

# Pulsed-resource mast systems and the movement, demographic storage, and diet breadth of consumers

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**Running head:** Masting and consumers

## Abstract

Mast-fruiting trees constitute a pulsed resource that both supports and destabilizes consumer populations. Whereas a reliable resource is abundant on average, with limited variation in time and space, masting events are volatile and localized (near seed-bearing trees), and that variability ramifies throughout food webs. The life histories and foraging patterns of mast consumers should be regulated by covariance structure in time, in space, and across a diverse diet. Theory is developed to evaluate how the space-time structure of masting interacts with the capacities of consumers to exploit alternative hosts, to forage widely in space, and to store reserves in time. Application to data is made possible with Mast Inference and Forecasting (MASTIF), a state-space autoregressive model that predicts resource availability within the canopy and on the forest floor, applied as an example here to trees in the genus *Pinus* across a network of inventory sites.

Theoretical contributions include the integration of space-time-species covariance in resource supply with the space-time-diet breadth of consumers. As foraging capacity increases, the volatility of an unreliable resource that varies

widely in space, time, or both, shifts from a variance cost to the mean benefit. Consumers foraging in the canopy (arboreal arthropods and rodents, song birds) experience space-time covariance between host trees. Consumers on the forest floor (rodents, ground-nesting birds and larger mammals) experience a redistribution of that covariance by dispersal. For consumers lacking mobility, demographic storage in episodic recruitment following mast years is important for population persistence. Consumers compensate volatility in time and space with diet breadth. Depending on the dominant masting strategies of host tree species in the diet, habitats differentially limit specific life history strategies that are misaligned. A resource score can be assigned to each consumer-habitat pair that combines the benefits it offers in mean supply weighed against the variance cost. It is scale-dependent, accommodating the space-time-diet ambit of each consumer. The impact of adding or subtracting a diet item can be gauged with the standard error (SE) rule, the mean benefit of an added diet item balanced against the variance cost, both of which depend on the existing diet, the abundance of the new host, and the consumer's foraging ambit. Results rank habitats by their capacities to support wildlife and other consumers from a resource perspective.

**Keywords:** diet breadth, foraging, portfolio effect, resource score, seed predation, seed-shadow models, spatio-temporal covariance, standard error rule

**Supplementary files:** A. Modeling and Computation; B. Parameter estimates; C. MASTIF package ([github url](#))

## INTRODUCTION

Masting trees and shrubs offer a pulsed resource that constitutes the base of forest food chains, both supports and destabilizes consumer populations, and mediates the spatio-temporal structure of communities (Janzen, 1970; Jones et al., 1998; Ostfeld and Keesing, 2000; McShea, 2000; Curran and Leighton, 2000; Koenig and Knops, 2001; Clotfelter et al., 2007; Schmidt and Ostfeld, 2003; Bogdziewicz et al., 2016; McMeans et al., 2016; Rosin and Poulsen, 2016). Seed-shadow models (SSMs) are widely used to describe masting, because they passively monitor both fecundity and dispersal simultaneously for all species that can be recovered and identified in seed traps. Estimates from SSMs provide insights on dispersal and recruitment limitation

11 (Ribbens et al., 1994; Clark et al., 1998, 1999; Nathan and Muller-Landau, 2000;  
12 Bullock and Clarke, 2000; Greene et al., 2004; Fricke and Wright, 2017), gene flow  
13 and hybridization (Garant et al., 2007; Jones and Muller-Landau, 2008; Moran and  
14 Clark, 2011; Moran et al., 2012), migration (Clark et al., 2001), environmental controls  
15 on reproductive effort and sex ratio (Clark et al., 2004; Uriarte et al., 2005; Schurr  
16 et al., 2008; Martinez and Gonzalez-Taboada, 2009; Clark et al., 2011; Uriarte et al.,  
17 2012; Clark et al., 2013, 2014; Canham et al., 2014; Detto et al., 2018), and allocation  
18 (Ladeau and Clark, 2006; Clark et al., 2013; Crone and Rapp, 2014; Berdanier and  
19 Clark, 2016). Some studies examine a single fruiting season, while others track seed  
20 production on inventory plots over time (table 1). Despite the diverse applications,  
21 current models omit key features of most data sets, and they do not estimate the  
22 time-, space-, and tree-dependence, which is often quasi-periodic and synchronous  
23 across individuals (Bogdziewicz et al., 2016; Zwolak et al., 2016; Wang et al., 2017).  
24 This variability ramifies throughout food webs, starting with the seed predators that  
25 forage at spatial scales from a few meters to entire landscapes. Synchronicity is one  
26 type of variation that has been of broad interest, primarily focused on correlation  
27 indices of population sizes over time (Tilman et al., 1998; Loreau and de Mazancourt,  
28 2008; Schindler et al., 2010). A diverse diet of masting hosts raises the more general  
29 problem of covariance in space-time and host-tree-time, across alternative hosts in the  
30 diet that vary in quality and are dispersed throughout the canopy and forest floor. To  
31 complicate inference, the seeds of many species can only be identified in seed traps to  
32 the genus level (fig. 1). Important next steps include theory to connect masting scales  
33 with their consumers and modeling advances to provide the inference and prediction,  
34 with full diagnostics, and demonstrable reproducibility. In this paper, we derive the  
35 space-time and host-time covariance structure faced by consumers that vary in diet  
36 and foraging strategies. We provide a modeling framework and computation that can  
37 be applied broadly for data synthesis.

38 Theory is needed to gauge the capacity of forests to support food webs by regulating  
39 the types of consumers that can persist and the predation risk faced by their masting  
40 hosts (Janzen, 1970; Connell, 1970; Ostfeld and Keesing, 2000; McMeans et al., 2016).  
41 We interpret the term consumers broadly to include seed-attacking fungi and damping-  
42 off pathogens. A reliable resource is abundant on average, with limited variation in  
43 time and space. How does the space-time structure of masting interact with the  
44 capacities of consumers to exploit alternative hosts, to forage widely in space, and

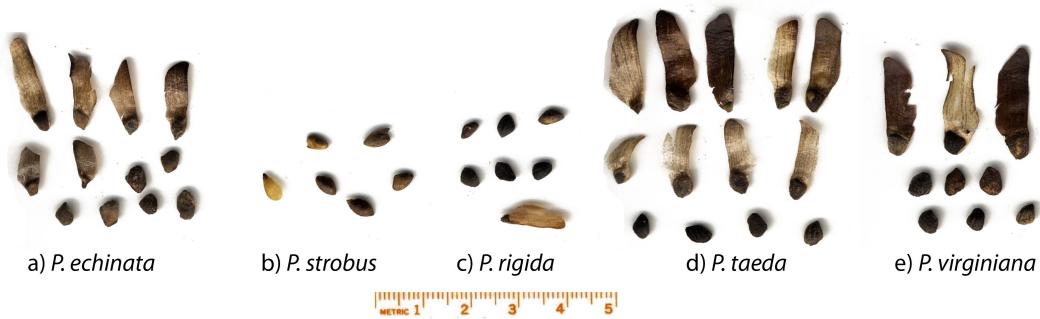


Figure 1: Three seed predators on *Pinus* spp. (above) and five seed types (below). The gray jay (*Perisoreus canadensis*) forages in the canopy (left), the eastern chipmunk (*Tamias striatus*) on the forest floor (center), and the eastern gray squirrel (*Sciurus carolinensis*) in both locations (right). Seeds extracted from seed traps (*Pinus* in this study) can often be identified only to genus level. Upper photos from Roland Kays.

45 to store reserves in time? Spatial variation in mast availability exists within stands  
 46 and across regions (August, 1983; Stein et al., 2014), and it differs in the canopy and  
 47 the understory (Carbone et al., 2005; Sheldon and Nadkarni, 2013). In the canopy,  
 48 host trees are accessed by song birds and arboreal-foraging arthropods and mammals  
 49 (Curran and Leighton, 2000; McShea, 2000; Koenig and Knops, 2001; Perea et al., 2011;  
 50 Schmidt and Ostfeld, 2003; Milleron et al., 2013; Bell and Clark, 2016) (fig. 1). Canopy  
 51 foragers must locate host individuals where and when resources are concentrated—

the *tree-time* covariance between hosts, over years. The density and aggregation of mast trees can vary widely between stands. Many mammals and ground-nesting birds respond to *space-time* covariance on the forest floor (Janzen, 1970; Moore et al., 2007; Zwolak et al., 2016), which combines host location with dispersal to the forest floor (fig. 2d). Arthropod seed consumers exhibit a range of foraging tactics (Janzen, 1970; Bonal and Munoz, 2008; Espelta et al., 2009; Bell and Clark, 2016). Damping-off pathogens appear to have limited dispersal capacity, but can extend dormancy (\*\*) to disperse in time.

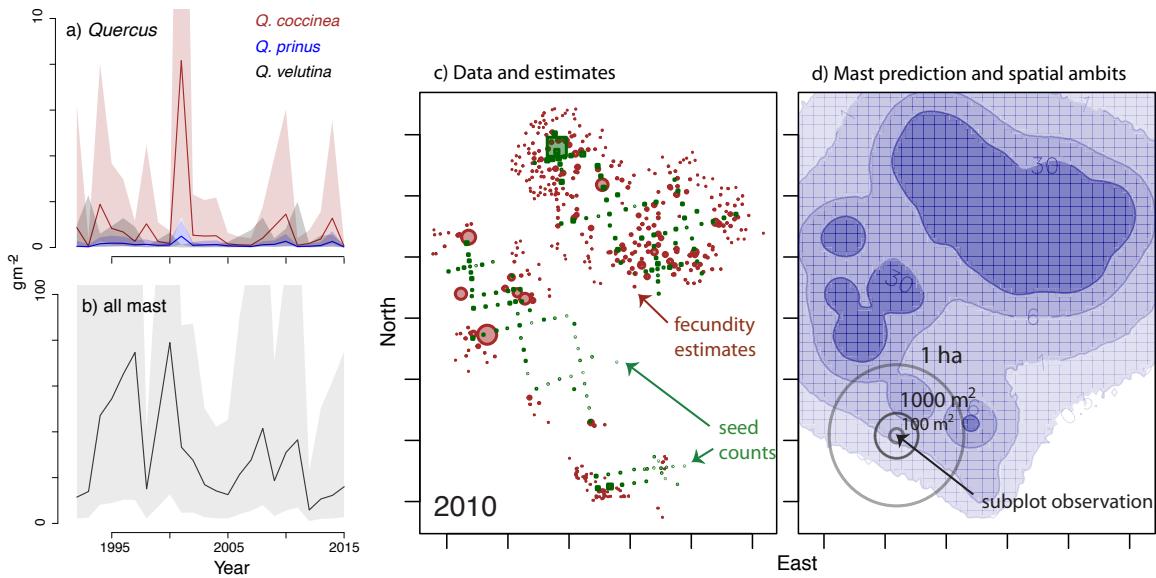


Figure 2: Space-time scales for seeds and consumers. a) Masting by three species in the S Appalachians is erratic. Shading spans 80% of the predictive variation at the  $1 \text{ m}^2$  scale. b) A generalist like *Sciurus* (fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*, *Nyssa*, *Cornus*). c) Fecundity estimates in brown and seed counts in green for *Pinus* in 2010 in the SE Piedmont. d) Predictive mean mast density from data in (c), showing spatial variation with superimposed ambits for species that can be sampled in subplots, including  $100 \text{ m}^2$  (e.g., flightless insects, larder hoarding rodents),  $1000 \text{ m}^2$  (e.g., scatter hoarding grey squirrel, chipmunk), and 1 ha (larger vertebrates).

Variance in space is not decoupled from variance in time and diet breadth. Quasi-periodic mast years can be spaced up to a decade apart (fig. 2a). Host species differ in total seed production, the degree of variation in time, and synchronicity between individuals (Clark et al., 2010). Diet generalists can abide spatio-temporal variation through diet switching, a *portfolio effect* (Tilman et al., 1998; Schindler et al., 2010),

65 while specialization exposes consumers to the full heterogeneity offered by a specific  
 66 host (Devictor et al., 2010; Clavel et al., 2011) (fig. 2a, b). We refer to a consumer's  
 67 *ambit* in space (host trees or ground area), time ( life span, storage potential, and/or  
 68 dormancy), and diet breadth (Carbone et al., 2005; Pelisson et al., 2013; Sainmont  
 69 et al., 2014; Rodel et al., 2016). The combination of these three dimensions determine if  
 70 consumers can abide variation in their hosts and if hosts can benefit by spatio-temporal  
 71 escape (Janzen, 1970; Curran and Leighton, 2000; Grotan et al., 2009; Schmidt and  
 72 Ostfeld, 2003; Lichti et al., 2014). Theory is needed to relate estimates of fecundity  
 73 and dispersal at these tree-space-time covariance scales of the consumer ambit.

74 The genus *Pinus* is used as an example application of theory and analysis developed  
 75 here. Important for a diversity of ground and canopy foragers (fig. 1), this wide-  
 76 ranging and multi-species genus tests our capacity to estimate and predict elements of  
 77 theory when challenged with observation error in seed identification. Arthropod seed  
 78 predators on *Pinus* species forage mainly in the canopy (Cibrian-Tovar et al., 1986).  
 79 Canopy vertebrates include crossbills (*Loxia* spp.) and other finches (Fringillidae),  
 80 nuthatches (*Sitta* spp.), gray jay (*Perisoreus canadensis*), and red-bellied woodpeckers  
 81 (*Melanerpes carolinus*). Ground foraging seed predators include eastern chipmunk  
 82 (*Tamias striatus*), white-footed mice (*Peromyscus leucopus*), and red-backed voles  
 83 (*Clethrionomys gapperi*) (Abbott and Quink, 1970; Ogawa et al., 2017). Eastern gray  
 84 squirrel (*Sciurus carolinensis*) forages in the canopy and on the ground (fig. 1).

85 A solution to the theoretical challenge is of little use without a model that offers  
 86 the necessary estimates. SSMs relate the sizes and locations of host trees and seed  
 87 counts from traps to estimate seed production and dispersal from each tree (fig. 2c).  
 88 SSMs include a likelihood for count data, such as a Poisson distribution, coupled to  
 89 seed production and dispersion processes, which can be written as

$$E[y_s] = A\lambda_s = A \sum_{i=1}^n \mathbf{S}_{s,i} f_i$$

90 where  $E[\cdot]$  is an expectation,  $y_s$  is the number of seeds counted in a trap at location  $s$ ,  
 91  $\lambda_s$  is the expected seed density (seeds  $m^{-2}$   $yr^{-1}$ ),  $A$  is sample effort, the area of a seed  
 92 trap times fraction of fruiting season it was deployed (traps are damaged by tree falls  
 93 and bears) ( $m^2 yr$ ),  $\mathbf{S}_{s,i}$  is the density of seed produced by tree  $i$  dispersed to location  
 94  $s$  ( $m^{-2}$ ), and  $f_i$  is seed production by tree  $i$  (table SA1.1). For a length- $S$  vector of  
 95 seed traps, a length- $n$  vector of fecundities, and a  $S \times n$  kernel matrix  $\mathbf{S}$ , there is a

96 length- $S$  vector of seed density

$$\boldsymbol{\lambda} = \mathbf{S}\mathbf{f} \quad (1)$$

97 Because both fecundity  $\mathbf{f}$  and dispersal capacity  $\mathbf{S}$  are unknown, the efficacy of these  
98 models should depend on the amount of data and its space-time structure.

Table 1: Attributes of some SSMs with examples.

Individuals <sup>a</sup>	Maturation <sup>b</sup>	Time <sup>a</sup>	Examples
eq. (2)	—	—	Clark et al. (1998, 1999); Greene et al. (2004); Uriarte et al. (2005); Jones et al. (2005); Jones and Muller-Landau (2008); Charco et al. (2017)
FE (A)	—	IND	Martinez and Gonzalez-Taboada (2009); Milleron et al. (2013); Canham et al. (2014)
FE (A)	—	RE	Muller-Landau et al. (2008)
—	ZIP	—	LaDeau and Clark (2001)
RE (A, D)	HM	AR(1) (C)	Clark et al. (2004)
RE (A, D)	HM	FE (B)	Ladeau and Clark (2006); Clark et al. (2010, 2011, 2013, 2014)

<sup>a</sup> IND - independent fits to each year; RE - random effect; FE - fixed effect; A - D are terms in table SA1.1.

<sup>b</sup> HM - hidden Markov submodel; ZIP - zero-inflated Poisson

99 Before turning to challenges with SSMs, we summarize why they can often be  
100 preferable to more direct analyses, such as stable isotope labels (Carlo et al., 2009;  
101 Cortes and Uriarte, 2013) or genotyping seeds or seedlings (Godoy and Jordano, 2001;  
102 Grivet et al., 2005; Jones et al., 2005; Pairon et al., 2006; Burczyk et al., 2006; Robledo-  
103 Arnuncio and Garcia, 2007; Jones and Muller-Landau, 2008; Moran and Clark, 2011;  
104 Schupp and Jordano, 2011; Bontemps et al., 2013). Due to labor and expense, typically  
105 only a small sample of seeds or seedlings can be labeled or genotyped, most often from  
106 a single species. Both data types provide information on dispersal, but not fecundity  
107 (Moran and Clark, 2011; Milleron et al., 2013). Because seed traps sample passively,  
108 SSMs provide an efficient option to gather fecundity and dispersal estimates from all  
109 species that can be identified in seed traps simultaneously, naturally integrating space

110 (trap area) and time (trap deployment period).

111 Seed traps record seed rain following any consumption losses that occur in the  
112 canopy. Canopy attack can be recorded by damage classes, such as exit holes by  
113 arthropods and husk removal from fleshy fruits (Bell and Clark, 2016). Other seeds are  
114 consumed, thus reducing total seeds recovered from traps. Some studies that employ  
115 seed traps together with direct access to the canopy directly (LaDeau and Clark, 2001;  
116 LaDeau and Clark, 2006) or observe seeds from the ground (Minor and Kobe, 2017)  
117 find substantial agreement. A tropical study found more liana seeds in seed traps  
118 placed directly in the canopy than in traps placed above the forest floor (Sheldon  
119 and Nadkarni, 2013). In general, seed trap estimates are recognized as potentially  
120 underestimating total fecundity.

121 Countering the advantages, SSMs are difficult to evaluate, because both seed pro-  
122 duction and dispersal must be estimated. For known  $\mathbf{S}$  and mean seed counts (an  
123 estimate of  $\boldsymbol{\lambda}$ ) eq. (1) can be solved directly,  $\hat{\mathbf{f}} = (\mathbf{SS}')^{-1} \mathbf{S}' \hat{\boldsymbol{\lambda}}$  (Clark et al., 2010).  
124 However, there is a unique solution only if there are more seed traps than there are  
125 trees, i.e.,  $S > n$ . Even with few trees, a solution would often include negative values,  
126 which is, of course, impossible. A model for  $f_i$  as simple as a prior distribution that ex-  
127 cludes negative values would fix the negative-fecundity problem, but there might still  
128 be insufficient information in the  $S$  seed counts. The early SSMs did not confront this  
129 problem, because they projected the  $n$  sources down to a few parameters, replacing  
130 individual fecundity in the vector  $\mathbf{f}$  with a function that is shared by all trees, e.g.,

$$f_i = a \times \text{size}_i^b \quad (2)$$

131 (first line of table 1). While such models can converge rapidly, it can be hard to deter-  
132 mine if global parameters  $(a, b)$  accurately describe population heterogeneity. Many  
133 trees might be needed to estimate parameters  $(a, b)$ , but high density of trees degrades  
134 the estimate of dispersal  $\mathbf{S}$ , due to the large overlap in seed shadows. Poorly estimated  
135 dispersal, in turn, degrades the information on fecundity  $\mathbf{f}$ . The question becomes, can  
136 SSMs estimate dispersal, the effects of size  $(a, b)$ , and the fecundities,  $f_i, i = 1, \dots, n$ ?

137 Extensions to eq. (2) have addressed some of the challenges, but they do not offer  
138 the synthesis needed to explain and predict spatio-temporal structure. Initial efforts to  
139 capture heterogeneity at the data stage, with over-dispersed data models (e.g., negative  
140 binomial) (Clark et al., 1998; Muller-Landau et al., 2008), appear less effective than  
141 allowing for heterogeneity between trees and over time (Clark et al., 2004; Martinez

142 and Gonzalez-Taboada, 2009; Uriarte et al., 2012; Clark et al., 2013).

143 Subsequent joint modeling of maturation and fecundity combined with in- and  
144 out-of-sample prediction showed that aggregate models like eq. (2) miss the pervasive  
145 heterogeneity. Inventory plots sampled over multiple years provide opportunity to  
146 quantify not only time-dependence (Clark et al., 2004, 2010), but also quasi-periodic  
147 variation and synchronicity (Koenig and Knops, 2001; Boutin et al., 2006; Bergeron  
148 et al., 2011; Wang et al., 2017). Binary maturation status  $\rho_{i,t}$  for an individual  $i$   
149 in year  $t$ , together with conditional fecundity  $\psi_{i,t}|\rho_{i,t} = 1$ , were introduced dynami-  
150 cally to allow for maturation schedules, as a hidden Markov (HM) process (table 1).  
151 Results showed that few individuals are reproductively mature. For mature trees, fe-  
152 cundity ranges over orders of magnitude and is only weakly related to tree size; it is  
153 often concentrated within few individuals (Clark et al., 2004, 2010; Nanos et al., 2010;  
154 Moran and Clark, 2011; Milleron et al., 2013; Minor and Kobe, 2017). Environmental  
155 predictors are often needed to estimate maturation and fecundity (Clark et al., 2004;  
156 Minor and Kobe, 2017). Tree-level random effects allow for the large differences be-  
157 tween individual trees that cannot be explained by covariates. Year effects account for  
158 variation in time that is shared across individuals (Clark et al., 2010, 2013). Autore-  
159 gressive (AR( $p$ )) models allow for lag effects up to  $p$  years. Thus far, only the AR(1)  
160 model has been implemented (Clark et al., 2004), whereas masting commonly involves  
161 multi-year lags (Koenig and Knops, 2001). Joint models for growth, survival, and  
162 fecundity provide estimates of allocation responses to the environment (Clark et al.,  
163 2010, 2014; Berdanier and Clark, 2016), but they cannot be used where only seed data  
164 are available or of interest.

165 In summary, at least three advances are needed to translate data to estimates of  
166 masting impacts on consumers. First is the missing theory for space-time covariance  
167 structure that could guide model development. Second is a modeling framework that  
168 delivers the necessary estimates. Finally, computation that is accessible to a commu-  
169 nity of users is needed to promote synthesis. Ideally, that framework would include  
170 simulation, to learn about the conditions where all elements can be identified. The  
171 potential to integrate data sets could help determine the controls on the site-to-site  
172 variation in consumers and their dynamics over time.

173 The goals of this paper are ambitious, yet focused. Here we provide both the theory  
174 and the modeling needed to synthesize space, time, and diet breadth with masting data,  
175 packaged in a computational framework that provides the critical estimates. It fills an

176 important gap in species-distribution modeling, which has thus far emphasized climate  
 177 and soils, but omitted food. By deriving the resource value of forest stands, based on  
 178 their means and covariance structures, we hope to enrich the potential to predict food  
 179 web structure. We leave the application of theory to a subsequent paper. A more  
 180 sweeping comparison of theory and data is needed, because resource supply, while  
 181 critical, must be analyzed in combination with the more traditional climate and habitat  
 182 variables across a network sites (Nuñez et al, in prep). The next section provides  
 183 background theory and the model framework used to estimate masting structure.

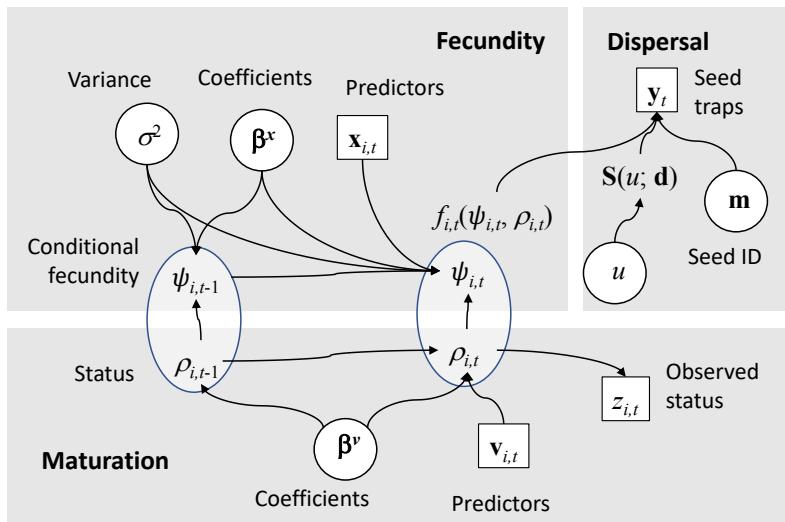


Figure 3: Graphical model for main elements of the model, including fecundity (above),  
 maturation (below), and dispersal (right), showing estimates (circles) and observed  
 variables (squares), with dynamics ( $t - 1, t$ ). Variables are defined in table SA1.1.

184

## MODEL DEVELOPMENT

185 Following a model summary, we incorporate masting effects on covariance between  
 186 host trees, in space, and over years, and we translate that covariance to the generalist  
 187 consumer with multiple hosts.

188 Consider an inventory plot where trees mature, after which they are capable of  
 189 seed production (fig. 3). The event that tree  $i$  can produce seed in year  $t$  is the  
 190 *maturity state*,  $\rho_{i,t} \in \{0, 1\}$ . Maturation is a hidden Markov probit with coefficients

<sup>191</sup>  $\beta^v$  describing covariate effects on maturation probability (eq. (SA1.7)). Observations  
<sup>192</sup> of maturation state  $z_{i,t} \in \{0, 1\}$  contribute to estimates (eq. (SA1.6)) (see also Clark  
<sup>193</sup> et al. (2010)).

<sup>194</sup> Annual seed production by a mature individual ( $\rho_{i,t} = 1$ ) is termed *conditional fe-*  
<sup>195</sup> *cundity*,  $\psi_{i,t} > 0$ . Like maturation, conditional fecundity is a dynamic process, modeled  
<sup>196</sup> with fixed and random effects, year effects, and/or autoregressive terms (table SA1.1,  
<sup>197</sup> submodel A). Coefficients in  $\beta^x$  can include tree size (eq. (2)), environment, and in-  
<sup>198</sup> teractions (Clark et al., 2010, 2013). *Random effects* (REs)  $\beta_i^w$  accommodate the het-  
<sup>199</sup> erogeneity of responses across individual trees (table SA1.1, submodel D). Year effects  
<sup>200</sup>  $\gamma_t$  are an alternative to a large covariance matrix across individuals (table SA1.1, sub-  
<sup>201</sup> model B). Alternatively, quasi-periodic variation can be described by an *autoregressive*  
<sup>202</sup> *model AR(p)* with  $l = 1, \dots, p$  lag terms  $\alpha_l$  (table SA1.1, submodel C). Year and lag  
<sup>203</sup> effects can be random across species and/or region groups, recognizing that masting  
<sup>204</sup> may be coherent within, but not between, groups. *Actual fecundity* is  $f_{i,t} = \psi_{i,t}\rho_{i,t} \geq 0$ .

<sup>205</sup> Seeds accumulate in traps  $s = 1, \dots, S$  from nearby trees, depending on dispersal.  
<sup>206</sup> A *dispersal kernel*  $\mathbf{S}(\mathbf{u})$  includes fitted parameters  $\mathbf{u} = u_1, \dots, u_H$  for each species  $h$   
<sup>207</sup> eq. (SA1.1) (eq. (1)). The seed count  $y_{sm,t}$  is the number of seeds of type  $m$  counted in  
<sup>208</sup> a trap at  $s$  in year  $t$ . Seeds are counted by species or, if species identity is unclear, then  
<sup>209</sup> genus (section SA1.4). When multiple species  $h = 1, \dots, H$  contribute to the same  
<sup>210</sup> seed type(s), as when some seeds are identified only to genus, then the  $m = 1, \dots, M$   
<sup>211</sup> seed types must be included in the model with the  $H$  species that could have produced  
<sup>212</sup> them. Observation error enters by a  $H \times M$  matrix  $\mathbf{M}$  holding probabilities that a  
<sup>213</sup> seed of species  $h$  will be assigned to type  $m$ . The *likelihood* is Poisson and incorporates  
<sup>214</sup> sample effort (trap area  $\times$  active period). The full model and prior distributions are  
<sup>215</sup> discussed in section SA1.2 and section SA1.5, respectively.

<sup>216</sup> All else being equal, a habitat that offers an abundant (large mean) and reliable  
<sup>217</sup> (small variance) food supply benefits a specialist consumer. We wish to evaluate how  
<sup>218</sup> the mean and spatio-temporal covariance impact consumers of multiple host species  
<sup>219</sup> that differ both in abundance and quality,

$$q_{i,t} = r_{h[i]} f_{i,t} \quad (3)$$

<sup>220</sup> where  $r_{h[i]}$  is the quality of a seed of species  $h$  corresponding to tree  $i$ . Here we use seed  
<sup>221</sup> mass as an index for quality. Dispersal translates resource abundance experienced by  
<sup>222</sup> a canopy forager on host tree  $i$ ,  $q_{i,t}$  (kg per host tree), to abundance on the ground at

223 location  $s$ ,  $g_{s,t}$  ( $\text{g m}^{-2}$ ).

224 A consumer that forages widely realizes the mean resource availability, through  
225 movement, storage, and/or diet breadth. Movement scale in the canopy is summarized  
226 by the  $n$  hosts visited by a consumer. On the forest floor, the movement scale is  
227 represented by the number of contiguous sites  $S$ , with a site defined at  $5 \text{ m} \times 5 \text{ m}$ .  
228 Time dependence enters when the proceeds of a high mast year can be 'stored' within  
229 individuals, by dormancy (fungal pathogens) or so-called *capital breeding* (mammals)  
230 (Karasov, 1986; Sainmont et al., 2014; Rodel et al., 2016), or within populations,  
231 the latter here termed *demographic storage*. Demographic storage describes pulsed  
232 recruitment following masting events (McShea, 2000; Koenig and Knops, 2001; Boutin  
233 et al., 2006; Clotfelter et al., 2007; Descamps et al., 2008; Bergeron et al., 2011; Schmidt  
234 and Ostfeld, 2003; Pelisson et al., 2013; Ogawa et al., 2017), stored as a cohort that can  
235 survive subsequent non-mast years, during which recruitment might not be sufficient  
236 for population persistence. Diet generalists experience dependence across individuals  
237 of multiple host species.

238 Let  $Q_{nT} = \sum_{i,t} q_{i,t}$  be the yield to a canopy consumer from  $n$  host trees over  $T$   
239 years, with expectation

$$E_{nT}(Q) = nT \cdot E_{it}(q) \quad (4)$$

240 where  $E_{it}(q)$  is the per-host, per-year expected yield. A consumer on the forest floor  
241 obtains yield  $G_{ST} = \sum_{s,t} g_{s,t}$ , with expectation

$$E_{ST}(G) = ST \cdot E_{st}(g) \quad (5)$$

242 If  $n$  or  $S$  are small and  $T$  is small, these totals will have large variances.

243 A consumer with restricted space-time foraging and narrow diet breadth is vulner-  
244 able to the variance; individuals and populations suffer in places and times of resource  
245 limitation. To weigh the benefits of high mean resource supply,  $E_{it}(q)$  or  $E_{st}(g)$ ,  
246 against the variance cost,  $Var(Q_{nT})$  or  $Var(G_{ST})$ , we build from a familiar index used  
247 to describe masting, the coefficient of variation,  $CV = \sqrt{Var(Q_{nT})}/E_{nT}(Q)$  (Herrera  
248 et al., 1998; LaMontagne and Boutin, 2009; Pesendorfer et al., 2016), but extend it to  
249 the problem of scale-dependence across multiple host species of variable resource qual-  
250 ity (eq. (3)). The traditional  $CV$  is inadequate, because masting intervals of 2 to 10  
251 years having the same  $CV$  will not have the same impacts on consumers that differ in

space-time-resource ambit. Our *resource score* inverts the  $CV$  (a score increases with the mean and declines with the variance), makes it scale-dependent, and expresses it on a proportionate (log) scale,  $R_{nT} = -\log CV_{nT}$  (tree-time) and  $R_{ST} = -\log CV_{ST}$  (space-time).

As a baseline for scale-dependence, we first evaluate the scale-independent resource score. The expected yields in eq. (4) and eq. (5) have corresponding expected variances,

$$E(Var(Q_{nT})) = nT \cdot Var_{it}(q) \quad (6)$$

$$E(Var(G_{ST})) = ST \cdot Var_{st}(g) \quad (7)$$

The baseline resource score in the canopy increases with scale at a rate of  $\log(nT)/2$ ,

$$E(R_{nT}) = -\log CV_{nT} = \log E_{it}(q) + \frac{\log n + \log T - \log Var_{it}(q)}{2} \quad (8)$$

By substituting  $n$  for the subscript  $nT$ , the resource score applies to  $n$  host trees in a single year. A subscript  $T$  applies to a single host over  $T$  years. Likewise, for the forest floor there is a resource score for  $T$  years in one site, for  $S$  sites in a single year, and for  $ST$  site-years.

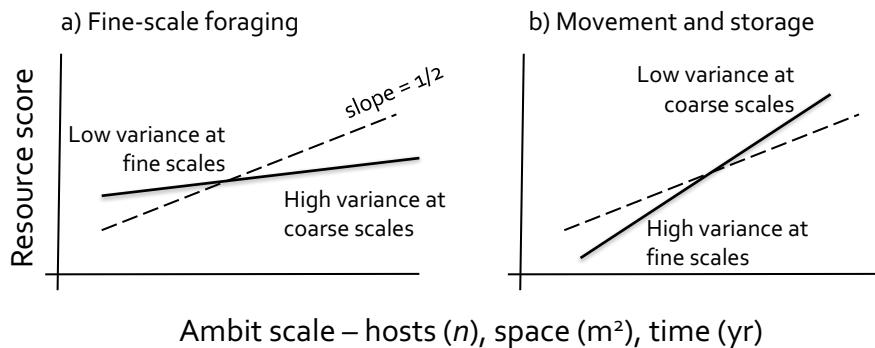


Figure 4: For scale-independent variation, the resource score increases with a slope of 1/2 on a log scale with  $n$  (host trees), space (area), and time (years) (eq. (8)). Especially beneficial for consumers with limited ambit are stands offering high mean and low variance at fine scales (a) and vice versa (b). [HORIZONTAL AXIS MUST SAY LOG SCALE]

The baseline eq. (8) provides an index to compare forest stands that differ in scale dependence (fig. 4). Extended mobility and storage may be of limited benefit where

265 fine-scale variation is low (fig. 4a). All else equal, high space-time variance at fine  
266 scales benefits the consumer that moves (fig. 4b), where the incremental increase in  
267 the total resource more than compensates for the scale-dependent variance. Again,  
268 space-time must be considered together, because a local forager, favored by (fig. 4a)  
269 may solve high-spatial variance with storage or dormancy in time (*Diet breadth and*  
270 *variance perceived by the consumer*). The covariances required to evaluate the resource  
271 score are described in the next section.

## 272 *Tree-time and space-time covariance*

273 Differences in masting structure experienced by consumers in the canopy and on the  
274 ground are summarized by stand-specific mean and covariance structure that will sub-  
275 stitute for the scale-independent values in eq. (8). In the canopy, the relevant covari-  
276 ance is between individual host trees, i.e., fecundity before seeds are dispersed. This  
277 is *individual-time* or *tree-time* covariance. On the forest floor, the relevant covariance  
278 is *space-time*; it follows dispersal.

279 Space- and time-dependence can be evaluated for estimated or for predicted tree-  
280 by-tree covariance, which is then combined with spatial covariance induced by disper-  
281 sal. Functional forms from the geospatial literature summarize space-time structure  
282 with a relatively small number of parameters (Gneiting, 2002; Banerjee et al., 2014).  
283 For the case of tree covariance, there is no evidence for a distance-related covariance  
284 between trees within stands (Clark et al., 2010), consistent with widely observed re-  
285 gional coherence (Liebhold et al., 2004; Fernandez-Martinez et al., 2017). For this  
286 reason, within-stand canopy covariance is between trees, rather than over distance.  
287 On the forest floor, spatial covariance combines tree covariance with dispersal. We  
288 do not introduce a geospatial model, because it is already imposed by the kernel  $\mathbf{S}$ .  
289 For covariance over time, we use the covariance in the estimated fecundity from the  
290 model. Although model fitting can include AR( $p$ ) or year terms (table SA1.1), we  
291 expect fecundity predictions to often include wide uncertainty. Fecundity estimates  
292 can be much more accurate than predictions (section SA1).

293 The analysis begins with a fecundity matrix  $\mathbf{F}_{(n \times T)}$  consisting of elements  $f_{i,t}$  with  
294 expectation and covariance

$$\begin{aligned} E(\mathbf{f}_{(nT)}) &= \boldsymbol{\psi}_{(nT)} \\ Cov(\mathbf{F}_{(n \times T)}) &= \mathbf{C} \end{aligned} \tag{9}$$

where  $\mathbf{f}_{(nT)} = vec(\mathbf{F}_{(n \times T)})$  and  $\boldsymbol{\psi}_{(nT)}$  are length- $nT$  vectors, and  $\mathbf{C}$  is the  $nT \times nT$  covariance matrix that incorporates both the relationships between individual trees and their variation over time (table SA3.2). The  $vec(\cdot)$  operator stacks the columns of a matrix to obtain a vector. An element  $\mathbf{C}_{it,i't'}$  holds the covariance between individual  $i$  in year  $t$  and individual  $i'$  in year  $t'$ . We cannot estimate the tree-time matrix  $\mathbf{C}$ , because each  $(i, i', t, t')$  combination happens once. Below we introduce the *tree-lag* covariance. First we note two special cases, i) a  $n \times n$  (tree-to-tree) covariance  $\mathbf{C}_n$  holding the covariances experienced by a consumer that moves between  $n$  host trees in a random year, and ii) a  $T \times T$  (year-to-year) covariance  $\mathbf{C}_T$ , holding the covariances experienced by a consumer that tracks a random host over  $T$  years (table SA3.2).

In contrast to tree-time covariance in the canopy, ground foragers respond to space-time covariance, which depends on tree locations, the individual-time covariance, and dispersal. For year  $t$  with tree fecundity vector  $\mathbf{f}_{(n)}$  there are expected seed intensities at the locations  $\mathcal{S} = 1, \dots, S$

$$\begin{aligned} E(\mathbf{y}_{(S)} | \mathbf{f}_{(n)}) &= \mathbf{\Lambda} | \mathbf{f}_{(n)} \\ &= \mathbf{S}_{(S \times n)} \mathbf{f}_{(n)} \end{aligned}$$

The conditional covariance in intensity is

$$Cov(E(\mathbf{y} | \mathbf{f})) = Cov(\mathbf{\Lambda} | \mathbf{f}) = \mathbf{S} \mathbf{C}_n \mathbf{S}'$$

(table SA3.2). The total covariance additionally includes the Poisson variance,

$$\begin{aligned} \mathbf{G}_S = Cov(\mathbf{y}) &= Cov(E(\mathbf{y} | \mathbf{f})) + E(var(\mathbf{y} | \mathbf{f})) \\ &= \mathbf{S} \mathbf{C}_n \mathbf{S}' + diag(\mathbf{S} \mathbf{f}) \end{aligned} \tag{10}$$

Combining these terms confirms that they describe covariance in simulated data (fig. 5, right). The first term in eq. (10) combines the covariance between trees with seed dispersal (fig. 5, left). There can be negative covariances (blue in fig. 5), depending on covariance structure in  $\mathbf{C}_n$ , but positive values dominate, imposed by dispersal.

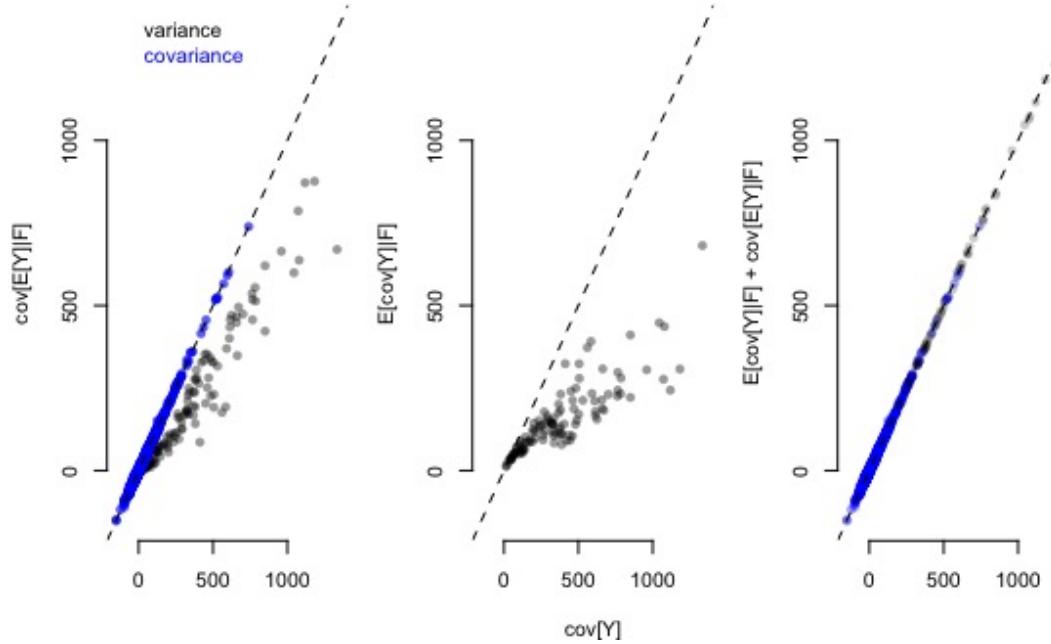


Figure 5: Contributions to space covariance  $\mathbf{G}_S$  from terms in eq. (10) plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in section SA2.

This effect will vary for each forest stand, depending on the distributions of hosts, their fecundities, and their dispersal distances. The second term in eq. (10) contributes only (positive) variance (fig. 5, center), acting like the nugget of geospatial models (Banerjee et al., 2014)<sup>1</sup>. The next section extends these results to multiple consumers.

### **Diet breadth and variance perceived by the consumer**

Because consumers exploit multiple resources, the covariance structure describes their combined supply, accounting for differences in nutritional quality and space-time availability. For the canopy, the aggregate seeds available to the consumer of  $n$  hosts over  $T$  years is  $C_{nT} = \mathbf{1}_n \mathbf{F} \mathbf{1}_T$ , for  $n \times T$  fecundity matrix  $\mathbf{F}$ . The total resource is

$$Q_{nT} = \mathbf{r}'_n \mathbf{F} \mathbf{1}_T \quad (11)$$

where  $\mathbf{r}_n = r_{h[1]}, \dots, r_{h[n]}$  is the vector of seed quality associated with each tree with elements given by eq. (3). Note that  $\mathbf{r}_n$  combines all host species and individuals in

---

<sup>1</sup>However, a nugget is not needed here to make  $\mathbf{G}_n$  positive definite, as  $\mathbf{S} \mathbf{C}_n \mathbf{S}'$  is typically positive definite.

326 the diet. There are also aggregate variances for a random year on  $n$  host trees, and  
 327 for a random host tree over  $T$  years. For example, the aggregate variance over all host  
 328 trees in the diet is,

$$Q_n = \mathbf{r}'_n \mathbf{C}_n \mathbf{r}_n = \mathbf{1}'_n \mathbf{Q}_n \mathbf{1}_n \quad (12)$$

329 where  $\mathbf{Q}_n$  is the covariance for resource yield between trees (eq. (3), table SA3.2).

330 To combine the contributions of mean and variance, the resource score for the  
 331 consumer foraging over  $n$  trees replaces terms in eq. (8) with those that come from  
 332 the scale-dependent space-time covariance. For example, foraging over  $n$  hosts and  $T$   
 333 years gives the score

$$R_n = \log Q_{nT} - \frac{\log Var(Q_{nT})}{2} \quad (13)$$

334 where  $Q_{nT}$  and  $Var(Q_{nT})$  are given in table SA3.2. This variation can be compared  
 335 to that expected for scale-independent variation in eq. (8).

336 We can combine eq. (8) with eq. (13) to quantify the potential advantage to a  
 337 consumer if it could expand the diet to include a new host  $\tilde{h}$  that brings  $\tilde{n}$  new host  
 338 individuals into the diet. The aggregate resource from eq. (11) increases by a term

$$Q_{(n+\tilde{n})T} = Q_{nT} + \mathbf{r}'_{\tilde{n}} \tilde{\mathbf{F}}_{\tilde{n}} \mathbf{1}_T \quad (14)$$

339 where  $r_{\tilde{h}}$  is the quality of the new resource, which can be concatenated into a length- $\tilde{n}$   
 340 vector  $\mathbf{r}_{\tilde{n}}$ , and  $\tilde{\mathbf{F}}_{\tilde{n}}$  is the  $\tilde{n} \times T$  matrix of seed produced by new host individuals. The  
 341 expected addition to the diet from the second term in eq. (14) is

$$E(\mathbf{r}'_{\tilde{n}} \tilde{\mathbf{F}}_{\tilde{n}} \mathbf{1}_T) = r_{\tilde{h}} \tilde{n} T \cdot E_{it}(\tilde{f}) = \tilde{n} T \cdot E_{it}(\tilde{q}) \quad (15)$$

342 where  $E_{it}(\tilde{f})$  is the expected seed production by the new host. From eq. (12), the  
 343 aggregate variance adds two terms,

$$Var(Q_{(n+\tilde{n})T}) = Var(Q_{nT}) + \mathbf{r}'_{\tilde{n}T} \mathbf{C}_{\tilde{n}T} \mathbf{r}_{\tilde{n}T} + 2\mathbf{r}'_{\tilde{n}T} \mathbf{C}_{\tilde{n}T, nT} \mathbf{r}_{nT} \quad (16)$$

344 where  $\mathbf{C}_{\tilde{n}T}$  is the  $\tilde{n}T \times \tilde{n}T$  covariance for new host trees, and  $\mathbf{C}_{\tilde{n}T, nT}$  is the  $\tilde{n}T \times nT$   
 345 covariance between new and original hosts in the diet. Of course, strong negative  
 346 covariance with hosts now in the diet (third term in eq. (16)) decreases aggregate  
 347 variance, with obvious benefits. Not so obvious is the fact that, even if independent of

348 the current diet, the resource score is expected to increase whenever the contribution  
 349 to the aggregate mean compensates for the increase in variance. For independent  
 350 variation eq. (16) simplifies to

$$Var(Q_{(n+\tilde{n})T}) = Var(Q_{nT}) + r_h^2 T \cdot Var_{it}(\tilde{f}) \quad (17)$$

$$= Var(Q_{nT}) + \tilde{n} T \cdot Var_{it}(\tilde{q}) \quad (18)$$

351 The new host increases the consumer's resource score if this inequality is satisfied:

$$Q_{nT} + \tilde{n} \cdot E_{it}(\tilde{q}) > \sqrt{var(Q_n) + \tilde{n} \cdot Var_{it}(\tilde{q})} \quad (19)$$

352 (CHECK T) As the number of new hosts becomes large,  $\tilde{n} > n$ , this inequality tends  
 353 to

$$E(\tilde{q}) > \sqrt{\frac{Var(\tilde{q})}{\tilde{n}}} \quad (20)$$

354 If the consumer were a statistician, she would recognize the right-hand side of eq. (20)  
 355 to be her standard error (SE) for yield on the left-hand side. A large yield from  
 356 the new host on the left combines with the averaging effects of scale  $\tilde{n}$  on the right  
 357 to increase the score. It is a consumer-specific SE, because it is referenced to the  
 358 consumer's ambit, including current diet breadth. Hereafter, we refer to the *SE rule*  
 359 as a rule-of-thumb for the advantage of diet breadth.

360 We use resource scores to compare the resource value of stands and how they can  
 361 vary with consumer ambit, including total yield,  $G_{ST}$  or  $Q_{nT}$  (eq. (11)), and score  
 362 (eq. (13)). The contributions of covariance structure across the diet are compared  
 363 with

$$\Delta \text{ score}_{nT} = R_{nT} - E(R_{nT}) \quad (21)$$

364 from eq. (13) and eq. (8) and  $\Delta \text{ score}_{ST}$ .

365 The same analysis leads to a resource score for ground foragers,  $R_{ST}$ . Despite  
 366 positive and negative covariance elements in the canopy, the forest floor covariances  
 367 in  $\mathbf{G}_S$  tend to be positive at the characteristic scales of dispersal (fig. 5). This is  
 368 not necessarily so at broader spatial scales, where the pattern of clumping of trees of  
 369 different species will dominate. Space-lag covariance structure used for  $\mathbf{Q}$  and  $\mathbf{G}$  in  
 370 this section is expanded in section SA3.1.

371

## METHODS

372 For posterior simulation, we implemented Gibbs sampling, a Markov chain Monte  
 373 Carlo (MCMC) technique, including Metropolis and Hamiltonian Markov chain steps  
 374 (section SA8). Predictive distributions were generated for maturation and fecundity,  
 375 which, in turn, predict seeds in-sample (i.e., at seed trap locations and sampling years)  
 376 and out-of-sample (other locations and/or years) (section SA1.6). Partial autocorre-  
 377 lation functions (PACF) quantify the contribution of each lag, while controlling for  
 378 shorter lags. Complex eigenvalues for the AR( $p$ ) model (section SA4) indicate quasi-  
 379 periodic variation. A stationary AR( $p$ ) process has all eigenvalues of less than unit  
 380 modulus (real plus complex parts, section SA4). The tree-lag (canopy) and space-lag  
 381 (forest-floor) covariances (*Space-lag covariance*) were generated with resource scores  
 382 for each plot. Overall structure is summarized by diet-wide entropy experienced by a  
 383 consumer over trees, sites, and years (section SA3.4).

384 The structure and methodology in MODEL DEVELOPMENT was implemented both  
 385 as a generative simulation and as an (inverse) fitting algorithm in the R package Mast  
 386 Inference and Forecasting (MASTIF), <http://rpubs.com/jimclark/281413>. Simula-  
 387 tion validates the model and identifies conditions where an SSM can recover parameters  
 388 and predict data. We follow with application to field data, demonstrating inference  
 389 and spatio-temporal structure.

390

## *Simulation*

391 Rather than offer an exhaustive compilation of simulation studies, we supply the full  
 392 MASTIF package with simple examples for application (section SA2). We adopt this  
 393 approach, because fitting depends on the structure of each stand (density and distri-  
 394 bution of mature trees), dispersal characteristics of each species, and spatio-temporal  
 395 sampling design, including density and dispersal of traps, and the classification of  
 396 seeds into types. As with any model, useful estimates are only expected where there  
 397 is 'signal' in data. Simulation determines if, given signal, the model can recover pa-  
 398 rameters and predict data. We illustrate where an SSM can be successful, and we  
 399 discuss aspects of data structure that can lead to poor performance. The value of the  
 400 simulator is this first opportunity it affords to examine a full range of potential data  
 401 sets.

402

## Application to field data

403 From up to 25 years of continuous seed collections across sites in the eastern US (section SA6), we analyzed mast production for the genus *Pinus*. Multiple species on the  
 404 same plots meant that species identity of most seeds was unknown (fig. 1). Throughout  
 405 this multi-decade study methods emphasized minimizing false-positive seed identifica-  
 406 tions, thus restricting species-specific classifications to unambiguous cases. Field and  
 407 lab methods are detailed in (Clark et al., 1998, 2004, 2010; Moran and Clark, 2011;  
 408 Bell and Clark, 2016). Data summaries are provided in section SA6.

410 For this focus on methodology, predictors are limited to tree diameter, making the  
 411 model comparable with most literature on this subject. The omission of environmental  
 412 predictors that control fecundity (Clark et al., 2004, 2010, 2014) sacrifices predictive  
 413 skill for transparency—our goal here is to focus on space-time structure that is linked  
 414 solely to a size model. Model fitting is demonstrated two ways, with AR(4) and with  
 415 year effects for conditional fecundity (table SA1.1). Prior distributions are provided  
 416 in the section SA1.5.

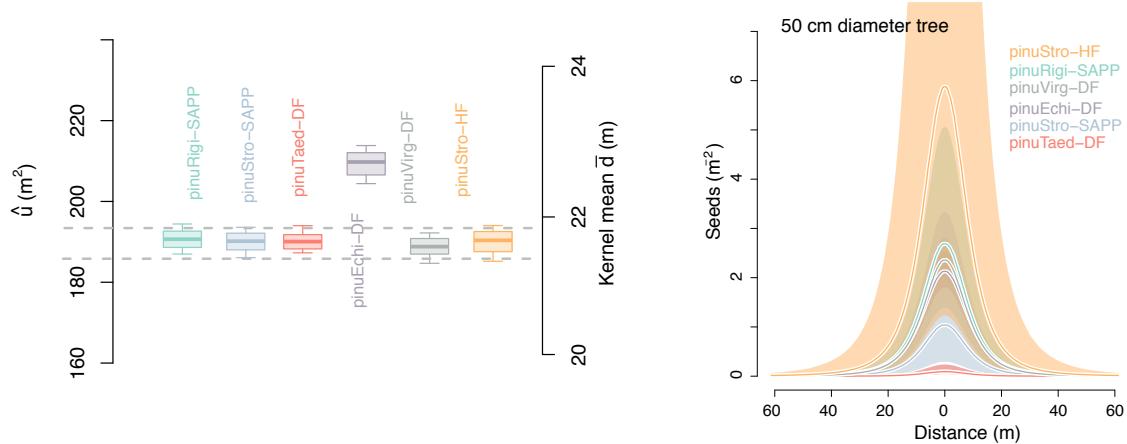


Figure 6: a) Estimates of dispersal parameters  $u_h$  for *Pinus* species-region groups. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. The kernel mean scale at right is eq. (SA5.15). b) Seed shadows predicted from the posterior distribution, with 95% predictive intervals.

417

## RESULTS

418

### *Simulation studies*

419 Simulation studies found that the model can recover parameters and latent states for  
 420 all species, even when most of the seeds (80%) are identified only to genus level. A  
 421 stochastic simulation example is summarized for  $M = 4$  seed types and  $H = 3$  species  
 422 on a mean of  $J = 8$  plots,  $T = 5$  years,  $n = 25$  trees, and  $S = 50$  traps. Parameter  
 423 recovery is approximate, because, as in real data, few trees in a plot of a given species  
 424 are mature. For the simulation shown in fig. SA7.3, the number of trees per plot  
 425 ranges from 4 to 23. Trees far from seed traps supply little information. However, if  
 426 too many trees are close to the same traps, information can be limited by extensive  
 427 overlap. Coefficients for maturation and conditional fecundity are close to values used  
 428 to generate data, but they are 'damped' (fig. SA7.3a, b), as would be expected from a  
 429 noisy fit. The composition vectors for seed identification  $\mathbf{m}_h$  are recovered precisely,  
 430 with 20% of seed from each species being assigned to the species and the remainder  
 431 to the undifferentiated class "querUNKN" (fig. SA7.3c).

432 Prediction from the fitted model is shown for observed seed counts (fig. SA7.4a,  
 433 b) and for unobserved fecundity (fig. SA7.4c). Seed counts can be predicted from  
 434 two stages in the model, as discussed in section SA1. Good prediction from the  
 435 maturation and fecundity estimates (fig. SA7.4b) requires that the model can identify  
 436 these latent states, but it does not require that covariates in the model can predict those  
 437 states. Good prediction from the full posterior (fig. SA7.4a) additionally requires that  
 438 environmental variables are available that predict maturation and fecundity, which,  
 439 in turn, predict seed counts. The fact that the model is capable of both here is not  
 440 surprising, because we are fitting the 'correct' model; the only predictor in the model  
 441 is known to be tree diameter. The predictions in (a) could be poor while those in (b)  
 442 are good in cases where the model finds good *estimates* of fecundity without finding  
 443 variables that can *predict* fecundity. The ability to recover unobserved fecundity, which  
 444 ranges widely over six orders of magnitude (fig. SA7.4c), verifies that the fit captures  
 445 each of the key features in the model. Again, the simulation mode in MASTIF permits  
 446 evaluation of designs applicable to specific studies.

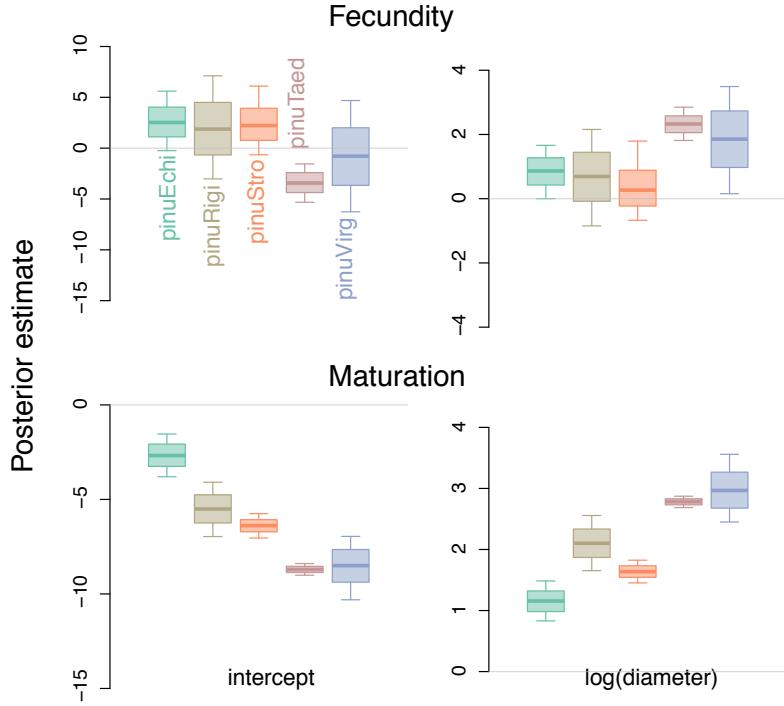


Figure 7: Estimates of fecundity coefficients  $\beta^x$  (above) and maturation coefficients  $\beta^v$  (below) (see table SA1.1) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively.

### ***Application to Pinus***

As for simulated data, fecundity estimates do predict seed rain (fig. SA7.6b), even as the model omits environmental variables needed to predict fecundity (fig. SA7.6a), as expected from previous studies that identified important environmental predictors (Clark et al., 2004, 2013, 2014). Estimates of maturation and fecundity coefficients show positive effects of tree diameter on both state variables (fig. 7). The similarities in diameter effects across species are not an artifact of treating them as random effects—they are fixed effects and, thus, are not responding to a hyperprior. The especially large diameter effect on maturation in *P. virginiana* is consonant with reproduction at comparatively small sizes for this short-statured species.

Dispersal parameter estimates  $\hat{u}_h$ , shown with kernel mean distances  $\bar{d}_h$ , (section SA5) are similar across species (fig. 6a). The random effects prior on  $\mathbf{u}$  borrows strength across all trees on all plots. Predicted seed shadows show expected and 95% uncertainty for seed arrival with distance from a 50 cm diameter tree (fig. 6b).

Partial autocorrelation identifies clear species differences. The southern yellow

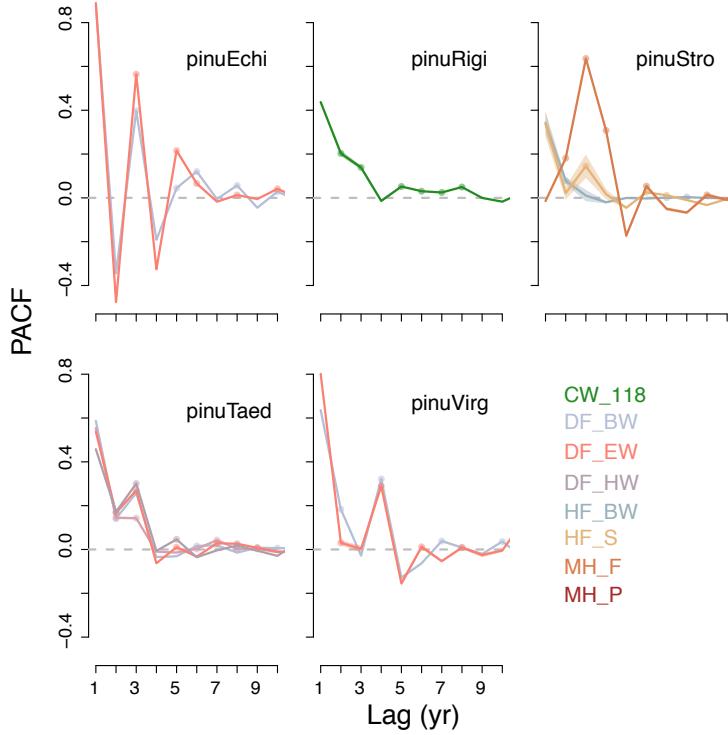


Figure 8: Partial autocorrelation for fecundity in *Pinus* by random groups, defined by species and plot.

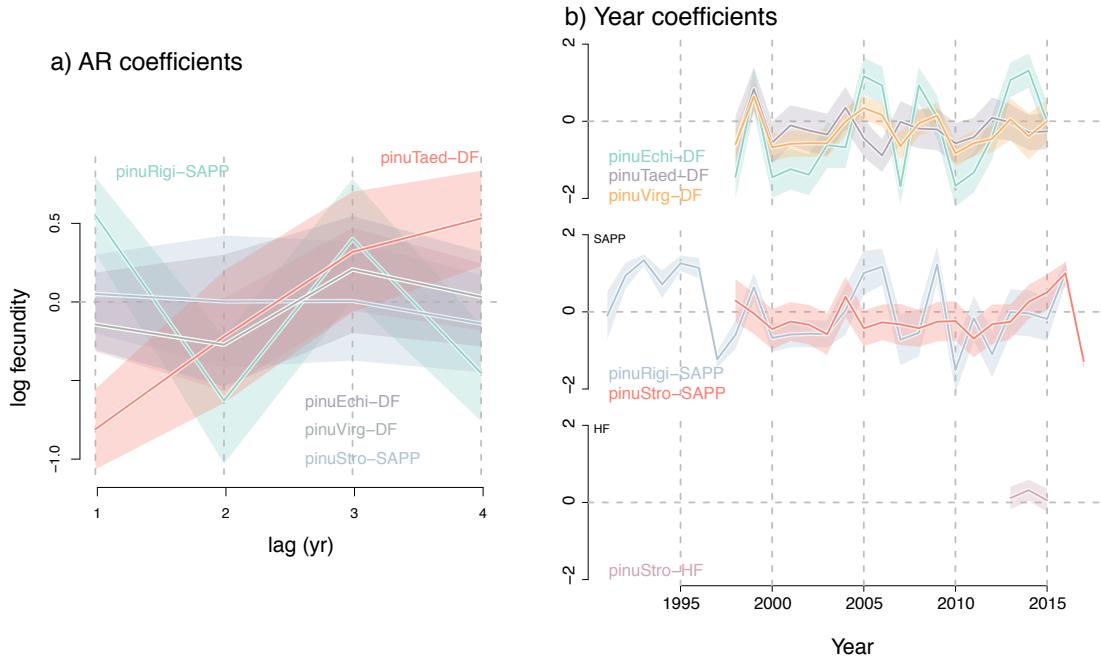


Figure 9: a) Coefficients for random species-region groups in the AR(4) model (a) and the year model (b). NEED SAME COLOR LEGEND.

<sup>462</sup> pines show one-year lags with strong three-yr (*P. echinata*, *P.*, *taeda*) and four-year  
<sup>463</sup> (*P. virginiana*) cycles, respectively (fig. 8). *P. strobus* also shows periodicity at two of

464 three sites. By contrast, *P. rigida* PACF declines gradually over a four-year period.  
 465 The AR(4) coefficients pick up this signal in *P. rigida*, with pronounced positive effects  
 466 at a lag of 3 years for the same species and sites (fig. 9a).

467 The model with year effects finds correlation between species, such as high values  
 468 in 1999 and negative values from 2000 - 2003 and from 2010 - 2011 in both the Pied-  
 469 mont and southern Appalachians (fig. 9b). However, species are decoupled at other  
 470 times. Eigenvalues identify both stationarity and quasi-periodic variation. Real and  
 471 imaginary parts lie within the unit circle (fig. 10), consistent with stabilizing variation  
 472 over the long term. Large imaginary parts indicate instabilities, including for species  
 473 that do not show strong effects at specific lags (fig. 9a).

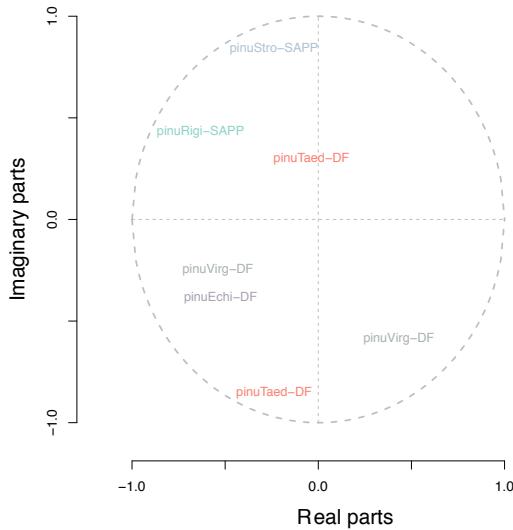


Figure 10: Eigenvalues, real and imaginary parts, lie within the unit circle.

474 Although the full tree-lag covariance  $\mathbf{C}_L$  and space-lag covariance  $\mathbf{G}_L$  are too  
 475 large to visualize for thousands of trees and locations across sites and decades (sec-  
 476 tion SA3.1), a random selection of trees and locations highlights the extent of the  
 477 covariance decline from canopy to forest floor. Warm colors in the lag zero plots show  
 478 that the weak tendency for synchronicity between trees (fig. 11a) is amplified by dis-  
 479 persal across the forest floor (fig. 11b). At higher lags there is evidence of year-to-year  
 480 correlation, with some trees remaining at high or low levels over successive years. The  
 481 positive correlations on the forest floor switch to negative after lag year three.

482 Resource scores do not correlate with mean resource supply, instead balancing the  
 483 benefit of high availability on average with uncertainty. In fig. 12 we evaluated scores  
 484 assuming consumers can visit 20 trees or 20 sites. Generally higher scores on the forest

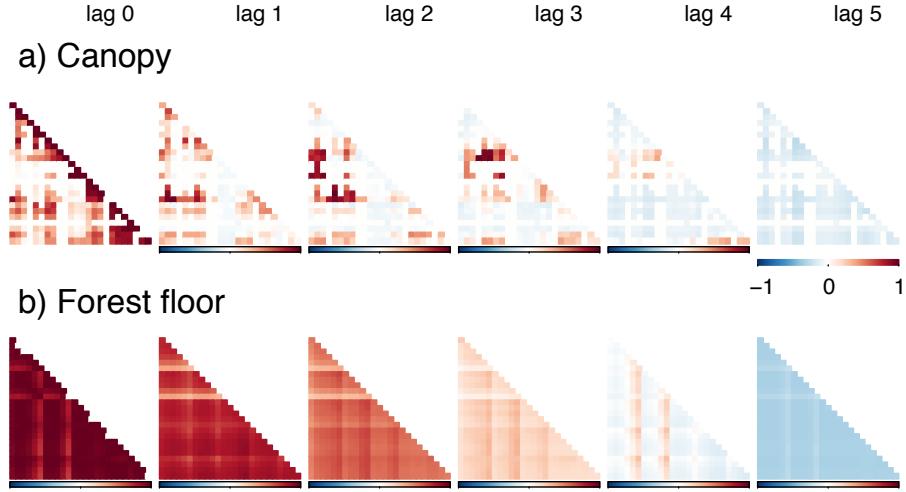


Figure 11: a) Tree-by-lag covariance structure in the canopy at DFBW, developed from  $\mathbf{C}_L$  eq. (9) and b) space-by-lag structure on the forest floor, developed from  $\mathbf{G}_L$  eq. (10). Each pixel represents an individual host tree (a) or site on the forest floor (b), tracked over successive lag years.

floor result from positive covariance imposed by dispersal (green). For example, MHF offers the largest total yield in the canopy at these spatial scales for a given year, but its low score is penalized by high variance (fig. 12a). The low variance over time in the *P. rigida*-dominated CW118 puts it ahead of other stand in fig. 12b, despite modest total productivity of this species.

To highlight the contribution of variance to the resources scores, we plotted  $\Delta$  scores from eq. (21) by spatial and temporal scale. For a given year, the decline of resource scores below the random expectation with spatial scale, indicates that spatial variance increases rapidly (fig. 13, upper panels), thus discouraging movement at the scale of tens of trees in the canopy and fractions of a hectare on the forest floor as a means for averaging spatial variation within a given year. The increase in variance with scale is consonant with large tree-to-tree variation (canopy) and non-uniform distributions of trees and, thus, their seed shadows (forest floor). However, the year-to-year variance is diminished over the same spatial scales in the canopy and on the ground (fig. 13, lower panels), increasing scores and making movement at this scale beneficial for reducing the interannual variance in resource supply. This benefit of movement between years reflects the limited synchronicity within and between host species—a good environment this year will be followed by a good environment somewhere else the next year.

Storage benefits consumers with limited spatial ambit (three host trees or 100 m<sup>2</sup>),

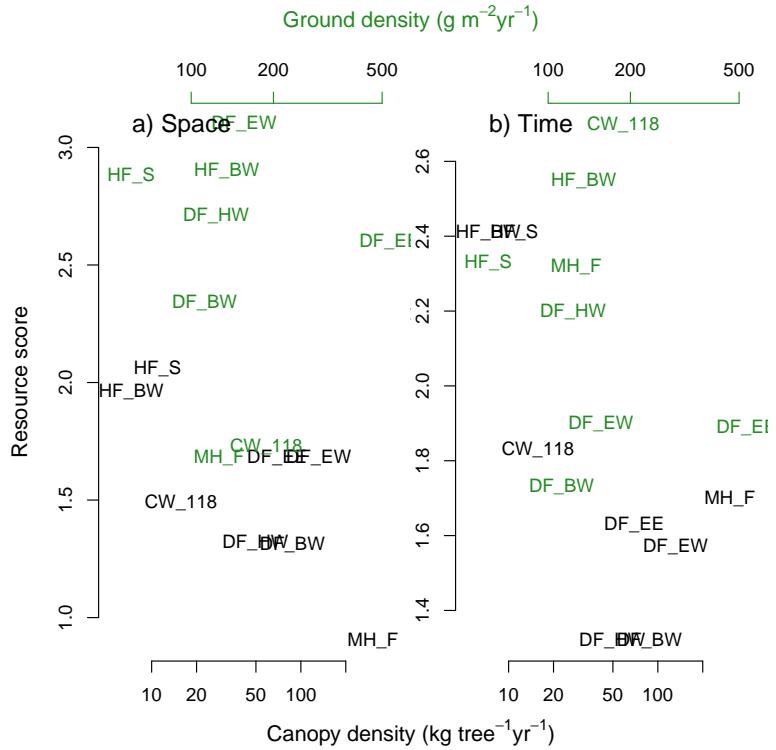


Figure 12: Resource scores (eq. (13)) plotted against mean resource supply (eq. (11)) for a) space [between host trees- (black) and sites on the ground (green) in a given year] and b) over years in a single host or site. Standard deviations are plotted in fig. SA7.5.

reducing the tree-to-tree and site-to-site variance (fig. 14, upper panels). Demographic storage, capital breeding, and dormancy effectively reduce variance for consumers with restricted mobility, thereby increasing scores. However, consumers restricted to a single host or site feel high variance at longer lags, meaning that storage must be coupled with at least some movement, the combined message of lower panels in fig. 13 and fig. 14.

## DISCUSSION

Quantifying the resource value of forested sites, based on their supply of both abundant and reliable mast, is a venerable challenge in ecology (Janzen, 1970; August, 1983; Ostfeld and Keesing, 2000; Curran and Leighton, 2000; Schmidt and Ostfeld, 2003; Cortes and Uriarte, 2013; McMeans et al., 2016). As foraging capacity increases, the variance-cost of an unreliable resource that fluctuates widely shifts to a mean-benefit: the scale-dependent averaging. The stability properties of mast cycles can be

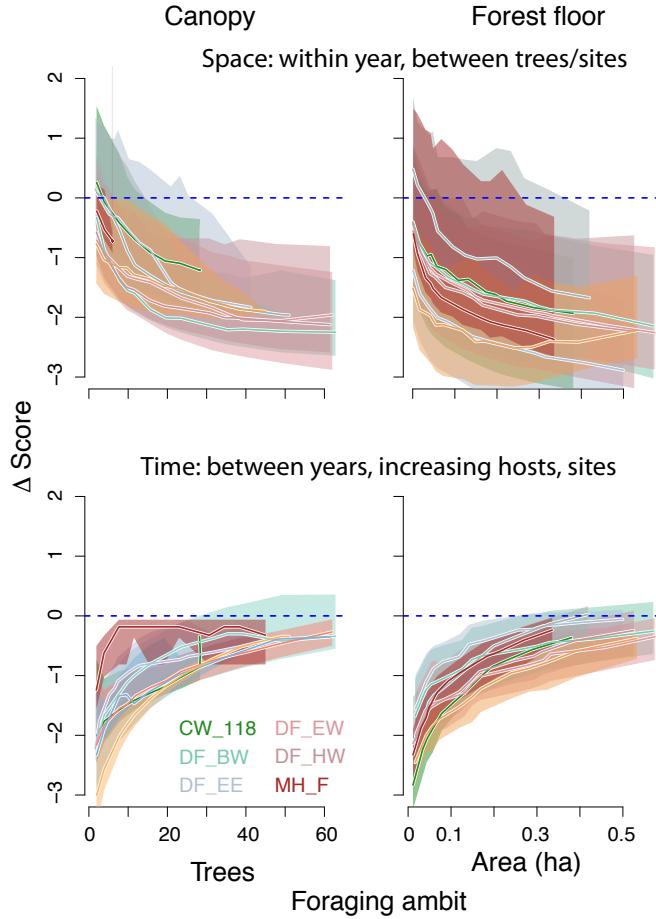


Figure 13: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers that can store resources up for two years. Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance.

517 quantified and compared, showing large differences between species and stands, per-  
 518 vasive quasi-periodicity, but evidence for long-term stability (fig. 10). Because spatial  
 519 foraging, storage, and diet breadth represent alternative solutions to the fluctuating  
 520 resource base, they cannot be analyzed independently. Combining episodic fruiting  
 521 and synchronicity of the multiple hosts in the diet with the consumer’s limited capac-  
 522 ity to forage and variable resource quality, we develop a simple resource score that can  
 523 apply across a network of inventory sites (fig. 12). Theoretical results combined with  
 524 a methodology that makes estimates widely available can help to synthesize a grow-  
 525 ing body of data for application to understanding and management. We summarize  
 526 the role of methodology, followed by potential to improve biogeographic prediction of  
 527 masting and consumers of it.

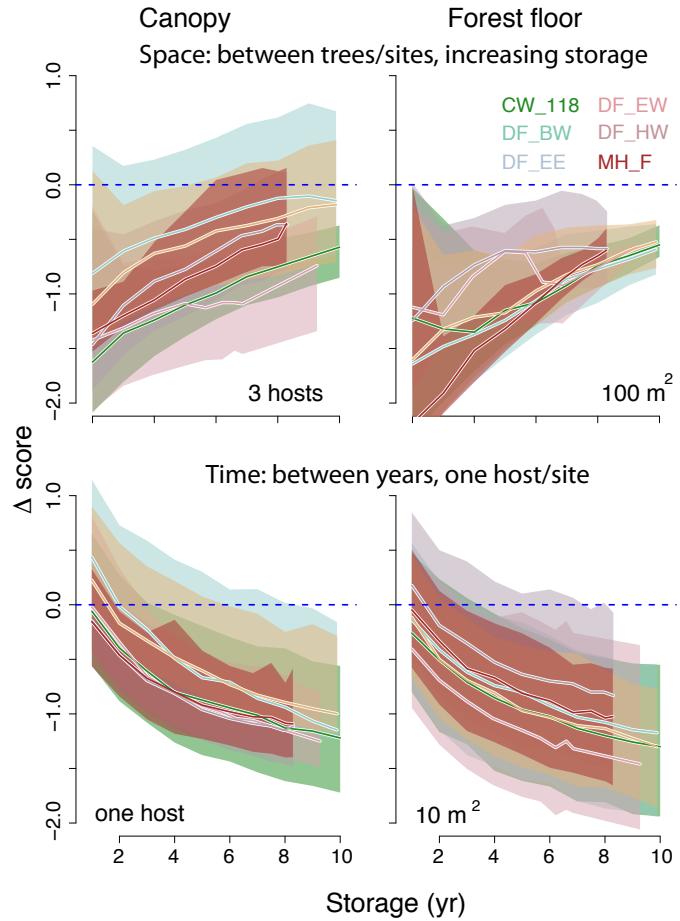


Figure 14: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers with storage capacity of two years to 10 years, assuming that the foraging space is three host trees or  $100 \text{ m}^2$ . Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance within one host or site.

528

### ***Mast estimates and prediction***

529 MASTIF offers a flexible platform that can facilitate synthesis across a large and grow-  
 530 ing literature (table 1), including the implications for different consumer types. The  
 531 model specification can include main effects, interactions, year effects, lag effects, and  
 532 random effects (table SA1.1), while accommodating the uncertainty in seed identifica-  
 533 tion (fig. SA7.3b). From the example application we find high confidence in estimates  
 534 (fig. 6, 7, 9 and Supplement B), and this can only improve when environmental pre-  
 535 dictors are included in the model (Clark et al. (2004); Uriarte et al. (2005); Ladeau  
 536 and Clark (2006); Clark et al. (2010, 2013, 2014); Uriarte et al. (2012), Nuñez et al.,  
 537 in prep.). Simulation in MASTIF can be used to explore the efficacy of study designs

538 for specific applications.

539 Inference and prediction break down when trees are either too abundant or too  
540 rare. When too abundant, overlapping seed shadows may not be resolved to specific  
541 trees. When reproductive trees are too few, there is an insufficient range of values,  
542 and estimates of slope coefficients for predictor variables are reduced in magnitude, as  
543 expected for noisy data (fig. SA7.3). Because the same seed traps are used to estimate  
544 all species on a plot, estimates will vary in the accuracy—each species offers a different  
545 distribution of distances and numbers and sizes and trees.

546 MASTIF’s Bayesian implementation exploits the accumulating knowledge of mat-  
547 uration, fecundity, and dispersal. A rich posterior distribution is efficiently explored  
548 with prior parameter values that integrate previous understading. For dispersal, these  
549 estimates can learn from a large literature that includes low-dimensional models that  
550 converge rapidly for simple assumptions about fecundity (table 1). Use of truncated  
551 priors (flat, with bounds) can specify acceptable ranges, within which the posterior  
552 shape is governed by the likelihood (Clark et al., 2013). Data sets that include multiple  
553 stands (a network) and years increase the range of effects contributing to estimates.  
554 Group-level random effects stabilize estimates across plots (fig. 6) that individually  
555 would not provide useful estimates. The flexibility to combine uncertainty in seed  
556 identifications and a wide range of predictor variables makes our approach amenable  
557 to many data sets. The tree-time and space-time covariance, visualized in fig. 11 and  
558 summarized by entropy, gauge the average supply and its reliability. The methodology  
559 extends to consumers with a generalized diet, implemented in a separate paper (Núñez  
560 et al, in prep).

### 561 ***Consumer ambit and resource score***

562 The scale-dependent resource score recognizes a shift from variance-penalty to mean-  
563 benefit with increasing consumer ambit (fig. 13, 14). It is important to evaluate the  
564 score at the space-time scale that describes a specific consumer, while integrating  
565 diet breadth. Continuing frustration with the standard coefficient of variation (CV)  
566 includes this omission of scale (Herrera et al., 1998; LaMontagne and Boutin, 2009).  
567 On the other hand, autocorrelation models applied to seed data, without estimates  
568 of maturation and fecundity, do not reflect availability in the canopy (Clark et al.,  
569 2004; Pesendorfer et al., 2016), due to redistribution by dispersal. The resource score

570 extends the value of CV as an index that combines mean and variance by making it  
571 scale-specific both for canopy and forest floor.

572 The standard error (SE) rule (eq. (20)) provides a simple index to quantify the  
573 advantage of expanding or contracting diet breadth. Losses from the diet decrease the  
574 mean and, except where there is positive covariance with current diet items, decrease  
575 the score through increased contribution of the variance. For example, the abundant  
576 American chestnut (*Castanea dentata*) in the Appalachian and northeastern forests  
577 had an unknown masting structure. Knowledge of extant species can provide guidance  
578 on the impacts of future threats. The value of the SE rule is not limited to cases where  
579 consumers possess the capacity to change their diets or where diet changes are imposed  
580 by changing host availability. It can be used to evaluate the consequences of resource  
581 supply potential of stands supporting a full range of tree species.

582 ***Biogeographic implications***

583 For biogeographic understanding, including impacts of climate change, the resource  
584 score can offer a more direct index of habitat suitability than is available through the  
585 variables currently used in habitat models and species distribution models (SDMs),  
586 which emphasize climate, land cover, and soils, but omit availability of food. The  
587 resource score can assign value to individual host tree species and to forest stands  
588 (fig. 12) for consumers that differ in diet breadth and foraging capacity. Ecologists  
589 and wildlife managers have long recognized that mastング provides the base of the food  
590 chain, and space-time variation can be just as critical as the mean resource supply  
591 (Ostfeld and Keesing, 2000; Curran and Leighton, 2000; McShea, 2000; Boutin et al.,  
592 2006; Bergeron et al., 2011; Bogdziewicz et al., 2016).

593 We did not offer a full predictive analysis of resources scores in this paper, because  
594 resources alone cannot predict trophic structure. That analysis includes a full range of  
595 climate and habitat variables (Nuñez et al., in prep). The tree species that contribute  
596 mast production are well-known. But there has not been a mechanism for combining  
597 pulsed-resource supply with life histories of consumers. The important contribution  
598 to biogeographic understanding includes the basic theory and computation that can  
599 use species-size structure to quantify resource supply in a way that can be combined  
600 with the traditional climate and habitat variables in SDMs. The translation of seed  
601 production and dispersal to spatio-temporal resource availability (fig. 11) and the

602 summary of its effect by forest stands (fig. SA7.5) can supplement the variables now  
603 used for SDM.

604

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