

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).

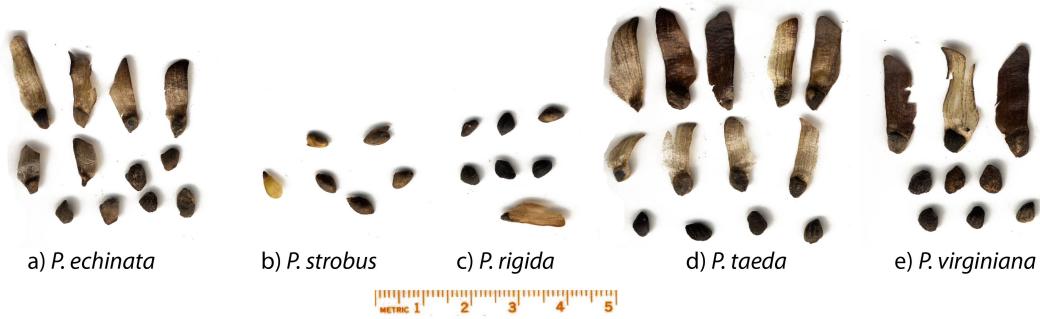


Figure 1: Three seed predators on *Pinus* spp. (above) and five seed types (below). The gray jay (*Perisoreus canadensis*) forages in the canopy (left), the eastern chipmunk (*Tamias striatus*) on the forest floor (center), and the eastern gray squirrel (*Sciurus carolinensis*) in both locations (right).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

In the canopy, host trees are accessed by song birds and arboreal-foraging arthropods and mammals (Curran and Leighton, 2000; McShea, 2000; Koenig and Knops, 2001; Perea et al., 2011; Milleron et al., 2013; Bell and Clark, 2016) (fig. 1). Canopy 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 (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.

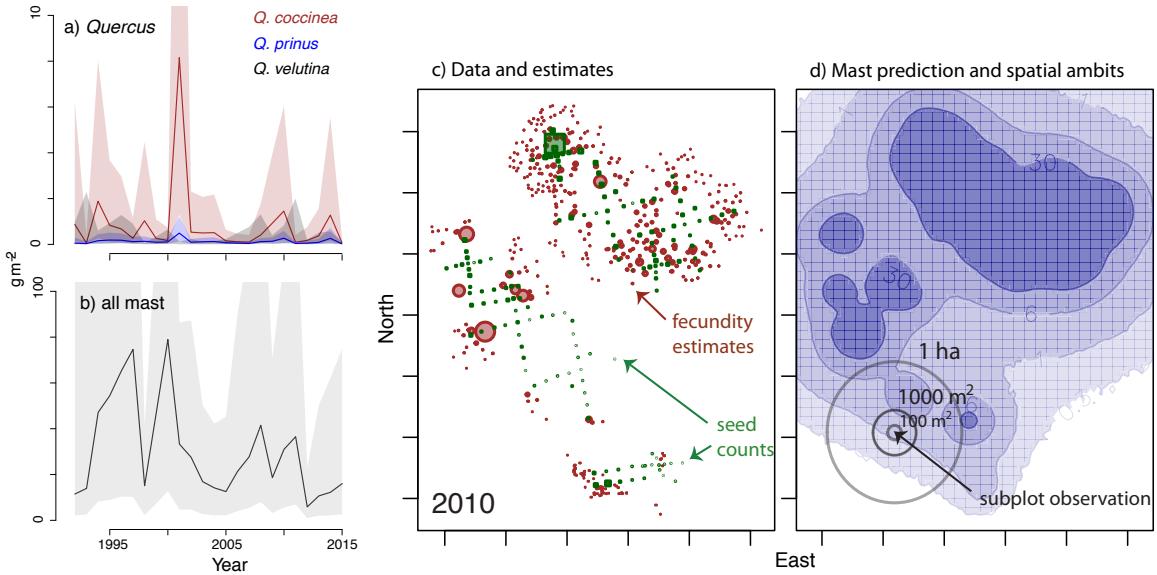


Figure 2: Space-time scales for seeds and consumers. a) Masting by three species in the S Appalachians is erratic. Shading spans 80% of the predictive variation at the 1 m² scale. b) A generalist like *Sciurus* (fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*, *Nyssa*, *Cornus*, *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.

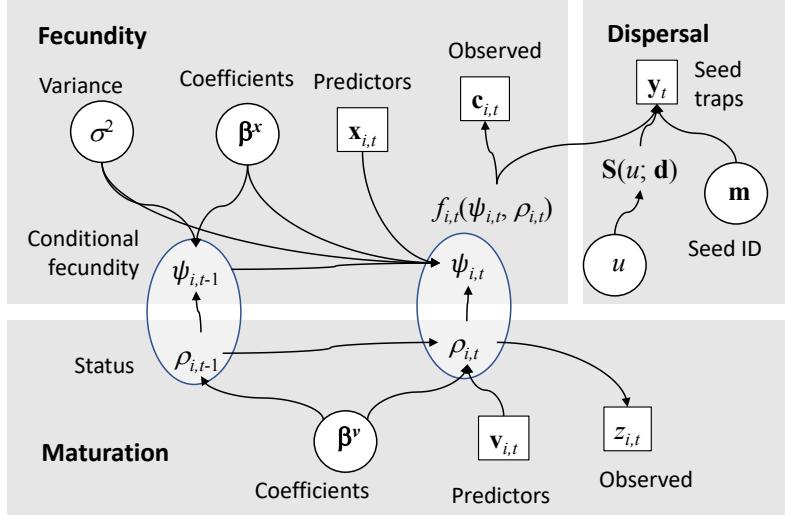


Figure 3: Graphical model for main elements of the model, including fecundity (above), maturation (below), and dispersal (right), showing estimates (circles) and observed variables (squares), with dynamics ($t - 1, t$). Variables are defined in table S1.1.

180 MODEL DEVELOPMENT

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

187 Annual seed production by a mature individual ($\rho_{i,t} = 1$) is termed *conditional fe-*
 188 *cundity*, $\psi_{i,t} > 0$. Like maturation, conditional fecundity is a dynamic process, modeled
 189 with fixed and random effects, year effects, and/or autoregressive terms (table S1.1,
 190 submodel A). Coefficients in β^x can include tree size (eq. (2)), environment, and inter-

actions (Clark et al., 2010, 2013). *Random effects* (REs) β_i^w accommodate the heterogeneity of responses across individual trees (table S1.1, submodel D). Year effects γ_t are an alternative to a large covariance matrix across individuals (table S1.1, submodel B). Alternatively, quasi-periodic variation can be described by an *autoregressive model* AR(p) with $l = 1, \dots, p$ lag terms α_l (table S1.1, submodel C). Year and lag effects can be random across species and/or region groups, recognizing that masting may be coherent within, but not between, groups. *Actual fecundity* is $f_{i,t} = \psi_{i,t}\rho_{i,t} \geq 0$. In some cases, actual fecundity may be observed, from direct counts in the canopy (Ladeau and Clark, 2006) or on the ground (Minor and Kobe, 2017). Observed fecundity enters here as minimum and maximum estimates in the vector $\mathbf{c}_{i,t} = (c_{i,t,min}, c_{i,t,max})$ (fig. 3).

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

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

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

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

A consumer that forages widely realizes the mean resource availability, through movement, storage, and/or diet breadth. Movement scale in the canopy is summarized by the n hosts visited by a consumer. On the forest floor, the movement scale is

represented by the number of contiguous sites S , with a site defined at 5 m \times 5 m.
 Time dependence enters when the proceeds of a high mast year can be 'stored' within
 individuals, by dormancy (fungal pathogens) or so-called *capital breeding* (mammals)
 (Karasov, 1986; Sainmont et al., 2014; Rodel et al., 2016), or within populations,
 the latter here termed *demographic storage*. Demographic storage describes pulsed
 recruitment following masting events (McShea, 2000; Boutin et al., 2006; Descamps
 et al., 2008; Bergeron et al., 2011; Schmidt and Ostfeld, 2003; Pelisson et al., 2013;
 Ogawa et al., 2017), stored as a cohort that can survive subsequent non-mast years,
 during which recruitment might not be sufficient for population persistence. Diet
 generalists experience dependence across individuals of multiple host species.

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

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

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

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

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

A consumer with restricted space-time foraging and narrow diet breadth is vulnerable
 to the variance; individuals and populations suffer in places and times of resource
 limitation. To weigh the benefits of high mean resource supply, $E_{it}(q)$ or $E_{st}(g)$,
 against the variance cost, $Var(Q_{nT})$ or $Var(G_{ST})$, we build from a familiar index used
 to describe masting, the coefficient of variation, $CV = \sqrt{Var(Q_{nT})}/E_{nT}(Q)$ (Herrera
 et al., 1998; LaMontagne and Boutin, 2009; Pesendorfer et al., 2016), but extend it to
 the problem of scale-dependence across multiple host species of variable resource qual-
 ity (eq. (3)). The traditional CV is inadequate, because masting intervals of 2 to 10
 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

252 score. The expected yields in eq. (4) and eq. (5) have corresponding expected variances,

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

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

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

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

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

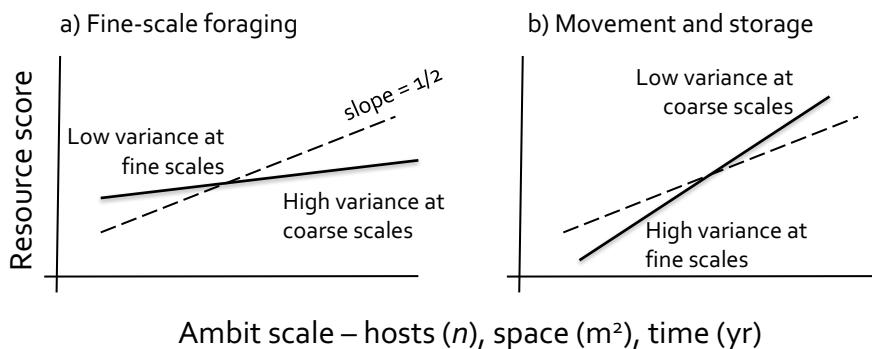


Figure 4: For scale-independent variation, the resource score increases with a slope of 1/2 on a log scale with n (host trees), space (area), and time (years) (eq. (8)). Especially beneficial for consumers with limited ambit are stands offering high mean and low variance at fine scales (a) and vice versa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

258 The baseline eq. (8) provides an index to compare forest stands that differ in scale
 259 dependence (fig. 4). Extended mobility and storage may be of limited benefit where
 260 fine-scale variation is low (fig. 4a). All else equal, high space-time variance at fine
 261 scales benefits the consumer that moves (fig. 4b), where the incremental increase in
 262 the total resource more than compensates for the scale-dependent variance. Again,
 263 space-time must be considered together, because a local forager, favored by (fig. 4a)
 264 may solve high-spatial variance with storage or dormancy in time (*Diet breadth and*

265 variance perceived by the consumer). The covariances required to evaluate the resource
266 score are described in the next section.

267 ***Tree-time and space-time covariance***

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

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

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

287 where $\mathbf{f}_{(nT)} = vec(\mathbf{F}_{(n \times T)})$ and $\boldsymbol{\psi}_{(nT)}$ are length- nT vectors, and \mathbf{C} is the $nT \times nT$
288 covariance matrix that incorporates both the relationships between individual trees
289 and their variation over time. The $vec(\cdot)$ operator stacks the columns of a matrix to
290 obtain a vector. An element $\mathbf{C}_{it,i't'}$ holds the covariance between individual i in year
291 t and individual i' in year t' . We cannot estimate the tree-time matrix \mathbf{C} , because
292 each (i, i', t, t') combination happens once. Below we introduce the *tree-lag* covariance.
293 First we note two special cases, i) a $n \times n$ (tree-to-tree) covariance \mathbf{C}_n holding the

294 covariances experienced by a consumer that moves between n host trees in a random
 295 year, and ii) a $T \times T$ (year-to-year) covariance \mathbf{C}_T , holding the covariances experienced
 296 by a consumer that tracks a random host over T years.

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

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

301 The conditional covariance in intensity is

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

302 The total covariance additionally includes the Poisson variance,

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

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

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

312 Because consumers exploit multiple resources, the covariance structure describes their
 313 combined supply, accounting for differences in nutritional quality and space-time avail-

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.

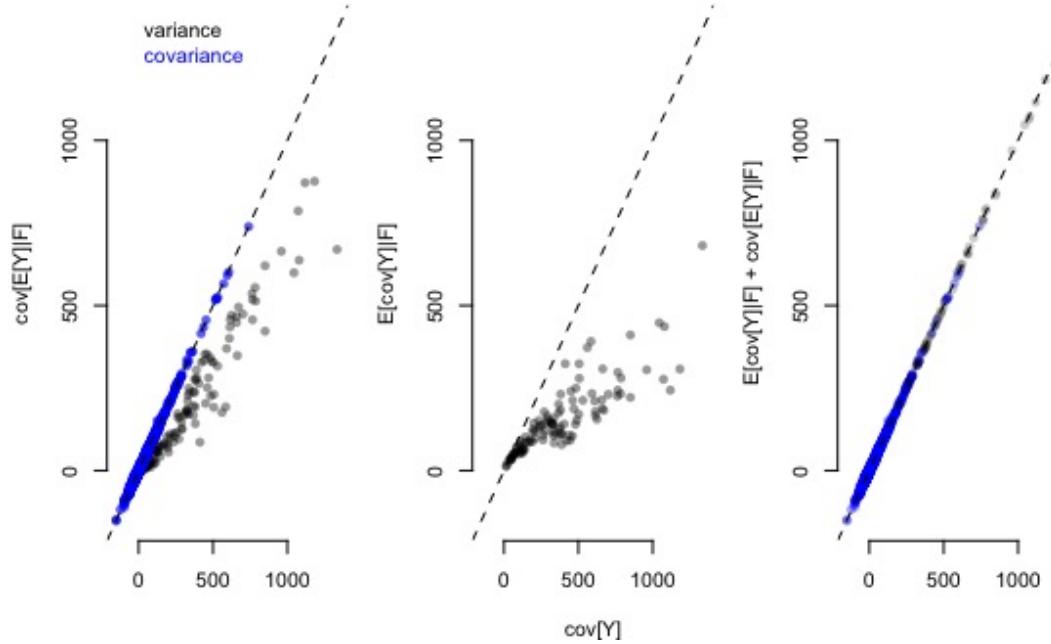


Figure 5: Contributions to space covariance \mathbf{G}_S from terms in eq. (10) plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in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

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

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

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

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

³²⁵ years gives the score

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

³²⁶ This variation can be compared to that expected for scale-independent variation in
³²⁷ eq. (8).

³²⁸ We can combine eq. (8) with eq. (13) to quantify the potential advantage to a
³²⁹ consumer if it could expand the diet to include a new host \tilde{h} that brings \tilde{n} new host
³³⁰ individuals into the diet. The aggregate resource from eq. (11) increases by a term

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

³³¹ where $r_{\tilde{h}}$ is the quality of the new resource, which can be concatenated into a length- \tilde{n}
³³² 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
³³³ expected addition to the diet from the second term in eq. (14) is

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

³³⁴ where $E_{it}(\tilde{f})$ is the expected seed production by the new host. From eq. (12), the
³³⁵ aggregate variance adds two terms,

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

³³⁶ 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 $\tilde{n}T \times nT$
³³⁷ covariance between new and original hosts in the diet. Of course, strong negative
³³⁸ covariance with hosts now in the diet (third term in eq. (16)) decreases aggregate
³³⁹ variance, with obvious benefits. Not so obvious is the fact that, even if independent of
³⁴⁰ the current diet, the resource score is expected to increase whenever the contribution
³⁴¹ to the aggregate mean compensates for the increase in variance. For independent
³⁴² variation eq. (16) simplifies to

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

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

³⁴³ The new host increases the consumer's resource score if this inequality is satisfied:

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

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

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

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

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

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

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

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

362 METHODS

363 For posterior simulation, we implemented Gibbs sampling, a Markov chain Monte
364 Carlo (MCMC) technique, including Metropolis and Hamiltonian Markov chain (HMC)
365 steps (section S8). Due to a high-dimensional state space (all trees over all years), pos-
366 terior simulation suffers well-known scaling limitations of MCMC, as the parameter
367 set is overwhelmed by the volume of parameter space (Neal, 2011); random-walk algo-
368 rithms cannot explore the parameter space in finite time. HMC exploits the geometry
369 of the typical parameter set to efficiently target proposals (Betancourt and Girolami,
370 2015). Because it relies on vector fields (a differentiable surface), HMC does not apply

371 to discrete maturation state. However, it does apply to conditional fecundity, and is
372 used for that purpose here (section S8.2). With the exception of maturation, condi-
373 tional fecundity, and the dispersal parameters (a low-dimensional vector), all other
374 parameters are sampled directly (section S8).

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

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

391 *Simulation*

392 Rather than offer an exhaustive compilation of simulation studies, we supply the full
393 MASTIF package with simple examples for application (section S2). We adopt this
394 approach, because fitting depends on the structure of each stand (density and distri-
395 bution of mature trees), dispersal characteristics of each species, and spatio-temporal
396 sampling design, including density and dispersal of traps, and the classification of
397 seeds into types. As with any model, useful estimates are only expected where there
398 is 'signal' in data. Simulation determines if, given signal, the model can recover pa-
399 rameters and predict data. We illustrate where an SSM can be successful, and we
400 discuss aspects of data structure that can lead to poor performance. The value of the
401 simulator is this first opportunity it affords to examine a full range of potential data
402 sets.

Application to field data

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

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

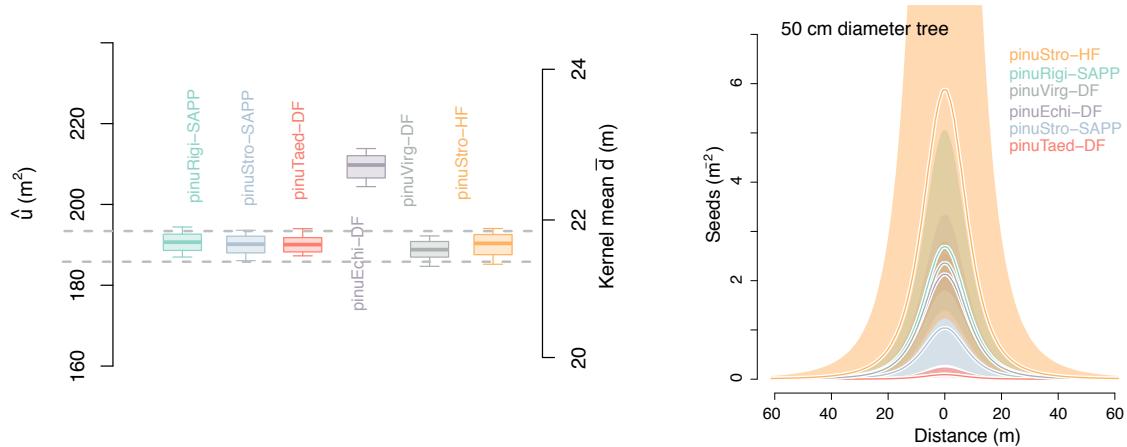


Figure 6: a) Estimates of dispersal parameters u_h for *Pinus* species-region groups. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. The kernel mean scale at right is eq. (S5.14). b) Seed shadows predicted from the posterior distribution, with 95% predictive intervals.

418

RESULTS

419

Simulation studies

420 Simulation studies found that the model can recover parameters and latent states
 421 for all species, even when most of the seeds (80%) are identified only to genus level.
 422 A stochastic simulation example is summarized for $M = 4$ seed types and $H = 3$
 423 species on a mean of $J = 8$ plots, $T = 5$ years, $n = 25$ trees, and $S = 50$ traps.
 424 Parameter recovery is approximate, because, as in real data, few trees in a plot of a
 425 given species are mature. For the simulation shown in fig. S7.3, the number of trees per
 426 plot ranges from 4 to 23. Trees far from seed traps supply little information. However,
 427 if too many trees are close to the same traps, information can be limited by extensive
 428 overlap. Coefficients for maturation and conditional fecundity are close to values used
 429 to generate data, but they are 'damped' (fig. S7.3a, b), as would be expected from a
 430 noisy fit. The composition vectors for seed identification \mathbf{m}_h are recovered precisely,
 431 with 20% of seed from each species being assigned to the species and the remainder
 432 to the undifferentiated class "querUNKN" (fig. S7.3c).

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

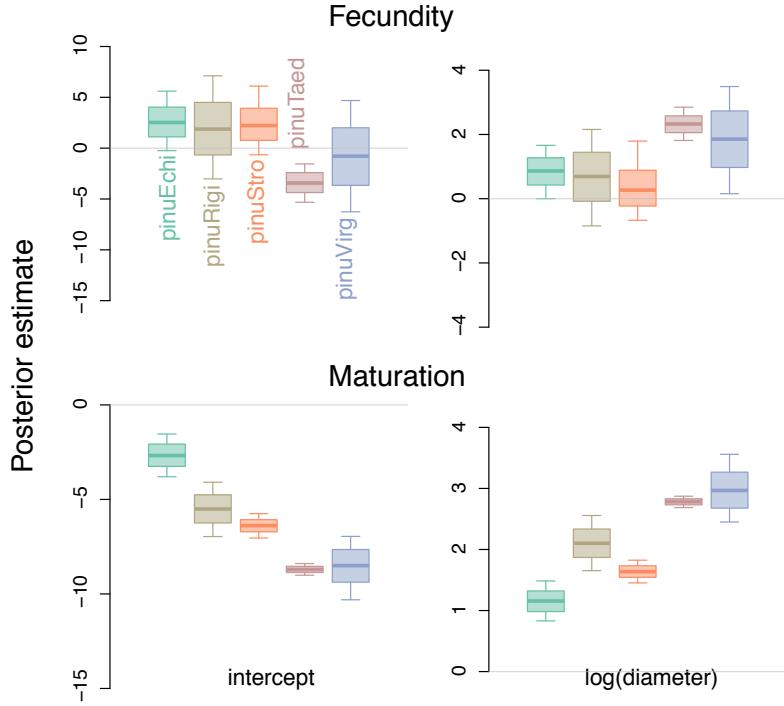


Figure 7: Estimates of fecundity coefficients β^x (above) and maturation coefficients β^v (below) (see table S1.1) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively.

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

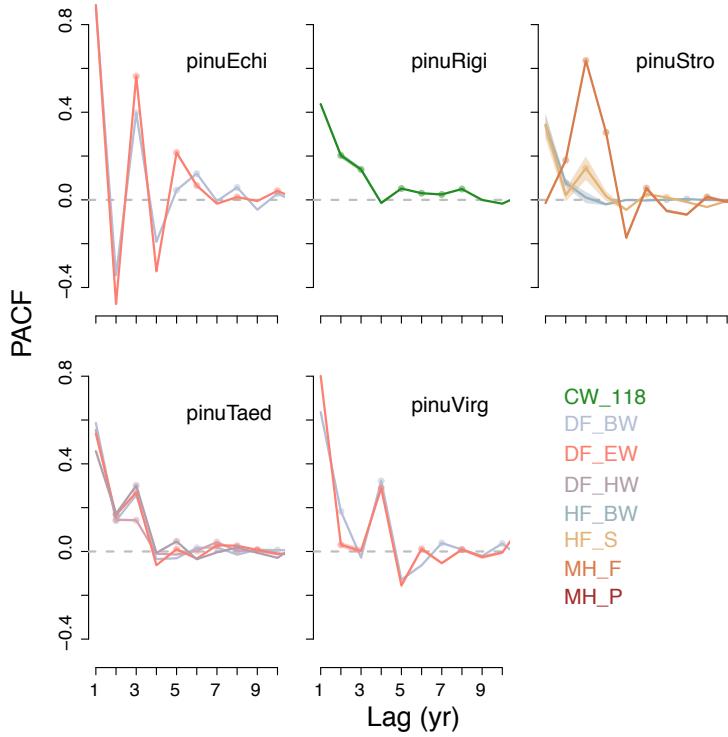


Figure 8: Partial autocorrelation for fecundity in *Pinus* by random groups, defined by species and plot.

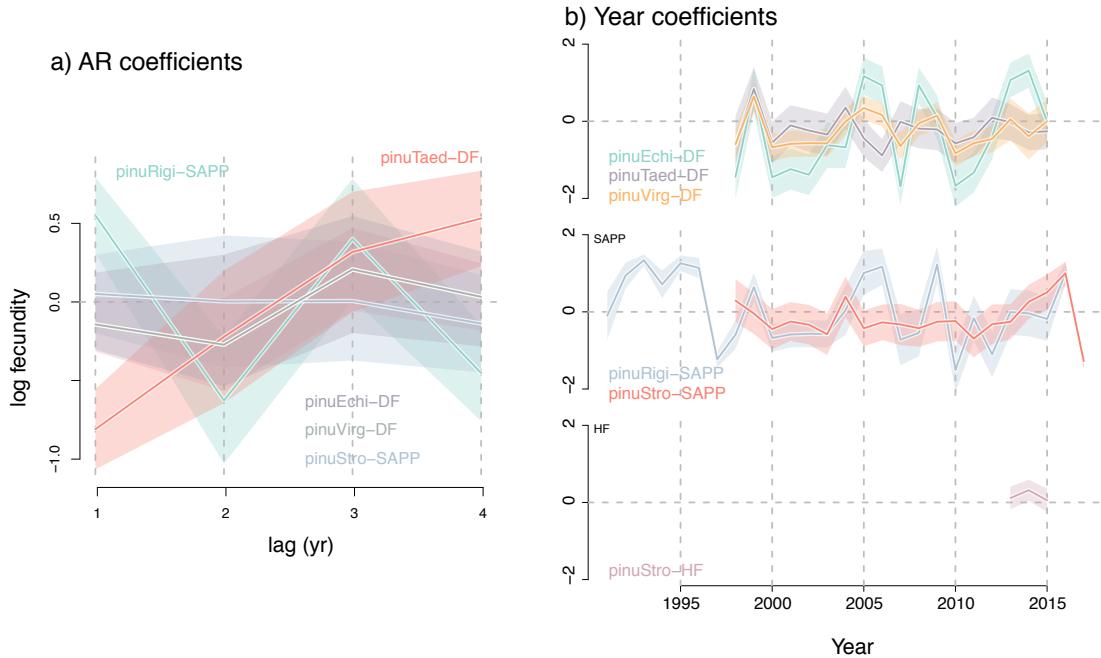


Figure 9: a) Coefficients for random species-region groups in the AR(4) model (a) and the year model (b). NEED SAME COLOR LEGEND.

⁴⁶³ pines show one-year lags with strong three-yr (*P. echinata*, *P.*, *taeda*) and four-year
⁴⁶⁴ (*P. virginiana*) cycles, respectively (fig. 8). *P. strobus* also shows periodicity at two of

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

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

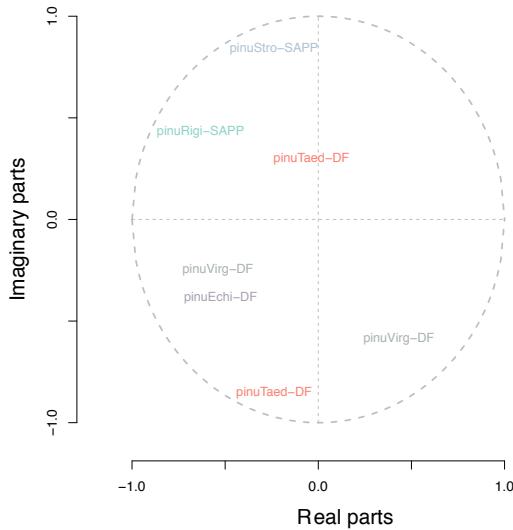


Figure 10: Eigenvalues, real and imaginary parts, lie within the unit circle.

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

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

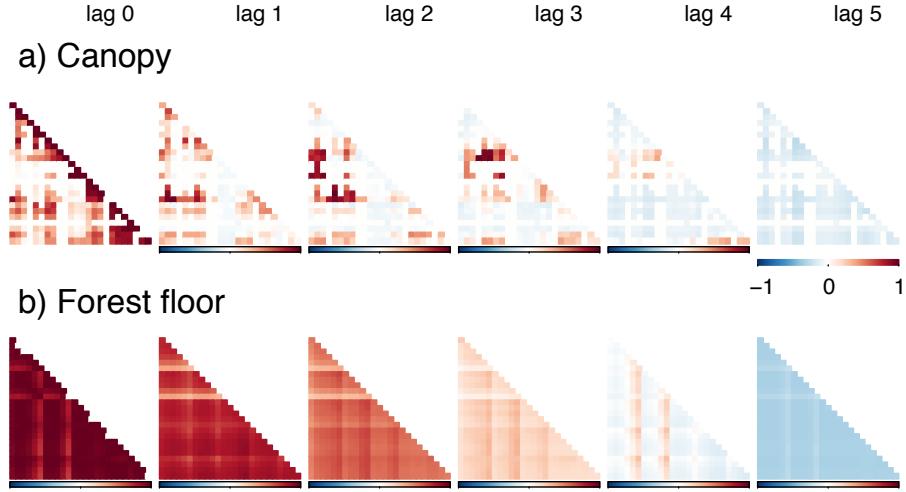


Figure 11: a) Tree-by-lag covariance structure in the canopy at DFBW, developed from \mathbf{C}_L eq. (9) and b) space-by-lag structure on the forest floor, developed from \mathbf{G}_L eq. (10). Each pixel represents an individual host tree (a) or site on the forest floor (b), tracked over successive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

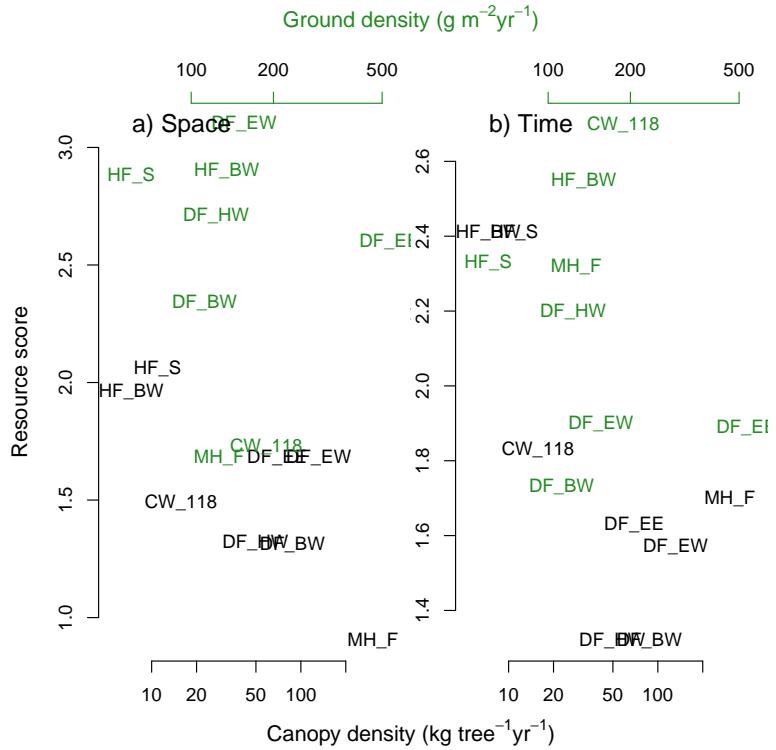


Figure 12: Resource scores (eq. (13)) plotted against mean resource supply (eq. (11)) for a) space [between host trees- (black) and sites on the ground (green) in a given year] and b) over years in a single host or site. Standard deviations are plotted in fig. S7.5.

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 habitats, based on their supply of reliable mast, is a venerable challenge in ecology (Janzen, 1970; August, 1983; Ostfeld and Keesing, 2000; Curran and Leighton, 2000; Cortes and Uriarte, 2013; McMeans et al., 2016). As foraging capacity and/or storage increase, the variance-cost of an unreliable resource shifts to a mean-benefit: the scale-dependent averaging. The stability properties of mast cycles can be quantified and compared, showing evidence for long-

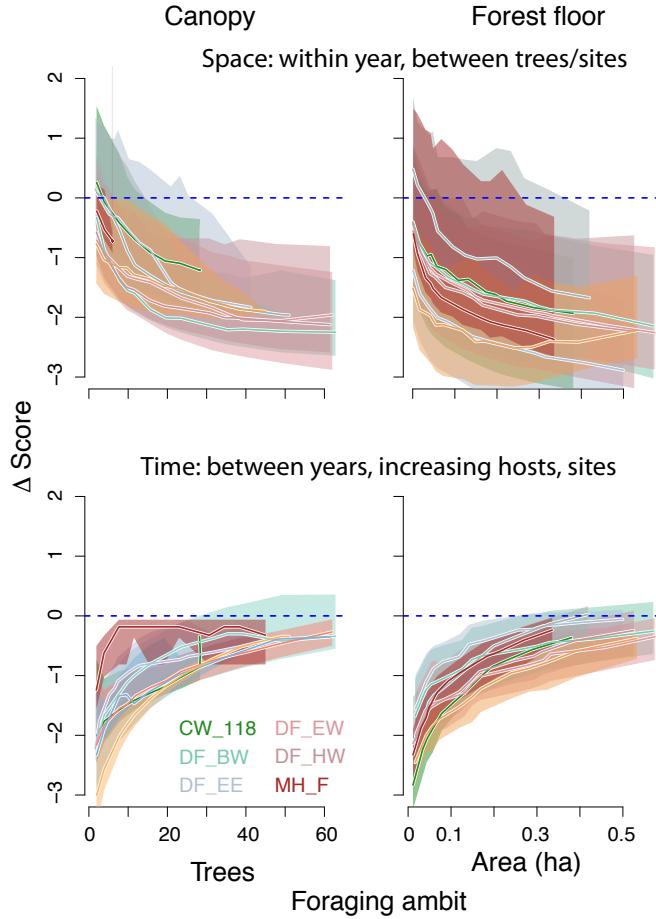


Figure 13: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers that can store resources up for two years. Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance.

term stability, but pervasive quasi-periodicity and large differences between habitats (fig. 10). Spatial foraging, storage, and diet breadth represent alternative solutions to the fluctuating resource base is aligned with episodic fruiting and synchronicity of the multiple hosts in the diet with variable quality. A simple resource score can apply across a network of inventory sites (fig. 12). Theoretical results are combined with a methodology that makes estimates widely available for synthesis. We summarize the methodological advance, followed by potential to improve biogeographic prediction of masting and consumers of it.

526

Mast estimates and prediction

527 MASTIF offers a flexible platform that can facilitate synthesis across a large and grow-
 528 ing literature (table 1). The model specification can include main effects, interactions,

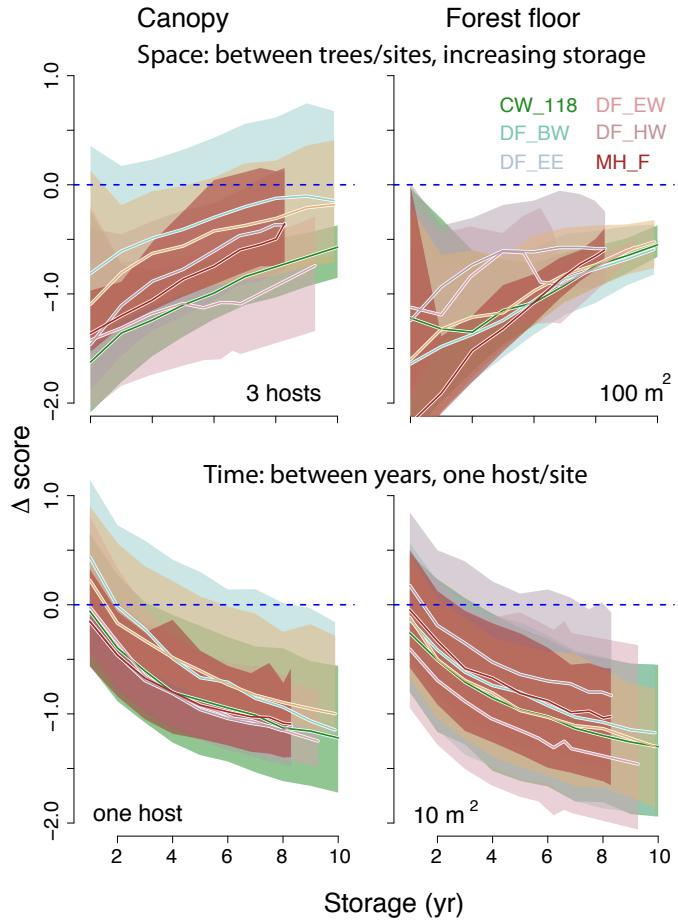


Figure 14: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers with storage capacity of two years to 10 years, assuming that the foraging space is three host trees or 100 m^2 . Above is the tree-to-tree and site-to-site variance within a given year. Below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

529 year effects, lag effects, and random effects (table S1.1), while accommodating the
 530 uncertainty in seed identification (fig. S7.3b). From the example application we find
 531 high confidence in estimates (fig. 6, 7, 9 and Supplement B), and this can only improve
 532 when environmental predictors are included in the model (Clark et al. (2004); Uriarte
 533 et al. (2005); Ladeau and Clark (2006); Clark et al. (2010, 2013, 2014); Uriarte et al.
 534 (2012), Nuñez et al., in prep.). Simulation in MASTIF can be used to explore the
 535 efficacy of study designs for specific applications.

536 Inference and prediction break down when trees are either too abundant or too
 537 rare, an inherent tension between inference on dispersal versus fecundity. When too
 538 abundant, overlapping seed shadows may not be resolved to specific trees. When

539 reproductive trees are too few, there is an insufficient range of values, and estimates
540 of slope coefficients for predictor variables are reduced in magnitude, as expected for
541 noisy data (fig. S7.3). Because the same seed traps are used to estimate all species on
542 a plot, model fit will vary for species, each of which offers a different distribution of
543 distances and numbers and sizes and trees.

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

557 ***Consumer ambit and resource score***

558 The scale-dependent resource score recognizes a shift from variance-penalty to mean-
559 benefit with increasing consumer ambit (fig. 13, 14). Limitations of the standard
560 coefficient of variation (CV) include this omission of scale (Herrera et al., 1998; La-
561 Montagne and Boutin, 2009). On the other hand, autocorrelation models applied to
562 seed trap data alone, without estimates of maturation and fecundity, do not reflect
563 availability in the canopy (Clark et al., 2004; Pesendorfer et al., 2016). The resource
564 score extends the value of CV as an index that combines mean and variance by making
565 it scale-specific both for canopy and forest floor.

566 The standard error (SE) rule (eq. (20)) provides a simple index to quantify the
567 advantage of expanding or contracting diet breadth. Losses from the diet decrease the
568 mean and, except where there is positive covariance with current diet items, decrease
569 the score through increased contribution of the variance. For example, the abundant
570 American chestnut (*Castanea dentata*) in the Appalachian and northeastern forests

571 had an unknown masting structure. Knowledge of extant species can provide guidance
572 on the impacts of future threats. The value of the SE rule is not limited to cases where
573 consumers possess the capacity to change their diets or where diet changes are imposed
574 by changing host availability. It can be used to evaluate the consequences of resource
575 supply potential of stands supporting a full range of tree species.

576

Biogeographic implications

577 For biogeographic understanding, including impacts of climate change, the resource
578 score can offer a more direct index of habitat suitability than is available through the
579 variables currently used in habitat models and species distribution models (SDMs),
580 which emphasize climate, land cover, and soils, but omit availability of food. Ecologists
581 and wildlife managers have long recognized that masting provides the base of the food
582 chain, and space-time variation can be just as critical as the mean resource supply
583 (Ostfeld and Keesing, 2000; Curran and Leighton, 2000; McShea, 2000; Boutin et al.,
584 2006; Bergeron et al., 2011; Bogdziewicz et al., 2016).

585 We did not offer a full predictive analysis of resources scores in this paper, because
586 resources alone cannot predict trophic structure, requiring instead a full range of cli-
587 mate and habitat variables (Nuñez et al., in prep). The important contribution to
588 biogeographic understanding includes the basic theory and computation that can use
589 species-size structure to quantify resource supply in a way that can be combined with
590 the traditional climate and habitat variables in SDMs. The translation of seed produc-
591 tion and dispersal to spatio-temporal resource availability (fig. 11) and the summary of
592 its effect by forest stands (fig. S7.5) can supplement the variables now used for SDM.

593

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