

# Foodwebs based on unreliable foundations: spatiotemporal masting merged with consumer movement, storage, and diet

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*Abstract.* Mast-fruited trees represent 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 is volatile and localized, and that variability ramifies throughout food-webs. Theory is developed to evaluate how the space–time structure of masting interacts with consumers who exploit alternative hosts, forage widely in space, and store reserves in time. We derive the space–time–species covariance in resource supply and combine 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 predicts resource availability within the canopy and on the forest floor with full uncertainty. A resource score can be assigned to each consumer–habitat combination that integrates the benefits of a high mean supply weighed against the variance cost. As the consumer ambit increases, the volatility of an unreliable resource shifts from a variance cost to a 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 the form of 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 depending on the misalignment between consumer ambit and spatiotemporal covariance of hosts. The impact of adding or subtracting a diet item can be gauged with the standard error (SE) rule or 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.

*Key words:* diet breadth; dispersal; fecundity; foraging; portfolio effect; resource score; seed predation; seed-shadow models; spatiotemporal covariance; standard error rule.

## 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, McShea 2000, Ostfeld and Keesing 2000, Clotfelter et al. 2007, McMeans et al. 2016, Rosin and Poulsen 2016). Anticipating how foodwebs respond to a changing climate and habitat requires theory that connects data on the space-time delivery of this foundational resource with the capacities of

consumers to abide variation. Seed-shadow models (SSMs) are widely used to quantify masting, with 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, Detto et al. 2018). Despite the diverse applications, current models omit key features of most data sets, and they do not estimate the spatiotemporal 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 seed predators and frugivores that forage at scales from a few meters to landscapes and ranging in diet from specialist to generalist (Fig. 1 top). To complicate inference, the seeds of many species are identified only to genus level

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FIG. 1. Example seed predators on *Pinus* spp. (above), a 1-m tall pile of cone remnants processed by ground squirrels following the 2017 mast at Niwot Ridge (center), and five seed types from traps (*Pinus* in this study) often identified only to genus (below). From left to right above, the Mountain Chickadee (*Poecile gambeli*) forages primarily in the canopy, the Eastern Turkey (*Meleagris gallopavo silvestris*) and the yellow-pine chipmunk (*Tamias amoenus*) primarily on the ground, and the American red squirrel (*Tamiasciurus hudsonicus*) commonly in both locations. Photos J. S. Clark.

(Fig. 1 bottom). The mast–consumer connection is a missing link in global change science; all serious efforts to anticipate future biodiversity include diverse climate and habitat variables, but omit the most basic

requirement of all food. Similarly, food-web analyses omit the joint relationships between consumers and multiple host plants, instead building from pairwise relationships that are estimated or simulated independently of



one another (May 2001, Boit et al. 2012, Thompson et al. 2012, Jonsson et al. 2018). Important next steps include theory to connect variation in masting with consumers, including full inference and prediction. 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 framework that can synthesize the growing network data on mast production with consumers that see this variation each 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). A reliable mast resource is abundant on average, with limited variation in time and space. A *host* is defined here as a tree or shrub species that contributes fruit or seed (*mast*) to the diet of a consumer. *Consumers* include not only invertebrates and vertebrates, but also seed-attacking fungi and damping-off pathogens. The consumer ambit consists of three dimensions, space (number of host individuals or forest-floor area typically visited by an individual consumer), time (storage by several mechanisms), and diet breadth (host species that differ in quantity and quality of mast they offer a given consumer). Spatial variation exists within habitats and across regions (August 1983, McShea 2000, Stein et al. 2014), and it differs for foragers in the canopy vs. on the forest floor (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). Reliability depends on a *host-time covariance* between mast-producing trees, over years. Conversely, many mammals and birds (including ground-nesters) respond to *space-time covariance* on the forest floor (Moore et al. 2007, Zwolak et al. 2016), depending on host locations with superimposed fruit and seed 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). Many song birds and some rodents forage both in the canopy and on the forest floor Fig. 1. A consumer experiences this host–space–time variation depending on these ambit dimensions of spatial foraging, storage, and diet breadth.

The three-dimensional ambit is not captured by current metrics used to quantify masting. Most common is the coefficient of variation for mast abundance  $y$ ,  $CV = E(y)/\sqrt{\text{Var}(y)}$ , which has an implicit scale determined by data collection. CVs in the literature are sometimes taken over spatial locations (e.g., seed traps), other times over trees, other times over years (Herrera et al. 1998, Buonaccorsi et al. 2003). For example, if a CV is calculated on the basis of seed traps, it has the implicit scale of seed-trap area (e.g., trap area in  $\text{m}^2$ ). If it is

calculated on a tree-to-tree basis, it has an implicit scale of an individual tree. The variance in yield obtained by consumers that forage over  $10 \text{ m}^2$  on the forest floor or 10 host trees in the canopy is not  $10 \times \text{Var}(y)$ , because resources are spatially clumped, and host production is correlated (Fig. 2b). Likewise, a CV evaluated over time (Buonaccorsi et al. 2003) applies to a year, without information on quasi-periodic mast years that can be spaced up to a decade apart (Fig. 2a) and differ between host species in mean and variance, in synchronicity between individuals, and in dispersal characteristics (Clark et al. 2010).

The three dimensions of a consumer’s ambit are not only scale-dependent, but also interdependent with one another (Janzen 1970, Grotan et al. 2009, Pelisson et al. 2013, Lichti et al. 2014, Sainmont et al. 2014, Rodel et al. 2016). Limited movement can be offset by storage in time, such as the extended dormancy of damping-off pathogens (Dworkin and Shah 2010), hoarding by rodents and birds (Abbott and Quink 1970, Moore et al. 2007), elevated body condition that supports future reproduction in large mammals (Fernandez-Llario et al. 1999), and vigorous post-mast cohorts that insure at least some survival through subsequent lean years (Bieber and Ruf 2005, Boutin et al. 2006). Diet generalists abide spatiotemporal variation through diet switching, sometimes termed a *portfolio effect* (Tilman et al. 1998, Loreau and de Mazancourt 2008, Schindler et al. 2010), while specialization exposes consumers to the full heterogeneity offered by a specific host (Devictor et al. 2010, Clavel et al. 2011) (Fig. 2a, b). Most importantly, none of the data-collection scales implicit in the CV (i.e., a tree, a seed trap, a year) are necessarily relevant for consumers that move, store energy, and forage on multiple host species.

The cost borne by consumers that depend on unreliable resources is missing from models that are used to predict both the distribution and abundance of species and the structure and dynamics of food-webs. Species distribution models (SDMs) (Calabrese et al. 2014) rely on relationships between the presence/absence of species and climate or habitat variables, generally lacking information on availability of food. Food-web models (May 2001, Boit et al. 2012, Thompson et al. 2012, Jonsson et al. 2018) are constructed from pairwise interaction coefficients that are taken in isolation of one another. These coefficients come either from literature on “who eats whom” or from allometric assumptions (e.g., “big eats small”). This information is sometimes combined with frequency of co-occurrence in observations (Bohan et al. 2011) or from simulations that draw coefficients at random. The independent, pairwise coefficients omit the indirect relationships that cause consumption rate of any one resource (functional response) to change with changing availability of others. Food-web analyses of linkage structure and food-web simulations (including stability at equilibrium) do not yet address the

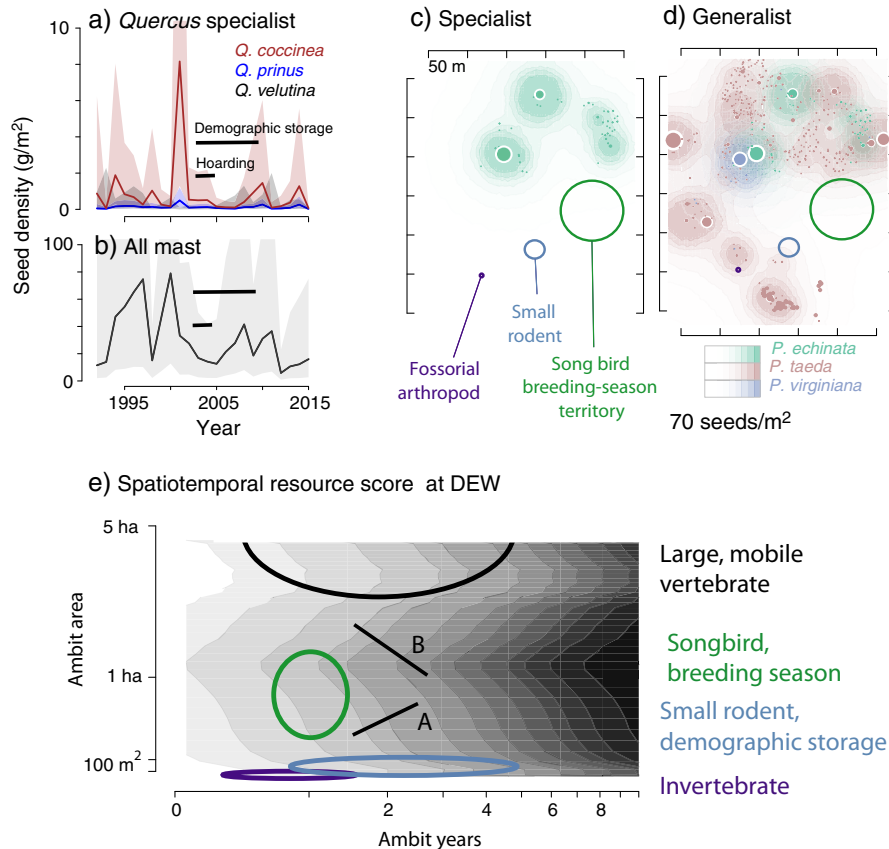


FIG. 2. Space-time scales for seeds and consumers. (a) Mastings by three *Quercus* species in the southern Appalachians is erratic. Shading spans 80% of the predictive variation at the 1-m<sup>2</sup> scale. Consumers experience variation in time depending on storage, such as hoarding from season to season or in large post-mast reproduction. (b) The generalist *Sciurus* (Fig. 1) averages variation over multiple hosts (combined *Quercus*, *Carya*, *Nyssa*, *Cornus*, *Pinus*). Horizontal lines indicate a time interval for averaging over year-to-year variation by different mechanisms. (c,d) Spatial variation is likewise experienced by consumers depending on foraging ambit, here comparing supply for on host (c) and multiple hosts (d), shown for *Pinus* in 2013 at DBW in the SE Piedmont. Superimposed ambits in panels c and d provide scale for <10 m<sup>2</sup> (e.g., flightless insects), 100 m<sup>2</sup> (e.g., larder hoarding rodents), up to 1 ha (such as breeding-season territories for song birds) and large, mobile vertebrates. (e) Resource score as a function of ambit. Straight lines indicate ambit domains where resource scores can increase with increasing (A) or decreasing (B) foraging area.

long-standing concerns that pairwise coefficients extracted from one time and place do not translate to another (Paine 1988, Shaner and Macko 2011, Bond and Lavers 2014). Beyond SDMs and food-web models, 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 spatiotemporal mast supply that might be offered by SSMs. Exploiting that information requires theory that connects the variability in any one host on the variability and the consumer’s access to others. This is the connection between host–space–time scales and the consumer ambit.

A solution to the theoretical challenges is of little use without a model that offers estimates, which first requires a solution to problems with current SSMs (Fig. 2c). SSMs provide insights on dispersal and recruitment limitation (Ribbens et al. 1994, Clark et al. 1998, 1999, Nathan and Muller-Landau 2000, 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 potential (Clark et al. 2001), environmental controls on reproductive effort and sex ratio (Clark et al. 2004, 2011, Uriarte et al. 2005, 2012, Schurr et al. 2008, Martinez and Gonzalez-Taboada 2009, Canham et al. 2014, Detto et al. 2018), and allocation (LaDeau and Clark 2006, Berdanier and Clark 2016). SSMs include a likelihood for seed-count data, such as a Poisson distribution with intensity expressed as expected seeds per trap

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

where  $y_s$  is the number of seeds in trap  $s$ ,  $A$  is sample effort [seed trap area (m<sup>2</sup>)],  $\lambda_s$  is the expected seed density (seeds per trap),  $S_{s,i}$  is the density of seed produced by tree  $i$  that is dispersed to location  $s$  (seeds/m<sup>2</sup>), and  $f_i$  is seed production by tree  $i$  (Table 3). The  $S \times n$  kernel

matrix  $\mathbf{S}$  has rows that can include attributes of seed traps. It has columns that include attributes of trees. For a length- $S$  vector of seed traps, a length- $n$  vector of fecundities, and a  $S \times n$  kernel matrix  $\mathbf{S}$ , there is a length- $S$  vector of seed density

$$\lambda = \mathbf{Sf}. \tag{1}$$

Because both fecundity  $\mathbf{f}$  and dispersal capacity  $\mathbf{S}$  are unknown, the efficacy of these models should be sensitive to the amount of data and its space-time structure.

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  $\mathbf{S}$ , we might take mean seed counts as an estimate of  $\lambda$  (Eq. 1) and solve directly for fecundity,  $\hat{\mathbf{f}} = (\mathbf{SS}')^{-1}\mathbf{S}'\hat{\lambda}$  (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, the vector  $\hat{\mathbf{f}}$  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 the negative-fecundity problem, but there might still be insufficient information in the  $S$  seed observations. 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.,

$$f_i = a \times \text{size}_i^b \tag{2}$$

(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 then 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 (Table 1), but they do not offer the synthesis needed to explain and predict spatiotemporal 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, 2013, Martinez and Gonzalez-Taboada 2009, Uriarte et al. 2012).

Subsequent joint modeling of maturation and fecundity combined with in- and out-of-sample prediction showed that aggregate models like Eq. 2 miss the pervasive heterogeneity. Few individuals are reproductively mature. Fecundity ranges over orders of magnitude, only weakly related to tree size, and often concentrated within few individuals (Clark et al. 2004, 2010, Nanos et al. 2010, Moran and Clark 2011, Milleron et al. 2013, Minor and Kobe 2017). Environmental predictors

TABLE 1. Attributes of some some seed-shadow models (SSMs) with examples.

Individuals	Maturation	Time	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)

*Notes:* IND, independent year effects; FE, RE fixed and random effects; A, B, C, and D are terms in Table 3; HM, hidden Markov submodel; ZIP, zero-inflated Poisson; AR(1), autoregressive model 1.

together with tree-level random effects allow for the large differences between individuals. Year effects account for annual variation that is shared across individuals (Clark et al. 2010, 2013). Autoregressive (AR( $p$ )) models allow for lag effects up to  $p$  years. Thus far, only the AR(1) model has been implemented (Clark et al. 2004), whereas masting commonly involves multi-year lags (Koenig and Knops 2001). Joint models for growth, survival, and fecundity provide estimates of allocation responses to the environment (Clark et al. 2010, 2014, Berdanier and Clark 2016), but they cannot be used where only seed data are available or of interest.

Despite these challenges with SSMs, they can be preferable to direct seed tracking methods, such as stable isotope labels (Carlo et al. 2009, Cortes and Uriarte 2013) or genotyping seeds or seedlings (Godoy and Jordano 2001, Grivet et al. 2005, Jones et al. 2005, Burczyk et al. 2006, Paireon et al. 2006, Robledo-Arnuncio and Garcia 2007, Jones and Muller-Landau 2008, Moran and Clark 2011, Schupp and Jordano 2011, Bontemps et al. 2013). Due to labor and expense, typically few seeds or seedlings can be labeled or genotyped, most often a single species. Labels provide information on dispersal, but not fecundity (Moran and Clark 2011, Milleron et al. 2013). Because seed traps sample passively, SSMs provide an efficient option to gather fecundity and dispersal estimates from all species that can be identified in seed traps simultaneously, naturally integrating space (trap area) and time (trap deployment period). Because seed traps record seed rain following any consumption losses that occur in the canopy (Bell and Clark 2016) they yield conservative estimates of fecundity.

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

The goals of this paper are ambitious, yet focused. We leave synthesis of network data to a subsequent, more sweeping comparison that combines food with traditional climate and habitat variables (C. Nuñez and J. S. Clark, *unpublished manuscript*). Here we do not directly extend results to SDMs or food-web models, but rather provide the framework that could be exploited by a range of applications. Results from this study complement existing foraging theory with formal inference on mast structure that links to consumer ambit. We fill a gap in species-distribution models (SDMs), which has emphasized climate, land cover, and soils, but omitted food. Habitat valuation based on resource reliability can improve the potential to predict food-web structure with covariance in supply across the diet. The next section summarizes theory needed to link mast with consumers and the model framework used to estimate it. We follow with a modeling approach, tested with simulation and applied to a large network, where we estimate parameters from the theoretical analysis. Finally, we show how the components of mast structure combine to “score” the environment for consumers that see this structure each in its own way.

### MODEL DEVELOPMENT

The two elements of this analysis yield estimates of habitat value for consumers that differ in foraging ambit. First we develop the connection between mast observations and the underlying dynamic processes of tree maturation, fecundity, and seed dispersal. Second, we translate these individual tree-scale estimates to the space-time supply to consumers that differ in ambit.

#### *Mast data to dynamic process*

Following from the process and data models in Clark et al. (2013), consider a forest habitat where trees mature and subsequently produce seed (Fig. 3). The event that tree  $i$  can produce seed in year  $t$  is the *maturation state*,  $\rho_{i,t} \in \{0, 1\}$ , a hidden Markov process (Table 2). Coefficients  $\beta^v$  describe covariate effects on maturation probability. Where available, observations of maturation state  $z_{i,t} \in \{0, 1\}$  contribute to estimated  $\rho_{i,t}$ .

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 3, submodel A). Coefficients in  $\beta^v$  can include tree size, environment, and interactions. *Random effects* (REs)  $\beta^w$  accommodate the heterogeneity of responses across individual trees (Table 3, submodel D). Annual variation can be described

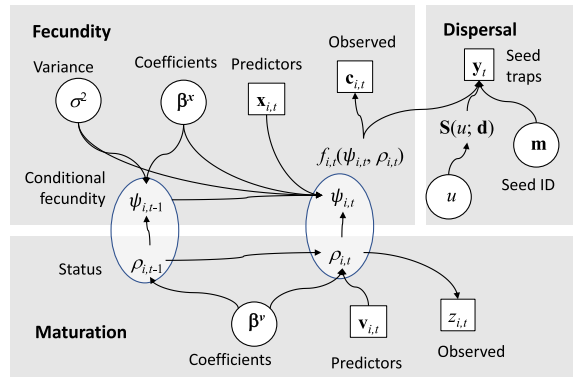


FIG. 3. Probabilistic graphical model, showing estimates (circles) and observed variables (squares), with dynamics ( $t - 1, t$ ). Variables are defined in Table 3.

TABLE 2. Terms.

Term	Definition	Reference
Ambit	Consumer movement/ storage in space ( $m^2$ on ground or host trees in canopy), time (yr), diet breadth (no. host spp.)	<i>Introduction</i>
Demographic storage	Large consumer cohort follows masting event	<i>Habitat reliability</i>
Error matrix, $\mathbf{M}$	Uncertain seed identification	Appendix S1: section S2.4
Maturation state	$\{0, 1\}$ , true $\rho_{i,t}$ , observed $z_{i,t}$	Eqs. S2.5 and S8.15
Fecundity Quality, ground, $g_{s,t}$	Conditional $\psi_{i,t}$ , true $f_{i,t}$ Resource density at location $s$ in yr $t$ ( $g/m^2$ ); space $\times$ yr covariance $\mathbf{G}_{SL}$ , total $G_{SL}$ (g)	Eq. 2 <i>Habitat reliability</i>
Quality, host, $q_{i,t}$	Resource from host tree $i$ in yr $t$ ( $g/tree$ ); host $\times$ yr covariance $\mathbf{Q}_{nL}$ , total $Q_{nL}$ (g)	Eq. 8
Quality, seed, $r_h$	Resource value of seed/ fruit of host species $h$	Eq. 8
Kernel, $\mathbf{S}$	Redistribution from trees to ground ( $m^{-2}$ )	Eq. 1, Eq. S2.1
Resource score	Quality/reliability of mast	<i>Habitat reliability</i>

*Note:* Table 3 contains variable definitions. In addition,  $S$  is the area over which a consumer forages,  $n$  is the number of trees visited by the typical consumer, and  $L$  is the number of lag years that a resource is stored.

by year effects  $\gamma_t$ , quantifying shared variation across individuals (Table 3, submodel B), or as quasi-periodic variation through an *autoregressive*  $AR(p)$  model, with lag terms  $\alpha_l, l = 1, \dots, p$  (Table 3, 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 the product of conditional fecundity and maturation (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 seed, fruit, or cone count  $c_{i,t}^n$ , the fraction of the fruit-bearing canopy observed  $c_{i,t}^f$ , and the standard error assigned to the canopy fraction  $c_{i,t}^s$ . These three numbers are held in the vector  $\mathbf{c}_{i,t} = (c_{i,t}^n, c_{i,t}^f, c_{i,t}^s)$  (Fig. 3), where counts are fruits or seeds,  $c_{i,t}^n$  is taken in units of seeds. 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.

TABLE 3. Terms for conditional fecundity,  $\log \psi_{i,t} \sim N(\mu_{i,t}, \sigma^2)$ , and variable list.

Terms and variables	Definitions
<b>Terms in <math>\mu_{i,t}</math></b>	
$\mathbf{x}'_{i,t} \boldsymbol{\beta}^x$	A, fixed effects
$\gamma_t + \gamma_{g[l],t}$	B, fixed year, random by group
$\sum_{l=1}^p (\alpha_l + \alpha_{g[l],t}) \psi_{i,t-l}$	C, AR( $p$ ) fixed lag, random group $g$
$\mathbf{w}'_{i,t} \boldsymbol{\beta}_i^w$	D, random individual effect
<b>Variables/parameters (dimension)</b>	
$A_{s,t}$	Sample effort ( $m^2$ )
$\mathbf{A}_\alpha (G \times G)$	Random group covariance for AR( $p$ )
$\alpha_l, \alpha_{l,g}$	AR( $p$ ) lag effect $l = 1, \dots, p$ , random group $g$
$\mathbf{B}_w (q^w \times q^w)$	Random individual covariance ( $x^{-2}$ )
$\boldsymbol{\beta}^v (q^v \times 1)$	Maturation coefficients ( $v^{-1}$ )
$\boldsymbol{\beta}^x (q^x \times 1), \boldsymbol{\beta}_i^w (q^w \times 1)$	Fecundity fixed, random coefficients ( $x^{-1}$ )
$\mathbf{c}_{i,t} (2 \times 1)$	Seed count on trees, canopy fraction counted
$f_{i,t}$	Fecundity (seeds)
$g_{sh,t}$	Seed mass on the ground ( $g/m^2$ )
$\lambda_{sm,t}$	Expected seed density (no. seeds/ $m^2$ )
$\psi_{i,t}$	Conditional fecundity (no. seeds)
$\gamma_t$	Year effect $t = 1, \dots, T$
$\mathbf{m}_h (M \times 1), \mathbf{M} (H \times M)$	Seed-type composition for species $h$
$q_{i,t}$	Seed mass on the tree ( $kg/tree$ )
$\rho_{i,t}$	Maturation status
$\mathbf{S} (S \times n)$	Redistribution kernel matrix ( $m^{-2}$ )
$\sigma^2$	Log fecundity residual variance
$\tau^2$	Year variance
$u_g$ or $u_h, \mathbf{u} (G \times 1)$	Random dispersal parameter ( $m^2$ )
$\tilde{u}, \tilde{V}$	Fixed dispersal mean ( $m^2$ ) and variance ( $m^4$ )
$\mathbf{v}_{i,t} (q^v \times 1)$	Maturation design ( $x$ )
$\mathbf{x}_{i,t} (q^x \times 1), \mathbf{w}_{i,t} (q^w \times 1)$	Fecundity fixed, random design ( $x$ )
$y_{sm,t}$	Seed count
$z_{i,t}$	Observed maturation status

Notes: Subscripts reference trap  $s$ , seed type  $m$ , individual  $i$ , species  $h$ , year  $t$ .  $g[l]$  refers to membership of individual  $i$  in group  $g$ . There are  $n$  trees,  $S$  traps,  $H$  species,  $M$  seed types, and  $G$  random groups used to model year effects, lag effects, or dispersal. Variables lacking units at right are dimensionless.

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 counts can be missing or censored, the latter when traps are inoperative during part of a collection interval or when seed counts are recorded in bins (e.g., Bourg et al. 2013).

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), and Poisson variation in counts  $\mathbf{Y}$ .

The full posterior distribution includes parameters and latent states (maturation and conditional fecundity). It can also include random effects, year effects, and lag effects (Table 3). In its most basic form (main effects only) the model has parameters

$$\boldsymbol{\theta} = \{\boldsymbol{\beta}^x, \boldsymbol{\beta}^v, \sigma^2, \mathbf{u}, \mathbf{M}\} \quad (3)$$

(Table 3). The posterior distribution is

$$[\boldsymbol{\theta} | \mathbf{X}, \mathbf{V}, \mathbf{Y}, \mathbf{c}] \propto \prod_{s,m,j} \prod_{t=1}^{T_{sj}} \text{Poi}(y_{smj,t} | A_{sj,t} \lambda_{smj,t}) \quad (4)$$

$$\times \prod_{i,j} \prod_{t \in T_{ij}} \text{Bernoulli}(\rho_{ij,t} | \rho_{ij,t-1} + (1 - \rho_{ij,t-1}) \Phi(\mathbf{v}'_{ij,t} \boldsymbol{\beta}^v)) \quad (5)$$

$$\times \prod_{i,j} \prod_{t=1}^{T_j} \text{binom}(c_{ij,t}^n | \psi_{ij,t}, c_{ij,t}^f) \quad (6)$$

$$I(\psi_{ij,t} \geq c_{ij,t}^n) \text{beta}(c_{ij,t}^f | a_{ij,t}, b_{ij,t}) \quad (7)$$

$$\times \prod_{i,j} \prod_{t=1}^{T_j} N(\log \psi_{ij,t} | \mathbf{x}'_{ij,t} \boldsymbol{\beta}^x + \dots, \sigma^2)$$

$$I(\psi_{ij,t} \leq 1)^{1-\rho_{ij,t}} I(\psi_{ij,t} > 1)^{\rho_{ij,t}}$$

$$\times [\boldsymbol{\theta}]$$

where  $\lambda_{smj,t}$  is an element of  $S_{j,t} \times M$  matrix  $\boldsymbol{\lambda}_{j,t} = \mathbf{S}_{j,t}(\mathbf{u}) \mathbf{F}_{j,t}(\psi_{ij,t}, \rho_{ij,t}, \mathbf{M})$ . The  $n_{j,t} \times M$  matrix  $\mathbf{F}_{j,t}$  has elements given by Eq. S2.6.  $\mathbf{S}(\mathbf{u})$  is the  $S_{j,t} \times n_{j,t}$  kernel matrix, and  $A_{sj,t}$  is the trap area. Years lacking observed status  $z_{ij,t}$  make up the set  $T_{ij}$  in Eq. 5. The binomial parameter  $\psi_{ij,t}$  in Eq. 6 is rounded to the nearest integer value. The uncertainty in observed crop fraction  $c_{ij,t}^f$  in Eq. 6 has beta parameters determined from the standard deviation assigned in the field  $c_{ij,t}^s$ . Terms in + in Eq. 7 can include random effects, year effects, or AR( $p$ ) terms. The prior distribution is discussed in Appendix S1: section S2.5. Sampling distributions are given in Appendix S1: section S8.

The posterior distribution makes clear how the model accommodates spatiotemporal dependence in data. Because maturation Eq. 5 and fecundity Eq. 7 are latent at the process stage, there is a posterior covariance for the full set of maturation and fecundity estimates.

#### *Dynamic process to habitat value*

The estimates of fecundity of all trees in all years describe a dynamic process in the canopy. Combined with spatial distributions of trees and dispersal, fecundity is used to predict the distribution of seed across for the forest floor. In this section, we translate the dynamic maturation–fecundity process to the spatiotemporal covariance experienced by consumers of differing ambit in the canopy and on the ground and then to a score that accounts for consumer yield that weighs the cost of variation.

*Habitat reliability.*—The cost of search time in a variable environment is central to foraging theory and a goal of inference in tracking studies (Owen-Smith et al. 2010, Avgar et al. 2013, Benhamou 2014). Taken in isolation, scale dependence in space determines whether or not to forage widely. In an extreme case of an island where the cost of movement may outweigh the low probability of encountering food, adaptations can include loss of flight (including seabirds, e.g., the Galapagos Cormorant (*Phalacrocorax harrisi*)). For masting, 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  $S$ .

Time dependence determines whether to store (e.g., periodic variation) or not (constant availability). A high mast year can be stored at the individual scale through dormancy (fungal pathogens), hoarding (Abbott and Quink 1970, Moore et al. 2007), and 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, Schmidt and Ostfeld 2003, Boutin et al. 2006, Descamps et al. 2008, Bergeron et al. 2011, 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. The time scale can be represented by lag year  $l$ .

Space–time interaction determines the benefit-cost of movement before next year. Invertebrate seed predators may have sedentary larvae that feed on one host, but widely dispersing adults (e.g., nut weevils of the genus *Curculio*), an important strategy where an individual host is not reliable from year to year. The advantages of expanding the diet or, conversely, the cost of losing a host species depend on a host’s covariance with other diet items at the space–time scale describing the consumer ambit.

We derive a simple *resource score* to summarize combined effects of mean resource abundance and variance. For a patchy resource (Fig. 2c), consumers with a

narrow foraging ambit are restricted to dense-resource habitats; concentrated resources make limited ambit possible within, but not between, these patchy habitats. Conversely, by averaging, the wide-ambit consumer can satisfy its requirements where spatial variation is high.

When variation in space is combined with variation in time (Fig. 2a) the resource score forms a surface (Fig. 2e). A consumer with restricted spatial ambit increases its score by foraging more broadly in space and storage in time along direction A in Fig. 2e). The surface is increasing in this direction because the increased total yield outweighs the variance cost *at this scale*. In the same habitat, a consumer of broader spatial ambit increases its score by *decreasing* its spatial ambit along direction B, due to the cost posed by scale-dependent variance in this habitat. When habitats are both patchy and ephemeral, shifting location from year to year, consumers with limited movement can compensate with a dispersal stage between years (e.g., a larval seed predator and flighted adult). Diet generalists depend on masting behavior of host individuals of multiple species. Diet breadth increases the height of the surface provided that alternative hosts are not highly synchronized in space and time, shown by comparing (Fig. 2a with Fig. 2b and Fig. 2c with Fig. 2d). This effect draws on the spatiotemporal covariance in resource supply, highlighted by interaction surface in Fig. 2e).

To translate the spatial and temporal components of variance in Fig. 2a–d to a scale- and diet-dependent resource score like Fig. 2d, we begin with *host quality*, the product of per-seed or per-fruit reward and seed/fruit abundance

$$q_{i,t} = r_{h[i]} f_{i,t} \quad (8)$$

where  $r_{h[i]}$  is the seed quality of host species  $h$  corresponding to tree  $i$ . Here we use seed mass as an index for quality (Table 2), but quality can be defined on alternative scales, including nutritional value. Dispersal translates host quality  $q_{i,t}$  (kg/host tree) to *resource quality* on the ground  $g_{s,t}$  (g/m<sup>2</sup> summed over all hosts in the diet).

The mast benefit is the accumulated resource over the consumer ambit. Let  $Q_{nL} = \sum_{i,l} q_{i,l}$  be the yield to a canopy consumer that searches  $n$  host trees over  $L$  years, with expectation

$$E(Q_{nL}) = nL \times E_{ii}(q) \quad (9)$$

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

$$E(G_{SL}) = SL \times E_{st}(g). \quad (10)$$

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



To weigh the benefits of a large mean,  $E_{ij}(q)$  or  $E_{sl}(g)$ , against the variance cost of an unreliable resource,  $\text{Var}(Q_{nL})$  or  $\text{Var}(G_{SL})$ , we build from the familiar coefficient of variation,  $\text{CV} = \sqrt{\text{Var}(Q_{nL})}/E_{nL}(Q)$  (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. 8). The traditional CV is inadequate, because the same CV could apply to masting intervals of 2–10 yr, having very different impacts on consumers depending on their space–time–diet ambit (Fig. 2e). 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,  $R_{nL} = -\log \text{CV}_{nL}$  (tree–time) for canopy foragers, and  $R_{SL} = -\log \text{CV}_{SL}$  (space–time) for ground foragers.

As a reference for the role of scale, the scale-independent resource score for a spatiotemporal Poisson process includes expected yields in Eqs. 9 and 10 and (scale-independent) expected variances

$$E(\text{Var}(Q_{nL})) = nT \times \text{Var}_{ij}(q) \quad (11)$$

$$E(\text{Var}(G_{SL})) = SL \times \text{Var}_{sl}(g). \quad (12)$$

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

$$E(R_{nT}) = -\log \text{CV}_{nL} = \log E_{ij}(q) + \frac{\log(nL) - \log \text{Var}_{ij}(q)}{2} \quad (13)$$

By substituting  $n$  for the subscript  $nL$ , the resource score applies to  $n$  host trees in a random year (lag  $L = 0$ ). A subscript  $L$  applies to a random host over  $L$  years ( $n = 1$ ). Likewise, for the forest floor there is a resource score for  $L$  years in one site, for  $S$  sites in a random year, and for  $SL$  site–years. The baseline Eq. 13 provides an index to compare habitats that differ in scale dependence.

*Tree–time and space–time covariance.*—Masting is experienced differently by consumers in the canopy and on the ground, described by covariance structures that make the resource score in Eq. 13 scale-dependent. For the canopy, there is no evidence for a distance-related covariance between trees within stands (Clark et al. 2010), consistent with widely observed regional coherence (Liebhold et al. 2004, Fernandez-Martinez et al. 2017). For this reason, within-stand canopy covariance is between trees, rather than over distance. On the forest floor, spatial covariance results from a combination of host-tree dispersion superimposed with seed dispersal from those trees. We do not introduce a geospatial model (e.g., Gneiting 2002, Banerjee et al. 2015), because spatial covariance is already induced by the dispersal kernel

S. For covariance over time, we use the covariance in the estimated fecundity from the SSM.

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

$$E(\mathbf{f}_{(nT)}) = \Psi_{(nT)} \quad (14)$$

$$\text{Cov}(\mathbf{F}_{(n \times T)}) = \mathbf{C}_{(nT \times nT)}$$

where  $\mathbf{f}_{(nT)} = \text{vec}(\mathbf{F}_{(n \times T)})$  and  $\Psi_{(nT)}$  are length- $nT$  vectors (to simplify notation, individuals are mature), and  $\mathbf{C}_{(nT \times nT)}$  is the  $nT \times nT$  covariance matrix that incorporates both the relationships between individual trees and their variation over time. The  $\text{vec}(\cdot)$  operator stacks the columns of a matrix to obtain a vector. An element  $C_{i,i't'}$  holds the covariance between host individual  $i$  in year  $t$  and host individual  $i'$  in year  $t'$ . We cannot estimate the tree-time matrix  $\mathbf{C}_{(nT \times nT)}$ , because each  $(i, i', t, t')$  combination happens once. The *tree-lag* covariance holds elements  $C_{i,i',l}$ , where time  $t$  and  $t'$  are replaced by time lag  $l$ . This matrix can be displayed as a lower triangular matrix for each lag (Fig. 4). At lag  $l = 0$  (Fig. 4, left) the positive variances (warm colors) occupy the diagonal. All other elements are covariances and can be positive or negative. A positive covariance between two individuals ( $i \neq i'$ ) at lag ( $l > 0$ ) (Fig. 4, right) indicates individuals that are offset from one another in time. This is the space–time interaction important for consumers that occupy a single host in a given year that will not offer that resource the next. Hereafter, matrix  $\mathbf{C}_{nL \times nL}$  or simply  $\mathbf{C}_{nL}$  refers to the tree-lag covariance that summarizes the entire covariance structure over host trees and lagged years.

We note two special cases, (1) a  $n \times n$  (tree-to-tree) covariance  $\mathbf{C}_n$  holding the covariances experienced by a consumer that moves between  $n$  host trees in a random year, and (2) an  $L \times L$  (year-to-year) covariance  $\mathbf{C}_L$ , holding the covariances experienced by a consumer that tracks a random host over  $L$  years.

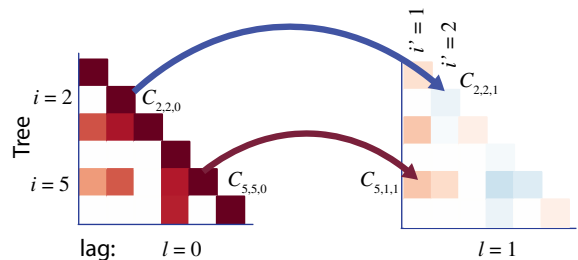


FIG. 4. Lower triangle of the tree-lag covariance matrix has elements  $C_{i,i',l}$ , shown for six trees at lags 0 and 1. At lag  $l = 0$  diagonal elements are all positive (they are variances), and most trees show positive covariances (warm colors), because there is tendency for synchrony. At lag  $l = 1$ , tree  $i = 2$  shows negative covariance with itself  $C_{2,2,1}$  (blue), and tree  $i = 5$  shows positive covariance with tree  $i' = 1$ . The same covariance matrix can be constructed for locations on the forest floor.

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

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

The conditional covariance in intensity is

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

The full covariance additionally includes the Poisson variance

$$\begin{aligned} \mathbf{G}_S = \text{Cov}(\mathbf{y}) &= \text{Cov}(E(\mathbf{y}|\mathbf{f})) + E(\text{Var}(\mathbf{y}|\mathbf{f})) \\ &= \mathbf{S}\mathbf{C}_n\mathbf{S}' + \text{diag}(\mathbf{S}\mathbf{f}). \end{aligned} \quad (15)$$

Combining these terms confirms that they describe covariance in simulated data (Fig. 5, right). The first term in Eq. 15 links the covariances 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 habitat, depending on the distributions of hosts, their fecundities, and their dispersal distances. The second term in Eq. 15 contributes only (positive) variance (Fig. 5, center), acting like the nugget of geospatial models (Banerjee et al. 2015) (However, a nugget is not needed here to make  $\mathbf{G}_n$  positive definite, as  $\mathbf{S}\mathbf{C}_n\mathbf{S}'$  is positive definite). The next section extends these results to multiple host species.

*Variance for a generalist consumer.*—Because consumers exploit multiple resources, the covariance structure must describe their combined supply, accounting for differences in nutritional quality. In this section, we evaluate the covariance in resource quantity to a canopy forager of  $n$  host trees and  $L$  lag years  $\mathbf{Q}_{nL}$  and to a ground forager over space  $S$  and  $L$  years  $\mathbf{G}_{SL}$ .

In the canopy, the aggregate resource available to the consumer of  $n$  hosts over  $L$  years is

$$Q_{nL} = \mathbf{r}'_n\mathbf{F}\mathbf{1}_L \quad (16)$$

where  $\mathbf{r}_n = r_{n[1]}, \dots, r_{n[n]}$  is the vector of seed quality associated with each tree (Eq. 8), and  $\mathbf{1}_L$  is a vector of ones. Note that  $\mathbf{r}_n$  combines individuals of all host species in the diet. There are also aggregate variances for a random year on  $n$  host trees, and for a random host tree over  $L$  years. For example, the aggregate variance over all host trees in the diet is

$$\text{Var}(Q_n) = \mathbf{r}'_n\mathbf{C}_n\mathbf{r}_n = \mathbf{1}'_n\mathbf{Q}_n\mathbf{1}_n \quad (17)$$

where  $\mathbf{Q}_n$  is the covariance for resource yield between trees (Eq. 8).

To combine the contributions of mean and variance, the resource score for the consumer foraging over  $n$  trees replaces terms in Eq. 13 with those that come from the scale-dependent space-time covariance. Foraging over  $n$  hosts and  $L$  years gives the score

$$R_{nT} = \log Q_{nL} - \frac{\log \text{Var}(Q_{nL})}{2} \quad (18)$$

where the variance in the second term comes from Eq. 17. This variation can be compared to that expected for scale-independent variation in Eq. 13.

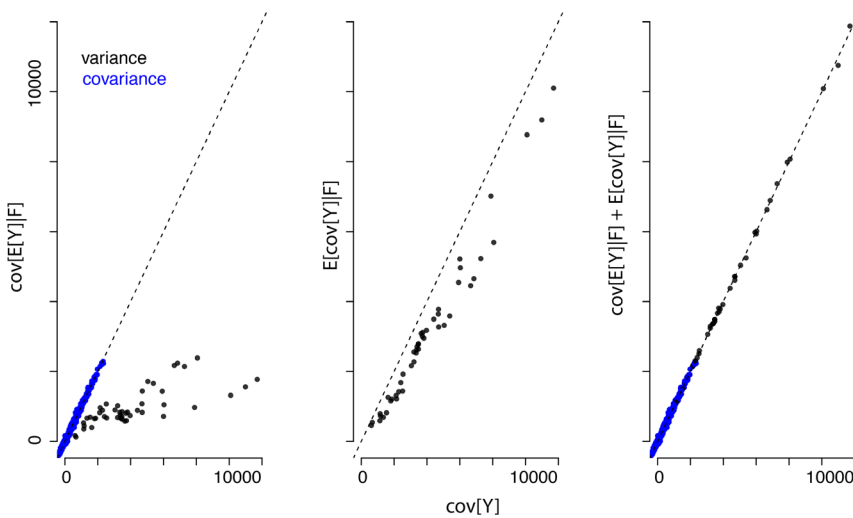


FIG. 5. Contributions to space covariance  $\mathbf{G}_S$  from terms in Eq. 15 plotted against the covariance in simulated data. Covariances (blue) are mostly positive, induced by dispersal. Variances (black) are necessarily positive and include the effects of sampling. The simulation is described in Appendix S1: section S3.

We can combine Eq. 13 with Eq. 18 to quantify the potential advantage to a consumer if it could expand the diet to include a new host  $\tilde{h}$  that brings  $\tilde{n}$  new host individuals into the diet and depends on densities of the current and new host species, their space–time. The aggregate resource from Eq. 16 increases by a term

$$Q_{(n+\tilde{n})L} = Q_{nL} + \mathbf{r}'_{\tilde{n}} \tilde{\mathbf{F}}_{\tilde{n}} \mathbf{1}_L \quad (19)$$

where  $r_{\tilde{h}}$  is the quality of the new resource, which can be concatenated into a length  $\tilde{n}$  vector  $\mathbf{r}_{\tilde{n}}$ , and  $\tilde{\mathbf{F}}_{\tilde{n}}$  is the  $\tilde{n} \times L$  matrix of seed produced by new host individuals. The expected addition to the diet from the second term in Eq. 19 is

$$E(\mathbf{r}'_{\tilde{n}} \tilde{\mathbf{F}}_{\tilde{n}} \mathbf{1}_L) = r_{\tilde{h}} \tilde{n} L \times E_{ii}(\tilde{f}) = \tilde{n} L \times E_{ii}(\tilde{q}) \quad (20)$$

where  $E_{ii}(\tilde{f})$  is the expected seed production by the new host. From Eq. 17, the aggregate variance adds two terms

$$\text{Var}(Q_{(n+\tilde{n})L}) = \text{Var}(Q_{nL}) + \mathbf{r}'_{\tilde{n}} \mathbf{C}_{\tilde{n}L} \mathbf{r}_{\tilde{n}L} + 2\mathbf{r}'_{\tilde{n}} \mathbf{C}_{\tilde{n}L, nL} \mathbf{r}_{nL} \quad (21)$$

where  $\mathbf{C}_{\tilde{n}L}$  is the  $\tilde{n}L \times \tilde{n}L$  covariance for new host trees, and  $\mathbf{C}_{\tilde{n}L, nL}$  is the  $\tilde{n}L \times nL$  covariance between new and current host trees. Of course, strong negative covariance with hosts now in the diet (third term in Eq. 21) decreases aggregate variance, with obvious benefits. Not so obvious is the fact that, even if independent of the current diet, the resource score is expected to increase whenever the contribution to the aggregate mean compensates for potential increases in variance. For independent variation, Eq. 21 simplifies to

$$\begin{aligned} \text{Var}(Q_{(n+\tilde{n})L}) &= \text{Var}(Q_{nL}) + r_{\tilde{h}}^2 L \times \text{Var}(\tilde{f}) \\ &= \text{Var}(Q_{nL}) + \tilde{n} L \times \text{Var}(\tilde{q}) \end{aligned}$$

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

$$Q_{nL} + \tilde{n} L \cdot E_{ii}(\tilde{q}) > \sqrt{\text{Var}(Q_{nL}) + \tilde{n} L \cdot \text{Var}(\tilde{q})}.$$

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

$$E(\tilde{q}) > \sqrt{\frac{\text{Var}(\tilde{q})}{\tilde{n} L}}. \quad (22)$$

If the consumer were a statistician, she would recognize the right-hand side of Eq. 22 to be her standard error (*SE*) for expected yield on the left-hand side. This is the consumer's uncertainty in the yield from the new host. It is a consumer- and habitat-specific *SE*, because it is referenced to the consumer's ambit, including current diet breadth ( $nL$ ) and number of host individuals it could exploit for the new resource ( $\tilde{n}L$ ). Hereafter, we

refer to the *SE rule* as a rule-of-thumb for the advantage of diet breadth.

We use resource scores to compare the value of habitats that vary with consumer ambit, including total yield,  $G_{SL}$  or  $Q_{nL}$  (Eq. 16), and score (Eq. 18). The contributions of covariance structure across the diet are compared using this difference:

$$\Delta_{nL} = R_{nL} - E(R_{nL}) \quad (23)$$

from Eqs. 13 and 18 and  $\Delta_{SL}$ .

The same analysis leads to a resource score for ground foragers,  $R_{SL}$ . Despite positive and negative covariances between canopy trees, the forest floor covariances in  $\mathbf{G}_S$  tend to be positive at the characteristic scales of dispersal (Fig. 5). This is not necessarily so at broader spatial scales, where the dispersion of host trees of different species can dominate spatial covariance.

The foregoing analysis also applies to loss of a diet item. Consequences are most severe for hosts with narrow diet breadth (host-specific consumers being the extreme case) and where the missing host is uncorrelated (or negatively correlated) with residual hosts. In other words, the host that is lost had previously bridged the consumer through times and locations of sparsity in other hosts. Space-lag covariance structure used for  $\mathbf{Q}$  and  $\mathbf{G}$  in this section is expanded in Appendix S1: section S4.1. Data that are introduced in the next section are fitted with the model and used to generate predictive distributions of covariance and resource scores.

## MAST DATA

To illustrate methods, we use the genus *Pinus* and its interacting species as an example. This wide-ranging and multi-species genus challenges the model with unbalanced data, observation error in seed identification, missing data, censored seed-trap values, and combinations of observed and unobserved fecundity estimates. Data come from 12 inventory plots initiated between the years of 1991 and 2011. Methods and site variables are detailed in a several previous publications (Clark et al. 2004, 2010, 2014, Bourg et al. 2013). Habitats include southeastern Piedmont mixed pine-hardwoods (DUKE EE, EW, BW, HW), Appalachian mountains (CWT 118, MARS F, P, SCBI), and New England mixed hardwoods (HARV BW, S). Numbers of trees, tree-years, seed and cone types, seed traps and trap-years are listed in Table 4. Data are unbalanced over time, combining plots observed from 4 to 27 yr. Within each plot, trees can differ in recruitment year, year of death, and year of maturation, the latter estimated as part of model fitting. Numbers of trees and seed traps differ between stands. Multiple species on the same plots meant that species identity of most seeds was unknown (Fig. 1). Throughout this multi-decade study, methods emphasized minimizing false-positive seed identifications, thus restricting





and distribution of mature trees, dispersal characteristics of each species, and spatiotemporal sampling design, including density and dispersion of traps and the classification of seeds into types. We emphasize that the simulator can never provide a direct interpretation of model performance with data, because real data are not generated by the model. The model necessarily simplifies complex processes that control tree maturation, seed production, and dispersal. It must be simple in order to be useful. As with any model, useful estimates are only expected where there is “signal” in data. We provide a concrete example using structure similar to the data set that follows to demonstrate that the model can recover parameters and predict data. We discuss aspects of data structure that can lead to poor performance. The value of the simulator is this first opportunity it affords to examine general design issues in seed-trap data.

#### *Parameter and latent state estimates through posterior simulation*

Posterior simulation is used to construct the distribution of parameters and latent states; all estimates are extracted from this posterior distribution. The structure and methodology in Model development was implemented both as a generative simulation and as an (inverse) fitting algorithm in the R package Mast Inference and Forecasting (MASTIF; available online).<sup>4</sup> Gibbs sampling, a Markov chain Monte Carlo (MCMC) technique, includes Metropolis and Hamiltonian Markov chain (HMC) steps (Appendix S1: section S8).

Due to a high-dimensional state space (maturation and fecundity of all trees over all years), posterior simulation suffers well-known scaling limitations of MCMC, as the parameter set is dwarfed by the volume of parameter space (Neal 2011); random-walk algorithms cannot explore the parameter space in finite time. HMC exploits the geometry of the typical parameter set to efficiently target proposals (Betancourt and Girolami 2015). Because it relies on vector fields (a differentiable surface), HMC does not apply to discrete maturation state. However, it does apply to conditional fecundity, and is used for that purpose here (section S8.3). Although fecundity can be sampled conditional on maturation, maturation cannot be sampled independent of conditional fecundity. With the exception of maturation, conditional fecundity, and the dispersal parameters (a low-dimensional vector), all other parameters are sampled directly (Appendix S1: section S8).

To evaluate the implications of lag structure for masting cycles, we translated  $AR(p)$  terms into eigenvalues (section S5). Partial autocorrelation functions (PACF) quantify the contribution of each lag  $p$ , while controlling for shorter lags  $0, \dots, p - 1$ . Complex eigenvalues for the  $AR(p)$  model (Appendix S1: section S5) would indicate quasi-periodic variation. A stationary  $AR(p)$

process has all eigenvalues of less than unit modulus (real plus complex parts, Appendix S1: section S5). The tree-lag (canopy) and space-lag (forest-floor) covariances (Appendix S1: section S4.1) were generated with resource scores for each plot. To summarize the diet-wide variation experienced by consumers in the canopy and on the ground, we evaluated entropy over the consumer ambit of trees, sites, and years (Appendix S1: section S4.2). Variable selection can be based on DIC values for fitted models, although the goal of this analysis is to relate resource availability to the simplest model. We follow with application to field data, demonstrating inference and spatiotemporal structure.

#### *Application to field data*

For this focus on methodology and transparency, we omit environmental variables known to influence maturation and fecundity (Clark et al. 2004, 2010, 2014). Model fitting is demonstrated with  $AR(4)$  and year effects for conditional fecundity (Table 3). Prior distributions are provided in Appendix S1: section S2.5.

## RESULTS

### *Simulation studies*

Because the basic approach has been detailed with diagnostics in both the ecological and statistical literature (Clark et al. 2004, 2010, 2013, Clark 2010) we focus here on the new innovations associated with seed identification errors.  $AR(p)$  effects are presented in the application to *Pinus*, because they are not available from the simulator.

An important addition to previous studies is the demonstration that the model admits the widespread practice of identifying many seeds only to genus level. Simulation studies show that the model can recover parameters and latent states even when most of the seeds (in this example, 2/3) are identified only to genus level. A stochastic simulation example is summarized for  $M = 6$  seed types and  $H = 5$  species on a mean of  $J = 8$  plots,  $T = 5$  years,  $n = 25$  trees, and  $S = 50$  traps. The composition vectors for seed identification  $\mathbf{m}_h$  are recovered, with one-third of seed from each species being assigned to the species and the remainder to the undifferentiated class “pinuUNKN” (Appendix S1: Fig. S7.3). Estimates with wide posterior distributions in Appendix S1: Fig. S7.3 come from plots where specific tree–seed-type combinations  $m_{h,m}$  are missing or rare. Because there is no effect on the likelihood for missing species–seed-type combinations, these unidentified values do not affect other aspect of the posterior distribution.

Parameter recovery for intercepts is approximate (Appendix S1: Fig. S7.2) for at least three reasons. First, tree diameters are measured only above a minimum diameter. There are no observations near the intercept at zero, which is extrapolated beyond the data. Second, the

<sup>4</sup><http://rpubs.com/jimclark/281413>

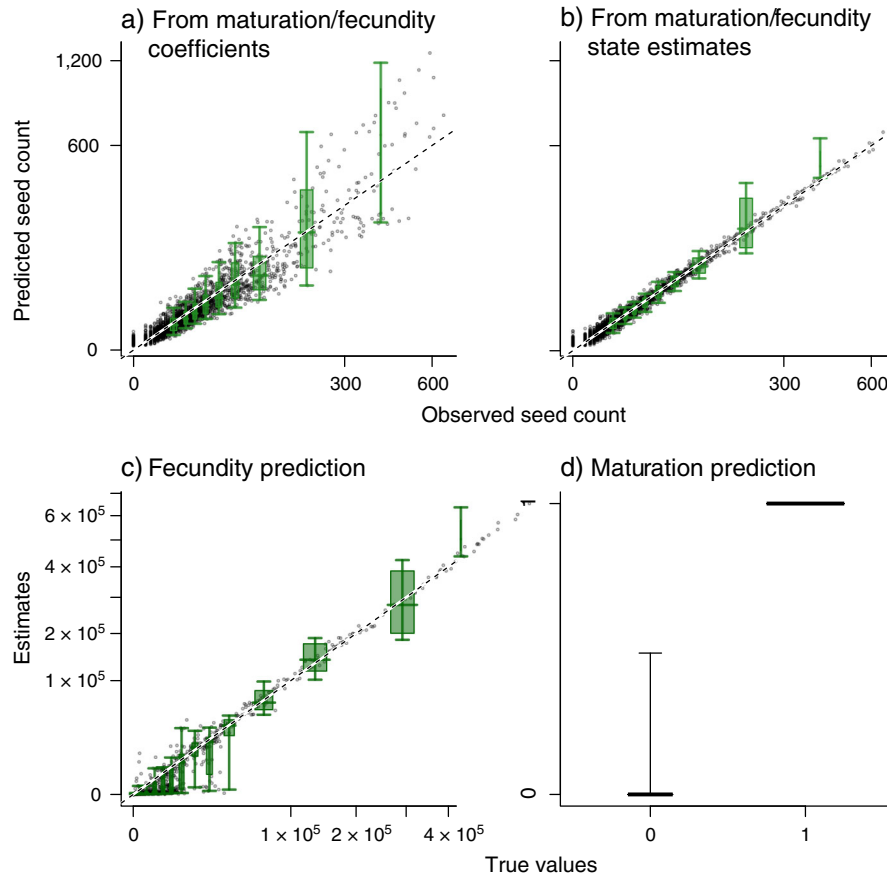


FIG. 6. Seed data prediction from the estimated coefficients (a) in the model and (b) from the estimated maturation/fecundity states compared with observations (Observed) for the simulated example. (c) The comparison of fecundity estimates with values used to simulate data (True values) (d) Predictions of maturation status vs. true values. Also shown is the dashed line of agreement. Box plot components are midline, median; box edges, 68%; whiskers, 95%.

product form for fecundity (maturation probability  $\times$  conditional fecundity) is not well identified near zero diameter where there is no reproduction; the model can only approximately identify the difference between an immature state vs. low conditional fecundity where both are zero or nearly so. Finally, fecundity coefficients are on the log scale, meaning that a unit difference near zero conditional fecundity (at zero diameter) is well below the noise level in terms of numbers of seeds. A unit difference from  $-6$  to  $-5$  in Appendix S1: Fig. S7.2b is the difference between the fractions  $0.0025$  vs.  $0.0067$  of a single seed, which, of course, is never observed. Despite these challenges typical of real data, coefficients are accurate for slope parameters, in this case the diameter effect. These coefficients quantify change in fecundity for a unit change in the predictor variable.

Prediction from the fitted model is shown for observed seed counts (Fig. 6a, b) and for unobserved fecundity (Fig. 6c) and maturation (Fig. 6d). Seed counts can be predicted from two stages in the model (Appendix S1: section S2). Accurate prediction from the maturation and fecundity estimates (Fig. 6b) requires that the model

can identify these latent states, but it does not require that covariates in the model can predict them. From Appendix S1: section S2, data are predicted from the latent states (through dispersal and seed identification error) as  $\{\psi, \rho, \mathbf{u}, \mathbf{M}\} \rightarrow \mathbf{Y}^*$ . In the case where there are more trees than seed traps, and those trees are close to seed traps, this prediction is vulnerable to overfitting.

Accurate prediction from the maturation and fecundity parameters (Fig. 6a) could only be subject to overfitting if there were a large number of predictors in the model. Again from Appendix S1: section S2, data are predicted from environment (fecundity and maturation coefficients) to the latent states (through dispersal and seed identification error) as  $[\{\beta^x, \beta^y, \sigma^2\} \rightarrow \{\psi, \rho\}, \{\mathbf{u}, \mathbf{M}\}] \rightarrow \mathbf{Y}^*$ . In other words, rather than predicting data from the estimated latent states, data are predicted from the environmental predictors in the model. In this case over fitting would be highly unusual, because estimating large numbers of coefficients, say dozens, would rarely be possible. Due to the indirect relationship between predictors and seed counts, a large number of predictors could only be identified for large data sets.



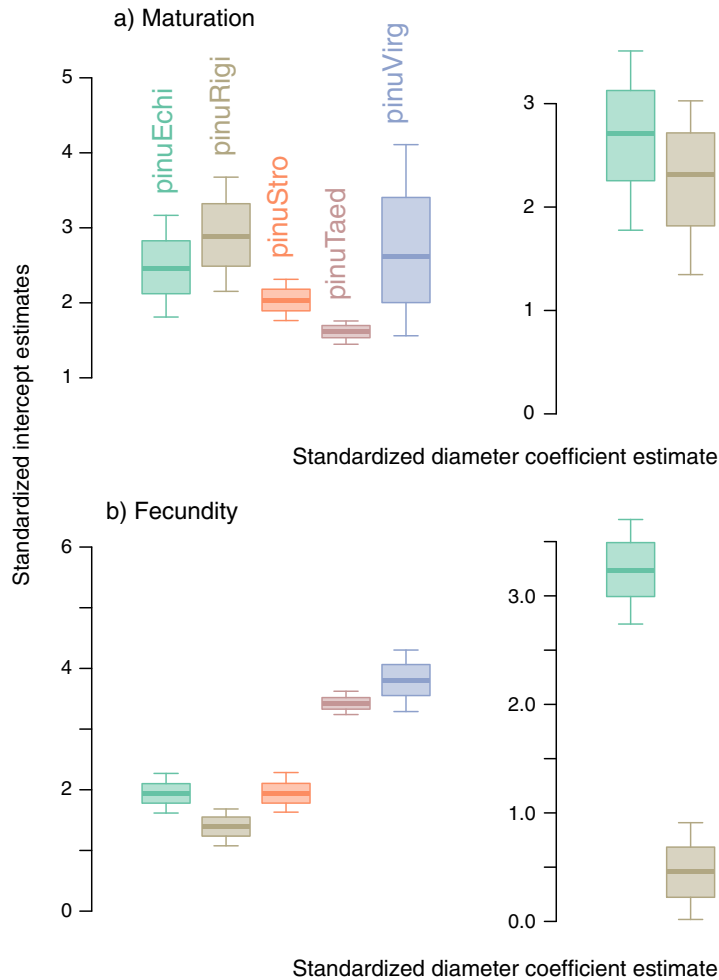


Fig. 7. Estimates of (a) fecundity coefficients  $\beta^x$  and (b) maturation coefficients  $\beta^y$  (see Table 3) for *Pinus*. Boxes and whiskers bound 68% and 95% of the posterior distribution, respectively. Symbolism follows Figure 6.

The model makes good prediction in both cases for this simulated example with only two parameters each for maturation and conditional fecundity. The ability to recover unobserved fecundity, which ranges widely over six orders of magnitude (Fig. 6c) verifies that the fit captures each of the key features in the model.

#### Application to Pinus

Estimates of maturation and fecundity coefficients show positive effects of tree diameter on both state variables. Fitted coefficients show species differences in fecundity responses (Fig. 7, below) and greater similarity in diameter effects on maturation (Fig. 7, above).

Dispersal parameter estimates combined with fecundity and the error matrix  $\mathbf{M}$  predict broadly overlapping seed shadows, but with large differences in expected values, as southern pines (*P. echinata*, *virginiana*, *taeda*) show much higher values than northern pines (*P. strobus*, *rigida*; Fig. 8). The 95% predictive intervals

apply to the square meter scale. They are scale-dependent and would decrease in width relative to the mean with increasing spatial scale, and vice versa.

Year effects show co-masting between southern pines (Fig. 9) that partially mutes the advantages of a diverse diet: the increase in expected yield with added host species does not alleviate the variance cost a consumer pays when those hosts are synchronized. The concentration of mast within the same years reduces the capacity for any one host species to bridge lean times in others. This effect is larger than it appears due to the log scale in Fig. 9. By contrast, there is limited support for co-masting of *P. rigida* and *P. strobus* in the southern Appalachians.

AR(4) terms show a tendency for positive lag-1 and lag-3 effects in all but *P. taeda* (Fig. 10a). In all cases, the lag-2 term is close to zero, and the lag-4 term is negative. Eigenvalues from lag terms having large imaginary parts identify quasi-periodic variation. Real and imaginary parts lie within the unit circle (Fig. 10b), consistent

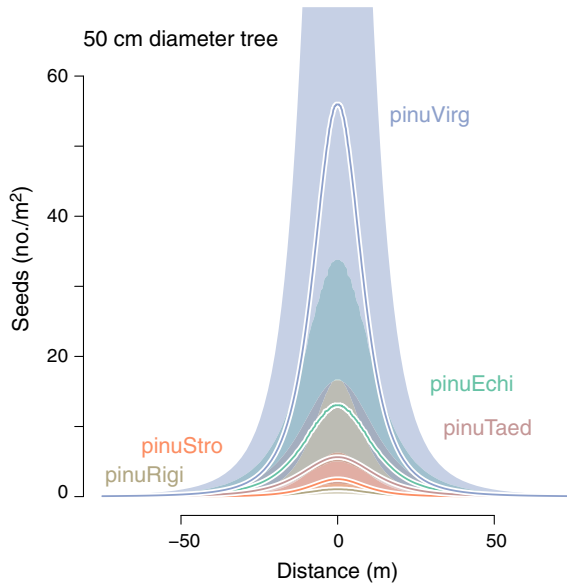


FIG. 8. Seed shadows are predicted from the posterior distribution, with 95% predictive intervals.

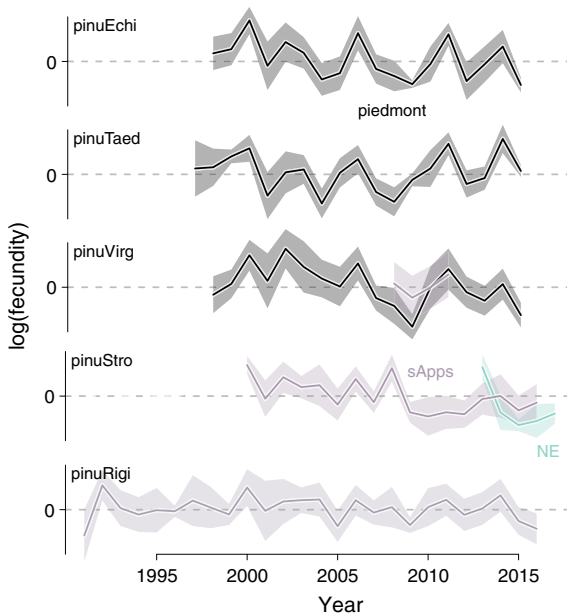


FIG. 9. Year effects show co-masting across Piedmont pines, but not for the southern Appalachians.

with stabilizing variation over the long term. Taken together, this shows a tendency toward damped, stable quasi-periodic masting.

The tree-lag covariance  $C_{nL}$  and space-lag covariance  $G_{SL}$  are shown for canopy foragers over  $n = 25$  host trees and ground foragers over an area of  $25 \times 25 \text{ m}^2$ . Each pixel in Fig. 11 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 evident at upper left, and recurring at lag 3. There is wide individual variation. Correlation on the forest floor (lower panels) is amplified by dispersal, which induces positive correlation at zero lag (Fig. 11b). This structure is lost by lag 1, with substantial patch-to-patch variation in subsequent years.

Resource scores that result from this covariance structure vary among sites, due to differences in host species composition, spatial aggregation, and host-tree quality (seed mass). Scores tend to be negative for canopy foragers (lower left of Fig. 12) due to the large variance among host fecundities. Southeastern sites with the highest yield also have high variance cost (DUKE in upper left of Fig. 12), also apparent from strong year effects showing synchronicity not only within, but also between host species (Fig. 9). This is true for two of three plantation sites (DUKE FACE), which have wide individual differences in fecundity (LaDeau and Clark 2006). The high variance costs at Coweeta (CWT) come from the *P. rigida* stand. The second CWT stand in this figure supports only a few *P. strobus* stands, where consumers would suffer from low total yield. The high score at one Harvard (HARV) site comes from *P. strobus* of relatively low mean fecundity but especially low variance cost. By contrast with the canopy, ground foragers pay a low variance cost (upper right of Fig. 12). The wide tree-to-tree variation in the canopy is smoothed by dispersal at this scale of  $25 \times 25 \text{ m}^2$ . Mean benefits on the forest floor generally follow trends in the canopy. These scores are scale specific.

To see the scale-dependent and space-time relationships, resource scores are shown as space-time surfaces (Fig. 13a) for two sites in the canopy and forest floor with maps (Fig. 13b). The tendency for score to increase with storage time (yr) is general. All else being equal, storage benefits consumers at all spatial scales on the forest floor. Demographic storage, capital breeding, and dormancy all effectively reduce variance, thereby increasing scores from left to right. Of course, this trend does not account for the costs for engaging in these different types of storage. Rather, it isolates the effect of resource variation. A space-for-time compensation (increasing surface from lower left to upper right) promotes movement between years, as shown by transect A in Fig. 2. Even in this example, the increasing score with spatial scale is not monotonic on the forest floor, due to the combination of two scales, that describing clumping of hosts and that describing the smoothing effect of dispersal. The valleys in surfaces for Fig. 13b are clearly evident in the maps of seed densities below. Canopy foragers that average over spatial displacement at this fine scale (e.g., song birds) do not experience this heterogeneity.

## DISCUSSION

Quantifying how an unreliable foundation impacts food-webs is a first step for understanding diversity and the biogeography of communities (Janzen 1970, August

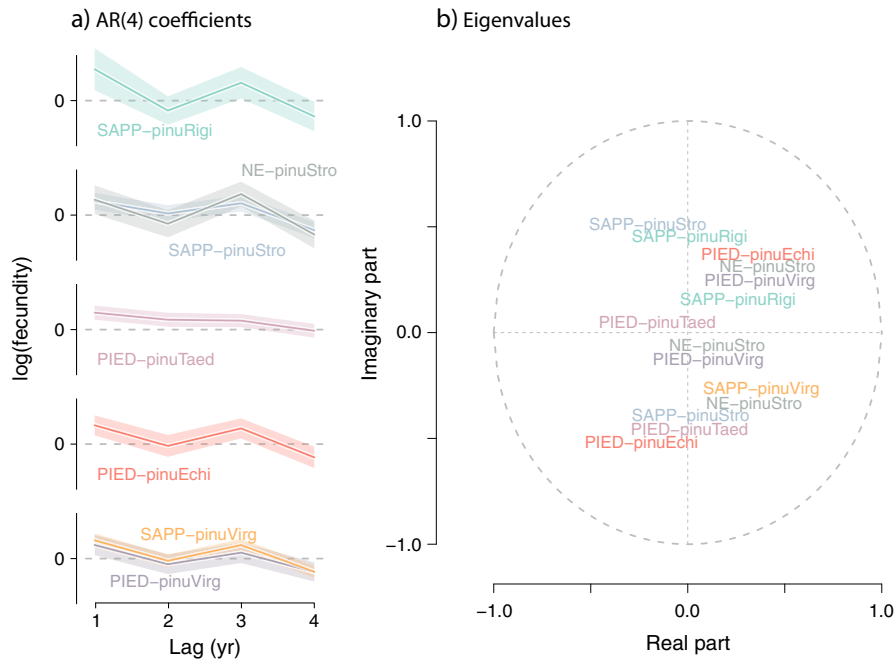


FIG. 10. (a) Lag coefficients in the AR(4) model by random region-species group fitted to *Pinus* data. (b) Eigenvalues from lag coefficients include large imaginary parts (oscillation) but lie within the unit circle (stability).

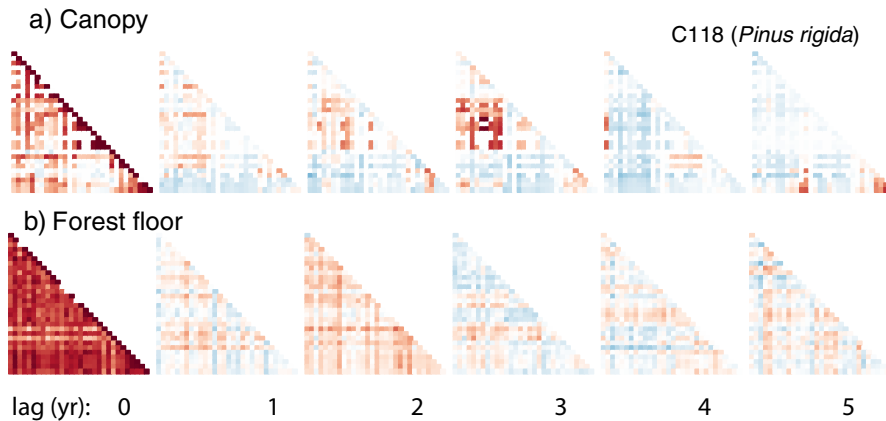


FIG. 11. Tree-by-lag covariance structure (a) in the canopy at C118, developed from  $C_{nL}$  (Eq. 14) and (b) space-by-lag structure on the forest floor, developed from  $G_{SL}$  (Eq. 15). Each pixel represents a pair of individual host trees (a) or sites on the forest floor (b), correlated over successive lag years. The site is dominated by *P. rigida*.

1983, Curran and Leighton 2000, Ostfeld and Keesing 2000, Cortes and Uriarte 2013, McMeans et al. 2016). Spatial foraging, storage, and diet breadth represent alternative solutions to the fluctuating resource base. As foraging capacity and/or storage increase, the variance-cost of an unreliable resource shifts to a mean-benefit: the scale-dependent averaging required for survival on variable resources. Spatiotemporal variance in mast production may limit not only the size of consumer populations in the near term, but also the potential adaptation of consumers to include new host plants in the diet (Williams 2007). Foraging theory weighs the costs of variable

resource supply for consumers that profit by minimizing unproductive search (Railsback and Harvey 2013). The resource score incorporates benefits and costs for consumers that see this variation each in its own way. A direct connection from theory to mast data can redefine habitat quality to include entropy in food supply at the scales relevant for consumers. The stability properties of mast cycles can be quantified and compared, in this case, showing evidence for long-term stability, but pervasive quasi-periodicity and large differences between habitats (Fig. 10). The effects of volatile masting of any one host species depends on all other hosts in the diet. We



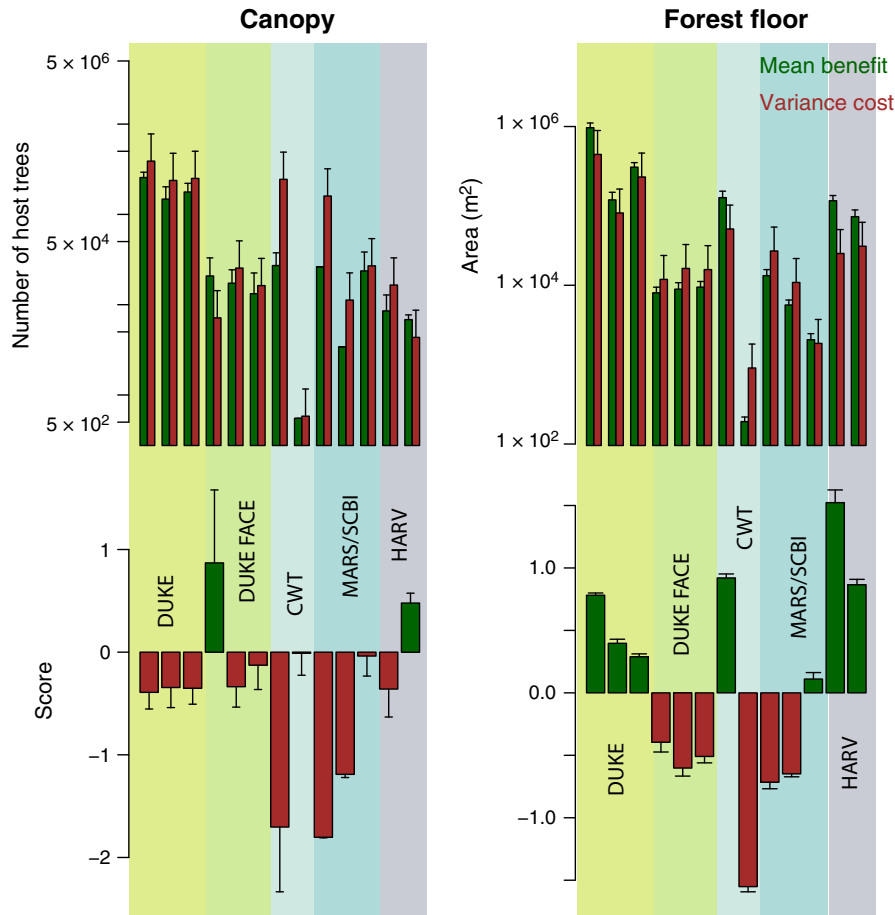


FIG. 12. Above are the contributions of mean benefit  $Q_{nL}$  (green) and variance cost  $\sqrt{\text{Var}(Q_{nL})}$  (brown) by sites summarized by region. Below are corresponding resource scores. Scores at left apply to a consumer that forages  $n = 25$  host trees. Scores at right apply to a consumer that forages  $S = 25 \times 25 \text{ m}^2$ . Error bars show plus 2 predictive standard errors.

summarize the methodological advance, followed by potential to improve biogeographic prediction of mast-ing and consumers of it.

*Mast estimates and prediction*

MASTIF offers a flexible platform that can facilitate synthesis across a large and growing literature (Table 1). Building on earlier analyses the allowance for individual host-plant heterogeneity (Clark et al. 2004, 2010, Nanos et al. 2010, Moran and Clark 2011, Uriarte et al. 2012, Milleron et al. 2013, Minor and Kobe 2017) is critical not only for useful estimates and predictions of mast supply. It also governs the space–time variance in the canopy and, through dispersal, provides the foundation for ground foragers. The model specification can include main effects, interactions, year effects, lag effects, and random effects (Table 3), while accommodating the uncertainty in seed identification (Appendix S1: Fig. S7.2b). As with previous models that led to this one (Clark et al. 2004, 2010), prediction is important for evaluating model fit, including potential overfitting. We find confident

estimates (Fig. 7; Appendix S1: Fig. S7.1). Predictions are accurate for even a simple model (Appendix S1: Fig. S7.6) and can only improve when environmental predictors are included in the model (Clark et al. 2004, 2014, Uriarte et al. 2005, 2012, LaDeau and Clark 2006).

Simulation in MASTIF can be used to explore potential design effects in mast studies. Inference and prediction break down when trees are either too abundant or too rare, an inherent tension between inference on dispersal vs. fecundity. When too abundant, overlapping seed shadows may not be resolved to specific trees. When reproductive trees are too few, there is an insufficient range of values to support inference on environmental effects. Because the same seed traps are used to estimate all species on a plot, model fit will vary for species, each of which offers a different distribution of distances and numbers and sizes and trees.

The approach of (Clark et al. 2004, 2010, Uriarte et al. 2012), extended here to include uncertain seed identification, addresses the concerns of (Nanos et al. 2010), while addressing the overfitting problem with their approach. Finding a better fit when seeds are

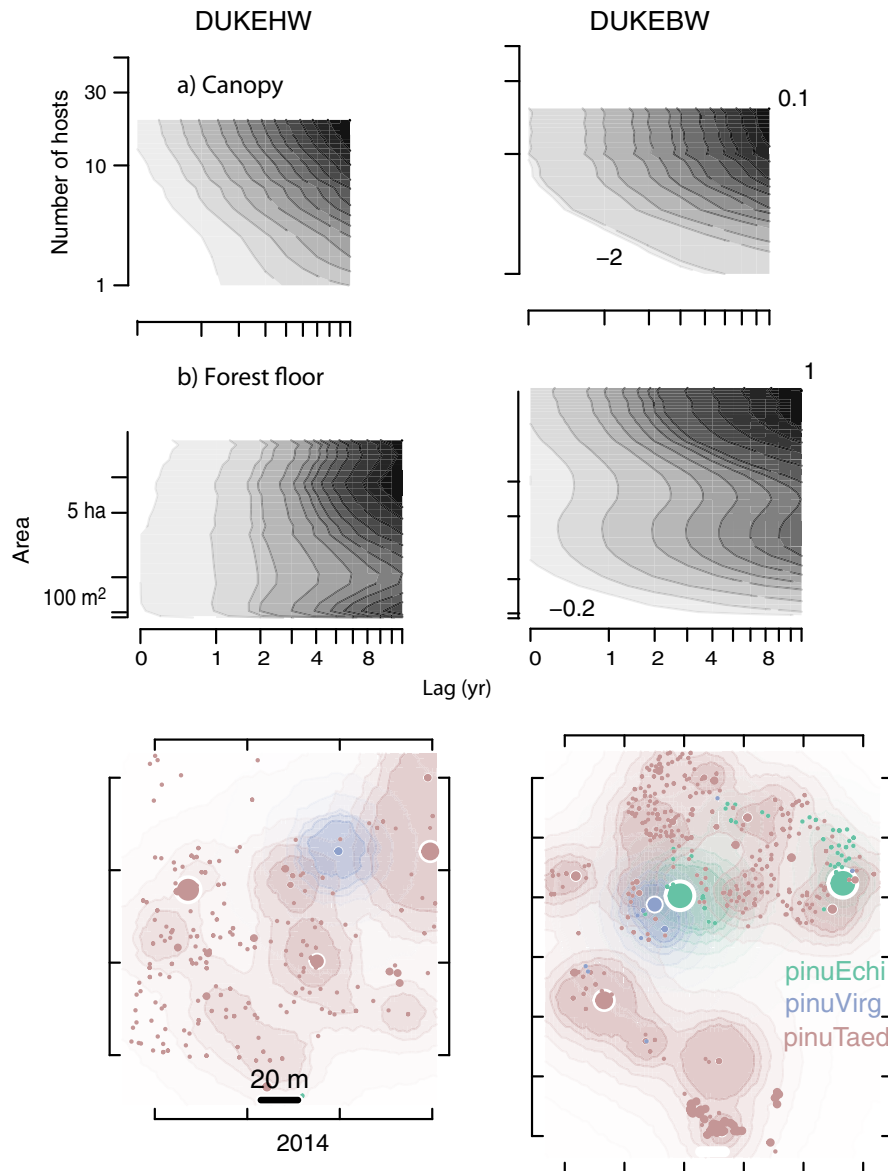


FIG. 13. Resource score surfaces at two sites experienced by a consumer (Eq. 23) that can store resources for 0–10 yr, forages over a range of (a) host trees or (b) forest-floor area, and consumes seeds from three host species. Space-for-time compensation occurs when surfaces increase from lower left 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. Shading intensity indicates high values.

predicted by  $n$  trees, rather than, say, two parameters (an intercept and an allometric coefficient on tree size), they argue for models that treat each tree as a separate parameter. Our approach allows that tree size is only one of a number of local and climate variables that control fecundity in a given tree year. Indeed, the effect of tree size can be “insignificant”. The fact that a constrained algorithm may predict precisely, does not change the fact that stands having  $n > S$  trees find too little information for inference on tree effects. Our approach allows for both a small number of predictors in the model and for the variance coming from individual differences, over time. Random variation is informed

by the hierarchical structure and the process model for maturation and fecundity.

The disadvantages of too many or too few host trees for confident model fitting on a single plot does not diminish their contribution to studies having multiple plots and/or prior information on dispersal distance. With multiple plots (or informative priors on dispersal), over- or under-populated plots can bring information on environmental effects because dispersal information comes from all plots.

MASTIF’s Bayesian implementation exploits the accumulating knowledge of maturation, fecundity, and dispersal (Appendix S1: Fig. S7.1). Prior parameter

values can integrate previous understanding, particularly for dispersal. The prior distribution combines data from multiple stands (a network) and years, thus increasing the range of effects that can be estimated. Group-level random effects stabilize estimates across plots (Fig. 8) that individually would not provide useful estimates. The flexibility to combine uncertainty in seed identifications, maturation and fecundity status of trees, and censored seed-trap observations makes our approach amenable to many data sets.

#### *Resource score as a cost–benefit index*

A single index cannot capture the complexity of habitat–host–consumer interactions. Limitations of the coefficient of variation (CV) include this omission of scale (Herrera et al. 1998, LaMontagne and Boutin 2009). Autocorrelation models applied to seed trap data alone, do not reflect availability in the canopy (Clark et al. 2004, Pesendorfer et al. 2016). Conversely, time series analyses of canopy counts miss the role of dispersal for ground foragers. For food-web studies, indices such as the CV, the simple mast interval, and AR coefficients suffer the same limitation: two consumers with different space–time–diet ambits see this variation differently. The specific resource score proposed here was motivated by simplicity and its close connection to current practice, the CV (Herrera et al. 1998, Pesendorfer et al. 2016), but extended to diet breadth and spatiotemporal dependence.

The generality of this approach comes from the spatiotemporal covariance structure of an arbitrarily diverse diet that can be estimated directly from data. The scale-dependent resource score recognizes a shift from variance-penalty to mean-benefit with expanding consumer ambit (Fig. 13). The approximations for covariance between individuals vs. covariance within an individual over time offered by Buonaccorsi et al. (2003) differs from our approach. They note the challenges of relating the two. By constructing the full space–time and space–tree covariance matrix we can examine the dual effects of correlated trees (or correlated space) and correlated years (Fig. 11). The principle steps in this derivation take us from the quality of seed or fruit combined with the fecundity of an individual tree in a given year (Eq. 8), to a tree  $\times$  tree  $\times$  lag covariance structure for hosts (Eq. 14; Appendix S1: section S4), to a spatiotemporal covariance on the forest floor (Eq. 15), decomposed by host species (Eqs. 19 and 21). It can be generalized to address a generic landscape characterized by spatial structure, rather than explicit spatial locations (Appendix S1: section S1). The resource score represents only one of many possible ways to summarize space-time-diet covariance. We expect other summaries to be equally valuable, depending on specific applications.

The *standard error rule* (Eq. 22) is a further summary index for the impact of introduction or loss of a diet item with direct applications to real habitats. Like the

resource score, it is not the most important product of this analysis, but rather a summary of it. Losses from the diet decrease the mean yield. Where there is weak or negative covariance with current diet items, the consumer may also lose a bridge resource that is important at times when alternatives are rare. For example, the abundant American chestnut (*Castanea dentata*) in the Appalachian and northeastern forests had an unknown masting structure (Diamond et al. 2000). If there were a strong tendency to co-mast with species in the genus *Quercus* then this loss would have less impact that it would if masting were independent. Knowledge of important extant mast species can provide guidance on the impacts of future threats.

#### *A second look at food-webs*

One of the most basic features of foraging is interaction: the rate of consumption of a resource depends on a consumer's alternatives. Food-web theory based on analysis of networks emphasizes presence or absence of specific consumer-prey interactions (Allesina et al. 2009, D'Alelio et al. 2016) and/or fixed coefficients representing prey dependence (McDonald-Madden et al. 2016). Generalized Lotka-Volterra models (Allesina and Tang 2012, Haerter et al. 2016) and resource-ratio models (Haegeman and Loreau 2015) assume consumption in proportion to supply of a diet item, traditionally termed the functional response (Kalinkat et al. 2013). If the consumption rate of each diet item is to depend on the availability of others, then the covariance structure across host species is needed, and it has to include the differing qualities of those resources. The capacity to quantify covariance in supply at consumer-specific scales has direct application to dynamic network analysis, where trophic connections are interdependent.

Our results show dependence between diet items in space and time, including co-masting (Fig. 9), which affects the resource variance experienced by a consumer. The dependence structure is expected to differ for each habitat. It is experienced differently by each consumer. As food-web theory continues to develop, this capacity to integrate resource dependence could affect the interpretation of food-web stability properties.

#### *Biogeographic implications*

For biogeographic understanding, including impacts of climate change, summaries of mean-variance structure like our resource score can offer a more direct index of habitat suitability than is available through the variables currently used in habitat models and species distribution models (SDMs), which emphasize climate, land cover, and soils, but omit availability of food. Ecologists and wildlife managers have long recognized that masting provides a base of forest food chains, and that space–time variation can be just as critical as the mean resource supply (McShea 2000, Ostfeld and Keesing 2000, Boutin

et al. 2006, Bergeron et al. 2011, Bogdziewicz et al. 2016). We do not offer a full predictive analysis of resource scores in this paper, because resources alone cannot predict trophic structure, requiring instead a full range of climate and habitat variables (C. Nuñez and J. S. Clark, *unpublished manuscript*). The important contribution to biogeographic understanding includes the basic theory and computation that can use species-size structure to quantify resource supply, which can be combined with the traditional climate and habitat variables in SDMs. The translation of seed production and dispersal to spatiotemporal resource availability (Fig. 11) and the summary of its effect by forest stands (Fig. 12) can supplement the variables now used for SDM.

#### ACKNOWLEDGMENTS

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1381/full>

## DATA AVAILABILITY

Data are available from CRAN: <https://CRAN.R-project.org/package=mastif>.