

# 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, 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, on the forest floor, and across sites in a regional network. The model is applied to *Pinus* species across a network of inventory sites.

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

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

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

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

## INTRODUCTION

Masting trees and shrubs offer a pulsed resource that constitutes the base of forest food chains, both supports and destabilizes consumer populations, and mediates the spatio-temporal structure of communities (Janzen, 1970; Jones et al., 1998; Ostfeld and Keesing, 2000; McShea, 2000; Curran and Leighton, 2000; Koenig and Knops, 2001; Clotfelter et al., 2007; Schmidt and Ostfeld, 2003; Boutin et al., 2006; Bergeron et al., 2011; Bogdziewicz et al., 2016; McMeans et al., 2016). Seed-shadow models (SSMs) are widely used to describe masting, because they passively monitor both fecundity and dispersal simultaneously for all species that can be recovered and identified in seed traps. Estimates from SSMs provide insights on dispersal and recruitment limitation

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

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

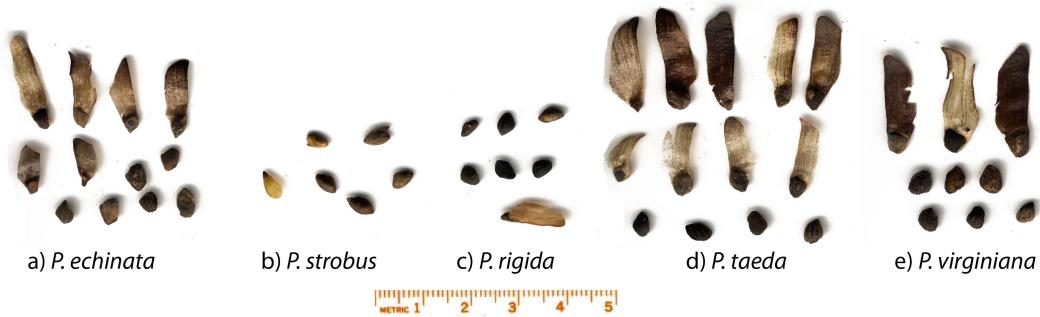


Figure 1: Three seed predators on *Pinus* spp. (above) and five seed types (below). The gray jay (*Perisoreus canadensis*) forages in the canopy (left), the eastern chipmunk (*Tamias striatus*) on the forest floor (center), and the eastern gray squirrel (*Sciurus carolinensis*) in both locations (right).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

and across regions (August, 1983; Stein et al., 2014). Spatial variation within stands presents challenges that differ for foragers in the canopy versus the understory (Carbone et al., 2005; Sheldon and Nadkarni, 2013). In the canopy, host trees are accessed by song birds and arboreal-foraging arthropods and rodents (Curran and Leighton, 2000; McShea, 2000; Koenig and Knops, 2001; Perea et al., 2011; Schmidt and Ostfeld, 2003; 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* co-

52 variance between hosts, over years. The density and aggregation of mast trees can vary  
53 widely between stands. Ground foraging mammals and ground-nesting birds respond  
54 to *space-time* covariance following dispersal to the forest floor (Janzen, 1970; Moore  
55 et al., 2007; Zwolak et al., 2016), which combines host location with dispersal (fig. 2d).  
56 Arthropod seed consumers exhibit a range of foraging tactics (Janzen, 1970; Bonal  
57 and Munoz, 2008; Espelta et al., 2009; Bell and Clark, 2016). Damping-off pathogens  
58 appear to have limited dispersal capacity, but can extend dormancy (\*\*) to disperse  
59 in time. Depending on diet breadth, life span, storage potential, and/or dormancy  
60 (Carbone et al., 2005; Pelisson et al., 2013; Sainmont et al., 2014; Rodel et al., 2016),  
61 seed predators and pathogens experience mast variation at temporal scales of a single  
62 season to multiple years.

63 Variance in space is not decoupled from variance in time and diet breadth. Quasi-  
64 periodic mast years can be spaced up to a decade apart (fig. 2a). Host species differ  
65 in total seed production, the degree of variation in time and synchronicity between  
66 individuals (Clark et al., 2010). Synchronicity between hosts reduces spatial varia-  
67 tion during mast years (production at high spatial density), but increases temporal  
68 variation between years.

69 Diet generalists can abide spatio-temporal variation through diet switching, a *port-*  
70 *folio effect* (Tilman et al., 1998; Schindler et al., 2010). Diet specialization exposes  
71 consumers to the full heterogeneity offered by a specific host (Devictor et al., 2010;  
72 Clavel et al., 2011), while the generalist averages the variation in multiple hosts (fig. 2a,  
73 b). For a consumer species  $c$ , there is space, time, and resource breadth  $|S, T, R|_c$ , or  
74 *ambit*. The combination of these three dimensions determine if consumers can abide  
75 variation in their hosts and if hosts can benefit by spatio-temporal escape (Janzen,  
76 1970; Curran and Leighton, 2000; Grotan et al., 2009; Schmidt and Ostfeld, 2003;  
77 Lichti et al., 2014). Theory is needed to relate estimates of fecundity and dispersal at  
78 these tree-space-time covariance scales of the consumer ambit.

79 The genus *Pinus* is used as an example application of theory and analysis devel-  
80 oped here. Important for a diversity of ground and canopy foragers (fig. 1), this wide-  
81 ranging and multi-species genus tests our capacity to estimate and predict elements of  
82 theory when challenged with observation error in seed identification. Arthropod seed  
83 predators on *Pinus* species forage mainly in the canopy (Cibrian-Tovar et al., 1986).  
84 Canopy vertebrates include crossbills (*Loxia* spp.) and other finches, nuthatches,  
85 gray jay (*Perisoreus canadensis*), and red-bellied woodpeckers. Ground foraging seed

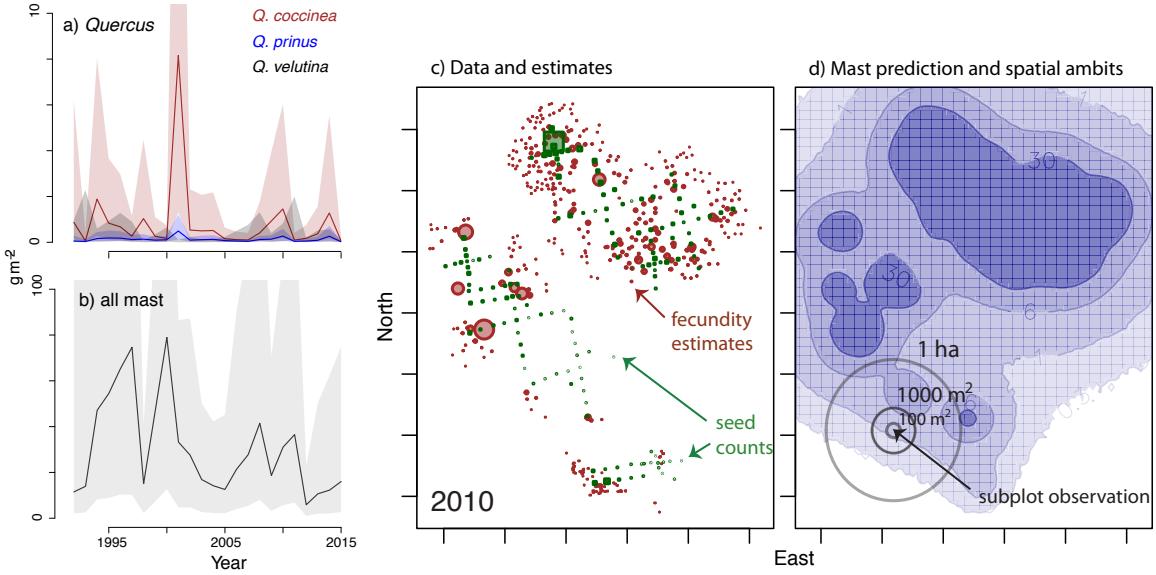


Figure 2: Space-time scales for seeds and consumers. a) Masting by three species in the S Appalachians is erratic. Shading spans 80% of the predictive variation at the  $1 \text{ m}^2$  scale. b) A generalist like *Sciurus* (fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*,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

predators include eastern chipmunk (*Tamias striatus*), wood mice, yellow-necked mice, white-footed mice (*Peromyscus leucopus*) and red-backed voles (*Clethrionomys gapiperi*) (Abbott and Quink, 1970; Ogawa et al., 2017). Eastern gray squirrel (*Sciurus carolinensis*) forages in the canopy and on the ground.

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

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

where  $E[\cdot]$  is an expectation,  $y_s$  is the number of seeds counted in a trap at location

<sub>96</sub>  $s$ ,  $\lambda_s$  is the expected seed density (seeds m<sup>-2</sup>),  $A$  is the area of a seed trap (m<sup>2</sup>),  $\mathbf{S}_{s,i}$   
<sub>97</sub> is the density of seed produced by tree  $i$  dispersed to location  $s$  (m<sup>-2</sup>), and  $f_i$  is seed  
<sub>98</sub> production by tree  $i$  (table 2). For a length- $S$  vector of seed traps, a length- $n$  vector  
<sub>99</sub> of fecundities, and a  $S \times n$  kernel matrix  $\mathbf{S}$ , there is a length- $S$  vector of seed density

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

<sub>100</sub> Because both fecundity  $\mathbf{f}$  and dispersal capacity  $\mathbf{S}$  are unknown, the efficacy of these  
<sub>101</sub> models should depend on the amount of data and its space-time structure.

Table 1: Attributes of some SSMs with examples.

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

<sup>a</sup> IND - independent fits to each year; RE - random effect; FE - fixed effect; A - D are terms in table 2.

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

<sub>102</sub> Before summarizing the challenges with SSMs, we briefly mention why they can  
<sub>103</sub> often be preferable to more direct analyses, such as stable isotope labels (Carlo et al.,  
<sub>104</sub> 2009; Cortes and Uriarte, 2013) or genotyping seeds or seedlings (Godoy and Jor-  
<sub>105</sub> dano, 2001; Grivet et al., 2005; Jones et al., 2005; Pairon et al., 2006; Burczyk et al.,  
<sub>106</sub> 2006; Robledo-Arnuncio and Garcia, 2007; Jones and Muller-Landau, 2008; Moran  
<sub>107</sub> and Clark, 2011; Schupp and Jordano, 2011; Bontemps et al., 2013). Due to labor  
<sub>108</sub> and expense, typically only a subset of seeds or seedlings can be labeled or genotyped,  
<sub>109</sub> most often selected individuals of a single species. Both data types provide infor-

110 mation on dispersal, but they do not offer estimates of fecundity (Moran and Clark,  
111 2011; Milleron et al., 2013). Because seed traps sample passively, SSMs provides an  
112 efficient option to gather fecundity and dispersal estimates from all species that can  
113 be identified in seed traps simultaneously, naturally integrating space (trap area) and  
114 time (trap deployment period).

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

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

$$f_i = a \times size_i^b \quad (2)$$

135 (first line of table 1). While such models can converge rapidly, it can be hard to deter-  
136 mine if global parameters  $(a, b)$  accurately describe population heterogeneity, because  
137 fecundity is not observed. Many trees might be needed to estimate parameters  $(a, b)$ ,  
138 but high density of trees degrades the estimate of dispersal  $\mathbf{S}$ , due to the large overlap  
139 in seed shadows. Poorly estimated dispersal, in turn, degrades the information on  
140 fecundity  $\mathbf{f}$ . The question becomes, can SSMs estimate dispersal, the effects of size  
141  $(a, b)$ , and the fecundities,  $f_i, i = 1, \dots, n$ ?

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

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

171 In summary, at least three advances are needed to translate data to estimates of  
172 mastинг impacts on consumers. First is the missing theory for space-time covariance  
173 structure that could guide model development. Second is a modeling framework that  
174 delivers the necessary estimates. Finally, computation that is accessible to a commu-  
175 nity of users is needed to promote synthesis. Ideally, that framework would include

Table 2: Terms for conditional fecundity,  $\log \psi_{i,t} \sim N(\mu_{i,t}, \sigma^2)$  and variable list.

Term(s) in $\mu_{i,t}$	Definitions
$\mathbf{x}'_{i,t} \boldsymbol{\beta}^x$	A. Fixed effects
$\gamma_t + \gamma_{g[i],t}$	B. Fixed year, random by group
$\sum_{l=1}^p (\alpha_l + \alpha_{g[i],l}) \psi_{i,t-l}$	C. AR( $p$ ) fixed lag, random by group
$\mathbf{w}'_{i,t} \boldsymbol{\beta}_i^w$	D. Random individual effect
Variables/parameters (dimension)	(units)
$A_{s,t}$	sample effort ( $\text{m}^2 \text{ yr}$ )
$\mathbf{A}_\alpha (G \times G)$	random group covariance for AR( $p$ )
$\alpha_l$	AR( $p$ ) lag effect $l = 1, \dots, p$
$\mathbf{B}_w (q^w \times q^w)$	random individual covariance ( $x^{-2}$ )
$\boldsymbol{\beta}^v (q^v \times 1)$	maturity coefficients ( $v^{-1}$ )
$\boldsymbol{\beta}^x (q^x \times 1), \boldsymbol{\beta}_i^w (q^w \times 1)$	fecundity fixed, random coefficients ( $x^{-1}$ )
$f_{i,t}$	fecundity (seeds)
$g_{sh,t}$	seed mass on the ground ( $\text{g m}^{-2}$ )
$\lambda_{sm,t}$	expected seed density ( $\text{m}^{-2}$ )
$\psi_{i,t}$	conditional fecundity (seeds)
$\gamma_t$	year effect $t = 1, \dots, T$
$\mathbf{m}_h (M \times 1)$	seed-type composition for species $h$
$q_{i,t}$	seed mass on the tree ( $\text{kg tree}^{-1}$ )
$\rho_{i,t}$	maturity status
$\mathbf{S} (S \times n)$	redistribution kernel matrix ( $\text{m}^{-2}$ )
$\sigma^2$	log fecundity residual variance
$\tau^2$	random year variance
$u_g$	random dispersal parameter ( $\text{m}^2$ )
$\tilde{u}, \tilde{U}$	fixed dispersal mean ( $\text{m}^2$ ) and variance ( $\text{m}^4$ )
$\mathbf{v}_{i,t} (q^v \times 1)$	maturity design ( $x$ )
$\mathbf{x}_{i,t} (q^x \times 1), \mathbf{w}_{i,t} (q^w \times 1)$	fecundity fixed, random design ( $x$ )
$y_{sm,t}$	seed count
$z_{i,t}$	observed maturity status

Subscripts reference trap  $s$  and seed type  $m$  or individual  $i$  and species  $h$  in year  $t$ . The notation  $g[i]$  refers to the membership of individual  $i$  in group  $g$ . There are  $n$  trees,  $S$  traps,  $H$  species,  $M$  seed types, and  $G$  random groups. The dimension of non-scalar quantities is indicated. Variables lacking units at right are dimensionless. Consumer covariance matrices are separately defined in table SA5.1.

176 simulation, to learn about the conditions where all elements can be identified. The  
177 potential to integrate data sets could help determine the controls on the site-to-site  
178 variation in consumers and their dynamics over time.

179 Here we incorporate and predict spatio-temporal covariance in SSMs with an ap-  
180 proach that can be implemented in a general software application. This initial treat-  
181 ment focuses on methodology, including theory, modeling, computation, and applica-  
182 tion. A subsequent paper applies it to the community of masturing species and their  
183 consumers across a network sites (Nuñez et al, in prep). The next section provides  
184 background theory and the model framework used to estimate masturing structure.

## 185 MODEL DEVELOPMENT

186 [IS THIS PARAGRAPH NECESSARY?] Following a summary of the problem, we  
187 discuss masturing effects on covariance between host trees, in space, and over years (*Tree-*  
188 *time and space-time covariance*), and we translate that covariance to the generalist  
189 consumer with multiple hosts (*Diet breadth and variance perceived by the consumer*).  
190 We then summarize elements of the model that allow for inference (*Model components*).

191 Consider an inventory plot where trees mature, after which they are capable of  
192 seed production. The probability that tree  $i$  can produce seed in year  $t$ , termed  
193 *maturity*  $\rho_{i,t} \in \{0, 1\}$ , can increase with tree size, depending on the environment and  
194 on the individual. Annual seed production by a mature individual ( $\rho_{i,t} = 1$ ) is termed  
195 *conditional fecundity*,  $\psi_{i,t}$ . Actual fecundity is  $f_{i,t} = \psi_{i,t}\rho_{i,t}$ . Fecundity can depend not  
196 only on tree attributes, weather, and resources, but also on other trees (synchronicity).  
197 Seeds accumulate in seed trap  $s = 1, \dots, S$ , from the combined fecundities of nearby  
198 trees, dispersal capacities, and their distances, described by the kernel  $\mathbf{S}$  (eq. (1)).  
199 Seeds extracted from traps are counted by species or, if species identity is unclear,  
200 then genus. When multiple species  $h = 1, \dots, H$  contribute to the same seed type(s),  
201 as when some seeds are identified only to genus, then the  $m = 1, \dots, M$  seed types  
202 must be included in the model with the  $H$  species that could have produced them.  
203 The seed count  $y_{sm,t}$  is the number of seeds of type  $m$  counted in a trap at  $s$  in year  $t$ .

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

207 that differ both in abundance and quality,

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

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

211 A consumer with restricted space-time foraging and narrow diet breadth is vulner-  
212 able to the variance; populations suffer in places and times of resource limitation. A  
213 consumer that forages widely realizes the mean resource availability—it ”averages” the  
214 variance. Consumers may ”store” the proceeds of a high mast year within individuals,  
215 by dormancy (fungal pathogens) or so-called *capital breeding* (mammals) (Karasov,  
216 1986; Sainmont et al., 2014; Rodel et al., 2016), or within populations, the latter here  
217 termed *demographic storage*. Demographic storage describes pulsed recruitment fol-  
218 lowing mast events (McShea, 2000; Koenig and Knops, 2001; Boutin et al., 2006;  
219 Clotfelter et al., 2007; Descamps et al., 2008; Bergeron et al., 2011; Schmidt and Os-  
220 tfeld, 2003; Pelisson et al., 2013; Ogawa et al., 2017), stored as a cohort that can  
221 survive subsequent non-mast years, during which recruitment might not be sufficient  
222 for population persistence.

223 To weigh the benefits of high mean resource supply  $\bar{c}$  against the variance cost  $C$ , we  
224 build from a familiar index long used to describe mast, the coefficient of variation,  
225  $CV = \sqrt{C}/\bar{c}$  (Herrera et al., 1998; LaMontagne and Boutin, 2009; Pesendorfer et al.,  
226 2016), but extending it to the problem of scale-dependence across multiple host species  
227 of variable resource quality (eq. (3)). A coefficient of variation is inadequate, because  
228 mast intervals of 2 to 10 years having the same  $CV$  will not have the same impacts  
229 on consumers that differ in space-time-resource ambit. Likewise, a spatial  $CV$  must  
230 be evaluated at the scale relevant for the consumer ambit.

231 Scale-dependence can represent number of host individuals visited in the canopy  
232  $n$  or foraging ambit on the ground ( $S$  sites defined at  $5 \text{ m} \times 5 \text{ m}$ ). Where there  
233 is storage, there is dependence in time  $T$ . Diet generalists experience dependence  
234 across host species. Our *resource score* inverts the  $CV$  (a score increases with the  
235 mean and declines with the variance), makes it scale-dependent, and expresses it on a  
236 proportionate (log) scale.

237 As a baseline for scale-dependence, we first evaluate the scale-independent resource  
238 score. In the canopy, the expected yield to a consumer over  $n$  hosts and  $T$  years is

<sup>239</sup>  $nT\bar{c}$ . The scale-independent variance on this aggregate yield is  $nT\bar{C}$ . The baseline  
<sup>240</sup> resource score increases at a rate of  $\log(nT)/2$ ,

$$\overline{RS}_{nT} = \log(CV_{nT}^{-1}) = \log(\bar{c}_{nT}) + \frac{\log(nT) - \log\bar{C}_{nT}}{2} \quad (4)$$

<sup>241</sup> By substituting  $n$  for the subscript  $nT$ , the resource score applies to  $n$  host trees in a  
<sup>242</sup> single year. A subscript  $T$  applies to a single host over  $T$  years. For the forest floor  
<sup>243</sup> there is a resource score for  $T$  years in one site, for  $S$  sites in a single year, and for  $ST$   
<sup>244</sup> site-years.

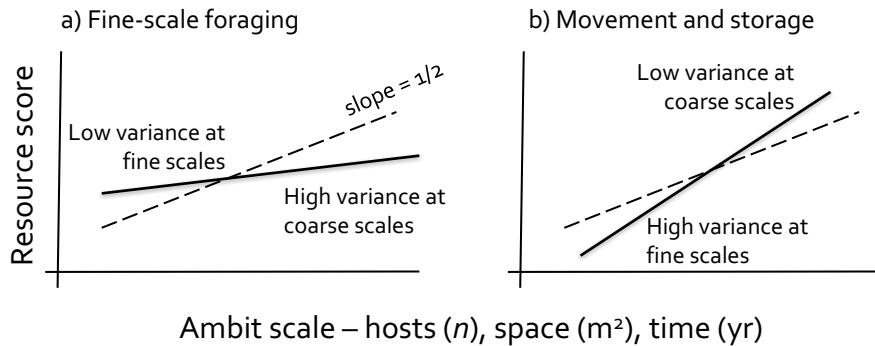


Figure 3: For scale-independent variation, the resource score increases with a slope of  $1/2$  on a log scale with  $n$  (host trees), space (area), and time (years) (eq. (4)). Especially beneficial for consumers with limited ambit are stands offering high mean and low variance at fine scales (a) and vice versa (b). [HORIZONTAL AXIS MUST SAY LOG SCALE]

<sup>245</sup> The baseline eq. (4) provides an index to compare forest stands that differ in their  
<sup>246</sup> scale dependence (fig. 3). Extended mobility and storage may be of limited benefit  
<sup>247</sup> where fine-scale variation is low (fig. 3a). All else equal, high space-time variance  
<sup>248</sup> at fine scales encourages movement for consumers capable of it (fig. 3b). Increased  
<sup>249</sup> foraging ambit is beneficial where the incremental increase in the total resource more  
<sup>250</sup> than compensates for the scale-dependent variance. Again, space-time must be con-  
<sup>251</sup>sidered together, because a local forager, favored by (fig. 3a) may solve high-spatial  
<sup>252</sup> variance with storage or dormancy in time (*Diet breadth and variance perceived by the*  
<sup>253</sup> *consumer*). The covariance required to evaluate the resource score are described in  
<sup>254</sup> the next section.

255        ***Tree-time and space-time covariance***

256        Differences in masting structure experienced by consumers in the canopy and on the  
 257        ground are summarized by stand-specific mean and covariance structure that will  
 258        substitute for the expected values in eq. (4). In the canopy, the relevant covariance  
 259        is between individual host trees, i.e., fecundity before seeds are dispersed. This is  
 260        *individual-time* or *tree-time* covariance. On the forest floor, the relevant covariance is  
 261        *space-time*; it follows dispersal.

262        Space- and time-dependence can be evaluated for estimated or for predicted tree-  
 263        by-tree covariance, which is then combined with spatial covariance induced by disper-  
 264        sal. Functional forms from the geospatial literature summarize space-time structure  
 265        with a relatively small number of parameters (Gneiting, 2002; Banerjee et al., 2014).  
 266        For the case of tree covariance, there is no evidence for a distance-related covariance  
 267        between trees within stands (Clark et al., 2010), consistent with widely observed re-  
 268        gional coherence (Liebhold et al., 2004; Fernandez-Martinez et al., 2017). For this  
 269        reason, within-stand canopy covariance is between trees, rather than over distance.  
 270        On the forest floor, spatial covariance combines tree covariance with dispersal. We do  
 271        not introduce a geospatial model, because it is already imposed by the kernel **S**. For  
 272        covariance over time, we use the covariance in the estimated fecundity from the model.  
 273        Although model fitting can include AR or year terms (*Model components*), we expect  
 274        fecundity predictions to often include wide uncertainty. Fecundity estimates can be  
 275        much more accurate than predictions (section SA1).

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

$$\begin{aligned} E [\mathbf{f}_{(nT)}] &= \boldsymbol{\psi}_{(nT)} \\ cov [\mathbf{F}_{(n \times T)}] &= \mathbf{C} \end{aligned} \tag{5}$$

278        where  $\mathbf{f}_{(nT)} = vec(\mathbf{F}_{(n \times T)})$  and  $\boldsymbol{\psi}_{(nT)}$  are length- $nT$  vectors, and  $\mathbf{C}$  is the  $nT \times nT$   
 279        covariance matrix that incorporates both the relationships between individual trees  
 280        and their variation over time (table SA5.1). The  $vec(\cdot)$  operator stacks the columns of  
 281        a matrix to obtain a vector. An element  $\mathbf{C}_{it,i't'}$  holds the covariance between individual  
 282         $i$  in year  $t$  and individual  $i'$  in year  $t'$ .

283        We cannot estimate the tree-time matrix **C**, because each  $(i, i', t, t')$  combination  
 284        happens once. Below we introduce the *tree-lag* covariance. First we note two special

cases, i) a  $n \times n$  (tree-to-tree) covariance  $\mathbf{C}_{\mathbf{F},n}$  holding the covariances experienced by a consumer that moves between  $n$  host trees in a random year, and ii) a  $T \times T$  (year-to-year) covariance  $\mathbf{C}_{\mathbf{F},T}$ , holding the covariances experienced by a consumer that tracks a random host over  $T$  years (table SA5.1).

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

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

The conditional covariance in intensity is

$$cov[E[\mathbf{y} | \mathbf{f}]] = cov[\mathbf{\Lambda} | \mathbf{f}] = \mathbf{S} \mathbf{C}_{\mathbf{F},n} \mathbf{S}'$$

(table SA5.1). The total covariance additionally includes the Poisson variance,

$$\begin{aligned} \mathbf{G}_{\mathbf{Y},S} = cov[\mathbf{y}] &= cov[E[\mathbf{y} | \mathbf{f}]] + E[var[\mathbf{y} | \mathbf{f}]] \\ &= \mathbf{S} \mathbf{C}_{\mathbf{F},n} \mathbf{S}' + diag(\mathbf{S} \mathbf{f}) \end{aligned} \quad (6)$$

Combining these terms confirms that they describe covariance in simulated data (fig. 4, right). The first term in eq. (6) combines the covariance between trees with seed dispersal (fig. 4, left). There can be negative covariances (blue in fig. 4), depending on covariance structure in  $\mathbf{C}_{\mathbf{F},n}$ , but positive values dominate, imposed by dispersal. This effect will vary for each forest stand, depending on the distributions of hosts, their fecundities, and their dispersal distances. The second term in eq. (6) contributes only (positive) variance (fig. 4, center), acting like the nugget of geospatial models (Banerjee et al., 2014)<sup>1</sup>. The next section extends these results to multiple consumers.

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

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

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

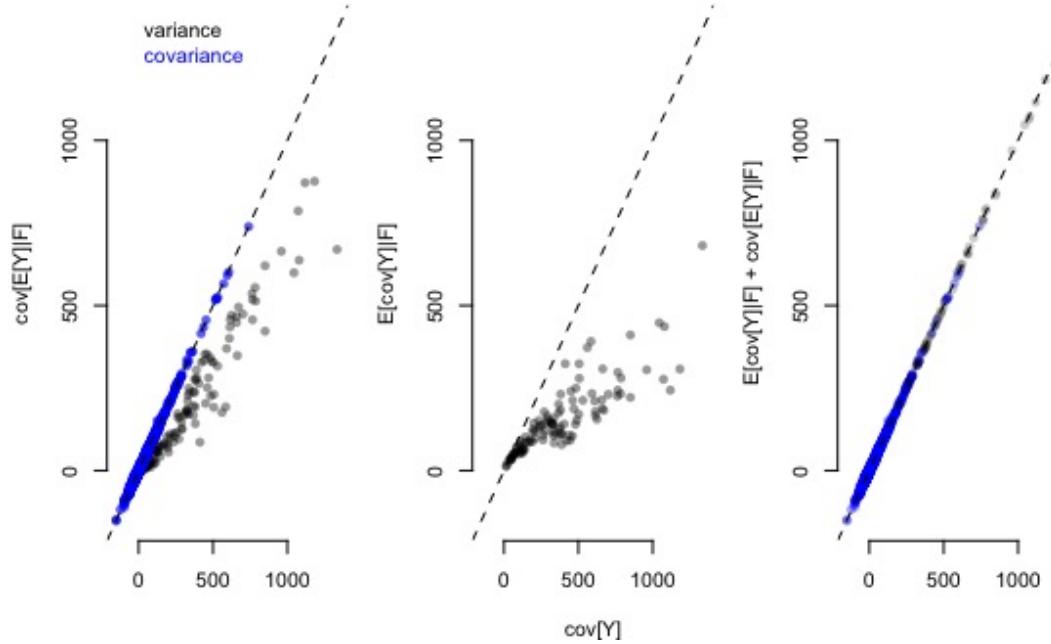


Figure 4: Contributions to space covariance  $\mathbf{C}_{\mathbf{Y},n}$  from terms in eq. (6) plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in section SA4.

ability. For the canopy, the aggregate seeds available to the consumer of  $n$  hosts over  $T$  years is

$$c_{\mathbf{F},nT} = \mathbf{1}_n \mathbf{F} \mathbf{1}_T \quad (7)$$

for  $n \times T$  fecundity matrix  $\mathbf{F}$ . The total resource is

$$\begin{aligned} c_{\mathbf{Q},nT} &= \mathbf{r}'_n \mathbf{F} \mathbf{1}_T \\ &= \mathbf{1}_n \mathbf{Q} \mathbf{1}_T \end{aligned} \quad (8)$$

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

In addition to the aggregate total of eq. (8), 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,

$$\begin{aligned} C_{\mathbf{Q},n} &= \mathbf{r}'_n \mathbf{C}_{\mathbf{F},n} \mathbf{r}_n \\ &= \mathbf{1}'_n \mathbf{C}_{\mathbf{Q},n} \mathbf{1}_n \end{aligned} \quad (9)$$

315 where  $\mathbf{C}_{\mathbf{F},n}$  is the  $n \times n$  covariance of fecundity  $\mathbf{F}$  between trees, and  $\mathbf{C}_{\mathbf{Q},n}$  is the  
 316 covariance of their product (eq. (3)). The means, covariances, and aggregated means  
 317 and variances are given in table SA5.1.

318 To combine the contributions of mean and variance, the resource score for consumer  
 319  $c$  foraging over  $n$  trees replaces terms in eq. (4) with those that come from the actual  
 320 space-time covariance. For example, foraging over  $n$  hosts gives the score

$$RS_n = \log c_{\mathbf{Q},nT} - \frac{\log C_{\mathbf{Q},n}}{2} \quad (10)$$

321 where  $c_{\mathbf{Q},nT}$  and  $C_{\mathbf{Q},n}$  are given in table SA5.1. This variation can be compared to  
 322 that expected for scale-independent variation in eq. (4).

323 Despite positive and negative covariance elements in the canopy, the forest floor  
 324 covariances that contribute to  $\mathbf{G}_{\mathbf{Q},S}$  tend to be positive at the characteristic scales of  
 325 dispersal (fig. 4). This is not necessarily so at broader spatial scales, where the pattern  
 326 of clumping of trees of different species will dominate.

327 We can combine eq. (4) with eq. (10) to quantify the potential advantage to a  
 328 consumer if it could expand the diet to include a new host  $h'$  that brings  $n'$  new host  
 329 individuals into the diet. The aggregate resource from eq. (8) increases by a term

$$c_{\mathbf{Q}',(n+n')T} = c_{\mathbf{Q},nT} + \mathbf{r}'_{n'} \mathbf{F}_{n'} \mathbf{I}_T \quad (11)$$

330 where  $r_{h'}$  is the quality of the new resource, which can be concatenated into a length- $n'$   
 331 vector  $\mathbf{r}_{n'}$ , and  $\mathbf{F}_{n'}$  is the  $n' \times T$  matrix of seed produced by new host individuals. The  
 332 expected addition to the diet from the second term in eq. (11) is

$$r_{h'} n' T \bar{c}_{\mathbf{F}',n'T} = n' T \bar{c}_{\mathbf{Q}',n'T} \quad (12)$$

333 where  $\bar{c}_{\mathbf{F}',n'T}$  is the seed produced by the new host averaged over individuals and years.

334 From eq. (9), the aggregate variance adds two terms,

$$C_{\mathbf{Q}',(n+n')T} = C_{\mathbf{Q},nT} + \mathbf{r}'_{n'T} \mathbf{C}_{\mathbf{F},n'T} \mathbf{r}_{n'T} + 2 \mathbf{r}'_{n'T} \mathbf{C}_{\mathbf{F},n'T,nT} \mathbf{r}_{nT} \quad (13)$$

335 where  $\mathbf{C}_{\mathbf{F},n'T}$  is the  $n'T \times n'T$  covariance for new host trees, and  $\bar{\mathbf{C}}_{\mathbf{F},n'T,nT}$  is the  $n'T \times nT$   
 336 covariance between new and original hosts in the diet. Of course, strong negative  
 337 covariance with hosts now in the diet (third term in eq. (13)) decreases aggregate  
 338 variance, with obvious benefits. Not so obvious is the fact that, even if independent of  
 339 the current diet, the resource score is expected to increase whenever the contribution  
 340 to the aggregate mean compensates for the increase in variance. For independent  
 341 variation eq. (13) simplifies to

$$C_{\mathbf{Q}',(n+n')T} = C_{\mathbf{Q},nT} + r_h^2 n' T \bar{\mathbf{C}}_{\mathbf{Q}',n'T} \quad (14)$$

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

$$\bar{c}_{\mathbf{Q}',n'T} > \sqrt{\frac{\bar{\mathbf{C}}_{\mathbf{Q}',n'T}}{n'T}} \quad (15)$$

343 If the consumer were a statistician, she would recognize the right-hand side of eq. (15)  
 344 to be her standard error (SE) for yield on the left-hand side. A large yield from the  
 345 new host on the left combines with the averaging effects of scale  $n'T$  on the right  
 346 to increase the score. It is a consumer-specific SE, because it is referenced to the  
 347 consumer's ambit, including current diet breadth. Hereafter, we refer to the *SE rule*  
 348 as a rule-of-thumb for the advantage of diet breadth in a scale-independent setting.

349 We use resource scores to compare the resource value of stands and how they can  
 350 vary with consumer ambit. Stands differences in mean mast supply across the diet are  
 351 compared with  $c_{\mathbf{Q}}$  (eq. (8)). The contributions of covariance structure across the diet  
 352 are compared with

$$\Delta \text{ score} = RS_n - \bar{RS}_n \quad (16)$$

353 from eq. (10) and eq. (4).

### 354 *Lag structure*

355 For a canopy arthropod that forages on a single host, the space-time covariance deter-  
 356 mines the potential advantages of a dispersal stage between years. In section SA5.1 we  
 357 summarize lag structure with a matrix  $\mathbf{C}_L$  (canopy) and  $\mathbf{G}_L$  (ground) that hold auto-  
 358 and cross-covariance terms over  $-p, \dots, 0, \dots, p$  lags between  $n$  trees or  $S$  sites. Tree-  
 359 to-year covariances determine the advantages of movement between years, as when

360 a good year for this tree might be followed by a good year for a different tree next  
361 year ( $L_{ii',\pm 1} > 0$ ). A consumer might abide pulsed availability ( $L_{ii,\pm 1} < 0$ ) if it has  
362 the capacity to switch hosts, and hosts are not synchronized ( $L_{ii',0} < 0$ ). The same  
363 principles apply to ground foragers with limited spatial ambit. We use the lag matrix  
364 to evaluate the advantages of movement between host trees between years.

365 ***Model components***

366 Space-time structure derived in *Tree-time and space-time covariance* requires a model  
367 that is sufficiently flexible to admit relationships between individuals and over time,  
368 summarized in table 2. This section summarizes the detailed section SA2. Because we  
369 explicitly consider multiple plots, we extend notation to include plots  $j = 1, \dots, J$ .

370 *Maturation* is a hidden Markov probit submodel. Because binary maturation is  
371 poorly observed and, for a given individual, can only happen once, the hidden Markov  
372 submodel for  $\rho_{ij,t}$  is limited to fixed effects with coefficients  $\beta^v$  (eq. (SA2.10)). Observations  
373 of maturation state contribute to estimates (eq. (SA2.9))(see also Clark et al.  
374 (2010)).

375 *Conditional fecundity* terms are summarized in table 2, starting with *fixed effects*  
376 in design  $\mathbf{x}_{ij,t}$ . The variation spanned by individuals, plots, and years determines  
377 confidence in estimates of coefficients  $\beta^x$  (table 2, submodel A). At minimum, the  
378 fixed effect is an intercept, and in traditional models. Traditional models include tree  
379 size (eq. (2)). Many predictors can be used that are plot-referenced (e.g., the soil  
380 type of plot  $j$ ), time-referenced (temperature in year  $t$ ), individual-referenced (species,  
381 health status, or gender of individual  $ij$ ), plot-time-referenced (climate for plot  $j$  in  
382 year  $t$ ), or individual-plot-time (diameter of individual  $ij$  in year  $t$ ). There can be  
383 interactions (Clark et al., 2010, 2013). For simplicity, predictors are limited here to  
384 size attributes.

385 *Random effects* (REs)  $\beta_i^w$  accommodate the heterogeneity of responses across individual  
386 trees (table 2, submodel D). REs may not be a good idea if there are a number  
387 of individual-referenced variables in the design  $\mathbf{x}_{ij,t}$  (e.g., tree size, tree canopy area).  
388 The random effects design  $\mathbf{w}$  (table 2) can include all or part of the full design  $\mathbf{x}$ .

389 As an alternative to a large covariance matrix across individuals, *year effects* assign  
390 a coefficient  $\gamma_t$  to each year (table 2, submodel B). When multiple groups are specified  
391 for year effects, there is a (shared) fixed year effect  $\gamma_t$  and a random year effect  $\gamma_{g,t}$  for

392 group  $g$ . Groups might be defined by species and/or region. Regional groups can be  
393 used to determine if plots in different regions share a group-level year effect, as when  
394 masting years differ between them.

395 Quasi-periodic variation can be described by an *autoregressive model* AR( $p$ ) with  
396  $l = 1, \dots, p$  lag terms  $\alpha_l$  (table 2, submodel C). At minimum, the fixed effect is an  
397 intercept, and in traditional models, tree size (eq. (2)). If there are multiple groups,  
398 then these groups are random (subscript  $g$ ), defined by plots within a region and/or  
399 species.

400 *Seed identification* is detailed in section SA2.2. *Dispersal* includes a fitted param-  
401 eter  $u_h$  for each species  $h$  eq. (SA1.1). The *likelihood* for seed data is Poisson and  
402 incorporates seed trap area and down time, as when a trap is inactive due to damage  
403 (section SA2.3). The full model and prior distributions are discussed in section SA2  
404 and section SA3, respectively.

## 405 *Estimates and predictions*

406 Gibbs sampling is a Markov chain Monte Carlo (MCMC) technique used for posterior  
407 simulation. Our implementation includes Metropolis and Hamiltonian Markov chain  
408 steps (section SA10). *Estimates* of parameters (including year and lag effects) and  
409 latent states (maturation and conditional fecundity) come from quantiles of MCMC  
410 chains. *Predictions* marginalize the posterior distribution to predict maturation and  
411 fecundity, which, in turn, predict seeds in-sample (i.e., at seed trap locations and  
412 sampling years) and out-of-sample (other locations and/or years) (section SA1.2). The  
413 *partial autocorrelation function* (PACF) quantifies the contribution of each lag, while  
414 controlling for shorter lags. PACF is evaluated for empirical seed rain and for estimated  
415 fecundity of all mature trees at each plot-species combination. *Eigenvalues* for time  
416 series quantify quasi-periodic behavior, estimated here for lag coefficients in the AR( $p$ )  
417 model (section SA6). A quasi-periodic process has complex eigenvalues. A stationary  
418 AR( $p$ ) process has all eigenvalues of less than unit modulus (real plus complex parts).  
419 Eigenvalues are evaluated for the fecundity of each mature tree and summarized by  
420 plot and species (section SA6). Seed production and aggregate mean and variance  
421 resource supplies are estimated and predicted for the canopy (table SA5.1). The  
422 tree-lag (canopy) and space-lag (forest-floor) matrices (*Lag structure*) were evaluated  
423 for each plot. The structure is summarized by diet-wide entropy experienced by a

424 consumer over trees, sites, and years (section SA5.4).

## 425 METHODS

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

### 432 *Simulation*

433 Rather than offer an exhaustive compilation of simulation studies, we supply the full  
434 MASTIF package with simple examples for application (section SA4). We adopt this  
435 approach, because fitting depends on the structure of each stand (density and distri-  
436 bution of mature trees), dispersal characteristics of each species, and spatio-temporal  
437 sampling design, including density and dispersal of traps, and the classification of  
438 seeds into types. As with any model, useful estimates are only expected where there  
439 is 'signal' in data. Simulation determines if, given signal, the model can recover pa-  
440 rameters and predict data. We illustrate where an SSM can be successful, and we  
441 discuss aspects of data structure that can lead to poor performance. The value of the  
442 simulator is this first opportunity it affords to examine a full range of potential data  
443 sets.

### 444 *Application to field data*

445 From up to 25 years of continuous seed collections across sites in the Southeast and  
446 Northeast US (section SA8), we applied the model to estimate mast production. We  
447 use the genus *Pinus* as an example, because multiple species on the same plots in-  
448 sure uncertainty in species identity of seeds (fig. 1). Throughout this multi-decade  
449 study methods emphasized minimizing false-positive seed identifications, thus restrict-  
450 ing species-specific classifications to unambiguous cases. Field and lab methods are  
451 detailed in (Clark et al., 1998, 2004, 2010; Moran and Clark, 2011; Bell and Clark,  
452 2016). Data summaries are provided in section SA8.

453 For this focus on methodology, predictors are limited to tree diameter, making the  
 454 model comparable with most literature on this subject. The omission of environmental  
 455 predictors that control fecundity (Clark et al., 2004, 2010, 2014) sacrifices predictive  
 456 skill for transparency—our goal here is to focus on space-time structure that is linked  
 457 solely to a size model. Model fitting is demonstrated two ways, with AR(5) and with  
 458 year effects for conditional fecundity (table 2). Prior distributions are provided in the  
 459 section SA3.

## RESULTS

### Simulation studies

462 Simulation studies show that the model can recover parameters and latent states for  
 463 all species, even when most of the seeds (80%) are identified only to genus level. A  
 464 stochastic simulation example is summarized for  $M = 4$  seed types and  $H = 3$  species  
 465 on a mean of  $J = 8$  plots,  $T = 5$  years,  $n = 25$  trees, and  $S = 50$  traps.

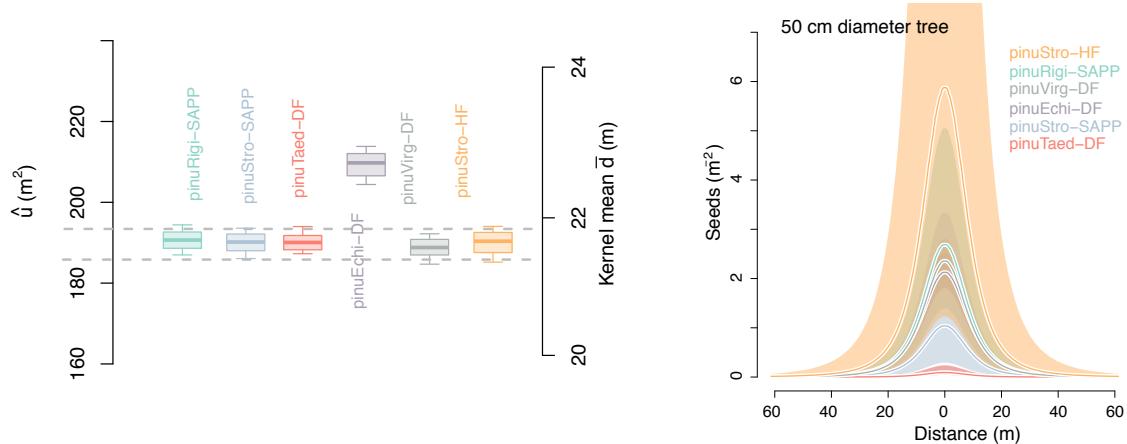


Figure 5: a) Estimates of dispersal parameters  $u_h$  for *Pinus* species-region groups. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. The kernel mean scale at right is eq. (SA7.16). b) Seed shadows predicted from the posterior distribution, with 95% predictive intervals.

466 Parameter recovery is approximate, because, as in real data, few trees in a plot  
 467 of a given species are mature. For the simulation shown in fig. SA9.3, the number of  
 468 trees per plot ranges from 4 to 23. Trees far from seed traps supply little information.  
 469 However, if too many trees are close to the same traps, information can be limited

470 by extensive overlap. Coefficients for maturation and conditional fecundity are close  
471 to values used to generate data, but they are 'damped' (fig. SA9.3a, b), as would  
472 be expected from a noisy fit. The composition vectors for seed identification  $\mathbf{m}_h$  are  
473 recovered precisely, with 20% of seed from each species being assigned to the species  
474 and the remainder to the undifferentiated class "querUNKN" (fig. SA9.3c).

475 Prediction from the fitted model is shown for observed seed counts (fig. SA9.4a,  
476 b) and for unobserved fecundity (fig. SA9.4c). Seed counts can be predicted from  
477 two stages in the model, as discussed in section SA1. Good prediction from the  
478 maturation and fecundity estimates (fig. SA9.4b) requires that the model can identify  
479 these latent states, but it does not require that covariates in the model can predict those  
480 states. Good prediction from the full posterior (fig. SA9.4a) additionally requires that  
481 environmental variables are available that predict maturation and fecundity, which,  
482 in turn, predict seed counts. The fact that the model is capable of both here is not  
483 surprising, because we are fitting the 'correct' model; the only predictor in the model  
484 is known to be tree diameter. The predictions in (a) could be poor while those in (b)  
485 are good in cases where the model finds good *estimates* of fecundity without finding  
486 variables that can *predict* fecundity. The ability to recover unobserved fecundity, which  
487 ranges widely over six orders of magnitude (fig. SA9.4c), verifies that the fit captures  
488 each of the key features in the model. Again, the simulation mode in MASTIF permits  
489 evaluation of designs applicable to specific studies.

## 490 Application

491 Comparing predictions from the full posterior versus the fecundity estimates, as dis-  
492 cussed above for simulated data, shows that fecundity estimates do predict seed rain  
493 (fig. SA9.6b), even as the model omits environmental variables needed to predict fe-  
494 cundity (fig. SA9.6a), as expected from previous studies that identified important  
495 environmental predictors (Clark et al., 2004, 2013, 2014).

496 Dispersal parameter estimates  $\hat{u}_h$  with kernel mean distances  $\bar{d}_h$  (section SA7) are  
497 similar across species (fig. 5a). Because most species tend to occur sporadically across  
498 multiple plots, independent dispersal estimates for each could show large differences,  
499 simply due to the specific arrangements of trees and traps. The random effects prior on  
500  $\mathbf{u}$  borrows strength across all trees on all plots. Predicted seed shadows show expected  
501 and 95% uncertainty for seed arrival with distance from a 50 cm diameter tree (fig. 5b).

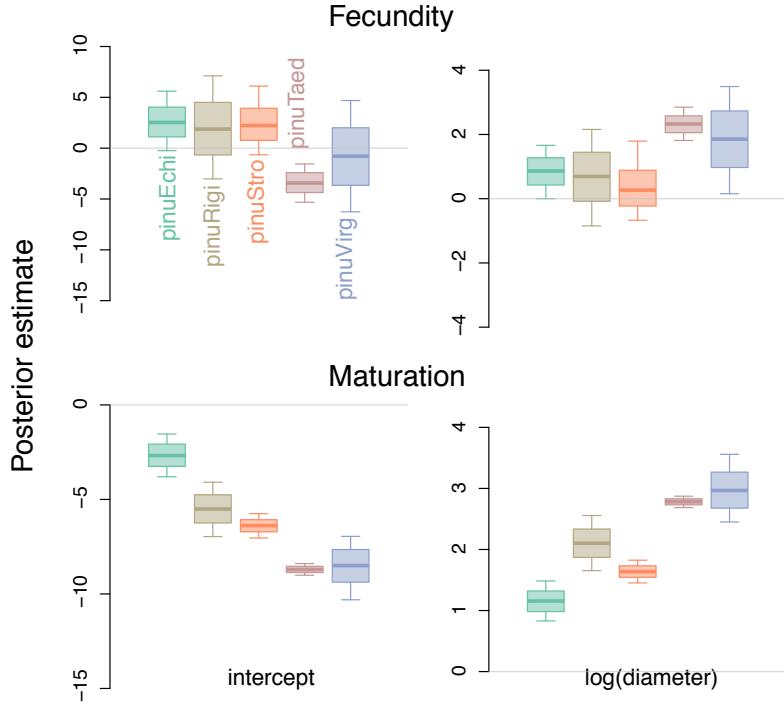


Figure 6: Estimates of fecundity coefficients  $\beta^x$  (above) and maturation coefficients  $\beta^v$  (below) (see table 2) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively.

Estimates of maturation and fecundity coefficients show positive effects of tree diameter on both state variables (fig. 6). 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.

Partial autocorrelation identifies clear species differences. The southern yellow pines show one-year lags with strong three-yr (*P. echinata*, *P.*, *taeda*) and four-year (*P. virginiana*) cycles, respectively (fig. 7). *P. strobus* also shows periodicity at two of three sites. By contrast, *P. rigida* PACF declines gradually over a four-year period. The AR(4) coefficients pick up this signal in *P. rigida*, with pronounced positive effects at a lag of 3 years for the same species and sites (fig. 8a).

The model with year effects finds correlation between species, such as high values in 1999 and negative values from 2000 - 2003 and from 2010 - 2011 in both the Piedmont and southern Appalachians (fig. 8b). However, species are decoupled at other

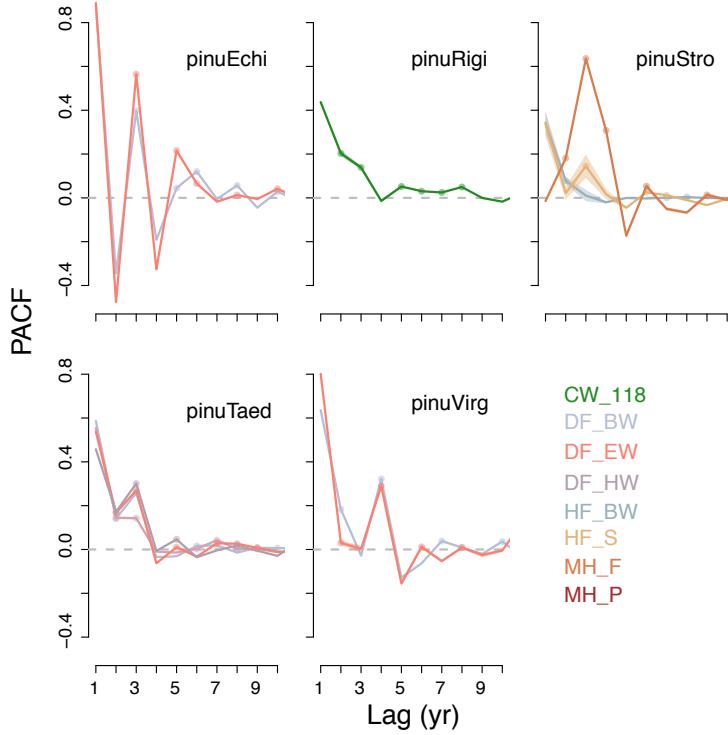


Figure 7: Partial autocorrelation for fecundity in *Pinus* by random groups, defined by species and plot.

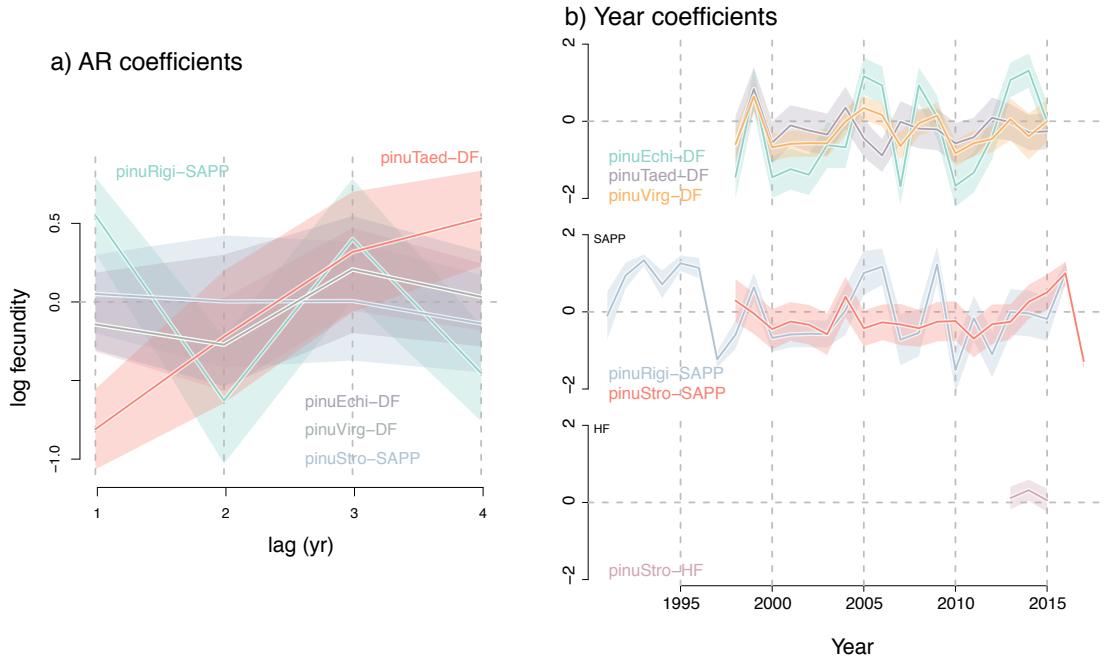


Figure 8: a) Coefficients for random species-region groups in the AR(4) model (a) and the year model (b). NEED SAME COLOR LEGEND.

times. Eigenvalues identify both stationarity and quasi-periodic variation. Real and imaginary parts lie within the unit circle (fig. 9), consistent with stabilizing variation

519 over the long term. Large imaginary parts indicate instabilities, including for species  
 520 that do not show strong effects at specific lags (fig. 8a).

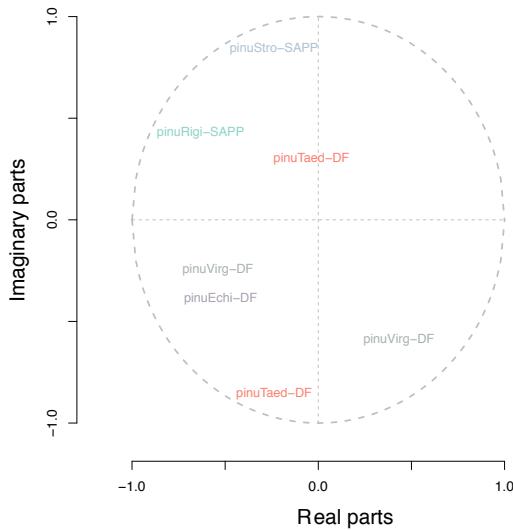


Figure 9: Eigenvalues, real and imaginary parts, lie within the unit circle.

521 Although the full tree-lag covariance  $\mathbf{C}_L$  and space-lag covariance  $\mathbf{G}_L$  are too  
 522 large to visualize for thousands of trees and locations across sites and decades (sec-  
 523 tion SA5.1), a random selection of trees and locations highlights the extent of the  
 524 covariance decline from canopy to forest floor. Warm colors in the lag zero plots show  
 525 that the weak tendency for synchronicity between trees (fig. 10a) is amplified by dis-  
 526 persal across the forest floor (fig. 10b). At higher lags there is evidence of year-to-year  
 527 correlation, with some trees remaining at high or low levels over successive years. The  
 528 positive correlations on the forest floor switch to negative after lag year three.

529 Resource scores do not correlate with mean resource supply, instead balancing the  
 530 benefit of high availability on average with uncertainty In fig. 11 we evaluated scores  
 531 assuming consumers that can visit 20 trees or 20 sites. Generally higher scores on the  
 532 forest floor results from lower variance, due to positive covariance imposed by dispersal  
 533 (green). Sites are similar in their rankings in the canopy and on the forest floor. For  
 534 example, MHF offers the largest total yield in the canopy at these spatial scales for a  
 535 given year, but its low score is penalized by high variance (fig. 11a). The low variance  
 536 over time in the *P. rigida*-dominated CW118 puts it ahead of other stand in fig. 11b,  
 537 despite modest total productivity of this species.

538 To highlight the contribution of variance to the resources scores, we plotted  $\Delta$  scores  
 539 from eq. (16) by spatial and temporal scale. For a given year, the decline of resource

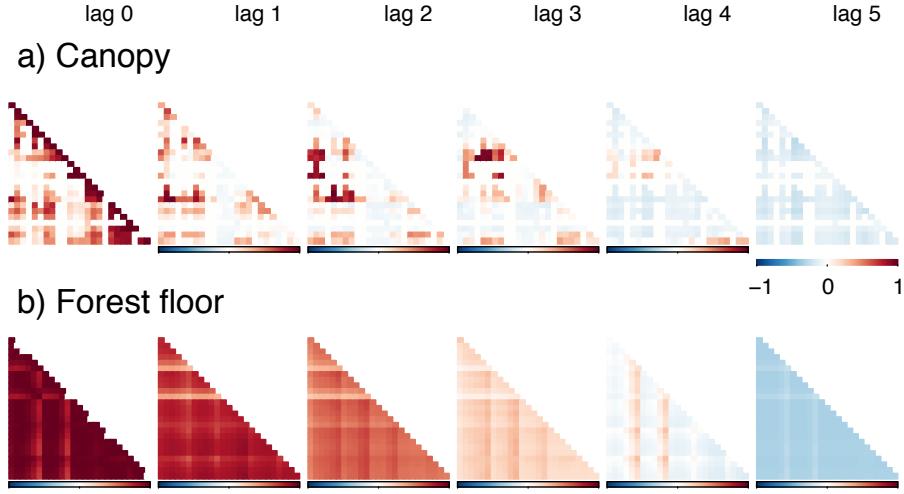


Figure 10: a) Tree-by-lag covariance structure in the canopy at DFBW, developed from  $\mathbf{C}_L$  eq. (5) and b) space-by-lag structure on the forest floor, developed from  $\mathbf{G}_L$  eq. (6). Each pixel represents an individual host tree (a) or site on the forest floor (b), tracked over successive lag years.

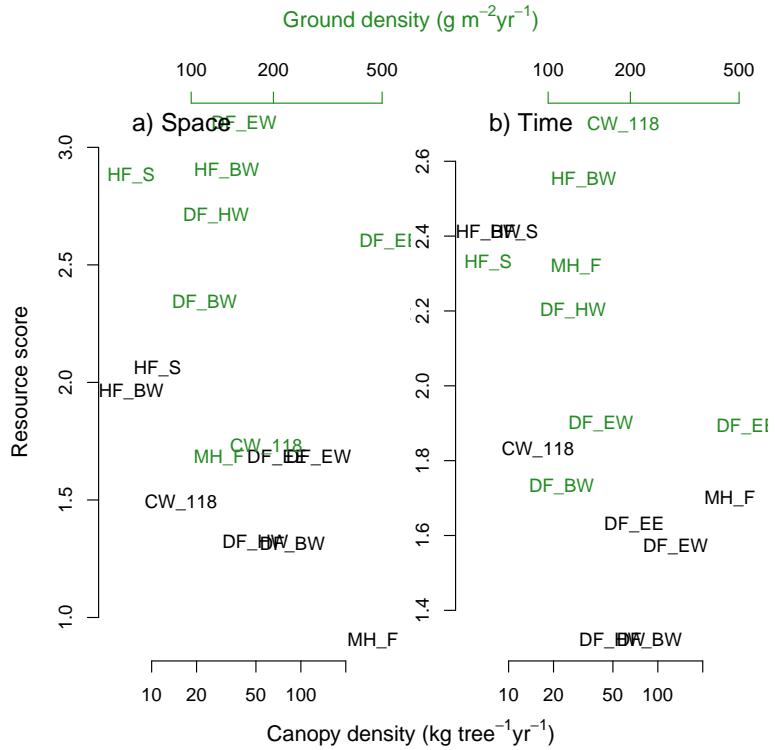


Figure 11: Resource scores (eq. (10)) plotted against mean resource supply (eq. (8)) for a) space [between host trees- (black) and sites on the ground (green) in a given year] and b) over years in a single host or site. Standard deviations are plotted in fig. SA9.5.

540 scores below the random expectation with spatial scale, indicates that spatial variance  
 541 increases rapidly (fig. 12, upper panels), thus discouraging movement at the scale of  
 542 tens of trees in the canopy and fractions of a hectare on the forest floor as a means for  
 543 averaging spatial variation within a given year. The increase in variance with scale is  
 544 consonant with large tree-to-tree variation (canopy) and non-uniform distributions of  
 545 trees and, thus, their seed shadows (forest floor). However, the year-to-year variance is  
 546 diminished over the same spatial scales in the canopy and on the ground (fig. 12, lower  
 547 panels), increasing scores and making movement at this scale beneficial for reducing  
 548 the interannual variance in resource supply. This benefit of movement between years  
 549 reflects the limited synchronicity within and between host species—a good environment  
 550 this year will be followed by a good environment somewhere else the next year.

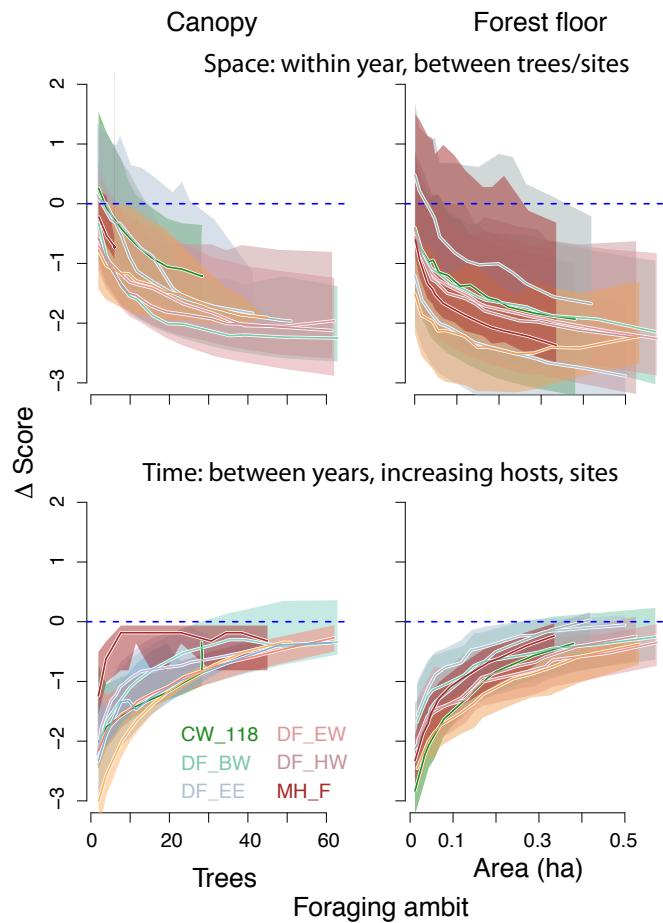


Figure 12: Resource scores as a departure from the independent expectation in eq. (16) evaluated for consumers that can store resources up for two years. Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance.

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

552 reducing the tree-to-tree and site-to-site variance (fig. 13, upper panels). Demographic  
 553 storage, capital breeding, and dormancy effectively reduce variance for consumers with  
 554 restricted mobility, thereby increasing scores. However, consumers restricted to a single  
 555 host or site feel high variance at longer lags, meaning that storage must be coupled  
 556 with at least some movement, the combined message of lower panels in fig. 12 and  
 557 fig. 13.

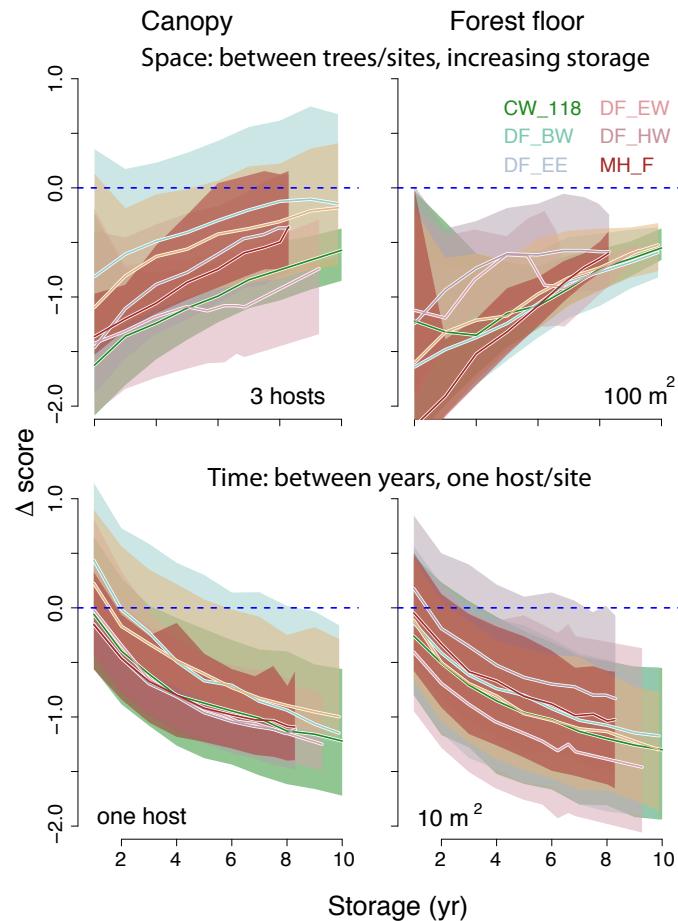


Figure 13: Resource scores as a departure from the independent expectation in eq. (16) evaluated for consumers with storage capacity of two years to 10 years, assuming that the foraging space is three host trees or  $100 \text{ m}^2$ . Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance within one host or site.

558 Prediction scores mentioned here (Gneiting and Raftery, 2007).

559

## DISCUSSION

560 Quantifying the resource value of forested sites, based on their supply of both abundant  
561 and reliable mast, is a venerable challenge in ecology that integrates space, time, and  
562 diet across hosts of variable quality (Janzen, 1970; August, 1983; Ostfeld and Keesing,  
563 2000; Curran and Leighton, 2000; Schmidt and Ostfeld, 2003; Cortes and Uriarte,  
564 2013; McMeans et al., 2016). Consumer ambit in spatial foraging, storage, and diet  
565 breadth provide alternative solutions to the fluctuating resource base—they must be  
566 examined together. Combining episodic fruiting and synchronicity of the multiple  
567 hosts in the consumer diet with the consumer’s limited capacity to forage and variable  
568 resource quality, we develop a simple resource score that can apply across a network  
569 of inventory sites (fig. 11). As foraging capacity increases, the variance-cost of an  
570 unreliable resource that fluctuates widely shifts to a mean-benefit: the scale-dependent  
571 averaging. Generalists additionally average over multiple resource types. Theoretical  
572 results combined with methodology that makes estimates widely available can help to  
573 synthesize a growing body of data. for application to understanding and management.  
574 We summarize the role of methodology, followed by potential to improve biogeographic  
575 prediction of masting and consumers of it.

576

### Mast estimates and prediction

577 MASTIF offers a flexible platform that can facilitate synthesis across a large and grow-  
578 ing literature (table 1). When there is signal in data, MASTIF can provide inference  
579 and prediction, including the implications for different consumer types. Models can in-  
580 clude main effects, interactions, year effects, lag effects, and random effects (table 2).  
581 They allow for the uncertainty in seed identification (include figure of rmat coeffs  
582 in Supplement). From the example application we find high confidence in estimates  
583 (fig. 5, 6, 8 and Supplement B), and this can only improve when environmental pre-  
584 dictors are included in the model (Clark et al. (2004); Uriarte et al. (2005); Ladeau  
585 and Clark (2006); Clark et al. (2010, 2013, 2014); Uriarte et al. (2012), Nuñez et al.,  
586 in prep.). Simulation in MASTIF provides capacity to explore the efficacy of study  
587 designs for specific applications.

588 MASTIF’s Bayesian implementation exploits the growing legacy of understanding  
589 of maturation, fecundity, and dispersal. A rich posterior distribution is efficiently  
590 explored with prior parameter values that integrate previous knowledge. For dispersal,

591 these estimates can learn from a large literature that includes low-dimensional models  
592 that converge rapidly to values that apply to simple assumptions about fecundity  
593 (table 1). Use of truncated priors (flat, with bounds) can specify acceptable ranges,  
594 within which the shape is governed by the prior (Clark et al., 2013).

595 Inference and prediction break down when trees are either too abundant or too  
596 rare. When too abundant, overlapping seed shadows may not be resolved to specific  
597 trees. When reproductive trees are too few, there is an insufficient range of values,  
598 and estimates of slope coefficients for predictor variables are reduced in magnitude,  
599 as expected for noisy data (fig. SA9.3). Because the same ensemble of seed traps is  
600 used to estimate all species, estimates from the same inventory plots will vary in the  
601 accuracy—each species offers a different distribution of distances and numbers and sizes  
602 and trees. The value of multiple stands (a network) comes from the range of stand  
603 structures it can provide. Estimates are improved by sample size, including multiple  
604 years and plots. Group-level random effects stabilize estimates across plots (fig. 5)  
605 that individually would not provide useful estimates.

606 The generalized modeling and computational option with flexibility to combine  
607 uncertainty in seed identifications and a wide range of predictor variables makes our  
608 approach amenable to many data sets, from many forest types. The tree-time and  
609 space-time covariance, visualized in fig. 10 and summarized by entropy gauge the  
610 average supply and its reliability. The methodology extends to consumers with a  
611 generalized diet, implemented in a separate paper (Núñez et al, in prep).

## 612 Consumer ambit and resource score

613 The scale-dependent resource score recognizes a shift from variance-penalty to mean  
614 benefit with increasing consumer ambit (fig. 12, 13). It is important to evaluate the  
615 score at the space-time scale that describes a specific consumer, while integrating  
616 diet breadth. Continuing frustration with the standard coefficient of variation (CV)  
617 includes this omission of scale (Herrera et al., 1998; LaMontagne and Boutin, 2009).  
618 Other alternatives, such as autocorrelation models applied to seed data, need not  
619 reflect availability in the canopy (Clark et al., 2004; Pesendorfer et al., 2016). The  
620 resource score extends the value of CV as an index that combines mean and variance  
621 by making it scale-specific.

622 The standard error (SE) rule (eq. (15)) 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 southern Appalachian and north-eastern 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 inquire about the stand characteristics where generalists are advantaged, including selective pressures.

To focus on theory and methods, the analysis presented here does not include all species in the diets of any individual consumers. That analysis is the subject of a separate paper (Nuñez et al., in prep). However, the methodology here scales to all hosts in the consumer diet.

## 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. The resource score can assign value to individual host tree species and to forest stands (fig. 11) for consumers that differ in diet breadth and foraging capacity. Ecologists and wildlife managers have long recognized that mastング 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). The tree species that contribute mast production are well-known. But there has not been a mechanism for combining pulsed-resource supply with life histories of consumers. The translation of seed production and dispersal to spatio-temporal resource availability (fig. 10) and the summary of its effect by forest stands (fig. SA9.5) can supplement the variables now used for SDM.

652

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