

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

JAMES S. CLARK^{1,2}, CHASE NUNES¹, and BRADLEY TOMASEK¹

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¹ Nicholas School of the Environment, Duke University, Durham NC 27708, USA

² Department of Statistical Science, Duke University, Durham NC 27708, USA

Running head: Masting and consumers

Abstract

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

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

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

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

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

INTRODUCTION

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

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

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

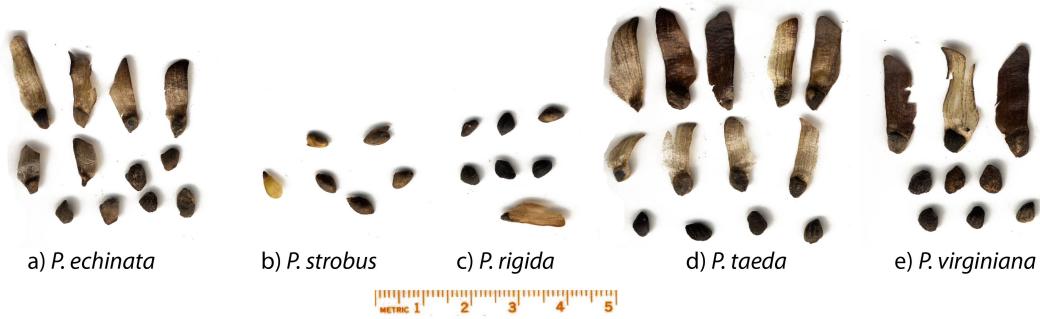


Figure 1: Three seed predators on *Pinus* spp. (above) and five seed types (below). The gray jay (*Perisoreus canadensis*) forages in the canopy (left), the eastern chipmunk (*Tamias striatus*) on the forest floor (center), and the eastern gray squirrel (*Sciurus carolinensis*) in both locations (right).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

store reserves in time? Spatial variation in mast availability exists within stands and across regions (August, 1983; Stein et al., 2014), and it differs in the canopy and 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 mammals (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

52 tree-time covariance between hosts, over years. The density and aggregation of mast
 53 trees can vary widely between stands. Many mammals and ground-nesting birds re-
 54 spond to space-time covariance on the forest floor (Janzen, 1970; Moore et al., 2007;
 55 Zwolak et al., 2016), which combines host location with dispersal to the forest floor
 56 (fig. 2d). Arthropod seed consumers exhibit a range of foraging tactics (Janzen, 1970;
 57 Bonal and Munoz, 2008; Espelta et al., 2009; Bell and Clark, 2016). Damping-off
 58 pathogens appear to have limited dispersal capacity, but are capable of extended dor-
 59 mancy (Dworkin and Shah, 2010) to disperse in time.

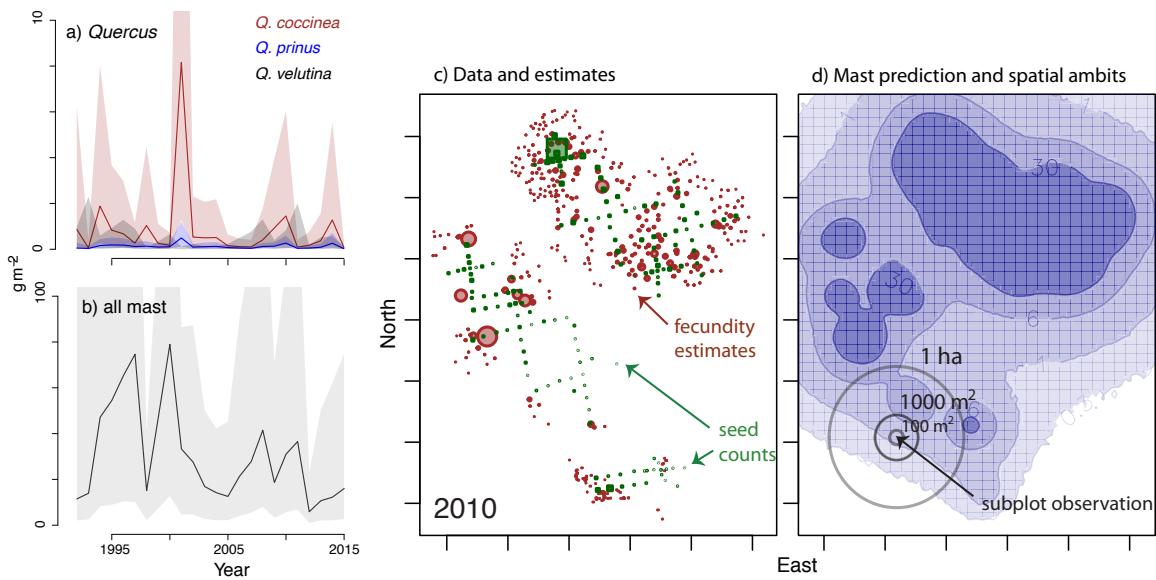


Figure 2: Space-time scales for seeds and consumers. a) Masting by three species in the S Appalachians is erratic. Shading spans 80% of the predictive variation at the 1 m^2 scale. b) A generalist like *Sciurus* (fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*, *Nyssa*, *Cornus*). 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 m^2 (e.g., flightless insects, larder hoarding rodents), 1000 m^2 (e.g., scatter hoarding grey squirrel, chipmunk), and 1 ha (larger vertebrates).

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

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

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

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

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

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

96 length- S vector of seed density

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

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

Table 1: Attributes of some SSMs with examples.

Individuals ^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	—	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)

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

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

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

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

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

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

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

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

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

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

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

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

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

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

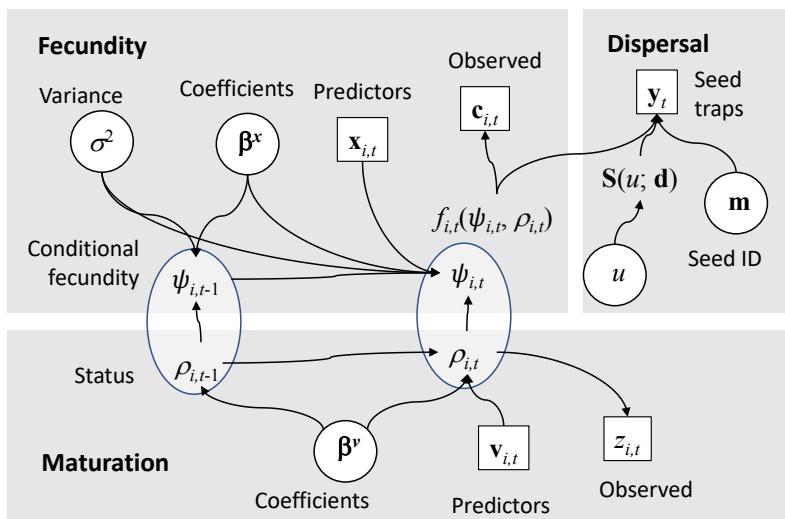


Figure 3: Graphical model for main elements of the model, including fecundity (above),
 maturation (below), and dispersal (right), showing estimates (circles) and observed
 variables (squares), with dynamics ($t - 1, t$). Variables are defined in table SA1.1.

184

MODEL DEVELOPMENT

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

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

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

¹⁹⁴ Annual seed production by a mature individual ($\rho_{i,t} = 1$) is termed *conditional*
¹⁹⁵ *fecundity*, $\psi_{i,t} > 0$. Like maturation, conditional fecundity is a dynamic process,
¹⁹⁶ modeled with fixed and random effects, year effects, and/or autoregressive terms (ta-
¹⁹⁷ ble SA1.1, submodel A). Coefficients in β^x can include tree size (eq. (2)), environ-
¹⁹⁸ ment, and interactions (Clark et al., 2010, 2013). *Random effects* (REs) β_i^w accom-
¹⁹⁹ modate the heterogeneity of responses across individual trees (table SA1.1, submodel
²⁰⁰ D). Year effects γ_t are an alternative to a large covariance matrix across individuals
²⁰¹ (table SA1.1, submodel B). Alternatively, quasi-periodic variation can be described by
²⁰² an *autoregressive model* AR(p) with $l = 1, \dots, p$ lag terms α_l (table SA1.1, submodel
²⁰³ C). Year and lag effects can be random across species and/or region groups, recogniz-
²⁰⁴ ing that masting may be coherent within, but not between, groups. *Actual fecundity*
²⁰⁵ is $f_{i,t} = \psi_{i,t}\rho_{i,t} \geq 0$. In some cases, actual fecundity may be observed, from direct
²⁰⁶ counts in the canopy (Ladeau and Clark, 2006) or on the ground (Minor and Kobe,
²⁰⁷ 2017). Observed fecundity enters here as minimum and maximum estimates in the
²⁰⁸ vector $\mathbf{c}_{i,t} = (c_{i,t,min}, c_{i,t,max})$ (fig. 3).

²⁰⁹ Seeds accumulate in traps $s = 1, \dots, S$ from nearby trees, depending on dispersal.
²¹⁰ A *dispersal kernel* $\mathbf{S}(\mathbf{u})$ includes fitted parameters $\mathbf{u} = u_1, \dots, u_H$ for each species h
²¹¹ eq. (SA1.1) (eq. (1)). The seed count $y_{sm,t}$ is the number of seeds of type m counted in
²¹² a trap at s in year t . Seeds are counted by species or, if species identity is unclear, then
²¹³ genus (section SA1.4). When multiple species $h = 1, \dots, H$ contribute to the same
²¹⁴ seed type(s), as when some seeds are identified only to genus, then the $m = 1, \dots, M$
²¹⁵ seed types must be included in the model with the H species that could have produced
²¹⁶ them. Observation error enters by a $H \times M$ matrix \mathbf{M} holding probabilities that a
²¹⁷ seed of species h will be assigned to type m . The *likelihood* is Poisson and incorporates
²¹⁸ sample effort (trap area \times active period). The full model and prior distributions are
²¹⁹ discussed in section SA1.2 and section SA1.5, respectively.

²²⁰ All else being equal, a habitat that offers an abundant (large mean) and reliable
²²¹ (small variance) food supply benefits a specialist consumer. We wish to evaluate how
²²² the mean and spatio-temporal covariance impact consumers of multiple host species

223 that differ both in abundance and quality,

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

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

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

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

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

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

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

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

247 A consumer with restricted space-time foraging and narrow diet breadth is vulner-
248 able to the variance; individuals and populations suffer in places and times of resource
249 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 masturing, 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 quality (eq. (3)). The traditional CV is inadequate, because masturing 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 score. The expected yields in eq. (4) and eq. (5) have corresponding expected variances,

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

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

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

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

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

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

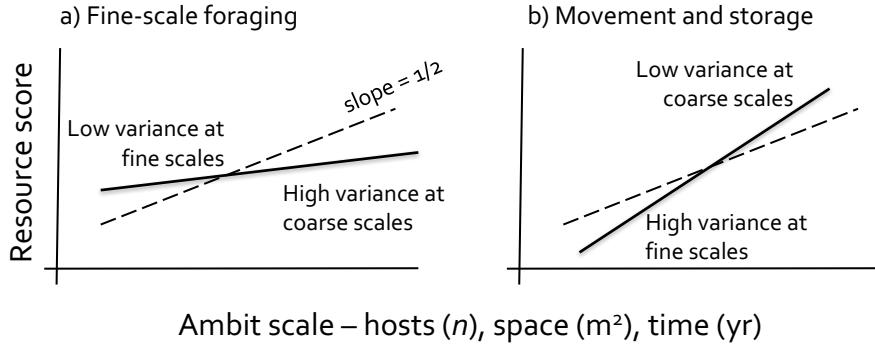


Figure 4: For scale-independent variation, the resource score increases with a slope of $1/2$ on a log scale with n (host trees), space (area), and time (years) (eq. (8)). Especially beneficial for consumers with limited ambit are stands offering high mean and low variance at fine scales (a) and vice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

276

Tree-time and space-time covariance

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

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

296 can be much more accurate than predictions (section SA1).

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

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

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

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

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

313 The conditional covariance in intensity is

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

314 (??). The total covariance additionally includes the Poisson variance,

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

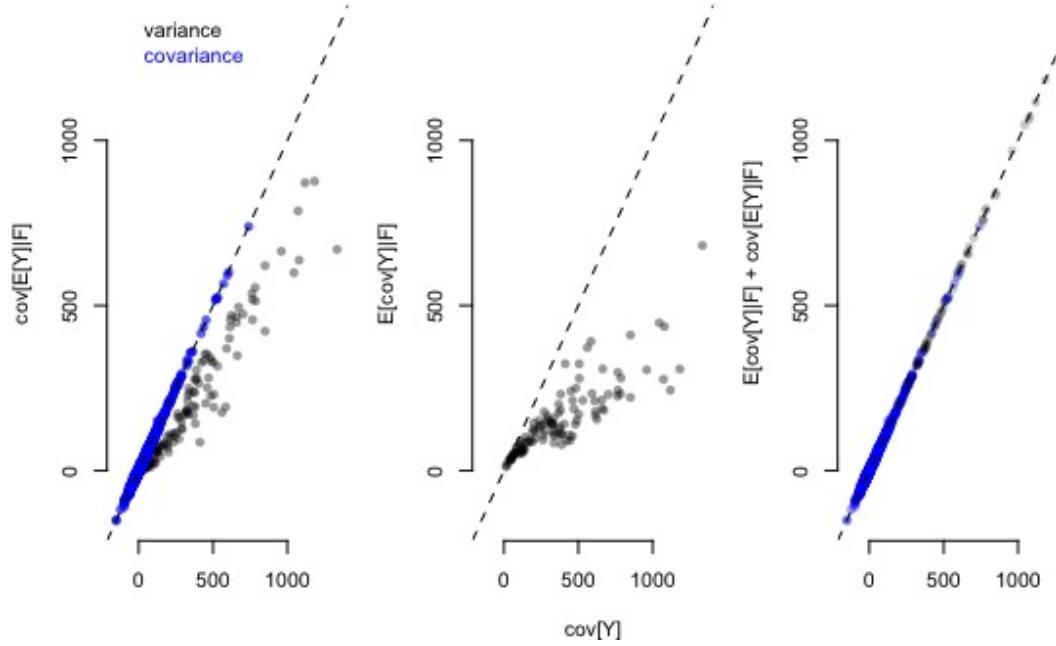


Figure 5: Contributions to space covariance \mathbf{G}_S from terms in eq. (10) plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in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

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

Diet breadth and variance perceived by the consumer

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

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.

³²⁷ 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

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

³²⁸ where $\mathbf{r}_n = r_{h[1]}, \dots, r_{h[n]}$ is the vector of seed quality associated with each tree with
³²⁹ elements given by eq. (3). Note that \mathbf{r}_n combines all host species and individuals in
³³⁰ the diet. There are also aggregate variances for a random year on n host trees, and
³³¹ for a random host tree over T years. For example, the aggregate variance over all host
³³² trees in the diet is,

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

³³³ where \mathbf{Q}_n is the covariance for resource yield between trees (eq. (3), ??).

³³⁴ To combine the contributions of mean and variance, the resource score for the
³³⁵ consumer foraging over n trees replaces terms in eq. (8) with those that come from
³³⁶ the scale-dependent space-time covariance. For example, foraging over n hosts and T
³³⁷ years gives the score

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

³³⁸ where Q_{nT} and $Var(Q_{nT})$ are given in ???. This variation can be compared to that
³³⁹ expected for scale-independent variation in eq. (8).

³⁴⁰ We can combine eq. (8) with eq. (13) to quantify the potential advantage to a
³⁴¹ consumer if it could expand the diet to include a new host \tilde{h} that brings \tilde{n} new host
³⁴² individuals into the diet. The aggregate resource from eq. (11) increases by a term

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

³⁴³ where $r_{\tilde{h}}$ is the quality of the new resource, which can be concatenated into a length- \tilde{n}
³⁴⁴ 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
³⁴⁵ expected addition to the diet from the second term in eq. (14) is

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

³⁴⁶ where $E_{it}(\tilde{f})$ is the expected seed production by the new host. From eq. (12), the
³⁴⁷ aggregate variance adds two terms,

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

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

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

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

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

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

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

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

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

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

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

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

369 The same analysis leads to a resource score for ground foragers, R_{ST} . Despite
 370 positive and negative covariance elements in the canopy, the forest floor covariances

371 in \mathbf{G}_S tend to be positive at the characteristic scales of dispersal (fig. 5). This is
372 not necessarily so at broader spatial scales, where the pattern of clumping of trees of
373 different species will dominate. Space-lag covariance structure used for \mathbf{Q} and \mathbf{G} in
374 this section is expanded in section SA3.1.

375

METHODS

376 For posterior simulation, we implemented Gibbs sampling, a Markov chain Monte
377 Carlo (MCMC) technique, including Metropolis and Hamiltonian Markov chain (HMC)
378 steps (section SA8). Because SSMs engage a high-dimensional state space (all trees
379 over all years), posterior simulation suffers well-known scaling limitations of MCMC,
380 specifically the volume of the parameter set is overwhelmed by the volume of parameter
381 space (Neal, 2011). Standard MCMC algorithms cannot explore the parameter space
382 in finite time. HMC exploits the geometry of the typical parameter set to efficiently
383 target proposals (Betancourt and Girolami, 2015). Because it relies on vector fields (a
384 differentiable surface), HMC cannot apply to discrete maturation state. However, it
385 does apply to conditional fecundity, and is used for that purpose here (section SA8.2).
386 With the exception of maturation, conditional fecundity, and the dispersal parameters
387 (a low-dimensional vector), all other parameters are sampled directly (section SA8).

388 Predictive distributions were generated for maturation and fecundity, which, in
389 turn, predict seeds in-sample (i.e., at seed trap locations and sampling years) and
390 out-of-sample (other locations and/or years) (section SA1.6). Partial autocorrelation
391 functions (PACF) quantify the contribution of each lag, while controlling for shorter
392 lags. Complex eigenvalues for the AR(p) model (section SA4) indicate quasi-periodic
393 variation. A stationary AR(p) process has all eigenvalues of less than unit modulus
394 (real plus complex parts, section SA4). The tree-lag (canopy) and space-lag (forest-
395 floor) covariances (*Space-lag covariance*) were generated with resource scores for each
396 plot. Overall structure is summarized by diet-wide entropy experienced by a consumer
397 over trees, sites, and years (section SA3.3).

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

403 and spatio-temporal structure.

404 ***Simulation***

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

416 ***Application to field data***

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

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

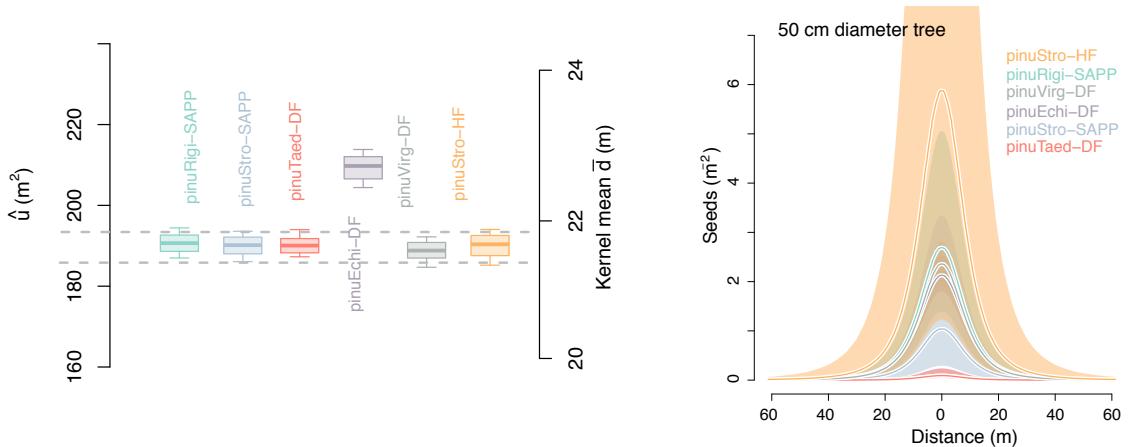


Figure 6: a) Estimates of dispersal parameters u_h for *Pinus* species-region groups. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. The kernel mean scale at right is eq. (SA5.14). b) Seed shadows predicted from the posterior distribution, with 95% predictive intervals.

RESULTS

Simulation studies

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

444 Prediction from the fitted model is shown for observed seed counts (fig. SA7.4a,
 445 b) and for unobserved fecundity (fig. SA7.4c). Seed counts can be predicted from
 446 two stages in the model, as discussed in section SA1. Good prediction from the

449 maturation and fecundity estimates (fig. SA7.4b) requires that the model can identify
 450 these latent states, but it does not require that covariates in the model can predict those
 451 states. Good prediction from the full posterior (fig. SA7.4a) additionally requires that
 452 environmental variables are available that predict maturation and fecundity, which,
 453 in turn, predict seed counts. The fact that the model is capable of both here is not
 454 surprising, because we are fitting the 'correct' model; the only predictor in the model
 455 is known to be tree diameter. The predictions in (a) could be poor while those in (b)
 456 are good in cases where the model finds good *estimates* of fecundity without finding
 457 variables that can *predict* fecundity. The ability to recover unobserved fecundity, which
 458 ranges widely over six orders of magnitude (fig. SA7.4c), verifies that the fit captures
 459 each of the key features in the model. Again, the simulation mode in MASTIF permits
 460 evaluation of designs applicable to specific studies.

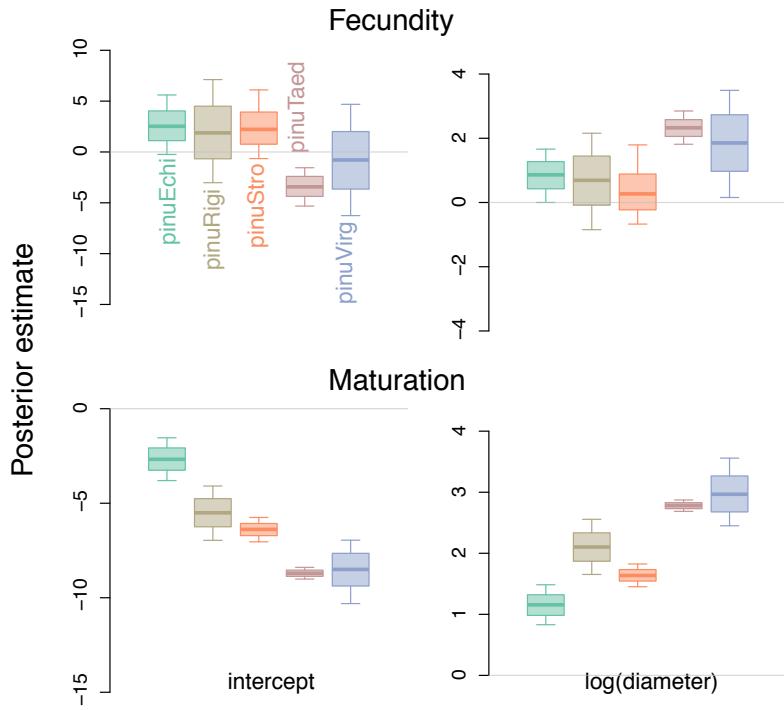


Figure 7: Estimates of fecundity coefficients β^x (above) and maturation coefficients β^v (below) (see table SA1.1) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively.

461

Application to Pinus

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

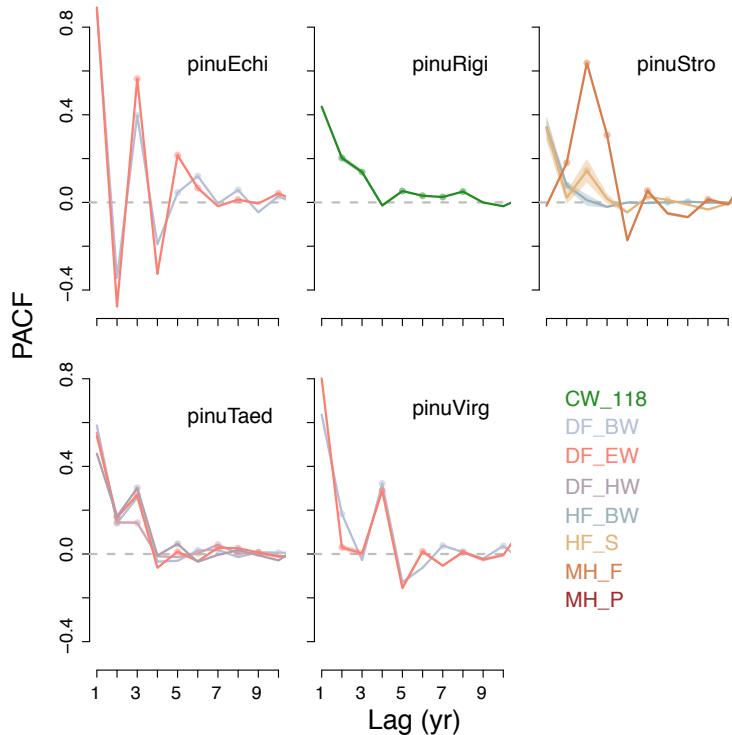


Figure 8: Partial autocorrelation for fecundity in *Pinus* by random groups, defined by species and plot.

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

475 Partial autocorrelation identifies clear species differences. The southern yellow
 476 pines show one-year lags with strong three-yr (*P. echinata*, *P.*, *taeda*) and four-year
 477 (*P. virginiana*) cycles, respectively (fig. 8). *P. strobus* also shows periodicity at two of

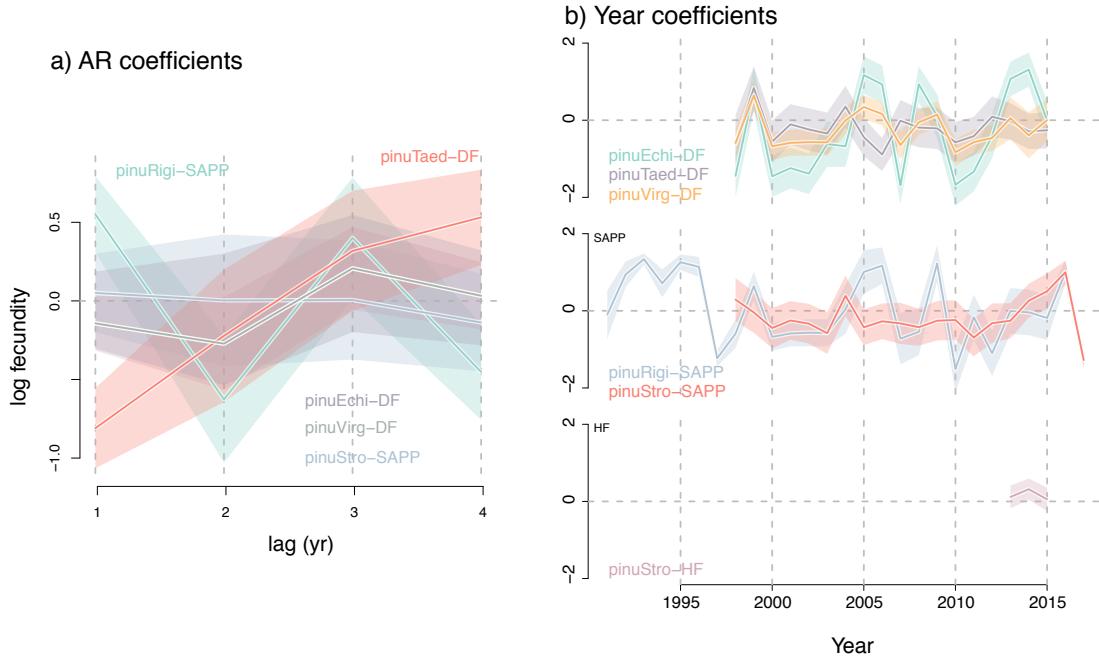


Figure 9: a) Coefficients for random species-region groups in the AR(4) model (a) and the year model (b). NEED SAME COLOR LEGEND.

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

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

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

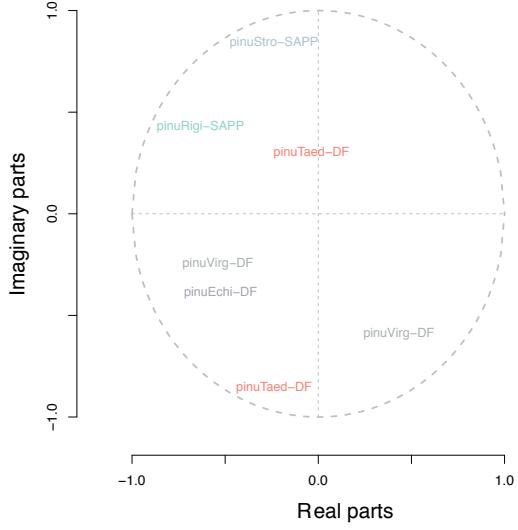


Figure 10: Eigenvalues, real and imaginary parts, lie within the unit circle.

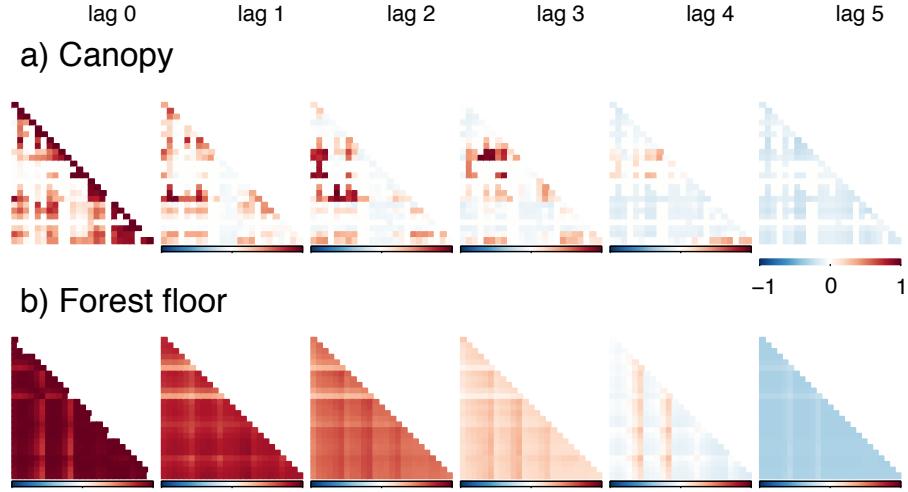


Figure 11: a) Tree-by-lag covariance structure in the canopy at DFBW, developed from \mathbf{C}_L eq. (9) and b) space-by-lag structure on the forest floor, developed from \mathbf{G}_L eq. (10). Each pixel represents an individual host tree (a) or site on the forest floor (b), tracked over successive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

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

503 total productivity of this species.

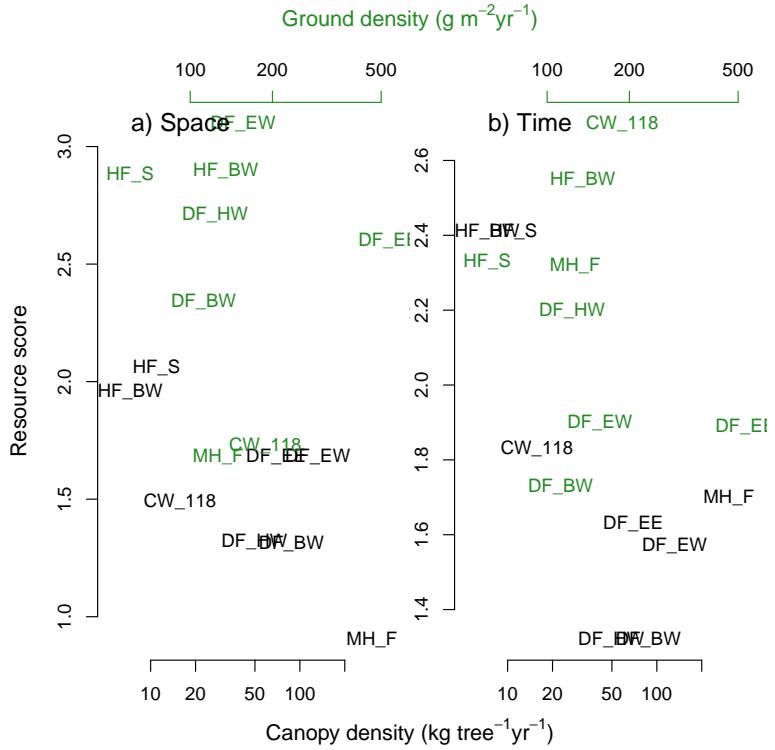


Figure 12: Resource scores (eq. (13)) plotted against mean resource supply (eq. (11)) for a) space [between host trees- (black) and sites on the ground (green) in a given year] and b) over years in a single host or site. Standard deviations are plotted in fig. SA7.5.

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

517 Storage benefits consumers with limited spatial ambit (three host trees or 100 m²),

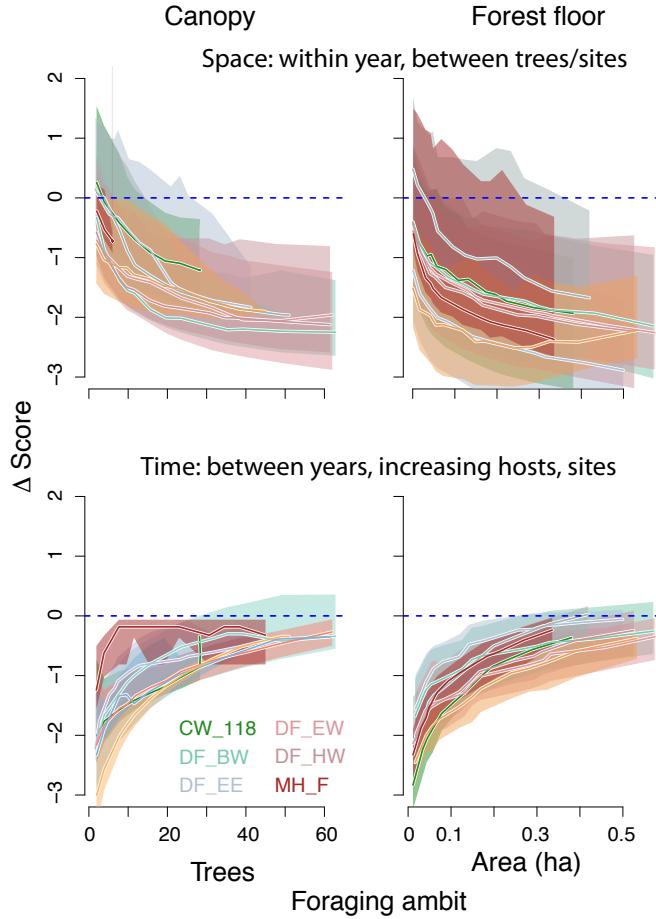


Figure 13: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers that can store resources up for two years. Above is the tree-to-tree and site-to-site variance within a given year. Below is the year-to-year variance.

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

DISCUSSION

524 Quantifying the resource value of forested sites, based on their supply of both abundant
 525 and reliable mast, is a venerable challenge in ecology (Janzen, 1970; August,
 526 1983; Ostfeld and Keesing, 2000; Curran and Leighton, 2000; Schmidt and Ostfeld,
 527

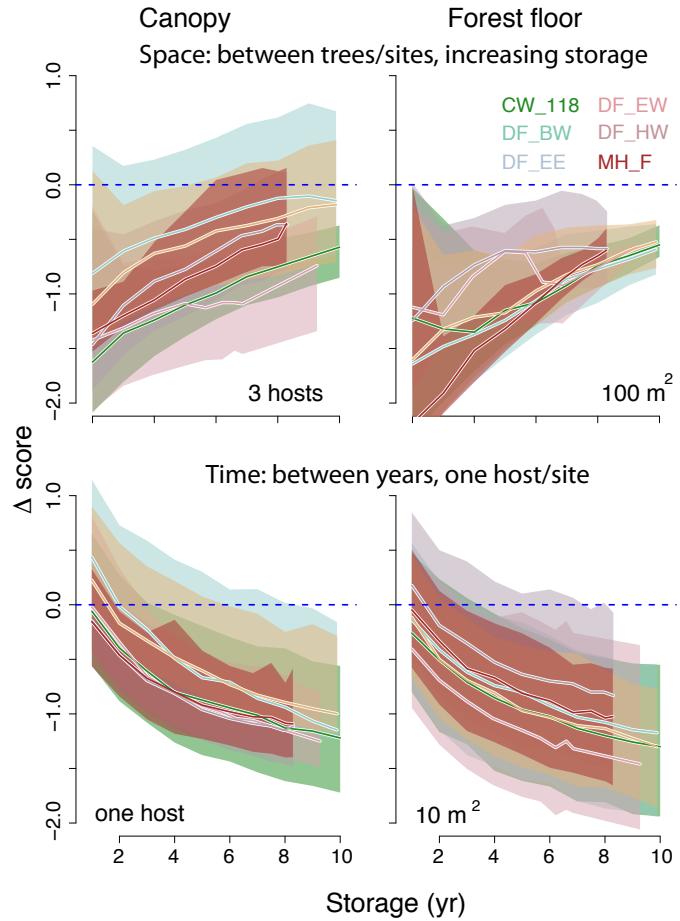


Figure 14: Resource scores as a departure from the independent expectation in eq. (21) evaluated for consumers with storage capacity of two years to 10 years, assuming that the foraging space is three host trees or 100 m^2 . Above is the tree-to-tree and site-to-site variance within a given year. Below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

528 2003; Cortes and Uriarte, 2013; McMeans et al., 2016). As foraging capacity increases,
 529 the variance-cost of an unreliable resource that fluctuates widely shifts to a mean-
 530 benefit: the scale-dependent averaging. The stability properties of mast cycles can be
 531 quantified and compared, showing large differences between species and stands, per-
 532 vasive quasi-periodicity, but evidence for long-term stability (fig. 10). Because spatial
 533 foraging, storage, and diet breadth represent alternative solutions to the fluctuating
 534 resource base, they cannot be analyzed independently. Combining episodic fruiting
 535 and synchronicity of the multiple hosts in the diet with the consumer’s limited capac-
 536 ity to forage and variable resource quality, we develop a simple resource score that can
 537 apply across a network of inventory sites (fig. 12). Theoretical results combined with

538 a methodology that makes estimates widely available can help to synthesize a grow-
539 ing body of data for application to understanding and management. We summarize
540 the role of methodology, followed by potential to improve biogeographic prediction of
541 masting and consumers of it.

542 ***Mast estimates and prediction***

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

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

560 MASTIF’s Bayesian implementation exploits the accumulating knowledge of mat-
561 uration, fecundity, and dispersal. A rich posterior distribution is efficiently explored
562 with prior parameter values that integrate previous understading. For dispersal, these
563 estimates can learn from a large literature that includes low-dimensional models that
564 converge rapidly for simple assumptions about fecundity (table 1). Use of truncated
565 priors (flat, with bounds) can specify acceptable ranges, within which the posterior
566 shape is governed by the likelihood (Clark et al., 2013). Data sets that include multiple
567 stands (a network) and years increase the range of effects contributing to estimates.
568 Group-level random effects stabilize estimates across plots (fig. 6) that individually
569 would not provide useful estimates. The flexibility to combine uncertainty in seed

identifications and a wide range of predictor variables makes our approach amenable to many data sets. The tree-time and space-time covariance, visualized in fig. 11 and summarized by entropy, gauge the average supply and its reliability. The methodology extends to consumers with a generalized diet, implemented in a separate paper (Núñez et al., in prep).

Consumer ambit and resource score

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

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

Biogeographic implications

For biogeographic understanding, including impacts of climate change, the resource score can offer a more direct index of habitat suitability than is available through the variables currently used in habitat models and species distribution models (SDMs), which emphasize climate, land cover, and soils, but omit availability of food. The

resource score can assign value to individual host tree species and to forest stands (fig. 12) for consumers that differ in diet breadth and foraging capacity. Ecologists and wildlife managers have long recognized that masting provides the base of the food chain, and space-time variation can be just as critical as the mean resource supply (Ostfeld and Keesing, 2000; Curran and Leighton, 2000; McShea, 2000; Boutin et al., 2006; Bergeron et al., 2011; Bogdziewicz et al., 2016).

We did not offer a full predictive analysis of resources scores in this paper, because resources alone cannot predict trophic structure. That analysis includes a full range of climate and habitat variables (Nuñez et al., in prep). The tree species that contribute mast production are well-known. But there has not been a mechanism for combining pulsed-resource supply with life histories of consumers. The important contribution to biogeographic understanding includes the basic theory and computation that can use species-size structure to quantify resource supply in a way that can be combined with the traditional climate and habitat variables in SDMs. The translation of seed production and dispersal to spatio-temporal resource availability (fig. 11) and the summary of its effect by forest stands (fig. SA7.5) can supplement the variables now used for SDM.

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References

- Abbott, H. G., and T. F. Quink. 1970. Ecology of Eastern White Pine Seed Caches Made by Small Forest Mammals. *Ecology* **51**:271–278. URL <[GotoISI](#)>://WOS:A1970G625900011.
- August, P. V. 1983. The Role of Habitat Complexity and Heterogeneity in Structuring Tropical Mammal Communities. *Ecology* **64**:1495–1507. URL <[GotoISI](#)>://WOS:A1983RU21500017.

- 630 Banerjee, S., B. P. Carlin, and A. E. Gelfand. 2014. Hierarchical Modeling and Analysis
631 for Spatial Data. 2nd edition. Monographs on Statistics and Applied Probability,
632 CRC Press, Boca Raton, Florida.
- 633 Bell, D. M., and J. S. Clark. 2016. Seed predation and climate impacts on reproductive
634 variation in temperate forests of the southeastern USA. *Oecologia* **180**:1223–1234.
635 URL <GotoISI>://WOS:000373186100029.
- 636 Berdanier, A. B., and J. S. Clark. 2016. Divergent reproductive allocation trade-offs
637 with canopy exposure across tree species in temperate forests. *Ecosphere* **7**:e01313–
638 n/a. URL <http://dx.doi.org/10.1002/ecs2.1313>.
- 639 Bergeron, P., D. Reale, M. M. Humphries, and D. Garant. 2011. Anticipation and
640 tracking of pulsed resources drive population dynamics in eastern chipmunks. *Ecology*
641 **92**:2027–2034. URL <GotoISI>://WOS:000296426000003.
- 642 Betancourt, M., and M. Girolami. 2015. Hamiltonian Monte Carlo for Hierarchical
643 Models, Book section 4, pages 79–96 . CRC Press, New York.
- 644 Bogdziewicz, M., R. Zwolak, and E. E. Crone. 2016. How do vertebrates respond to
645 mast seeding? *Oikos* **125**:300–307. URL <http://dx.doi.org/10.1111/oik.03012>.
- 646 Bonal, R., and A. Munoz. 2008. Seed growth suppression constrains the growth
647 of seed parasites: premature acorn abscission reduces Curculio elephas larval size.
648 *Ecological Entomology* **33**:31–36. URL <GotoISI>://WOS:000252495600004.
- 649 Bontemps, A., E. K. Klein, and S. Oddou-Muratorio. 2013. Shift of spatial pat-
650 terns during early recruitment in *Fagus sylvatica*: Evidence from seed dispersal
651 estimates based on genotypic data. *Forest Ecology and Management* **305**:67–76.
652 URL <GotoISI>://WOS:000324222800008.
- 653 Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi, and A. A.
654 Dhondt. 2006. Anticipatory reproduction and population growth in seed predators.
655 *Science* **314**:1928–1930. URL <GotoISI>://WOS:000242996800049.
- 656 Bullock, J. M., and R. T. Clarke. 2000. Long distance seed dispersal by wind:
657 measuring and modelling the tail of the curve. *Oecologia* **124**:506–521. URL
658 <GotoISI>://WOS:000089509700005.

- 659 Burczyk, J., W. T. Adams, D. S. Birkes, and I. J. Chybicki. 2006. Using ge-
660 netic markers to directly estimate gene flow and reproductive success parameters
661 in plants on the basis of naturally regenerated seedlings. *Genetics* **173**:363–372.
662 URL <GotoISI>://WOS:000237990600031.
- 663 Canham, C. D., W. A. Ruscoe, E. F. Wright, and D. J. Wilson. 2014. Spatial and
664 temporal variation in tree seed production and dispersal in a New Zealand temperate
665 rainforest. *Ecosphere* **5**. URL <GotoISI>://WOS:000335955500003.
- 666 Carbone, C., G. Cowlishaw, N. Isaac, and J. Rowcliffe. 2005. How Far Do Animals Go?
667 Determinants of Day Range in Mammals. *The American Naturalist* **165**:290–297.
668 URL <http://www.journals.uchicago.edu/doi/abs/10.1086/426790>.
- 669 Carlo, T. A., J. J. Tewksbury, and C. Martinez Del Rio. 2009. A new method to track
670 seed dispersal and recruitment using ^{15}N isotope enrichment. *Ecology* **90**:3516–25.
671 URL <https://www.ncbi.nlm.nih.gov/pubmed/20120818>.
- 672 Charco, J., M. Venturas, L. Gil, and N. Nanos. 2017. Effective Seed Dispersal and
673 Fecundity Variation in a Small and Marginal Population of *Pinus pinaster* Ait.
674 Growing in a Harsh Environment: Implications for Conservation of Forest Genetic
675 Resources. *Forests* **8**. URL <GotoISI>://WOS:000411523700011.
- 676 Cibrian-Tovar, D., S. F. E. S. A. N.C.), U. A. Chapingo., and U. S. F. Service. 1986.
677 Cone and seed insects of the Mexican conifers = Insectos de conos y semillas de las
678 coniferas de Mexico. Southeastern Forest Experiment Station, Asheville, N.C.
- 679 Clark, J., D. M. Bell, M. Kwit, A. Powell, and K. Zhu. 2013. Dynamic inverse
680 prediction and sensitivity analysis with high-dimensional responses: application to
681 climate-change vulnerability of biodiversity. *Journal of Biological, Environmental,*
682 and Agricultural Statistics
- 683 Clark, J., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-
684 competition hypothesis. *Ecological Monographs* **74**:415–442.
- 685 Clark, J., M. Lewis, and L. Horvath. 2001. Invasion by extremes: Population spread
686 with variation in dispersal and reproduction. *American Naturalist* **157**:537–554.
- 687 Clark, J., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment
688 limitation in southern Appalachian forests. *Ecological Monographs* **68**:213–235.

- 689 Clark, J., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed
690 dispersal near and far: Patterns across temperate and tropical forests. *Ecology*
691 **80**:1475–1494.
- 692 Clark, J. S., D. M. Bell, C. Chu, B. Courbaud, M. Dietze, M. H. Hersh, J. HilleRisLam-
693 bers, I. Ibanez, S. LaDeau, S. McMahon, J. Metcalf, J. Mohan, E. Moran, L. Pangle,
694 S. Pearson, C. Salk, Z. Shen, D. Valle, and P. Wyckoff. 2010. High-dimensional
695 coexistence based on individual variation: a synthesis of evidence. *Ecological Mono-
696 graphs* **80**:569–608.
- 697 Clark, J. S., D. M. Bell, M. H. Hersh, and L. Nichols. 2011. Climate change vulnera-
698 bility of forest biodiversity: climate and competition tracking of demographic rates.
699 *Global Change Biology* **17**:1834–1849.
- 700 Clark, J. S., D. M. Bell, M. C. Kwit, and K. Zhu. 2014. Competition-interaction
701 landscapes for the joint response of forests to climate change. *Glob Chang Biol*
702 **20**:1979–91. URL <https://www.ncbi.nlm.nih.gov/pubmed/24932467>.
- 703 Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species:
704 toward a global functional homogenization? *Frontiers in Ecology and the Environ-
705 ment* **9**:222–228. URL <http://dx.doi.org/10.1890/080216>.
- 706 Clotfelter, E. D., A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and
707 E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird
708 populations. *Oecologia* **154**:493–503. URL <Go to ISI>://WOS:000251146900006.
- 709 Connell, J., 1970. Herbivores and the Number of Tree Species in Tropical Forests,
710 Page 298312 . Pudoc, Wageningen.
- 711 Cortes, M. C., and M. Uriarte. 2013. Integrating frugivory and animal movement: a
712 review of the evidence and implications for scaling seed dispersal. *Biol Rev Camb
713 Philos Soc* **88**:255–72. URL <https://www.ncbi.nlm.nih.gov/pubmed/23136896>.
- 714 Crone, E. E., and J. M. Rapp. 2014. Resource depletion, pollen coupling, and the
715 ecology of mast seeding. *Year in Ecology and Conservation Biology* **1322**:21–34.
716 URL <Go to ISI>://WOS:000340899900002.

- 717 Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation
718 in seed production of mast-fruiting dipterocarpaceae. Ecological Monographs
719 **70**:101–128. URL <Goto^{ISI}>://WOS:000085208500005.
- 720 Descamps, S., S. Boutin, D. Bertheaux, A. G. McAdam, and J. M. Gaillard. 2008.
721 Cohort effects in red squirrels: the influence of density, food abundance and temperature
722 on future survival and reproductive success. Journal of Animal Ecology
723 **77**:305–314. URL <Goto^{ISI}>://WOS:000252810400013.
- 724 Detto, M., S. J. Wright, O. Calderon, and H. C. Muller-Landau. 2018. Resource
725 acquisition and reproductive strategies of tropical forest in response to the El Niño-
726 Southern Oscillation. Nat Commun **9**:913. URL <https://www.ncbi.nlm.nih.gov/pubmed/29500347>.
- 728 Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail,
729 S. Villeger, and N. Mouquet. 2010. Defining and measuring ecological specialization.
730 Journal of Applied Ecology **47**:15–25. URL <Goto^{ISI}>://WOS:000274191300003.
- 731 Dworkin, J., and I. M. Shah. 2010. Exit from dormancy in microbial organisms. Nature
732 Reviews Microbiology **8**:890–896. URL <Goto^{ISI}>://WOS:000284308200014.
- 733 Espelta, J. M., R. Bonal, and B. Sanchez-Humanes. 2009. Pre-dispersal acorn predation
734 in mixed oak forests: interspecific differences are driven by the interplay among
735 seed phenology, seed size and predator size. Journal of Ecology **97**:1416–1423. URL
736 <Goto^{ISI}>://WOS:000270787100033.
- 737 Fernandez-Martinez, M., S. Vicca, I. A. Janssens, J. M. Espelta, and J. Penuelas. 2017.
738 The North Atlantic Oscillation synchronises fruit production in western European
739 forests. Ecography **40**:864–874. URL <Goto^{ISI}>://WOS:000405455800008.
- 740 Fricke, E. C., and S. J. Wright. 2017. Measuring the demographic impact of conspecific
741 negative density dependence. Oecologia **184**:259–266. URL <https://www.ncbi.nlm.nih.gov/pubmed/28382478>.
- 743 Garant, D., S. E. Forde, and A. P. Hendry. 2007. The multifarious effects of dispersal
744 and gene flow on contemporary adaptation. Functional Ecology **21**:434–443. URL
745 <Goto^{ISI}>://WOS:000246708200005.

- 746 Gneiting, T. 2002. Nonseparable, stationary covariance functions for space-time data.
747 Journal of the American Statistical Association **97**:590–600. URL <GotoISI>://
748 WOS:000176078300025.
- 749 Godoy, J. A., and P. Jordano. 2001. Seed dispersal by animals: exact identification of
750 source trees with endocarp DNA microsatellites. Molecular Ecology **10**:2275–2283.
751 URL <GotoISI>://WOS:000171127700015.
- 752 Greene, D. F., C. D. Canham, K. D. Coates, and P. T. LePage. 2004. An evaluation
753 of alternative dispersal functions for trees (vol 92, pg 758, 2004). Journal of Ecology
754 **92**:1124–1124. URL <GotoISI>://WOS:000225631400015.
- 755 Grivet, D., P. E. Smouse, and V. L. Sork. 2005. A novel approach to an old problem:
756 tracking dispersed seeds. Molecular Ecology **14**:3585–3595. URL <GotoISI>://WOS:
757 000231800900023.
- 758 Grotan, V., B. E. Saether, S. Engen, J. H. van Balen, A. C. Perdeck, and M. E.
759 Visser. 2009. Spatial and temporal variation in the relative contribution of density
760 dependence, climate variation and migration to fluctuations in the size of great
761 tit populations. Journal of Animal Ecology **78**:447–459. URL <GotoISI>://WOS:
762 000263038800017.
- 763 Herrera, C. M., P. Jordano, J. Guitian, and A. Traveset. 1998. Annual variability
764 in seed production by woody plants and the masting concept: Reassessment of
765 principles and relationship to pollination and seed dispersal. American Naturalist
766 **152**:576–594. URL <GotoISI>://WOS:000076014900006.
- 767 Janzen, D. 1970. Herbivores and the Number of Tree Species in Tropical Forests.
768 The American Naturalist **104**:501–528. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282687>.
- 770 Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998.
771 Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk.
772 Science **279**:1023–1026. URL <GotoISI>://WOS:000072006400045.
- 773 Jones, F. A., J. Chen, G. J. Weng, and S. P. Hubbell. 2005. A genetic evaluation of
774 seed dispersal in the neotropical tree Jacaranda copaia (Bignoniaceae). American
775 Naturalist **166**:543–555. URL <GotoISI>://WOS:000232832700006.

- 776 Jones, F. A., and H. C. Muller-Landau. 2008. Measuring long-distance seed dis-
777 persal in complex natural environments: an evaluation and integration of classical
778 and genetic methods. *Journal of Ecology* **96**:642–652. URL <GotoISI>://WOS:
779 000256635800009.
- 780 Karasov, W. H. 1986. Energetics, Physiology and Vertebrate Ecology. *Trends in*
781 *Ecology and Evolution* **1**:101–104. URL <GotoISI>://WOS:A1986F726600007.
- 782 Koenig, W. D., and J. M. H. Knops. 2001. Seed-crop size and eruptions of North
783 American boreal seed-eating birds. *Journal of Animal Ecology* **70**:609–620. URL
784 <GotoISI>://WOS:000170005700008.
- 785 LaDouce, S. L., and J. S. Clark. 2001. Rising CO₂ levels and the fecundity of forest
786 trees. *Science* **292**:95–8. URL <https://www.ncbi.nlm.nih.gov/pubmed/11292871>.
- 787 Ladeau, S. L., and J. S. Clark. 2006. Elevated CO₂ and tree fecundity: the role of tree
788 size, interannual variability, and population heterogeneity. *Global Change Biology*
789 **12**:822–833. URL <http://dx.doi.org/10.1111/j.1365-2486.2006.01137.x>.
- 790 LaMontagne, J. M., and S. Boutin. 2009. Quantitative methods for defining mast-
791 seeding years across species and studies. *Journal of Vegetation Science* **20**:745–753.
792 URL <GotoISI>://WOS:000267755000018.
- 793 Lichti, N. I., M. A. Steele, H. Zhang, and R. K. Swihart. 2014. Mast species com-
794 position alters seed fate in North American rodent-dispersed hardwoods. *Ecology*
795 **95**:1746–1758. URL <GotoISI>://WOS:000339470500005.
- 796 Liebhold, A., V. Sork, M. Peltonen, W. Koenig, O. N. Bjornstad, R. Westfall, J. Elk-
797 inton, and J. M. H. Knops. 2004. Within-population spatial synchrony in mast
798 seeding of North American oaks. *Oikos* **104**:156–164. URL <GotoISI>://WOS:
799 000187962200017.
- 800 Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neu-
801 tral and nonneutral community dynamics in fluctuating environments. *Am Nat*
802 **172**:E48–66. URL <https://www.ncbi.nlm.nih.gov/pubmed/18598188>.
- 803 Martinez, I., and F. Gonzalez-Taboada. 2009. Seed dispersal patterns in a temperate
804 forest during a mast event: performance of alternative dispersal kernels. *Oecologia*
805 **159**:389–400. URL <GotoISI>://WOS:000263424800014.

- 806 McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2016.
807 Food web structure in temporally-forced ecosystems (vol 30, pg 662, 2015). Trends
808 in Ecology and Evolution **31**:408–408. URL <GotoISI>://WOS:000375737200016.
- 809 McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and
810 bird populations. Ecology **81**:228–238. URL <GotoISI>://WOS:000084913400019.
- 811 Milleron, M., U. L. de Heredia, Z. Lorenzo, J. Alonso, A. Dounavi, L. Gil, and
812 N. Nanos. 2013. Assessment of spatial discordance of primary and effective seed
813 dispersal of European beech (*Fagus sylvatica* L.) by ecological and genetic methods.
814 Molecular Ecology **22**:1531–1545. URL <GotoISI>://WOS:000316209500006.
- 815 Minor, D. M., and R. K. Kobe. 2017. Masting synchrony in northern hardwood
816 forests: super-producers govern population fruit production. Journal of Ecology
817 **105**:987–998. URL <GotoISI>://WOS:000403549500017.
- 818 Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007.
819 Determinants of seed removal distance by scatter-hoarding rodents in deciduous
820 forests. Ecology **88**:2529–2540. URL <GotoISI>://WOS:000250714200014.
- 821 Moran, E. V., and J. S. Clark. 2011. Estimating seed and pollen movement in a mon-
822 noecious plant: a hierarchical Bayesian approach integrating genetic and ecological
823 data. Molecular Ecology **20**:1248–1262. URL <GotoISI>://WOS:000288074600015.
- 824 Moran, E. V., J. Willis, and J. S. Clark. 2012. Genetic Evidence for Hybridization in
825 Red Oaks (*Quercus* Sect. *Lobatae*, Fagaceae). American Journal of Botany **99**:92–
826 100. URL <GotoISI>://WOS:000299167700020.
- 827 Muller-Landau, H. C., S. J. Wright, O. Calderon, R. Condit, and S. P. Hubbell. 2008.
828 Interspecific variation in primary seed dispersal in a tropical forest. Journal of
829 Ecology **96**:653–667. URL <GotoISI>://WOS:000256635800010.
- 830 Nanos, N., K. Larson, M. Milleron, and S. Sjostedt-de Luna. 2010. Inverse modeling for
831 effective dispersal: Do we need tree size to estimate fecundity? Ecological Modelling
832 **221**:2415–2424. URL <GotoISI>://WOS:000282403700001.
- 833 Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their
834 determinants and consequences for recruitment. Trends in Ecology and Evolution
835 **15**:278–285. URL <GotoISI>://WOS:000087831100008.

- 836 Neal, R., 2011. MCMC Using Hamiltonian Dynamics, Book section 5, pages 1–49 .
837 CRC Press, New York, New York.
- 838 Ogawa, R., A. Mortelliti, J. W. Witham, and M. L. Hunter. 2017. Demographic
839 mechanisms linking tree seeds and rodent population fluctuations: insights from
840 a 33-year study. *Journal of Mammalogy* **98**:419–427. URL <GotoISI>://WOS:
841 000398033100010.
- 842 Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of con-
843 sumers in terrestrial ecosystems. *Trends in Ecology and Evolution* **15**:232–237. URL
844 <http://www.sciencedirect.com/science/article/pii/S0169534700018620>.
- 845 Pairon, M., M. Jonard, and A. L. Jacquemart. 2006. Modeling seed dispersal of black
846 cherry, an invasive forest tree: how microsatellites may help? *Canadian Journal*
847 of Forest Research-Revue Canadienne De Recherche Forestiere **36**:1385–1394. URL
848 <GotoISI>://WOS:000238286600004.
- 849 Pelisson, P. F., C. Bernstein, D. Francois, F. Menu, and S. Venner. 2013. Dispersal and
850 dormancy strategies among insect species competing for a pulsed resource. *Ecological*
851 *Entomology* **38**:470–477. URL <GotoISI>://WOS:000323848500005.
- 852 Perea, R., A. S. Miguel, and L. Gil. 2011. Flying vs. climbing: Factors control-
853 ling arboreal seed removal in oak-beech forests. *Forest Ecology and Management*
854 **262**:1251–1257. URL <GotoISI>://WOS:000294143100011.
- 855 Pesendorfer, M. B., W. D. Koenig, I. S. Pearse, J. M. H. Knops, and K. A. Funk. 2016.
856 Individual resource limitation combined with population-wide pollen availability
857 drives masting in the valley oak (*Quercus lobata*). *Journal of Ecology* **104**:637–
858 645. URL <GotoISI>://WOS:000379014900003.
- 859 Ribbens, E., J. A. Silander, and S. W. Pacala. 1994. Seedling Recruitment in Forests
860 - Calibrating Models to Predict Patterns of Tree Seedling Dispersion. *Ecology*
861 **75**:1794–1806. URL <GotoISI>://WOS:A1994PE26700026.
- 862 Robledo-Arnuncio, J. J., and C. Garcia. 2007. Estimation of the seed dispersal kernel
863 from exact identification of source plants. *Molecular Ecology* **16**:5098–5109. URL
864 <GotoISI>://WOS:000251205200019.

- 865 Rodel, H. G., T. G. Valencak, A. Handrek, and R. Monclus. 2016. Paying the en-
866 ergetic costs of reproduction: reliance on postpartum foraging and stored reserves.
867 Behavioral Ecology **27**:748–756. URL <GotoISI>://WOS:000381224500015.
- 868 Rosin, C., and J. R. Poulsen. 2016. Hunting-induced defaunation drives increased
869 seed predation and decreased seedling establishment of commercially important tree
870 species in an Afrotropical forest. Forest Ecology and Management **382**:206–213.
871 URL <GotoISI>://WOS:000387519700020.
- 872 Sainmont, J., K. H. Andersen, O. Varpe, and A. W. Visser. 2014. Capital versus
873 Income Breeding in a Seasonal Environment. American Naturalist **184**:466–476.
874 URL <GotoISI>://WOS:000342281100007.
- 875 Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers,
876 and M. S. Webster. 2010. Population diversity and the portfolio effect in an
877 exploited species. Nature **465**:609–12. URL <https://www.ncbi.nlm.nih.gov/pubmed/20520713>.
- 879 Schmidt, K. A., and R. S. Ostfeld. 2003. Songbird populations in fluctuating en-
880 vironments: Predator responses to pulsed resources. Ecology **84**:406–415. URL
881 <GotoISI>://WOS:000181482600014.
- 882 Schupp, E. W., and P. Jordano. 2011. The full path of Janzen-Connell effects: genetic
883 tracking of seeds to adult plant recruitment. Molecular Ecology **20**:3953–3955. URL
884 <GotoISI>://WOS:000295230000002.
- 885 Schurr, F. M., O. Steinitz, and R. Nathan. 2008. Plant fecundity and seed dispersal in
886 spatially heterogeneous environments: models, mechanisms and estimation. Journal
887 of Ecology **96**:628–641. URL <GotoISI>://WOS:000256635800008.
- 888 Sheldon, K. S., and N. M. Nadkarni. 2013. Spatial and Temporal Variation of Seed
889 Rain in the Canopy and on the Ground of a Tropical Cloud Forest. Biotropica
890 **45**:549–556. URL <GotoISI>://WOS:000323829800003.
- 891 Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal
892 driver of species richness across taxa, biomes and spatial scales. Ecology Letters
893 **17**:866–880. URL <http://dx.doi.org/10.1111/ele.12277>.

- 894 Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *Am Nat* **151**:277–82.
895
896 URL <https://www.ncbi.nlm.nih.gov/pubmed/18811358>.
- 897 Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2005.
898 Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-
899 dependence and the spatial distribution of parent trees. *Journal of Ecology* **93**:291–
900 304. URL <GotoISI>://WOS:000227721400006.
- 901 Uriarte, M., J. S. Clark, J. K. Zimmerman, L. S. Comita, J. Forero-Montana, and
902 J. Thompson. 2012. Multidimensional trade-offs in species responses to disturbance:
903 implications for diversity in a subtropical forest. *Ecology* **93**:191–205. URL
904 <GotoISI>://WOS:000301996100021.
- 905 Wang, Y. Y., J. Zhang, J. M. LaMontagne, F. Lin, B. H. Li, J. Ye, Z. Q. Yuan, X. G.
906 Wang, and Z. Q. Hao. 2017. Variation and synchrony of tree species mast seeding
907 in an old-growth temperate forest. *Journal of Vegetation Science* **28**:413–423. URL
908 <GotoISI>://WOS:000397559100018.
- 909 Zwolak, R., M. Bogdziewicz, and L. Rychlik. 2016. Beech masting modifies the re-
910 sponse of rodents to forest management. *Forest Ecology and Management* **359**:268–
911 276. URL <GotoISI>://WOS:000366789500028.