THE EFFECTS OF TREE SIZE, NUTRIENT AVAILABILITY, INTERACTIONS WITH NEIGHBORS, AND MASTING SYNCHRONY ON FRUIT PRODUCTION IN TROPICAL AND TEMPERATE FORESTS

By

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ABSTRACT

THE EFFECTS OF TREE SIZE, NUTRIENT AVAILABILITY, INTERACTIONS WITH NEIGHBORS, AND MASTING SYNCHRONY ON FRUIT PRODUCTION IN TROPICAL AND TEMPERATE FORESTS

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Tree regeneration can be limited by the number of fruit produced by mature trees. Fruit production may influenced by tree size, soil nutrient availability, and competition with neighbors. In addition, synchronized reproduction in masting events may increase reproductive success of individuals. Differences in soil characteristics and biotic communities in tropical versus temperate regions may affect fruit production. Fruit production was individually measured for ∼3600 trees of 17 tropical species in La Selva, Costa Rica, and 10 temperate species in the Manistee National Forest, Michigan, USA. In both regions, tree size was the dominant influence on fruit production, with larger trees producing more. Soil nutrient availability had little effect on fruit production in both regions. In tropical species, the presence of larger neighboring trees reduced fruit production. This effect is consistent with competition for light, and may suggest that carbon balance is important for reproduction in these species.

In temperate species, I combined individual fruit production measurements with long term seed and seedling density data to assess the synchrony of individuals during masting events. In two species, *Acer saccharum* and *Fagus grandifolia*, I found that a small subset of individuals fruited more often and were responsible for a large proportion of fruit production in their populations. In contrast, in *Tila americana* different subsets of individuals were responsible for different masting events. These results highlight the importance of considering individual trees in studies of masting and environmental effects on reproduction.

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Chapter 1

Introduction

Tree reproduction has long-lasting effects on the forest community. Future canopy composition depends on the reproductive success of adult trees. Often, seedling recruitment is limited by seed availability, acting as a bottleneck to species' presence in the future forest community (Caspersen and Saprunoff 2005, De Steven and Wright 2002, Svenning and Wright 2005). Fruit abundance influences the animal community, affecting frugivore survival and causing cascading trophic effects which can influence human health (Wright et al. 1999, Milton et al. 2005, Ostfeld et al. 1996, Jensen et al. 2012).

Climate change and nitrogen deposition may alter tree species' reproduction in varied and unpredictable ways, and responses may differ between temperate and tropical forests (Ibanez et al. 2007, HilleRisLambers et al. 2009). By improving our understanding of individual reproduction in multiple species and biomes, we can better understand how the environment influences allocation to reproduction, and improve our ability to predict how global change will influence reproduction and the future of forest communities.

Fruit production occurs at the individual level and must be measured at this scale in order to answer certain questions (Żywiec et al. 2012, LaMontagne and Boutin 2007, Herrera 1998). Many tree species exhibit interannual masting cycles, where peaks in reproduction are synchronized for a population in a given year (Silvertown 1980, Kelly 1994, Kelly and Sork 2002). However, population cycles are the cumulative result of individual reproductive cycles, and the degree of synchrony can only be assessed with individual data. Individual measurements of reproduction are also necessary for understanding how environmental factors such as soil nutrient availability or competition from neighboring trees affect fruit production.

In many tree populations reproductive success is highly unequal among individuals, with a small portion of the population parenting most of the offspring (Moran and Clark 2012, Herrera and Jovani 2010, González-Martínez et al. 2006). Some of the disparity among individuals is due to tree size. Trees must reach a certain size before reaching reproductive maturity, which varies among species, even relative to their maximum size (Owens 1995, Thomas 1996b, Wright et al. 2005). The relative size at which species become mature may be related to other life history traits like shade tolerance, with fast-growing shade intolerant species reproducing earlier in their life than slower-growing shade tolerant species. After reaching a reproductive size, larger trees may be able to acquire and store more resources, leading to more fruit production (Greene and Johnson 1994, Snook et al. 2005, Han et al. 2008, Carbone et al. 2013). Although differences in size may account for some of the reproductive variation in a population, environmental factors such as nutrient availability and competition are also likely to affect fruit production.

The availability of soil nutrients may cause unequal fruit production among individuals (Satake and Bjørnstad 2008). The soil nutrients that limit fruit production may vary by species and location, with nitrogen typically being limiting in temperate forests and phosphorus in tropical forests (Vitousek and Howarth 1991b, Vitousek et al. 2010). However, this presumed difference between temperate and tropical forests may be over-emphasized. Nitrogen can increase fruit production in both temperate and tropical forests (Kaspari et al. 2008, Callahan et al. 2008, Lovett et al. 2013), and phosphorus is also important in temperate areas (Gradowski and Thomas 2008). In addition, there is increasing evidence for the importance of base cations such as calcium, magnesium and potassium for growth and reproduction in both regions (Gradowski and Thomas 2008, Kaspari et al. 2008, Holste 2010, Baribault et al. 2010; 2012). However, much of the previous research on nutrient limitation has focused on the population or community reproductive response, averaging across species and individuals. By measuring species separately, at the individual level, we can investigate differences in species nutrient requirements and how nutrient availability affects maturation and fecundity.

Competition from neighboring trees may restrict individual access to soil nutrients and light. Light availability tends to increase fruit production, likely because recently produced carbohydrates are used for reproduction (Greene et al. 2002, Ichie et al. 2013). Shading from larger neighbors may decrease the amount of fruit produced by an individual or delay maturation (Wright et al. 2005). The incorporation of competition extends the possible effects of resource limitation to biotic interactions.

In this thesis, I compared fruit production in tropical and temperate forests in two parallel studies. In both forest types, I investigated how fruit production is influenced by tree size, nutrient availability, and neighborhood competition at the individual level in common tree species. I used fruiting measurements across a natural range of soil nutrient availability to determine how these species varied in their reproductive nutrient requirements. Variation in forest community structure was used to assess how competition may decrease fruit production.

In Chapter 2, I examined the effects of environmental factors on fruit production in tropical trees. I also determined whether fruit production is associated with community composition. Greater conspecific density increases pollen availability and may increase fruit production in pollen-limited species (Knight et al. 2005). In Chapter 3, using long-term measurements of population seed availability in conjunction with individual measurements of fruit production, I examine fruit production and masting synchrony in temperate species.

The research presented in this thesis expands upon previous studies of tree reproduction by using individual measurements to examine nutrient limitation, rather than data collected at the population or community level. Ascertaining the effects that size, nutrient limitation, and competition have on fruit production can lead to increased understanding of the causes of reproductive inequality among individuals and better prediction of forest community regeneration.

Chapter 2

Fruit Production is Influenced by Tree Size and Size-asymmetric Competition in a Wet Tropical Forest

2.1 Abstract

In tropical forest communities seedling recruitment can be limited by the number of fruit produced by adults. Fruit production may be affected by physiological constraints, such as tree size; local environmental factors, such as soil nutrient availability; and biotic factors, such as competition. The number of fruit produced was observed for ∼2000 trees of 17 species across three years in a wet tropical forest in Costa Rica. Fruit production was modeled as a function of tree size, nutrient availability and neighborhood competition. In all species, larger trees were more likely to produce fruit, and more of it. In addition, fruit production was negatively related to presence of larger neighboring trees in 13 species. Soil nutrient availability (sum of base cations) was positively associated with fruit production in only two species. I also examined site-level effects, where average fruit production increased with conspecific basal area for two palm species. This pattern indicates a community constraint to individual fecundity and is consistent with pollen limitation. Nitrogen and phosphorus availability were positively related to fruit production in two species at the site level. Overall, these results suggest that direct influences on fruit production tend to be biotic, through tree size, competition from neighboring trees, or facilitation by pollination from conspecifics. Nutrient availability influenced fruit production little, but may operate indirectly through the dominant effect of tree size.

2.2 Introduction

Tree reproduction affects species composition of the forest understory, as well as future canopy composition, having long-lasting effects on the forest community. Regeneration is often limited by seed availability in tropical tree species, with the abundance of suitable sites for germination being greater than the number of seeds that reach these sites (De Steven and Wright 2002, Svenning and Wright 2005, Hubbell et al. 1999). Fruit is also a vital food source for frugivore populations in tropical forests, which often have high mortality rates during periods of low fruit production (Fleming et al. 1987, Wright et al. 1999, Milton et al. 2005). While fruit is necessary for survival of plant and animal populations, its production represents a major resource investment for trees (Bazzaz et al. 1987). Allocation to reproduction may reduce allocation to growth (Charlesworth and Morgan 1991). Allocation in response to environmental factors is particularly important to understanding carbon cycling in forests.

Fruit production by individual trees is influenced by multiple factors, including tree size, soil nutrient availability, and crowding from neighboring trees. Tree size affects reproductive output in at least two ways. First, a tree must reach a certain developmental stage or size before reaching reproductive maturity, although the size at which this stage occurs varies based on an individual's physiology and environment (Owens 1995). The size at which trees reach maturity also varies among species, even relative to their maximum size (Wright et al. 2005, Thomas 1996b). Second, after reaching maturity, larger trees are likely to produce more fruit (Greene and Johnson 1994, Snook et al. 2005), possibly due to greater access to resources (Carbone et al. 2013, Han et al. 2008). However, even among large, potentially reproductive individuals of the same species, reproduction tends to be very unequal, with most of the fruit being produced by a few individuals (González-Martínez et al. 2006, Herrera and Jovani 2010, Moran and Clark 2012). This variation among individuals indicates that there are additional factors that influence fruit production in trees.

Soil nutrient availability may limit fruit production in some species, and explain some intraspecific variability in fruit output. The effect of nutrients on fruit production has been extensively studied in crop species (Dordas 2006, Bishnoi et al. 2007, Burton et al. 2000), but less is known about nutrient requirements in naturally established forests. Fertilization with nitrogen (N) and phosphorus (P) increased reproductive litter in a tropical forest community, but it is unknown how these responses vary among species (Wright et al. 2011, Kaspari et al. 2008). In addition, high concentrations of N, P, and base cations (calcium (Ca), potassium (K) and magnesium (Mg)) in fruits (Chidumayo 1997, Pregitzer and Burton 1991, Karlsson and Örlander 2002) could indicate high demand for these nutrients by trees for fruit production, or may simply indicate high availability in the environment.

The surrounding forest community also could influence fruit production. Neighboring trees may cast shade and compete for soil nutrients (Baribault and Kobe 2011, Canham et al. 2006). Competition among neighbors may be size-asymmetric, with larger neighbors being stronger competitors, limiting the light and nutrients available to smaller trees for reproduction (Wright et al. 2005). In addition, pollination success may increase with greater conspecific density, subsequently increasing fruit set and production, and resulting in an Allee effect (Knight et al. 2005).

The goal of this study was to investigate how size, soil nutrients, and neighborhood crowding influence fruit production in tropical tree species. I estimated fruit production for 17 common species in a wet tropical forest. By measuring reproduction of trees across locations with a range of nutrient availability, I aimed to determine which nutrients limit reproduction in these species, and how competition among neighboring individuals interacts with nutrient limitations. I predict that for all species fruit production would 1) be positively correlated with tree size, 2) increase with nutrient availability, 3) decrease with greater neighborhood crowding, but 4) be positively correlated with stand density of conspecifics.

2.3 Methods

2.3.1 Study site

This study was conducted at La Selva Biological Station, Costa Rica (longitude, latitude). La Selva is located in a wet tropical forest, receiving approximately 4000 cm of precipitation annually. Fruit production measurements and soil samples were taken from five 41 m x 240 m plots which varied in N, P, and base cation availability. The large variation in soil characteristics at La Selva allowed me to sample areas with differing nutrient availability within a relatively small area. Three of these plots are located on older, lower-fertility, volcanic soils, and two are on younger, richer soils deposited by rivers (McDade and Hartshorn 1994). All trees 5 cm or greater in diameter at breast height (DBH) within each plot have been mapped and DBH was measured approximately annually.

2.3.2 Fruit production measurements

In order to get direct, individual-level estimates and to avoid potential confounding with animal predation, fruit production was estimated while fruit was still on the tree (Żywiec et al. 2012, LaMontagne and Boutin 2007, Herrera 1998). The majority of studies of tree fruit production utilize litter traps. This approach provides a population-level estimate of the number of fruit produced, but does not account for losses due to predation and requires modeling of dispersal or incorporating genetic data in order to detect intraspecific variation in reproductive output (Clark et al. 2010; 2004, Moran and Clark 2011). It was important to have measurements at the individual level in order to understand the factors controlling the amount of fruit produced.

At each plot, fruit production of 17 common canopy and subcanopy tree species was estimated for all mapped individuals. These species were chosen because there were at least 50 individuals of the species present across the five plots, for a total of approximately 2,200 trees (Table 1). I will refer to species by genus throughout the paper. Species tended to be well represented across their size range, although some species' size distributions were skewed toward an abundance of smaller individuals (Figure 1). Fruit production was estimated for each individual three times: September–November 2007, April–June 2008, and November 2009–May 2010. At each observation, the number of fruit was visually estimated and placed into one of six categories (Table 2). Visual estimates were made from the ground using binoculars with 10X magnification.

Categories were used instead of full counts in order to increase the speed of data collection. In order to assess the accuracy of this method, a more detailed count was performed in March 2010 on a subset of 675 individuals using a more powerful telescope (20X–60X magnification). This estimate was performed by counting the number of fruit on three reproductive branches dispersed throughout the crown. The average of these three counts was multiplied by the total number of reproductive branches on the tree to gain an estimate of the total number of fruit. These count estimates were compared to categorical estimates taken within two weeks of each other. The two estimates agreed for >80% of individuals and were positively correlated ($R = 0.53$ for all comparisons; $R = 0.71$ for 56 comparisons where both estimates were greater than zero), supporting the use of the much faster categorical method.

2.3.3 Soil resource measurements

Soil samples were taken at a relatively fine spatial scale at each plot. Three subsamples were taken from the upper 20 cm of soil and composited from each meter of a 200-m transect down the center of the plot. In addition, samples were taken in a lattice structure in the rest of the plot with 10 m spacing between samples (Holste 2010). Samples were measured for nitrate (NO_3^-), ammonium (NH_4^+), total extractable phosphorus (P), potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}). To estimate the potential nitrogen mineralization rate (NMin), nitrate and ammonium were also measured after 30-day incubations. NMin was used in the analyses here because it better represents nitrogen availability over time than NO_3^- or NH_4^+ (Pastor et al. 1984). Also, because K, Ca, and Mg availabilities strongly covaried, they were added and used in these analyses as the sum of base cation availability (SBC). Nutrient availability for each tree was calculated as a distance-weighted average of the five closest soil sample points, using the R package yaImpute (Crookston and Finley 2008).

2.3.4 Data analysis

Fruit production was modeled as a function of tree size, soil nutrients, and neighborhood crowding. The dataset was analyzed in three ways with different data subsets to test the effects of these factors. First, a binomial logistic regression was used to isolate which factors influence the probability of being reproductive in each species, ignoring variation in the amount of fruit produced. Second, including all individuals, I modeled fruit production in each species with a multinomial logistic regression. Third, a multinomial regression including only reproductive individuals (with fruit observed at least once during the study) was used to determine which of the factors measured are important for the amount of fruit produced following reproductive maturity. These models were fit in a hierarchical Bayesian framework (Clark et al. 2010; 2004), using R and WinBUGS statistical software (R Core Team 2013, Lunn et al. 2000).

2.3.5 Neighborhood competition index

Following Baribault and Kobe (2011) and Canham et al. (2006), the neighborhood competition index (NCI) was defined as:

$$\mathrm{NCI} = \sum_{i=1}^{n} (\mathrm{DBH}_i^{\alpha_j} \exp^{-\nu_j/\mathrm{dist}_i}) \tag{1}$$

where α and ν are random variables controlling the influence of neighbor DBH and distance to focal tree, respectively. Both of these variables were drawn from $\mathrm{Gamma}(1.0, 1.0)$ distributions. The effect is summed for $i = 1, \ldots, n$ neighbors within a 10-m radius of the focal tree. Two sets of neighbors were tested: 1) all trees within 10 m, and 2) only individuals that were larger DBH than the focal tree, in order to test for asymmetric neighborhood competition (ANCI). To keep the number of estimated variables manageable, α and ν were unique for each focal species j, but assumed to be equal for all neighbor species.

2.3.6 Binomial regression

I used binomial regression to characterize the probability of reproduction, as a function of tree size, nutrient availability, and neighborhood competition. If fruit production observations were >0 for an individual, its reproductive success was set to 1. Reproductive status of individual i of species j (R_{ij}) was distributed as:

$$R_{ij} \sim \mathrm{Bernoulli}(\pi_{ij}) \tag{2}$$

$$\operatorname{logit} \pi_{ij} = \boldsymbol{X'}_j \boldsymbol{\beta}_j + \epsilon_i \tag{3}$$

where π is the probability of being reproductive, $\boldsymbol{X}_j$ is the matrix of covariate values for individuals of species j, and $\boldsymbol{\beta}_j$ is a vector of species-specific coefficients drawn from:

$$\boldsymbol{\beta}_j \sim \text{MVNormal}(\boldsymbol{\mu}, \boldsymbol{\Sigma}) \tag{4}$$

Individual random effects were included such that: $\epsilon_i \sim \text{Normal}(0.0, \tau)$. Random variables μ, Σ, and τ were drawn from vague prior distributions. There was no effect of plot, so it was not included explicitly in the model.

Six alternative models were considered for reproductive status (Table 3). Models were fit via the Markov Chain Monte Carlo (MCMC) technique. The models were run for three chains of 50,000 iterations each, following a burn-in of at least 10,000 iterations to reach convergence based on Gelman and Rubin's convergence criterion (Gelman and Rubin 1992). Therefore, conclusions were drawn from a posterior distribution of $3 * 50,000 = 150,000$ samples. I compared models using deviance information criterion (DIC) and proper scoring rules. DIC is smaller for better fitting models and includes a penalty for additional parameters (Spiegelhalter et al. 2002). For an explanation of proper scoring rules, see the Appendix (Table 10).

2.3.7 Multinomial regression

Although the binomial regression can provide useful information about the factors that are associated with reproductive status, it does not reveal how these factors influence the quantity of fruit produced. Therefore, I used a multinomial regression. Because data were collected in ordered categories, I used an ordinal multinomial regression to investigate how tree size, nutrient availability, and neighborhood competition influenced the number of fruit.

Observations in some fruit production categories were rare so the categories were collapsed (see Table 2). Because trees reproduce in mast cycles, fruit output, F_{ij} was defined as the maximum fruiting category observed for each individual i of species j. This model was fit as an ordinal logistic regression such that:

$$F_{ij} \sim \text{Multinomial}(\pi_{ijk}) \tag{5}$$

$$\pi_{ijk} = Q_{ijk} - Q_{ijk-1} \tag{6}$$

$$\text{logit}\, Q_{ijk} = \gamma_k - (\boldsymbol{X'}_j \boldsymbol{\beta}_j + \epsilon_i) \tag{7}$$

where k is the fruit number category, π_k is the probability of producing k fruit, Q_k is the cumulative probability of producing k fruit, and γ_k is the cut point (or boundary) between categories k and $k+1$. A total of $K = 4$ categories were used, as described above, with $K - 1$ ordered cut points such that:

$$\gamma_1 = 0 < \gamma_2 < \gamma_3 \tag{8}$$

$\boldsymbol{\beta}$ and ϵ were given the same vague priors as in the binomial regression.

The same six alternative sets of covariates were considered for the multinomial regression as in the binomial model (Table 3). Alternative models were compared with DIC and proper scoring rules. The model was run for three chains of 100,000 iterations each, following a burn-in of at least 10,000 iterations to reach convergence based on Gelman and Rubin's convergence criterion (Gelman and Rubin 1992). Chains were thinned to every tenth iteration, so conclusions were drawn from a posterior distribution of $3 * 100,000/10 = 30,000$ samples.

The same multinomial model was used to examine fruit production in the subset of individuals that were reproductive. The same alternative sets of covariates were used (Table 3). I again compared models using DIC and proper scoring rules (Tables 11–12).

2.3.8 Plot level analysis

Because the effects of nutrient availability and crowding may operate at a coarser spatial scale than the individual tree, I also tested for plot-level trends in fruit production. For each plot p and species j, mean fruit production category ($\overline{F_{jp}}$) and mean reproductive status ($\overline{R_{jp}}$) were calculated. Simple linear regressions of $\overline{F_{jp}}$ and $\overline{R_{jp}}$ on plot-level NMin, P, SBC, and total conspecific basal area were considered for each species.

2.4 Results

Although fruit production was observed for all 17 species, many individuals did not produce any fruit (Table 1). *Virola* was excluded from analyses because only one individual of this species produced fruit during the study. Across all species, fruit production was observed in each category, with fruit production being more rare in higher categories (Figure 1), which may be partly attributed to the relative scarcity of larger individuals.

In all species, larger individuals were more likely to produce fruit, and more of it (Figures 2–3). However, the rate at which fruit production increased varied among species. For example, among the three canopy species *Goethalsia*, *Laetia*, and *Pentaclethra*, I saw a drastic difference in how rapidly fruit production increased with tree size (Figure 2). In *Goethalsia*, moderate levels of fruit production were rare; if an individual was reproductive, it was likely to be capable of producing more than 1,000 fruits. *Laetia* individuals were likely to become reproductive at a similar size as *Goethalsia* individuals, but had a larger size range where moderate levels of fruit production were likely. Finally, even large individuals of *Pentaclethra* produced relatively few fruit.

Competition from larger neighbors was negatively associated with fruit production. The number of fruit produced was negatively related to ANCI in 13 species, and inclusion of DBH and ANCI had the strongest support among the multinomial models (Table 11). Based on DIC, there was also support for the influence of competition from the total neighborhood (NCI) on the probability of fruiting and fruit production (Tables 10, 12), but this relationship was not statistically significant for any species.

In the plot level analysis, significant relationships between fruit production and community composition were most common in palm species (Arecaceae). Two palm species (*Cryosophila* and *Welfia*) showed positive relationships between conspecific basal area and both probability of fruiting ($\overline{R_{js}}$), and amount of fruit produced ($\overline{F_{jp}}$; Figure 4). These positive relationships may indicate pollination limitation in these species, or that these species generally perform better at certain sites leading to both higher densities and higher reproductive output. In addition, one palm species (*Euterpe*) had a negative relationship between $\overline{F_{jp}}$ and heterospecific basal area. There were also negative relationships between $\overline{R_{jp}}$ and heterospecific basal area in two canopy species: *Laetia* and the nitrogen-fixing *Pentaclethra*.

SBC had a positive relationship with fruit production in the subcanopy species *Prestoea* and *Rinorea*, suggesting base cation limitation. No other nutrients were associated with individual fruit production (see Appendix).

In contrast, I found that multiple nutrients were related to fruit production at the plot level, mostly affecting subcanopy species (Figures 12–17). *Coussarea* and *Faramea* had positive relationships between number of fruit ($\overline{F_{jp}}$) and NMin. In *Coussarea* only, NMin was also positively related to reproductive status ($\overline{R_{jp}}$). In Faramea only, P availability positively affected reproductive status and number of fruit produced. On the other hand, there was a negative relationship between reproductive status and NMin in the palm species *Euterpe*. In palm species *Iriartea* and *Socratea*, reproductive status and number of fruit were negatively related to SBC availability. Canopy nitrogen-fixer *Pentaclethra* had a negative relationship between reproductive status and P availability.

2.5 Discussion

The goal in this study was to determine if there was a relationship between resources in a tree's environment and fruit production. Species differences in reproductive requirements may influence their reproductive output, affecting seed availability and ultimately future forest composition. Trees also must split their resources between reproduction and growth (Primack and Kang 1989), so allocation priorities could affect forest carbon balance. Reproduction occurs at the individual level, so fruit production data collected at this level are necessary to assess how environmental factors affect allocation to fruit production.

Tree size was the primary predictor of individual fruit production in all species. Smaller trees are unable to reproduce until they reach a certain size, which depends on the species of the individual (Figure 3; Wright et al. 2005, Thomas 1996b). Larger trees may have a greater ability to acquire and store nutrients and carbohydrates, and they tend to produce more fruit (Figure 2; Han et al. 2008, Carbone et al. 2013, Greene and Johnson 1994). Even after accounting for this trend, reproduction tends to be unequal among conspecifics (Moran and Clark 2012, Herrera and Jovani 2010, González-Martínez et al. 2006), with many individuals not producing fruit at all (Figure 1).

The negative association between fruit production and the competition from larger neighbors, as opposed to all neighbors, may indicate that competition for light affects reproduction more than competition for soil resources. Carbohydrates which were recently produced from photosynthesis are important for fruit production (Ichie et al. 2013), and decreased light availability decreases fruit production (Greene et al. 2002, Wright et al. 2005). In contrast, competition negatively affected growth of individuals in only 3 out of 15 species examined at these same plots (Baribault et al. 2012), versus 13 out of 17 species for fruit production. If competition decreases fruit production, but not growth, there may be preferential allocation of carbohydrates to growth in these species. An important caveat is that the competition index in Baribault et al. (2012) included all neighbors instead of only larger neighbors, and a larger neighborhood area.

The effects of soil nutrients on fruit production varied among species. At the individual tree level, there were no significant relationships between number of fruit produced and nutrient availability. High spatial and temporal variability in fruit production can make it difficult to detect the effects of nutrient availability (Wright et al. 2011). However, base cations were positively associated with reproductive status at the individual tree scale in *Prestoea* and *Rinorea*. At the plot level, N and P availability was positively associated with fruit production for *Coussarea* and *Faramea*, suggesting that these nutrients may limit fruit production in these species, and that soil nutrient availability is important at a larger spatial range for some species. Adult trees may be less affected by fine scale variations in soil resources than seedlings and saplings due to a larger root network. In addition, the forest floor is composed of a network of mycorrhyzal fungi and fine roots, which provides soil nutrients to trees (Hertel et al. 2003). The extent of the root and mycorrhyzal fungal networks suggest that some species can access nutrients from a much greater surrounding area, potentially averaging nutrient availability over this area, and decreasing the apparent affect of nutrient availability in the few meters immediately surrounding the stem. This greater access to resources, mediated by tree size, may increase fruit production.

Similarly, larger trees may be averaging nutrient availability across time. Trees are able to store nutrients, and in some species storage of N or P may control interannual fruit production cycles (e.g. masting) (Han et al. 2011; 2008, Ichie and Nakagawa 2011). If soil nutrients are stored for use in periodic masting events, or if the amount of resources used by annual fruit production is small compared to the amount stored, fruit production may be decoupled from environmental nutrient availability.

Larger trees may have a larger storage capacity, contributing to the positive effect of tree size on fruit production. Alternatively, effects of tree size on fruit production may result indirectly from nutrient availability; i.e., larger trees grew to that size as a result of higher nutrient availability (e.g. Baribault et al. 2012), and because of their size are able to produce more fruit.

Although I did observe some direct influence of soil nutrient availability on fruit production, these effects occurred in relatively few species, and were inconsistent. Despite an apparent lack of influence of soil nutrient availability on fruit production, it seems unlikely to be completely unimportant. Plants invest on average more N in reproductive structures than any other structure (Bazzaz et al. 1987), and fertilization with N (Kaspari et al. 2008) or a suite of nutrients (Li et al. 2006) increases the biomass of reproductive structures in tropical forests. I surprisingly found some negative relationships of fruit production with soil nutrient availability, which may indicate that some species are less able to acquire nutrients for fruit production in high resource, competitive environments. Nutrient availability also could have an effect on fruit quality, which was not measured in this study. A trade-off between the number of fruit produced and the amount of nutrients invested in an individual fruit would allow trees in different nutrient environments to produce similar numbers of fruit by adjusting the fruit quality (Primack and Kang 1989, Venable 1992). Future research combining individual estimates of fruit production over time, and fertilization across a range of spatial scales may help to clarify how soil nutrient availability influences reproduction in tropical forests.

There were also broader scale community effects on individual tree fruit production, with fruit production increasing with conspecific basal area in two species. This pattern may be due to an unobserved factor which increases both survival and fruit production, but is also consistent with pollen limitation (Knight et al. 2005). A greater density of large, mature individuals increases the probability of pollination and subsequently fruit production. In this study, palm species may be especially affected by pollen limitation, accounting for both species for which this effect was observed. Both species are insect pollinated, which was not unique among the species studied (insects pollinate 15 out of the 17 species; Chazdon et al. 2003).

Despite accounting for physiological factors (tree size and nutrient availability) and community factors (neighborhood crowding and conspecific density), there was substantial uncertainty in predicting the reproductive status of an individual (Table 10). The contribution to overall seed availability is highly unequal among individuals, with many not producing fruit during the study (Figure 1). Even during mast fruiting events it is common for trees to not produce fruit, even among individuals of reproductive size (Herrera and Jovani 2010). Lack of reproduction may be due to insufficient nutrient storage by the tree (Han et al. 2008) or a trade-off with investment in growth (Charlesworth and Morgan 1991). The three-year timespan of this study, may not have included a mast year for all species. During a mast year, I would expect the peak in fruit production to make resource limitation more apparent than in other years. Without a longer time series of reproductive data, it is difficult to determine if this study included a peak in fruit production for all species. There are also many environmental and stochastic factors that influence the reproductive status of an individual tree, including liana competition/parasitism (Wright et al. 2005), tree health (Silvertown et al. 2001), weather events (Wright et al. 1999), and location within the species' geographical range (Hampe 2005, Garcia et al. 2000, Pigott and Huntley 1981). Although this pattern of unequal fruit production may be exaggerated by the short duration of this study relative to the lifetime of a tree, it may persist in the long term, with most individuals producing low or moderate amounts of fruit (Moran and Clark 2012, Herrera and Jovani 2010).

Although it is not surprising that larger trees are likely to produce more fruit, species differences in the size at which fruit production first occurs, and the rate at which fruit production increases, provide insight into how seed availability may vary over time. Greater nutrient availability may increase reproduction and seed availability in certain species (Kaspari et al. 2008, Callahan et al. 2008), but variability in fruit production makes this effect difficult to assess (Wright et al. 2011). However, competition for light and nutrients from larger trees can delay reproductive maturity (Wright et al. 2005), and decrease reproductive output of an individual. This delay in maturation may be caused by resource allocation to growth being prioritized over reproduction in some species, as competition has less influence on growth in these species (Baribault et al. 2012).

In many cases, seedling abundance of a species is limited by the number of seeds that reach the forest floor, with seedling recruitment being higher following greater fruit production (De Steven and Wright 2002, Turnbull et al. 2000). The number of seeds that reach suitable sites is limited by the number of fruit produced, dispersal ability, and seed predation (Svenning and Wright 2005, Hubbell et al. 1999). In species that quickly reach high levels of fruit production, reproductive individuals may have the advantage of greater numbers of offspring reaching suitable locations over their lifetime.

Chapter 3

Masting synchrony in northern hardwood forests: super-producers dominate population fruit production

3.1 Abstract

Peaks in fruit production via interannual masting cycles are a common phenomena in tree populations. Masting cycles require some level of synchronization in fruit production among individuals. The level of synchrony is largely unknown because most studies of masting measure fruit production at a population level, rather than for individuals. By measuring individual fruit production, I investigated the degree to which individuals were synchronized, and how much fruit each individual contributed to a mast event. Through direct canopy counts, I estimated the number of fruit produced by 1635 individuals of 10 temperate tree species across 4 years in northern lower Michigan. I also used a longterm dataset of seed and seedling density on the forest floor to place the individual tree data into a broader context of population mast cycles. Three species had mast events during the 4-year period of the study, in addition to some minor peaks in fruit production in these and other species. In *Acer saccharum* and *Fagus grandifolia*, which had multiple peaks in reproduction, a small subset of the population reproduced more often and was responsible for a large portion of the total number of fruit produced in the population. In *Tilia americana*, different subsets of individuals were responsible for multiple peaks in reproduction. This suggests that it is important to incorporate individual measures of fruit production when investigating mast cycles, as small subsets of trees may dominate population patterns. The large amount of variation in the number of fruit produced suggests that other environmental or biotic factors may be affecting tree reproduction. Larger trees tended to produce more fruit in all species and were more likely to be reproductively mature, although even large trees often produced zero or few fruit. There were no direct effects of nutrient availability or competition on fruit production. Although the cause is unclear, in some species a small number of trees dominate

the number of fruit produced and the frequency of mast cycles. By producing more fruit, more often than their conspecifics, these individuals increase their chance of successfully producing offspring over time.

3.2 Introduction

Tree reproduction has long-lasting effects on the forest community. Seedling recruitment is often limited by seed production, placing a bottleneck on the species available to make up the future canopy (Caspersen and Saprunoff 2005). Seed availability also affects animal population sizes, causing trophic cascades that can affect disease prevalence in humans (Ostfeld et al. 1996, Jensen et al. 2012). Tree regeneration may respond in unpredictable ways to climate change and nitrogen deposition, with responses varying by species (Ibanez et al. 2007, HilleRisLambers et al. 2009). Understanding fruit production in individual trees, and in the entire forest community, will improve our ability to predict how global change may influence reproduction and the forest community in the future.

Many temperate tree species have interannual cycles in fruit production (masting), with synchronized high fruit production across a population in certain years (Silvertown 1980, Kelly 1994, Kelly and Sork 2002). Drastic increases in fruit availability during mast years can increase seedling recruitment (Caspersen and Saprunoff 2005) and animal population sizes, causing trophic cascades that can affect disease prevalence in humans (Ostfeld et al. 1996, Jensen et al. 2012). Much of the research on fruit production in temperate tree species focuses on masting, and usually fruit production at the population scale (Herrera 1998, Monks and Kelly 2006). Although masting is a population-level phenomenon, reproduction occurs at the individual level.

Masting is the cumulative result of individual reproductive cycles. By definition, individual cycles must be synchronized to some extent for masting to occur. Fruit production is typically low between masting events, although some individuals may produce fruit out of sync with the rest of the population (LaMontagne and Boutin 2007, Koenig et al. 2003). Even if mast years are observed in a population, it is difficult to tell how synchronized individual trees actually are. Peaks in population-level reproduction could be caused by multiple scenarios, including:

1) Completely synchronized: all individuals produce large amounts of fruit in mast years and very little in non-mast years;
2) Somewhat synchronized: Majority of individuals reproduce together and a few individuals with high fruit output reproduce in other years;
3) Frequent fruiters: A few individuals with high fruit output consistently reproduce together, more frequently than the rest of the population;

The latter scenarios are possible because within a population the number of fruit produced tends to be highly unequal among individuals, with some individuals producing far more fruit than their conspecifics (Moran and Clark 2012, Herrera and Jovani 2010, González-Martínez et al. 2006). However, I do not know how well these high fruit producing trees are synchronized with the rest of the population. For this reason, I have used individual fruit production to assess synchrony in temperate tree populations, and to determine how individual variation in fruit production contributes to masting events.

Because variation in fruit production among individuals determines the extent of masting synchrony in a population, it is also important to understand the cause of this variation. Inequality in fruit production by individual trees may be influenced by several factors, including tree size, soil nutrient availability, and competition from neighboring trees. Size may have two effects on reproduction. First, there is a minimum size a tree must reach before it becomes reproductively mature (Owens 1995). This size threshold tends to vary among species, even relative to their maximum size (Thomas 1996b, Wright et al. 2005). Although trees continue to grow following maturation, after this point allocation is divided between growth and reproduction (Wesselingh et al. 1997). Second, once a tree is mature, the number of fruit produced may increase with size (Greene and Johnson 1994). Larger trees may have greater access to resources, and greater nutrient and carbohydrate storage capability (Carbone et al. 2013, Han et al. 2008).

Resources in the local environment may also limit fruit production (Satake and Bjørnstad 2008) In temperate forests, nitrogen (N) is typically considered to be the most important nutrient that limits growth and productivity (Vitousek and Howarth 1991a). Other nutrients that limit growth and potentially fruit production include phosphorus (P) and base cations such as calcium (Ca), potassium (K), and magnesium (Mg) (Vitousek et al. 2010, Baribault et al. 2010, Gradowski and Thomas 2008). Although fertilization has shown a positive relationship between nutrient availability and reproduction for some species (Lovett et al. 2013, Callahan et al. 2008, Drenovsky and Richards 2005), the strength of this relationship may vary based on site conditions and tree species (HilleRisLambers et al. 2009, Magill et al. 2000). In addition, neighboring trees may indirectly influence fruit production through competition for resources (Baribault and Kobe 2011, Canham et al. 2006). Larger neighbors may present stronger competition by casting shade and limiting nutrient uptake by smaller trees (Greene et al. 2002, Wright et al. 2005).

The goal of this study was to investigate how individual fruit production in temperate tree species contributes to masting events. Specifically, I assessed masting synchrony among individuals, and the effect of tree size, soil nutrient availability, and neighborhood competition on individual fecundity. I measured fruit production in 10 common species in a northern hardwood forest in Michigan, USA. I investigated how individual trees contribute to masting events using individual fruit production data in conjunction with longterm seed and seedling census data. By observing fruit production across a natural range of nutrient availability, and experimentally fertilizing, I determined how nutrients may influence reproduction in these species. I also used the variation in tree density across sites to assess how neighborhood crowding may inhibit fruit production. I predicted that more fruit would be produced in larger trees, with greater nutrient availability, and with lower competition.

3.3 Methods

3.3.1 Site description

This study was conducted at 12 sites in the Manistee National Forest in the lower peninsula of Michigan, USA. Each site was located in a mixed hardwood stand ranging from 80–100 years old (Host et al. 1988). These sites were located on a variety of glacial landforms, and have differences in soil fertility and forest community composition corresponding to the landform (Zak et al. 1989, Host and Pregitzer 1992). Soil fertility is lowest at outwash sites and highest at moraine sites, with N, Ca, and water availability increasing along this gradient (Baribault et al. 2010). I measured fruit production for 10 common species at these sites (Table 4). Community composition shifts along the fertility gradient, with the lowest fertility sites being dominated by *Quercus alba* and *Quercus velutina* and the highest fertility being dominated by *Acer saccharum.* Where possible, site dimensions were 41 m x 240 m. However, one site was split into two 41 m x 120 m areas and another was 21 m x 240 m. All trees greater than 10 cm in diameter at breast height (DBH) were mapped and measured for

DBH. Along the center axis of each site I established a 200 m x 1 m seedling transect, that was censused for newly germinated seedlings annually from 1998–2013. Positioned next to the seedling transect at 10 m intervals were 1 m x 1 m seed traps, which were collected annually from 2001–2012. Seeds were sorted by species and viability (based on seed development), and counted.

3.3.2 Fruit estimation

At each site, the number of fruit was estimated for all trees within a 41 m x 41 m area (21 m x 41 m at one site). For uncommon species, fruit production was estimated for all trees within the full 41 m x 240 m area in order to obtain a sufficient sample size. The number of fruit was estimated from direct counts in tree canopies because an estimate of pre-dispersal, pre-predation fruit production more accurately reflects a tree's resource investment. This method also obtains an estimate of individual fruit production, while avoiding the uncertainty associated with modeling dispersal to seed traps (Clark et al. 2010; 2004, Moran and Clark 2011). For each tree, fruit production was estimated by counting the number of fruit on each of three fruiting branches. Branches were chosen haphazardly, with an effort to disperse samples vertically in the crown when possible. Counting was done from the ground using a telescope with 20–60x magnification. All counts were performed by a single observer, in order to eliminate inter-observer variation (Chapman et al. 1992). The average number of fruit from these three branches was multiplied by the number of fruiting branches to obtain a whole tree estimate of fruit production. The number of fruit was estimated for each individual annually from 2008–2011 (2009–2011 for *A. rubrum* and *P. grandidentata*).

3.3.3 Soil nutrient measurements

Soil nutrient analyses were performed on composite samples, each consisting of three soil cores from each sampling location. Samples were taken from the central 200-m transect of each site in a lattice plus fill-in design (Diggle and Lophaven 2006), and from parallel transects located 5 and 15 m to either side of the central transect at 20-m intervals. Samples were analyzed for ammonium, nitrate, phosphorus, calcium, potassium, and magnesium concentrations. Potential net N mineralization (NMin) was measured through aerobic mineralization (see Baribault et al. 2010, for details). NMin was used in analyses to better estimate nitrogen availability over time (Pastor et al. 1984). Because of collinearity among them, calcium, potassium, and magnesium were combined as the sum of base cations (SBC) for analyses. To obtain nutrient availability estimates for each tree I used distance-weighted averages of each nutrient from the five nearest soil samples using the R package yaImpute (Crookston and Finley 2008).

3.3.4 Fertilization experiment

At 11 of the sites I also fertilized trees outside of the main plot area to determine if fruit production was limited by specific nutrients. The four most common species were fertilized (*Acer rubrum*, *Acer saccharum*, *Quercus alba*, and *Quercus rubra*). Approximately 100 individuals of each species were included, divided evenly among five treatments: control, N only, Ca only, N and Ca, and a complete nutrient treatment consisting of N, P, K, Ca, and micronutrients. Fertilizer was applied 2008–2011 in mid-May and mid-June within a 4-m radius around each tree (Table 5), and was effective at increasing nutrient availability (Baribault 2011). Fruit production was estimated 2009–2011 for all fertilized trees in the same way as the trees in the main plot. I tested for differences in the number of fruit produced among treatments using an analysis of covariance (ANCOVA), with DBH as a covariate.

3.3.5 Individual fruit production modeling

Fruit production was modeled as a combination of tree maturity and number of fruit produced. A hierarchical Bayesian approach was used so that my inferences could draw upon information from the entire community, while also ascertaining species differences (Clark et al. 2004). In all analyses, *Q. rubra* and *Q. velutina* were analyzed as one species. These two species commonly hybridize (Moran et al. 2012) and could not always be distinguished. Analyses were performed using the rstan package in R statistical software (R Core Team 2013, Stan Development Team 2013).

To model maturity each tree was assumed to have an underlying reproductive status, R_i, and an observed status r_i. R_i would be zero for individuals that are not yet reproductive, and one for mature individuals. Because the duration of this study was relatively short (4 years) relative to the longevity of the trees being studied, I assumed R_i did not change over the course of the study. If an individual could be identified as reproductive, either by observing fruit during the study or evidence of previous reproduction (e.g. the previous year's acorn caps still attached), it was classified as $r_i = 1$, otherwise, $r_i = 0$. The probability of maturity,

$$p(R_i) = \text{Bernoulli}(R_i|\pi_i) \tag{1}$$

increases with size. This relationship was represented as a logistic regression with diameter

(D_i):

$$r_i \sim \text{Bernoulli}(\pi_i) \tag{2}$$

$$\text{logit}(\pi_i) = \boldsymbol{D}_i' \boldsymbol{\alpha}_j \tag{3}$$

where $\boldsymbol{\alpha}_j$ was a vector of regression coefficients for species j.

$$\boldsymbol{\alpha}_j \sim \text{MVNormal}(\boldsymbol{\alpha}_\mu, \boldsymbol{\Sigma}_\alpha) \tag{4}$$

Random variables $\boldsymbol{\alpha}_\mu$ and $\boldsymbol{\Sigma}_\alpha$ were drawn from vague prior distributions.

Observed reproductive staus (r_i) may not exactly reflect the true status (R_i). While I can be confident that an individual was actually mature when $r_i = 1$ (i.e. there were no false positives), there is more uncertainty when $r_i = 0$. If no fruit production was observed, an individual may have truly been immature ($r_i = R_i = 0$). However, if fruit production occurred and was not observed due to detection error, or if a mature tree happened to not reproduce during the study, then the observed status would not reflect the true status ($r_i = 0, R_i = 1$). To incorporate this uncertainty into the model of number of fruit produced, estimated status, ρ_i, was defined as the probability of $R_1 = 1$ based on the value of r_1. When $r_1 = 0$, the estimated reproductive status (ρ_i) is based on a probability of maturity (π_i) rather than directly on the value of r_i.

$$\rho_i = p(R_i = 1 | r_i) = \begin{cases} 1 & r_i = 1 \\ \pi_i & r_i = 0 \end{cases} \tag{5}$$

Because the data were overdispersed and had a high frequency of zero fruit production, a zero-inflated negative binomial distribution was used (Martin et al. 2005, Joe and Zhu 2005). The zero-inflation parameter, δ_i was based on the estimated reproductive status:

$$\delta_i \sim \text{Bernoulli}(\rho_i) \tag{6}$$

The negative binomial regression was parameterized as a Poisson-gamma mixture:

$$F_i \sim \text{Poisson}(\delta_i \eta_i e^{\boldsymbol{X'}_i \boldsymbol{\beta}_j}) \tag{7}$$

where F_i was the maximum number of fruit produced by tree i. Maximum number of fruit was used in order to represent the maximum investment capable by an individual. I also tested the average number of fruit produced by an individual, which had similar results to the maximum. Random variables in Equation 7 were η_i, the gamma-distributed error; $\boldsymbol{X}_i$, the vector of covariates; and $\boldsymbol{\beta}_j$, the vector of regression coefficients for species j drawn from

$$\boldsymbol{\beta}_j \sim \text{MVNormal}(\boldsymbol{\beta}_\mu, \boldsymbol{\Sigma}_\beta) \tag{8}$$

Random variables $\boldsymbol{\beta}_\mu$, $\boldsymbol{\Sigma}_\beta$, and η_i were drawn from vague prior distributions.

Three alternate sets of covariates were tested for the regression in Equation 7 (see Table 6): Covariates included DBH, soil nutrient availability, and neighborhood competition index (NCI). Following Baribault and Kobe (2011), NCI was defined as:

$$\text{NCI}_i = \sum_{k=1}^{n} (\text{DBH}_k^{\gamma_j} \exp^{-1/\text{dist}_k}) \tag{9}$$

where γ is a random variable controlling the influence of neighbor DBH, and was drawn from a Gamma$(1.0, 1.0)$ distribution. The effect is summed for $k = 1, \ldots, n$ neighbors within a 10-m radius of the focal tree, including only neighbors with a larger DBH than the focal tree. For approximately 10% of individuals, the 10-m neighborhood was not completely mapped. Therefore, an estimated NCI (ENCI) was drawn from a normal distribution, with NCI of the known area as the mean, and variance as a function of the proportion of the area known (p_i).

$$\mathrm{ENCI}_i \sim N(\mathrm{NCI}_i, e^{\eta - \nu * p_i}) \tag{10}$$

For individuals with the complete neighborhood known, the variance is small, and grows larger as the known proportion shrinks. The parameters η and ν are random variables with vague priors. Each alternative model was run for 4 chains of 2000 iterations, following a 2000 iteration burn-in. All parameters reached convergence based on Gelman and Rubin's convergence criterion (Gelman and Rubin 1992). Alternative sets of parameters were compared using Akaike Information Criterion (AIC; Burnham and Anderson 2002).

3.3.6 Relative size at onset of maturity

The binomial portion of the zero-inflated regression described above was used to define a reproductive diameter threshold (D_{thres}), at which the probability of being reproductively mature was 0.5 (Figure 5). D_{thres} varied among species, but this could be due to differences in the maximum size of species. Because tree height growth reaches a limit more so than diameter growth, I used height to calculate the relative size at onset of maturity for each species ($RSOM$) (Thomas 1996b). First, an allometric function was fit using diameter and height measurements of all individuals in the population (Thomas 1996a).

$$H = H_{max}(1 - e^{-aD^{b}}) \tag{11}$$

H and D were height and diameter, respectively. H_{max} was the asymptotic maximum height for the species, and a and b were random variables. This function was then used to compute H_{thres} from D_{thres}, and RSOM = H_{thres}/H_{max}.

3.3.7 Synchrony in masting cycles

To understand individual fruit production in the context of population mast cycles, I used long-term seed trap and seedling census data. *Populus grandidentata* was not included in this analysis because no seeds or seedlings were found of this species during the study period. To check for consistency among these three data sources, I correlated direct fruit observations with newly germinated seedling and viable seed density in the 4 year period for which all data sources were available, accounting for a time lag in seedling density relative to fruit counts and seed density. The time lag was 0, 1, or 2 years based on which lag maximized Pearson's r in a correlation between seed and seedling density in each species. I expected most species to have a 1-year lag, but seeds could remain in the seed bank for multiple years.

Because mast years require high allocation of resources to fruit production, and trees are more likely to produce near their maximum capacity, the effects of nutrient limitation should be most apparent during a mast year. I used the long-term seed density time series to determine when mast years had occurred for each species, and if they coincided with the four year window of direct fruit counts used in the model above. Mast years were determined based on standardized deviates from the long-term mean seed density. The annual deviate of seed density was the deviation from the longterm mean seed density divided by the standard deviation of seed density (LaMontagne and Boutin 2009). Any years for which the annual deviate was greater than the absolute value of the minimum annual deviate was designated as a mast year.

The occurrence of a mast year at the population level does not imply that all individuals produced fruit in that year. Synchrony among individuals across the 4 years of direct fruit counts was measured using Spearman's rank correlation (Żywiec et al. 2012, Buonaccorsi et al. 2001). The mean of all pairwise correlations among individuals that reproduced at least once was used to calculate the mean synchrony for each species (ρ_s). For example, 56 *Acer saccharum* individuals produced fruit during the study. The amount of fruit produced by a given tree in each year was individually correlated with the amount produced by each other tree, for a total of 1540 combinations. The mean of all 1540 correlation coefficients was taken to produce ρ_s. Spearman's correlation was used because the data were not normally distributed. I also calculated the percentage of each reproductive population that produced fruit in each year, and how much these individuals contributed to total fruit produced in the reproductive population. The reproductive population was defined as all individuals greater in size than the reproductive size threshold (D_{thresh}) for each species, which accounted for $\geq 90\%$ of the fruit produced in each species.

3.4 Results

Larger trees were more likely to produce fruit (Figure 5) in seven out of nine species; larger trees also produced more fruit in all species (Figure 6). In *P. grandidentata* and *F. americana*, the failure to detect a relationship between probability of producing fruit and tree size was probably due to the under-representation of smaller trees in the dataset. Consistent with other forest communities, relative size at onset of maturity (RSOM: height at first reproduction / maximum height) varied among species (Figure 7, Thomas 1996b, Wright et al. 2005), although there was no obvious pattern to this variation, such a connection to life history strategy. No evidence of direct effects of soil nutrients or neighborhood competition on fruit production were found, and these factors were not included in the best model (Table 6). In addition, there was no effect of fertilization treatment on number of fruit produced (*A. rubrum*: $F = 0.8, p = 0.5$; *A. saccharum*: $F = 0.6, p = 0.7$; *Q. alba*: $F = 1.0, p = 0.4$; *Q. rubra*: $F = 0.9, p = 0.5$). However, a longer time period may be required for a fertilization effect to be observed in mature trees.

In the longterm dataset, there was a 1-year time lag between the number of seeds produced and number of newly germinated seedlings, with the exception of *F. americana* which had a 2-year lag (Table 7). Low correlations between seed and seedling density in some species suggest a low germination rate, high seed predation, or that seeds are remaining in the seed bank for a longer time period. The average annual fruit production from canopy counts in 2008–2011 corresponded well to density of seeds and seedlings found at each site, with the number of seeds having a stronger correlation (Table 8). In the longer time series dataset for seed density (2001–2011), *A. saccharum*, *F. americana*, and *T. americana* experienced a mast year during the four years of canopy counts (Figure 8). In addition, *F. grandifolia*, *P. serotina*, and *Q. rubra/velutina* had at least a moderate (minor mast) fruit production year.

Synchronization also varied among species. Based on Spearman's rank correlation (ρ_s), synchrony was low in *A. rubrum*, *P. grandidentata*, and *Q. rubra/velutina*; moderate in *F. grandifolia*, *P. serotina*, *Q. alba*, and *T. americana*; and high in *A. saccharum*, and

F. americana (Table 9). In *A. rubrum* and *F. americana*, very few individuals produced fruit in non-mast years. In *A. saccharum*, *F. grandifolia*, *P. serotina*, and *T. americana*, there were years with zero or near-zero fruit production, but also minor mast years when 10–18% of reproductively mature individuals produced fruit.

In the three species that had both a mast year and a minor mast year, or two minor mast years (*A. saccharum*, *F. grandifolia*, and *T. americana*), 3–8% of the population reproduced in both years (Figure 9). In *A. saccharum* and *F. grandifolia* the individuals that reproduced in both mast years account for approximately 40–70% of fruit produced in a single event, suggesting that a small subset of individuals are responsible for a large proportion of the fruit production in these populations. In *A. saccharum*, this subset included the largest tree measured, which by itself accounted for 20% of the fruit produced in the 2008 mast year. The other high fruit producing *A. saccharum* trees were not extraordinarily large, but the high fruit producing *F. grandifolia* trees were all in the 80th percentile for size in this species. The highly reproductive trees in both of these species did not have extraordinarily high nutrient availability or low neighborhood index. On the other hand, the *T. americana* individual that reproduced in both events accounted for <10% of the fruit produced in a given event, suggesting that in this species different subsets of trees are likely to be reproductive in different events.

3.5 Discussion

Tree size was the key factor for predicting individual fruit production in most of the nine species sampled in this study, and the probability of an individual being reproductively mature increased with size. Species varied in relative size at the onset of maturity (RSOM), possibly indicating different allocation strategies among species, although there was no obvious connection to life history traits, such as shade tolerance. A smaller RSOM allows trees to reproduce for a longer portion of their life, but if there is a trade-off between growth and reproduction (Charlesworth and Morgan 1991), then becoming mature at a small size may be at the expense of lifetime growth rate (Wright et al. 2005, Thomas 1996b, Wesselingh et al. 1997). However, in high resource environments, individuals may be able to allocate to both growth and reproduction (Moran and Clark 2012).

Highly unequal reproduction among individuals is typical for many tree species (Moran and Clark 2012, Herrera and Jovani 2010, González-Martínez et al. 2006), and this variation suggests that environmental factors influence individual fruit production.Fruit production requires a large investment of carbohydrate and mineral nutrients. Plants invest more nitrogen in reproductive parts than any other structure (Bazzaz et al. 1987). Therefore, it is surprising that I found no effect of the availability of nitrogen or other soil nutrients on fruit production, neither across a natural soil nutrient gradient, nor following experimental fertilization. Nitrogen fertilization has previously increased seed production in multiple temperate species (Lovett et al. 2013, Callahan et al. 2008). A longer time period of fertilization may be necessary before a fruit production response can be observed. Also, none of the four species which were part of the fertilizer experiment were observed during a mast year, when nutrient limitation may be more apparent. Alternatively, previous studies which have observed an increase in seed production following fertilization have quantified seed biomass rather than number, possibly combining changes in fruit quantity and quality into one effect.

Although I found no direct effects of soil nutrient availability on fruit production, there may have been unobserved indirect effects mediated through tree size. Tree growth is influenced by nitrogen and base cation availability (Baribault et al. 2010), so larger trees may have grown to that size because of the locally available soil nutrients, eventually translating into greater fruit production. Additionally, large trees may have a greater capacity to store nutrients (Han et al. 2008), allowing them to produce more fruit.

Carbohydrates are also heavily invested in reproduction, so increased light availability would be expected to increase fruit production (Ichie et al. 2013, Greene et al. 2002, Wright et al. 2005), but I found no evidence of a negative effect of competition from larger neighboring trees. This is in contrast to findings in some tropical species, which had a negative fruit production response to asymmetric competition (See Chapter 2). Competition may be more intense in tropical forests, or fruit production may be a lower priority for tropical species when light is limiting. Also, productivity at these temperate sites is negatively related to competition (Baribault and Kobe 2011), suggesting that resource allocation to reproduction may be higher priority than growth. However, the high variability in fruit production across years and individuals makes it difficult to compare with growth over the relatively short time period in this study. The lack of evidence for resource limitation from soil nutrients or carbohydrates may indicate that other factors such as disease, insect attack, or genetics may explain some of the reproductive inequality among individuals.

Species differed in the extent to which variation in individual reproduction contributed to masting. Some species were almost completely synchronized, with very little fruit production occurring outside of mast years. Other species had minor mast years in addition to full mast years. The minor mast years were due to a subset of individuals reproducing more often than their conspecifics, or by different groups of trees reproducing in different years. Consistent with other studies, not more than 40% of the reproductive-size trees in a population reproduced in a given mast year, and very few contributed to multiple peak reproduction years (Żywiec et al. 2012).

The lack of synchrony in *T. americana* and unequal fruit production among individuals in *A. saccharum* and *F. grandifolia* could have consequences for reproductive success at both the population and individual level. One of the possible benefits of masting is predator satiation (Kelly 1994). This benefit relies on seed predator populations being reduced in non-mast years, and producing more seeds than the predator population can consume in mast years. If different subsets of the population reproduce in consecutive years (as in *T. americana*), a large predator population could be maintained. Fruits produced by individuals in the second year may be completely consumed, and if this pattern continued the reproductive success of the entire tree population could decrease (Żywiec et al. 2012). Similarly, if an individual tree reproduces out of sync with the rest of the rest of the population, its seeds may be consumed, reducing its reproductive success. However, if peak years are intermittent (as in *A. saccharum* and *F. grandifolia*), and there is a subset of the population which produces more often and makes a disproportionately large amount of fruit, then these super-producers will have higher relative fitness without sacrificing the reproductive success of the population.

If the reproductive inequality observed in all species (Figure 6 persists, it may influence future forest composition. In some tree species, seedling recruitment is limited by the number of seeds (Caspersen and Saprunoff 2005), and if seeds are only consistently produced by a few individuals (Table 9, Figure 8), then spatial heterogeneity of seed availability may be high (Moran and Clark 2012). This could lead to greater seedling competition and mortality near highly reproductive individuals, decreasing their reproductive success relative to the number of seeds they produce (Venable 1992, Moran and Clark 2012). In addition, there may be a trade-off between number of fruit produced and the quality of fruit, reducing germination rates in fruits from highly reproductive individuals (Primack and Kang 1989). Although fruit production and seed availability tend to be positively correlated with seedling germination and establishment (Venable 1992, González-Martínez et al. 2006, Moran and Clark 2012), successful transition from fruit to established seedling is uncertain due to the high mortality at this life stage. Although I have been able to examine the reproductive efforts of individual trees by estimating individual fruit production, in order to get a full picture of the reproductive success of individuals, and the resulting changes in the forest community, established seedlings or saplings must also be observed (Moran and Clark 2012).

In conclusion, individual measurements provide key insights into tree reproduction that would have been obscured by population level sampling. I was able to detect differences in maturation schedules among species and determine that reproduction is highly unequal within populations. By combining individual and population data, I was able to examine how synchrony among individuals contributes to masting, revealing that in some species there may be individual cycles that are not apparent at the population level due to a lack of synchronization among individuals across years. Individual trees that produce more fruit more often may have greater lifetime reproductive success and greatly influence the surrounding forest community.

Chapter 4

Conclusion

4.1 Conclusion

Future forest composition depends on the reproductive success of individual trees, and seedling recruitment is often limited by seed availability (Caspersen and Saprunoff 2005, De Steven and Wright 2002, Svenning and Wright 2005). Allocation to fruit production may be limited by different resources in temperate and tropical forest species (Greene et al. 2002, Kaspari et al. 2008, Callahan et al. 2008, Lovett et al. 2013, Ichie et al. 2013). The goal of the studies in this thesis was to gain a better understanding of how tree size, nutrient availability, and competition affect an individual tree's production of fruit.

Among both tropical and temperate species, there was a consistent positive effect of tree size on maturation and fruit production. The size at which trees became reproductive differed among species in both tropical and temperate forests (Thomas 1996b, Wright et al. 2005). In temperate species, the relative size of maturation also varied among species. The relative size at which species become mature may reflect species differences in allocation to growth versus reproduction, but was not related to shade tolerance. Future research is necessary to determine if relative size at the onset of maturity is consistently related to other life history traits.

Among reproductive individuals, the distribution of fruit production was skewed. Consistent with previous studies, most of the fruit was produced by a small number of individuals, while many trees produces few or no fruits (Moran and Clark 2012, LaMontagne and Boutin 2007, Herrera 1998). In addition, some highly reproductive individuals in temperate species reproduce more frequently than the rest of the population (Żywiec et al. 2012). These individuals produce a large portion of the fruit in the population, dominating population reproductive cycles, and underscoring the importance of individual measurements for assessing synchrony. This inequality in fruit production among individuals may cause spatial heterogeneity in seed arrival and seedling recruitment in the environment, leading to increased competition among seedlings (Moran and Clark 2012).

Nutrient availability had less influence on fruit production than expected. Soil nutrients had no association with fruit production in temperate species, and varied effects in tropical species. Reproduction in four tropical species was affected by nutrients, with different species being limited by nitrogen, phosphorus, and base cations. The relative lack of effects of soil nutrients and consistent effect of tree size may be caused by soil nutrients acting indirectly through tree size. Large trees may have grown to their present size because of greater access to nutrients, and larger trees may be able to acquire and store more nutrients (Han et al. 2008, Baribault et al. 2010; 2012).

The influence of competition on fruit production was the starkest difference between temperate and tropical species. The number of fruit produced was negatively associated with neighborhood competition in the majority of tropical species and none of the temperate species. This may suggest that biotic interactions are more intense in the tropics, leading to a greater response to competition. Alternatively, tropical and temperate species may differ in allocation priorities. In some temperate species competition negatively affects growth, while there is a lack of competitive influence on growth in tropical species (Baribault and Kobe 2011, Baribault et al. 2012). This may indicate that resources tend to be preferentially allocated to reproduction in temperate species and growth in tropical species. However, a study directly comparing fruit production and growth in relation to competition and local resource environment is necessary to confirm this trend.

This study of reproduction in a broad set of species across tropical and temperate forest types demonstrated that soil nutrients may have less direct effect on fruit production than previously thought, but that tree size and competition influence maturation and the number of fruit produced. Individual differences in fruit production and reproductive cycles demonstrate the importance of individual measurements in order to determine population synchrony, environmental effects on reproduction, and the source of seeds in a population.

APPENDICES

Appendix A

Tables and figures for Chapter 2

Table 1: **Study species at La Selva, Costa Rica.** For each speces, the number of individuals measured and the number of individuals which were observed fruiting at least once during the study.

Species	Family	No. trees	No. observed fruiting
Capparis pittieri	Capparaceae	74	48
Casearia arborea	Salicaceae	206	123
Coussarea hondensis	Rubiaceae	65	28
Cryosophila warscewiczii	Arecaceae	114	41
Dendropanax arboreus	Araliaceae	60	5
Euterpe precatoria	Arecaceae	57	16
Faramea parvibractea	Rubiaceae	85	30
Goethalsia meiantha	Malvaceae	55	30
Iriartea deltoidea	Arecaceae	374	32
Laetia procera	Salicaceae	48	19
Pentaclethra macroloba	Fabaceae	367	188
Prestoea decurrens	Arecaceae	112	44
Rinorea deflexiflora	Violaceae	99	42
Socratea exorrhiza	Arecaceae	198	40
Virola sebifera	Myristicaceae	51	1
Warszewiczia coccinea	Rubiaceae	86	18
Welfia regia	Arecaceae	173	76
Total		2173	780

Table 2: **Fruit production categories.** The range of number of fruit present on a tree in each category. Six categories were used in field observations, but were collapsed to four categories for data analysis.

Category	Observed range	Collapsed range
1	0	0
2	1–10	1–100
3	11–100	101–1,000
4	101–1,000	>1,000
5	1,001–10,000	
6	>10,000	

Table 3: **Model evaluation.** Evaluation of the alternative models for the binomial regression (Binom), multinomial regression fit to all individuals (AMulti), and multinomial regression fit to reproductive individuals (RMulti). For each model, DIC is reported. Smaller values of DIC indicate better model fit.

		DIC	
Covariates	Binom	AMulti	RMulti
Intercept only	2419	3489	993
DBH	1703	2749	936
DBH+ soil	1705	2755	929
DBH + NCI	1670	2728	**884**
DBH + ANCI	1674	**2718**	900
DBH + soil + NCI	**1659**	2738	888
DBH + soil + ANCI	1679	2732	910

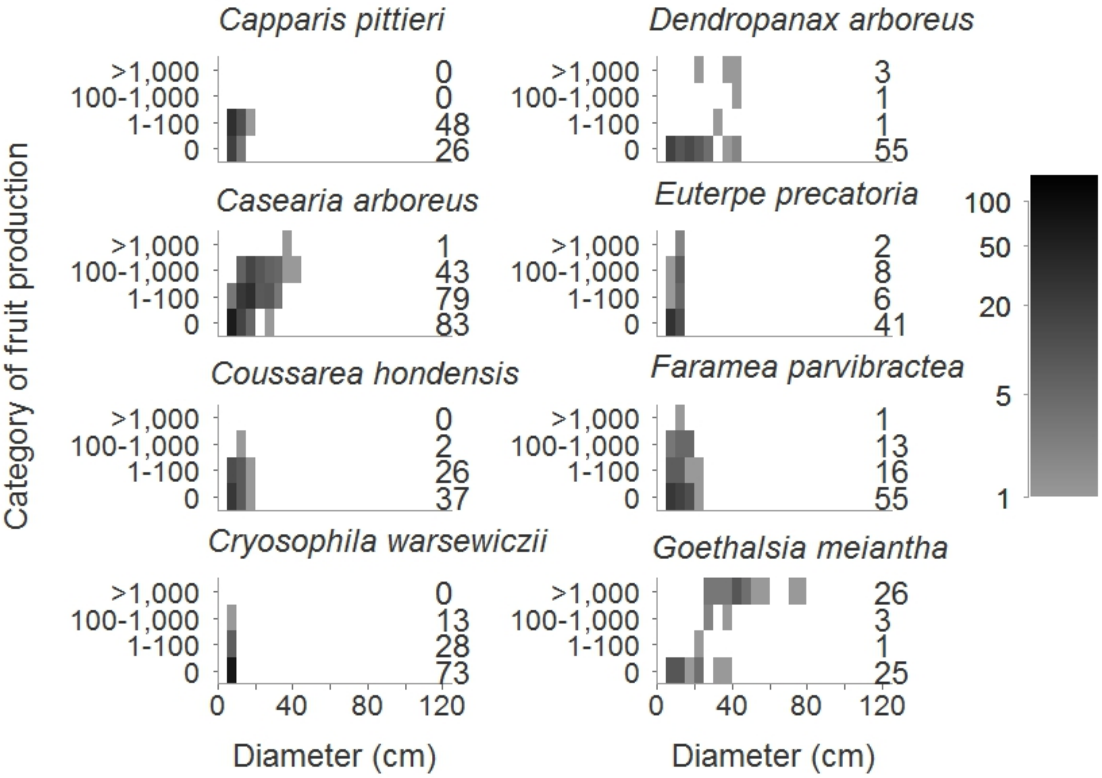
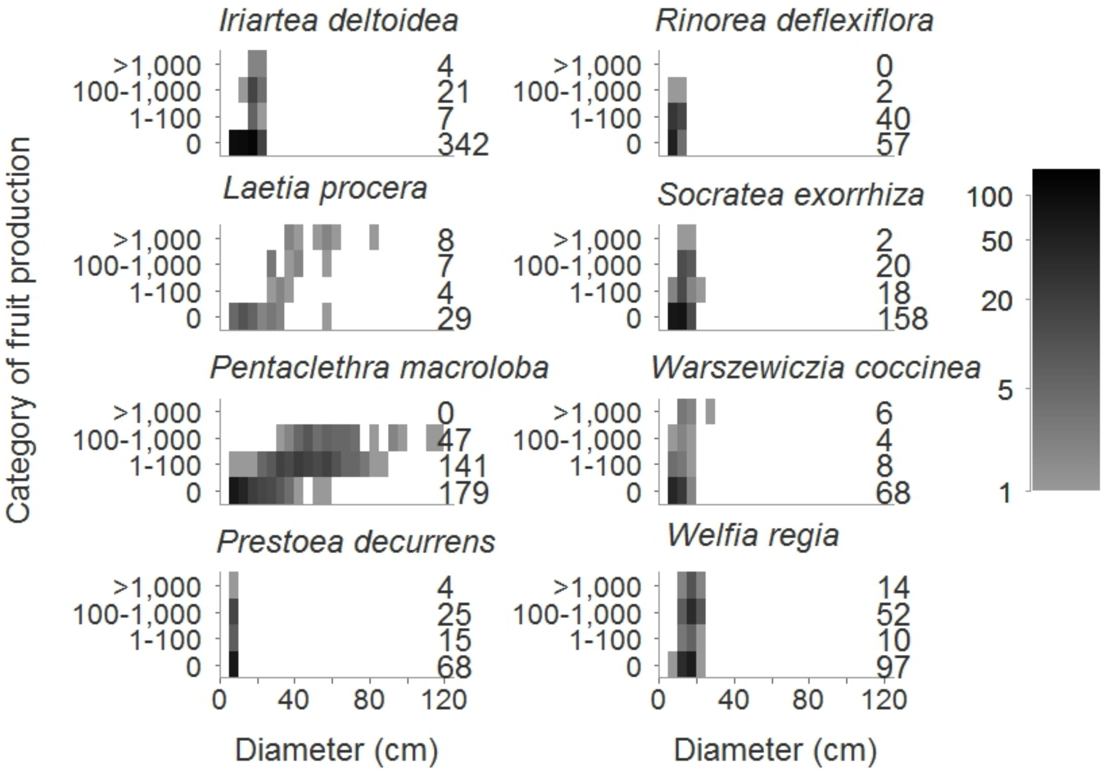


Figure 1: **2-dimensional histogram of fruit production, divided by category and DBH.** Number of trees in each fruit production category (vertical axis) for each species divided into 5-cm DBH classes. Categories are 1: 0 fruit, 2: 1–100 fruits, 3: 101–1,000 fruits, and 4: >1,000 fruits. Total number of individuals in each size class are to the right of each graph. This figure shows the size range for each species, how many individuals were in each fruiting category, and the size distribution for the individuals in each category.

Figure 1 (cont'd)



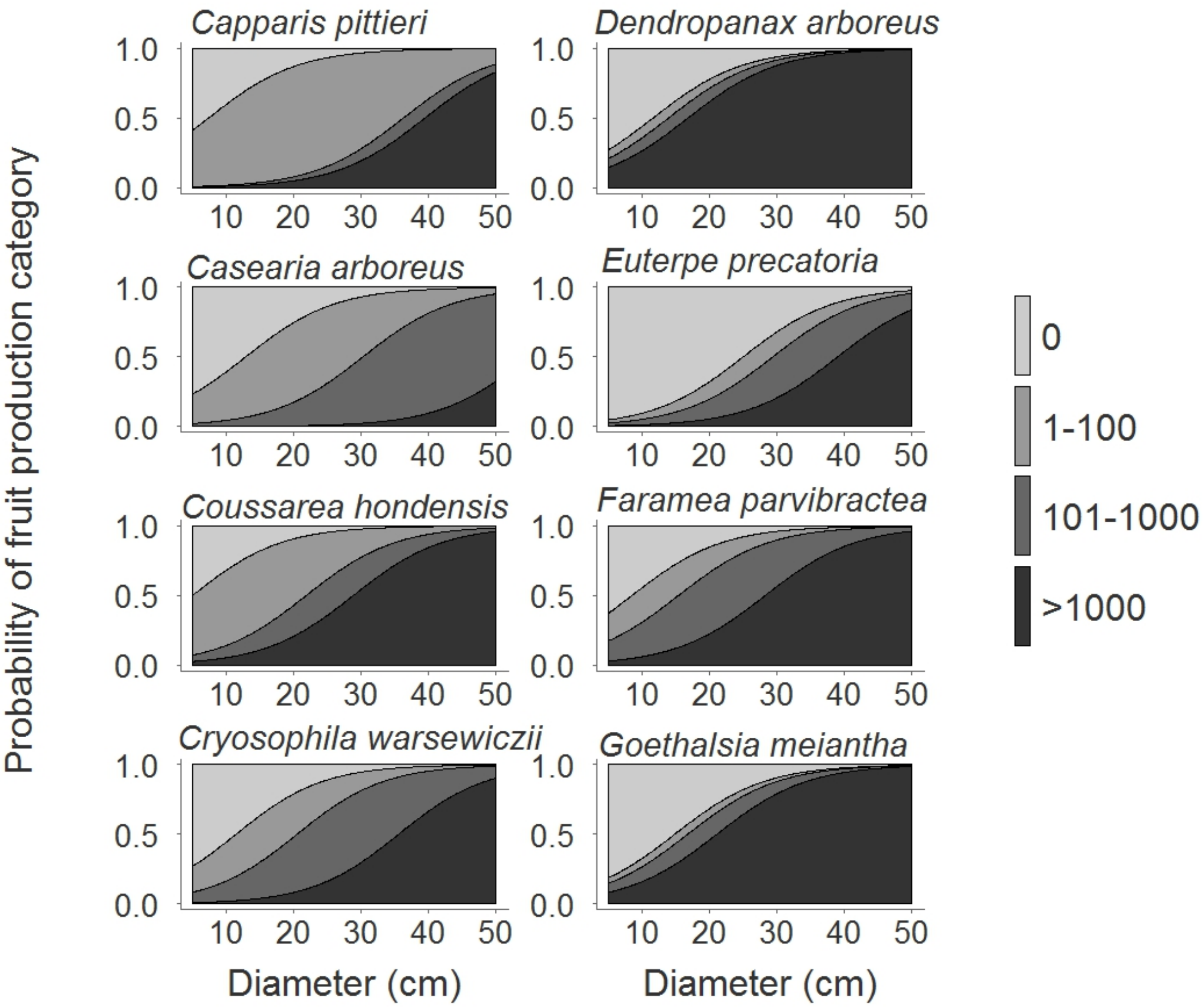
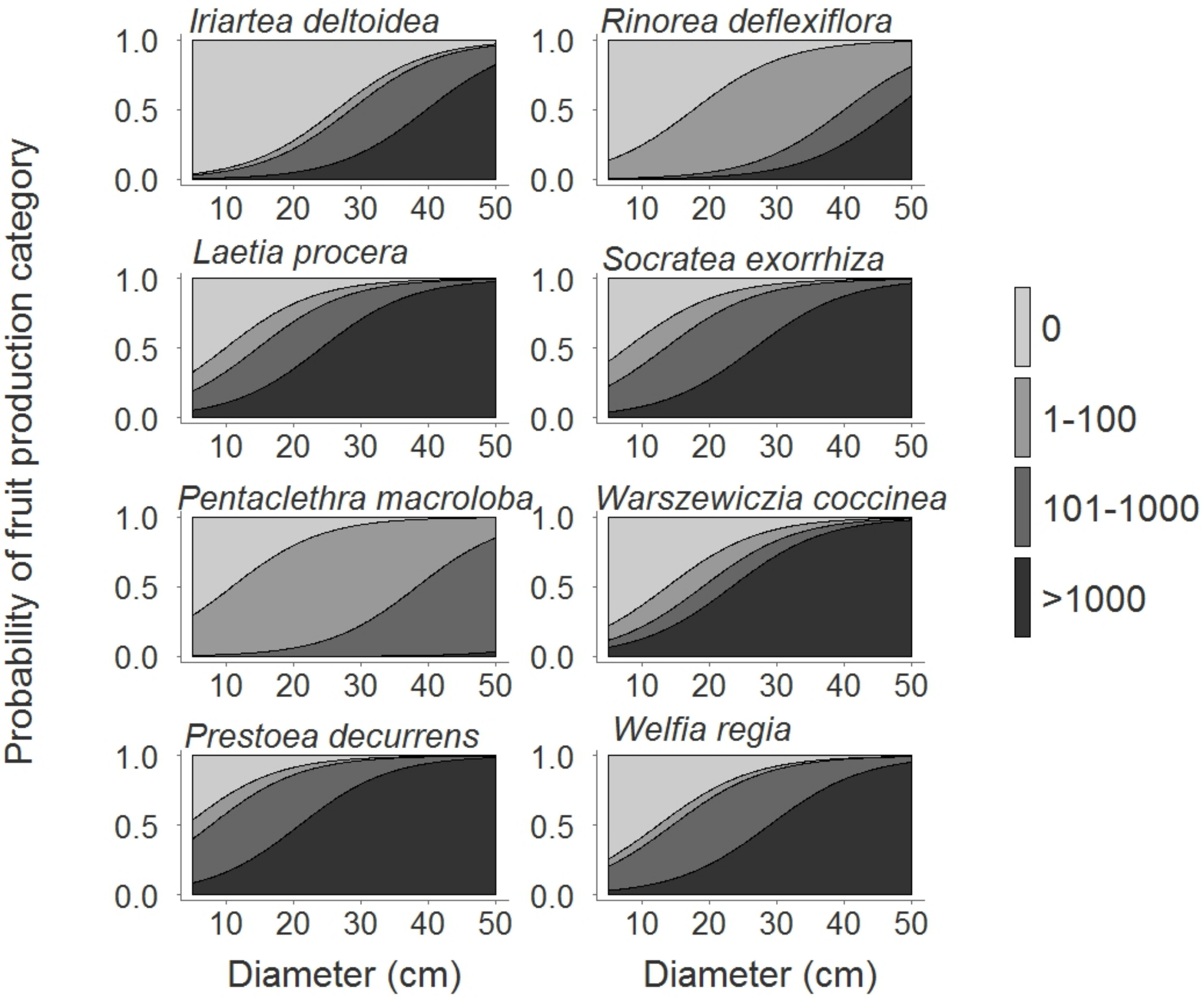


Figure 2: **Multinomial relationship between DBH and probability of fruit production for each species.** Shaded areas represent the probability of each fruit production category relative to DBH. Darker shaded areas indicate greater fruit production categories.

Figure 2 (cont'd)



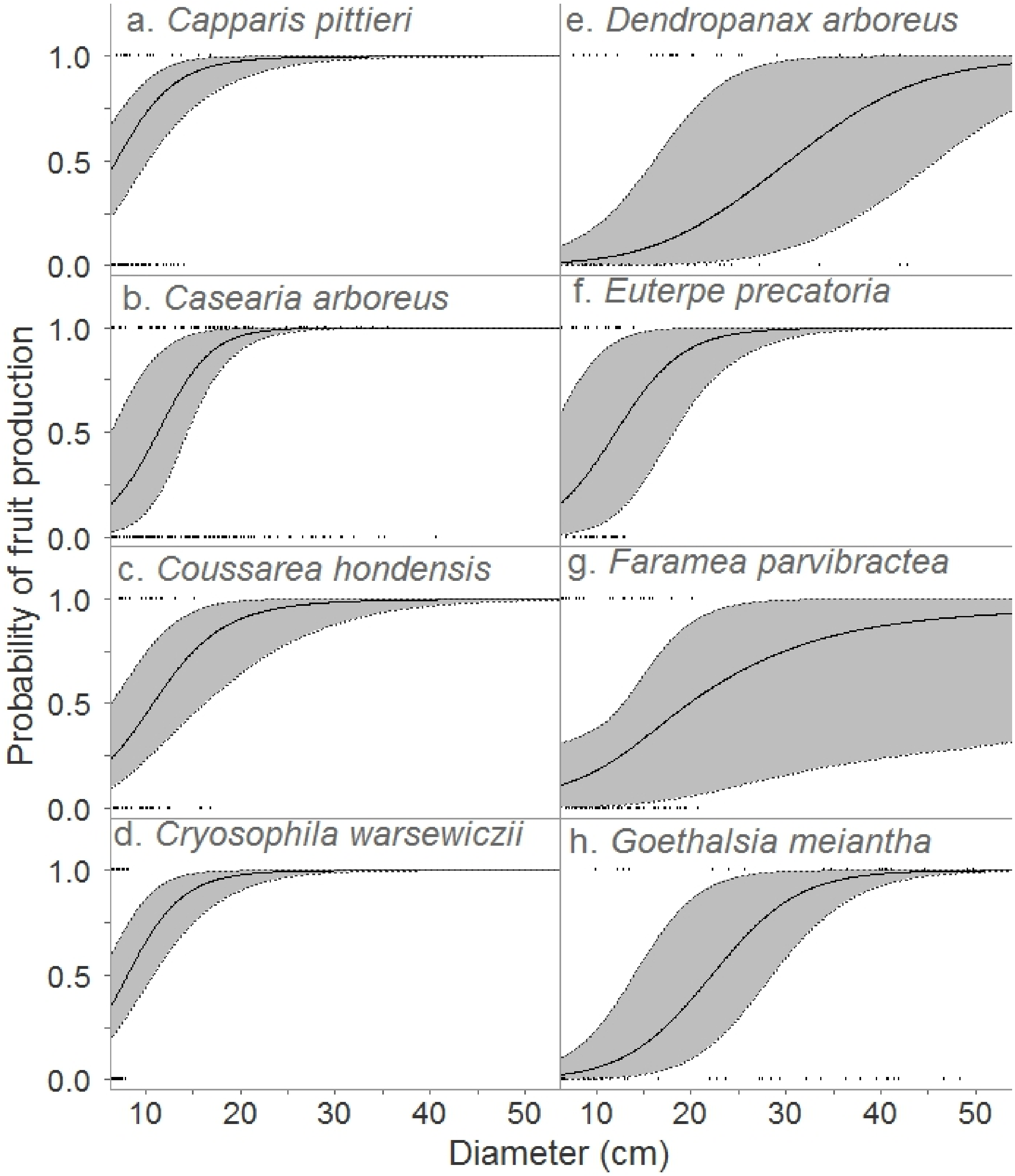
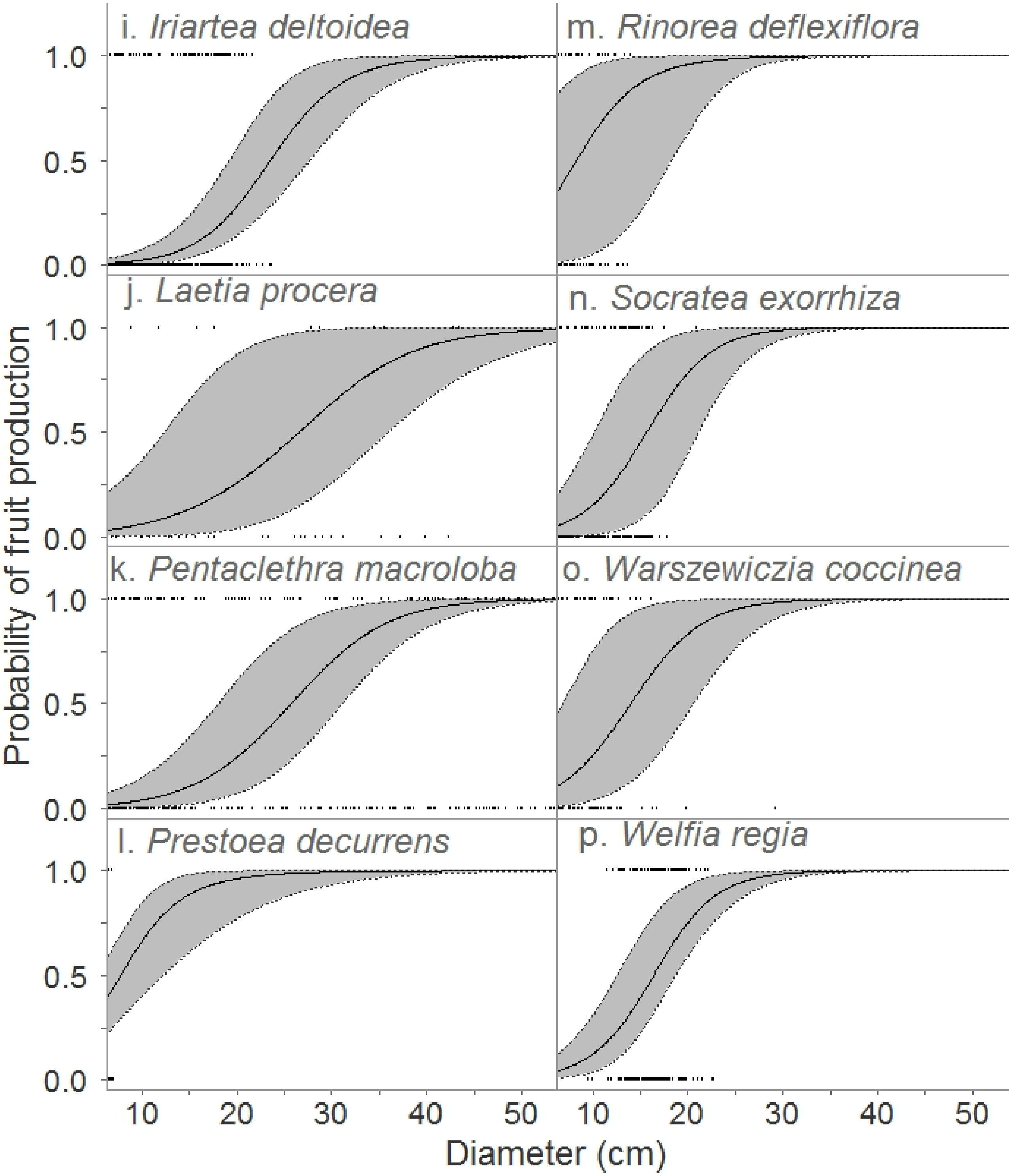


Figure 3: **Probability of reproducing as a function of tree diameter.** Posterior mean probability for individual species are presented with 95% credible intervals indicated with gray shading. Data points are the observed reproductive status of each individual sampled (r_i).

Figure 3 (cont'd)



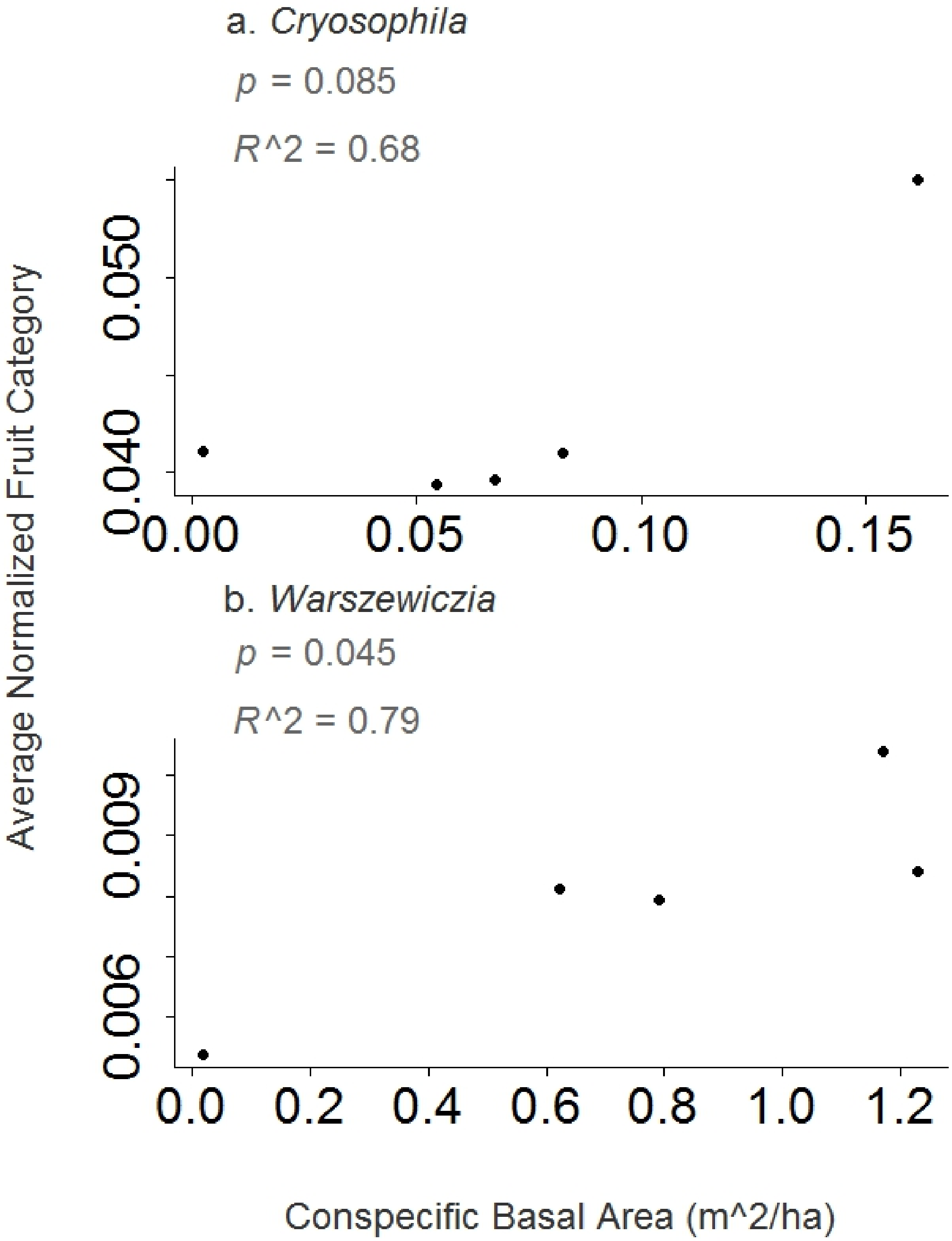


Figure 4: **Conspecific basal area vs. average maximum fruiting category by plot for two species.** Each point represents one plot at La Selva, Costa Rica. The average fruit category of each plot was normalized by the mean size of individuals (as basal area). Simple linear regressions were performed for each species. R^2 and p-values are reported.

Appendix B

Tables and figures for Chapter 3

Table 4: **Study species in Manistee National Forest, MI.** For each species, the number of individuals measured over all years and sites, and the number of individuals which were observed fruiting at least once during the study.

Species	Family	No. trees	No. observed fruiting
Acer rubrum	Aceraceae	423	173
Acer saccharum	Aceraceae	284	56
Fagus grandifolia	Fagaceae	205	89
Fraxinus americana	Oleaceae	57	25
Populus grandidentata	Salicaceae	148	16
Prunus serotina	Rosaceae	37	23
Quercus alba	Fagaceae	193	91
Quercus rubra/velutina	Fagaceae	231	177
Tilia americana	Tiliaceae	57	43
Total		1635	699

Table 5: **Fertilizer application rates.** Amount of fertilizer applied annually (g/yr) in the four different fertilizer treatments of the fertilization study. Micromax® (The Scotts Company) is a fertilizer containing a suite of micronutrients, including Ca, Mg, manganese (Mn), molybdenum (Mo), copper (Cu), iron (Fe), and zinc (Zn).

Treatment	$CaSO_4$	$(NH_4)_2SO_4$	NPK (12-12-12)	Micromax
Ca	3000	–	–	–
N	–	1900	–	–
Ca + N	3000	1900	–	–
Complete	2790	–	3325	700

Table 6: **Model evaluation for the zero-inflated regression on number of fruits produced using AIC.** Smaller AIC values indicate better model fit.

Covariates	AIC
DBH	10053
DBH+ soil	10134
DBH + NCI	16664

Table 7: **Correlation between seed and newly germinated seedling density.** The correlation was tested at different time lags (0-2 years), allowing for species differences in the time spent in the seed bank before germination. Pearson's r is reported, with the largest positive correlation in bold for each species.

Species	0 years	1 year	2 years
A. rubrum	-0.24	**-0.07**	-0.23
A. saccharum	-0.24	**0.71**	-0.42
F. grandifolia	-0.20	**0.80**	-0.27
F. americana	-0.33	-0.33	**0.70**
P. serotina	-0.25	**0.20**	-0.32
Q. alba	-0.28	**0.57**	-0.25
Q. rubra/velutina	0.20	**0.86**	-0.14
T. americana	-0.33	**0.16**	<0.01

Table 8: **Pearson's correlation of annual average fruit production from direct counts with annual seed or seedling density.** The number of fruit observed was correlated with seed density from the same year, and seedling density from the following year. For *Fraxinus americana* fruit production was correlated with seedling density from the second following year (see Table 7).

Species	Seed	Seedling
A. rubrum	0.96	-0.97
A. saccharum	0.94	0.96
F. grandifolia	0.93	0.94
F. americana	0.99	0.99
P. serotina	0.87	0.95
Q. alba	0.64	0.34
Q. rubra/velutina	0.14	0.15
T. americana	0.94	0.76

Table 9: **Degree of masting synchrony within species.** Synchrony within each species as the mean of all pairwise Spearman's correlations (ρ_s). For each year, the percent of the reproductive population ($D > D_{thres}$) which produced more fruit than the average fruit production necessary for a mast year is shown. This masting threshold was calculated from the absolute value of the minimum annual deviate of seed density, and the relationship between direct counts and seed density. Only species with a strong relationship between direct counts and seed density were included (see Table 8). Mast events are shown in bold. For species that had two mast or minor mast events, the percentage of reproductive individuals that produced fruit in both events is shown (R_{tw}), as well as the percentage of the total fruit production these overlapping individuals contributed to the two events (P_1, P_2).

Species	ρ_s	2008	2009	2010	2011	R_{tw}	P_1	P_2
A. rubrum	0.02	–	0.0	0.0	0.0			
A. saccharum	0.73	**35.4**	0.0	0.0	10.4	6.3 (3)	46.6	67.5
F. grandifolia	0.45	13.6	0.0	3.4	14.8	8.0 (7)	38.1	63.2
F. americana	0.90	0.0	0.0	0.0	**32.6**			
P. grandidentata	-0.06							
P. serotina	0.39	0.0	3.0	6.1	18.2			
Q. alba	0.59							
Q. rubra/velutina	0.09							
T. americana	0.50	0.0	0.0	**40.0**	14.0	2.0 (1)	6.6	9.5

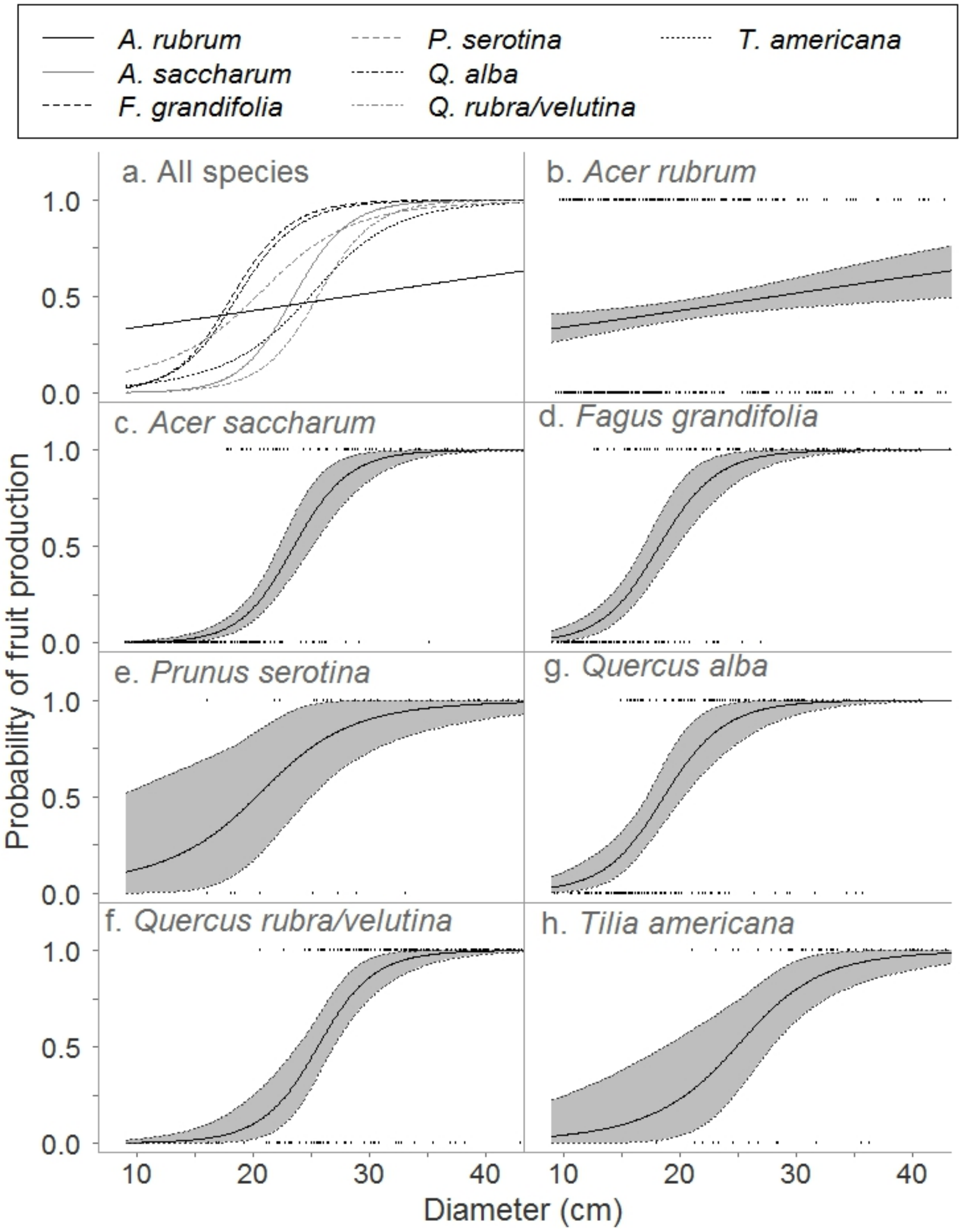


Figure 5: **Probability of reproducing as a function of tree diameter.** Posterior mean probability for (a) all species and (b–h) individual species. Posterior means for individuals are presented with 95% credible intervals indicated with gray shading. Data are the observed reproductive status of each individual sampled (r_i).

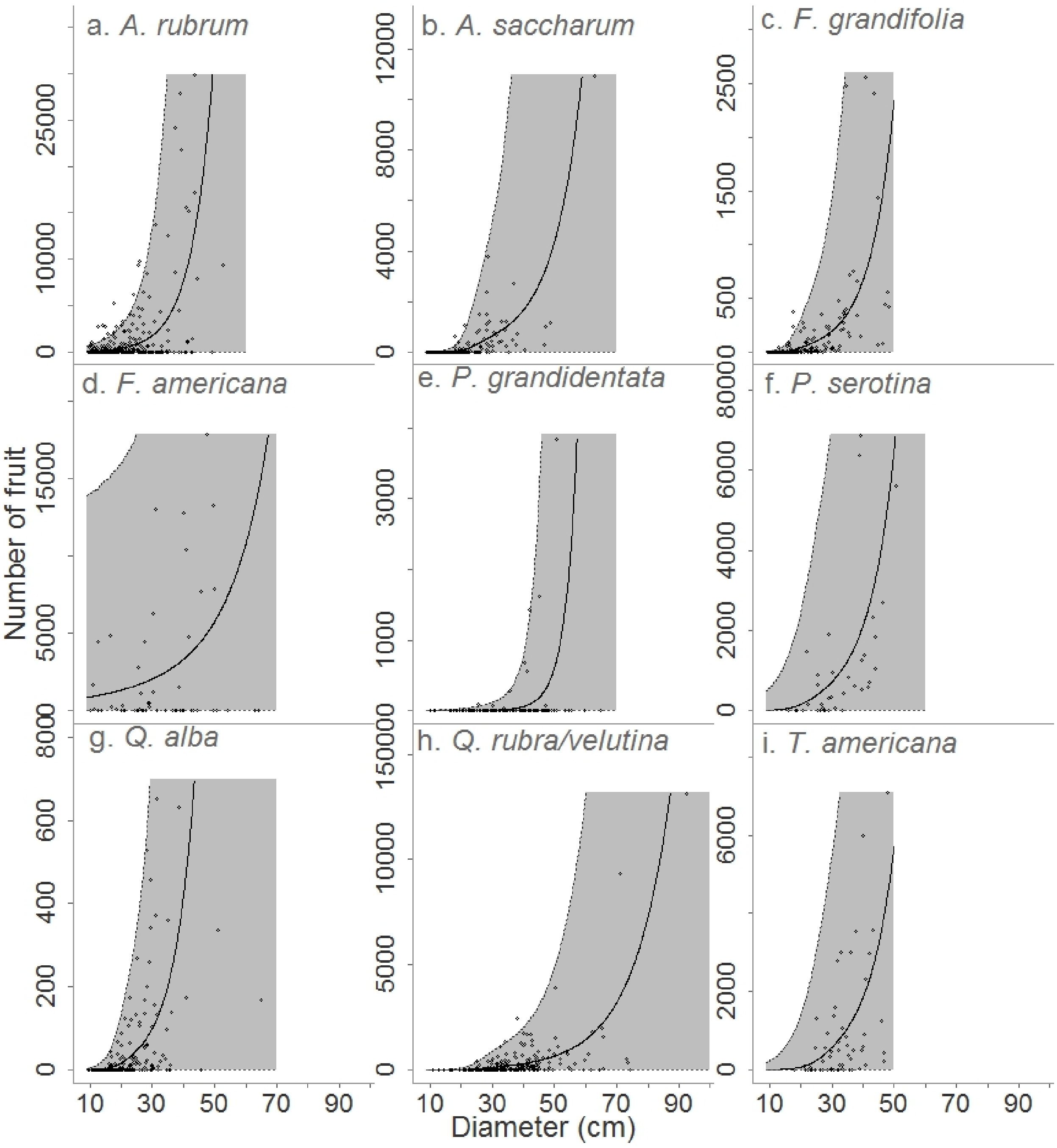


Figure 6: **Maximum number of fruit produced by each individual in relation to stem diameter.** The solid trendline represents the mean value of the negative binomial regression. The gray area surrounded by dashed lines is the 95% credible interval of each regression.

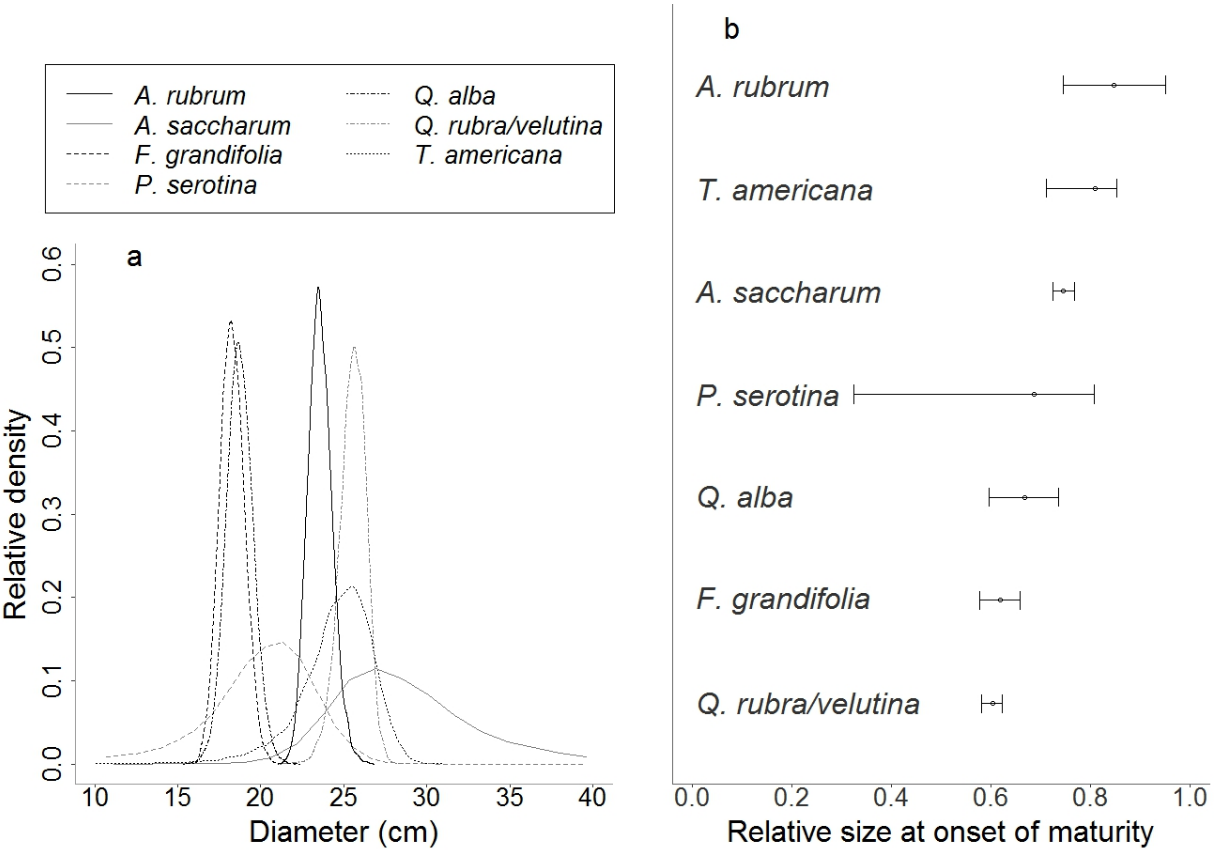


Figure 7: **Size at onset of maturity.** (a) Probability density function of $P(\text{mature}) = 0.5$ for all species with legend above. (b) Relative size at onset of maturity. Error bars indicate the 95% credible intervals.

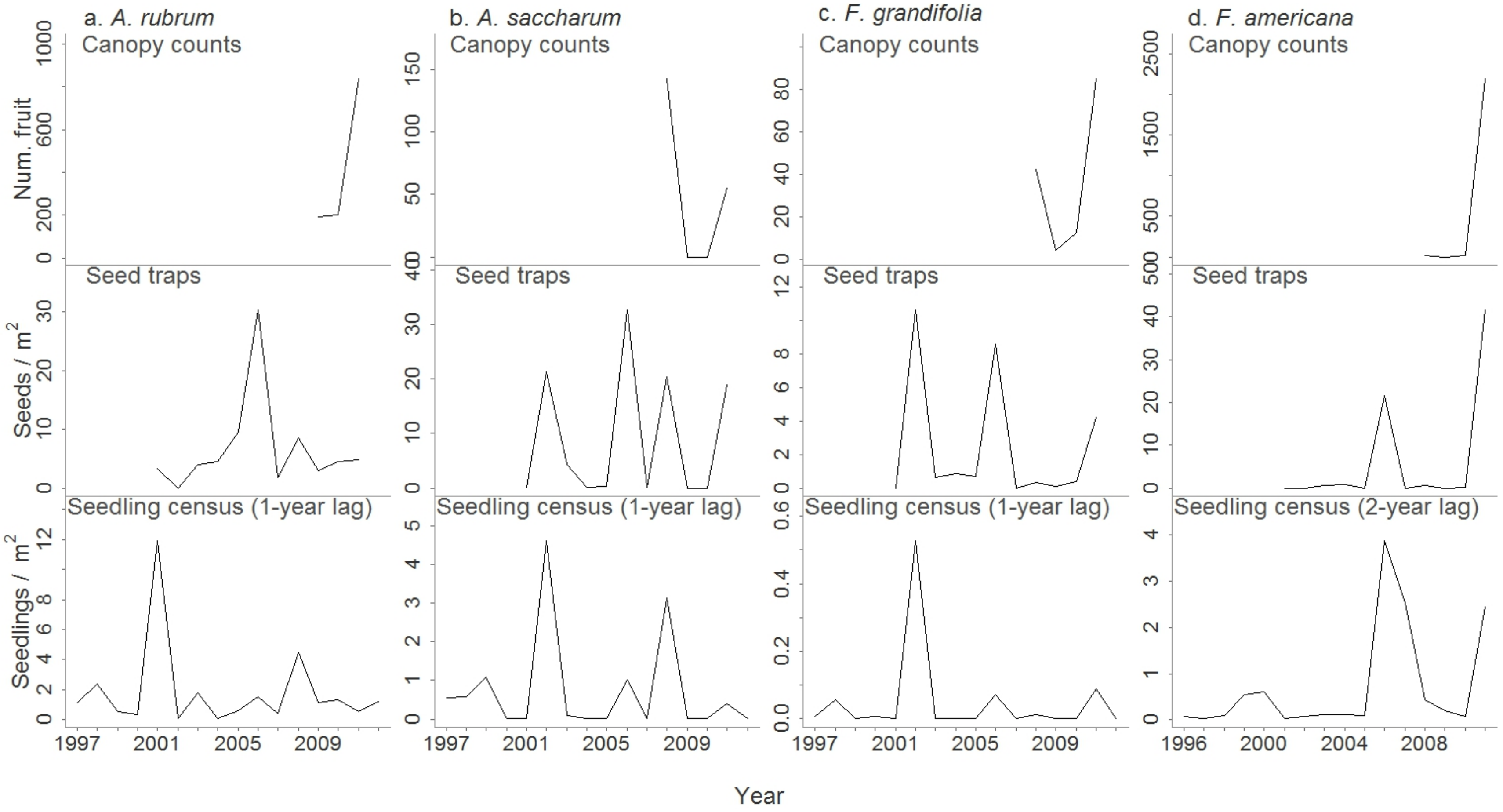
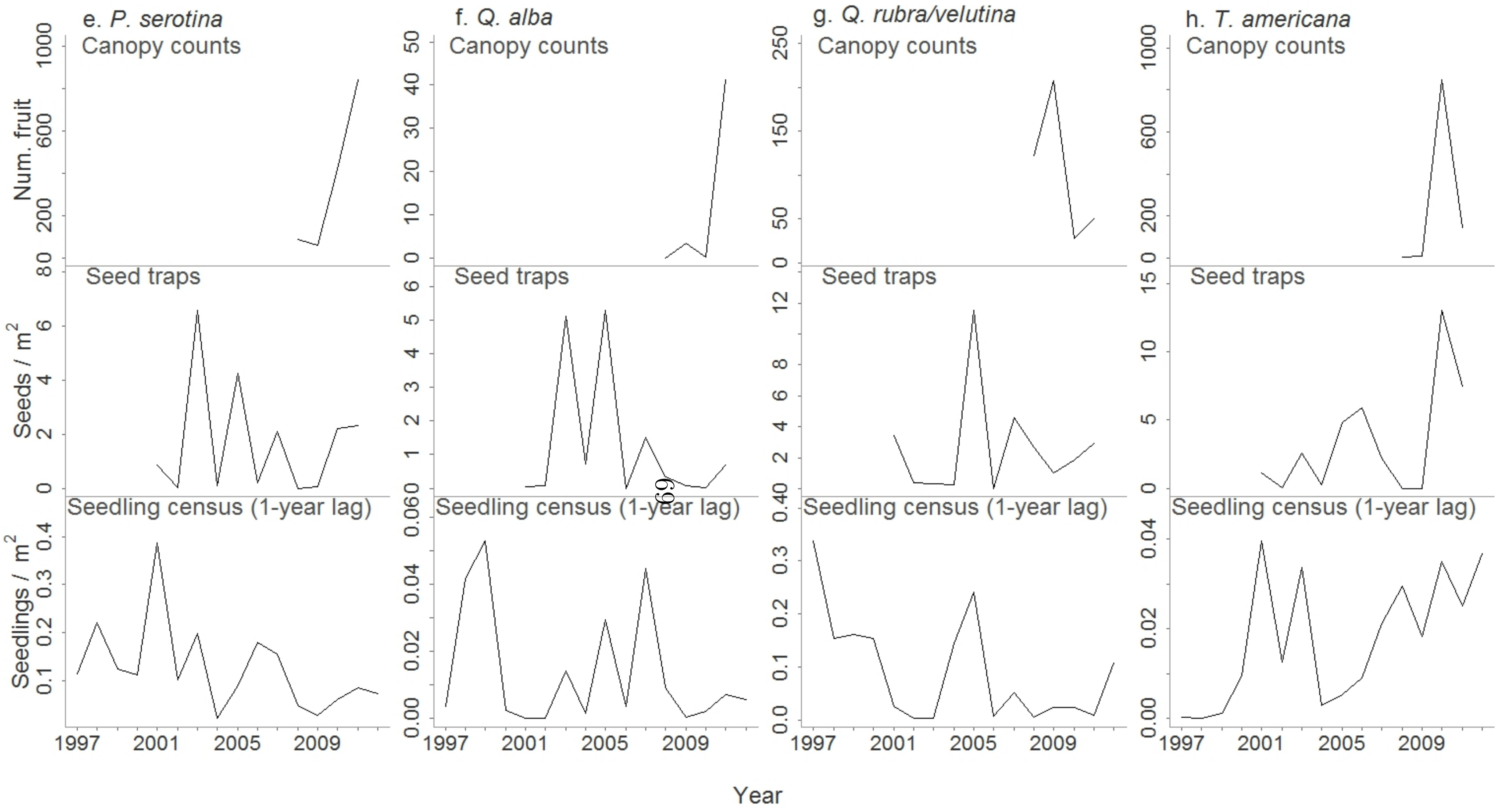


Figure 8: **Time series of fruit production.** Average fruit production (from direct counts of fruit on trees), seed density, and seedling density observed each year for nine common species in the Manistee National Forest, Michigan, USA. Seedling density for year t is displayed at year $t-1$ to account for the 1-year lag between fruit production and seed germination, except for *F. americana* (d), which is displayed at year $t-2$. Vertical dashed lines indicate mast years based on seed density.

Figure 8 (cont'd)



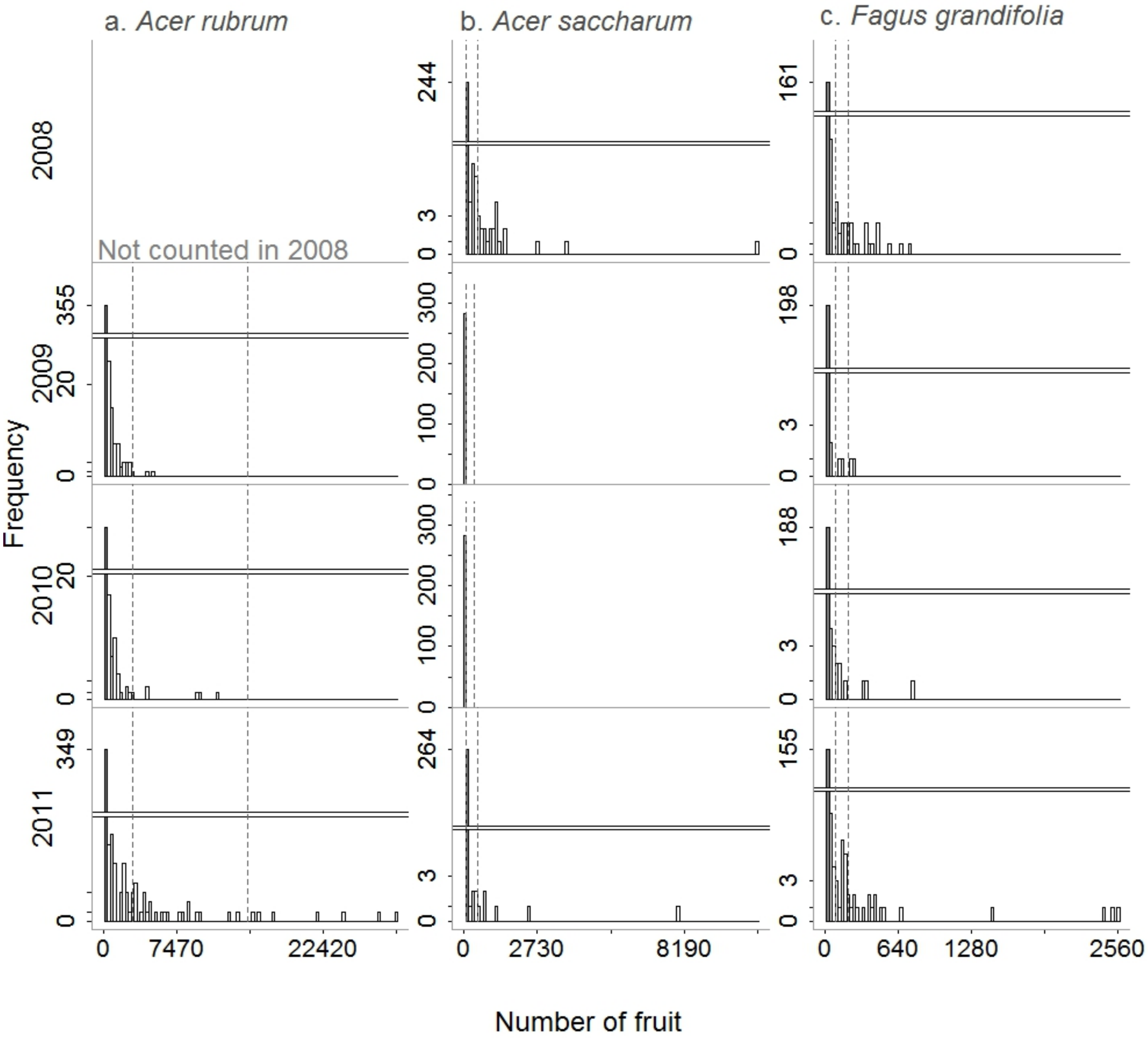
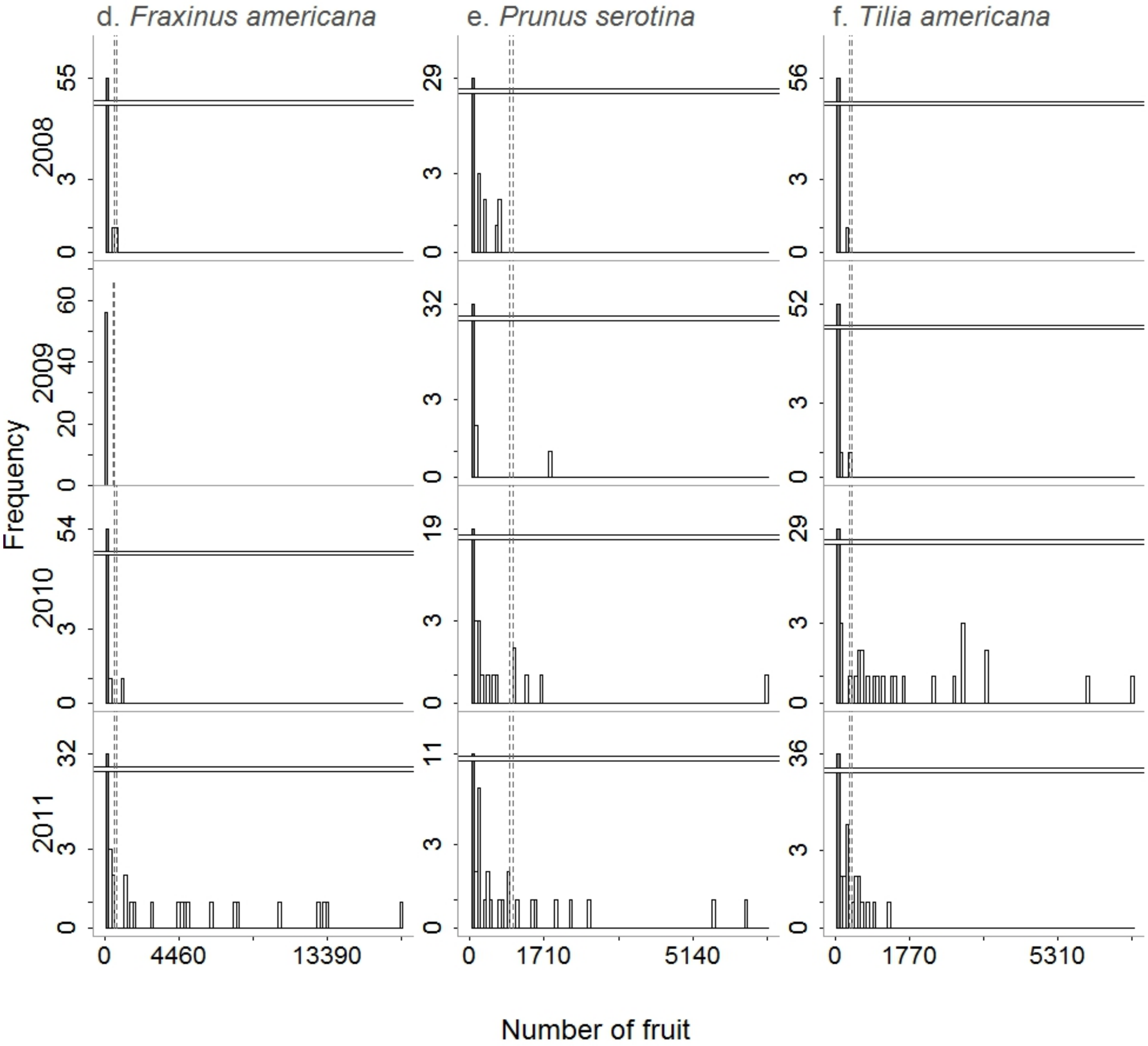


Figure 9: **Annual density of fruit production.** Vertical dashed lines indicate the average fruit production in a mast year based on all individuals in the population (left), or only the individuals above the reproductive size threshold (right).

Figure 9 (cont'd)



Appendix C

Model Evaluation for Chapter 2

We compared models using deviance information criterion (DIC) for both the binomial and multinomial models. DIC is smaller for better fitting models and includes a penalty for additional parameters (Spiegelhalter et al. 2002).

Because I am interested in being able to predict fruit output, I also used proper scoring rules to compare and assess alternative models. Proper scoring rules are used to evaluate the quality of predictions made from probabilistic models. They provide a measure of predictive performance of the model based on observed data and the predictive distribution, $\boldsymbol{\pi} = \{\pi_i, \ldots, \pi_K\}$ (Gneiting and Raftery 2007). The scoring rule function $S(\boldsymbol{\pi}, i)$ was calculated for each individual i in a holdout set. The holdout set consisted of 100 individuals from the full dataset which was used in the binomial and complete multinomial models. A holdout set of 75 individuals was used from the subset of reproductive individuals. It is common to use multiple scoring rules to evaluate a model, each of which incorporates information from the observed data and predictive distribution in a different way. Four scoring rules for categorical variables were used:

$$\text{Zero-one: } S(\pi, i) = \begin{cases} 1 & \text{if } \pi_i = \max\{\pi_1, \ldots, \pi_K\} \\ 0 & \text{if otherwise} \end{cases} \tag{1}$$

$$\text{Quadratic: } S(\pi, i) = 2\pi_i - \sum_{k=1}^{K} \pi_k^2 - 1 \tag{2}$$

$$\text{Spherical: } S(\pi, i) = \frac{\pi_i}{(\sum_{k=1}^{K} \pi_k^2)^{\frac{1}{2}}} \tag{3}$$

$$\text{Logarithmic: } S(\pi, i) = \log \pi_i \tag{4}$$

The zero-one rule (Equation 1) ignores variability in the predictive distribution, returning zero or one for each individual, resulting in the rate at which the correct category was predicted. The logarithmic rule (Equation 4) also uses a limited amount of information, being based only on the probability of the category of which individual i is a part. The quadratic and spherical rules (Equations 2–3) incorporate information from the entire predictive distribution, evaluating the probability of predicting the correct category in relation to the probability of predicting incorrect categories. Higher scores indicate better predictive performance. For the zero-one and spherical rules this means scores closer to 1, but for the quadratic and logarithmic rules (which are negative) this means scores closer to zero. The median and 95% credible intervals were obtained for the posterior mean of each scoring rule.

Table 10: **Model evaluation for the binomial regression.** For each model, DIC and the median and 95% credible intervals of four proper scoring rules are reported. For DIC, smaller values indicate better model fit. For proper scoring rules, larger values indicate better predictive performance of the model.

Covariates	DIC	Zero-one			Quadratic			Spherical			Logarithmic		
Intercept only	2419	0.28	0.30	0.34	-0.98	-0.94	-0.90	0.46	0.47	0.49	-1.31	-1.22	-1.13
DBH	1703	0.14	0.15	0.17	-1.30	-1.24	-1.19	0.30	0.32	0.34	-2.51	-2.21	-2.00
DBH+ soil	1705	0.15	0.21	0.33	-1.27	-1.13	-0.95	0.31	0.37	0.47	-2.47	-2.05	-1.70
DBH + NCI	1670	0.14	0.20	0.33	-1.34	-1.23	-1.01	0.29	0.33	0.45	-3.88	-2.32	-1.91
DBH + ANCI	1674	0.13	0.15	0.18	-1.29	-1.22	-1.16	0.30	0.33	0.35	-2.47	-2.17	-1.94
DBH + soil + NCI	**1659**	0.16	0.21	0.29	-1.37	-1.26	-1.12	0.28	0.33	0.39	-6.27	-2.76	-2.09
DBH + soil + ANCI	1679	0.13	0.16	0.19	-1.29	-1.23	-1.17	0.30	0.32	0.35	-2.53	-2.25	-2.01

Table 11: **Model evaluation for the multinomial regression fit to all individuals.** For each model, DIC and the median and 95% credible intervals of four proper scoring rules are reported. For DIC, smaller values indicate better model fit. For proper scoring rules, larger values indicate better predictive performance of the model.

Covariates	DIC	Zero-one			Quadratic			Spherical			Logarithmic		
Intercept only	3489	0.63	0.68	0.68	-0.45	-0.43	-0.42	0.73	0.74	0.75	-0.79	-0.77	-0.74
DBH	2749	0.74	0.77	0.79	-0.34	-0.32	-0.31	0.80	0.81	0.82	-0.60	-0.58	-0.56
DBH+ soil	2755	0.73	0.76	0.79	-0.35	-0.33	-0.32	0.79	0.80	0.81	-0.63	-0.60	-0.57
DBH + NCI	2728	0.74	0.77	0.79	-0.34	-0.32	-0.31	0.80	0.81	0.82	-0.61	-0.58	-0.55
DBH + ANCI	**2718**	0.75	0.77	0.80	-0.34	-0.33	-0.32	0.80	0.81	0.82	-0.62	-0.60	-0.57
DBH + soil + NCI	2738	0.73	0.76	0.79	-0.36	-0.34	-0.32	0.79	0.80	0.81	-0.63	-0.60	-0.57
DBH + soil + ANCI	2732	0.74	0.78	0.80	-0.35	-0.33	-0.32	0.80	0.81	0.82	-0.63	-0.60	-0.57

Table 12: **Model evaluation for the multinomial regression fit to only reproductive individuals.** For each model, DIC and the median and 95% credible intervals of four proper scoring rules are reported. For DIC, smaller values indicate better model fit. For proper scoring rules, larger values indicate better predictive performance of the model.

Covariates	DIC	Zero-one			Quadratic			Spherical			Logarithmic		
Intercept only	993	0.68	0.71	0.73	-0.42	-0.40	-0.38	0.75	0.77	0.78	-0.67	-0.63	-0.60
DBH	936	0.68	0.72	0.75	-0.40	-0.38	-0.36	0.77	0.78	0.80	-0.64	-0.61	-0.58
DBH+ soil	929	0.68	0.72	0.76	-0.42	-0.39	-0.36	0.76	0.78	0.79	-0.68	-0.63	-0.58
DBH + NCI	**884**	0.65	0.71	0.75	-0.42	-0.39	-0.37	0.75	0.77	0.79	-0.67	-0.62	0.58
DBH + ANCI	900	0.61	0.69	0.75	-0.54	-0.41	-0.37	0.69	0.76	0.79	-1.18	-0.68	-0.60
DBH + soil + NCI	888	0.67	0.72	0.76	-0.42	-0.39	-0.36	0.76	0.78	0.79	-0.67	-0.62	-0.58
DBH + soil + ANCI	910	0.64	0.71	0.75	-0.49	-0.42	-0.37	0.72	0.76	0.79	-0.95	-0.67	-0.60

Appendix D

Site level fruit production relationships for Chapter 2

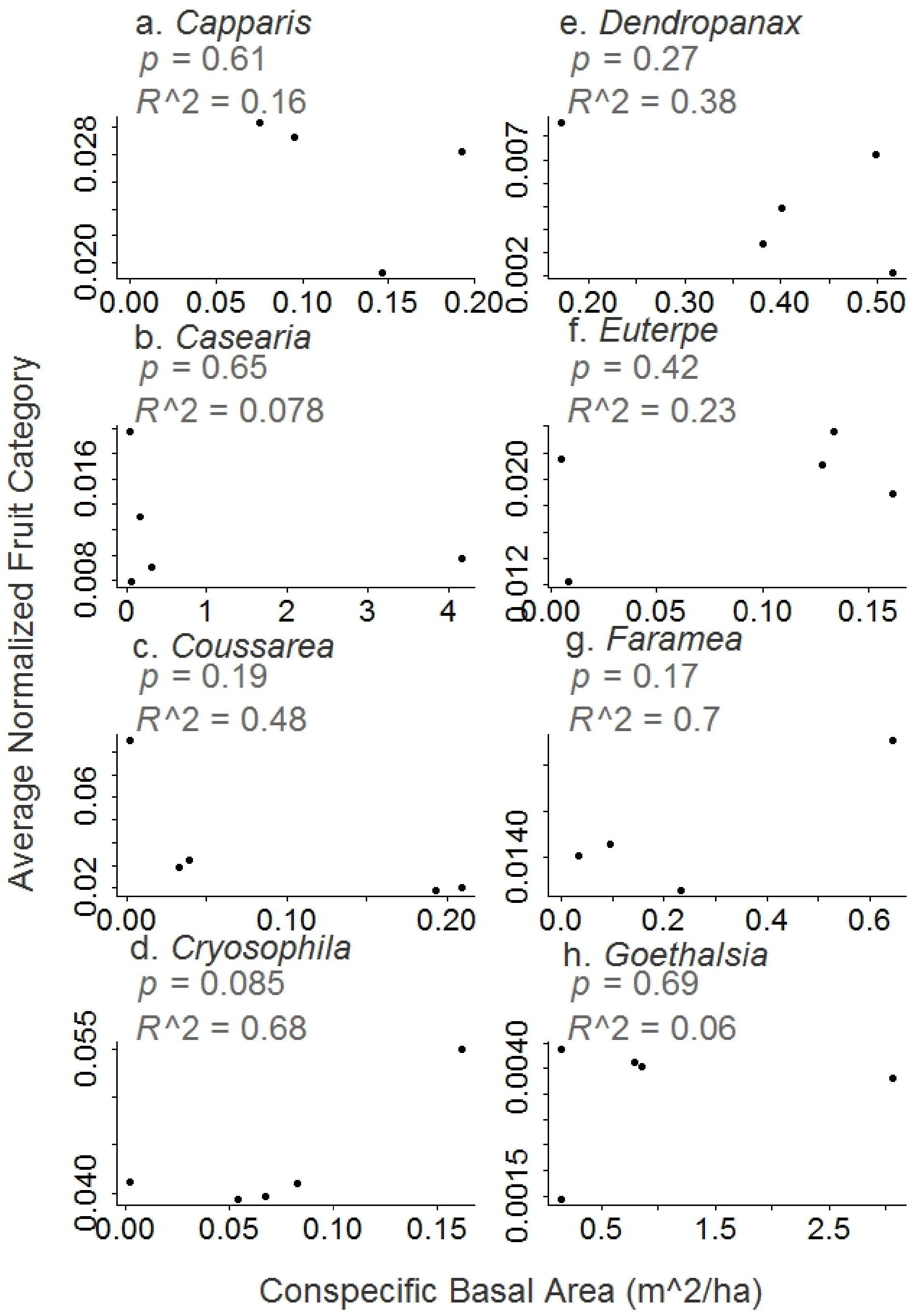
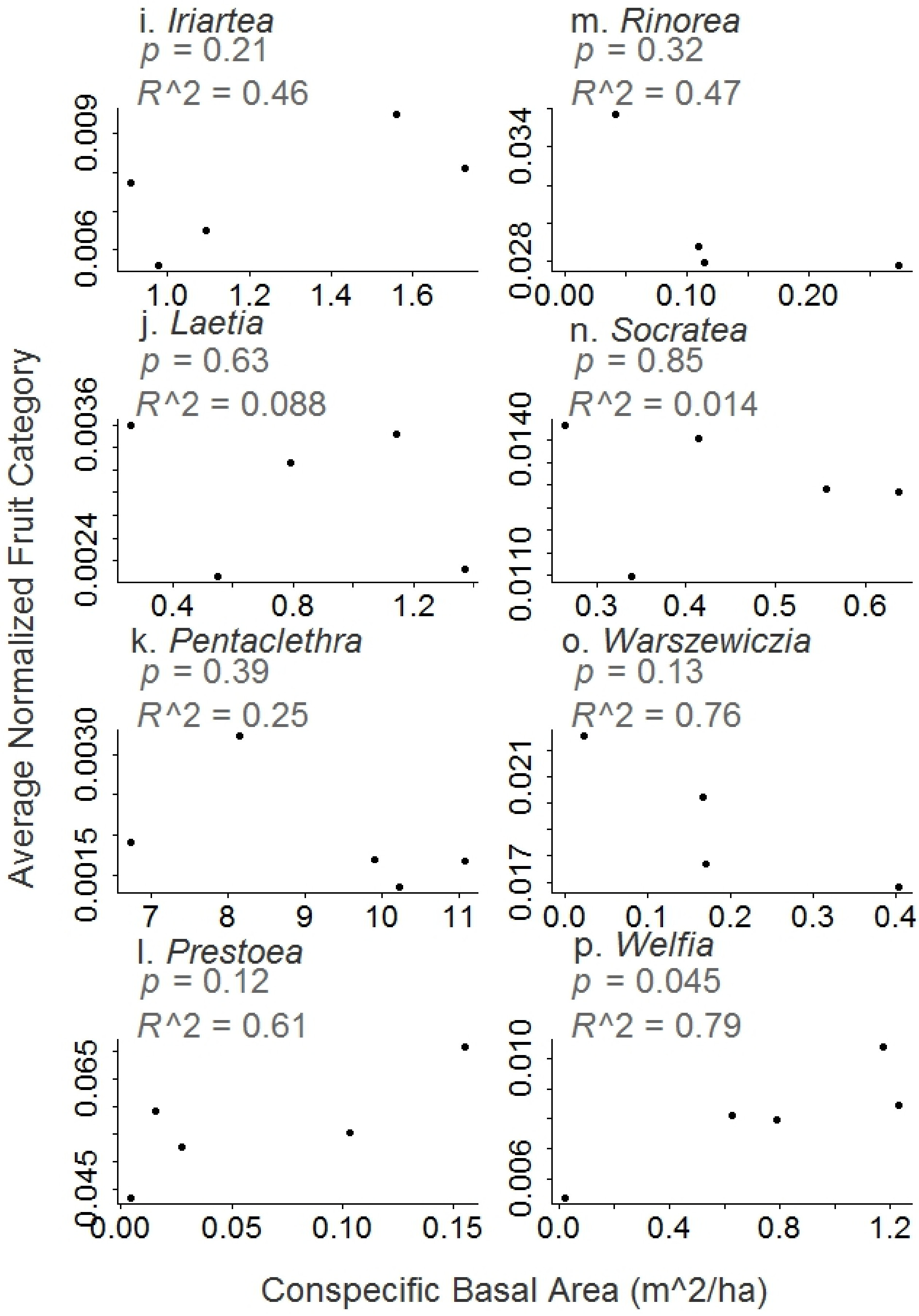


Figure 10: **Conspecific basal area vs. average maximum fruiting category by plot for each species.** Each point represents one plot at La Selva, Costa Rica. The average fruit category of each plot was normalized by the mean size of individuals (as basal area). Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 10 (cont’d)



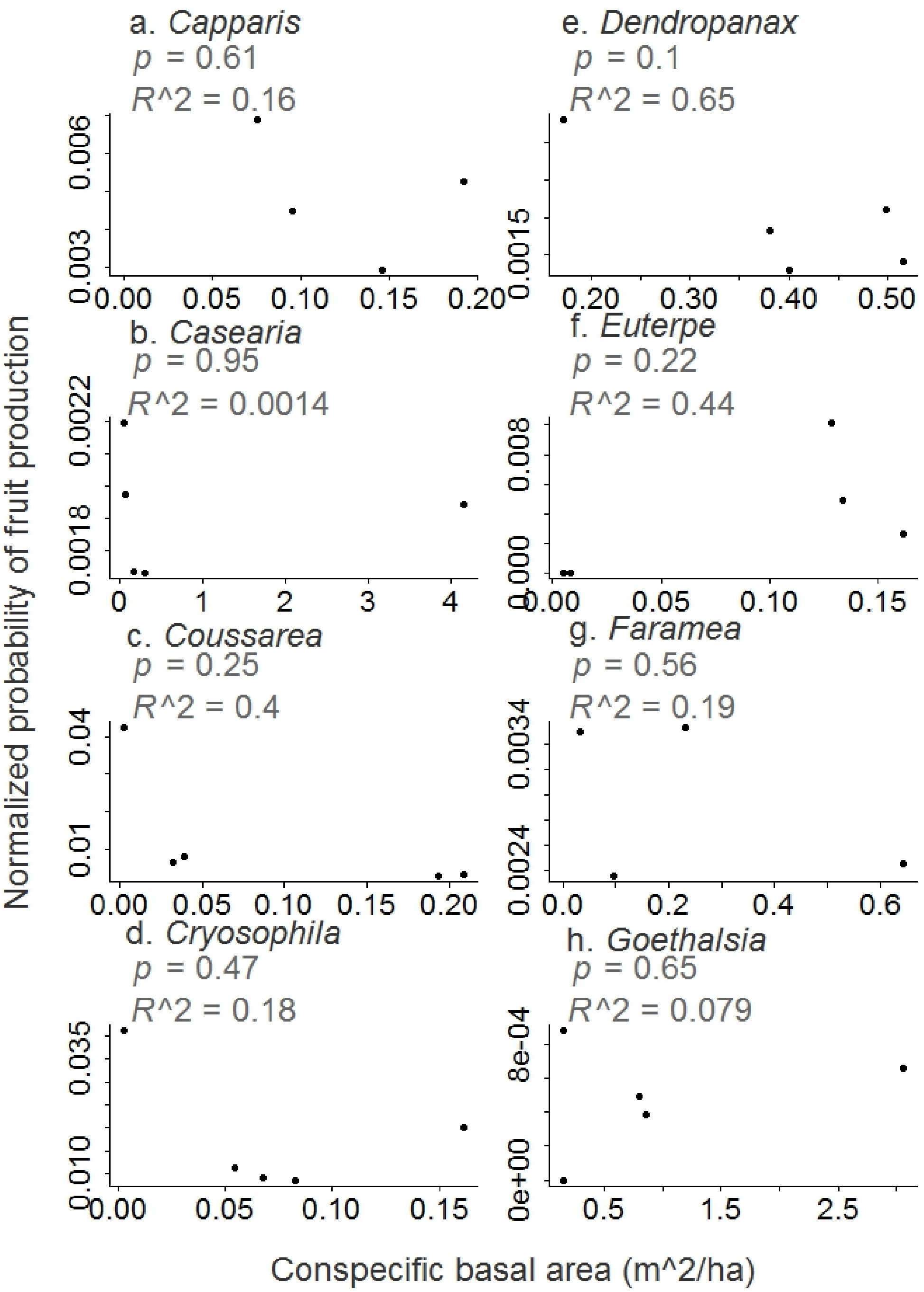
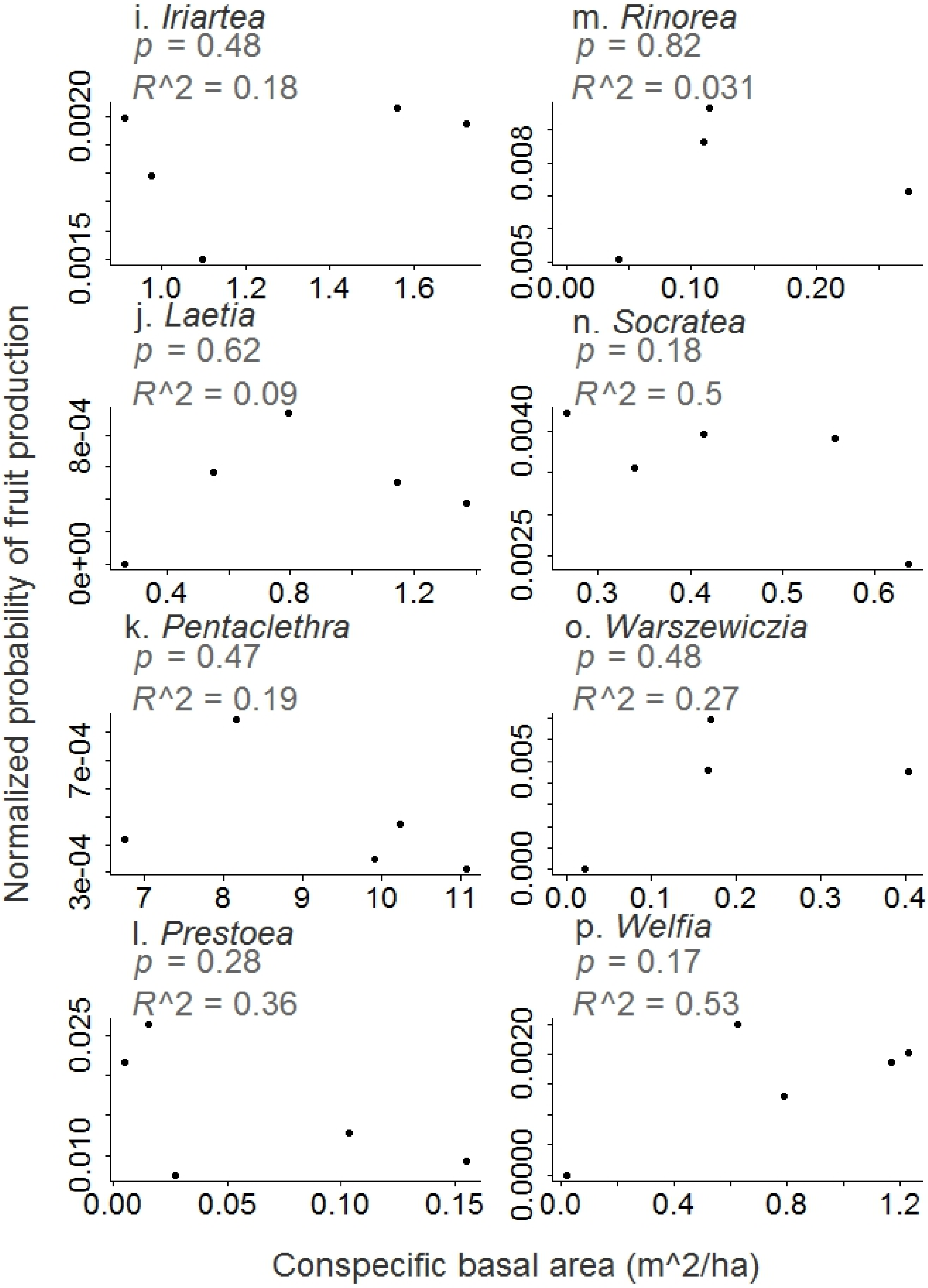


Figure 11: **Conspecific basal area vs. probability of fruit production by plot for each species. Each point represents one plot.** Each point represents one plot at La Selva, Costa Rica. The probability of fruiting for each plot was normalized by the mean size of individuals (as basal area). Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 11 (cont'd)



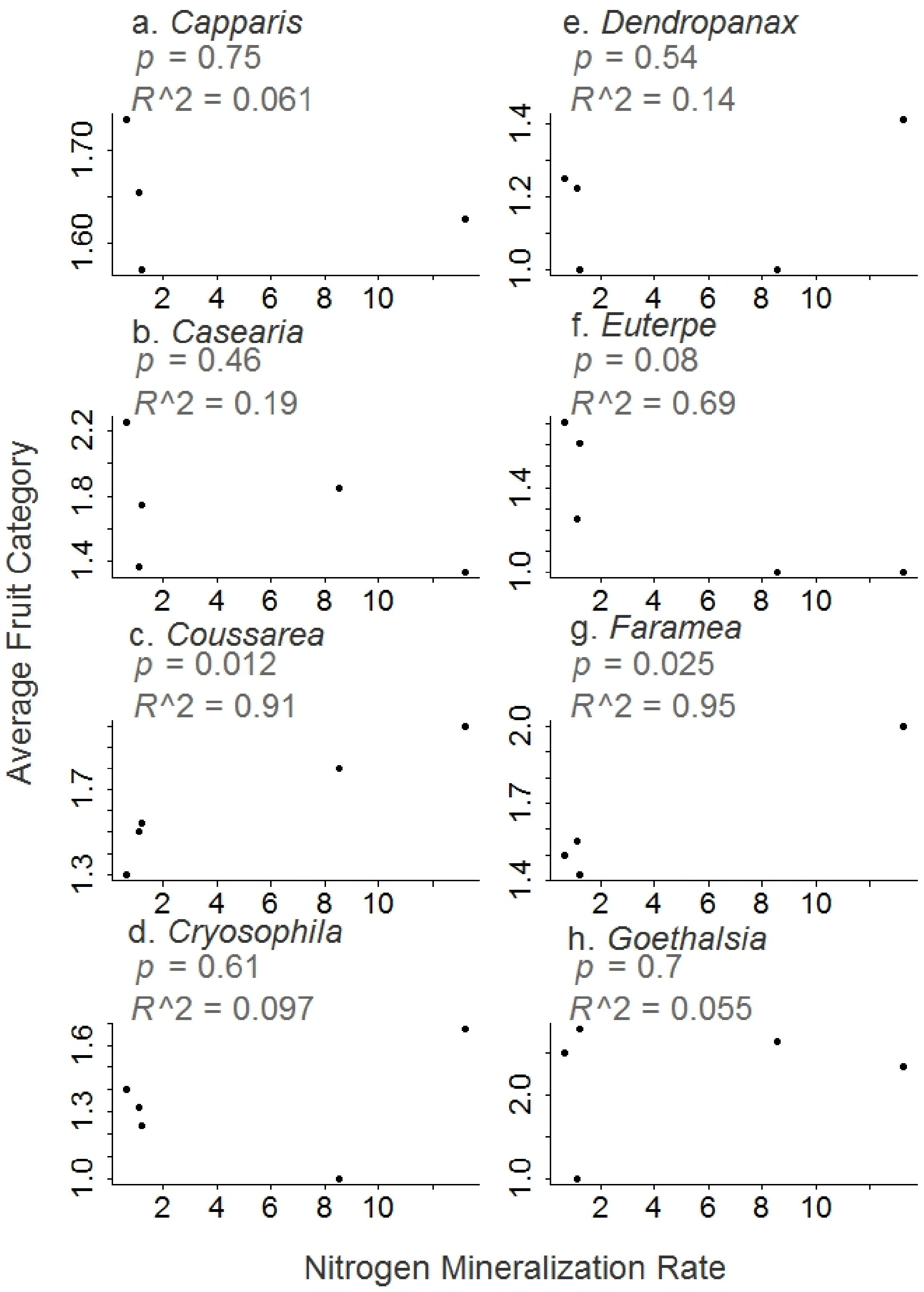
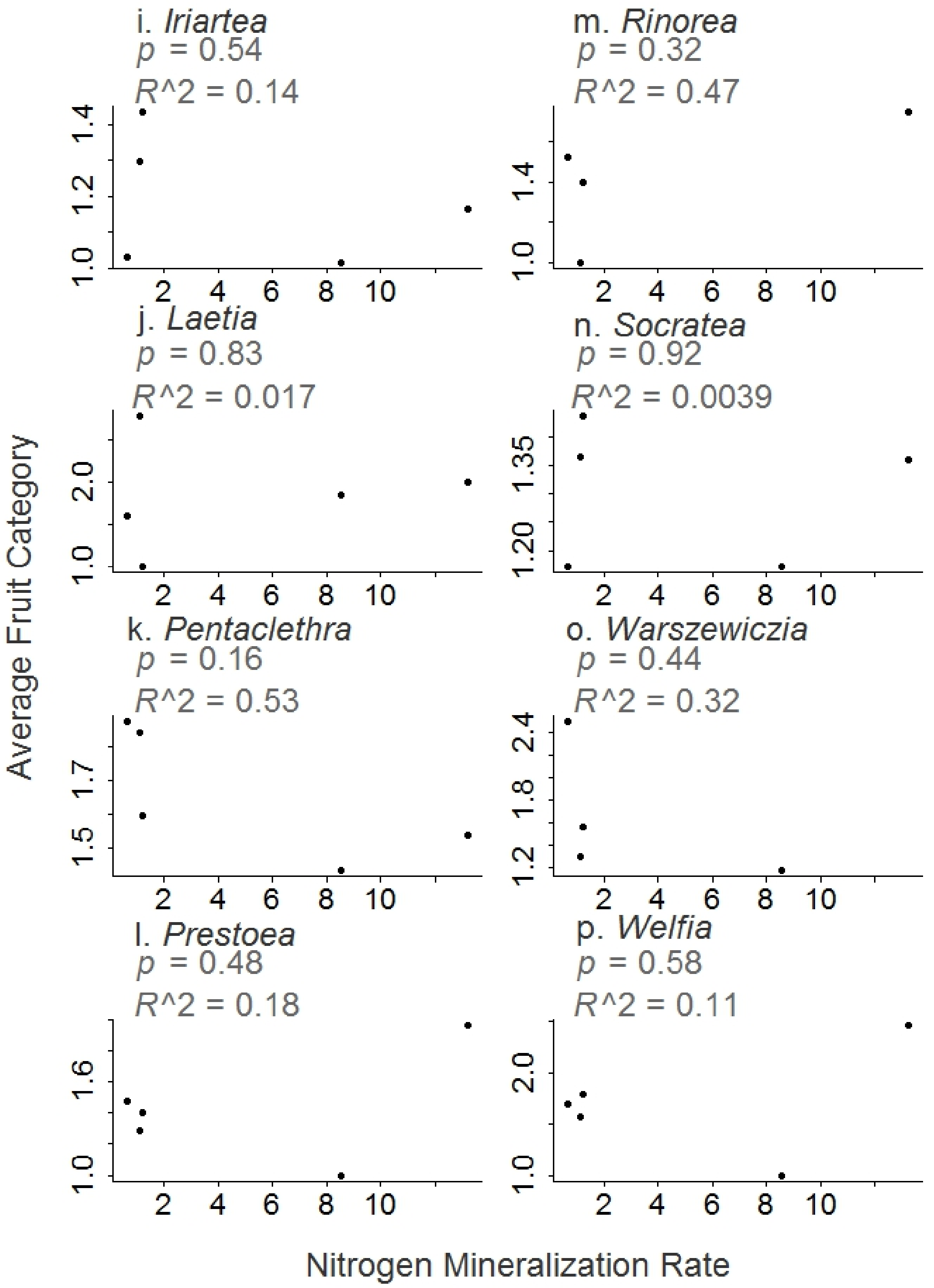


Figure 12: **Nitrogen mineralization rate vs. average maximum fruiting category by plot for each species.** Each point represents one plot at La Selva, Costa Rica. Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 12 (cont'd)



i. *Iriartea* p = 0.54 R^2 = 0.14

m. *Rinorea* p = 0.32 R^2 = 0.47

j. *Laetia* p = 0.83 R^2 = 0.017

n. *Socratea* p = 0.92 R^2 = 0.0039

k. *Pentaclethra* p = 0.16 R^2 = 0.53

o. *Warszewiczia* p = 0.44 R^2 = 0.32

l. *Prestoea* p = 0.48 R^2 = 0.18

p. *Welfia* p = 0.58 R^2 = 0.11

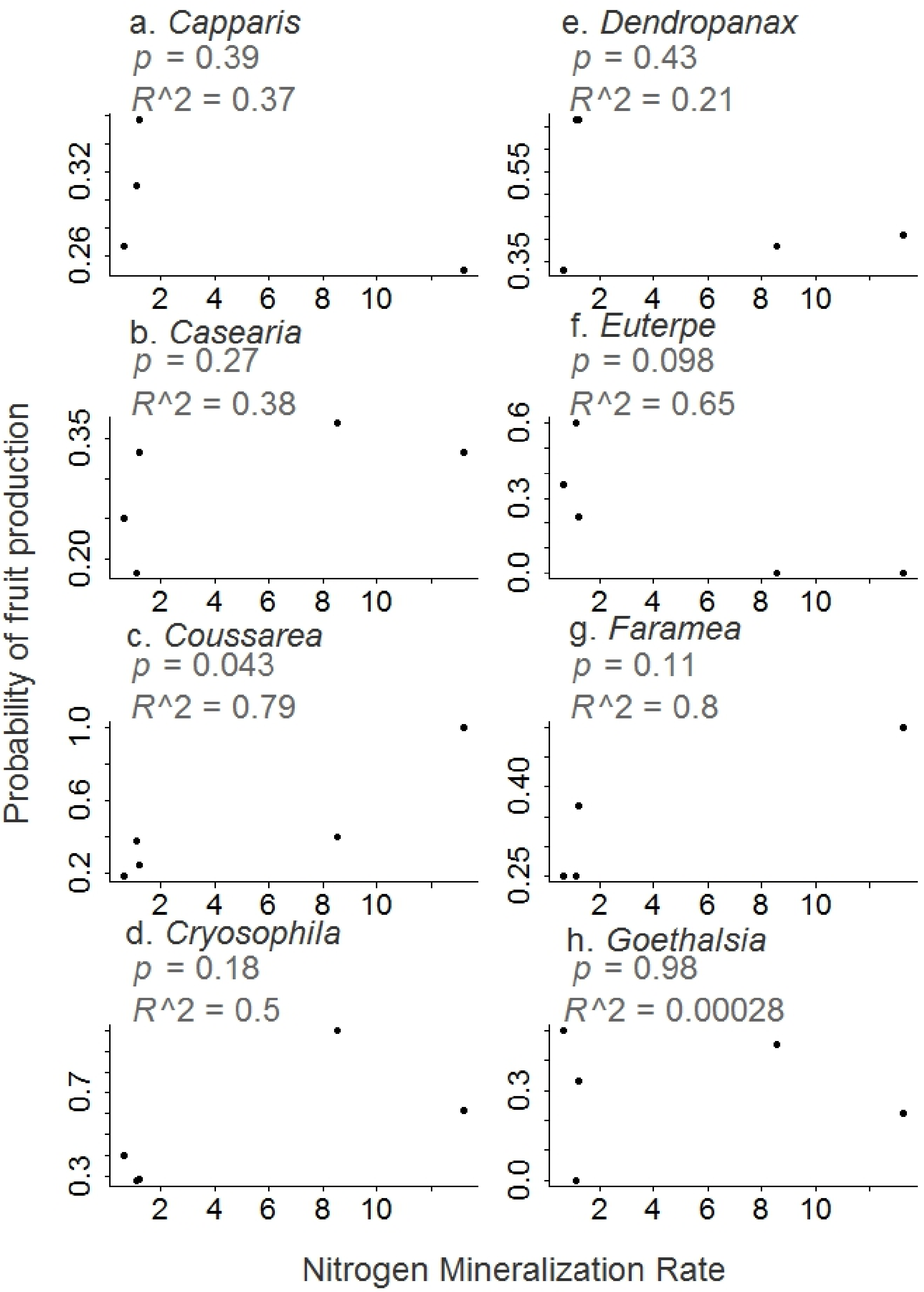
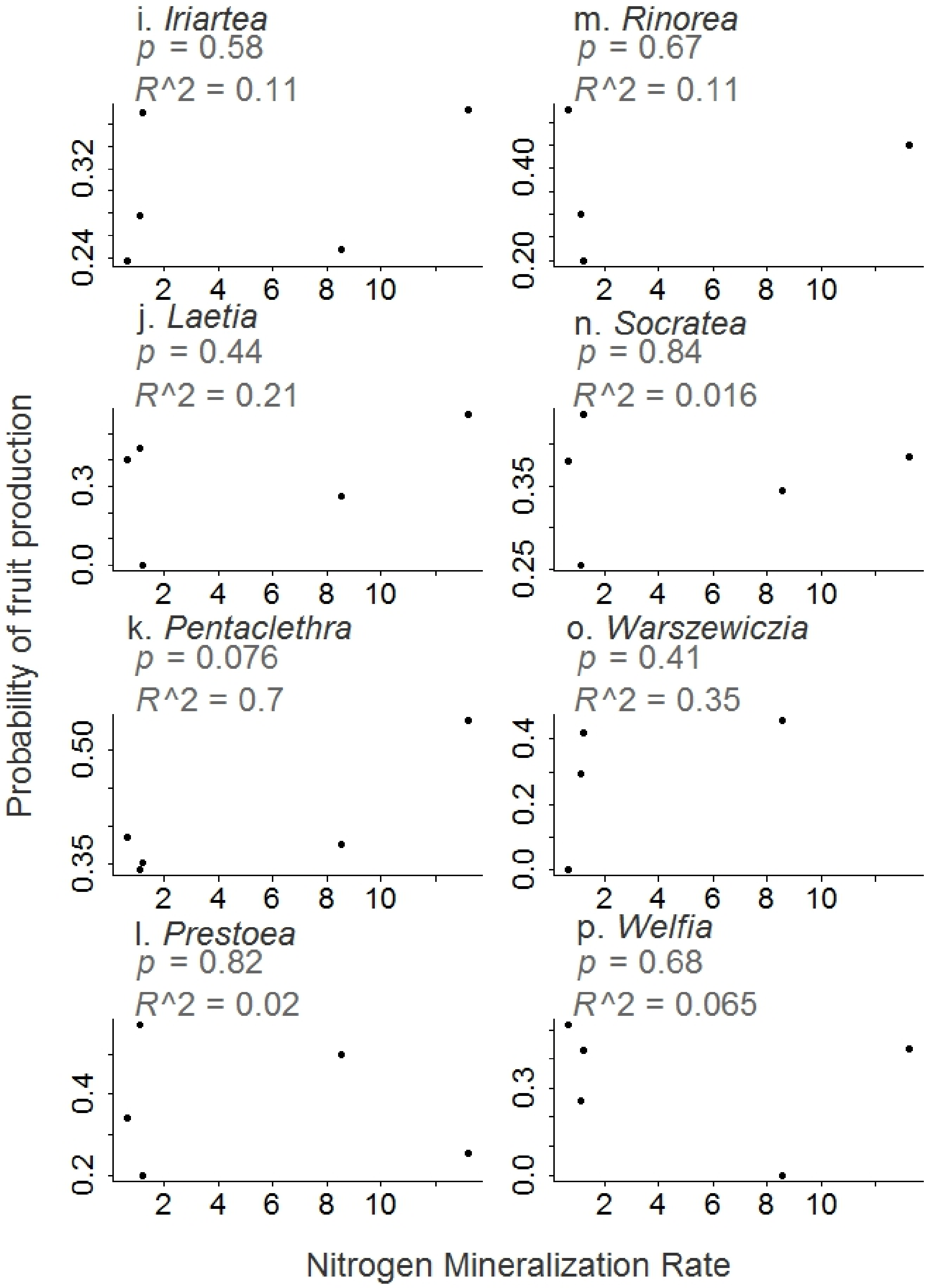


Figure 13: **Nitrogen mineralization rate vs. probability of fruit production by plot for each species.** Each point represents one plot at La Selva, Costa Rica. Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 13 (cont'd)



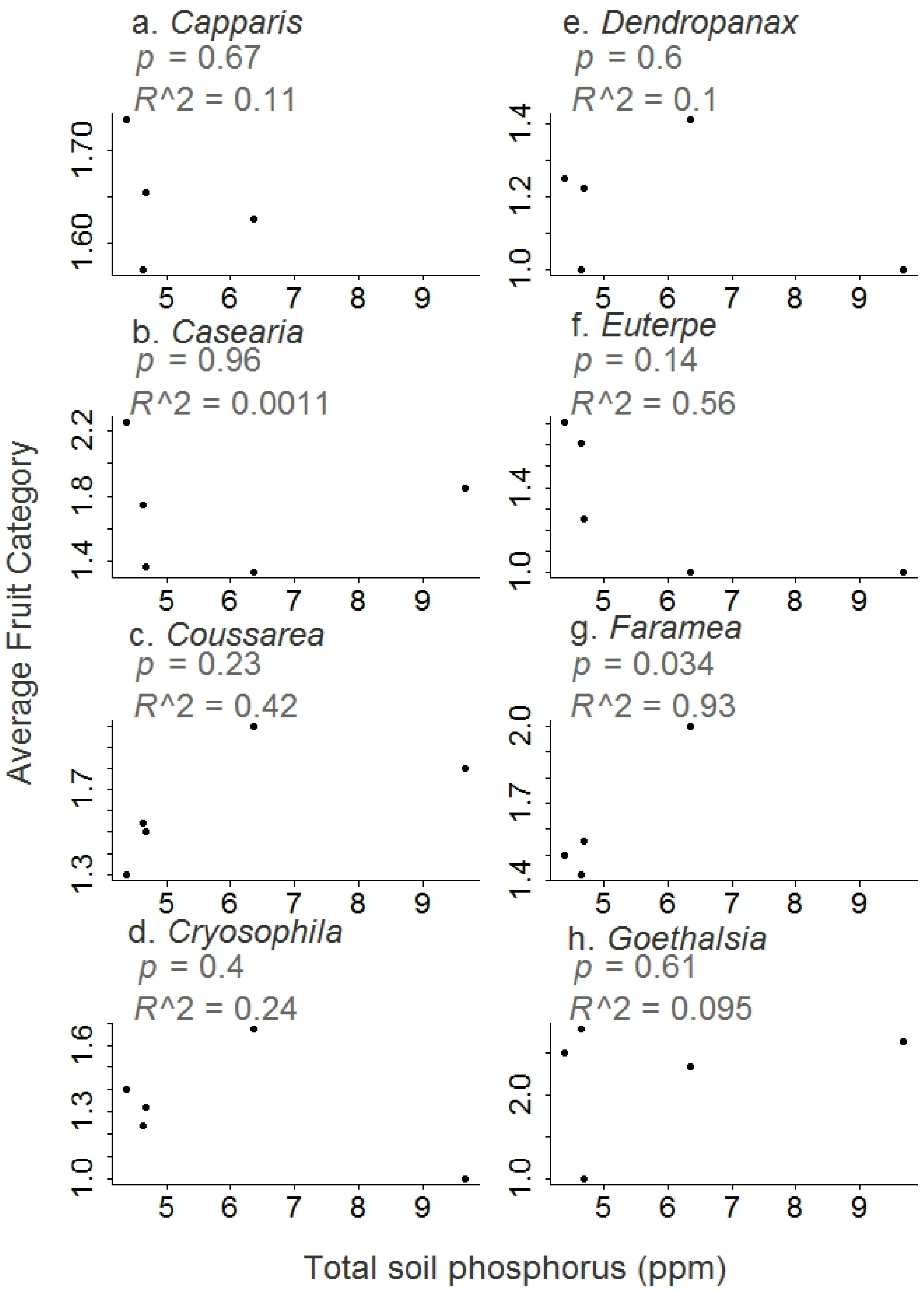
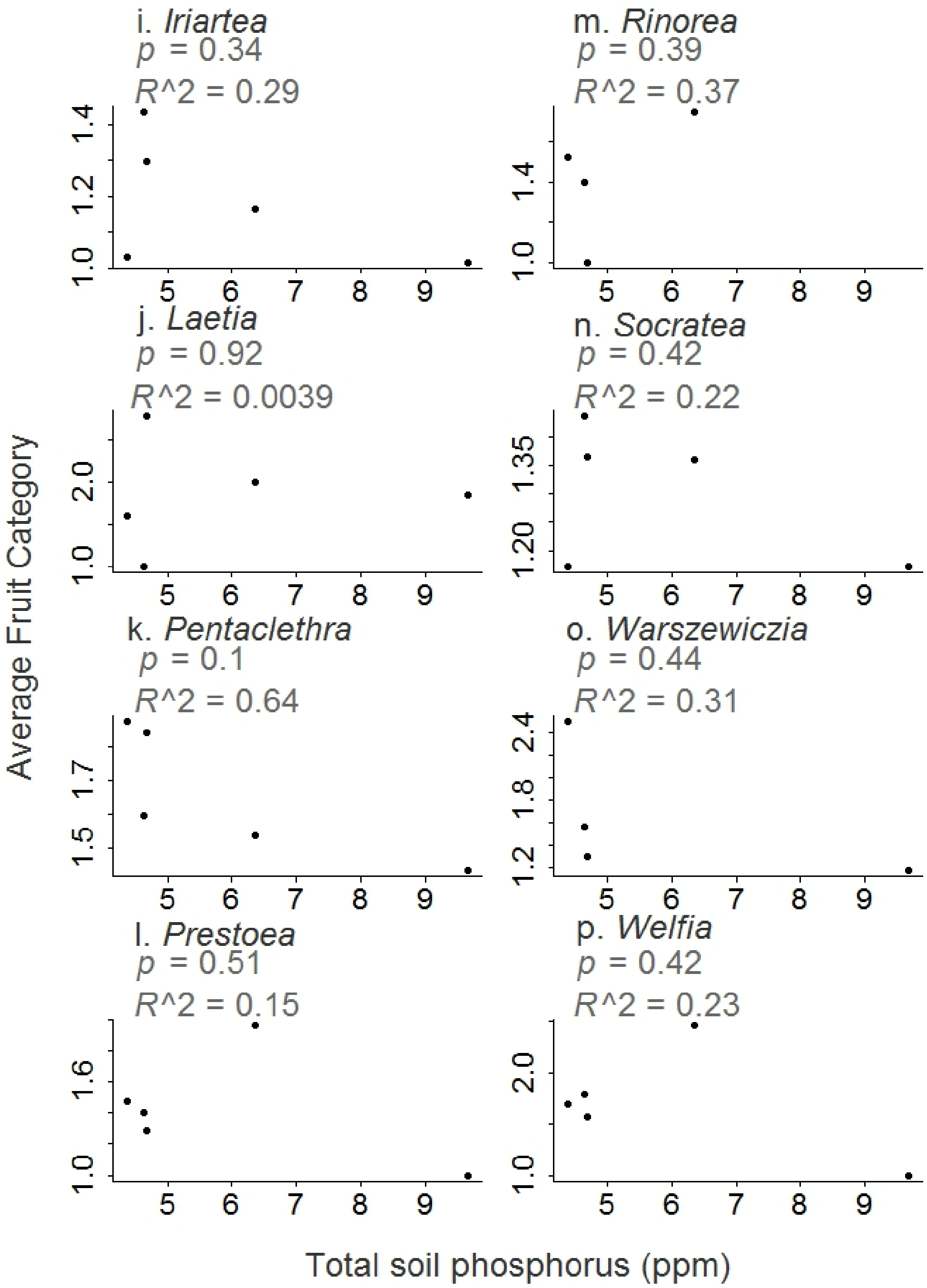


Figure 14: **Phosphorus availability vs. average maximum fruiting category by plot for each species.** Each point represents one plot at La Selva, Costa Rica. Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 14 (cont'd)



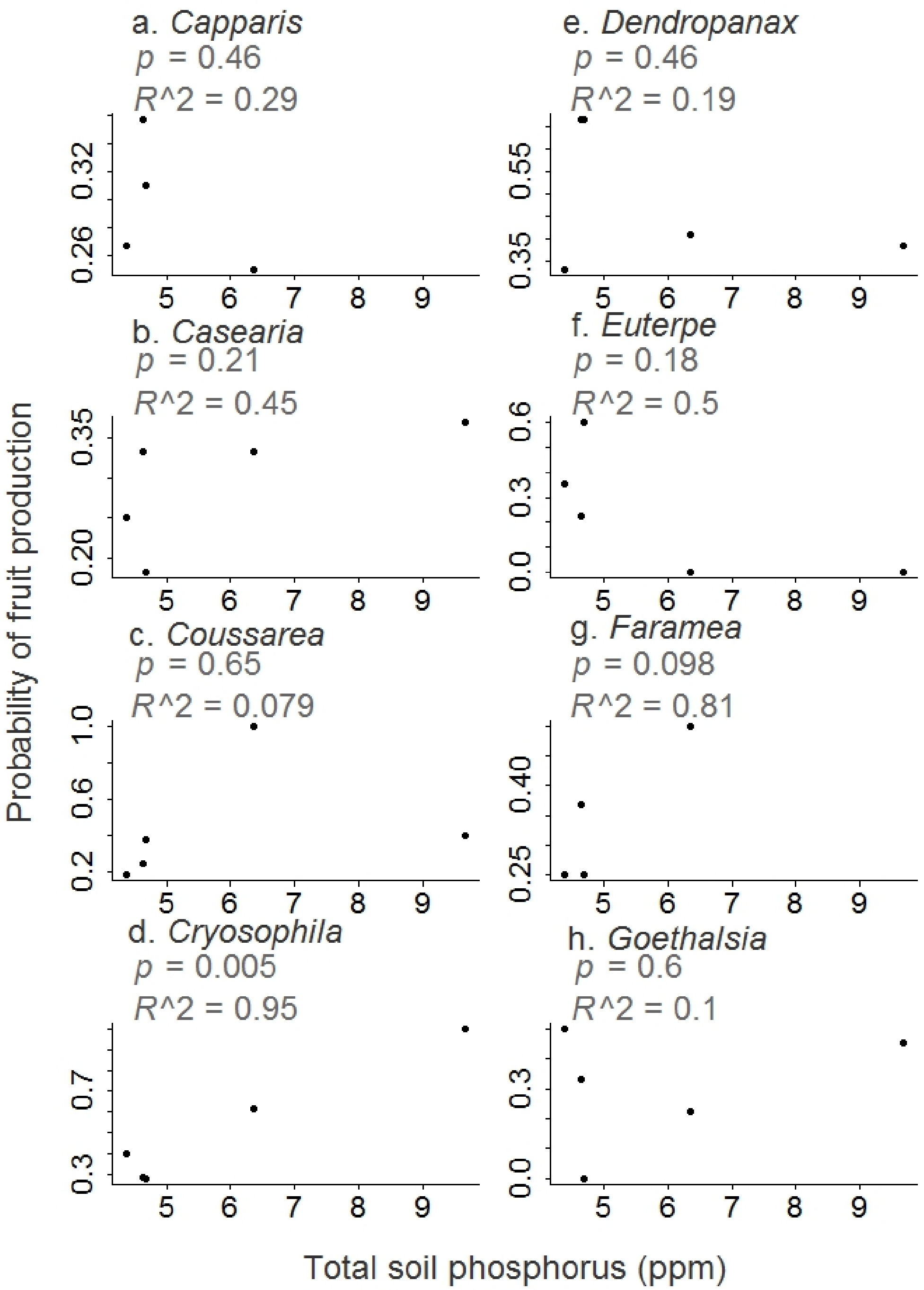
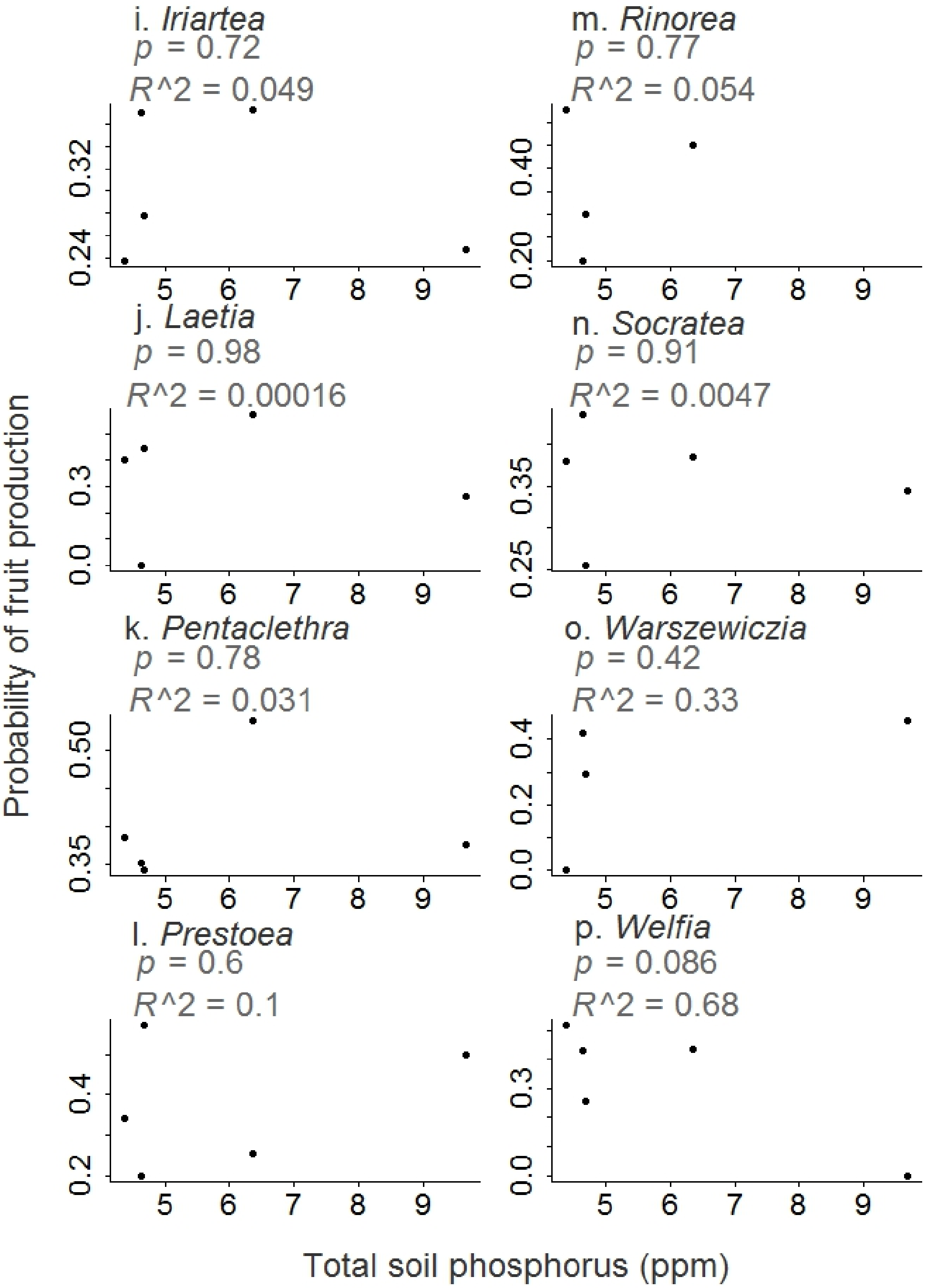


Figure 15: **Phosphorus availability vs. probability of fruit production by plot for each species.** Each point represents one plot at La Selva, Costa Rica. Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 15 (cont'd)



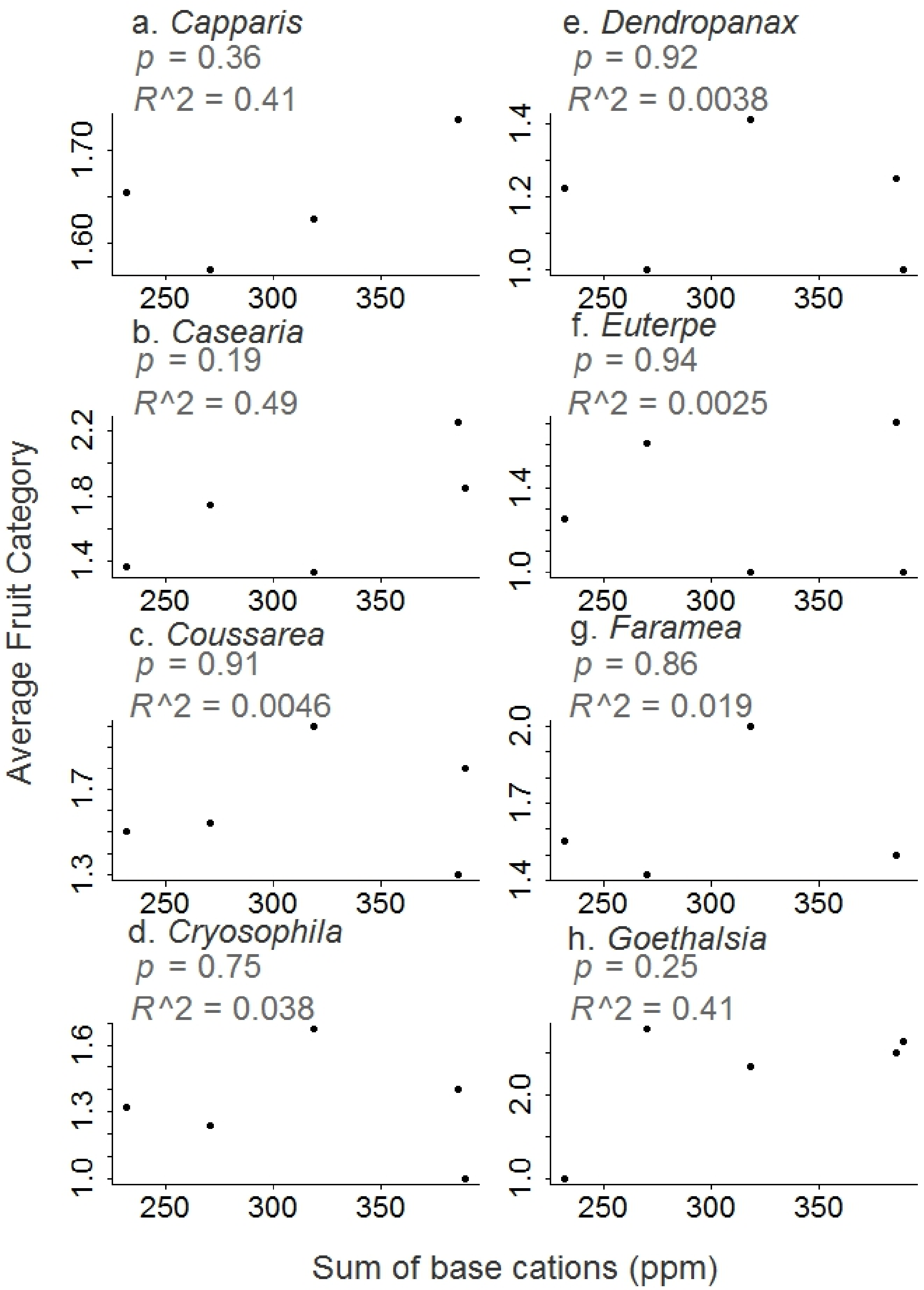
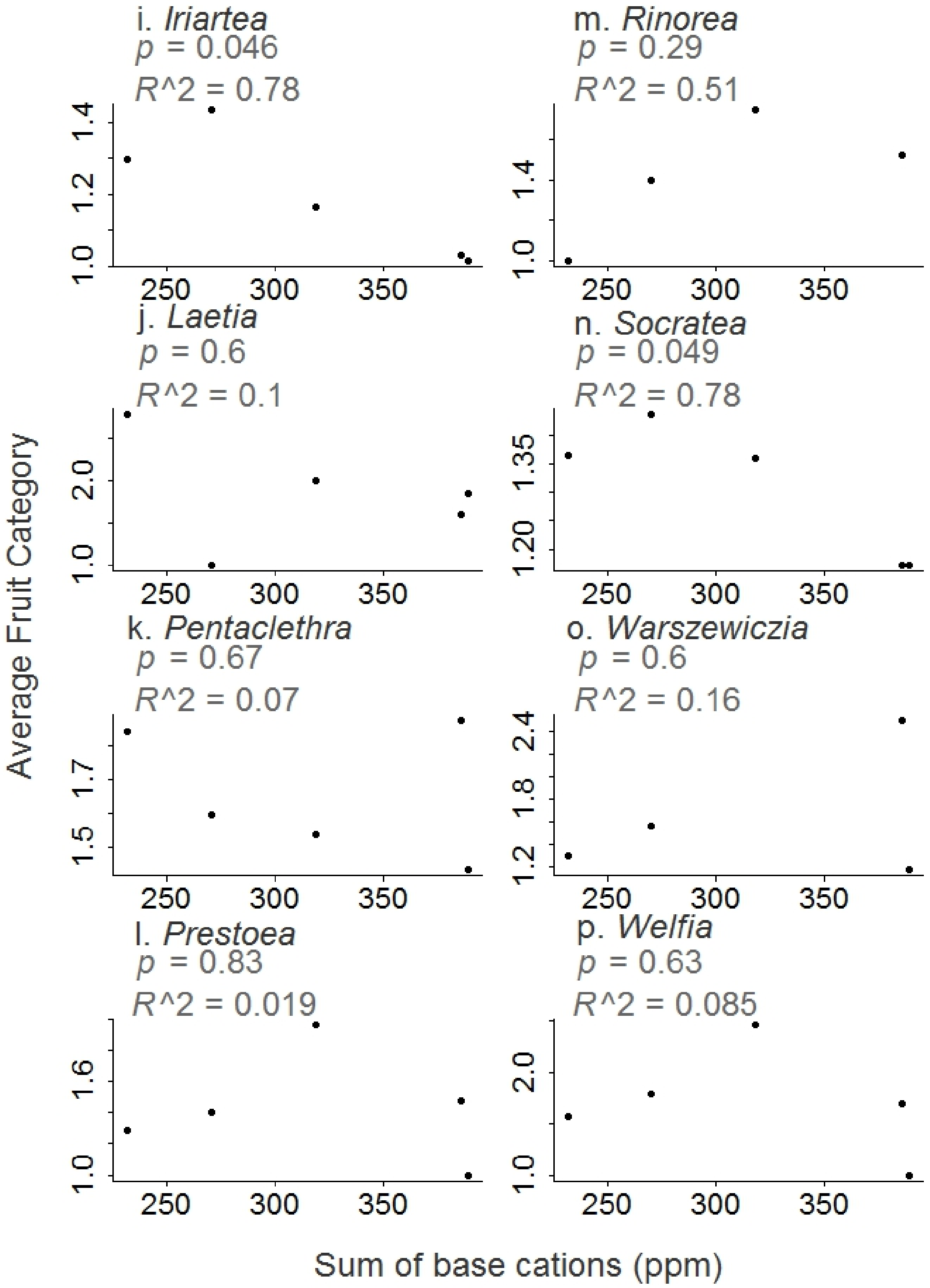


Figure 16: **Sum of base cation availability vs. average maximum fruiting category by plot for each species.** Each point represents one plot at La Selva, Costa Rica. Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 16 (cont'd)



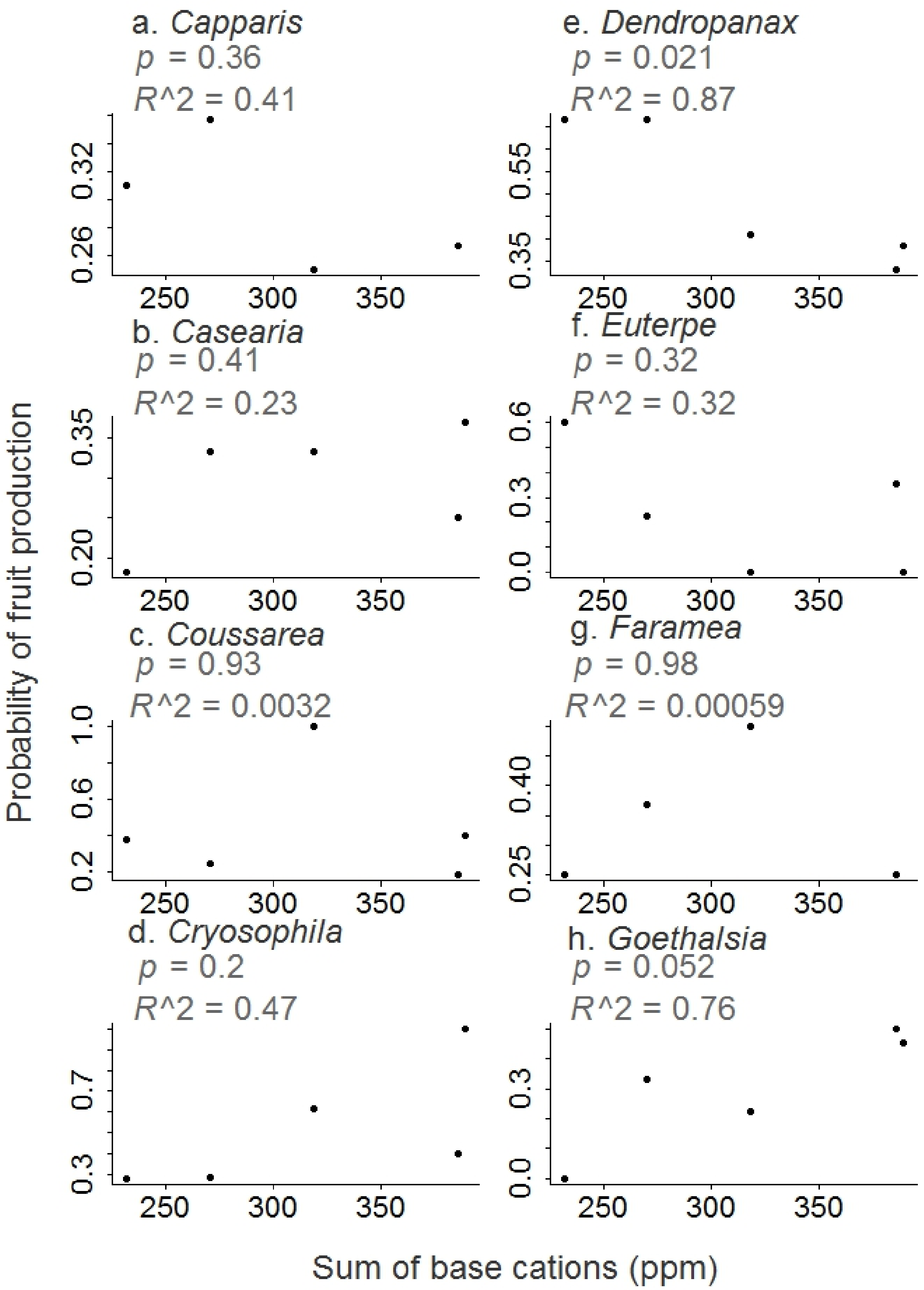
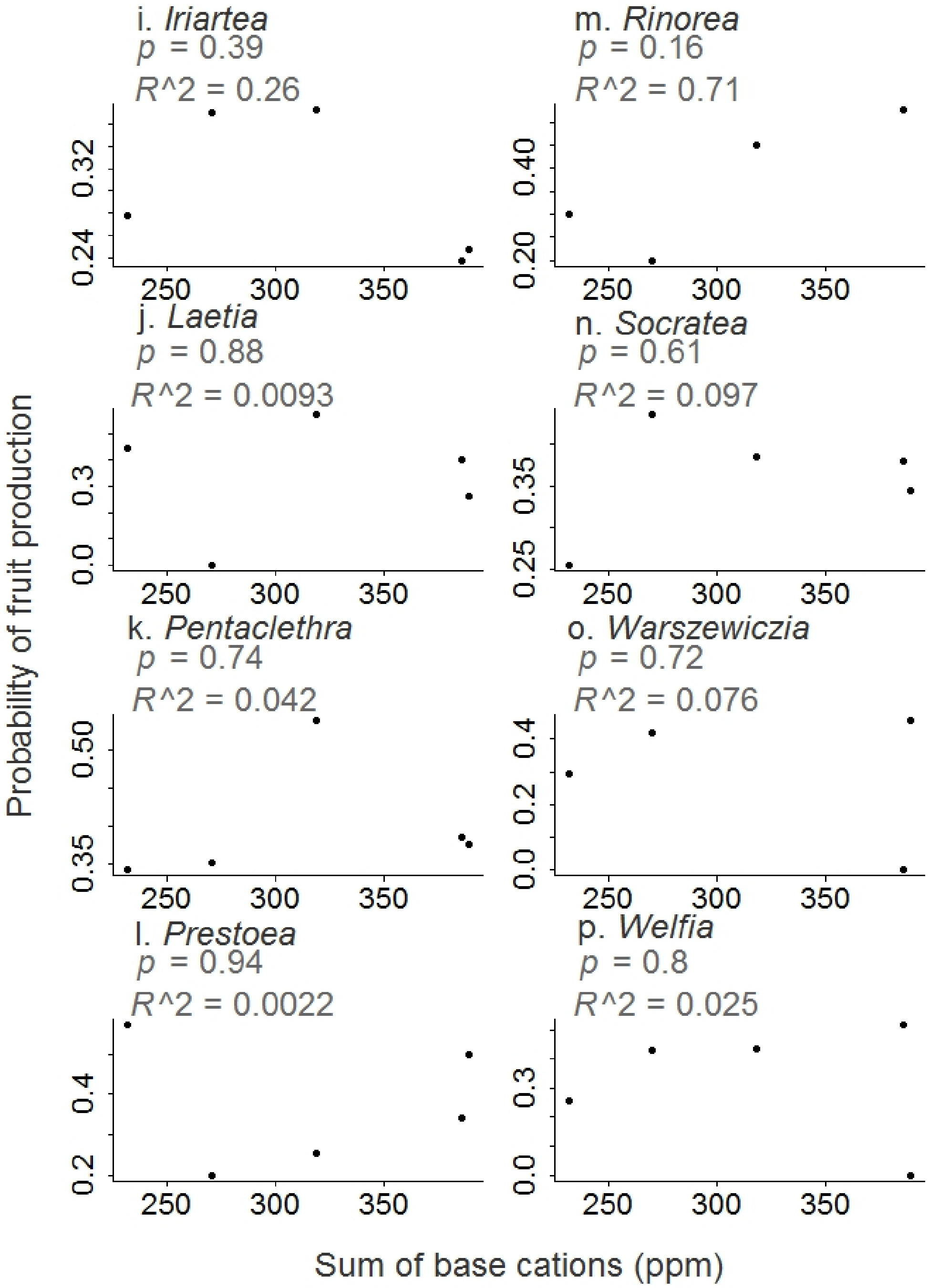


Figure 17: **Sum of base cation availability vs. probability of fruit production by plot for each species.** Each point represents one plot at La Selva, Costa Rica. Simple linear regressions were performed for each species. R^2 and p-values are reported.

Figure 17 (cont'd)



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