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A resource budget model to explain intraspecific variation in mast reproductive dynamics

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Abstract Rowan, *Sorbus aucuparia* L., exhibits conspicuous geographic variation in its inter-annual patterns of reproduction across southern Norway. Along the southern west coast, trees flower and produce clusters of succulent berries every other year, while in the east, trees mast every 3 years. We investigate two hypotheses for this variation: local adaptation to environmental conditions that favors different reproductive schedules at different locations or variation arising from single stereotyped reproductive strategy in the face of a geographic variation in productivity. To assess the theoretical plausibility of each of these hypotheses, we develop a refined resource budget model for mast reproduction. The refined model assumes that there is a lower bound on the amount of resource that may be allocated to reproduction, which allows the prediction of the relation between reproductive schedules and productivity. From the analysis of the model, we find that the observed geographic transition in rowan mast is caused if either productivity in the east is lower than that in the west or if plants in the eastern populations have evolved to pause reproduction until energy reserves are replenished to higher levels. The prediction by the productivity gradient hypothesis match with the empirical finding that the productivity is, in fact, likely to be lower in the east than the west, although we lack empirical data to test the likelihood of the local adap-

tion hypothesis. There is a need for experimental studies to clarify the validity of the local adaptation hypothesis.

Keywords Masting · Mast seeding · Geographic variation · Local adaptation · Productivity · Reproductive allocation · Life history

Introduction

Plant reproductive tactics vary widely among taxa, as some species exhibit a more or less constant flowering effort through time, while others exhibit a highly variable effort. In the face of the wide diversity of reproductive tactics, it is conspicuous as to how many long-lived perennials employ a masting strategy: most individuals in a population reproduce in synchrony, but with large inter-annual variation in effort (Kelly 1994). Masting is a common phenomenon reported in diverse taxonomic groups and from most continents (Herrera et al. 1998; Sork et al. 1993; Koenig et al. 1994; Shibata et al. 1998; Yasaka et al. 2003; Kon et al. 2005; Janzen 1971; Ashton et al. 1988). Moreover, it is widely reported that the abundance of seeds results in major resource pulses to seed consumer populations that cascade through ecosystems (Ostfeld et al. 1996; Ostfeld and Keesing 2000; Satake et al. 2004; Boutin et al. 2006).

A variety of hypotheses, both adaptive and non-adaptive, have been proposed to explain this phenomenon (Kelly and Sork 2002; Koenig and Knops 2005). The growing consensus is that masting is evolutionarily favored as a means to swamp seed predators and/or enhance pollination rates (Ims 1990; Norton and Kelly 1988; Kelly et al. 2001; Kelly and Sork 2002). Moreover, a family of resource budget models has recently been shown to provide both a physiological mechanism by which plants may successfully generate such intermittent and synchronous reproduction (Isagi et al. 1997; Satake and Iwasa 2000, 2002a, 2000b) and provide conditions

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for which masting is adaptive (Rees et al. 2002; Satake and Bjørnstad 2004).

A not uncommon but less well understood observation is the existence of intraspecific variation in mast seeding. Rowan (*Sorbus aucuparia* L.), for instance, exhibits large-scale geographic variation in masting across southern Norway. Along the west coast, trees mast in alternate years, while in the east, the mast crops are every 3 years (Kobro et al. 2003; Satake et al. 2004). Intraspecific variation in masting has also been described in snow tussocks (*Chionochloa* spp.) (e.g., Kelly et al. 2000), masting oaks (*Quercus* sp.) (e.g., Liebhold et al. 2004), and many other tree species (Koenig and Knops 1998, 2000; Schaubert et al. 2002; Suzuki et al. 2005). There are two intuitive hypotheses for such variation: local adaptation to local ecological conditions or variation arising from gradients in productivity. The former may occur if the costs of lost reproduction/recruitment opportunities and enhanced seedling competition versus the benefits of masting (Rees et al. 2002) varies among habitats or regions. Intuitively, the latter may occur if the recovery of energy loss by reproduction is faster in high productivity habitats so that plants are capable of reproduction more frequently.

In this paper, we seek to elucidate the theoretical plausibility of these hypotheses. We are fortunate in the existence of previously developed models for the physiological mechanism of mast seeding (Satake and Iwasa 2000) that have been validated against several sets of data (Rees et al. 2002; Crone et al. 2005). In our enquiry, we found it useful to focus on the transition from 2- to 3-year periodicity in rowan reproduction as moving from the west to east across southern Norway. We use the details of this transition to contrast the relative merit of local adaptation versus productivity gradients and, thereby, highlight—and resolve—an intuitive conundrum of the most current mechanistic model (Isagi et al. 1997; Satake and Iwasa 2000; Rees et al. 2002): the standard resource budget model predicts there to be no qualitative relation between reproductive dynamics and productivity—high productivity is predicted to yield higher mast crops but without altering the inter-mast interval. In the face of this, we analyze a modified resource budget model and show that the inclusion of a minimum bound to resource depletion can account for productivity-dependent variation in mast intervals in general, and a productivity-dependent transition from 2- to 3-year reproductive cycles in particular. Using the results from our analysis of the modified resource budget model, we discuss the relative merits of the two hypotheses.

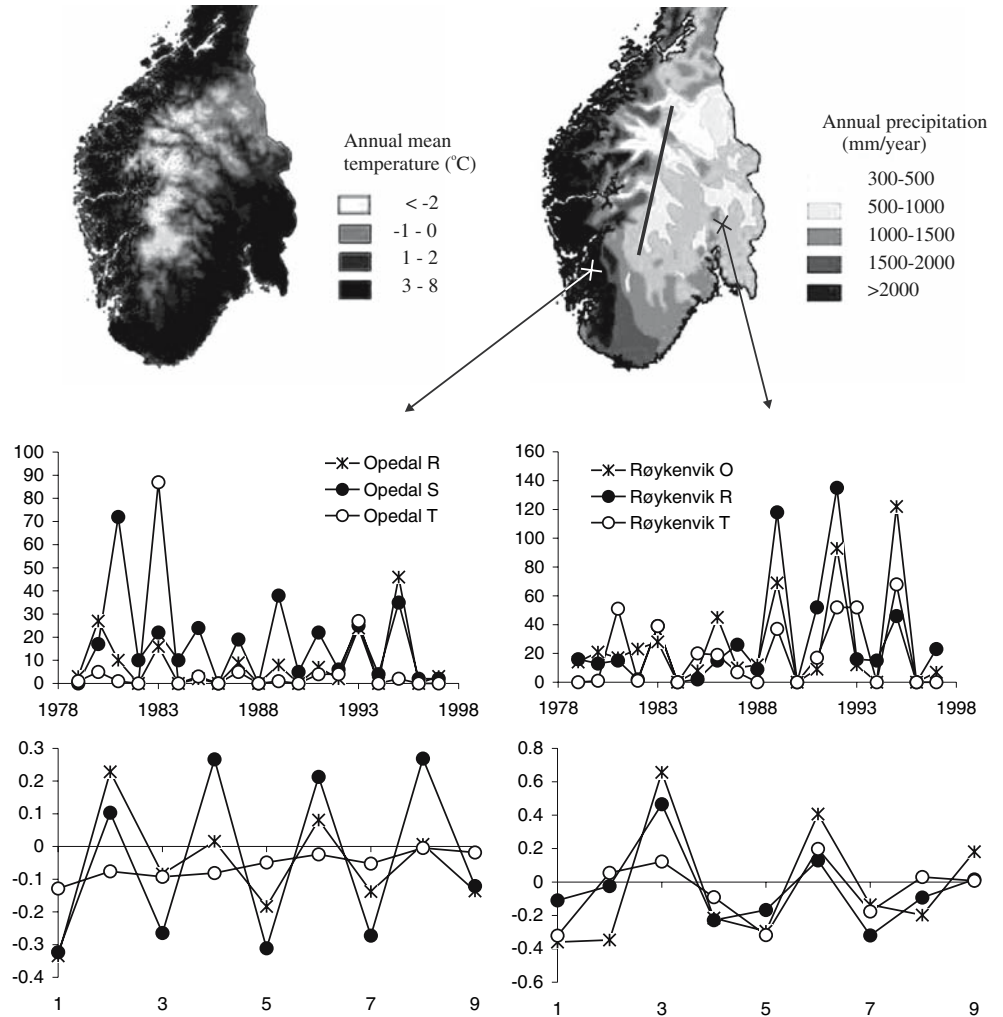
Preamble: geographic variation in rowan masting

Rowan is widely distributed throughout Europe and grow as far north as 70°N in Norway. The clusters of white flowers are produced in the early summer and its

berries ripen in conspicuous red clusters in the fall. Flower and berry production vary greatly between years in a typical masting fashion (Sperens 1997; Kobro et al. 2003; Satake et al. 2004). From long-term data on berry production by rowan trees on commercial apple farms across southern Norway, Satake et al. (2004) documented geographically distinct reproductive patterns among the rowan trees: a 2-year cycle in southwest Norway and a 3-year cycle in southeast Norway. Figure 1 represents a refined illustration of this based on the data available for six individual trees between 1979 and 1997 at two different sites, Opedal (west) and Røykenvik (east). The geographic difference in the flowering dynamics is readily seen from the autocorrelation functions (ACFs) of the time series (Fig. 1e, f). The reproductive patterns of the three Opedal trees (west) exhibit strong positive autocorrelation at lags 2, 4, 6, etc., and negative autocorrelation at lags 1, 3, 5, etc. (though the ACF of one of the trees is swamped by the outliers in 1983 and 1993). In contrast, the three trees in Røykenvik (east) show positive autocorrelations at lags 3 and 6 and negative ones at lags 1, 2, 4, 5, and 7. Satake et al. (2004) provide a comprehensive description of this phenomenon across 49 geographic locations (though, as detailed therein, those time series represent aggregates across multiple trees at each site, as opposed to the individual data presented in Fig. 1).

Motivated by the productivity gradient hypothesis, we reviewed the relevant climatic information reported by the Norwegian Meteorological Institute (<http://www.met.no>) for the two different regions (Fig. 1a, b). The mean annual temperature did not differ markedly between the two. However, the east is more continental and shows wider fluctuations. The meteorological station at Gardermoen (east; 41 km from Røykenvik), for instance, has an average of 167 days a year with minimum temperatures below freezing, as compared to 57 days for Bergen (west; 140 km from Opedal). Moreover, the number of days for which the maximum temperature exceeds 20°C is 52 at Gardermoen (east) but only 5 at Bergen (west). With respect to precipitation, the relevant stations in the eastern region typically receive an average of 500–1,000 mm a year, while the relevant stations in the west receive more than twice that amount (Fig. 1); Ullensvang County (west; where Opedal is situated) reports an annual precipitation of 1,350 mm compared to 770 mm in Gran County (east; where Røykenvik is situated). The average annual temperatures for the two counties is 6.8°C (January mean −0.2°C, July mean 15.0) versus 3.0°C (January mean −9.6°C, July mean 15.3). Taken as a whole—and given the general relationship between soil moisture, temperature, and productivity (e.g., Richardson et al. 2005)—we have a reason to speculate that productivity is higher in the west. The theoretical challenge, then, is to investigate the consequences for altered productivity on mast seeding dynamics.

Fig. 1a-f Map of southern Norway showing the locations of the study sites (**a** and **b**), time series data of the annual flower production of rowan trees (**c** and **d**), and the autocorrelation functions (ACFs) (e and f). Western Norway (Opedal) and eastern Norway (Røykenvik) includes three individuals each



A thresholded resource budget model

We here build on the theoretical formalism of Satake and Iwasa (2000). In the model, each individual, i , has a

the ratio of fruiting cost to flowering cost. With these assumptions, the energy dynamics of an individual can be written as:

$$S_i(t+1) = \begin{cases} S_i(t) + P_S & \text{if } S_i(t) + P_S \leq L_T \\ S_i(t) + P_S - (k+1)(S_i(t) + P_S - L_T) & \text{otherwise} \end{cases} \quad (1)$$

stored resource, $S_i(t)$, at the beginning of the year, t . The plants are subsequently assumed to accumulate P_S energy units during the season. When the stored resource $S_i(t) + P_S$ exceeds some critical level, L_T , the plant invests in reproduction. Otherwise, it saves its resources towards reproduction in a subsequent year. We call L_T the “reproductive threshold.” Upon reproduction, the energy invested in flowering is assumed to be proportional to its excess resources, i.e., $S_i(t) + P_S - L_T$. The energetic costs of fruit development following flower pollination is determined by k , which is

In this model, a large k means that a plant depletes resources to a lower level during reproduction. We, therefore, call k the “depletion coefficient.”

Here, we incorporate an additional level of realism into the model: a minimum as to how deep resource levels can be drawn during fruiting (after which the selective abortion of pollinated flowers occurs). Theoretically speaking, this translates to the assumption that the plant’s stored resource level cannot be negative (i.e., $S_i(t) \geq 0$ must be satisfied). As detailed in previous studies (Satake and Iwasa 2000, 2002a, 2000b), the non-dimensional

variable, $Y_i(t) = \frac{S_i(t) + P_S - L_T}{P_S}$, allows a complete mathematical analysis of the resulting masting dynamics. With the requirement that $S_i(t) \geq 0$, the non-dimensional variable has the following constraint:

$$Y_i(t) \geq 1 - \frac{L_T}{P_S} \quad (2)$$

From a biological perspective, the above inequality means that, when the ratio of the reproductive threshold (L_T) to the rate of productivity (P_S) is very large, the minimum threshold represented by the right-hand term in Eq. 2 can be very low after heavy reproduction. Hence, the modified model behaves according to the standard model (analyzed by Satake and Iwasa 2000, 2002a, 2000b). In contrast, when the ratio L_T/P_S is finite, $Y_i(t)$ is constrained to be above the level of $1 - \frac{L_T}{P_S}$, even after major flowering effort. We will see that such a minimum threshold greatly affects the general predictions with respect to masting dynamics, including the possibility of a productivity-induced transition from 2- to 3-year mast intervals.

Using the non-dimensional variable $Y_i(t)$ with the constraint of Eq. 2, the energy allocation dynamics become:

$$Y_i(t+1) = \begin{cases} Y_i(t) + 1 & \text{if } Y_i(t) \leq 0 \\ -k[Y_i(t)]_{\min} + 1 & \text{otherwise} \end{cases} \quad (3a)$$

where $[Y_i(t)]_{\min}$ is given by:

$$[Y_i(t)]_{\min} = \begin{cases} Y_i(t) & \text{if } Y_i(t) \leq \frac{L_T}{kP_S} \\ \frac{L_T}{kP_S} & \text{otherwise} \end{cases} \quad (3b)$$

Equations 3a and 3b mean that, if the variable representing the level of stored resources, $Y_i(t)$, is negative, the plant does not reproduce; otherwise, it reproduces with some effort to deplete its resources. However, the effort is constrained due to abortion such that the energy depletion is at most up to the minimum threshold, $1 - \frac{L_T}{P_S}$.

Two hypotheses: local adaptation versus productivity gradient

Armed with the thresholded resource budget model, we can clarify the two hypotheses for geographic variation in masting—local adaptation and productivity gradient—using the following definitions.

The local adaptation hypothesis considers how intraspecific variation in masting may be caused by geographic differentiation among the genes that control the reproductive strategy. Although the detailed relation between genetic and physiological mechanisms regarding resource allocation is largely unknown, it is reasonable to assume that both the depletion coefficient (k) and the reproductive threshold (L_T) are genetically determined, since fruit display (the size, number, nutrient quality, and morphology) are important determinants of the reproductive success of plants. Plants

employing a higher magnitude of k invest more resources on seed production against flower production, and, consequently, higher quality fruits are produced. In contrast, as L_T is increased, the maximum capacity of resource investment for fruiting per year is increased, resulting in an increase in the maximum number of fruits that can be produced in any given year. If the resource requirement for fruiting, $k(S_i(t) + P_S - L_T)$, exceeds L_T , the abortion of fertilized flowers occurs. The local adaptation hypothesis implies that either k and/or L_T varies locally to match the local optimum with respect to the reproductive strategy, given the local environmental and ecological conditions. Geographic differences in these parameters are then hypothesized to cause geographic variation in masting dynamics, such as that exemplified by the transition from 2- to 3-year mast in rowan across southern Norway.

The productivity gradient hypothesis assumes that the underlying biological parameters do not vary geographically—in particular, parameters k and L_T would be regarded as constant among populations—and that the differences in masting dynamics result from geographic variation in productivity, P_S , due to different environmental conditions, such as variations in temperature and precipitation levels. Based on the climatic data for southern Norway, we conjecture that the west has larger productivity than the east, as explained in the previous section.

Theoretical plausibility of the local adaptation and productivity gradient hypotheses

The purpose of this section is to explore which hypothesis is more likely to predict a shift from 2- to 3-year cycles in the reproductive dynamics of the rowan populations as proceeding from west to east in southern Norway (Fig. 1). For this purpose, we first provide a brief analysis of how the presence of a minimum threshold to resource depletion (Eqs. 3a and 3b) affects masting dynamics.

A shift from a 2- to a 3-year cycle in masting is not predicted to result from any parameter changes in the classic resource budget model. As detailed by Satake and Iwasa (2000), as the plant invests more resources to fruiting (i.e., as the depletion coefficient, k , increases), the plant's reproductive dynamics is predicted to change from annual constant reproduction to a quasi 2-year cycle with high and low reproductive activity in alternating years; these fluctuations are not strictly cyclic because they are, in fact, chaotic (Satake and Iwasa 2000). However, statistically speaking, they have a strong and dominant 2-year signal. As k increases further, the quasi 2-year cycle is replaced by irregular and strongly chaotic fluctuations without any statistical periodicity.

Varying k , therefore, cannot produce a shift from (quasi) 2- to 3-year cycles if there is no lower bound on resource depletion. Moreover, variations in the repro-

ductive threshold, L_T , or productivity, P_S , do not influence the reproductive dynamics qualitatively because the underlying (non-dimensionalized) resource dynamics is independent of the magnitude of L_T and P_S (for details, see Satake and Iwasa 2000). This result is somewhat counter-intuitive and results from the fact that, in a high-productivity environment, an individual will accumulate energy faster, but it will also allocate more energy to flower production upon deciding to reproduce. As a consequence, its resource level will be depleted to a lower level and, ultimately, it takes the same amount of time to replenish the energy reserves to above the threshold as in a lower productivity environment. This effect depends, however, on the biologically unreasonable, implicit assumption that energy reserves can be depleted to arbitrary low levels.

The refined model that we introduced above (Eqs. 3a and 3b) reveals an important effect of an explicit minimum threshold on the dynamics. The presence of such a threshold can push chaotic fluctuations (Fig. 2a, b) to strictly periodic ones (Fig. 2c, d). This indicates that the minimum threshold provides a stabilizing effect—if there is a bound on how deep plants can deplete their energy resources, chaos is replaced by cyclic patterns. The consequence of changing the minimum threshold is shown in the bifurcation diagram in Fig. 3a. This bifurcation diagram shows the long-term trajectories of reproductive levels across a range of values of the depletion coefficient, k , for a minimum threshold arbitrarily set to -1.2 . We calculated the power spectrum of the time series generated from the model in order to elucidate the statistical periodicities (Fig. 3b). Recall that dominant fluctuations at a frequency of 0.5 represents a 2-year cycle (and 0.25 a 4-year cycle, etc.). As predicted by the original model, we initially find a shift from annual quasi periodic 2-year cycles to chaotic dynamics as the depletion coefficient, k , increases. However, we also observe a transition from chaotic to

periodic behavior for high values of k that is not predicted by the standard model. Importantly, there is a parameter region with a conspicuous 3-year cycle in reproduction (Fig. 3b) that is absent from the model without the minimum threshold.

The predicted transition from 2- to 3-year reproductive cycles with a change of the depletion coefficient, k , (Fig. 3) provides a theoretically plausible mechanism for how local adaptation may give rise to geographic variation in masting dynamics. In particular, the results indicate that the transition from 2- to 3-year reproductive cycles is possible if the plant population in eastern Norway employs a much larger depletion coefficient (more than double) than that in western Norway (Fig. 3). However, biologically speaking, it does not seem realistic that there is such a large difference in fruit quality between individuals in the two different areas. We conclude that, while the refined model produces a theoretically feasible transition from a 2- to a 3-year cycle because of local adaptation, the implication regarding geographic variation in fruit quality is so extreme that the local adaptation hypothesis by changing the depletion coefficient, k , seems unlikely to be responsible for the patterns.

We now turn to explore the theoretical plausibility of the productivity gradient hypothesis and the local adaptation hypothesis by changing the reproductive threshold, L_T . We study the reproductive dynamics and the spectral density as a function of the minimum threshold, $1 - \frac{L_T}{P_S}$. As the minimum threshold increases, the reproductive dynamics become more cyclic (as opposed to chaotic), showing a clear periodicity in reproduction (Fig. 4). The result further shows that there is a transition from 3- to 2-year cycles as the minimum threshold increases, even for a fixed value of k . The minimum threshold decreases as L_T increases. Therefore, this result implies that the observed shift in rowan populations in southern Norway is possible if the plant

Fig. 2a–d Return maps (a, c) and time series (b, d) of the energy dynamics of a single tree. **a** and **b** indicate the results without a minimum threshold at energy level, while **c** and **d** assume an existence of a minimum threshold ($\frac{1-L_T}{P_S} = -1.2$). The depletion coefficient, k , is set as 4.5

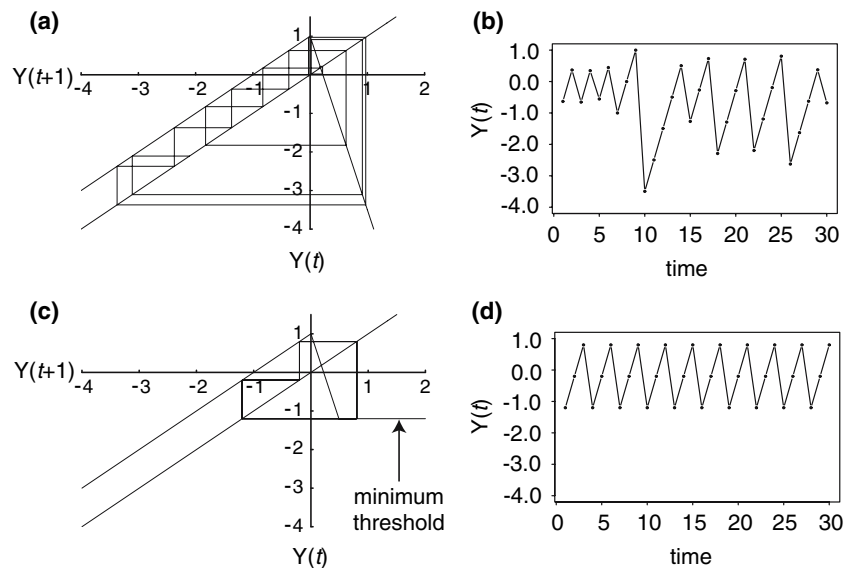


Fig. 3a, b The bifurcation diagram (a) and the spectrum density (b) of the reproductive dynamics of a single tree generated from the model with a minimum threshold $\left(1 - \frac{L_T}{P_S} = -1.2\right)$. In a bifurcation diagram, we plotted a long-term orbit for the amount of resources invested for fruiting (i.e., $k[Y(t)]_{\min}$) along the depletion coefficient k

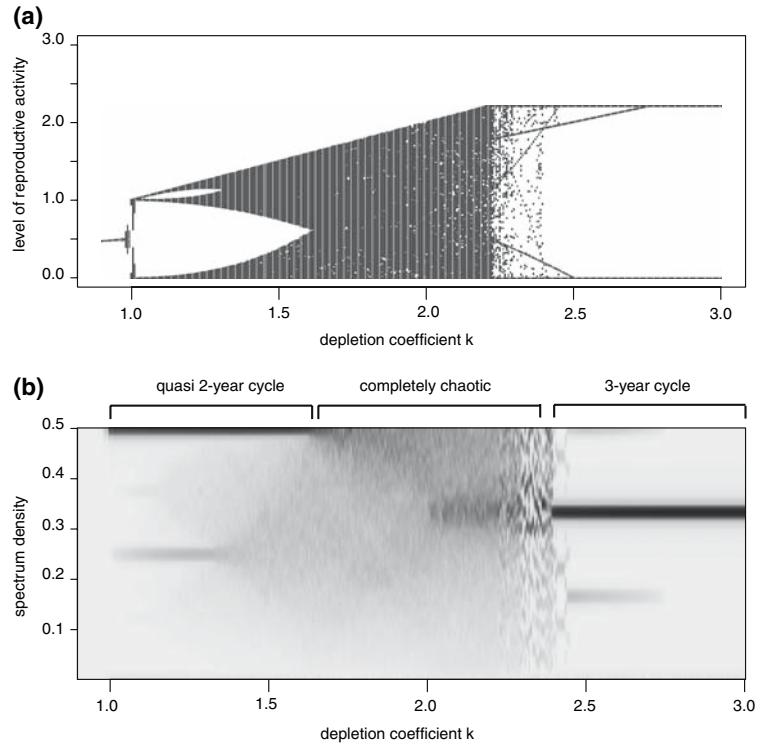
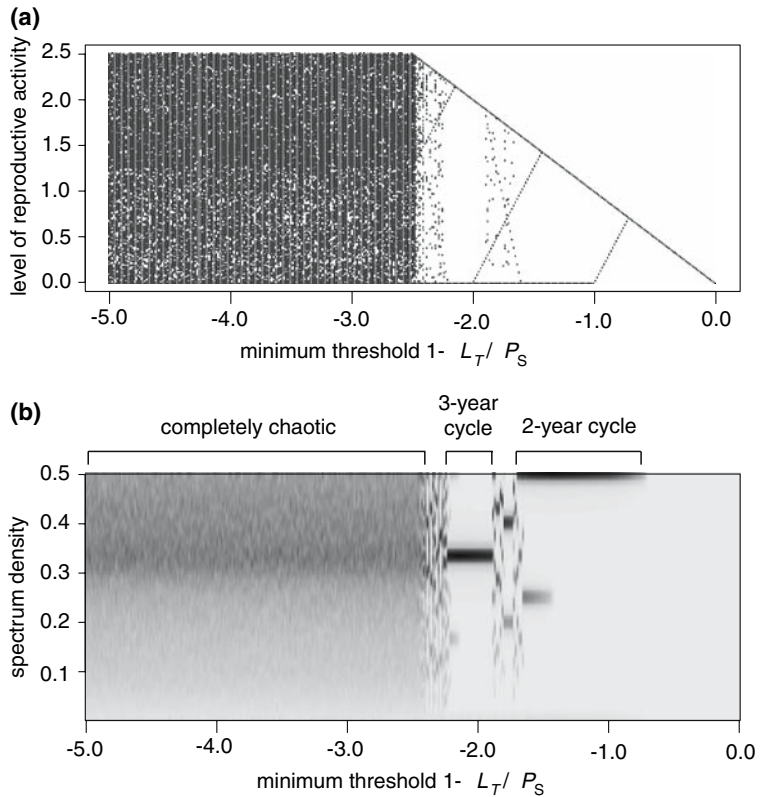


Fig. 4a, b The bifurcation diagram (a) and the spectrum density (b) of the reproductive dynamics of a single tree plotted against minimum thresholds $\left(1 - \frac{L_T}{P_S} = -1.2\right)$. In a bifurcation diagram, we plotted a long-term orbit for the amount of resources invested for fruiting (i.e., $k[Y(t)]_{\min}$) along the depletion coefficient k . Parameter $k = 2.5$



population in eastern Norway employs a larger reproductive threshold than that in western Norway. Moreover, the minimum threshold increases with P_S , which means that the observed shift is also expected if the plant

population in eastern Norway experiences lower productivity than that in western Norway. Based on our review of climatic data (temperature and precipitation), we conjecture that productivity is, in fact, lower in

eastern than western Norway, based on the analysis of environmental factors. If this is true, the productivity gradient hypothesis is supported both theoretically and empirically. The local adaptation hypothesis by altering the magnitude of the reproductive threshold is supported at least theoretically, but we lack empirical evidence.

Discussion

Our theoretical explorations of masting were motivated by how rowan trees exhibit significant intraspecific variation in reproductive dynamics with a 2-year cycle in western but a 3-year cycle in eastern Norway (Fig. 1; Satake et al. 2004). We investigated two intuitively plausible mechanisms to explain such a dramatic transition in reproductive dynamics: local adaptation versus productivity gradient. The original resource budget model by Isagi et al. (1997) and Satake and Iwasa (2000) assumes that plants accumulate resources every year, and set flowers and seeds when the stored resource exceeds some threshold level. If large resources are invested to set flowers and seeds, energy reserves are exhausted and the plants cannot flower until the energy reserves are replenished. One may intuit that increased productivity should decrease the inter-mast interval so as to generate geographic variation in masting patterns. However, the original resource budget model does not predict such a relation. Nor is it able to generate 3-year mast cycles. We proposed a more biologically realistic model to resolve this theoretical puzzle.

We found that the reason that the original resource budget model (Isagi et al. 1997; Satake and Iwasa 2000) does not predict the transition from 2- to 3-year cycles in reproduction is because it assumes there to be no bound on how deep plants can deplete their energy resources. We showed that an addition of such a bound results in a potential for productivity-related geographic variation in masting dynamics. Using the new model, we assessed the theoretical plausibility of the two different hypotheses—local adaptation versus productivity gradient—in generating the observed geographic variation in masting.

The local adaptation by altering the maximum amount of investment for fruiting (i.e., the reproductive threshold, L_T) was shown to produce the intraspecific variation observed in rowan populations in southern Norway if the eastern population employs a higher L_T . The productivity gradient hypothesis also was supported. The model reproduced the observed geographic variation if productivity in the east is smaller than that in the west. The prediction by the productivity gradient hypothesis matched with the empirical finding that the productivity is, in fact, likely to be lower in the east than in the west (Fig. 1), although we lack empirical data to test the likelihood of the local adaptation hypothesis.

Having said that, we currently lack empirical methods to rigorously test for local adaptation. We see some

potentially fruitful approaches towards tackling the issue of local adaptation. The experimental approach would be one of reciprocal transplantations—which should be doable though awkward given the size of mature rowan trees. A more indirect method would be a comparison of the extent of predation pressure by the apple fruit moth between the west and east. The apple fruit moth, *Argyresthia conjugella* Zeller, is a major pre-dispersal seed predator of rowan trees. Although the overall attack rates by the apple fruit moth was not significantly different between the regions (Satake et al. 2004), it is conceivable that a more subtle difference in moth populations, such as the timing of emergence and dormant strategies, may result in selection for different reproductive strategies. Finally, it would be of interest to follow up on the statistical approach of Rees et al. (2002) to estimate the depletion coefficient, k , from time series. However, that method would need to be modified to be applicable to the modified model that includes a lower threshold to depletion.

Theoretical models are increasingly providing useful insights for explaining spatio-temporal patterns in ecology (Tilman and Kareiva 1997; Hanski 1999; Dieckmann et al. 2000). Many of these insights have come from adapting general (“strategic”) models to specific case studies involving long-term data. Often, specific details of biology are essential in order for the models to capture key features. Our analysis illustrates the usefulness of applying this approach in the study of masting dynamics.

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