klein *et al.*, 2007; Roubik, 1995; Roubik 2002). Reciprocally, plants provide their pollinators with necessary energetic resources in the form of nectar: energetic reward from plants strongly influences pollinator behavior (Heinrich, 1975; Heinrich and Raven, 1972; Heithaus *et al.*, 1975; Klinkhamer and Lugt, 2004; Schaffer and Schaffer, 1979). Factors such as plant population density, bloom time, and nectar award amount strongly influence pollinator abundance (Cotton, 2007; Heinrich and Raven, 1972). Therefore, the complex webs of interdependent relationships in global ecosystems are largely reliant upon pollination services.

Concerning the urgency in addressing global threats to pollination, there is a need for developing tools to monitor, evaluate, and quantify variables which support functional pollination services. Particularly, quantifying pollinator resources is critical to better understand the effects of anthropogenic landscape alterations on pollinators and their behavior. Maintaining and nurturing these intricate pollinator-plant systems requires further understanding of resources across landscapes. However, there is a lack of assessment of these resources at the scales at which pollinators interact with them. As resources are significant drivers of pollinator behavior and distribution, this translates into a relatively unexplored aspect of pollinator-plant relationships. By evaluating resources at fine scales, it is possible to further examine the repercussions of anthropogenic landscape alterations on pollination services, ultimately ensuring their long-term continuation and health.

2.1 INTRODUCTION

Pollination is a fundamental service upon which the majority of plants and numerous species worldwide rely for reproduction (Ollerton *et al.*, 2011). Globally, pollinators and the services they provide are threatened, with parallel declines observed in both plants and their pollinators (Biesmeijer *et al.*, 2006; Fründ *et al.*, 2010; Weiner *et al.*, 2014). The most prominent factor of this global pollination crisis is landscape change. Due to the closely bound relationship between pollinators and their plant resources, drastic alterations of these resources (i.e. via deforestation, pesticides) across landscapes have compounding consequences. As habitat is lost, fragmented, and degraded, pollinators alter their movement patterns and behavior in search of adequate resources (Hadley and Betts, 2009), often perishing if unsuccessful (Potts *et al.*, 2010). Thus, understanding the distribution of floral resources and how they influence pollinators and their services is imperative. This requires quantifying of flowering plants at the fine scales that correspond with pollinator behavior and movement.

2.1.1 A NEED FOR NEW RESOURCE MODELING TOOLS

Despite widespread acknowledgement of the crucial role of energetics in pollinator distribution and behavior (Cotton, 2007; Heinrich and Raven, 1972; Heithaus *et al.*, 1975; Klinkhamer and Lugt, 2004; Schaffer and Schaffer, 1979), quantifying high-resolution resource availability at a landscape scale is a relatively new and undeveloped aspect of pollination ecology (Kremen *et al.*, 2007). Recent efforts have attempted to map distributions of nesting resources (Lonsdorf *et al.*, 2009) and floral resources at broad spatial extents (Feldman and McGill, 2014). However there was a mismatch between the scale and resolution of resource quantification in this work and the scale at which pollinators interacted with them, limiting usefulness of these models for understanding fine scale pollinator distributions and behavior.

Quantifying resources at scales where individual foraging decisions occur across broad spatial extents has not been attempted. Such evaluations are necessary to effectively examine the site scale habitat selection, foraging behavior, and effects of landscape change on pollinators. By discerning the amount of available energetic resources across a large space, we can determine how resource distribution, configuration, and abundance influence pollinator behavior. This may

ultimately aid in developing more effective management methods to combat the global pollination crisis.

We outline a method that uses existing ecological tools and broadly available environmental layers to provide a flexible option for quantifying pollinator resources. Our primary objective was to develop a technique that can be used to quantify energetic resources for pollinators at high resolution across entire landscapes. Our end result was a high-resolution map of calories across a large scale. We incorporated observed flower presences with nectar volume and sugar content to predict a spatial distribution of caloric resources. Through this model, there exists novel opportunities to examine drivers of pollinator behavior and potentially predict movement based upon energetics.

2.1.2 TESTING A CALORIC LANDSCAPE MODEL IN COSTA RICA

In order to test this model, we investigated hummingbird-pollinated systems in the fragmented tropical landscape of Coto Brus, southern Costa Rica. Hummingbirds (family *Trochilidae*) are renowned for having the fastest metabolism in the vertebrate subphylum (Diamond, 1990; Pearson, 1950; Suarez and Gass, 2002). Both hummingbird morphology (small endotherms) and behavior (hovering) demand a frequent and high caloric intake (Feinsinger *et al.*, 1979; Suarez and Gass, 2002). Consequently, the quality (sugar concentration), quantity (nectar volume), and spatial distributions of nectar resources are primary drivers of hummingbird behavior (López-Calleja *et al.*, 1997; Stiles, 1975). Recently, our laboratory discovered three key findings that provide clear evidence of these global threats to hummingbird pollination services. First, hummingbird movement is restricted by forest cover (Hadley and Betts, 2009). Second, there is reduced ornithophilous² plant reproductive success in smaller forest fragments (Hadley *et al.*, 2014). Third, pollinator communities differ in forest patches, with fewer specialized, long-billed hummingbird pollinators in smaller patches (Hadley *et al.*, *in prep*). Understanding and quantifying pollinator resources could help explain the mechanism behind the effects these studies reported.

² Bird-pollinated.

2.2 METHODS

2.2.1 STUDY SYSTEM

Costa Rica has an extensive history of severe landscape alteration (Arroyo-Mora, 2005; Boucher *et al.*, 1983; Grainger, 1993; Lopez, 2013). The landscape, composed of remnant forest fragments embedded within an agricultural matrix, is ideal for examining effects of land use changes on pollinator systems. The study occurred in a ~33,000 ha region in Coto Brus County of southern Costa Rica (Figure 1; see Appendix 1 for elevation map). Roughly 42% is premontane tropical wet forest. Las Cruces Biological Station lies at the approximate center of the study landscape (8° 47' 7" N, 82° 57' 32" W). An estimated 2000 plant species are extant in Las Cruces alone, with roughly 20 hummingbird species represented (OTS, 2014). Seasons are categorized as wet (May-Dec) and dry (Jan-Apr). This study focuses on the ornithophilous³ dry season flower community.

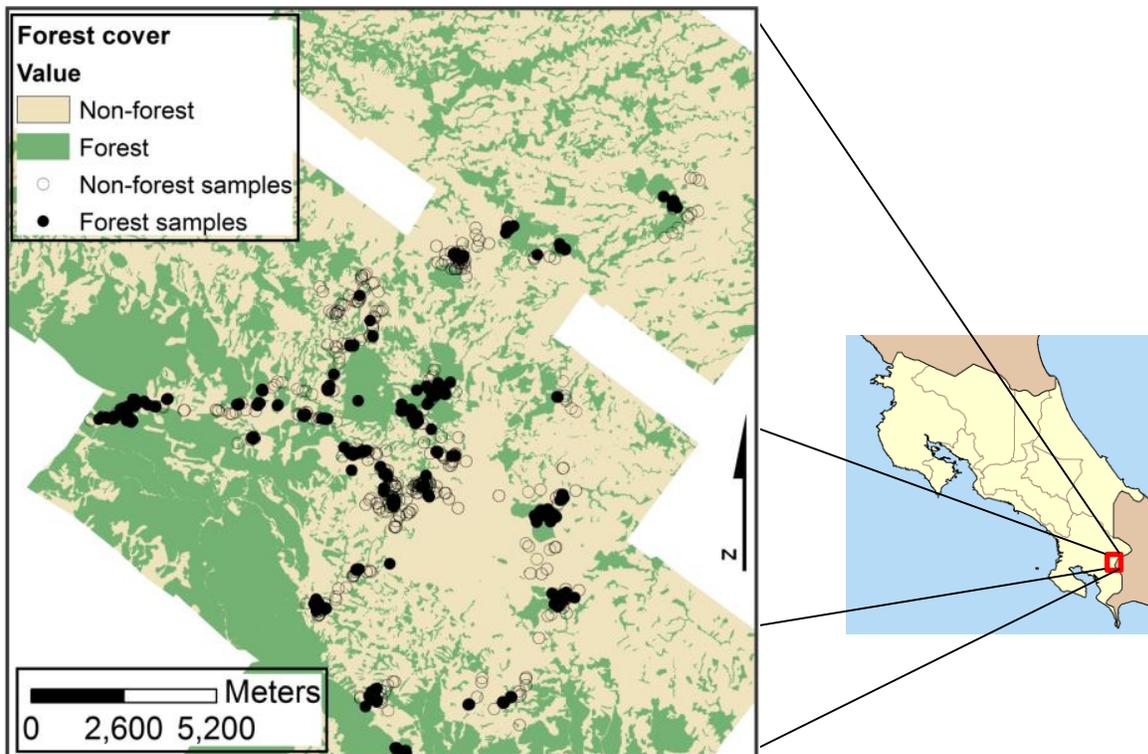


Figure 1. Map of plant presence data superimposed upon forest cover and elevation of study landscape. The white spaces are locations with absences in remotely-sensed environmental data. Costa Rica map from Wikimedia commons.

³ Bird-pollinated.

2.2.2 PLANT PRESENCE SAMPLING

We used a dataset containing 5456 flowering plant locations across gradients in elevation (909-1555 m), forest cover, and forest patch size (68% in forest fragments and 32% in non-forested areas) (Figure 1, section 2.2.1). We selected the 13 most abundant ornithophilous species using observed presence data. These species all had observed visitations from hummingbirds and contained morphological traits that suggested hummingbird pollination. We determined that our study species account for 73% of existing dry season flowers in the study region. This information was surmised from comparing the observed presences for all study species to the total observed presences of ornithophilous dry season flowers. **Table 1** summarizes key ecological traits of the study species. We collected floral resource location data during peak dry season (Jan-Mar) using three different techniques. In 2010 and 2011 we sampled flowers in 37 forest patches representing a gradient in patch size, forest amount and elevation (Hadley *et al.*, 2014) as part of a study on pollination success of *Heliconia*. Flowers were sampled in 7 ± 4 , 20 m radius locations within each forest patch (1186 total locations). In 2012 we collected flower location data at 2787 sites visited by radio-tagged hummingbirds and 1204 randomly selected points within 500m of these locations (see Volpe *et al.* 2014 for detailed methods). All ornithophilous flowers within a 20m radius were recorded at each site. We collected additional presence data for non-forested areas through roadside surveys (752 flower locations) (Hadley *et al.*, 2014).

Abund Rank	Species	Morph.	Growth	Special.	Avg inflor.	Avg flowers per inflor.	Corolla length	Curved	Openness	Known <i>Trochilidae</i> nectarivores
1	<i>Calathea crotalifera</i>		Sh	Sp	1.25	5	S	N	C	1
2	<i>Heliconia tortuosa</i>		Sh	Sp	1	2	L	Y	C	7
3	<i>Palicourea padifolia</i>		Sh	G	40	5	S	N	O	9
4	<i>Glossoloma tetragonus</i>		Sh	Sp	1	4	L	N	O	4
5	<i>Musa x paradisiaca</i>		T	G	1	4	L	N	O	4
6	<i>Psychotropia poeppigiana</i>		Sh	G	5	2	S	N	O	2
7	<i>Renealmia cernua</i>		Sh	G	1	4	L	N	O	1
8	<i>Palicourea discolor</i>		Sh	G	40	5	S	N	O	5
9	<i>Centropogon granulatus</i>		Sh	Sp	1.25	4	L	Y	C	7
10	<i>Erythrina poeppigiana</i>		T	G	50	5	L	Y	O	6
11	<i>Musa velutina</i>		T	G	1	4	L	N	O	3
12	<i>Drymonia macrantha</i>		Sh	G	1.25	4	L	Y	O	7
13	<i>Columnea polyantha</i>		Sh	Sp	1.25	3	L	N	C	2

Table 1. Study species. This table reflects morphology, growth habits (Sh=shrub, T=tree), specialization (Sp=specialist, G=generalist), average inflorescences per plant, average open flowers per inflorescence, relative corolla length (S=short, L=long), flower curvature (N=not curved, Y=yes curved), flower openness (O=open, C=closed), and observed number of *Trochilidae* nectarivores.

2.2.3 NECTAR SAMPLING

We sampled cumulative nectar from covered flowers. Mature buds were covered with a fine mesh bag the night prior to anthesis⁴ to prevent pollinator access (following McDade and Weeks, 2004; Wolff *et al.*, 2006). Cumulative nectar was quantified the following late afternoon-evening by inserting microcapillary tubes into the open flower's nectary. We measured nectar quality through the temperature-corrected Brix percentage⁵ using a sugar refractometer. These nectar characteristics were used to quantify caloric availability as described in the caloric estimation section (2.2.6).

2.2.1 MODEL DESCRIPTION

A caloric landscape model requires two key elements: resource abundance distribution and caloric quantification of nectar. In order to build an accurate map, we needed to ensure that the majority of caloric resources are represented. Due to limitations of labor and time, it may not be possible to acquire such extensive data and areas will remain unsampled. Accordingly, the use of maximum entropy models (MaxEnt) permits an accurate predicted distribution across a large region based on presence-only data (Elith *et al.*, 2011; Phillips *et al.*, 2006; Phillips, 2008; Phillips and Dudik, 2008). We obtained caloric values through quantitative field estimates and from published results. These inputs were combined to generate a caloric landscape map. **Box 1** (section 2.2.7) summarizes the assumptions made to build this model.

2.2.4 RESOURCE DISTRIBUTION MODELING

We used maximum entropy modeling (MaxEnt; Phillips *et al.* 2006) to create a predictive map of each species' distribution based upon environmental features and Landsat reflectance bands (Shirley *et al.*, 2013). Topographic variables (elevation, slope, aspect) and landscape configuration variables (forest cover, distance to forest edge, distance to stream) were used to predict suitability for each species (Figure 4, section 2.3). Map resolution was at 35m x 35m pixels, as this was determined to be closest in size to the sampled 20m radii sites. We conducted

⁴ Blooming.

⁵ Brix percentage measures the grams of sucrose equivalents in 100 grams of solution (nectar, in this case).

a 10-fold cross-validation in our models. For all species, elevation alone accounted for over 50% of predicted environmental suitability (both percent contribution and permutation importance). The second strongest predictor variable was forest cover. We measured model performance through AUC (area under the curve) of the ROC⁶ (receiver operating characteristic) plot. Model variance with environmental variables was analyzed through jackknife resampling and analysis of variance (ANOVA) (Table 2, section 2.3).

2.2.6 CALORIC ESTIMATION

We quantified calories per plant using the average cumulative nectar of newly opened flowers, average temperature-corrected Brix, and applying the caloric multiplier (sensu Heinrich, 1975). Nectar is largely composed of sugar and water, with negligible amounts of amino acids and other components (Heinrich, 1975). The three primary sugars—sucrose, fructose, and glucose—all contain equivalent calories per gram (Stiles, 1975). Synergizing these factors, we derived **Equation 1** to estimate calories per plant (see Appendix 3 for explanation). Variables *I* and *F* are estimates deduced from averaging observations made for each plant species when gathering nectar data.

Equation 1. Estimating calories per plant:

$$C_i = \frac{N \cdot S \cdot V}{S/\rho_{ST} + (100-S)/\rho_{WT}} I_i \cdot F_i \quad \text{Eq. 1}$$

C=estimated calories per plant

i= species

I=estimated inflorescences per plant

F=estimated open flowers per inflorescence

S=average temperature-corrected Brix

V=average daily nectar output (mL)

N=4000 calories per 1 g sucrose (calorie multiplier)

ρ_{ST} =density of sucrose at average sample temp T

ρ_{WT} =density of water at average sample temp T

⁶ The ROC graph plots the true positive rate against the false positive rate of the predicted suitability using independent presence data. The area under the plotted curve measures how accurately the model predicts the suitability for the target species. An AUC of 0.5 suggests that the model is performing poorly and predicts no better than random chance. And AUC of or above 0.7 indicates the model is performing well.

2.2.7 MODELING CALORIC DISTRIBUTION

MaxEnt outputs a continuous gradient of values that represent how suitable the location is for a plant species according to observed presence data and environmental variables. We calibrated this suitability value as an index of flower abundance for each of our species using known flower densities. We partitioned the continuous range in suitability into 20% bins (i.e. 0-0.2 is the first bin) and applied the average observed flower abundances to each pixel within the category. We then reclassified the resource abundance distribution maps for each species by multiplying the mean plant abundance by calculated calories per plant. Finally, we summed the calories for all species at each pixel to generate the complete caloric landscape (Figure 5, section 2.3; See Appendix 4 for individual plant species' caloric maps). **Figure 2** describes the complete process used to synthesize the caloric landscape map.

Box 1. List of assumptions for this caloric landscape model

1. There is little variance in caloric output per individual flower, regardless of topographic variation in plant location.
2. There is little temporal variance in nectar availability within season
3. Study species are blooming during the entire season
4. Averages are an accurate representations of the actual nectar available
5. MaxEnt predicted suitability values are accurate representations of actual plant distributions

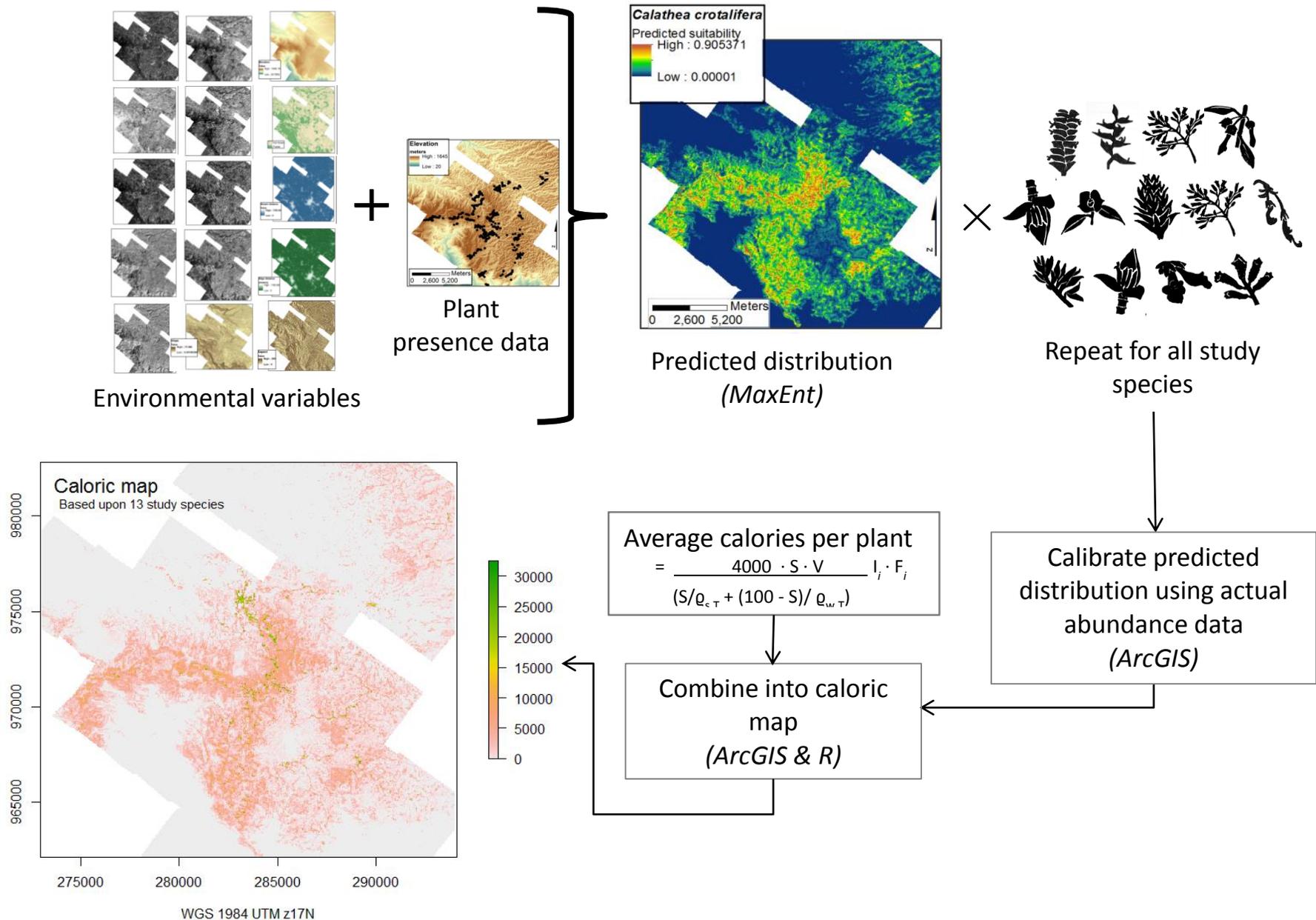


Figure 2. Process of modeling a caloric landscape. This flow chart visualizes the steps taken to synthesize a caloric landscape map. Parentheses indicate the program used to complete the step. Specifically, MaxEnt was used for obtaining a predicted distribution across the entire landscape for each species. ArcGIS was used for calibrating the suitability values for the predicted distribution into an actual abundance map. ArcGIS was then used to reclassify these abundance maps into caloric landscapes for each species. Finally, R statistical analysis was used to sum the rasters for all species into a single map.

2.3 RESULTS

For all species, elevation was the highest predictor variable for distribution (Table 2). Forest cover was the second strongest predictor for many species. We found that MaxEnt models predicted species' distributions with high accuracy. AUC ranged from 79% to 98%, with the majority of species containing an AUC over 90%. This indicates our predicted species distributions were representative of actual existing distributions (Figure 3). **Figure 4** reflects the predicted species distributions.

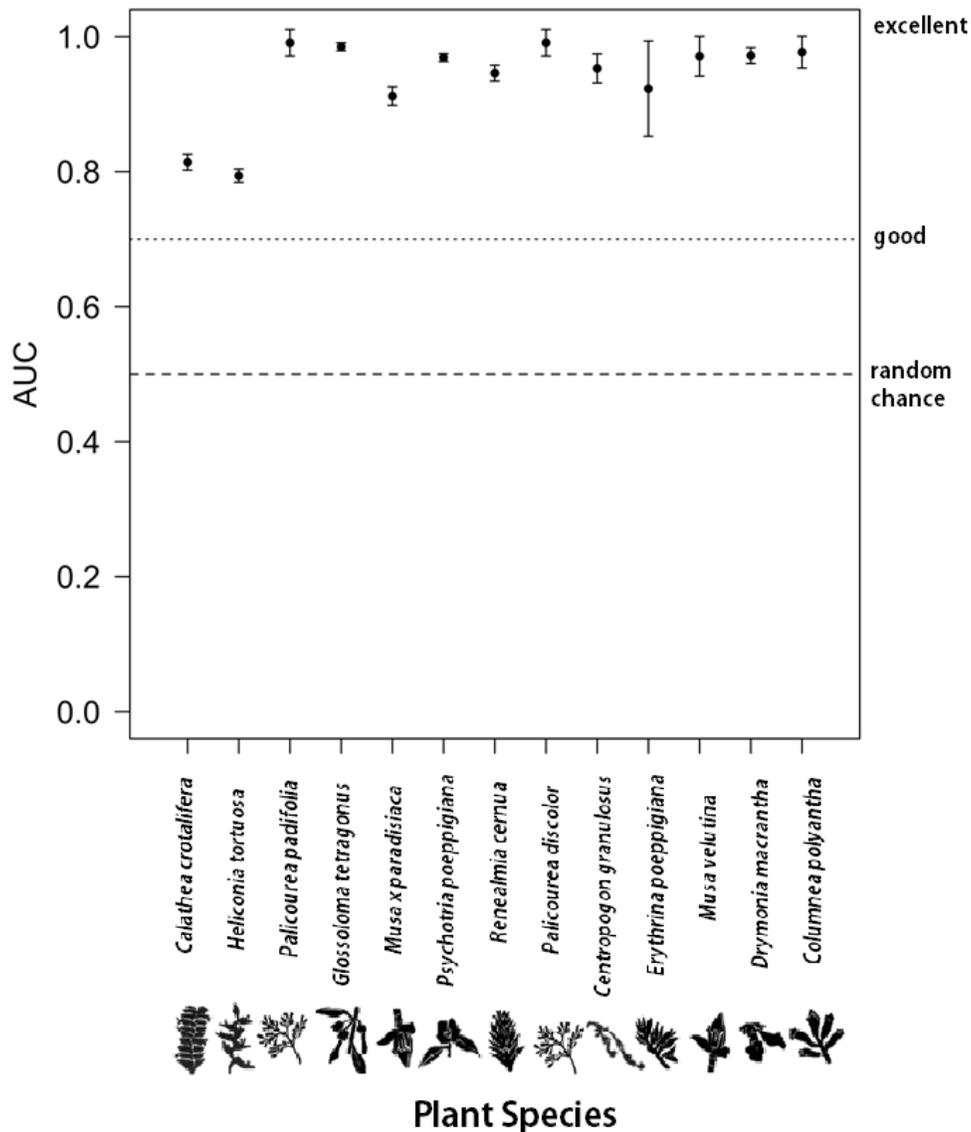


Figure 3. MaxEnt model performance in predicting suitability distributions. This graph compares the mean AUC values for each plant species' predicted suitability distributions. An AUC of 0.5 reflects a model that performs no better than random chance. An AUC above 0.7 is considered good, indicating a model is predicting with high accuracy. For all study plant species, the predicted suitability distributions were predicted well through maximum entropy modeling.

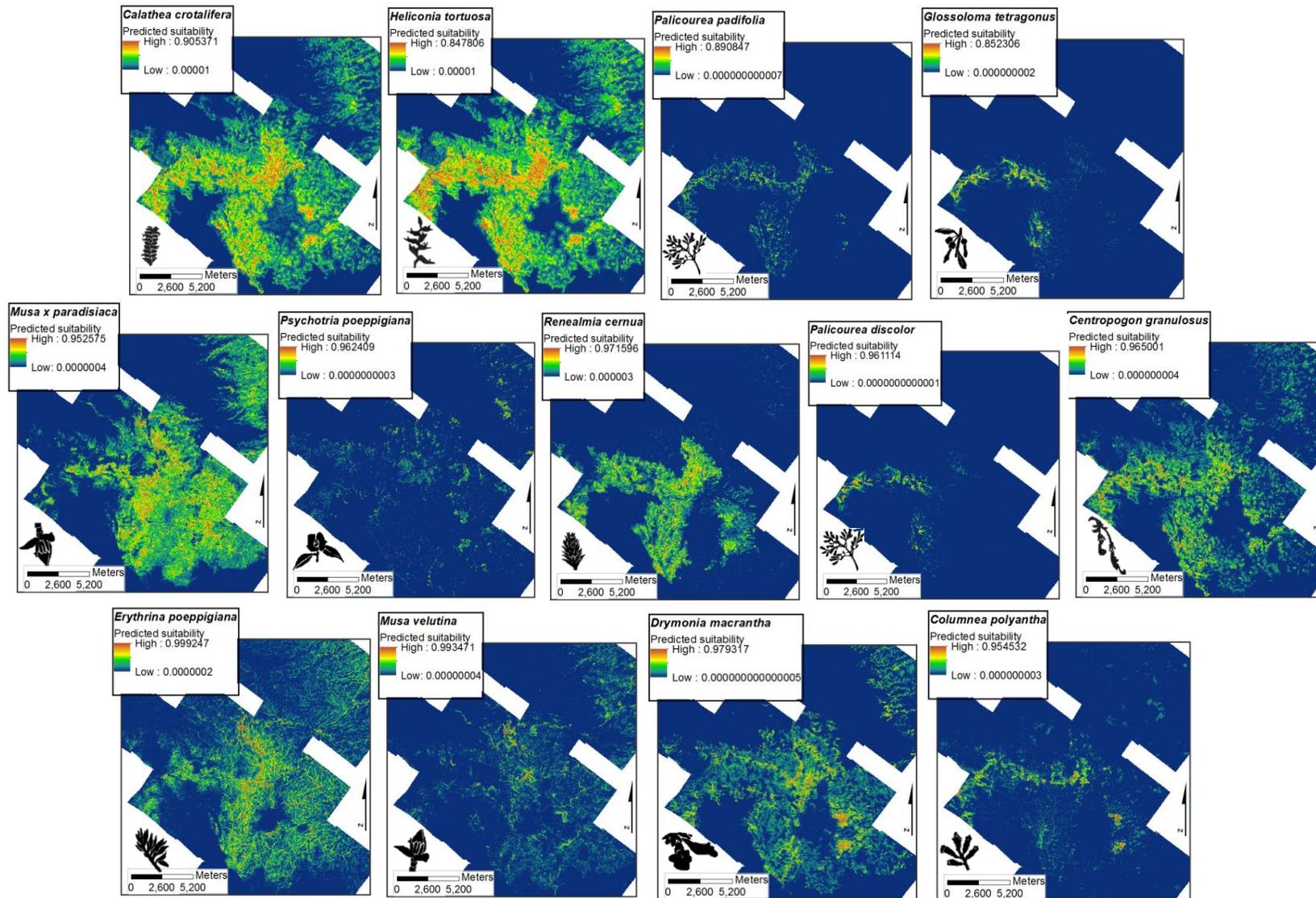


Figure 4. Predicted suitability of plant species across landscape. These maps are the outputs of MaxEnt (Phillips *et al.*, 2006) for our 13 study plant species. The predicted suitability at each pixel is determined from plant presence data and predictor environmental variables (Landsat reflectance bands, landscape configuration, topography). We treat this map as a form of predicted plant distribution across the landscape. Note that the suitability value ramp is not consistent across species.

Species	Mean AUC	St. dev. AUC	#1 permutation importance	#2 permutation importance	#1 percent contribution	#2 percent contribution	#1 jackknife resample test gain	#1 jackknife resample AUC
<i>Calathea crotalifera</i>	0.814	0.006	Elevation 73.8	Forest 6.8	Elevation 67.7	Forest 8	Elevation	Elevation
<i>Heliconia tortuosa</i>	0.794	0.005	Elevation 75.8	Forest 10.6	Elevation 73.4	Forest 10.1	Elevation	Elevation
<i>Palicourea padifolia</i>	0.991	0.01	Elevation 69.8	Edge 10.9	Elevation 50.9	Slope 11	Elevation (Aspect, slope)	Elevation (Aspect, Landsat b62, slope)
<i>Glossoloma tetragonus</i>	0.985	0.003	Elevation 95.1	Forest 1.9	Elevation 83.4	Forest 5	Elevation	Elevation (Aspect)
<i>Musa x paradisiaca</i>	0.912	0.007	Elevation 67.5	Landsat b62 6.1	Elevation 60.3	Slope 7.7	Elevation	Elevation (Slope)
<i>Psychotropia poeppigiana</i>	0.969	0.003	Elevation 67.3	Forest 8.7	Elevation 25.7	Landsat b40 24	Elevation (Slope, aspect)	Elevation (Slope, aspect)
<i>Renealmia cernua</i>	0.946	0.006	Elevation 88.3	Landsat b502 2.2	Elevation 80.2	Slope 6.3	Elevation	Elevation (Aspect, slope)
<i>Palicourea discolor</i>	0.991	0.01	Elevation 91.9	Forest 4.3	Elevation 70.4	Forest 15.7	Elevation	Elevation (Landsat b61, Landsat b62)
<i>Centropogon granulatus</i>	0.953	0.011	Elevation 70.3	l03_b61 5.1	Elevation 45.8	Edge 10.5	Elevation	Elevation
<i>Erythrina poeppigiana</i>	0.923	0.036	Elevation 51.8	Landsat b502 11.4	Elevation 42	Landsat b10 11.1	Elevation	Elevation
<i>Musa velutina</i>	0.971	0.015	Elevation 54.2	Landsat b10 30.3	Landsat b10 41.8	Elevation 31.5	Elevation	Elevation (Landsat b30, Landsat b10, slope)
<i>Drymonia macrantha</i>	0.972	0.006	Elevation 69.6	Stream 11	Elevation 62.2	Edge 7.5	Elevation	Elevation
<i>Columnnea polyantha</i>	0.977	0.012	Elevation 66.9	Aspect 5.5	Elevation 47.2	Landsat b61 13.1	Elevation	Elevation (Landsat b61, Landsat b62)

Table 2. MaxEnt summary. This table summarizes the prediction accuracy of maximum entropy models for study species (AUC) and importance of environmental variables for distribution prediction, according to ANOVA and jackknife resampling. The area under the curve (AUC) for each study species was high, thus the species' distributions were predicted well by MaxEnt. For all species, elevation was the strongest predictor variable according to ANOVA and jackknife analysis. See Phillips *et al.*, 2006 for further explanation of these outputs. Shirley *et al.*, 2013 explains the Landsat reflectance band variables. These variables are from Landsat 7 (2003) data.

Our caloric landscape model reflects a range in calories from 0 to 32,542 calories per 35m x 35m pixel (Figure 5). The map represents the mean cumulative calories available across the landscape in one typical day for 13 of the most abundant ornithophilous plants (~73% available ornithophilous flower resources represented) during peak dry season (Jan-Mar). **Appendix 4** depicts the average caloric estimations per flower for each species. *Erythrina poeppigiana* (37%), *Heliconia tortuosa* (31%), and *Musa x paradisiaca* (11%) contributed the largest proportion of total calories across the landscape (Table 3).

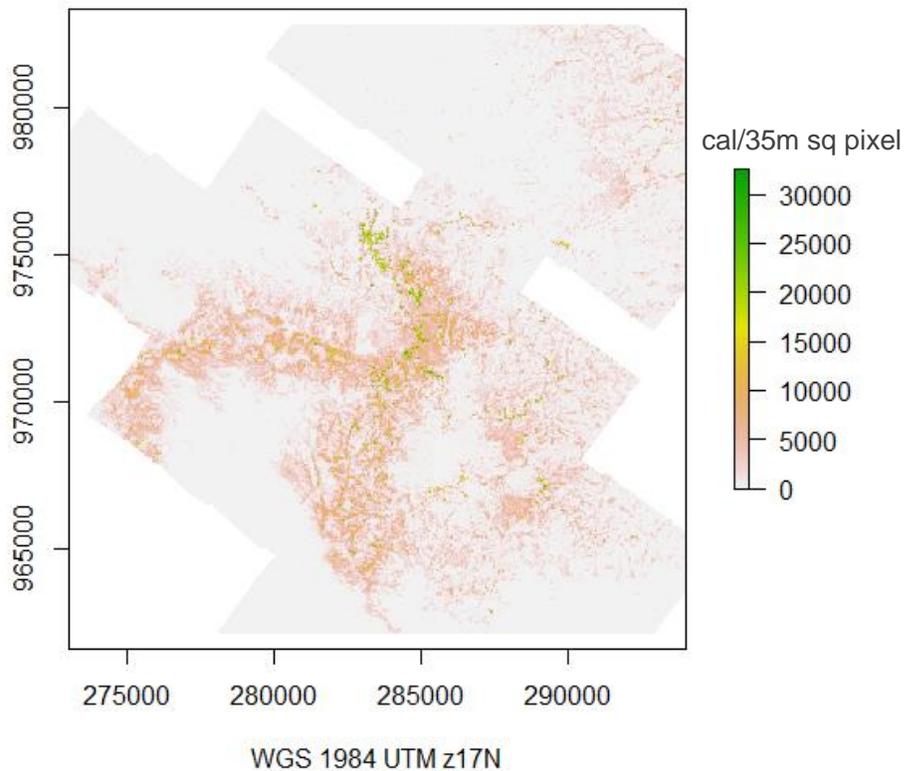


Figure 5. Map of caloric landscape. This map reflects the total calories available from 13 ornithophilous plant species in a typical day during the dry season (Jan- Mar) across the study landscape. The value ramp on the right represents the average cumulative calories available in one 35m x 35m pixel. We determined that this size of pixel had the closest area to the sampled 20m radii field data. This caloric map is a conservative estimate.

Species	Total cal in landscape	Proportion (%)
<i>Calathea crotalifera</i>	16876448	5.70
<i>Heliconia tortuosa</i>	89867126	30.57
<i>Palicourea padifolia</i>	4466994	1.52
<i>Glossoloma tetragonus</i>	4796147	1.63
<i>Musa x paradisiaca</i>	32995932	11.22
<i>Psychotria poeppigiana</i>	411249	0.14
<i>Renalmia cernua</i>	7885984	2.68
<i>Palicourea discolor</i>	2283469	0.78
<i>Centropogon granulosus</i>	15975698	5.43
<i>Erythrina poeppigiana</i>	108838531	37.02
<i>Musa velutina</i>	2951218	1.00
<i>Drymonia macrantha</i>	6531478	2.22
<i>Columnea polyantha</i>	103470	0.04
Total	293983744	100.00

Table 3. Caloric contributions by species. This table contains the total caloric output per study species across the entire landscape. *Erythrina poeppigiana*, *Heliconia tortuosa*, and *Musa x paradisiaca* were by far the largest caloric contributors.

2.4 DISCUSSION

Overall, we found that it is feasible to build an accurate caloric landscape model using simple modeling techniques and readily available remotely sensed environmental data. This model is a useful tool to add to an ecologist's toolbox. It is not intended to replace existing models for resource evaluation or pollinator prediction; however, it provides complementary fine-resolution knowledge about pollinator resources at large spatial scales. It allows for further examination of pollinator behavior and distributions in relation to available energetic rewards across landscapes. This is broadly useful, as the model is adaptable to other pollinator-plant systems.

2.4.1 ECOLOGICAL SIGNIFICANCE

A caloric map can serve as a useful tool to evaluate a landscape. Considering the high metabolism of hummingbirds, quantifying caloric availability has implications for predicting their movements and abundances. The general metabolism of a Green Hermit hummingbird (*Phaethornis guy*, a common, medium-sized pollinator within the study landscape) is, conservatively, 8,580 calories (8.58 Cal) per day (Schuchmann and Prizinger, 1988). Using this estimate, one dark green pixel (30,000 calories) has the potential to sustain daily needs of over 3 hummingbirds (Figure 5, section 2.3). Alternatively, an average hummingbird may require two light pink pixels (5000 calories) to achieve its caloric needs in one day. This caloric availability is a conservative estimate, as ~27% of the existing flowers are unaccounted for in the landscape. In addition to approximating potential for hummingbird abundances, the relative index of calories may serve as an indicator for hummingbird movement and path selection. In this manner, a caloric landscape model promises significant utility in examining pollinator-plant systems across a landscape.

2.4.2 EVALUATION OF A CALORIC MODEL

Model accuracy and predictive value could be measured through comparing pollinator abundance or movement to the caloric landscape. Using existing data from sampling points along the trajectories of radiotelemetrically tracked hummingbirds (Volpe *et al.*, 2014 *in press*), we will implement generalized linear mixed models to evaluate model accuracy. If the

hummingbirds are selecting trajectories along higher caloric locations, it is a good indicator of caloric map accuracy and prediction strength. Another method in evaluating model accuracy would be to compare pollinator abundances within patches. A caloric landscape could be modeled for each patch, with either point counts or capture data used to quantify pollinator abundances. This correlative evaluation could also be compared to an experimental manipulation of caloric rewards and examination of pollinator behavioral changes. These evaluations would substantiate whether the caloric resources have a strong effect on pollinator behavior and abundance.

2.4.3 MODEL CAVEATS AND FUTURE IMPROVEMENTS

As with any tool, this model is only useful if correctly used. MaxEnt models performed very well at mapping distributions of our plant species. These models are particularly useful in cases where presence-only data are available (i.e. common location data at broad scales), however, a disadvantage in these mapping techniques is that they result in maps of predicted suitability rather than actual abundance distributions. Thus, abundance modeling techniques such as Poisson regression and binomial mixture models would be advantageous (Kéry *et al.*, 2005; Vincent and Haworth, 1983), as they would eliminate the complication of relating suitability values to raw abundance data in order to derive caloric values at the pixel level. If sample region is relatively small, then direct abundance distribution data will provide the highest accuracy in caloric landscape modeling.

We intend to build upon this model following my graduation. In the near future, we aim to gather more extensive caloric and abundance data for a larger array of ornithophilous plant species. Our objective is to reduce potential sources of error through an alternative method of using both presence and absence data for species distributions (not just presence-only) and directly input these actual (not predicted from MaxEnt) abundance distributions into caloric maps.

As all models, the appropriate information must be gathered to generate an accurate output. This model's precision could be limited by the extent of caloric data gathered (sample size, controls) and the observed plant abundance values. The model's accuracy is constrained by prediction

accuracy of species distributions (MaxEnt AUC) and the percent of total ornithophilous species accounted for in that season. This model may only be applied for the season that the presence and nectar data were gathered during.

2.4.4 MODEL STRENGTHS

This model provides a fine scale relative index of calories available across broad spatial extents. We were able to model the majority of actual flower abundances and their daily caloric rewards. Another strength is that the model translates all resources into a single metric—calories—the energetic currency that provides the basis of pollination ecology. This allows for further analysis of pollinator movement in tandem with caloric resources.

2.4.5 INTERNATIONAL APPLICATIONS

This model holds promise as a tool for assessing global landscapes, as it is very adaptable to different systems. By adjusting parameters—such as environmental variables and plant species—and caloric estimations, the model may be calibrated to other pollinator systems. This means that it is possible to build caloric landscapes for passerine, insect, and mammal pollinators. There is also potential for modification for non-pollinator systems such as frugivory and seed dispersal. Our hope is that this tool will aid future endeavors in managing global landscapes to ensure the survival and health of pollinator systems. With this information, we can better understand the impacts of anthropogenic threats to pollination and ameliorate the current pollination crisis.

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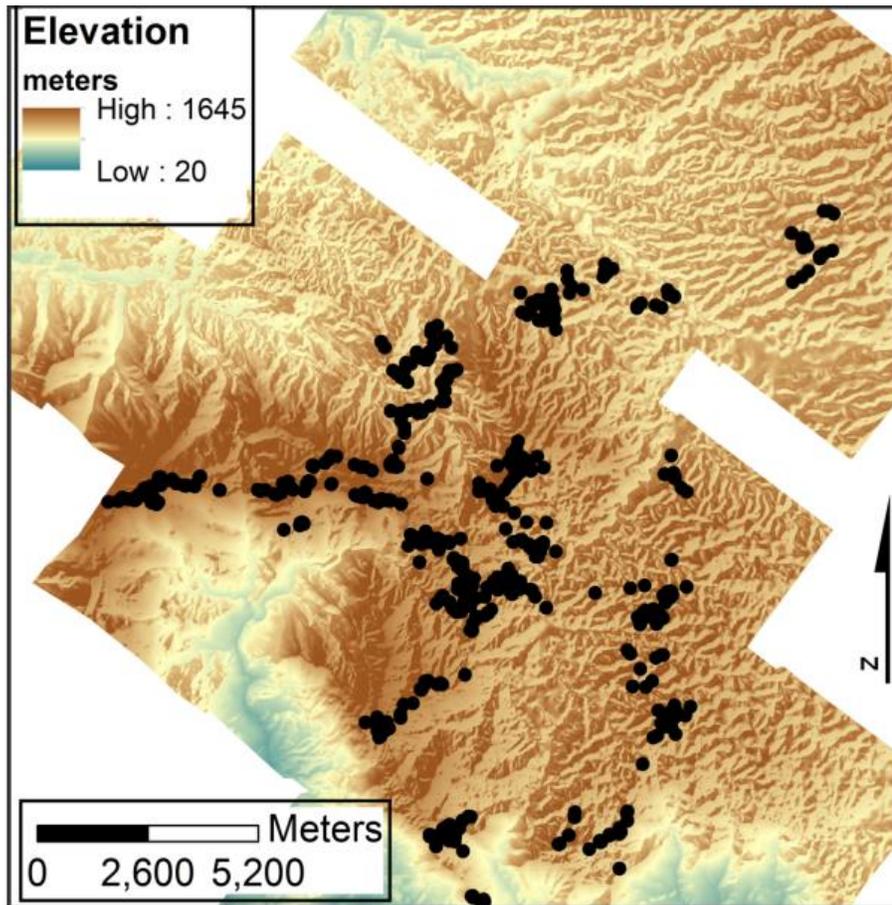
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APPENDICES

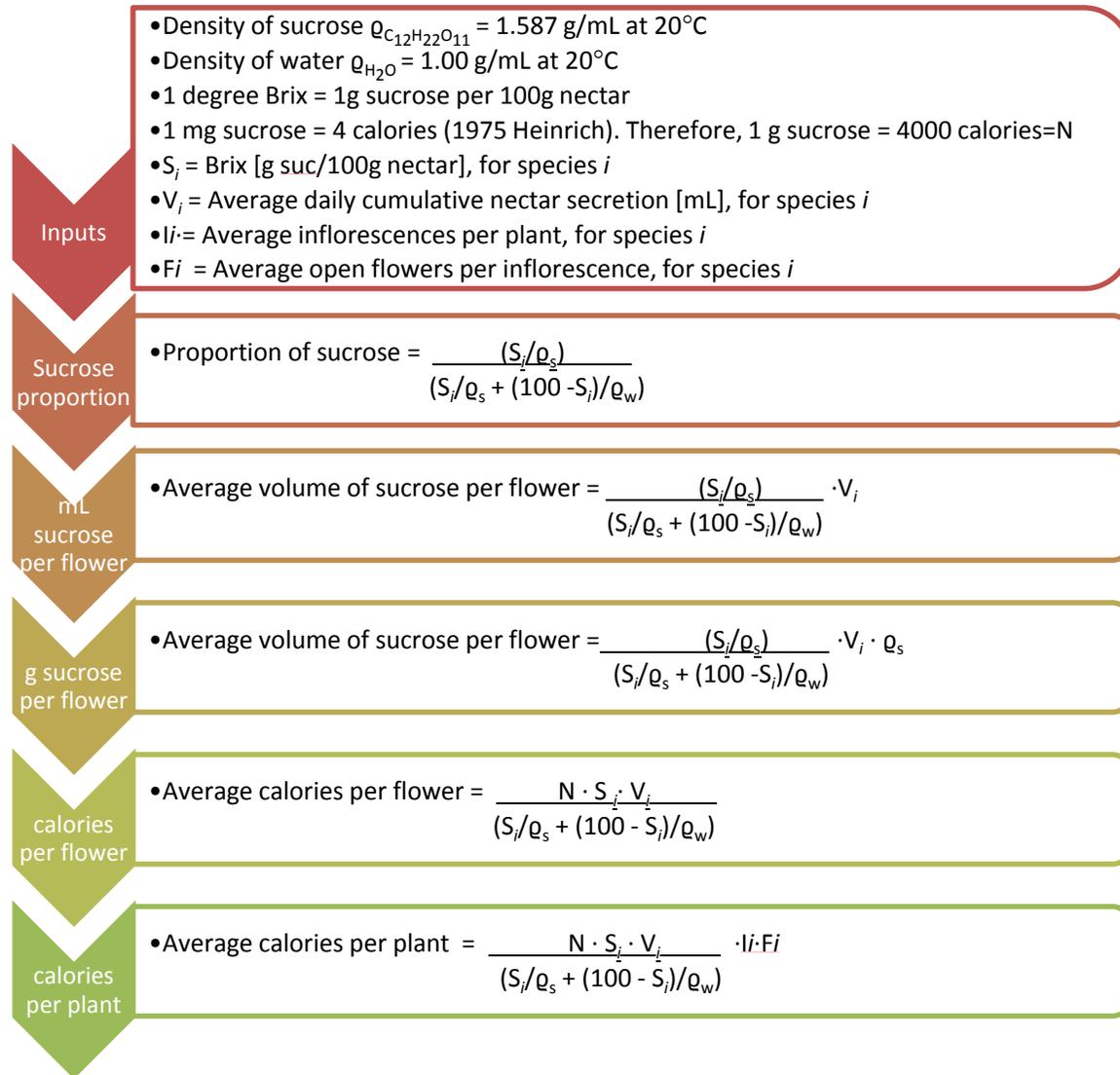


Appendix 1. Plant presence data superimposed upon elevation map. We sampled plant presence and abundances at a total of 5456 locations. At each of these locations, we counted all flowers within a 20 m radius.

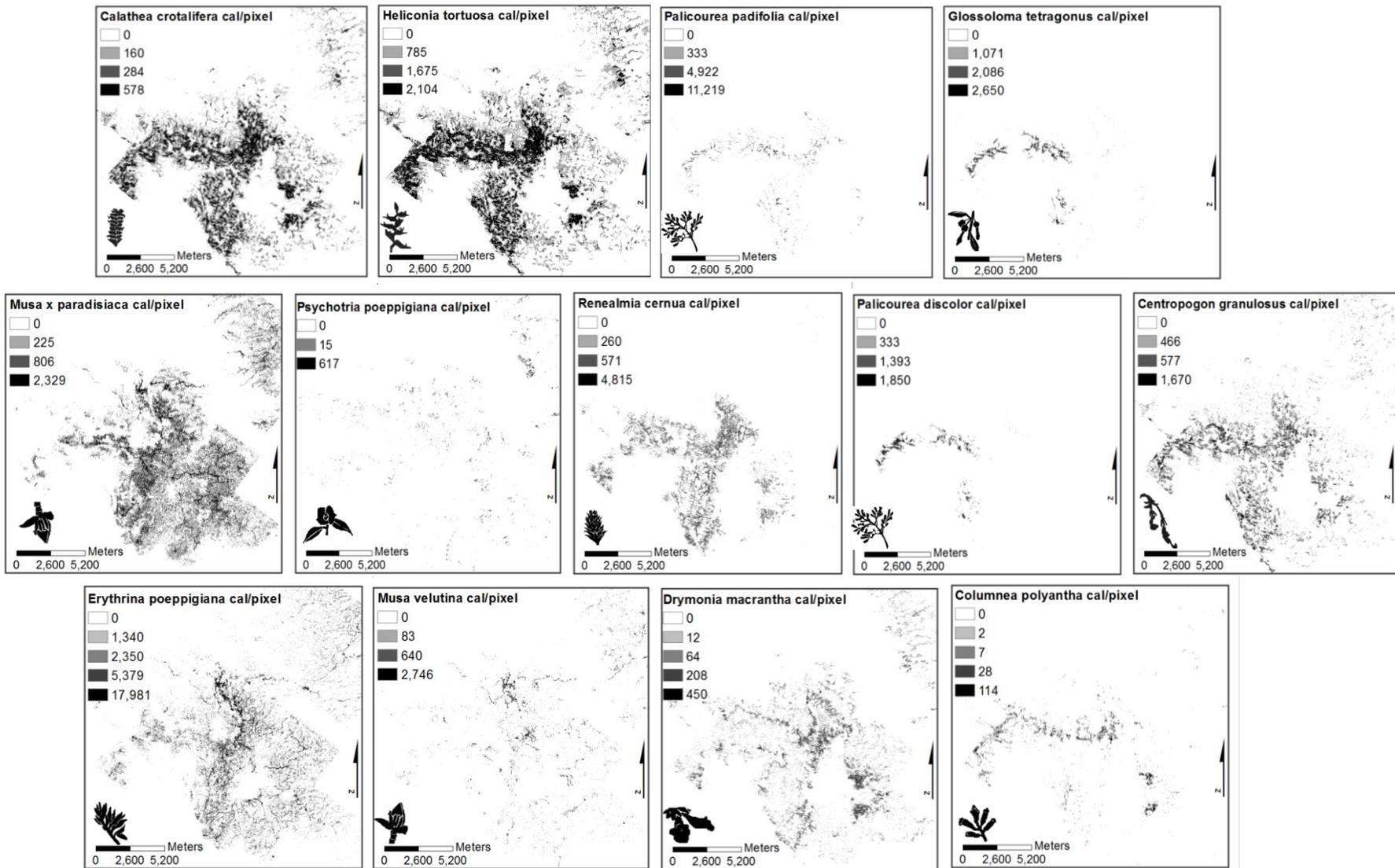
Species	Avg temp-corrected Brix (%)	Avg Brix st. dev (±%)	Sample size (Brix)	Avg volume (mL)	Avg volume st. dev (±mL)	Sample size (volume)	Avg cal per flower (lumped)	Avg cal per flower (individ)	Avg st. dev calories (individ)
<i>Calathea crotalifera</i>	29.73	5.14	22	0.0069	0.0032	16	9.18	9.33	4.55
<i>Heliconia tortuosa</i>	24.17	4.44	41	0.0789	0.0342	29	83.75	78.27	36.50
<i>Palicourea padifolia</i>	11.28	2.12	42	0.0271	0.0132	37	12.77	12.59	4.33
<i>Glossoloma tetragonus</i>	27.03	5.15	12	0.0414	0.0322	8	49.70	47.67	32.06
<i>Musa x paradisiaca</i>	14.45	3.78	16	0.0765	0.0955	2	46.70	30.08	35.38
<i>Psychotropa poeppigiana</i>	15.61	4.99	10	0.0067	0.0037	10	4.41	4.60	2.09
<i>Renalmia cernua</i>	24.65	2.59	5	0.0495	0.0177	7	53.70	44.27	32.24
<i>Palicourea discolor</i>	**11.28	**2.12	**	**0.0271	**0.0132	**	**12.77	**12.59	**4.33
<i>Centropogon granulatus</i>	26.15	3.82	19	0.0803	0.0758	5	93.00	101.08	93.23
<i>Erythrina poeppigiana</i>	*27.73	*2.79	*	*0.0323	*0.0029	*	*43.8	*43.8	*UNKN
<i>Musa velutina</i>	14.07	3.14	39	0.1051	0.1145	8	62.41	89.67	77.36
<i>Drymonia macrantha</i>	24.32	9.06	5	0.0263	0.0294	5	28.12	26.36	26.81
<i>Columnea polyantha</i>	29.77	1.26	14	0.0069	0.0049	14	9.18	12.79	2.94

*=derived from published values of *Erythrina* species in same genus (Neill, 1987); **=based upon gathered measurements of *Palicourea* species in same genus.

Appendix 2. Caloric summary. This table contains the summary caloric information for each plant species. Sample sizes for Brix and volume were different due to accidental dropping of the flowers when measuring nectar and nectar robbery that occurred despite bag presence. The lumped average calories per flower were calculated by first averaging the cumulative nectar and Brix for the species before inputting into the caloric estimator equation. The individual average calories per flowers were calculated for each sampled flower before averaging calories within the species. Figure 5 (section 2.3) depicts the lumped average calories across the landscape. Due to time constraints and the lengthy process required to generate each caloric map, it was not feasible to build the individual average map for this thesis.



Appendix 3. Derivation of caloric estimator equation. Ornithophilous flowers are dominated by sucrose (Percival, 1962). The remaining nectar content is primarily water. The average temperature when nectar was sampled was 20°C. We first calculated the proportion of sucrose in the nectar and applied it to the measured volume of nectar. We then converted this into weight of sucrose to estimate calories per flower. We then determined calories per plant through using the average open flowers per inflorescences, and the average



Appendix 4. Caloric map per individual plant species. These maps reflect the typical calories produced by each plant species in a day during the dry season (Jan-Mar) across the study landscape. The left-hand value legend quantifies the average cumulative calories output per 35m x 35m pixel. Note that the caloric value ramp for all species is not consistent across species.