Estimating the fitness of a local discrete-structured population: From uncertainty to an exact number

Dmitrii O. Logofet [a,b,*]

[a] Laboratory of Mathematical Ecology, A.M. Obukhov Institute of Atmospheric Physics, Russian Academy of Sciences, Moscow 119 017, Russia
[b] Institute of Forest Science, Russian Academy of Sciences, Uspenskoe 143030, Russia

ABSTRACT

The fitness of a local discrete-structured population is measured by the dominant eigenvalue λ_1 of its matrix model, L, calibrated on empirical data. The data mined in case studies on local populations of *Calamagrostis* spp., perennial long-rhizome grasses colonizing rapidly open spaces (such as forest clear-cuts or meadows) due to their fast vegetative propagation, do provide for the accurate calculation of the transition part T in canonical sum of $L = T + F$, but leave the reproduction summand F uncertain. This 'reproductive uncertainty' (which is still constrained by the data and botanical knowledge) was amenable to calibration under the hypothesis that the adaptation is maximal for the given data and constraints, while the need to test the hypothesis experimentally motivated a drastic change in the technique of field experiments: from the description of above-ground parts of clones on a sample plot to the excavation of the whole colonies and analysing its system of rhizome reproductive links. In this paper, I report on how the "evolution" of experimental design and calibration technique has achieved an exact number in the estimation of fitness measure. As a by-product of that evolution, a new phenomenon has been discovered in the ontogeny of *Calamagrostis epigeios*, which has induced unexpected situations where the ever-working $\lambda_1(L)$ fails in the accuracy and needs an adjustment. The data-vs.-model dialectics behind the story are also commented on.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Higher plants are widely known to adaptively respond to environmental "challenges" with 'a diversity of options' (Chapin et al., 2010, p. 246) including their responses at different levels, from physiology (Jaleel et al., 2009) to adaptive dynamics (Zhukova and Komarov, 1990; Kozlowski and Pallardy, 2002) and evolution (Grime, 1977, 2001; Sultan, 1987, 2000). An observable and measurable kind of those responses is generalized in the concept of *polyvariant ontogeny* meaning 'the realization of diverse pathways' of individuals of a species (Zhukova and Komarov, 1990, p. 451). Polyvariant ontogeny is considered the major mechanism of species adaptation at the local population level, and the quantitative measure of adaptation can be determined via constructing a proper matrix population model and calibrating it from available data as outlined below.

The 'diverse pathways in the ontogenesis' may be vividly seen in what is called *the life cycle graph* (*LCG*) for a discrete-structured population (Caswell, 1989, 2001): the vertices of the graph represent various *statuses* of individuals in a classification adopted (or *generalized stages*, Caswell, 2001), while the directed arcs represent possible (often alternative) transitions or reproductive contributions that individuals of certain statuses can do in one time step. An example is given in Fig. 1, where the classification was double: both in the chronological age and the ontogenetic stages of individuals along a so-called 'scale of ontogeny' (Ulanova et al., 2008). Those 'scales' are well developed in the Russian school of botany (Uranov, 1967, 1975; Rabotnov, 1978; Zhukova and Ermakova, 1985; Zaugolnova et al., 1988; Ulanova, 2000; Ulanova et al., 2002) from considering the continuous ontogenetic process as an ordered sequence of discrete stages, the stages being determined by the morphology of individual plants and given standard notations (*ibidem*).

Fig. 1 presents a sample of the LCGs that were used in our case studies of *Calamagrostis* spp., perennial long-rhizome grasses colonizing rapidly open spaces, such as forest clear-cuts or meadows, due to their fast vegetative propagation (Ulanova et al., 2002). The *vertices* (or *nodes*) of the graph constitute a finite set defined on a 2D lattice of nodes as the field data contain both the stage and the chronological age of individual plants (in years, *ibidem*). Note that,

* Tel.: +7 916 6286229; fax: +7 495 953 1652.
  E-mail address: danilal@postman.ru
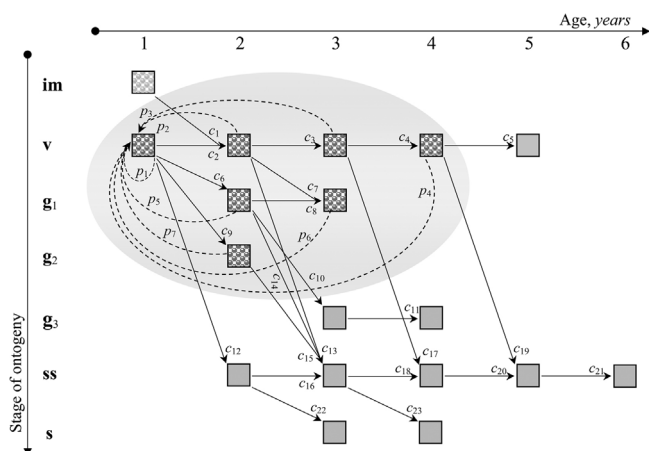
Fig. 1. Life cycle graph for a mature population of *C. epigeios* woodreed reproducing vegetatively. The stages are: **im**, immature; **v**, virginal; **g**, generative; **ss**, subsenile; **s**, senile. Empty boxes designate the age-stage states that were not observed in the field study, the patterned ones indicate states participating in reproduction. Solid arrows represent aging and ontogenetic transitions, the dashed ones correspond to reproduction. Latin letters attributed to arrows denote the corresponding, age-stage-specific vital rates (adapted from Ulanova et al., 2008).

according to the LCG in Fig. 1, there is only one single stage-specific group ($\mathbf{v^1}$) where the recruits occur.

Given an LCG and the vector, $\boldsymbol{x}(t)$, of population structure, the corresponding "projection matrix" (Caswell, 2001) provides for the basic model equation

$$\boldsymbol{x}(t) = \boldsymbol{L}\boldsymbol{x}(t-1), \quad t = 1, 2, \ldots, \tag{1}$$

where the elements of $\boldsymbol{L}$ represent the status-specific *vital rates* (i.e., *transition* and *reproduction* rates, *ibidem*). Once matrix $\boldsymbol{L}$ becomes quantitatively certain due to calibration from data, its dominant eigenvalue $\lambda_1(\boldsymbol{L})$, in spite of the asymptotic role it plays in model dynamics (1) (Caswell, 2001), does measure the adaptation that the local population possessed in the place where, and at the time when, the population data were collected to calibrate the matrix $\boldsymbol{L}$ (Logofet, 2013a; Logofet et al., 2014). The value of λ_1 thus serves as the basis for site- and time-specific comparative studies, where the problem reduces to reliable matrix calibration on the specific data.

The kind of data in which they monitor changes in the status of each individual at successive moments of time was called 'identified individuals' (Caswell, 2001, p. 134). It is advantageous as the status-specific transition rates can be calculated just as the frequencies of the corresponding transition events to be observed (*ibidem*). However, the data gained in our field studies 'on the ground' (RFBR, 2013; Logofet et al., 2014) should rather be called 'identified individuals with uncertain parents' (Logofet, 2010, p. 40; Logofet et al., 2012, p. 89) because they bear no information about the parent plants of recruiting individuals. The total number of recruits follows from the next-moment data, but the contribution by each of several status-specific reproductive groups still remains uncertain, generating the uncertainty in the status-specific reproduction rates ('reproductive uncertainty', Logofet et al., 2012, p. 99). As a result, $\lambda_1(\boldsymbol{L})$, the measure of adaptation, remains uncertain, too, yet being restricted to Eq. (1) and specific data.

To overcome reproductive uncertainty, various tricks were proposed in the literature, at various extents of arbitrariness (survey in Logofet, 2008), yet none of them conformed the idea of polyvariant ontogeny. Alternatively, an extremal principle to be substituted for the uncertainty suggested that $\lambda_1(\boldsymbol{L})$ takes on the maximal value among those admitted by Eq. (1) and the data (*ibidem*; Logofet, 2010). Aside the issue of whether the maximation hypothesis was evolutionary true, the calibration then reduced to a nonlinear

constraint maximization problem for $\lambda_1(\boldsymbol{L})$, thus providing for a single method of comparative studies.

A recent case study was aimed at testing the maximization hypothesis experimentally (Logofet et al., 2015) and focused on the parent-offspring links 'beneath the ground' (Logofet et al., 2014). Excavating the whole connected system of ramets from a sample plot and detecting all their rhizome links were supposed to enable directly calculating the contributions by status-specific reproductive groups to the recruitment. However, the reproductive uncertainty has still turned out to persist for a certain reason, yet be restricted so as $\lambda_1(\boldsymbol{L})$ to lie within certain (upper and lower) limits (Logofet et al., 2015), or 'the limits of adaptation in the local population of a clonal plant with multivariant ontogeny' (RFBR, 2013).

In the present paper, I report on how a modification of the experiment technique has totally eliminated the reproductive uncertainty and reduced the range of feasible $\lambda_1(\boldsymbol{L})$ values to a single number. That number has helped test the maximization hypothesis and refine its formulation for the further studies.

2. Materials and methods

2.1. Key species

The woodreed *Calamagrostis epigeios* (L.) Roth was taken as a key species for modelling. It is a perennial, clonal, long-rhizome, polycarpic grass, which propagates vegetatively, colonizing open areas, such as forest clear-cuts, and dominating 100% of the area (Ulanova, 1995). The morphology of individual ramets in a woodreed colony was well studied before (*ibidem*), so the chronological age of ramets can be determined from the pattern of annual growths in the tillering zone (*ibidem*; Ulanova et al., 2002; Schweingruber and Poschlod, 2005), while the ontogenetic stage of each ramet be determined by the 'scale of ontogeny' (Ulanova et al., 2007, 2008). In a case study by Janczyk-Weglarska (1997), the polyvariant ontogeny in *C. epigeios* was proved to be caused rather by phenotypic variability than genetic modifications.

2.2. Field experiments

The experiments were aimed at gaining data of the 'identified individuals' type without any reproductive uncertainty. As a means to avoid the uncertainty, the whole colonies were excavated from sample plots in order to dig up the system of parent–offspring rhizome links, thereafter to estimate the contribution of each status-specific reproductive group to the population recruitment.

The structures of local *C. canescens* populations, i.e., vectors $\boldsymbol{x}(t)$ of Eq. (1), were studied on a complete clear-cut area of spruce forest (Moscow Region, Russia), where the plots of woodreed phytocoenosis were totally dominated by *C. epigeios* (Logofet et al., 2015). In addition to the traditional analysis of the above-ground morphology at the moment of excavation, the population structures the year before, $\boldsymbol{x}(t-1)$, were also recovered as far as the last-year stage of each plant could also be determined from its current status and the pattern of dry shoots.

The experiments were conducted during 2013–2015, in the middle of each-year August, when the ramets have completed their developments in the current season. The experimental design was successively modified each year to improve the degree of uncertainty elimination.

2013. Three sample plots of $1 \times 1\,\text{m}^2$ size were analyzed: the 1st one with a 2-year-old part of the population, the 2nd with a 3-year-old part, and the 3rd with a 4-year-old part. The $1 \times 1\,\text{m}^2$ size turned out sufficient to specify the population structure as the number of ramets exceeded 100 in each plot (Logofet et al., 2014).