

## REPORT

## The scaling of reproductive variability in trees

Andrew J. Kerkhoff<sup>1</sup>\* and Ford Ballantyne IV<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

<sup>2</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

\*Correspondence: E-mail: kerkhoff@u.arizona.edu

### Abstract

Seed output in perennial plant populations is temporally variable and often synchronous over large regions. The similarly complex spatiotemporal dynamics of animal populations have been characterized by the power-law scaling of the variance in population numbers with mean abundance. Here we show that a large compilation of published reproductive time series exhibits largely invariant mean–variance scaling properties across both angiosperm and conifer tree species. A simple model of seed production in tree stands shows that observed values of the scaling exponent reflect very general aspects of plant ecology and life history as well as the temporal dynamics of seed production. Together, these results suggest that the continuum of reproductive variability and synchrony observed in trees may reflect the influence of a common set of ecological processes.

### Keywords

Macroecology, masting, mean–variance scaling, pollen coupling, reproductive strategies, Taylor’s power law.

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## INTRODUCTION

Variability in seed production by populations of perennial plants has long intrigued ecologists (Silvertown 1980; Kelly 1994; Kelly & Sork 2002). Despite large fluctuations in seed output, plant populations and even genera frequently exhibit high degrees of synchrony, sometimes over continental-scale distances (Koenig & Knops 1998, 2000). While many ecologists identify so-called masting as a discrete reproductive strategy (Janzen 1971; Kelly 1994; Kelly & Sork 2002), recent reviews suggest that reproductive variability may be extremely widespread and that plants exhibit a broad continuum of reproductive variability and synchrony (Herrera *et al.* 1998; Koenig & Knops 2000).

Traditionally, reproductive variability has been characterized using the coefficient of variation ( $CV = \sigma/M$ , where  $\sigma$  and  $M$  are the standard deviation and the mean) of reproductive output of a local population. However, the geographical scale and taxonomic breadth of patterns of reproductive variability demand characterization both across species and across local populations. Understanding how variability changes among populations could provide key insights on both the causes (Kelly 1994) and consequences (Ostfeld & Keesing 2000) of reproductive variability in perennial plants.

In population biology, similar spatiotemporal patterns of population dynamics are frequently summarized using the

power-law relationship between the mean ( $M$ ) and variance ( $V$ ) of population size.

$$V = aM^b, \quad (1)$$

where  $a$  is the coefficient and  $b$  the exponent of the  $M$ – $V$  scaling relationship. From this ‘synoptic’ perspective (Taylor & Woiwod 1982), the existence of strong scaling relationships implies that a general set of processes constrain local variation in abundance (Keitt *et al.* 2002; Maurer & Taper 2002). Since it was first brought to light (Taylor 1961),  $M$ – $V$  scaling has been shown to hold at scales from cell numbers within somatic tissues (Azevedo & Leroi 2001) to the temporal fluctuations of continental-scale, multi-species assemblages of North American breeding birds (Keitt *et al.* 2002; Maurer & Taper 2002).  $M$ – $V$  scaling relationships for animal populations typically exhibit exponents of  $1 \leq b \leq 2$ , and while a good deal of research has addressed variation in the value of the exponent, no clear consensus exists as to what determines its value (Keeling 2000; Kilpatrick & Ives 2003).

Here, we ask whether similar  $M$ – $V$  scaling relationships hold for patterns of reproductive output in trees. In this case, the value of the exponent is particularly important because it describes how variability changes across populations. From eqn 1,  $CV = V^{1/2}/M = (aM^b)^{1/2}/M = a^{1/2}M^{b/2-1}$ . Thus, the CV is a function of both the coefficient and the exponent of the  $M$ – $V$  scaling relationship

(Azevedo & Leroi 2001; Kilpatrick & Ives 2003). So while the CV is commonly used to assess relative variability of seed output, except when  $b = 2$ , it will change systematically with  $M$  across populations. If  $b < 2$ , the CV will systematically decrease with increasing  $M$ . Conversely, the CV will increase with  $M$  if  $b > 2$ . Thus, comparing reproductive CVs may be complicated by  $M$ - $V$  scaling, especially if there are differences in  $b$  among species.

Differences in the scaling exponent among tree species may also provide clues about species-specific selective pressures that affect patterns of reproductive variability. For example, endozoochorous (frugivore-dispersed) species, which are expected to exhibit more constant reproduction (Herrera 1998; Kelly & Sork 2002), might exhibit  $b < 2$ , i.e. less variable reproduction under more reproductively favorable (high  $M$ ) conditions. Alternatively, species under selection to satiate seed predators, which favours high variability, might exhibit  $b > 2$ , to increase their relative variability under favourable conditions (Janzen 1971; Kelly & Sork 2002).

We show that a large compilation of published reproductive time series (Koenig & Knops 2000) exhibits largely invariant scaling properties across tree species, which suggests that patterns of reproductive output for all studied species may be influenced by a common set of ecological and physiological processes. We also use a simple model of seed production in tree stands (Satake & Iwasa 2000) to show that values of the scaling exponent reflect very general aspects of plant ecology and life history as well as the temporal dynamics of seed production. This study presents the first evidence for  $M$ - $V$  scaling in reproductive output of trees and highlights the importance of patterns across populations and species for understanding the causes and consequences of reproductive variability.

## MATERIALS AND METHODS

### Seed production data

To examine the  $M$ - $V$  scaling of seed production, we used a subset of the data compiled by Koenig & Knops (2000) from a single study in which all sites were sampled using a standard methodology (Tallqvist 1978). In this survey, 28 species were monitored in northern Europe for 4–17 years (mean = 10.6), with a total of 148 reproductive time series.

In the scaling analyses, each data point represents a site, with the mean ( $M$ ) and variance ( $V$ ) of seed production (seeds per  $m^2$ ) calculated across years in that site. In order to look for differences among taxa, we also conducted separate scaling analyses for conifers and angiosperms, and for all individual genera and species represented by a sufficient number of data points ( $n > 5$ ). In all, we analysed six

individual species, four conifer genera and two angiosperm genera. We used both ordinary least squares (OLS) and reduced major axis (RMA) regression of log-transformed  $V$  against log-transformed  $M$  to estimate the exponents and coefficients of the scaling relationships. RMA is more appropriate when error is present in both the variables, as in this case (McArdle 1988; Henry & Aarssen 1999).

### A Model

To explore the ecological processes underlying the scaling of reproductive variability, we used a previously published model of seed production in tree stands (Satake & Iwasa 2000, 2002). The model is based on the assumption that reproduction is primarily constrained by internal energy reserve of the trees, and the availability of outcross pollen. In its simplest form, the dynamics of the energy reserve of a tree is modelled as

$$Y(t+1) = \begin{cases} Y(t) + 1 & \text{if } Y(t) \leq 0, \\ -\kappa P(t)Y(t) + 1 & \text{if } Y(t) > 0. \end{cases} \quad (2)$$

Here,  $Y(t)$  is the non-dimensionalized energy reserve of the tree, defined as  $Y(t) \equiv (S(t) + \mathcal{A} - L)/\mathcal{A}$ , where  $S$  is the energy reserve of the tree,  $\mathcal{A}$  is the net photosynthetic energy assimilation (here held constant), and  $L$  is the threshold energy reserve level above which the tree initiates reproduction (also held constant). The 'depletion coefficient',  $\kappa$ , represents the energy cost of reproduction, and is defined as  $\kappa \equiv \epsilon(R + 1) - 1$ , where  $R$  is the ratio of the energetic cost of fruiting to that of flowering and  $\epsilon$  is a constant of proportionality related to the efficiency of flower production. Finally,  $P$  is the pollen available to the  $i$ th tree defined as

$$P_i(t) = \left( \frac{1}{N-1} \sum_{j \neq i} [Y_j(t)]_+ \right)^\beta, \quad (3)$$

where  $[Y_j(t)]_+ = Y_j(t)$  if  $Y_j(t) > 0$ , and  $[Y_j(t)]_+ = 0$ , otherwise, and  $N$  is the number of trees in the population. The 'coupling exponent',  $\beta$  determines the degree to which a tree depends on other trees for pollen. As  $\beta$  approaches zero, seed production of the tree becomes independent of the other trees in the stand, as in selfing species, for example. Conversely, when  $\beta$  is large, seed production is potentially limited by pollen availability and seed production by the tree is highly dependent on the reproductive actions of the other trees in the stand, as in the case of dioecy.

Thus, the reproductive output of the entire stand in year  $t$  is simply

$$Z_{\text{TOT}}(t) = \kappa \sum_{i=1}^N P_i(t) [Y_i(t)]_+.$$

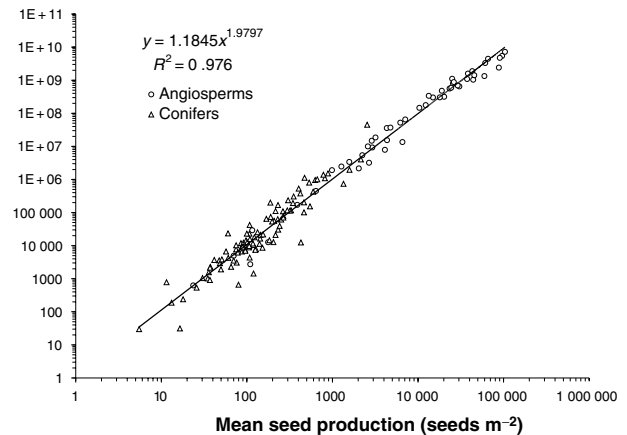
The model, with its two control parameters,  $\kappa$  and  $\beta$ , generates rich dynamics, ranging from completely asynchronous reproduction to synchronized reproduction (Satake & Iwasa 2000). Here, we investigate how model parameters influence the  $M$ – $V$  scaling of reproductive dynamics.

The model is simulated as a globally coupled map of  $N$  trees, with pollen availability  $P(t)$  calculated over the entire stand. While many physiological and ecological phenomena may affect mean seed production in natural stands, in the model variation in  $M$  is achieved by varying the size of the stand,  $N$ . We used stand sizes from 50 to 10 000 trees, with the initial condition for each tree drawn from a uniform distribution between 0 and 1. We ran all simulations for 1000 time steps and discarded the first 100 to eliminate transient behaviour. We then calculated  $M$  and  $V$  of  $Z_{TOT}$  for each stand across the 900-year reproductive time series, and used these values to calculate  $M$ – $V$  scaling exponents for the range of parameter values  $1.1 \leq \kappa \leq 4.1$  and  $0 \leq \beta \leq 2.2$ .

## RESULTS

### Empirical data

Across all species, the seed production data for trees exhibited very strong  $M$ – $V$  scaling over approximately four orders of magnitude in mean seed production (Fig. 1). The exponent is indistinguishable from  $b = 2$ , which implies that CV of population seed output should be independent of  $\log(M)$ , as described above. Empirical CV values exhibited no significant trend with  $\log(M)$  ( $F_{148} = 1.6$ ,  $P = 0.20$ ). The value of the regression intercept,  $\log(a)$ , was



**Figure 1**  $M$ – $V$  scaling of seed production for the Tallqvist (1978) data from northern Europe. The regression line (OLS) is for the angiosperms (circles) and conifers (triangles), combined.

not significantly different from zero, which indicates that  $a \approx 1$ . This result provides an estimate of the mean CV across species of approximately 1. From the empirical data we found the mean CV = 1.09.

Similar scaling relationships, in terms of both  $a$  and  $b$ , held for both conifers and angiosperms, and even for most of the individual genera and species (Table 1). The one species that did not show a significant  $M$ – $V$  relationship, *Larix sibirica*, was represented by five sites that differed little in the magnitude of  $M$  (190–465 seeds per  $m^2$ ). The exponents of the scaling relationships within genera and species were generally  $< 2$ , and in cases (*Betula* and *B. verrucosa*) the

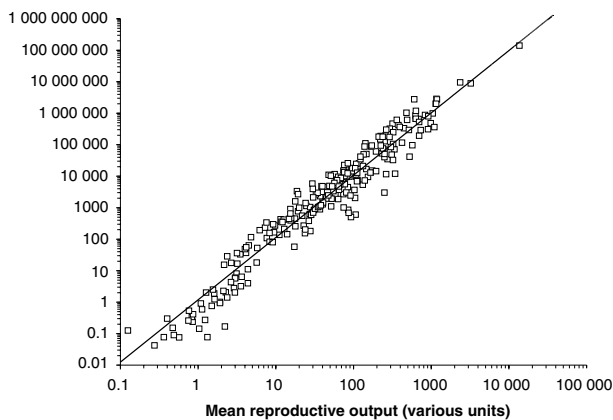
**Table 1** Regression results for the scaling analysis for the full data set and different subgroups. Estimates of the exponent ( $b$ ) and coefficient ( $a$ ) are given for both ordinary least squares (OLS) and reduced major axis (RMA) regression models. Standard errors for both the RMA estimates are the same those from OLS. Unless noted (n.s.), all regressions were highly significant ( $P < 0.01$  or less)

	$b_{OLS}$	$SE_b$	$b_{RMA}$	95% CI <sub>RMA</sub>	$\log(a)_{OLS}$	$SE_{\log(a)}$	$\log(a)_{RMA}$	$r^2$	$n$	$F$
All data	1.98	0.03	2.00	1.95–2.05	0.07	0.07	0.01	0.976	148	5929
Conifers	2.08	0.07	2.20	2.05–2.35	–0.01	0.16	–0.40	0.891	98	783
<i>Abies</i>	1.64	0.29	1.74	0.95–2.53	1.20	0.80	0.93	0.892	6	33
<i>Larix</i>	1.87	0.22	1.94	1.42–2.47	0.30	0.52	0.14	0.926	8	75
<i>L. sibirica</i>	0.62	0.35	0.88	–0.36–1.92	3.39	0.86	2.78	0.500	5	3 (n.s.)
<i>Picea</i>	1.78	0.18	1.98	1.61–2.35	0.79	0.45	0.31	0.808	25	97
<i>P. abies</i>	1.77	0.13	1.86	1.59–2.14	0.87	0.31	0.67	0.906	21	182
<i>Pinus</i>	1.92	0.13	2.15	1.88–2.41	0.09	0.26	–0.36	0.799	55	210
<i>P. sylvestris</i>	1.53	0.18	1.94	1.58–2.30	0.83	0.35	0.03	0.620	47	73
Angiosperms	1.96	0.04	1.98	1.91–2.06	0.11	0.15	0.06	0.983	50	2790
<i>Alnus</i>	1.83	0.30	1.95	1.18–2.72	0.51	1.07	0.09	0.882	7	37
<i>A. incana</i>	1.87	0.39	1.99	0.76–3.22	0.32	1.40	–0.09	0.887	5	24
<i>Betula</i>	1.77	0.06	1.80	1.70–1.91	0.96*	0.24	0.85	0.969	35	1020
<i>B. pubescens</i>	1.88	0.08	1.91	1.75–2.08	0.54	0.34	0.42	0.971	19	574
<i>B. verrucosa</i>	1.65	0.07	1.67	1.51–1.82	1.45*	0.30	1.34	0.976	15	519

\*Values of  $\log(a)$  significantly different from zero.

95% confidence intervals for the exponent did not overlap with that of the overall relationship (Table 1). Although the regression intercept was usually not significantly different from zero,  $\log(a)$  for *Betula* and *B. verrucosa* were significantly greater than zero. As the OLS results and the RMA results were qualitatively consistent, we were able to use ANCOVA to look for differences in the scaling exponent among taxa. Using generic identity as a factor produced no indication of unequal exponents ( $\mathcal{S}_{\text{III}} = 0.20$ ,  $F_9 = 0.25$ ,  $P = 0.99$ ). However, assuming equal slopes, there was a significant generic effect on  $\log(a)$  ( $\mathcal{S}_{\text{III}} = 3.76$ ,  $F_{12} = 3.73$ ,  $P < 0.001$ ).

The  $M$ - $V$  scaling relationship across species with  $b = 2$  implies that the scaling relationship should hold regardless of the units of measure of reproductive output (e.g. cones per tree vs. seeds per  $\text{m}^2$ ) as long as the transformation from one set of units to another is linear (e.g. seeds  $\text{m}^{-2} = \text{cones per tree} \times \text{seeds per cone} \times \text{tree per m}^2$ ). This implication arises because a linear transformation of the mean of a process is quadratic in its variance, which results in a slope of 2 for the  $M$ - $V$  scaling relationship under transformation (Kilpatrick & Ives 2003). This is illustrated by the fact that  $M$  and  $V$  from all other data sets compiled by Koenig & Knops (2000) lie directly along the extrapolated regression line from the Tallqvist (1978) data analysed above (Fig. 2). The units of measure varied widely among these 246 additional time series, and they were frequently unreported in the published database. Although it is inappropriate to perform a regression on such heterogeneous data, and the ancillary information necessary to rectify the units is unavailable, it is clear from Fig. 2 that linear transformation of the units would only move the data points along the existing regression line. Thus, the same  $M$ - $V$  scaling relationship probably holds across all 96 species in the Koenig and Knops database.



**Figure 2** Regression line extrapolated from the Tallqvist data (Fig. 1), shown together with the remaining reproductive data compiled by Koenig & Knops (2000).

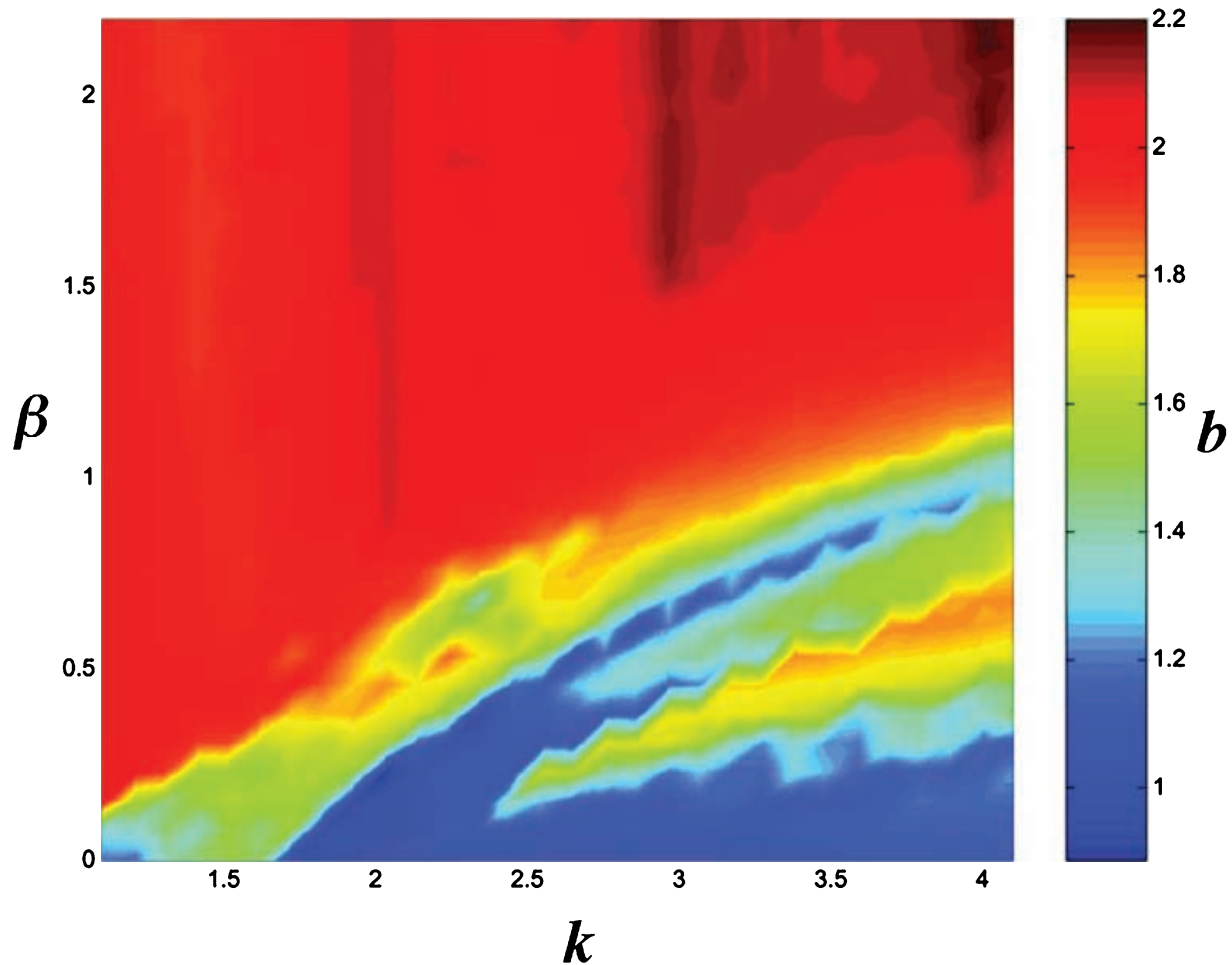
## Modelled scaling relationships

The temporal dynamics of the globally coupled map model fall into four general classes of behaviour (Satake & Iwasa 2000). When  $\kappa \leq 1$ , annual energy gain completely compensates for reproductive investment and the annual reproductive output of the population is constant, regardless of the degree of pollen coupling,  $\beta$ . As we are specifically interested in reproductive variability, we ignored this portion of the parameter space. For  $\kappa > 1$ , we found that the other three classes of dynamical behaviour delineated by Satake & Iwasa (2000) corresponded quite precisely to different ranges of scaling exponents (Fig. 3). The desynchronized phase, in which all individuals reproduce independently of one another, generated scaling exponents of  $b \approx 0.94$ – $1.75$  (the lower right region of blue and yellow in Fig. 3). The clustering phase, in which subpopulations within the stand reproduced synchronously, corresponded to exponents of  $b \approx 1.75$ – $1.9$  (the yellow-orange region along the narrow diagonal transition zone in Fig. 3). Finally, in the coherent phase, in which all individuals reproduced synchronously, we observed scaling exponents of  $b \approx 1.9$ – $2.2$  (the upper orange and red region of Fig. 3). The coherent phase can be further broken down into chaotic and periodic phases, depending on the dynamics of the synchronized population. The periodic phase occurs around integer values of  $\kappa$ , and in our analysis left the signature of characteristically high scaling exponents ( $b \approx 2.2$ ).

## DISCUSSION

Despite interspecific differences in ecology and life history, a common  $M$ - $V$  scaling relationship appears to hold across all species in this study. However, given the limited component of tree diversity represented by even the full database (96 species, 35 genera), we think that variation in the scaling exponent, as observed in animals (Taylor & Woiwod 1982), remains an important open question. Still, the fact that the  $M$ - $V$  scaling relationship was largely invariant across species, genera and divisions of plants suggests that reproductive variability across local populations may be constrained by very general processes, regardless of pronounced differences in ecologies and life histories of species.

The Satake and Iwasa model provides insights as to why such invariant  $M$ - $V$  scaling might arise, and cases in which it should break down. The model predicts that  $b \approx 2$  scaling should occur in a very broad region of the parameter space, as long as the degree of pollen coupling  $\beta$  is high relative to the ratio of the fruiting cost to flowering cost (which is directly proportional to  $\kappa$ ). Dynamically, this corresponds to locally clustered or synchronous reproduction of individuals in the stand, with pronounced interannual fluctuations.



**Figure 3** Response surface of  $M$ - $V$  scaling exponents ( $b$ ) with respect to the 'depletion coefficient' ( $k$ ), and the 'coupling exponent' ( $\beta$ ) of the Satake and Iwasa stand reproduction model.

Thus, synchronous and interannually variable patterns of reproduction (the hallmarks of masting; Kelly 1994; Herrera *et al.* 1998) may occur in species that differ considerably in their life-history characteristics, particularly for species with relatively high pollen coupling, i.e. dioecious and other primarily outcrossing species.

Conversely, species with high cost ratios of fruit to flowers under low pollen coupling should exhibit  $b < 2$ , with individuals within a stand producing asynchronously. Plants that bear energetically costly fleshy fruits, many of which are endozoochorous, probably have high fruit : flower costs, and thus high  $k$ . If pollen coupling is not too strong, these species could exhibit decreasing relative variability (CV) under increasingly favourable conditions. Thus, the relatively low reproductive variability observed in frugivore-dispersed plants (Jordano 1995; Herrera 1998; Kelly & Sork 2002) may have arisen 'preadaptively' as an epiphenomenon of selection for attractive (and costly)

fruits. Unfortunately, endozoochorous species were not sufficiently represented in the data to evaluate this hypothesis. Exploring variation in the exponent requires data for species of more varied life histories, as all species examined here are both pollinated and dispersed primarily by wind. In particular, important insights might be gained by applying  $M$ - $V$  scaling analyses to well known masting systems, e.g. the *Chionochloa* (Poaceae) of New Zealand (Kelly *et al.* 2000), or the Dipterocarps of Southeast Asia (Curran & Webb 2000).

Our results do not provide a formal test of the Satake and Iwasa model, but if the model did not produce  $M$ - $V$  scaling, it would have indicated an important schism between empirical patterns of reproductive variability and a model put forward to explain them. The major limitation of the model is the rather complex relationship between model parameters and the life-history attributes and ecological circumstances of plant species. While some clearly defined

attributes may relate intuitively to the parameters (e.g. cleistogamy and dioecy in the case of  $\beta$ ) many factors, both intrinsic and extrinsic to the species, can affect its position in the parameter space. For example, the coupling parameter  $\beta$  relates not only to the self-compatibility of a species, but also to the degree of pollen limitation imposed by the environment. Still, the relationships that the model suggests between the reproductive characters of plants and both the dynamics and statistical properties of population reproductive output warrant further investigation.

More generally, the model suggests that the slope of the  $M$ - $V$  scaling relationship in ecological time series may be closely related to the degree of correlation among individuals (or subpopulations) in a larger population. Here correlation is related to the degree of pollen coupling ( $\beta$ ), but in different contexts, such correlations could be induced by various ecological interactions, including intraspecific competition (Maurer & Taper 2002), predation (Kilpatrick & Ives 2003), dispersal (Ranta *et al.* 1999) and pathogen transmission (Keeling & Grenfell 1999), and also by environmental forcing (i.e. the Moran effect; Ranta *et al.* 1997). Together, these results suggest a general probabilistic framework for understanding  $M$ - $V$  scaling in ecological time series based on covariance among individuals (Ballantyne and Kerckhoff, unpublished data).

This analysis also provides insights concerning the proximate causes of reproductive variability. The spatial autocorrelation structure of the reproductive data analysed here has been shown to be similar to that of records of precipitation and temperature (Koenig & Knops 2000). However, because  $b \approx 2$  across species, reproductive CVs do not change systematically with changes in  $M$ , which contrasts with the systematic decrease in the CV with increasing mean observed for precipitation (Knapp & Smith 2001). Thus, while the spatial structure of the data implies that climatic forcing may play a role in generating reproductive synchrony among populations, this difference in  $M$ - $V$  scaling suggests that reproductive variability is not simply tracking climate in time. Koenig & Knops (2000) reach a similar conclusion based on the temporal autocorrelation structure of the reproductive data, which is also quite different from that of temperature and precipitation. The incomplete coupling between climatic variability and fluctuations in seed output has important implications for the spatiotemporal dynamics of granivorous animal populations (Koenig & Knops 2001; Stenseth *et al.* 2002) and the communities they interact with (Blasius *et al.* 1999; Ostfeld & Keesing 2000). A recent extension of the stand reproduction model which incorporates autocorrelated extrinsic forcing (Satake & Iwasa 2002) provides an opportunity to functionally link climate fluctuations, via seed production, to the population dynamics of granivores and their predators.

## CONCLUSIONS

Fluctuations in seed output have been shown to be autocorrelated over continental-scale distances (Koenig & Knops 2000). We apply  $M$ - $V$  scaling analysis to explore patterns of reproductive variability across populations and species in order to better understand both the proximate (physiological and ecological) and ultimate (evolutionary) causes of reproductive variability at larger spatiotemporal scales. This macroecological (Brown 1995) approach complements more intensive, localized studies of reproductive variability (Sork *et al.* 1993; Kelly & Sullivan 1997; Herrera 1998), by showing that strong regularity ( $M$ - $V$  scaling with tightly constrained, if not invariant, exponents) underlies complex patterns of reproductive variability and by generating testable predictions about how the ecological and life-history attributes of species influence spatiotemporal patterns of reproduction.

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