

Food webs built on unreliable foundations: Masting 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 and with limited variation in time and space, masting events are volatile and localized (near seed-bearing trees that have limited dispersal), and that variability ramifies throughout food webs. 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, deriving the space-time-species covariance in resource supply and combining it with the space-time-diet breadth of consumers, or *ambit*. Direct connection to data is made possible with Mast Inference and Forecasting (MASTIF), a state-space autoregressive model that fits seed-trap and canopy observations, and it predicts resource availability within the canopy and on the forest floor for individual habitats or networks of inventory plots.

As the consumer ambit increases, the volatility of an unreliable resource that varies widely 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 (seed and damping-off fungi, arthropods, rodents, ground-nesting birds, mammals) experience instead a redistribution of that covariance by dispersal. For consumers lacking mobility, demographic storage in episodic birth cohorts following mast years is important for population persistence. Consumers additionally compensate volatility with diet breadth. Depending on the dominant masting strategies of host tree species in the diet, habitats differentially limit consumers with misaligned life history strategies. A resource score can be assigned to each consumer-habitat pair that combines the benefits that habitat offers in mean supply weighed against the variance cost. The impact of adding or subtracting a diet item can be gauged with the standard error (SE) rule, the 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. Results are connected directly to data, with full uncertainty, by MASTIF.

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 supply a pulsed resource that constitutes the base of forest food chains, both supports and destabilizes consumer populations, and mediates the structure of communities in ways that are poorly understood (Jones et al., 1998; Ostfeld and Keesing, 2000; McShea, 2000; Clotfelter et al., 2007; McMeans et al., 2016; Rosin and Poulsen, 2016). Understanding how food webs respond to a changing climate and habitat requires theory that connects data on the space-time delivery of this foundational resource with the abilities of consumers to abide variation. Seed-shadow models (SSMs) are widely used to quantify masting, taking data that passively monitor fecundity and dispersal simultaneously for all tree and shrub species that can be recovered and identified in seed traps (Clark et al., 1998, 2004; Uriarte et al., 2005; Jones and Muller-Landau, 2008; Dettlo et al., 2018). Despite the diverse applications, current models omit key features of most data sets, and they do not estimate the spatio-temporal dependence, which is often quasi-periodic and synchronous across host individuals (Crone and Rapp, 2014; Bogdziewicz et al., 2016; Zwolak et al., 2016; Wang et al., 2017). This variability ramifies throughout food webs, starting with the seed predators and frugivores that forage at spatial scales from a few meters to landscapes and ranging in diet from specialist to generalist. To complicate inference, the seeds of many species are identified only to genus level (fig. 1). The mast-consumer connection is a missing link in global change science, explaining why all serious efforts to anticipate future biodiversity include diverse climate and habitat variables, but omit the most basic requirement of all-food. Important next steps include theory to connect variation in masting with consumers and modeling to provide the inference and prediction, with full diagnostics. In this paper, we derive the space-time and host-time covariance structure faced by consumers that vary in diet and foraging strategies. By extending SSMs, we provide a modeling framework that can synthesize the growing network data with direct inference on the capacities of habitats to supply consumers, each of which sees that variation in its own way.

The consequences of masting depend on an interaction between the space-time structure of resource supply and the capacities of consumers to exploit alternative hosts, to forage widely in space, and to store reserves in time (Janzen, 1970). The large literatures on foraging theory and interpretation of tracking data (Owen-Smith et al., 2010; Avgar et al., 2013; Benhamou, 2014) have not benefitted from estimates of

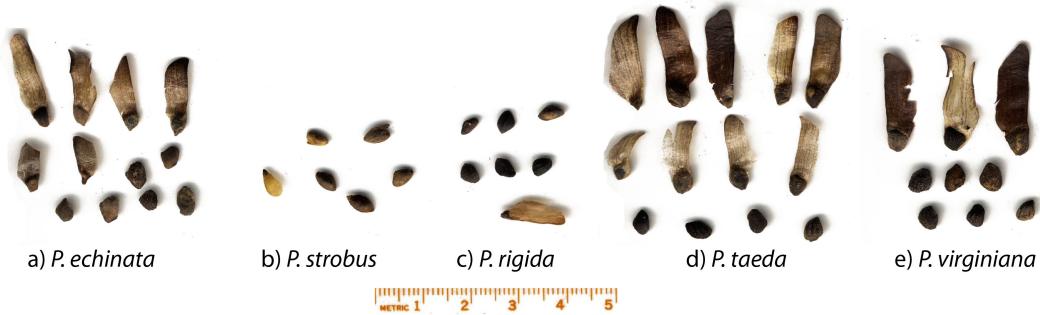


Figure 1: Three seed predators on *Pinus* spp. (above) and five seed types (below). The gray jay (*Perisoreus canadensis*) forages in the canopy (left), the eastern chipmunk (*Tamias striatus*) on the forest floor (center), and the eastern gray squirrel (*Sciurus carolinensis*) in both locations (right).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

the spatio-temporal structure of mast supply that might be offered by SSMs. A *host* is defined here as a tree or shrub that contributes to the diet of a consumer. *Consumers* include not only insects and vertebrates, but also seed-attacking fungi and damping-off pathogens. A reliable mast resource is abundant on average, with limited variation in time and space. Spatial variation exists within habitats 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; Milleron et al., 2013; Bell and Clark, 2016) (fig. 1) where and when resources are concentrated—the *host-time covariance* between host trees, over years. Mammals and ground-nesting birds respond to *space-time covariance* on the forest floor (Moore et al., 2007; Zwolak et al., 2016), which combines host location with dispersal (fig. 2d). Arthropod seed consumers exhibit a range of foraging tactics (Janzen, 1970; Bonal and Munoz, 2008; Espelta et al., 2009; Bell and Clark, 2016). A consumer experiences this host-space-time variation depending on its *ambit*, defined in three dimensions, i) area or number of hosts visited, ii) capacity to store resources over time, and iii) diet breadth.

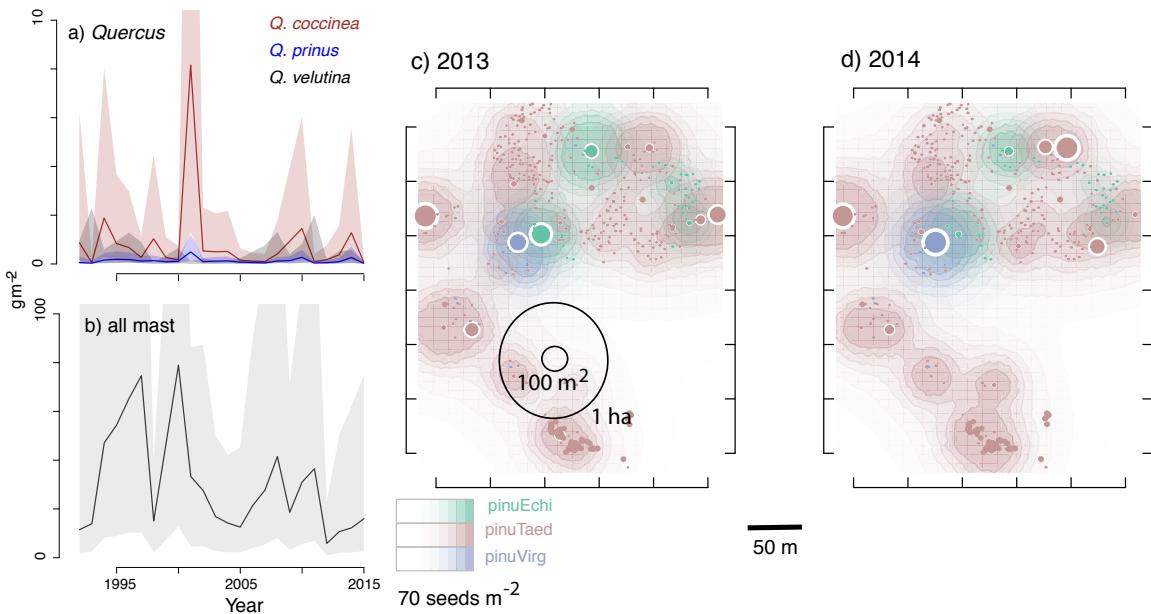


Figure 2: Space-time scales for seeds and consumers. a) Mast production by three *Quercus* species in the southern Appalachians is erratic. Shading spans 80% of the predictive variation at the 1 m² scale. b) The generalist *Sciurus* (fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*, *Nyssa*, *Cornus*, *Pinus*). c, d) Fecundity estimates (circles) and seed counts (squares) for *Pinus* in 2013, 2014 at DFBW in the SE Piedmont. Shading is the predictive mean mast density for three species. Superimposed ambits in (c) provide scale for 100 m² (e.g., flightless insects, larder hoarding rodents) and 1 ha (song birds and larger vertebrates).

The three dimensions of ambit are not decoupled from one another (Janzen, 1970; Grotan et al., 2009; Pelisson et al., 2013; Sainmont et al., 2014; Lichti et al., 2014; Rodel et al., 2016). Quasi-periodic mast years can be spaced up to a decade apart (fig. 2a) and differ between host species in mean and variance, in synchronicity between

55 individuals, and in dispersal distance (Clark et al., 2010). Limited movement can be
 56 offset by storage in time, such as the extended dormancy in damping-off pathogens
 57 (Dworkin and Shah, 2010). Diet generalists abide spatio-temporal variation through
 58 diet switching, a *portfolio effect* (Tilman et al., 1998; Loreau and de Mazancourt, 2008;
 59 Schindler et al., 2010), while specialization exposes consumers to the full heterogeneity
 60 offered by a specific host (Devictor et al., 2010; Clavel et al., 2011) (fig. 2a, b). The-
 61 ory is needed to relate estimates of fecundity and dispersal at these host-space-time
 62 covariance scales of the consumer ambit.

63 A solution to the theoretical challenge is of little use without a model that offers
 64 estimates, which depend in turn on resolving limitations with current SSMs (fig. 2c).
 65 Studies examine a single fruiting season, or they track inventory plots over time (ta-
 66 ble 1). Estimates provide insights on dispersal and recruitment limitation (Ribbens
 67 et al., 1994; Clark et al., 1998, 1999; Nathan and Muller-Landau, 2000; Fricke and
 68 Wright, 2017), gene flow and hybridization (Garant et al., 2007; Jones and Muller-
 69 Landau, 2008; Moran and Clark, 2011; Moran et al., 2012), migration potential (Clark
 70 et al., 2001), environmental controls on reproductive effort and sex ratio (Clark et al.,
 71 2004; Uriarte et al., 2005; Schurr et al., 2008; Martinez and Gonzalez-Taboada, 2009;
 72 Clark et al., 2011; Uriarte et al., 2012; Canham et al., 2014; Dettlo et al., 2018), and
 73 allocation (LaDeau and Clark, 2006; Berdanier and Clark, 2016). SSMs include a
 74 likelihood for count data, such as a Poisson distribution with intensity expressed as
 75 expected seeds per trap,

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

76 where y_s is the number of seeds in trap s , A is sample effort [seed trap area times
 77 fraction of fruiting season it was deployed (traps are damaged by tree falls and bears)
 78 ($\text{m}^2 \text{ yr}^{-1}$)], λ_s is the expected seed density (seeds per trap yr^{-1}), $\mathbf{S}_{s,i}$ is the density of
 79 seed produced by tree i dispersed to location s (m^{-2}), and f_i is seed production by
 80 tree i (table S2.1). The $S \times n$ kernel matrix \mathbf{S} has rows that include attributes of seed
 81 traps. It has columns that include attributes of trees, including a tree-specific dispersal
 82 parameter. For a length- S vector of seed traps, a length- n vector of fecundities, and a
 83 $S \times n$ kernel matrix \mathbf{S} , there is a length- S vector of seed density

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

⁸⁴ Because both fecundity \mathbf{f} and dispersal capacity \mathbf{S} are unknown, the efficacy of these
⁸⁵ models should be sensitive to 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 S2.1.

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

⁸⁶ Before turning to challenges with SSMs, we summarize why they can be preferable
⁸⁷ to direct seed tracking methods, such as stable isotope labels (Carlo et al., 2009; Cortes
⁸⁸ and Uriarte, 2013) or genotyping seeds or seedlings (Godoy and Jordano, 2001; Grivet
⁸⁹ et al., 2005; Jones et al., 2005; Pairon et al., 2006; Burczyk et al., 2006; Robledo-
⁹⁰ Arnuncio and Garcia, 2007; Jones and Muller-Landau, 2008; Moran and Clark, 2011;
⁹¹ Schupp and Jordano, 2011; Bontemps et al., 2013). Due to labor and expense, typically
⁹² few seeds or seedlings can be labeled or genotyped, most often a single species. Labels
⁹³ provide information on dispersal, but not fecundity (Moran and Clark, 2011; Milleron
⁹⁴ et al., 2013). Because seed traps sample passively, SSMs provide an efficient option
⁹⁵ to gather fecundity and dispersal estimates from all species that can be identified
⁹⁶ in seed traps simultaneously, naturally integrating space (trap area) and time (trap
⁹⁷ deployment period).

⁹⁸ Seed traps record seed rain following any consumption losses that occur in the
⁹⁹ canopy. Canopy attack can be recorded by damage classes, such as exit holes by

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

Countering the advantages, SSMs are difficult to evaluate, because estimates are needed for both fecundity and dispersal, and both degenerate when trees are too rare or too abundant. For known \mathbf{S} and mean seed counts (an 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). However, even with known \mathbf{S} there is a unique solution (i.e., \mathbf{SS}' is full rank) only if there are more seed traps than trees ($S > n$). Even with few trees, a solution would often include negative values, which is, of course, impossible. A model for f_i as simple as a prior distribution that excludes negative values fixes with the negative-fecundity problem, but there might still be insufficient information in the S seed counts. The early SSMs did not confront this problem, because they projected the n sources down to a few parameters, replacing individual fecundity in the vector \mathbf{f} with a function that is shared by all trees, e.g.,

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

(first line of table 1). While such models can converge rapidly, they cannot describe population heterogeneity. Many trees might be needed to estimate parameters (a, b) , but high density of trees degrades the estimate of dispersal \mathbf{S} , due to the large overlap in seed shadows. Poorly estimated dispersal, in turn, degrades the information on fecundity \mathbf{f} . The question becomes, can SSMs estimate dispersal, the effects of size (a, b) , and the fecundities, $f_i, i = 1, \dots, n$?

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

Subsequent joint modeling of maturation and fecundity combined with in- and

132 out-of-sample prediction showed that aggregate models like eq. (2) miss the perva-
133 sive heterogeneity. Few individuals are reproductively mature. Fecundity ranges over
134 orders of magnitude, only weakly related to tree size, and often concentrated within
135 few individuals (Clark et al., 2004, 2010; Nanos et al., 2010; Moran and Clark, 2011;
136 Milleron et al., 2013; Minor and Kobe, 2017). Environmental predictors together with
137 tree-level random effects allow for the large differences between individuals. Year ef-
138 fects account for annual variation that is shared across individuals (Clark et al., 2010,
139 2013). Autoregressive ($AR(p)$) models allow for lag effects up to p years. Thus far, only
140 the $AR(1)$ model has been implemented (Clark et al., 2004), whereas masting com-
141 monly involves multi-year lags (Koenig and Knops, 2001). Joint models for growth,
142 survival, and fecundity provide estimates of allocation responses to the environment
143 (Clark et al., 2010, 2014; Berdanier and Clark, 2016), but they cannot be used where
144 only seed data are available or of interest.

145 In summary, at least three advances are needed. First is the missing theory to
146 align space-time heterogeneity in mast with the ambitions of consumers. Second is a
147 modeling framework that delivers estimates. Finally, computation that is accessible to
148 a community of users is needed to promote synthesis. Ideally, that framework would
149 include simulation, to learn about the conditions where all elements can be identified.

150 For theory and the model that follows we use the genus *Pinus* as an example.
151 This wide-ranging and multi-species genus challenges the model with observation er-
152 ror in seed identification. A diversity of ground and canopy foragers include *Pinus*
153 (fig. 1) in the diet. Arthropod seed predators forage mainly in the canopy (Cibrian-
154 Tovar et al., 1986). Canopy vertebrates include crossbills (*Loxia* spp.) and other
155 finches (Fringillidae), nuthatches (*Sitta* spp.), gray jay (*Perisoreus canadensis*), and
156 red-bellied woodpeckers (*Melanerpes carolinus*). Ground foraging seed predators in-
157 clude eastern chipmunk (*Tamias striatus*), white-footed mice (*Peromyscus leucopus*),
158 and red-backed voles (*Clethrionomys gapperi*) (Abbott and Quink, 1970; Ogawa et al.,
159 2017). Eastern gray squirrel (*Sciurus carolinensis*) forages in the canopy and on the
160 ground (fig. 1).

161 The goals of this paper are ambitious, yet focused. We provide both theory and
162 the modeling needed to synthesize space, time, and diet breadth with masting data.
163 We complement existing foraging theory with formal inference on mast structure that
164 links to consumer ambit, and we fill a gap in species-distribution modeling, which has
165 emphasized climate, land cover, and soils, but omitted food. Habitat valuation based

on resource reliability can improve the potential to predict food web structure. We leave synthesis to a subsequent, more sweeping comparison of theory and data, because resource supply must be combined with traditional climate and habitat variables across a network of sites (Nuñez et al, in prep). The next section provides background theory and the model framework used to estimate masting structure. We follow with a modeling approach, tested with simulation and applied to a large network, where we estimate parameters from the theoretical analysis.

MODEL DEVELOPMENT

Dynamic process, observations

Consider an inventory plot where trees mature, after which they are capable of seed production (fig. 3). The event that tree i can produce seed in year t is the *maturity state*, $\rho_{i,t} \in \{0, 1\}$, a hidden Markov process (table 2). Coefficients β^v describe covariate effects on maturation probability. Observations of maturation state $z_{i,t} \in \{0, 1\}$ contribute to estimates of $\rho_{i,t}$.

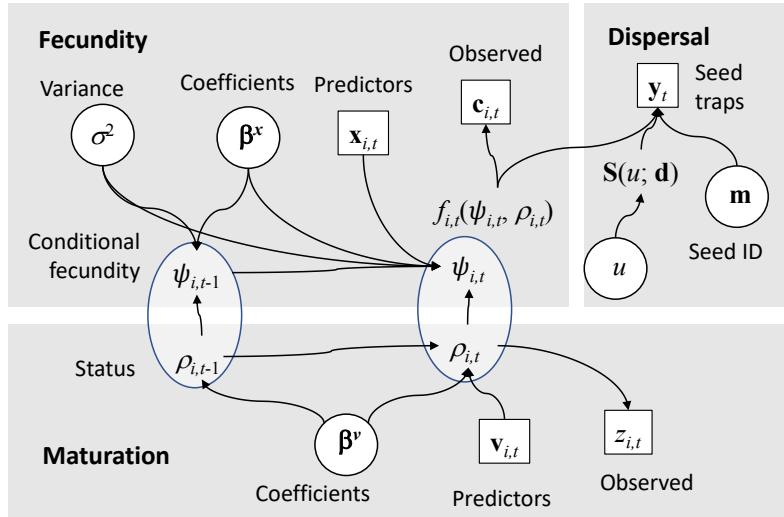


Figure 3: Probabilistic graphical model for main elements of the model, showing estimates (circles) and observed variables (squares), with dynamics ($t - 1, t$). Variables are defined in table S2.1.

Mature individuals ($\rho_{i,t} = 1$) have *conditional fecundity* $\psi_{i,t} \geq 1$ that depends on fixed and random effects, year effects, and/or autoregressive terms (table S2.1,

submodel A). Coefficients in β^x can include tree size, environment, and interactions. *Random effects* (REs) β_i^w accommodate the heterogeneity of responses across individual trees (table S2.1, submodel D). Annual variation can be described by year effects γ_t , quantifying shared variation across individuals (table S2.1, submodel B), or as quasi-periodic variation through an *autoregressive AR(p)* model, with lag terms α_l , $l = 1, \dots, p$ (table S2.1, submodel C). Year and lag effects can be random across species and/or regions, recognizing that masting may be coherent within, while not necessarily between groups. *Actual fecundity* $f_{i,t} = \psi_{i,t}\rho_{i,t} \geq 0$ is a latent variable (fig. 3). There are sometimes direct counts from the canopy (LaDeau and Clark, 2006) or from the ground (Minor and Kobe, 2017). When available, observed fecundity enters as a minimum and maximum estimate in the vector $\mathbf{c}_{i,t} = (c_{i,t,min}, c_{i,t,max})$ (fig. 3). Theory and methods developed here omit studies that lack seed trap data (e.g., Koenig and Knops (2001)), because we are concerned with not only seeds in the canopy, but also their redistribution by dispersal.

Seeds accumulate in traps $s = 1, \dots, S$ from nearby trees, depending on the *dispersal kernel* $\mathbf{S}(\mathbf{u})$, which includes fitted parameters $\mathbf{u} = u_1, \dots, u_H$ for each species h . The seed count $y_{sm,t}$ is the number of seeds of type m counted in trap s in year t .

Seed-identification uncertainty enters through a $H \times M$ error matrix \mathbf{M} . When multiple species $h = 1, \dots, H$ contribute to the same seed type(s) (e.g., some seeds identified only to genus), then the $m = 1, \dots, M$ seed types must be included in the model with the H species that could have produced them. Element \mathbf{M}_{hm} is the probability that a seed of species h will be assigned to type m . The *likelihood* for seed counts incorporates observation error \mathbf{M} , sample effort A (trap area \times active period), and Poisson variation in counts \mathbf{Y} . The full model and prior distributions are discussed in section S2.2 and section S2.5, respectively.

207 ***Habitat reliability***

The cost of search time in a variable environment is central to foraging theory and an objective for inference in tracking studies (Owen-Smith et al., 2010; Avgar et al., 2013; Benhamou, 2014). All else being equal, a habitat that offers an abundant (large mean) and reliable (small variance) mast supply benefits a consumer, depending on its ambit. A landscape that supports two resources, equal on average, but differing in distribution, is illustrated in fig. 4a. Useful definitions are *exceedance*, the fraction of landscape above a minimum resource density when experienced at the scale of the

Table 2: Terms with definitions.

Term	Definition	Reference
<i>ambit</i>	consumer movement/storage in space (m^2 on ground or host trees in canopy), time (yr), diet breadth (no. host spp.)	INTRODUCTION
<i>demographic storage</i>	post-mast event consumer cohort	<i>Habitat reliability</i>
<i>encounter distance</i>	nearest habitat exceeding minimal requirement	
<i>error matrix, M</i>	uncertain seed identification	section S2.4
<i>exceedence</i>	fraction of landscape exceeding minimal requirement	
<i>fecundity</i>	conditional $\psi_{i,t}$, true $f_{i,t}$, observed range $\mathbf{c}_{i,t}$	eq. (S2.8), eq. (2)
<i>quality, ground, $g_{s,t}$</i>	resource density at location s in yr t (g m^{-2}); space \times yr covariance \mathbf{G}_{SL} , total G_{SL} (g)	<i>Habitat reliability</i>
<i>quality, host, $q_{i,t}$</i>	resource from host tree i in yr t (g tree^{-1}); host \times yr covariance \mathbf{Q}_{nL} , total Q_{nL} (g)	eq. (3)
<i>quality, seed, r_h</i>	resource value of seed/fruit of host species h	eq. (3)
<i>kernel, S</i>	redistribution from trees to ground (m^{-2})	eq. (1), eq. (S2.1)
<i>maturity state</i>	$\{0,1\}$, true $\rho_{i,t}$, observed $z_{i,t}$	eq. (S2.6), eq. (S2.7)
<i>resource score</i>	balance quality, reliability of mast resource	<i>Habitat reliability</i>

table S2.1 contains variable definitions

consumer's foraging ambit (fig. 4b), and *encounter distance* to the nearest habitat from a consumer's range that exceeds the minimum requirement, also dependent on foraging ambit (fig. 4c). For a clumped resource, consumers with a narrow foraging ambit are restricted to dense-resource habitats that exceed the minimum requirement (brown in fig. 4a); concentrated resources make limited ambit possible within, but not between, these patchy habitats. High variance penalizes movement everywhere resource density is inadequate (fig. 4c), and the overall fraction of habitats exceeding threshold densities increases at a rate that is low relative to a scale-independent (diffuse) resource (fig. 4c).

Conversely, only a wide-ambit consumer can exceed its threshold on a diffuse resource; in fact a wide ambit becomes the preferred strategy (fig. 4c, d). Of course, a wide ambit should not discourage concentrated feeding in dense patches when they are encountered, or "search globally/orange locally".

We wish to recast basic foraging concepts to connect the mean and spatio-temporal covariance structure of masting trees with consumers of multiple host species that differ both in abundance and host quality. We develop a resource score that summarizes benefits and costs when there is scale-dependence in habitat quality, consumers differ in ambit, including diet breadth (fig. 4b). When variation is space is combined with variation in time, the resource score forms a surface (fig. 4e). A small-ambit consumer increases its score by foraging widely, along direction B in fig. 4e). These relationships further apply to space-time. The same consumer could increase its score with storage (direction A in fig. 4e). When habitats that are both patchy and ephemeral, shifting location from year to year, consumers with limited foraging can compensate with a dispersal stage between years (e.g., a larval seed predator and flighted adult). This effect draws on the spatio-temporal covariance in resource supply, highlighted by transect C in fig. 4e). These concepts are derived in *Variance for a generalist consumer*.

To translate a map like fig. 4a to a scale- and diet-dependent resource score like fig. 4d, we begin with *host quality*, the product of per-seed or per-fruit reward and seed/fruit abundance,

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

where $r_{h[i]}$ is the seed quality of species h corresponding to tree i . Here we use seed mass as an index for quality (table 2), but quality can be defined on any scale. Dispersal translates host quality $q_{i,t}$ (kg per host tree) to *resource quality* on the ground $g_{s,t}$ (g m⁻² summed over all hosts in the diet).

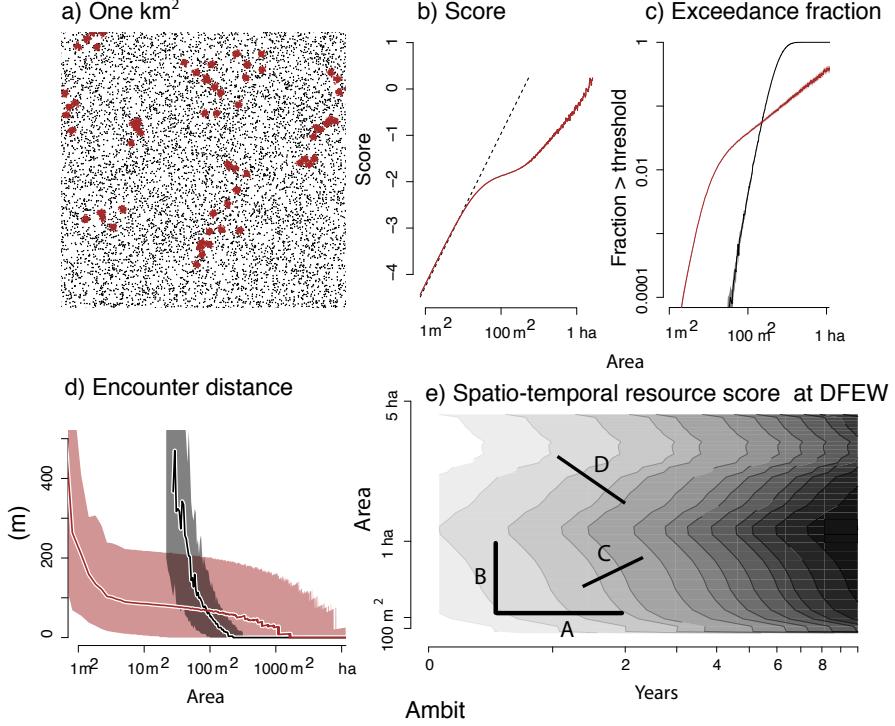


Figure 4: Search-globally/forage-locally, summarized as a resource score. a) Map of two resources, equal on average, one scale-independent, i.e., diffuse (black), another clumped (brown). b) A resource score, combining the mean benefits versus variance costs for the resources in (a) depend on the scale of foraging by a consumer on the diffuse resource (dashed) and the clumped resource (brown). c) The diffuse resource cannot support a consumer that requires resource densities above a threshold unless it can forage widely, while the clumped resource has lower yield for consumers that forage widely. d) For a clumped resource (brown), encounter distances decline slowly on average with foraging ambit, but there is a high variance cost (shaded). A diffuse resource is only available to consumers with sufficiently large ambit to meet threshold resource densities, but then encounter distances decline sharply and with low variance (black). e) Mean-benefits/variance-costs also exist in time, forming a space-time surface. Transects A through D are discussed in the text.

A consumer that forages widely realizes the mean resource availability, through movement, storage, and diet breadth. The movement scale in the canopy is summarized by the n hosts visited by a consumer. The movement scale on the forest floor is area. Time dependence enters when a high mast year can be 'stored' within individuals, either by dormancy (fungal pathogens) or by so-called *capital breeding* (mammals) (Karasov, 1986; Sainmont et al., 2014; Rodel et al., 2016). It can also be stored within

populations, here termed *demographic storage*, a pulse of births that follows masting events (McShea, 2000; Boutin et al., 2006; Descamps et al., 2008; Bergeron et al., 2011; Schmidt and Ostfeld, 2003; Pelisson et al., 2013; Ogawa et al., 2017). The mast-year cohort can be sufficiently large to offset mortality losses and low birth rates in subsequent non-mast years. Diet generalists depend on masting behavior of host individuals of multiple species, summarized by mean and covariance structure.

Mast benefit is the accumulated resource over the consumer ambit. Let $Q_{nT} = \sum_{i,t} q_{i,t}$ be the yield to a canopy consumer that searches n host trees over T years, with expectation

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

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

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

A consumer with restricted space-time foraging (small n, S, T) and narrow diet breadth is vulnerable to the variance in encounter of resource-rich habitats (fig. 4c).

To weigh the benefits of a large mean, $E_{it}(q)$ or $E_{st}(g)$, against the variance cost of an unreliable resource, $Var(Q_{nT})$ or $Var(G_{ST})$, we build from a familiar index used to describe masting, the coefficient of variation, $CV = \sqrt{Var(Q_{nT})}/E_{nT}(Q)$ (Herrera et al., 1998; LaMontagne and Boutin, 2009; Pesendorfer et al., 2016), but introduce scale-dependence across multiple host species of variable resource quality (eq. (3)). The traditional CV is inadequate, because mast intervals of 2 to 10 years having the same CV will not have the same impacts on consumers that differ in space-time-diet ambit; the mean-variance balance depends on scale (fig. 4). 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) for canopy foragers, and $R_{ST} = -\log CV_{ST}$ (space-time) for ground foragers.

As a reference for the role of scale, we first evaluate the scale-independent resource score, a spatio-temporal Poisson process (black in fig. 4a, b, c). The expected yields in eq. (4) and eq. (5) have corresponding expected variances,

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

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

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

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

282 (dashed line in fig. 4b). By substituting n for the subscript nT , the resource score
283 applies to n host trees in a random year. A subscript T applies to a random host over
284 T years. Likewise, for the forest floor there is a resource score for T years in one site,
285 for S sites in a random year, and for ST site-years. The baseline eq. (8) provides an
286 index to compare habitats that differ in scale dependence.

287 ***Tree-time and space-time covariance***

288 Masting is experienced differently by consumers in the canopy and on the ground, de-
289 scribed by covariance structures that make the resource score eq. (8) scale-dependent.
290 For the canopy, there is no evidence for a distance-related covariance between trees
291 within stands (Clark et al., 2010), consistent with widely observed regional coherence
292 (Liebhold et al., 2004; Fernandez-Martinez et al., 2017). For this reason, within-stand
293 canopy covariance is between trees, rather than over distance. On the forest floor,
294 spatial covariance combines host-tree dispersion with dispersal. We do not introduce
295 a geospatial model (e.g., Gneiting (2002); Banerjee et al. (2014)), because spatial co-
296 variance is already induced by the kernel \mathbf{S} . For covariance over time, we use the
297 covariance in the estimated fecundity from the SSM.

298 The covariance analysis begins with a fecundity matrix $\mathbf{F}_{(n \times T)}$ consisting of ele-
299 ments $F_{i,t}$ with expectation and covariance

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

300 where $\mathbf{f}_{(nT)} = vec(\mathbf{F}_{(n \times T)})$ and $\boldsymbol{\psi}_{(nT)}$ are length- nT vectors (to simplify notation,
301 individuals are mature), and \mathbf{C} is the $nT \times nT$ covariance matrix that incorporates
302 both the relationships between individual trees and their variation over time. The

303 $\text{vec}(\cdot)$ operator stacks the columns of a matrix to obtain a vector. An element $\mathbf{C}_{it,i't'}$
 304 holds the covariance between host individual i in year t and host individual i' in year
 305 t' . We cannot estimate the tree-time matrix \mathbf{C} , because each (i, i', t, t') combination
 306 happens once. Below we introduce the *tree-lag* covariance. First we note two special
 307 cases, i) a $n \times n$ (tree-to-tree) covariance \mathbf{C}_n holding the covariances experienced by a
 308 consumer that moves between n host trees in a random year, and ii) a $T \times T$ (year-to-
 309 year) covariance \mathbf{C}_T , holding the covariances experienced by a consumer that tracks a
 310 random host over T years.

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

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

315 The conditional covariance in intensity is

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

316 The total covariance additionally includes the Poisson variance,

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

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

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

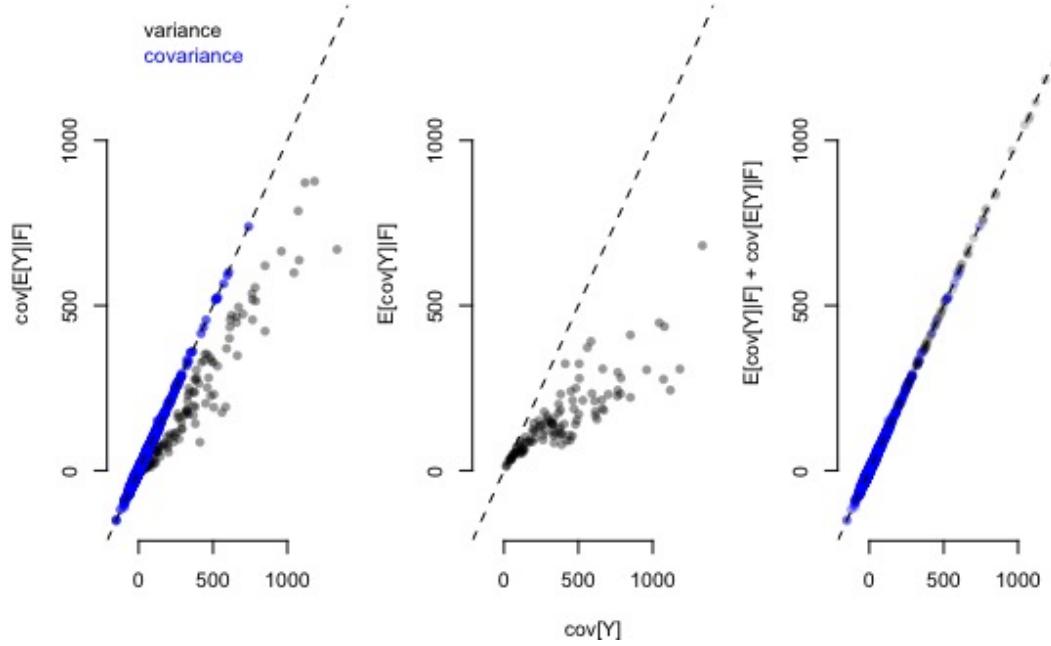


Figure 5: Contributions to space covariance \mathbf{G}_S from terms in eq. (10) plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in section S3.

325

Variance for a generalist consumer

326 Because consumers exploit multiple resources, the covariance structure must describe
 327 their combined supply, accounting for differences in nutritional quality. In this section
 328 we evaluate the covariance in resource quantity to a canopy forager of n host trees and
 329 L lag years \mathbf{Q}_{nL} and to a ground forager over space S and L years \mathbf{G}_{SL} . These
 330 quantities lead to the resource score.

331 In the canopy, the aggregate resource available to the consumer of n hosts over T
 332 years is

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

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

337 is,

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

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

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

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

343 This variation can be compared to that expected for scale-independent variation in
344 eq. (8). An example of this comparison is shown in fig. 4b.

345 We can combine eq. (8) with eq. (13) to quantify the potential advantage to a
346 consumer if it could expand the diet to include a new host \tilde{h} that brings \tilde{n} new host
347 individuals into the diet and depends on densities of the current and new host species,
348 their space-time covariance, and the consumer ambit. The aggregate resource from
349 eq. (11) increases by a term

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

350 where $r_{\tilde{h}}$ is the quality of the new resource, which can be concatenated into a length- \tilde{n}
351 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
352 expected addition to the diet from the second term in eq. (14) is

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

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

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

355 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 $\tilde{n}T \times nT$
356 covariance between new and original hosts in the diet. Of course, strong negative
357 covariance with hosts now in the diet (third term in eq. (16)) decreases aggregate
358 variance, with obvious benefits. Not so obvious is the fact that, even if independent of

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

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

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

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

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

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

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

364 If the consumer were a statistician, she would recognize the right-hand side of eq. (20)
 365 to be her standard error (SE) for yield on the left-hand side. A large yield from the
 366 new host on the left combines with the averaging effects of increasing \tilde{n} on the right to
 367 increase the score. It is a consumer- and habitat-specific SE, because it is referenced
 368 to the consumer's ambit, including current diet breadth (nT) and number of hosts
 369 it could exploit of the new resource ($\tilde{n}T$). Hereafter, we refer to the *SE rule* as a
 370 rule-of-thumb for the advantage of diet breadth.

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

$$\Delta_{nT} = R_{nT} - E(R_{nT}) \quad (21)$$

374 from eq. (13) and eq. (8) and Δ_{ST} .

375 The same analysis leads to a resource score for ground foragers, R_{ST} . Despite
 376 positive and negative covariance elements in the canopy, the forest floor covariances
 377 in \mathbf{G}_S tend to be positive at the characteristic scales of dispersal (fig. 5). This is not
 378 necessarily so at broader spatial scales, where the dispersion of host trees of different
 379 species can dominate. Space-lag covariance structure used for \mathbf{Q} and \mathbf{G} in this section
 380 is expanded in section S4.1.

381

METHODS

382 We implemented Gibbs sampling, a Markov chain Monte Carlo (MCMC) technique.
 383 Sampling includes Metropolis and Hamiltonian Markov chain (HMC) steps (section S9).
 384 Due to a high-dimensional state space (maturation and fecundity of all trees over all
 385 years), posterior simulation suffers well-known scaling limitations of MCMC, as the
 386 parameter set is dwarfed by the volume of parameter space (Neal, 2011); random-walk
 387 algorithms cannot explore the parameter space in finite time. HMC exploits the ge-
 388 ometry of the typical parameter set to efficiently target proposals (Betancourt and
 389 Girolami, 2015). Because it relies on vector fields (a differentiable surface), HMC does
 390 not apply to discrete maturation state. However, it does apply to conditional fecun-
 391 dity, and is used for that purpose here (section S9.2). Maturation cannot be sampled
 392 independent of conditional fecundity. The algorithm is thus a hybrid of [maturation,
 393 fecundity] updates and [maturation|fecundity] updates. With the exception of matu-
 394 ration, conditional fecundity, and the dispersal parameters (a low-dimensional vector),
 395 all other parameters are sampled directly (section S9).

396 Predictive distributions were generated for maturation and fecundity, which, in
 397 turn, predict seeds in-sample (i.e., at seed trap locations and sampling years) and
 398 out-of-sample (other locations and/or years) (section S2.6). Partial autocorrelation
 399 functions (PACF) quantify the contribution of each lag p , while controlling for shorter
 400 lags $0, \dots, p-1$. Complex eigenvalues for the AR(p) model (section S5) indicate quasi-
 401 periodic variation. A stationary AR(p) process has all eigenvalues of less than unit
 402 modulus (real plus complex parts, section S5). The tree-lag (canopy) and space-lag
 403 (forest-floor) covariances (*Space-lag covariance*) were generated with resource scores
 404 for each plot. Overall structure is summarized by diet-wide entropy experienced by a
 405 consumer over trees, sites, and years (section S4.2). Variable selection can be base on
 406 DIC values for fitted models.

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

413

Simulation

414 Rather than offer an exhaustive compilation of simulation studies, we supply the full
 415 MASTIF package with simple examples for application (section S3). We adopt this
 416 approach, because fitting depends on the structure of each stand (density and distri-
 417 bution of mature trees), dispersal characteristics of each species, and spatio-temporal
 418 sampling design, including density and dispersion of traps, and the classification of
 419 seeds into types. As with any model, useful estimates are only expected where there
 420 is 'signal' in data. Simulation determines if, given signal, the model can recover pa-
 421 rameters and predict data. We illustrate where an SSM can be successful, and we
 422 discuss aspects of data structure that can lead to poor performance. The value of the
 423 simulator is this first opportunity it affords to examine a full range of potential data
 424 sets.

425

Application to field data

426 From up to 25 years of continuous seed collections across sites in the eastern US (sec-
 427 tion S7), we analyzed mast production for the genus *Pinus*. Multiple species on the
 428 same plots meant that species identity of most seeds was unknown (fig. 1). Throughout
 429 this multi-decade study methods emphasized minimizing false-positive seed identifica-
 430 tions, thus restricting species-specific classifications to unambiguous cases. Field and
 431 lab methods are detailed in (Clark et al., 1998, 2004, 2010; Moran and Clark, 2011;
 432 Bell and Clark, 2016). Data summaries are provided in section S7.

433 For this focus on methodology, predictors are limited to tree diameter, making the
 434 model comparable with most literature on this subject. The omission of environmental
 435 predictors that control fecundity (Clark et al., 2004, 2010, 2014) sacrifices predictive
 436 skill for transparency—our goal here is to focus on space-time structure that is linked
 437 solely to a size model. Model fitting is demonstrated with AR(4) conditional fecundity
 438 (table S2.1). Prior distributions are provided in the section S2.5.

439

RESULTS

440

Simulation studies

441 Simulation studies found that the model can recover parameters and latent states for
 442 all species, even when most of the seeds (in , this example, 2/3) are identified only to
 443 genus level. A stochastic simulation example is summarized for $M = 4$ seed types and

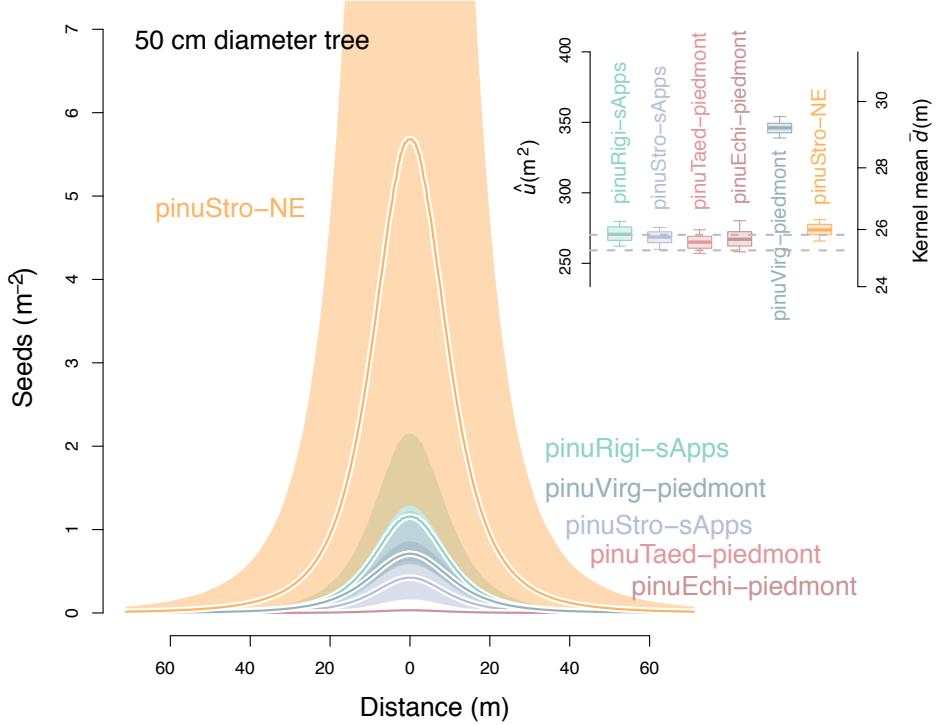


Figure 6: Dispersal and seed shadows. Seed shadows are predicted from the posterior distribution, with 95% predictive intervals. Estimates of dispersal parameters u_h for *Pinus* species-region groups in the AR(4) model are shown at right. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. The kernel mean scale at right is eq. (S6.15).

444 $H = 3$ species on a mean of $J = 8$ plots, $T = 5$ years, $n = 25$ trees, and $S = 50$ traps.
445 Parameter recovery is approximate, because, as in real data, few trees in a plot of a
446 given species are mature. For the simulation shown in fig. S8.4, the number of trees per
447 plot ranges from 4 to 23. Trees far from seed traps supply little information. However,
448 if many trees are close to the same traps, information is limited by extensive spatial
449 overlap. Coefficients for maturation and conditional fecundity are close to values used
450 to generate data, but they are 'damped' (fig. S8.4a, b), as would be expected from a
451 noisy fit. The composition vectors for seed identification \mathbf{m}_h are recovered precisely,
452 with 33% of seed from each species being assigned to the species and the remainder
453 to the undifferentiated class "querUNKN" (fig. S8.4c).

454 Prediction from the fitted model is shown for observed seed counts (fig. S8.5a, b)
455 and for unobserved fecundity (fig. S8.5c). Seed counts can be predicted from two stages
456 in the model, as discussed in section S2. Accurate prediction from the maturation and
457 fecundity estimates (fig. S8.5b) requires that the model can identify these latent states,

458 but it does not require that covariates in the model can predict those states. Accurate
 459 prediction from the full posterior (fig. S8.5a) additionally requires that environmental
 460 variables are available that predict maturation and fecundity, which, in turn, predict
 461 seed counts. The fact that the model is capable of both here is not surprising, because
 462 we are fitting the 'correct' model; the only predictor in the model is known to be tree
 463 diameter. The predictions in (a) could be poor while those in (b) are good in cases
 464 where the model finds good *estimates* of fecundity without finding variables that can
 465 *predict* fecundity. The ability to recover unobserved fecundity, which ranges widely
 466 over six orders of magnitude (fig. S8.5c), verifies that the fit captures each of the key
 467 features in the model. Again, the simulation mode in MASTIF permits evaluation of
 468 designs applicable to specific studies.

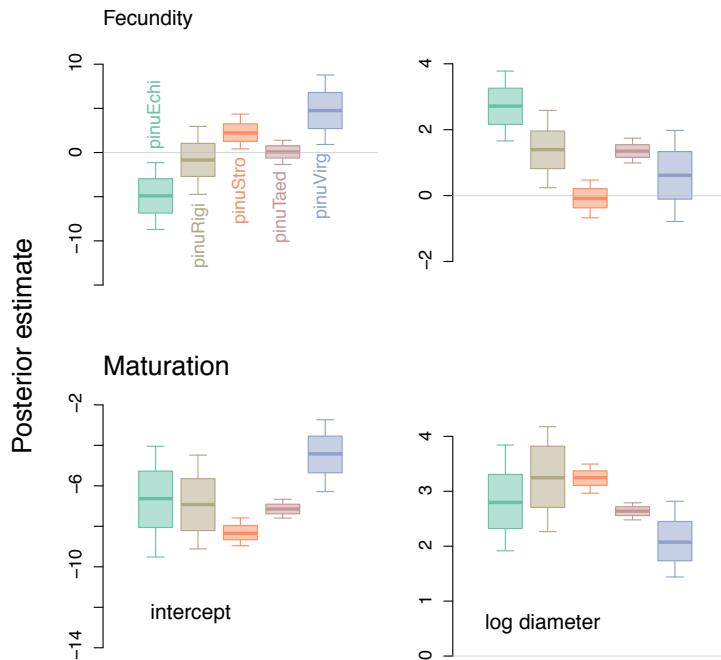


Figure 7: Estimates of fecundity coefficients β^x (above) and maturation coefficients β^v (below) (see table S2.1) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively.

469

Application to Pinus

470 As for simulated data, fecundity estimates accurately predict seed rain (fig. S8.7a,
 471 b). Estimates of maturation and fecundity coefficients show positive effects of tree
 472 diameter on both state variables (fig. 7). The similarities in diameter effects across
 473 species are not an artifact of treating them as random effects—they are fixed effects

474 and, thus, are not bound by a hyperprior.

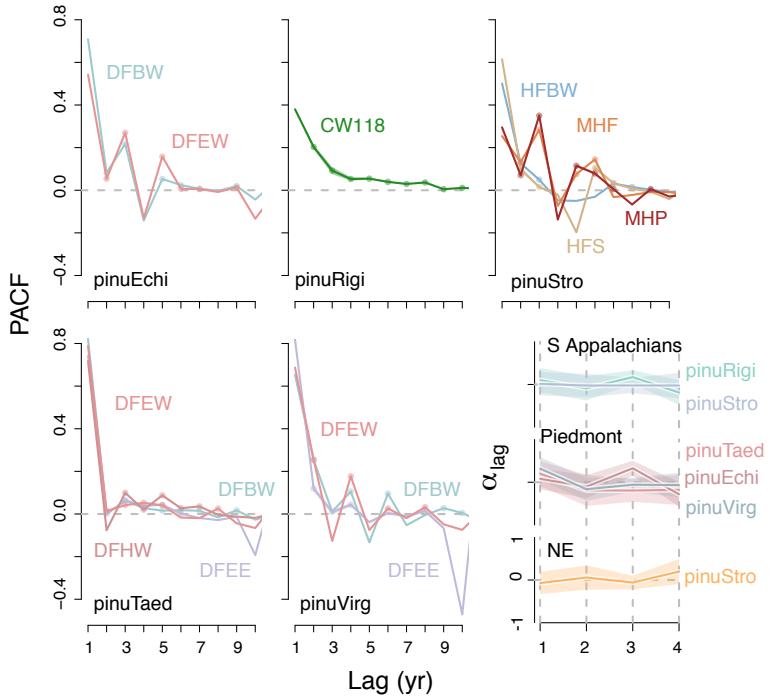


Figure 8: Partial autocorrelation for fecundity in *Pinus* by random groups, defined by species and plot. At lower right are coefficients for random species-region groups in the AR(4) model (a) and the year model

475 Dispersal parameter estimates \hat{u}_h , shown with kernel mean distances \bar{d}_h , (sec-
476 tion S6) are similar across species (fig. 6a). The random effects prior on \mathbf{u} borrows
477 strength across all trees on all plots. Predicted seed shadows show expected and 95%
478 uncertainty for seed arrival with distance from a 50 cm diameter tree (fig. 6b).

479 Partial autocorrelation identifies clear species differences in lag relationships. The
480 southern yellow pines show one-year lags with strong three-yr (*P. echinata*, *P.*, *taeda*)
481 and four-year (*P. virginiana*) cycles, respectively (fig. 8). *P. strobus* also shows pe-
482 riodicity at two of four sites. By contrast, *P. rigida* PACF declines gradually over a
483 four-year period. The AR(4) coefficients pick up this signal, with positive effects at a
484 lag of 3 years for the same species and sites (fig. 8, lower right). Eigenvalues with large
485 imaginary parts identify stationarity, but quasi-periodic variation. Real and imaginary
486 parts lie within the unit circle (fig. S5.1), consistent with stabilizing variation over the
487 long term. Large imaginary parts indicate instabilities, including for species that do
488 not show strong effects at specific lags (fig. 8a).

489 The full tree-lag covariance \mathbf{C}_L and space-lag covariance \mathbf{G}_L are too large to vi-
490 sualize for thousands of trees and locations across sites and decades, so we provide

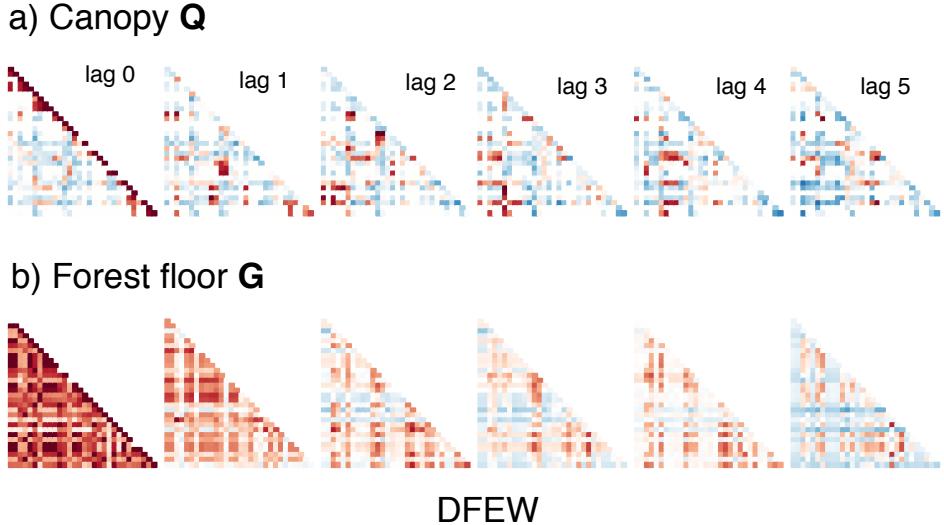


Figure 9: a) Tree-by-lag covariance structure in the canopy at DFEW, developed from \mathbf{C}_L eq. (9) and b) space-by-lag structure on the forest floor, developed from \mathbf{G}_L eq. (10). Each pixel represents pair of individual host trees (a) or sites on the forest floor (b), correlated over successive lag years.

examples. Each panel in fig. 9 shows a correlation between two host trees (above) or locations on the forest floor (below) in the same years (lag 0) or at lagged intervals. Synchronicity (warm colors at zero lag) is weak in these species, with some high correlations (fig. 9a). The limited synchronicity promotes a relatively reliable resource availability over years for canopy foragers. Correlation in space is amplified by dispersal across the forest floor, which induces positive correlation at zero lag (fig. 9b). The positive correlations on the forest floor switch to negative by lag 2.

Resource scores are not strongly correlated between canopy and forest floor. Comparing a canopy forager of five host trees with a ground forager of 500 m^2 shows generally higher scores on the forest floor resulting from redistribution that smooths variation between host trees in the canopy. 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. 10a). The low variance over time in the *P. rigida*-dominated CW118 puts it ahead of other stands in fig. 10, despite modest total productivity of this species.

Resource scores are shown for two sites in the canopy and forest floor (fig. 11). Each habitat combination offers a different space-time pattern. The tendency for score to increase with storage time (yr) is general, but not uniform between habitats. Storage benefits consumers at all spatial scales on the forest floor. Demographic storage, cap-

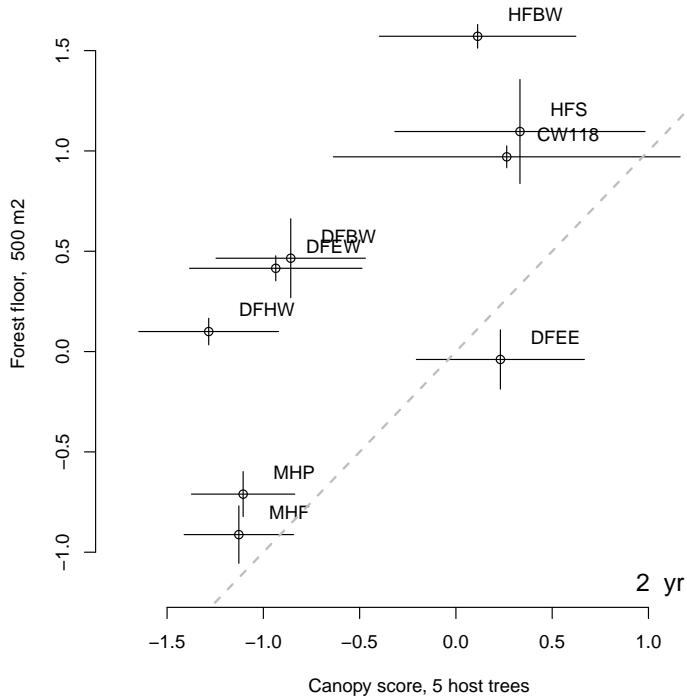


Figure 10: Resource scores (eq. (13)) plotted against mean resource supply (eq. (11)) for space [between host trees- (black) and sites on the ground (green) in a given year] and b) over years in a single host or site.

ital breeding, and dormancy all effectively reduce variance, thereby increasing scores. Space-for-time compensation (increasing surface from lower left to upper right) is only clearly evident on the forest floor at DFBW (fig. 11b, right). This is the pattern that promotes movement between years, as shown by transect C in fig. 2. Even here, the increasing score with spatial scale is not monotonic, with a decline at the hectare scale, due to clumped distributions of host trees. Canopy foragers that ignore spatial displacement at the scale (e.g., song birds) do not experience this heterogeneity. The maximum score at relatively small numbers of host trees at DFBW (fig. 11a) results from large variance between host individuals.

DISCUSSION

Quantifying the resource value of forested habitats, based on their supply of reliable mast, is a venerable challenge in ecology (Janzen, 1970; August, 1983; Ostfeld and Keesing, 2000; Curran and Leighton, 2000; Cortes and Uriarte, 2013; McMeans et al., 2016). As foraging capacity and/or storage increase, the variance-cost of an unreliable

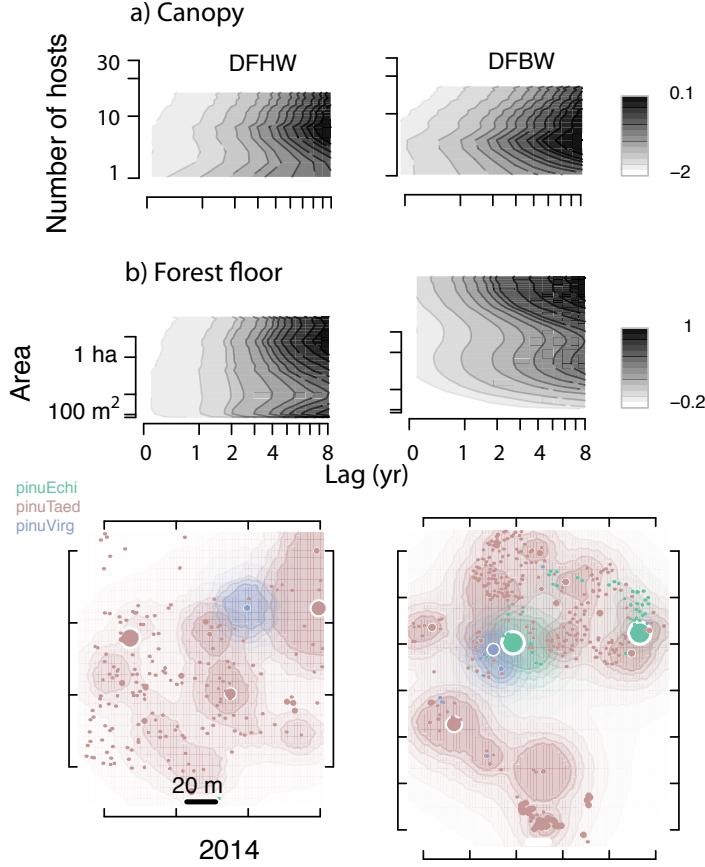


Figure 11: Resource scores at two sites experienced by a consumer (eq. (21)) that can store resources for zero to ten years, forages over a range of host trees (a) or forest-floor area (b), and consumes seeds from three host species. Space-for-time compensation occurs when surfaces increase from lower left to upper right in a, b. Below are mapped seed density surfaces for a high-productivity year, with trees (circles) scaled by their fecundity estimates.

resource shifts to a mean-benefit: the scale-dependent averaging. Habitats differ in the entropy in food supply they offer consumers section S4.2. The stability properties of mast cycles can be quantified and compared, showing evidence for long-term stability, but pervasive quasi-periodicity and large differences between habitats (fig. S5.1). Spatial foraging, storage, and diet breadth represent alternative solutions to the fluctuating resource base. They contend with episodic fruiting and synchronicity of the multiple hosts in the diet that differ in quality. A simple resource score can summarize habitat differences across a network of inventory sites (fig. 10). Theoretical results are combined with a methodology that makes estimates widely available for synthesis. We summarize the methodological advance, followed by potential to improve biogeographic prediction of masting and consumers of it.

535

Mast estimates and prediction

536 MASTIF offers a flexible platform that can facilitate synthesis across a large and grow-
537 ing literature (table 1). The model specification can include main effects, interactions,
538 year effects, lag effects, and random effects (table S2.1), while accommodating the
539 uncertainty in seed identification (fig. S8.4b). From the example application we find
540 high confidence in estimates (fig. 6, 7, and Supplement B), and this can only improve
541 when environmental predictors are included in the model (Clark et al. (2004); Uriarte
542 et al. (2005); LaDeau and Clark (2006); Clark et al. (2010, 2013, 2014); Uriarte et al.
543 (2012), Nuñez et al., in prep.).

544 Simulation in MASTIF can be used to explore the efficacy of study designs for
545 specific applications. Inference and prediction break down when trees are either too
546 abundant or too rare, an inherent tension between inference on dispersal versus fecun-
547 dity. When too abundant, overlapping seed shadows may not be resolved to specific
548 trees. When reproductive trees are too few, there is an insufficient range of values,
549 and estimates of slope coefficients for predictor variables are reduced in magnitude, as
550 expected for noisy data (fig. S8.4). Because the same seed traps are used to estimate
551 all species on a plot, model fit will vary for species, each of which offers a different
552 distribution of distances and numbers and sizes and trees.

553 MASTIF’s Bayesian implementation exploits the accumulating knowledge of mat-
554 uration, fecundity, and dispersal. A rich posterior distribution is efficiently explored
555 with prior parameter values that integrate previous understanding. For dispersal,
556 these estimates can learn from a large literature that includes low-dimensional models
557 that converge rapidly for simple assumptions about fecundity (table 1). Data sets that
558 include multiple stands (a network) and years increase the range of effects that can be
559 estimated. Group-level random effects stabilize estimates across plots (fig. 6) that in-
560 dividually would not provide useful estimates. The flexibility to combine uncertainty
561 in seed identifications and a wide range of predictor variables makes our approach
562 amenable to many data sets. The tree-time and space-time covariance, visualized in
563 fig. 9 and summarized by entropy section S4.2, gauge the average supply and its reli-
564 ability. The methodology extends to consumers with a generalized diet, implemented
565 in a separate paper (Nuñez et al, in prep).

566

Resource score as an index

567 The many ways in which a consumer experiences resource heterogeneity cannot be
 568 captured by a single index. The specific resource score proposed here was motivated
 569 by simplicity, including its close connection to current practice, but expanding the
 570 traditional coefficient of variation to accommodate a broad diet and spatio-temporal
 571 dependence. It is not the most important product of this analysis, but rather a sum-
 572 mary of it. The generality is rather the spatio-temporal covariance structure of an
 573 arbitrarily broad diet that can be estimated directly from data. The principle steps
 574 in this derivation take us from the quality of seed or fruit combined with the fecun-
 575 dity of an individual tree in a given year (eq. (3)), to a tree \times tree \times lag covariance
 576 structure for hosts (eq. (9), section S4), to a spatio-temporal covariance on the forest
 577 floor (eq. (10)), decomposed by host species (eq. (14), eq. (16)). It can be generalized
 578 to address a generic landscape characterized by spatial structure, rather than explicit
 579 spatial locations (section S1). The resource score represents only one of many possible
 580 ways to summarize it. We expect other summaries to be equally valuable, depending
 581 on specific applications.

582

Consumer ambit and resource score

583 The scale-dependent resource score recognizes a shift from variance-penalty to mean-
 584 benefit with increasing consumer ambit (fig. 11). Limitations of the standard coefficient
 585 of variation (CV) include this omission of scale (Herrera et al., 1998; LaMontagne and
 586 Boutin, 2009). On the other hand, autocorrelation models applied to seed trap data
 587 alone, without estimates of maturation and fecundity, do not reflect availability in the
 588 canopy (Clark et al., 2004; Pesendorfer et al., 2016). The resource score extends the
 589 value of CV as an index that combines mean and variance by making it scale-specific
 590 both for canopy and forest floor.

591 The standard error (SE) rule (eq. (20)) provides a simple index to quantify the
 592 advantage of expanding or contracting diet breadth. Losses from the diet decrease the
 593 mean and, except where there is positive covariance with current diet items, decrease
 594 the score through increased contribution of the variance. For example, the abundant
 595 American chestnut (*Castanea dentata*) in the Appalachian and northeastern forests
 596 had an unknown masting structure. Knowledge of extant species can provide guidance
 597 on the impacts of future threats. The value of the SE rule is not limited to cases where

598 consumers possess the capacity to change their diets or where diet changes are imposed
599 by changing host availability. It can be used to evaluate the consequences of resource
600 supply potential of stands supporting a full range of tree species.

601 *Biogeographic implications*

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

610 We did not offer a full predictive analysis of resources scores in this paper, be-
611 cause resources alone cannot predict trophic structure, requiring instead a full range
612 of climate and habitat variables (Nuñez et al., in prep). The important contribution
613 to biogeographic understanding includes the basic theory and computation that can
614 use species-size structure to quantify resource supply in a way that can be combined
615 with the traditional climate and habitat variables in SDMs. The translation of seed
616 production and dispersal to spatio-temporal resource availability (fig. 9) and the sum-
617 mary of its effect by forest stands (fig. 10) can supplement the variables now used for
618 SDM.

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624 References

- 625 Abbott, H. G., and T. F. Quink. 1970. Ecology of Eastern White Pine Seed Caches
626 Made by Small Forest Mammals. *Ecology* **51**:271–278. URL <GotoISI>://WOS:
627 A1970G625900011.

- 628 August, P. V. 1983. The Role of Habitat Complexity and Heterogeneity in Structuring
629 Tropical Mammal Communities. *Ecology* **64**:1495–1507. URL <GotoISI>://WOS:
630 A1983RU21500017.
- 631 Avgar, T., A. Mosser, G. S. Brown, and J. M. Fryxell. 2013. Environmental and
632 individual drivers of animal movement patterns across a wide geographical gradient.
633 *J Anim Ecol* **82**:96–106. URL <https://www.ncbi.nlm.nih.gov/pubmed/23020517>.
- 634 Banerjee, S., B. P. Carlin, and A. E. Gelfand. 2014. Hierarchical Modeling and Analysis
635 for Spatial Data. 2nd edition. Monographs on Statistics and Applied Probability,
636 CRC Press, Boca Raton, Florida.
- 637 Bell, D. M., and J. S. Clark. 2016. Seed predation and climate impacts on reproductive
638 variation in temperate forests of the southeastern USA. *Oecologia* **180**:1223–1234.
639 URL <GotoISI>://WOS:000373186100029.
- 640 Benhamou, S. 2014. Of scales and stationarity in animal movements. *Ecol Lett*
641 **17**:261–72. URL <https://www.ncbi.nlm.nih.gov/pubmed/24350897>.
- 642 Berdanier, A. B., and J. S. Clark. 2016. Divergent reproductive allocation trade-offs
643 with canopy exposure across tree species in temperate forests. *Ecosphere* **7**:e01313–
644 n/a. URL <http://dx.doi.org/10.1002/ecs2.1313>.
- 645 Bergeron, P., D. Reale, M. M. Humphries, and D. Garant. 2011. Anticipation and
646 tracking of pulsed resources drive population dynamics in eastern chipmunks. *Ecology*
647 **92**:2027–2034. URL <GotoISI>://WOS:000296426000003.
- 648 Betancourt, M., and M. Girolami, 2015. Hamiltonian Monte Carlo for Hierarchical
649 Models, Book section 4, pages 79–96 . CRC Press, New York.
- 650 Bogdziewicz, M., R. Zwolak, and E. E. Crone. 2016. How do vertebrates respond to
651 mast seeding? *Oikos* **125**:300–307. URL <http://dx.doi.org/10.1111/oik.03012>.
- 652 Bonal, R., and A. Munoz. 2008. Seed growth suppression constrains the growth
653 of seed parasites: premature acorn abscission reduces Curculio elephas larval size.
654 *Ecological Entomology* **33**:31–36. URL <GotoISI>://WOS:000252495600004.
- 655 Bontemps, A., E. K. Klein, and S. Oddou-Muratorio. 2013. Shift of spatial pat-
656 terns during early recruitment in *Fagus sylvatica*: Evidence from seed dispersal

- 657 estimates based on genotypic data. *Forest Ecology and Management* **305**:67–76.
658 URL <GotoISI>://WOS:000324222800008.
- 659 Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi, and A. A.
660 Dhondt. 2006. Anticipatory reproduction and population growth in seed predators.
661 *Science* **314**:1928–1930. URL <GotoISI>://WOS:000242996800049.
- 662 Burczyk, J., W. T. Adams, D. S. Birkes, and I. J. Chybicki. 2006. Using ge-
663 netic markers to directly estimate gene flow and reproductive success parameters
664 in plants on the basis of naturally regenerated seedlings. *Genetics* **173**:363–372.
665 URL <GotoISI>://WOS:000237990600031.
- 666 Canham, C. D., W. A. Ruscoe, E. F. Wright, and D. J. Wilson. 2014. Spatial and
667 temporal variation in tree seed production and dispersal in a New Zealand temperate
668 rainforest. *Ecosphere* **5**. URL <GotoISI>://WOS:000335955500003.
- 669 Carbone, C., G. Cowlishaw, N. Isaac, and J. Rowcliffe. 2005. How Far Do Animals Go?
670 Determinants of Day Range in Mammals. *The American Naturalist* **165**:290–297.
671 URL <http://www.journals.uchicago.edu/doi/abs/10.1086/426790>.
- 672 Carlo, T. A., J. J. Tewksbury, and C. Martinez Del Rio. 2009. A new method to track
673 seed dispersal and recruitment using ^{15}N isotope enrichment. *Ecology* **90**:3516–25.
674 URL <https://www.ncbi.nlm.nih.gov/pubmed/20120818>.
- 675 Charco, J., M. Venturas, L. Gil, and N. Nanos. 2017. Effective Seed Dispersal and
676 Fecundity Variation in a Small and Marginal Population of *Pinus pinaster* Ait.
677 Growing in a Harsh Environment: Implications for Conservation of Forest Genetic
678 Resources. *Forests* **8**. URL <GotoISI>://WOS:000411523700011.
- 679 Cibrian-Tovar, D., S. F. E. S. A. N.C.), U. A. Chapingo., and U. S. F. Service. 1986.
680 Cone and seed insects of the Mexican conifers = Insectos de conos y semillas de las
681 coniferas de Mexico. Southeastern Forest Experiment Station, Asheville, N.C.
- 682 Clark, J., D. M. Bell, M. Kwit, A. Powell, and K. Zhu. 2013. Dynamic inverse
683 prediction and sensitivity analysis with high-dimensional responses: application to
684 climate-change vulnerability of biodiversity. *Journal of Biological, Environmental,*
685 and Agricultural Statistics

- 686 Clark, J., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-
687 competition hypothesis. *Ecological Monographs* **74**:415–442.
- 688 Clark, J., M. Lewis, and L. Horvath. 2001. Invasion by extremes: Population spread
689 with variation in dispersal and reproduction. *American Naturalist* **157**:537–554.
- 690 Clark, J., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment
691 limitation in southern Appalachian forests. *Ecological Monographs* **68**:213–235.
- 692 Clark, J., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed
693 dispersal near and far: Patterns across temperate and tropical forests. *Ecology*
694 **80**:1475–1494.
- 695 Clark, J. S., D. M. Bell, C. Chu, B. Courbaud, M. Dietze, M. H. Hersh, J. HilleRisLam-
696 bers, I. Ibanez, S. LaDeau, S. McMahon, J. Metcalf, J. Mohan, E. Moran, L. Pangle,
697 S. Pearson, C. Salk, Z. Shen, D. Valle, and P. Wyckoff. 2010. High-dimensional
698 coexistence based on individual variation: a synthesis of evidence. *Ecological Mono-*
699 *graphs* **80**:569–608.
- 700 Clark, J. S., D. M. Bell, M. H. Hersh, and L. Nichols. 2011. Climate change vulnera-
701 bility of forest biodiversity: climate and competition tracking of demographic rates.
702 *Global Change Biology* **17**:1834–1849.
- 703 Clark, J. S., D. M. Bell, M. C. Kwit, and K. Zhu. 2014. Competition-interaction
704 landscapes for the joint response of forests to climate change. *Glob Chang Biol*
705 **20**:1979–91. URL <https://www.ncbi.nlm.nih.gov/pubmed/24932467>.
- 706 Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species:
707 toward a global functional homogenization? *Frontiers in Ecology and the Environ-
708 ment* **9**:222–228. URL <http://dx.doi.org/10.1890/080216>.
- 709 Clotfelter, E. D., A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and
710 E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird
711 populations. *Oecologia* **154**:493–503. URL <GotoISI>://WOS:000251146900006.
- 712 Cortes, M. C., and M. Uriarte. 2013. Integrating frugivory and animal movement: a
713 review of the evidence and implications for scaling seed dispersal. *Biol Rev Camb
714 Philos Soc* **88**:255–72. URL <https://www.ncbi.nlm.nih.gov/pubmed/23136896>.

- 715 Crone, E. E., and J. M. Rapp. 2014. Resource depletion, pollen coupling, and the
716 ecology of mast seeding. *Year in Ecology and Conservation Biology* **1322**:21–34.
717 URL <GotoISI>://WOS:000340899900002.
- 718 Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal vari-
719 ation in seed production of mast-fruited dipterocarpaceae. *Ecological Monographs*
720 **70**:101–128. URL <GotoISI>://WOS:000085208500005.
- 721 Descamps, S., S. Boutin, D. Bertheaux, A. G. McAdam, and J. M. Gaillard. 2008.
722 Cohort effects in red squirrels: the influence of density, food abundance and tem-
723 perature on future survival and reproductive success. *Journal of Animal Ecology*
724 **77**:305–314. URL <GotoISI>://WOS:000252810400013.
- 725 Detto, M., S. J. Wright, O. Calderon, and H. C. Muller-Landau. 2018. Resource
726 acquisition and reproductive strategies of tropical forest in response to the El Nino-
727 Southern Oscillation. *Nat Commun* **9**:913. URL <https://www.ncbi.nlm.nih.gov/pubmed/29500347>.
- 729 Devictor, V., J. Clavel, R. Julliard, S. Lavergne, D. Mouillot, W. Thuiller, P. Venail,
730 S. Villeger, and N. Mouquet. 2010. Defining and measuring ecological specialization.
731 *Journal of Applied Ecology* **47**:15–25. URL <GotoISI>://WOS:000274191300003.
- 732 Dworkin, J., and I. M. Shah. 2010. Exit from dormancy in microbial organisms. *Nature*
733 *Reviews Microbiology* **8**:890–896. URL <GotoISI>://WOS:000284308200014.
- 734 Espelta, J. M., R. Bonal, and B. Sanchez-Humanes. 2009. Pre-dispersal acorn predation
735 in mixed oak forests: interspecific differences are driven by the interplay among
736 seed phenology, seed size and predator size. *Journal of Ecology* **97**:1416–1423. URL
737 <GotoISI>://WOS:000270787100033.
- 738 Fernandez-Martinez, M., S. Vicca, I. A. Janssens, J. M. Espelta, and J. Penuelas. 2017.
739 The North Atlantic Oscillation synchronises fruit production in western European
740 forests. *Ecography* **40**:864–874. URL <GotoISI>://WOS:000405455800008.
- 741 Fricke, E. C., and S. J. Wright. 2017. Measuring the demographic impact of conspecific
742 negative density dependence. *Oecologia* **184**:259–266. URL <https://www.ncbi.nlm.nih.gov/pubmed/28382478>.

- 744 Garant, D., S. E. Forde, and A. P. Hendry. 2007. The multifarious effects of dispersal
745 and gene flow on contemporary adaptation. *Functional Ecology* **21**:434–443. URL
746 <GotoISI>://WOS:000246708200005.
- 747 Gneiting, T. 2002. Nonseparable, stationary covariance functions for space-time data.
748 *Journal of the American Statistical Association* **97**:590–600. URL <GotoISI>://
749 WOS:000176078300025.
- 750 Godoy, J. A., and P. Jordano. 2001. Seed dispersal by animals: exact identification of
751 source trees with endocarp DNA microsatellites. *Molecular Ecology* **10**:2275–2283.
752 URL <GotoISI>://WOS:000171127700015.
- 753 Greene, D. F., C. D. Canham, K. D. Coates, and P. T. LePage. 2004. An evaluation
754 of alternative dispersal functions for trees (vol 92, pg 758, 2004). *Journal of Ecology*
755 **92**:1124–1124. URL <GotoISI>://WOS:000225631400015.
- 756 Grivet, D., P. E. Smouse, and V. L. Sork. 2005. A novel approach to an old problem:
757 tracking dispersed seeds. *Molecular Ecology* **14**:3585–3595. URL <GotoISI>://WOS:
758 000231800900023.
- 759 Grotan, V., B. E. Saether, S. Engen, J. H. van Balen, A. C. Perdeck, and M. E.
760 Visser. 2009. Spatial and temporal variation in the relative contribution of density
761 dependence, climate variation and migration to fluctuations in the size of great
762 tit populations. *Journal of Animal Ecology* **78**:447–459. URL <GotoISI>://WOS:
763 000263038800017.
- 764 Herrera, C. M., P. Jordano, J. Guitian, and A. Traveset. 1998. Annual variability
765 in seed production by woody plants and the masting concept: Reassessment of
766 principles and relationship to pollination and seed dispersal. *American Naturalist*
767 **152**:576–594. URL <GotoISI>://WOS:000076014900006.
- 768 Janzen, D. 1970. Herbivores and the Number of Tree Species in Tropical Forests.
769 *The American Naturalist* **104**:501–528. URL <http://www.journals.uchicago.edu/doi/abs/10.1086/282687>.
- 771 Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998.
772 Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk.
773 *Science* **279**:1023–1026. URL <GotoISI>://WOS:000072006400045.

- 774 Jones, F. A., J. Chen, G. J. Weng, and S. P. Hubbell. 2005. A genetic evaluation of
775 seed dispersal in the neotropical tree Jacaranda copaia (Bignoniaceae). *American*
776 *Naturalist* **166**:543–555. URL <GotoISI>://WOS:000232832700006.
- 777 Jones, F. A., and H. C. Muller-Landau. 2008. Measuring long-distance seed dis-
778 persal in complex natural environments: an evaluation and integration of classical
779 and genetic methods. *Journal of Ecology* **96**:642–652. URL <GotoISI>://WOS:
780 000256635800009.
- 781 Karasov, W. H. 1986. Energetics, Physiology and Vertebrate Ecology. *Trends in*
782 *Ecology and Evolution* **1**:101–104. URL <GotoISI>://WOS:A1986F726600007.
- 783 Koenig, W. D., and J. M. H. Knops. 2001. Seed-crop size and eruptions of North
784 American boreal seed-eating birds. *Journal of Animal Ecology* **70**:609–620. URL
785 <GotoISI>://WOS:000170005700008.
- 786 LaDouce, S. L., and J. S. Clark. 2001. Rising CO₂ levels and the fecundity of forest
787 trees. *Science* **292**:95–8. URL <https://www.ncbi.nlm.nih.gov/pubmed/11292871>.
- 788 LaDouce, S. L., and J. S. Clark. 2006. Elevated CO₂ and tree fecundity: the role of tree
789 size, interannual variability, and population heterogeneity. *Global Change Biology*
790 **12**:822–833. URL <http://dx.doi.org/10.1111/j.1365-2486.2006.01137.x>.
- 791 LaMontagne, J. M., and S. Boutin. 2009. Quantitative methods for defining mast-
792 seeding years across species and studies. *Journal of Vegetation Science* **20**:745–753.
793 URL <GotoISI>://WOS:000267755000018.
- 794 Lichti, N. I., M. A. Steele, H. Zhang, and R. K. Swihart. 2014. Mast species com-
795 position alters seed fate in North American rodent-dispersed hardwoods. *Ecology*
796 **95**:1746–1758. URL <GotoISI>://WOS:000339470500005.
- 797 Liebhold, A., V. Sork, M. Peltonen, W. Koenig, O. N. Bjornstad, R. Westfall, J. Elk-
798 inton, and J. M. H. Knops. 2004. Within-population spatial synchrony in mast
799 seeding of North American oaks. *Oikos* **104**:156–164. URL <GotoISI>://WOS:
800 000187962200017.
- 801 Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neu-
802 tral and nonneutral community dynamics in fluctuating environments. *Am Nat*
803 **172**:E48–66. URL <https://www.ncbi.nlm.nih.gov/pubmed/18598188>.

- 804 Martinez, I., and F. Gonzalez-Taboada. 2009. Seed dispersal patterns in a temperate
805 forest during a mast event: performance of alternative dispersal kernels. *Oecologia*
806 **159**:389–400. URL <[Goto ISI](#)>://WOS:000263424800014.
- 807 McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2016.
808 Food web structure in temporally-forced ecosystems (vol 30, pg 662, 2015). *Trends*
809 in Ecology and Evolution
- 31**
- :408–408. URL <
- [Goto ISI](#)
- >://WOS:000375737200016.
- 810 McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and
811 bird populations. *Ecology* **81**:228–238. URL <[Goto ISI](#)>://WOS:000084913400019.
- 812 Milleron, M., U. L. de Heredia, Z. Lorenzo, J. Alonso, A. Dounavi, L. Gil, and
813 N. Nanos. 2013. Assessment of spatial discordance of primary and effective seed
814 dispersal of European beech (*Fagus sylvatica* L.) by ecological and genetic methods.
815 *Molecular Ecology* **22**:1531–1545. URL <[Goto ISI](#)>://WOS:000316209500006.
- 816 Minor, D. M., and R. K. Kobe. 2017. Masting synchrony in northern hardwood
817 forests: super-producers govern population fruit production. *Journal of Ecology*
818 **105**:987–998. URL <[Goto ISI](#)>://WOS:000403549500017.
- 819 Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007.
820 Determinants of seed removal distance by scatter-hoarding rodents in deciduous
821 forests. *Ecology* **88**:2529–2540. URL <[Goto ISI](#)>://WOS:000250714200014.
- 822 Moran, E. V., and J. S. Clark. 2011. Estimating seed and pollen movement in a monoecious
823 plant: a hierarchical Bayesian approach integrating genetic and ecological
824 data. *Molecular Ecology* **20**:1248–1262. URL <[Goto ISI](#)>://WOS:000288074600015.
- 825 Moran, E. V., J. Willis, and J. S. Clark. 2012. Genetic Evidence for Hybridization in
826 Red Oaks (*Quercus* Sect. *Lobatae*, Fagaceae). *American Journal of Botany* **99**:92–
827 100. URL <[Goto ISI](#)>://WOS:000299167700020.
- 828 Muller-Landau, H. C., S. J. Wright, O. Calderon, R. Condit, and S. P. Hubbell. 2008.
829 Interspecific variation in primary seed dispersal in a tropical forest. *Journal of*
830 *Ecology* **96**:653–667. URL <[Goto ISI](#)>://WOS:000256635800010.
- 831 Nanos, N., K. Larson, M. Milleron, and S. Sjostedt-de Luna. 2010. Inverse modeling for
832 effective dispersal: Do we need tree size to estimate fecundity? *Ecological Modelling*
833 **221**:2415–2424. URL <[Goto ISI](#)>://WOS:000282403700001.

- 834 Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their
835 determinants and consequences for recruitment. *Trends in Ecology and Evolution*
836 **15**:278–285. URL <GotoISI>://WOS:000087831100008.
- 837 Neal, R., 2011. MCMC Using Hamiltonian Dynamics, Book section 5, pages 1–49 .
838 CRC Press, New York, New York.
- 839 Ogawa, R., A. Mortelliti, J. W. Witham, and M. L. Hunter. 2017. Demographic
840 mechanisms linking tree seeds and rodent population fluctuations: insights from
841 a 33-year study. *Journal of Mammalogy* **98**:419–427. URL <GotoISI>://WOS:
842 000398033100010.
- 843 Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of con-
844 sumers in terrestrial ecosystems. *Trends in Ecology and Evolution* **15**:232–237. URL
845 <http://www.sciencedirect.com/science/article/pii/S0169534700018620>.
- 846 Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled:
847 the behavioural ecology of herbivore movement. *Philos Trans R Soc Lond B Biol
848 Sci* **365**:2267–78. URL <https://www.ncbi.nlm.nih.gov/pubmed/20566503>.
- 849 Pairon, M., M. Jonard, and A. L. Jacquemart. 2006. Modeling seed dispersal of black
850 cherry, an invasive forest tree: how microsatellites may help? *Canadian Journal
851 of Forest Research-Revue Canadienne De Recherche Forestiere* **36**:1385–1394. URL
852 <GotoISI>://WOS:000238286600004.
- 853 Pelisson, P. F., C. Bernstein, D. Francois, F. Menu, and S. Venner. 2013. Dispersal and
854 dormancy strategies among insect species competing for a pulsed resource. *Ecological
855 Entomology* **38**:470–477. URL <GotoISI>://WOS:000323848500005.
- 856 Perea, R., A. S. Miguel, and L. Gil. 2011. Flying vs. climbing: Factors control-
857 ling arboreal seed removal in oak-beech forests. *Forest Ecology and Management*
858 **262**:1251–1257. URL <GotoISI>://WOS:000294143100011.
- 859 Pesendorfer, M. B., W. D. Koenig, I. S. Pearse, J. M. H. Knops, and K. A. Funk. 2016.
860 Individual resource limitation combined with population-wide pollen availability
861 drives masting in the valley oak (*Quercus lobata*). *Journal of Ecology* **104**:637–
862 645. URL <GotoISI>://WOS:000379014900003.

- 863 Ribbens, E., J. A. Silander, and S. W. Pacala. 1994. Seedling Recruitment in Forests
864 - Calibrating Models to Predict Patterns of Tree Seedling Dispersion. *Ecology*
865 **75**:1794–1806. URL <GotoISI>://WOS:A1994PE26700026.
- 866 Robledo-Arnuncio, J. J., and C. Garcia. 2007. Estimation of the seed dispersal kernel
867 from exact identification of source plants. *Molecular Ecology* **16**:5098–5109. URL
868 <GotoISI>://WOS:000251205200019.
- 869 Rodel, H. G., T. G. Valencak, A. Handrek, and R. Monclus. 2016. Paying the en-
870 ergetic costs of reproduction: reliance on postpartum foraging and stored reserves.
871 *Behavioral Ecology* **27**:748–756. URL <GotoISI>://WOS:000381224500015.
- 872 Rosin, C., and J. R. Poulsen. 2016. Hunting-induced defaunation drives increased
873 seed predation and decreased seedling establishment of commercially important tree
874 species in an Afrotropical forest. *Forest Ecology and Management* **382**:206–213.
875 URL <GotoISI>://WOS:000387519700020.
- 876 Sainmont, J., K. H. Andersen, O. Varpe, and A. W. Visser. 2014. Capital versus
877 Income Breeding in a Seasonal Environment. *American Naturalist* **184**:466–476.
878 URL <GotoISI>://WOS:000342281100007.
- 879 Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers,
880 and M. S. Webster. 2010. Population diversity and the portfolio effect in an
881 exploited species. *Nature* **465**:609–12. URL <https://www.ncbi.nlm.nih.gov/pubmed/20520713>.
- 883 Schmidt, K. A., and R. S. Ostfeld. 2003. Songbird populations in fluctuating en-
884 vironments: Predator responses to pulsed resources. *Ecology* **84**:406–415. URL
885 <GotoISI>://WOS:000181482600014.
- 886 Schupp, E. W., and P. Jordano. 2011. The full path of Janzen-Connell effects: genetic
887 tracking of seeds to adult plant recruitment. *Molecular Ecology* **20**:3953–3955. URL
888 <GotoISI>://WOS:000295230000002.
- 889 Schurr, F. M., O. Steinitz, and R. Nathan. 2008. Plant fecundity and seed dispersal in
890 spatially heterogeneous environments: models, mechanisms and estimation. *Journal*
891 *of Ecology* **96**:628–641. URL <GotoISI>://WOS:000256635800008.

- 892 Sheldon, K. S., and N. M. Nadkarni. 2013. Spatial and Temporal Variation of Seed
893 Rain in the Canopy and on the Ground of a Tropical Cloud Forest. *Biotropica*
894 **45**:549–556. URL <Goto^{ISI}>://WOS:000323829800003.
- 895 Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal
896 driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*
897 **17**:866–880. URL <http://dx.doi.org/10.1111/ele.12277>.
- 898 Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships:
899 statistical inevitability or ecological consequence? *Am Nat* **151**:277–82.
900 URL <https://www.ncbi.nlm.nih.gov/pubmed/18811358>.
- 901 Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2005.
902 Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-
903 dependence and the spatial distribution of parent trees. *Journal of Ecology* **93**:291–
904 304. URL <Goto^{ISI}>://WOS:000227721400006.
- 905 Uriarte, M., J. S. Clark, J. K. Zimmerman, L. S. Comita, J. Forero-Montana, and
906 J. Thompson. 2012. Multidimensional trade-offs in species responses to distur-
907 bance: implications for diversity in a subtropical forest. *Ecology* **93**:191–205. URL
908 <Goto^{ISI}>://WOS:000301996100021.
- 909 Wang, Y. Y., J. Zhang, J. M. LaMontagne, F. Lin, B. H. Li, J. Ye, Z. Q. Yuan, X. G.
910 Wang, and Z. Q. Hao. 2017. Variation and synchrony of tree species mast seeding
911 in an old-growth temperate forest. *Journal of Vegetation Science* **28**:413–423. URL
912 <Goto^{ISI}>://WOS:000397559100018.
- 913 Zwolak, R., M. Bogdziewicz, and L. Rychlik. 2016. Beech masting modifies the re-
914 sponse of rodents to forest management. *Forest Ecology and Management* **359**:268–
915 276. URL <Goto^{ISI}>://WOS:000366789500028.