

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; Clotfelter et al., 2007; 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 (Ribbens et al., 1994; Clark et al., 1998, 1999; Nathan and Muller-Landau, 2000;

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

36 Theory is needed to gauge the capacity of forests to support food webs by regu-
37 lating the types of consumers that can persist and the predation risk faced by their
38 masting hosts (McMeans et al., 2016). We interpret the term *consumer* to include
39 seed-attacking fungi and damping-off pathogens. A reliable resource is abundant on
40 average, with limited variation in time and space. How does the space-time structure
41 of masting interact with the capacities of consumers to exploit alternative hosts, to for-
42 age widely in space, and to store reserves in time? Spatial variation in mast availability
43 exists within stands and across regions (August, 1983; Stein et al., 2014), and it differs
44 in the canopy and the understory (Carbone et al., 2005; Sheldon and Nadkarni, 2013).

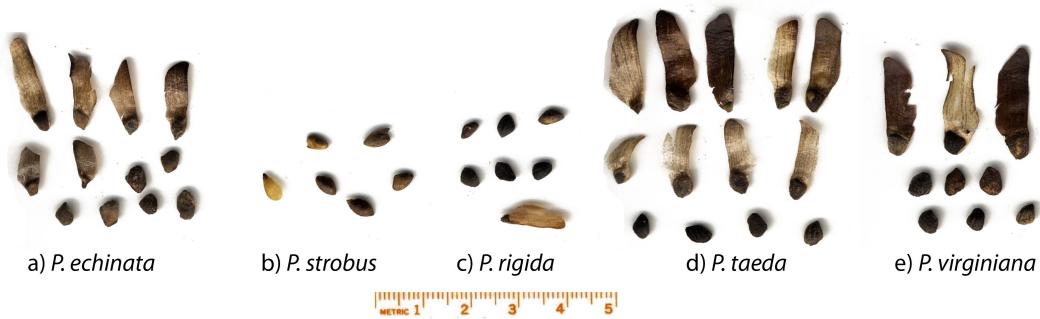


Figure 1: Three seed predators on *Pinus* spp. (above) and five seed types (below). The gray jay (*Perisoreus canadensis*) forages in the canopy (left), the eastern chipmunk (*Tamias striatus*) on the forest floor (center), and the eastern gray squirrel (*Sciurus carolinensis*) in both locations (right).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

45 In the canopy, host trees are accessed by song birds and arboreal-foraging arthropods
 46 and mammals (Curran and Leighton, 2000; McShea, 2000; Koenig and Knops, 2001;
 47 Perea et al., 2011; Milleron et al., 2013; Bell and Clark, 2016) (fig. 1). Canopy foragers
 48 must locate host individuals where and when resources are concentrated—the *tree-time*
 49 covariance between hosts, over years. The density and aggregation of mast trees can
 50 vary widely between stands. Many mammals and ground-nesting birds respond to
 51 *space-time* covariance on the forest floor (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 are capable of extended dormancy (Dworkin and Shah, 2010) to disperse in time.

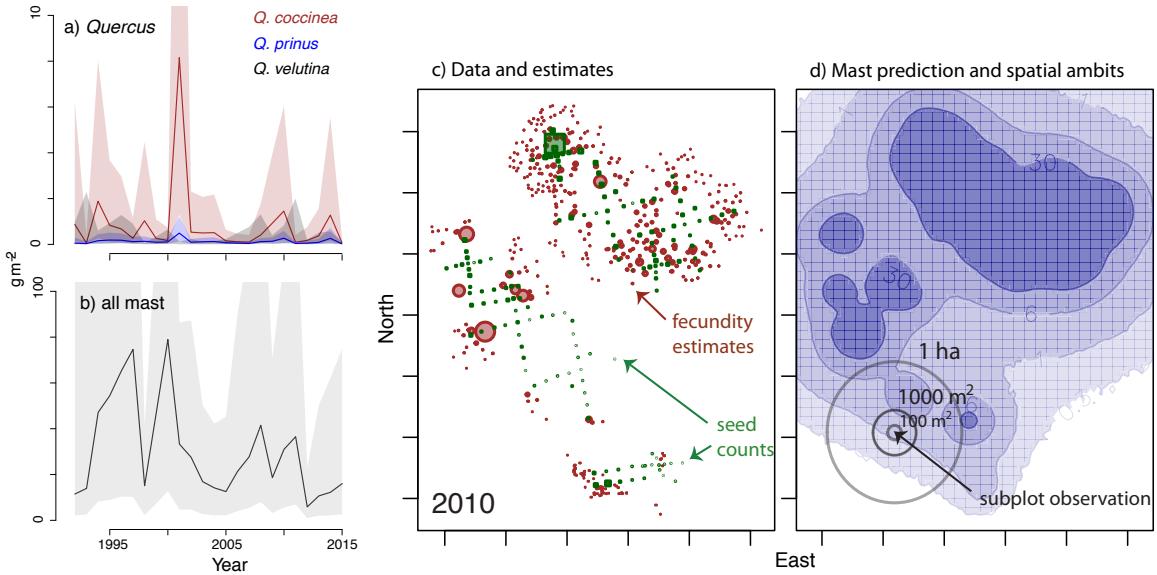


Figure 2: Space-time scales for seeds and consumers. a) Masting by three species in the S Appalachians is erratic. Shading spans 80% of the predictive variation at the 1 m² scale. b) A generalist like *Sciurus* (fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*, *Nyssa*, *Cornus*, *Pinus*). c) Fecundity estimates in brown and seed counts in green for *Pinus* in 2010 at DFBW in the SE Piedmont. d) Predictive mean mast density fitted to data in (c), with superimposed ambits for species that can be sampled in subplots, including 100 m² (e.g., flightless insects, larder hoarding rodents), 1000 m² (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), while specialization exposes consumers to the full heterogeneity offered by a specific host (Devictor et al., 2010; Clavel et al., 2011) (fig. 2a, b). We refer to a consumer's *ambit* in space (host trees or ground area), time (life span, storage potential, and/or

65 dormancy), and diet breadth (Carbone et al., 2005; Pelisson et al., 2013; Sainmont
 66 et al., 2014; Rodel et al., 2016). The combination of these three dimensions determine if
 67 consumers can abide variation in their hosts and if hosts can benefit by spatio-temporal
 68 escape (Janzen, 1970; Grotan et al., 2009; Lichti et al., 2014). Theory is needed to
 69 relate estimates of fecundity and dispersal at these tree-space-time covariance scales
 70 of the consumer ambit.

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

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

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

87 where $E(\cdot)$ is an expectation, y_s is the number of seeds counted in a trap at location
 88 s , λ_s is the expected seed density (seeds m^{-2} yr^{-1}), A is sample effort, the area of
 89 a seed trap times fraction of fruiting season it was deployed (traps are damaged by
 90 tree falls and bears) (m^2 yr^{-1}), $\mathbf{S}_{s,i}$ is the density of seed produced by tree i dispersed
 91 to location s (m^{-2}), and f_i is seed production by tree i (table S1.1). For a length- S
 92 vector of seed traps, a length- n vector of fecundities, and a $S \times n$ kernel matrix \mathbf{S} ,
 93 there is a length- S vector of seed density

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

⁹⁴ Because both fecundity \mathbf{f} and dispersal capacity \mathbf{S} are unknown, the efficacy of these
⁹⁵ models should depend on the amount of data and its space-time structure.

Table 1: Attributes of some SSMs with examples.

Individuals ^a	Maturation ^b	Time ^a	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	–	LaDreau 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)

^a IND - independent fits to each year; RE - random effect; FE - fixed effect; A - D are terms in table S1.1.

^b HM - hidden Markov submodel; ZIP - zero-inflated Poisson

⁹⁶ Before turning to challenges with SSMs, we summarize why they can often be
⁹⁷ preferable to more direct analyses, such as stable isotope labels (Carlo et al., 2009;
⁹⁸ Cortes and Uriarte, 2013) or genotyping seeds or seedlings (Godoy and Jordano, 2001;
⁹⁹ Grivet et al., 2005; Jones et al., 2005; Pairon et al., 2006; Burczyk et al., 2006; Robledo-
¹⁰⁰ Arnuncio and Garcia, 2007; Jones and Muller-Landau, 2008; Moran and Clark, 2011;
¹⁰¹ Schupp and Jordano, 2011; Bontemps et al., 2013). Due to labor and expense, typically
¹⁰² only a small sample of seeds or seedlings can be labeled or genotyped, most often from
¹⁰³ a single species. Both data types provide information on dispersal, but not fecundity
¹⁰⁴ (Moran and Clark, 2011; Milleron et al., 2013). Because seed traps sample passively,
¹⁰⁵ SSMs provide an efficient option to gather fecundity and dispersal estimates from all
¹⁰⁶ species that can be identified in seed traps simultaneously, naturally integrating space
¹⁰⁷ (trap area) and time (trap deployment period).

¹⁰⁸ Seed traps record seed rain following any consumption losses that occur in the
¹⁰⁹ canopy. Canopy attack can be recorded by damage classes, such as exit holes by

110 arthropods and husk removal from fleshy fruits (Bell and Clark, 2016). Other seeds are
 111 consumed, thus reducing total seeds recovered from traps. Some studies that employ
 112 seed traps together with direct access to the canopy directly (LaDeau and Clark, 2001;
 113 Ladeau and Clark, 2006) or observe seeds from the ground (Minor and Kobe, 2017)
 114 find substantial agreement. A tropical study found more liana seeds in seed traps
 115 placed directly in the canopy than in traps placed above the forest floor (Sheldon
 116 and Nadkarni, 2013). In general, seed trap estimates are recognized as potentially
 117 underestimating total fecundity.

118 Countering the advantages, SSMs are difficult to evaluate, because both seed pro-
 119 duction and dispersal must be estimated. For known \mathbf{S} and mean seed counts (an
 120 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).
 121 However, there is a unique solution only if there are more seed traps than there are
 122 trees, i.e., $S > n$. Even with few trees, a solution would often include negative values,
 123 which is, of course, impossible. A model for f_i as simple as a prior distribution that ex-
 124 cludes negative values would fix the negative-fecundity problem, but there might still
 125 be insufficient information in the S seed counts. The early SSMs did not confront this
 126 problem, because they projected the n sources down to a few parameters, replacing
 127 individual fecundity in the vector \mathbf{f} with a function that is shared by all trees, e.g.,

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

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

134 Extensions to eq. (2) have addressed some of the challenges, but they do not offer
 135 the synthesis needed to explain and predict spatio-temporal structure. Initial efforts to
 136 capture heterogeneity at the data stage, with over-dispersed data models (e.g., negative
 137 binomial) (Clark et al., 1998; Muller-Landau et al., 2008), appear less effective than
 138 allowing for heterogeneity between trees and over time (Clark et al., 2004; Martinez
 139 and Gonzalez-Taboada, 2009; Uriarte et al., 2012; Clark et al., 2013).

140 Subsequent joint modeling of maturation and fecundity combined with in- and
 141 out-of-sample prediction showed that aggregate models like eq. (2) miss the pervasive

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

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

169 The goals of this paper are ambitious, yet focused. Here we provide both the theory
170 and the modeling needed to synthesize space, time, and diet breadth with masting data,
171 packaged in a computational framework that provides the critical estimates. It fills an
172 important gap in species-distribution modeling, which has thus far emphasized climate
173 and soils, but omitted food. By deriving the resource value of forest stands, based on
174 their means and covariance structures, we hope to enrich the potential to predict food
175 web structure. We leave the application of theory to a subsequent paper. A more

176 sweeping comparison of theory and data is needed, because resource supply, while
 177 critical, must be analyzed in combination with the more traditional climate and habitat
 178 variables across a network sites (Nuñez et al, in prep). The next section provides
 179 background theory and the model framework used to estimate masting structure.

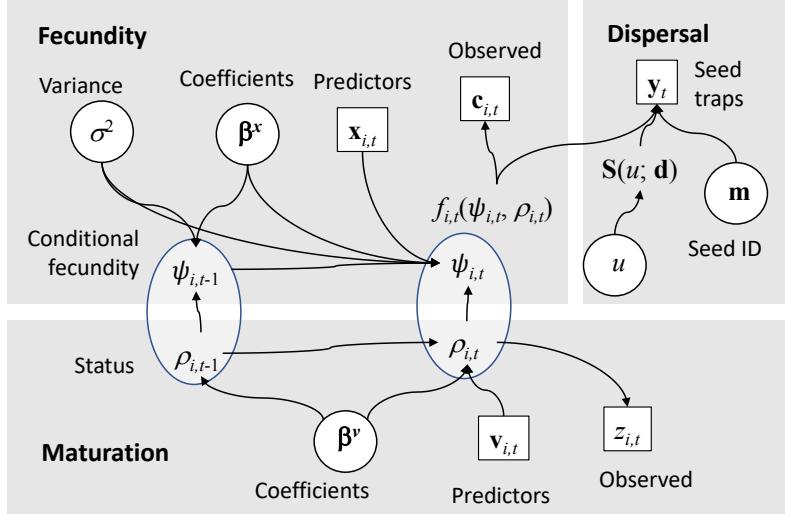


Figure 3: Graphical model for main elements of the model, including fecundity (above), maturation (below), and dispersal (right), showing estimates (circles) and observed variables (squares), with dynamics ($t - 1, t$). Variables are defined in table S1.1.

180 MODEL DEVELOPMENT

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

184 Consider an inventory plot where trees mature, after which they are capable of
 185 seed production (fig. 3). The event that tree i can produce seed in year t is the
 186 *maturity state*, $\rho_{i,t} \in \{0, 1\}$. Maturation is a hidden Markov probit with coefficients
 187 β^v describing covariate effects on maturation probability (eq. (S1.7)). Observations of
 188 maturation state $z_{i,t} \in \{0, 1\}$ contribute to estimates (eq. (S1.6))(see also Clark et al.
 189 (2010)).

190 Annual seed production by a mature individual ($\rho_{i,t} = 1$) is termed *conditional fe-*

191 *cundity*, $\psi_{i,t} > 0$. Like maturation, conditional fecundity is a dynamic process, modeled
 192 with fixed and random effects, year effects, and/or autoregressive terms (table S1.1,
 193 submodel A). Coefficients in β^x can include tree size (eq. (2)), environment, and inter-
 194 actions (Clark et al., 2010, 2013). *Random effects* (REs) β_i^w accommodate the hetero-
 195 geneity of responses across individual trees (table S1.1, submodel D). Year effects γ_t
 196 are an alternative to a large covariance matrix across individuals (table S1.1, submodel
 197 B). Alternatively, quasi-periodic variation can be described by an *autoregressive model*
 198 AR(p) with $l = 1, \dots, p$ lag terms α_l (table S1.1, submodel C). Year and lag effects can
 199 be random across species and/or region groups, recognizing that masting may be co-
 200 herent within, but not between, groups. *Actual fecundity* is $f_{i,t} = \psi_{i,t}\rho_{i,t} \geq 0$. In some
 201 cases, actual fecundity may be observed, from direct counts in the canopy (Ladeau and
 202 Clark, 2006) or on the ground (Minor and Kobe, 2017). Observed fecundity enters here
 203 as minimum and maximum estimates in the vector $\mathbf{c}_{i,t} = (c_{i,t,min}, c_{i,t,max})$ (fig. 3).

204 Seeds accumulate in traps $s = 1, \dots, S$ from nearby trees, depending on a *disper-*
 205 *sal kernel* $\mathbf{S}(\mathbf{u})$, which includes fitted parameters $\mathbf{u} = u_1, \dots, u_H$ for each species h
 206 eq. (S1.1) (eq. (1)). The seed count $y_{sm,t}$ is the number of seeds of type m counted
 207 in a trap at s in year t . Seeds are counted by species or, if species identity is unclear,
 208 then genus (section S1.4). When multiple species $h = 1, \dots, H$ contribute to the same
 209 seed type(s), as when some seeds are identified only to genus, then the $m = 1, \dots, M$
 210 seed types must be included in the model with the H species that could have produced
 211 them. Observation error enters by a $H \times M$ matrix \mathbf{M} holding probabilities that a
 212 seed of species h will be assigned to type m . The *likelihood* is Poisson and incorporates
 213 sample effort (trap area \times active period). The full model and prior distributions are
 214 discussed in section S1.2 and section S1.5, respectively.

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

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

219 where $r_{h[i]}$ is the quality of a seed of species h corresponding to tree i . Here we use seed
 220 mass as an index for quality. Dispersal translates resource abundance experienced by
 221 a canopy forager on host tree i , $q_{i,t}$ (kg per host tree), to abundance on the ground at
 222 location s , $g_{s,t}$ (g m^{-2}).

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

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

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

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

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

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

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

252 on a proportionate (log) scale, $R_{nT} = -\log CV_{nT}$ (tree-time) and $R_{ST} = -\log CV_{ST}$
 253 (space-time).

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

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

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

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

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

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

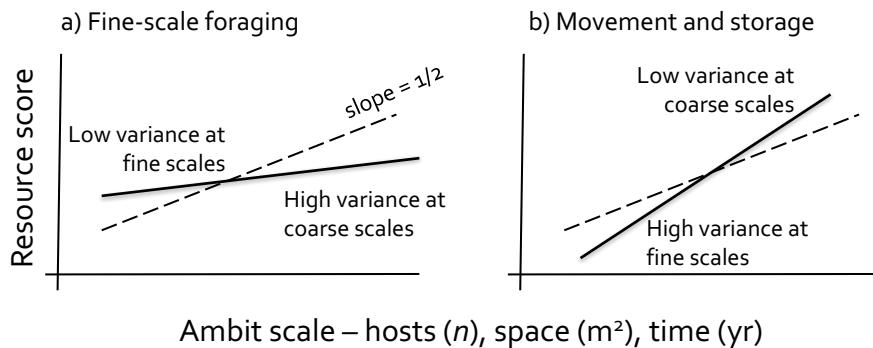


Figure 4: For scale-independent variation, the resource score increases with a slope of 1/2 on a log scale with n (host trees), space (area), and time (years) (eq. (8)). Especially beneficial for consumers with limited ambit are stands offering high mean and low variance at fine scales (a) and vice versa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

261 The baseline eq. (8) provides an index to compare forest stands that differ in scale
 262 dependence (fig. 4). Extended mobility and storage may be of limited benefit where
 263 fine-scale variation is low (fig. 4a). All else equal, high space-time variance at fine
 264 scales benefits the consumer that moves (fig. 4b), where the incremental increase in

the total resource more than compensates for the scale-dependent variance. Again, space-time must be considered together, because a local forager, favored by (fig. 4a) may solve high-spatial variance with storage or dormancy in time (*Diet breadth and variance perceived by the consumer*). The covariances required to evaluate the resource score are described in the next section.

Tree-time and space-time covariance

Differences in mastng structure experienced by consumers in the canopy and on the ground are summarized by stand-specific mean and covariance structure that will substitute for the scale-independent values in eq. (8). Space- and time-dependence can be evaluated for estimated or for predicted tree-by-tree covariance, which is then combined with spatial covariance induced by dispersal. Functional forms from the geospatial literature summarize space-time structure with a relatively small number of parameters (Gneiting, 2002; Banerjee et al., 2014). For the case of tree covariance, there is no evidence for a distance-related covariance between trees within stands (Clark et al., 2010), consistent with widely observed regional coherence (Liebhold et al., 2004; Fernandez-Martinez et al., 2017). For this reason, within-stand canopy covariance is between trees, rather than over distance. On the forest floor, spatial covariance combines tree covariance with dispersal. We do not introduce a geospatial model, because spatial covariance is already induced by the kernel \mathbf{S} . For covariance over time, we use the covariance in the estimated fecundity from the model. Although model fitting can include AR(p) or year terms (table S1.1), we expect fecundity predictions to often include wide uncertainty. Fecundity estimates can be much more accurate than predictions (section S1).

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

²⁹⁴ t and individual i' in year t' . We cannot estimate the tree-time matrix \mathbf{C} , because
²⁹⁵ each (i, i', t, t') combination happens once. Below we introduce the *tree-lag* covariance.
²⁹⁶ First we note two special cases, i) a $n \times n$ (tree-to-tree) covariance \mathbf{C}_n holding the
²⁹⁷ covariances experienced by a consumer that moves between n host trees in a random
²⁹⁸ year, and ii) a $T \times T$ (year-to-year) covariance \mathbf{C}_T , holding the covariances experienced
²⁹⁹ by a consumer that tracks a random host over T years.

³⁰⁰ In contrast to tree-time covariance in the canopy, ground foragers respond to space-
³⁰¹ time covariance, which depends on tree locations, the individual-time covariance, and
³⁰² dispersal. For year t with tree fecundity vector $\mathbf{f}_{(n)}$ there are expected seed intensities
³⁰³ at the locations $\mathcal{S} = 1, \dots, S$

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

³⁰⁴ The conditional covariance in intensity is

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

³⁰⁵ The total covariance additionally includes the Poisson variance,

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

³⁰⁶ Combining these terms confirms that they describe covariance in simulated data
³⁰⁷ (fig. 5, right). The first term in eq. (10) combines the covariance between trees with
³⁰⁸ seed dispersal (fig. 5, left). There can be negative covariances (blue in fig. 5), depend-
³⁰⁹ ing on covariance structure in \mathbf{C}_n , but positive values dominate, imposed by dispersal.
³¹⁰ This effect will vary for each forest stand, depending on the distributions of hosts, their
³¹¹ fecundities, and their dispersal distances. The second term in eq. (10) contributes only
³¹² (positive) variance (fig. 5, center), acting like the nugget of geospatial models (Banerjee
³¹³ et al., 2014)¹. The next section extends these results to multiple consumers.

¹However, 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.

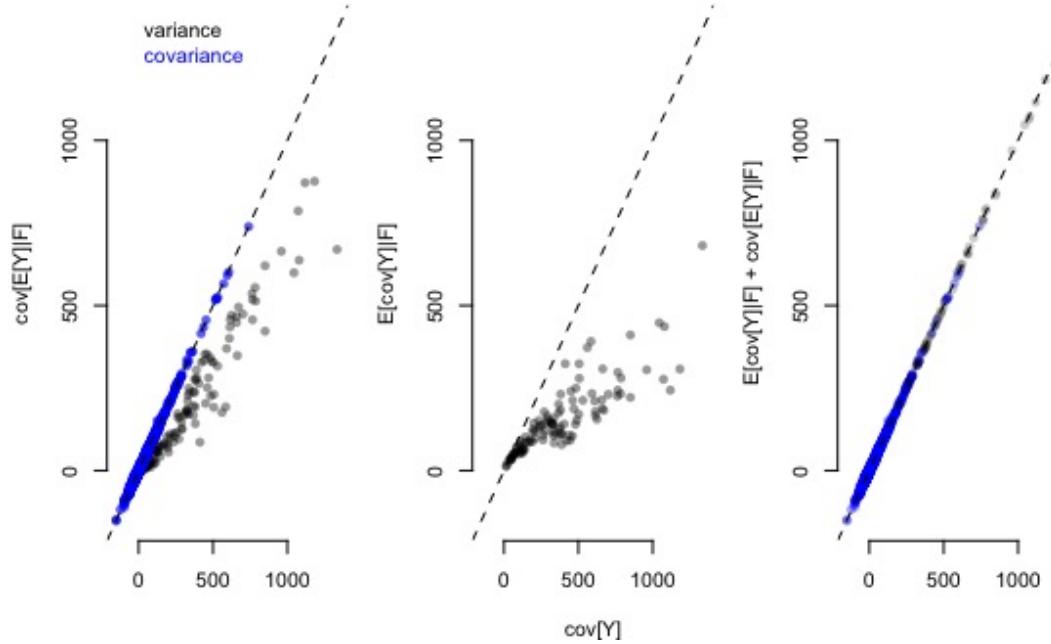


Figure 5: Contributions to space covariance \mathbf{G}_S from terms in eq. (10) plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in section S2.

314 Diet breadth and variance perceived by the consumer

315 Because consumers exploit multiple resources, the covariance structure describes their
316 combined supply, accounting for differences in nutritional quality and space-time avail-
317 ability. For the canopy, the aggregate seeds available to the consumer of n hosts over
318 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

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

319 where $\mathbf{r}_n = r_{h[1]}, \dots, r_{h[n]}$ is the vector of seed quality associated with each tree with
320 elements given by eq. (3). Note that \mathbf{r}_n combines all host species and individuals in
321 the diet. There are also aggregate variances for a random year on n host trees, and
322 for a random host tree over T years. For example, the aggregate variance over all host
323 trees in the diet is,

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

324 where \mathbf{Q}_n is the covariance for resource yield between trees (eq. (3)).

325 To combine the contributions of mean and variance, the resource score for the

326 consumer foraging over n trees replaces terms in eq. (8) with those that come from
 327 the scale-dependent space-time covariance. For example, foraging over n hosts and T
 328 years gives the score

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

329 This variation can be compared to that expected for scale-independent variation in
 330 eq. (8).

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

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

334 where $r_{\tilde{h}}$ is the quality of the new resource, which can be concatenated into a length- \tilde{n}
 335 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
 336 expected addition to the diet from the second term in eq. (14) is

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

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

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

339 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 $\tilde{n}T \times nT$
 340 covariance between new and original hosts in the diet. Of course, strong negative
 341 covariance with hosts now in the diet (third term in eq. (16)) decreases aggregate
 342 variance, with obvious benefits. Not so obvious is the fact that, even if independent of
 343 the current diet, the resource score is expected to increase whenever the contribution
 344 to the aggregate mean compensates for the increase in variance. For independent
 345 variation eq. (16) simplifies to

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

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

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

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

347 As the number of new hosts becomes large, $\tilde{n} > n$, this inequality tends to

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

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

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

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

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

359 The same analysis leads to a resource score for ground foragers, R_{ST} . Despite
360 positive and negative covariance elements in the canopy, the forest floor covariances
361 in \mathbf{G}_S tend to be positive at the characteristic scales of dispersal (fig. 5). This is
362 not necessarily so at broader spatial scales, where the pattern of clumping of trees of
363 different species will dominate. Space-lag covariance structure used for \mathbf{Q} and \mathbf{G} in
364 this section is expanded in section S3.1.

365 METHODS

366 For posterior simulation, we implemented Gibbs sampling, a Markov chain Monte
367 Carlo (MCMC) technique, including Metropolis and Hamiltonian Markov chain (HMC)
368 steps (section S8). Due to a high-dimensional state space (all trees over all years), pos-
369 terior simulation suffers well-known scaling limitations of MCMC, as the parameter

set is overwhelmed by the volume of parameter space (Neal, 2011); random-walk algorithms cannot explore the parameter space in finite time. HMC exploits the geometry of the typical parameter set to efficiently target proposals (Betancourt and Girolami, 2015). Because it relies on vector fields (a differentiable surface), HMC does not apply to discrete maturation state. However, it does apply to conditional fecundity, and is used for that purpose here (section S8.2). With the exception of maturation, conditional fecundity, and the dispersal parameters (a low-dimensional vector), all other parameters are sampled directly (section S8).

Predictive distributions were generated for maturation and fecundity, which, in turn, predict seeds in-sample (i.e., at seed trap locations and sampling years) and out-of-sample (other locations and/or years) (section S1.6). Partial autocorrelation functions (PACF) quantify the contribution of each lag, while controlling for shorter lags. Complex eigenvalues for the AR(p) model (section S4) indicate quasi-periodic variation. A stationary AR(p) process has all eigenvalues of less than unit modulus (real plus complex parts, section S4). The tree-lag (canopy) and space-lag (forest-floor) covariances (*Space-lag covariance*) were generated with resource scores for each plot. Overall structure is summarized by diet-wide entropy experienced by a consumer over trees, sites, and years (section S3.3).

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

394 *Simulation*

Rather than offer an exhaustive compilation of simulation studies, we supply the full MASTIF package with simple examples for application (section S2). We adopt this approach, because fitting depends on the structure of each stand (density and distribution of mature trees), dispersal characteristics of each species, and spatio-temporal sampling design, including density and dispersal of traps, and the classification of seeds into types. As with any model, useful estimates are only expected where there is 'signal' in data. Simulation determines if, given signal, the model can recover pa-

402 rameeters and predict data. We illustrate where an SSM can be successful, and we
403 discuss aspects of data structure that can lead to poor performance. The value of the
404 simulator is this first opportunity it affords to examine a full range of potential data
405 sets.

406 ***Application to field data***

407 From up to 25 years of continuous seed collections across sites in the eastern US (sec-
408 tion S6), we analyzed mast production for the genus *Pinus*. Multiple species on the
409 same plots meant that species identity of most seeds was unknown (fig. 1). Throughout
410 this multi-decade study methods emphasized minimizing false-positive seed identifica-
411 tions, thus restricting species-specific classifications to unambiguous cases. Field and
412 lab methods are detailed in (Clark et al., 1998, 2004, 2010; Moran and Clark, 2011;
413 Bell and Clark, 2016). Data summaries are provided in section S6.

414 For this focus on methodology, predictors are limited to tree diameter, making the
415 model comparable with most literature on this subject. The omission of environmental
416 predictors that control fecundity (Clark et al., 2004, 2010, 2014) sacrifices predictive
417 skill for transparency—our goal here is to focus on space-time structure that is linked
418 solely to a size model. Model fitting is demonstrated two ways, with AR(4) and with
419 year effects for conditional fecundity (table S1.1). Prior distributions are provided in
420 the section S1.5.

421 **RESULTS**

422 ***Simulation studies***

423 Simulation studies found that the model can recover parameters and latent states
424 for all species, even when most of the seeds (80%) are identified only to genus level.
425 A stochastic simulation example is summarized for $M = 4$ seed types and $H = 3$
426 species on a mean of $J = 8$ plots, $T = 5$ years, $n = 25$ trees, and $S = 50$ traps.
427 Parameter recovery is approximate, because, as in real data, few trees in a plot of a
428 given species are mature. For the simulation shown in fig. S7.3, the number of trees per
429 plot ranges from 4 to 23. Trees far from seed traps supply little information. However,
430 if too many trees are close to the same traps, information can be limited by extensive
431 overlap. Coefficients for maturation and conditional fecundity are close to values used

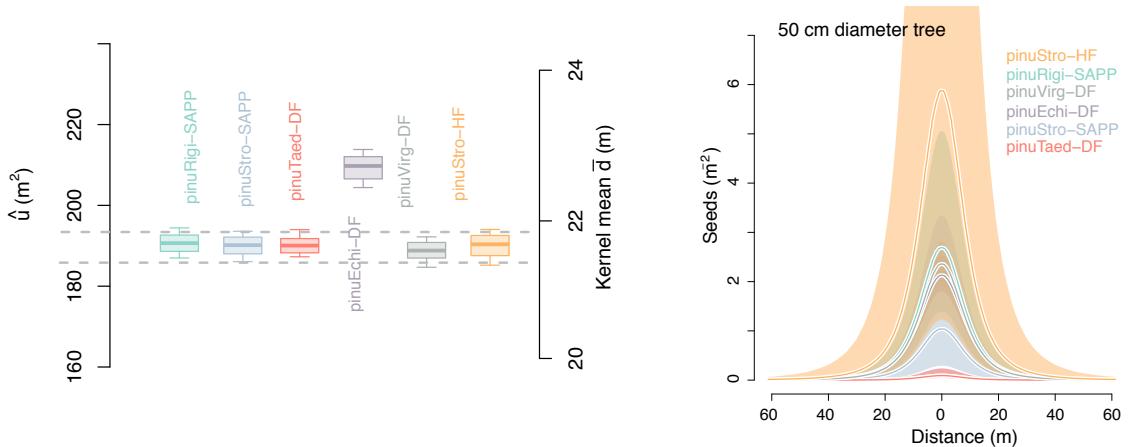


Figure 6: a) Estimates of dispersal parameters u_h for *Pinus* species-region groups. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. The kernel mean scale at right is eq. (S5.14). b) Seed shadows predicted from the posterior distribution, with 95% predictive intervals.

to generate data, but they are 'damped' (fig. S7.3a, b), as would be expected from a noisy fit. The composition vectors for seed identification \mathbf{m}_h are recovered precisely, with 20% of seed from each species being assigned to the species and the remainder to the undifferentiated class "querUNKN" (fig. S7.3c).

Prediction from the fitted model is shown for observed seed counts (fig. S7.4a, b) and for unobserved fecundity (fig. S7.4c). Seed counts can be predicted from two stages in the model, as discussed in section S1. Good prediction from the maturation and fecundity estimates (fig. S7.4b) requires that the model can identify these latent states, but it does not require that covariates in the model can predict those states. Good prediction from the full posterior (fig. S7.4a) additionally requires that environmental variables are available that predict maturation and fecundity, which, in turn, predict seed counts. The fact that the model is capable of both here is not surprising, because we are fitting the 'correct' model; the only predictor in the model is known to be tree diameter. The predictions in (a) could be poor while those in (b) are good in cases where the model finds good *estimates* of fecundity without finding variables that can *predict* fecundity. The ability to recover unobserved fecundity, which ranges widely over six orders of magnitude (fig. S7.4c), verifies that the fit captures each of the key features in the model. Again, the simulation mode in MASTIF permits evaluation of designs applicable to specific studies.

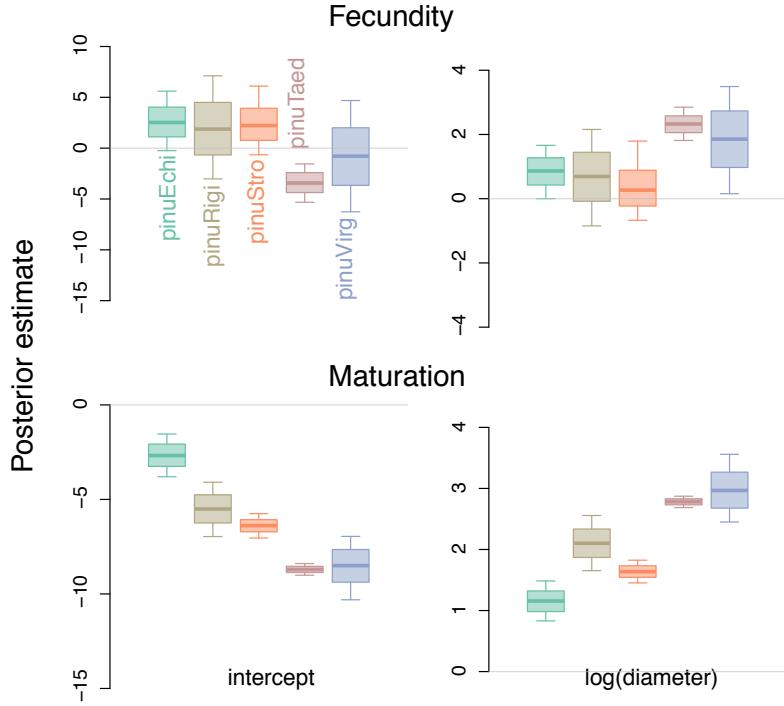


Figure 7: Estimates of fecundity coefficients β^x (above) and maturation coefficients β^v (below) (see table S1.1) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively.

Application to Pinus

As for simulated data, fecundity estimates do predict seed rain (fig. S7.6b), even as the model omits environmental variables needed to predict fecundity (fig. S7.6a), 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 S5) 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

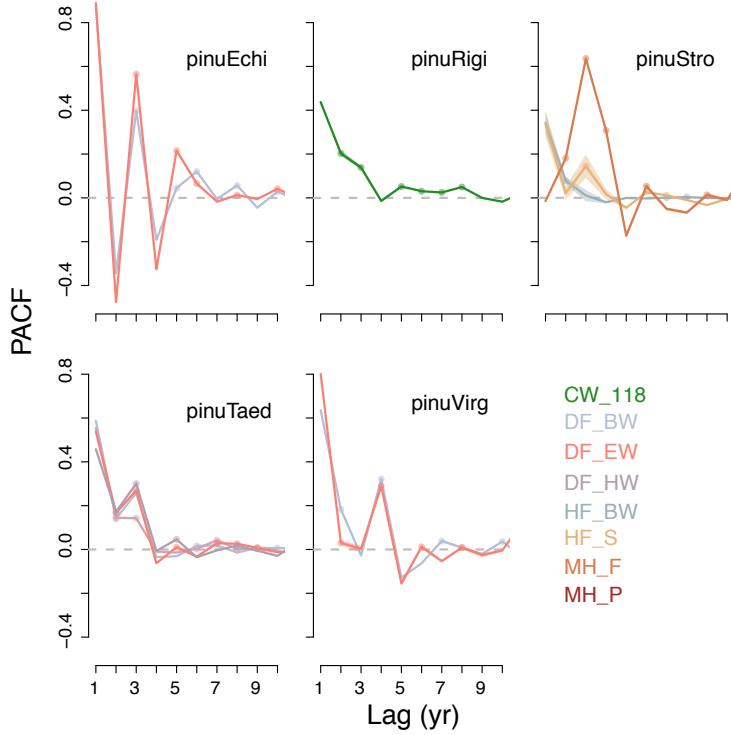


Figure 8: Partial autocorrelation for fecundity in *Pinus* by random groups, defined by species and plot.

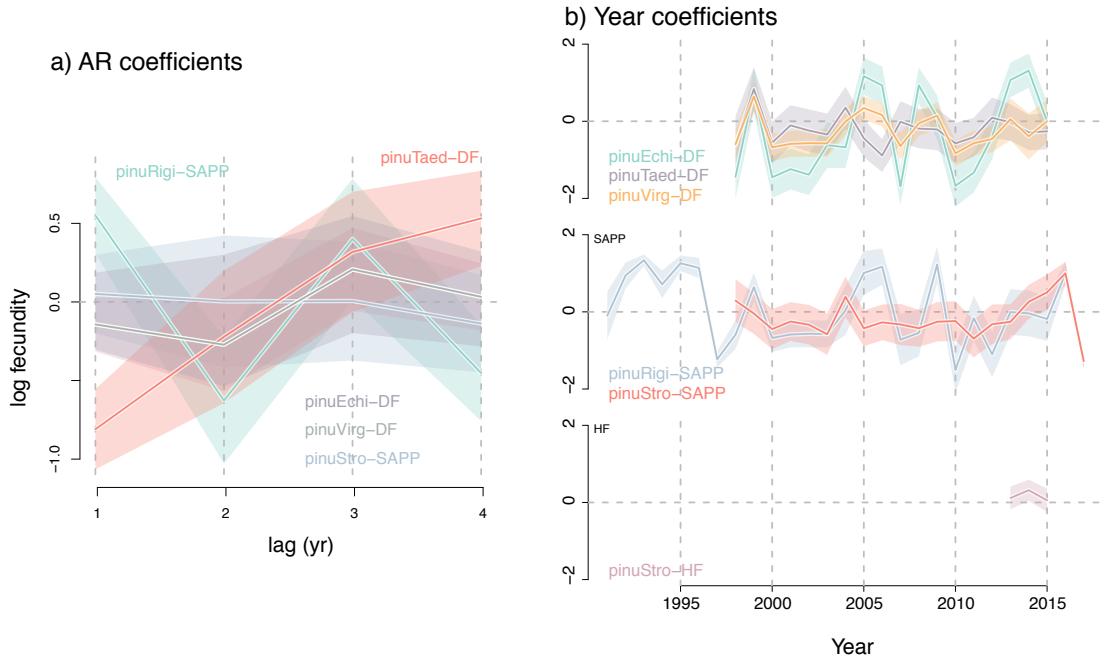


Figure 9: a) Coefficients for random species-region groups in the AR(4) model (a) and the year model (b). NEED SAME COLOR LEGEND.

⁴⁶⁶ pines show one-year lags with strong three-yr (*P. echinata*, *P.*, *taeda*) and four-year
⁴⁶⁷ (*P. virginiana*) cycles, respectively (fig. 8). *P. strobus* also shows periodicity at two of

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

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

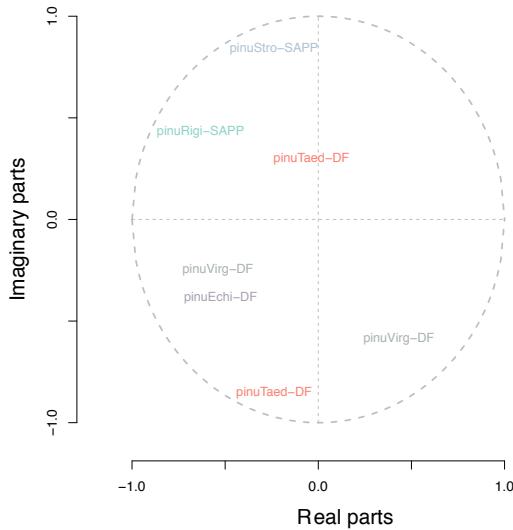


Figure 10: Eigenvalues, real and imaginary parts, lie within the unit circle.

478 Although the full tree-lag covariance \mathbf{C}_L and space-lag covariance \mathbf{G}_L are too large
 479 to visualize for thousands of trees and locations across sites and decades (section S3.1),
 480 a random selection of trees and locations highlights the extent of the covariance decline
 481 from canopy to forest floor. Warm colors in the lag zero plots show that the weak
 482 tendency for synchronicity between trees (fig. 11a) is amplified by dispersal across
 483 the forest floor (fig. 11b). At higher lags there is evidence of year-to-year correlation,
 484 with some trees remaining at high or low levels over successive years. The positive
 485 correlations on the forest floor switch to negative after lag year three.

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

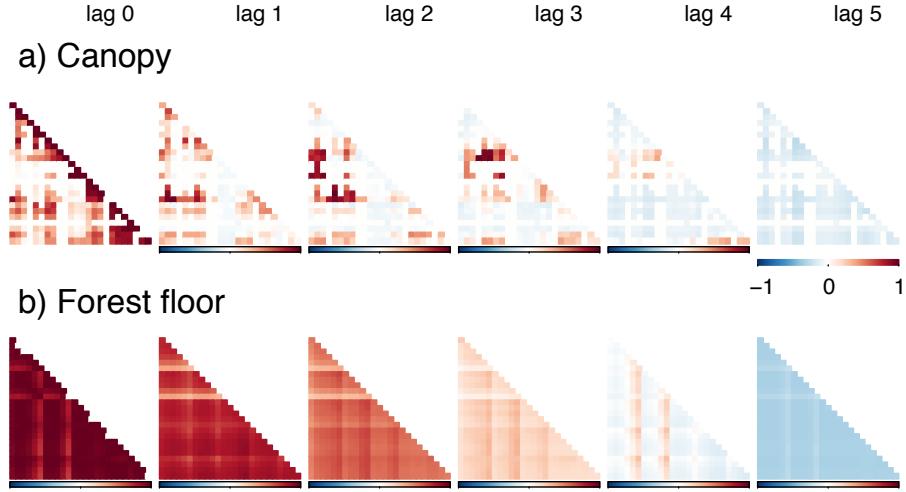


Figure 11: a) Tree-by-lag covariance structure in the canopy at DFBW, developed from \mathbf{C}_L eq. (9) and b) space-by-lag structure on the forest floor, developed from \mathbf{G}_L eq. (10). Each pixel represents an individual host tree (a) or site on the forest floor (b), tracked over successive 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 Δ 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 m²),

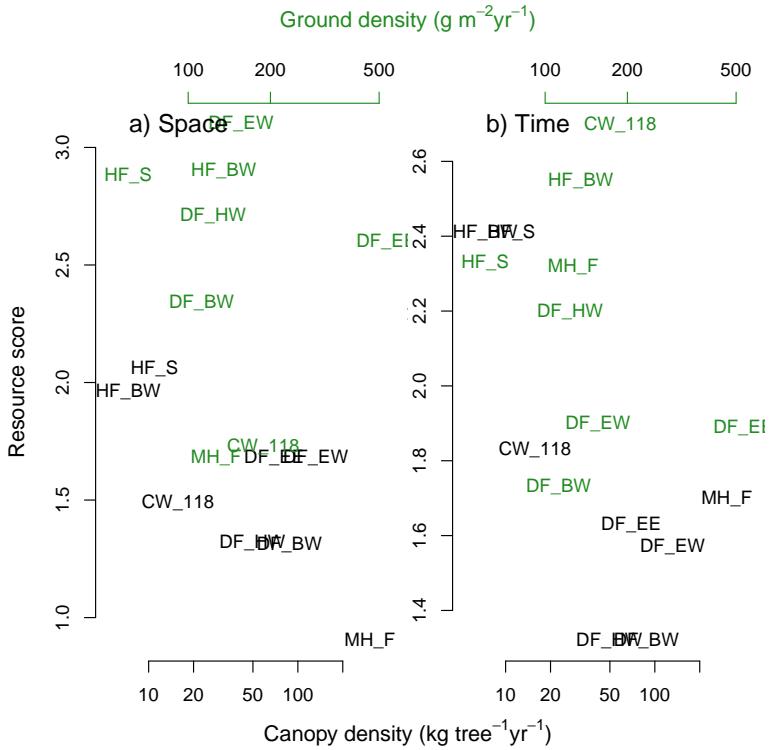


Figure 12: Resource scores (eq. (13)) plotted against mean resource supply (eq. (11)) for a) space [between host trees- (black) and sites on the ground (green) in a given year] and b) over years in a single host or site. Standard deviations are plotted in fig. S7.5.

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

DISCUSSION

515 Quantifying the resource value of forested sites, based on their supply of both abun-
 516 dant and reliable mast, is a venerable challenge in ecology (Janzen, 1970; August,
 517 1983; Ostfeld and Keesing, 2000; Curran and Leighton, 2000; Cortes and Uriarte,
 518 2013; McMeans et al., 2016). As foraging capacity increases, the variance-cost of an
 519 unreliable resource shifts to a mean-benefit: the scale-dependent averaging. The sta-
 520 bility properties of mast cycles can be quantified and compared, showing pervasive

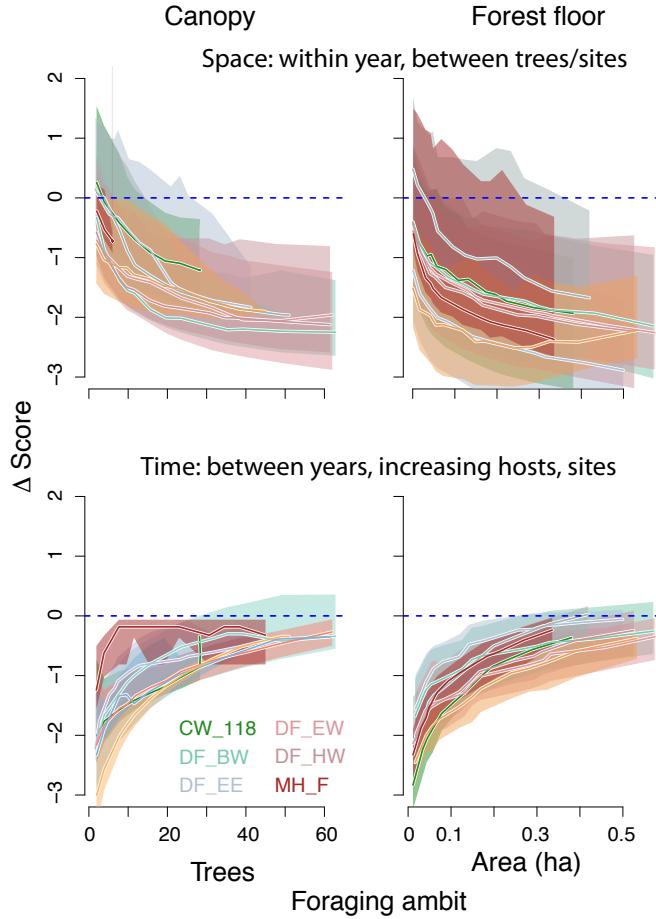


Figure 13: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers that can store resources up for two years. Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance.

quasi-periodicity, but evidence for long-term stability, but large differences between species and stands (fig. 10). Because spatial foraging, storage, and diet breadth represent alternative solutions to the fluctuating resource base, they cannot be analyzed independently. Combining episodic fruiting and synchronicity of the multiple hosts in the diet with the consumer's limited capacity to forage and variable resource quality, we develop a simple resource score that can apply across a network of inventory sites (fig. 12). Theoretical results combined with a methodology that makes estimates widely available can help to synthesize a growing body of data for application to understanding and management. We summarize the role of methodology, followed by potential to improve biogeographic prediction of masting and consumers of it.

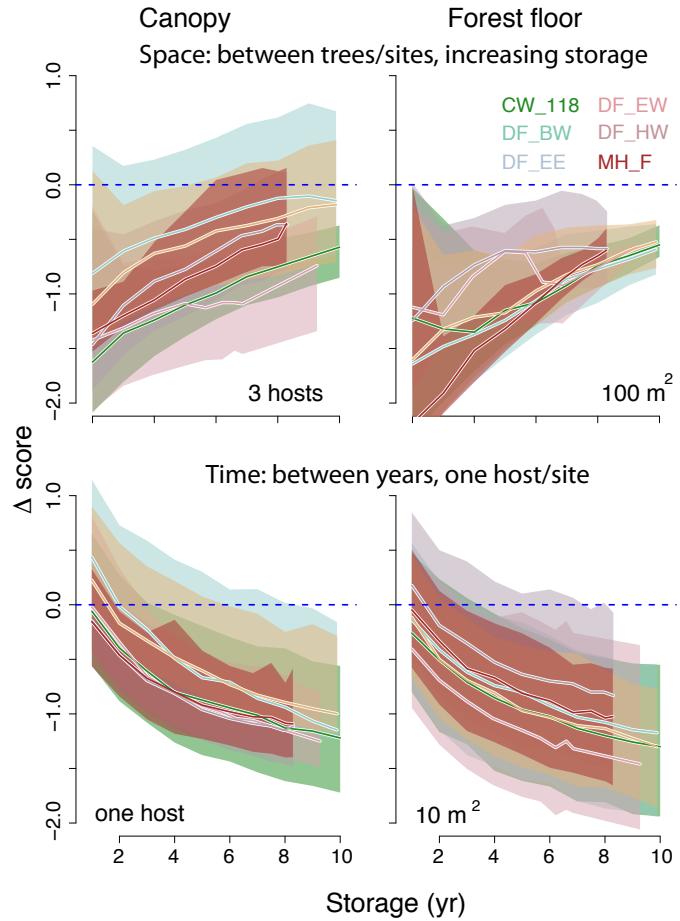


Figure 14: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers with storage capacity of two years to 10 years, assuming that the foraging space is three host trees or 100 m^2 . Above is the tree-to-tree and site-to-site variance within a given year. Below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

531

Mast estimates and prediction

532 MASTIF offers a flexible platform that can facilitate synthesis across a large and grow-
 533 ing literature (table 1). The model specification can include main effects, interactions,
 534 year effects, lag effects, and random effects (table S1.1), while accommodating the
 535 uncertainty in seed identification (fig. S7.3b). From the example application we find
 536 high confidence in estimates (fig. 6, 7, 9 and Supplement B), and this can only improve
 537 when environmental predictors are included in the model (Clark et al. (2004); Uriarte
 538 et al. (2005); Ladeau and Clark (2006); Clark et al. (2010, 2013, 2014); Uriarte et al.
 539 (2012), Nuñez et al., in prep.). Simulation in MASTIF can be used to explore the
 540 efficacy of study designs for specific applications.

541 Inference and prediction break down when trees are either too abundant or too
542 rare. When too abundant, overlapping seed shadows may not be resolved to specific
543 trees. When reproductive trees are too few, there is an insufficient range of values,
544 and estimates of slope coefficients for predictor variables are reduced in magnitude, as
545 expected for noisy data (fig. S7.3). Because the same seed traps are used to estimate
546 all species on a plot, model fit will vary for species, each of which offers a different
547 distribution of distances and numbers and sizes and trees.

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

563 ***Consumer ambit and resource score***

564 The scale-dependent resource score recognizes a shift from variance-penalty to mean-
565 benefit with increasing consumer ambit (fig. 13, 14). Continuing frustration with the
566 standard coefficient of variation (CV) includes this omission of scale (Herrera et al.,
567 1998; LaMontagne and Boutin, 2009). On the other hand, autocorrelation models
568 applied to seed trap data, without estimates of maturation and fecundity, do not
569 reflect availability in the canopy (Clark et al., 2004; Pesendorfer et al., 2016), due to
570 redistribution by dispersal. The resource score extends the value of CV as an index
571 that combines mean and variance by making it scale-specific both for canopy and forest
572 floor.

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

Biogeographic implications

For biogeographic understanding, including impacts of climate change, the resource score can offer a more direct index of habitat suitability than is available through the variables currently used in habitat models and species distribution models (SDMs), which emphasize climate, land cover, and soils, but omit availability of food. Ecologists and wildlife managers have long recognized that masturing provides the base of the food chain, and space-time variation can be just as critical as the mean resource supply (Ostfeld and Keesing, 2000; Curran and Leighton, 2000; McShea, 2000; Boutin et al., 2006; Bergeron et al., 2011; Bogdziewicz et al., 2016).

We did not offer a full predictive analysis of resources scores in this paper, because resources alone cannot predict trophic structure. That analysis includes a full range of climate and habitat variables (Nuñez et al., in prep). The tree species that contribute to mast production are well-known. But there has not been a mechanism for combining pulsed-resource supply with life histories of consumers. The important contribution to biogeographic understanding includes the basic theory and computation that can use species-size structure to quantify resource supply in a way that can be combined with the traditional climate and habitat variables in SDMs. The translation of seed production and dispersal to spatio-temporal resource availability (fig. 11) and the summary of its effect by forest stands (fig. S7.5) can supplement the variables now used for SDM.

603

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