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Transient and asymptotic demographics of the riparian species *Euptelea pleiospermum* in the Shennongjia area, central China

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ABSTRACT

Transient dynamics is a growing concern in population biology and is particularly relevant for rare species that colonize ecotones. *Euptelea pleiospermum* is a threatened species endemic to eastern Asia and a common component in riparian forests. Transient amplification and attenuation envelopes, as well as elasticities of population growth rates and population momentum, were explored based on stage-structured transition matrix models to articulate the population dynamics of this species. The results demonstrated that transient population growth rates and eventual population sizes (i.e. population momentum) differed sufficiently from asymptotic expectations. But transient population fluctuations as measured by amplification and attenuation envelopes were modest in size. The potential of transient amplification and attenuation are perhaps associated with reproduction of early mature individuals and the mortality of juveniles, respectively. Both asymptotic and transient population growth of *E. pleiospermum* are most sensitive to survival, less sensitive to tree growth, and largely insensitive to fecundity, whereas the importance of vegetative reproduction is pronounced over fecundity. Underrepresented or overrepresented stages in the initial structure relative to stable stage distribution have comparatively larger elasticities of transient population growth and population momentum, suggesting the importance of vital rates of "biased" stages in driving transient dynamics. Our results highlight the use of transient envelopes and elasticities in guiding the adaptive management for the target species.

1. Introduction

Riparian corridors, as ecotones between terrestrial and aquatic zones are some of the most biophysically complex and ecologically dynamic communities on the planet (Gregory et al., 1991; Naiman and Décamps, 1997). It has been suggested that riparian ecotones provide critical habitats for rare and threatened species (Naiman et al., 1993; Naiman and Décamps, 1997), which in turn make significant contributions to community structuring and ecosystem functioning (Cao et al., 1998; Lyons et al., 2005). There are a great many rare and threatened species concentrated in riparian forests, which repeatedly emerged in eastern Asia, west-central Europe and southeastern USA (Burkart, 2001; Galuszka and Kolb, 2002; Hampe and Arroyo, 2002; Sakio et al., 2002). This kind of biodiversity pattern is appealing to both biogeographers and conservation biologists.

As lucidly illustrated by Washitani (2001), "conserving local populations of certain species associated with unique habitats or ecological processes is a clear operational goal for ecosystem management" and one of the most important practical paths protecting global biodiversity. Consequently, population biology of rare and threatened species closely associated with riparian habitats ought to enjoy a high priority in ecological investigations for conservation (Washitani, 2001). Furthermore, the problem of transients (short-term dynamics) is particularly acute for rare and endangered species in riparian zones because of quite unstable habitats within ecotones and high susceptibility of small populations to stochasticity. Subjected to periodical perturbations and/or disturbances, populations of riparian species rarely reside in the stable (st)age distribution or grow at an asymptotic rate (λ). Traditional population modelling based on equilibrium assumptions (i.e. stable (st)age distribution and asymptotic rate) are inadequate to capture the essence of such population dynamics.

Demography deals with fundamentals of population biology and is a powerful tool in predicting and interpreting population dynamics, as well as proposing conservation and restoration schemes for rare and endangered species (Harper and White, 1974; Menges, 1990; Schemske et al., 1994). Sensitivity analyses often focus on the response of asymptotic population growth (λ) to changes in vital rates and provide in-depth insights into life-history evolution and wildlife management (Caswell, 1982;

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Silvertown et al., 1993, 1996; Benton and Grant, 1996). But asymptotic demography fails to recognize transient dynamics in natural populations, that is, the fluctuation and oscillation in both population growth rate and population size over short time intervals for populations with unstable (st)age distributions. The magnitude and direction of transient dynamics can depart substantially from those of asymptotic dynamics (Stott et al., 2010), and the response of transients to changes in vital rates differs qualitatively from that of asymptotics in some situations (McMahon and Metcalf, 2008; Buhnerkempe et al., 2011). The importance of transient behavior as an internal dimension of population dynamics was realized by early demographers (Keyfitz, 1971; Tuljapurkar, 1983; Law and Edley, 1990). But only recently were appropriate analytic methods developed (Fox and Gurevitch, 2000; Caswell, 2007), thereby prompting enthusiastic interests of transient analysis in population ecology and conservation (Hastings, 2004; Stott et al., 2011). Currently, the integration of both asymptotic and transient demography can yield a thorough understanding of the critical population processes and can be ideal for adaptive management goals as well (Ezard et al., 2010; Buhnerkempe et al., 2011).

Euptelea pleiospermum (Eupteleaceae) is a deciduous tree species and a common component of riparian forests. It is a Tertiary-relict and East-Asia endemic species. Although widely distributed in China, it has very small population sizes on isolated sites as a result of increased forest logging and habitat degradation. It is therefore considered a rare and threatened species and requiring conservation efforts (Fu and Chin, 1992). Ecological factors such as light and substrate influencing seed germination and seedling survival have been examined experimentally (Wei et al., 2010). Its population size, structure and spatial distribution were previously documented (Wei et al., 2008). Nevertheless, population dynamics are less reliably predicted just by individual demographic traits or the static size structure, but more convincingly by demographic models (Batista et al., 1998; Condit et al., 1998; Feeley et al., 2007; Stott et al., 2010). However, matrix models for structured dynamics of *E. pleiospermum* have not been developed.

Here, both asymptotic and transient dynamics of *E. pleiospermum* in the Shennongjia area were examined in detail, aiming at addressing the following two questions: (1) how do population growth rates and population sizes change in response to disturbed stage distributions? (2) How sensitive are population growth rates and population sizes to perturbations to vital rates in the short versus long term?

2. Materials and methods

2.1. Study area

The Shengnongjia (Shennungia in the Wade-Giles Romanization System) area (31.25°–31.95°N, 109.93°–110.97°E) is located in western Hubei (Hupeh in Wade-Giles Romanization System) Province, central China. It straddles the transition between the higher mountains of southwestern China and the low, hilly regions of southeastern China. Simultaneously, it is characterized by a north-south interface climate between temperate and subtropical zones. Monsoons moving north cross the area; annual precipitation ranges from 800 to 2500 mm with the majority in summer. Mean annual temperature ranges from 14.5 °C at 460 m to 4.8 °C at 2300 m above sea level. According the observation of the 1980 Sino-American Botanical Expedition (Bartholomew et al. 1983), microclimates in this area vary notably with the topographical features of high, steep mountains and deeply incised valleys, providing a diversity of habitats that "range from warm temperate-subtropical at the lowest elevations to essentially boreal at the summits of the highest peaks". Vertical vegetation zonation can be roughly classified into a subtropical zone below1100 m, a warm temperate zone between 1100 and 2600 m, and a temperate zone above 2600 m (Zheng et al., 1997; Zhu and Song, 1999). The geographic position, complex topography, high microclimate variability and floristic history of the Shennongjia area have presumably resulted in the development of a rich and varied flora (Bartholomew et al. 1983).

As an important biodiversity hot-spot in the south-central China, the Shennongjia area is notable for its richness in Tertiary-relict and endemic plant species such as *Davidia involucrate*, *Cercidiphyllum japonicum*, *Tetracentron sinense* and *Dipteronia sinensis* (Ying et al., 1979; Bartholomew, 1983; Myers et al., 2000). Particularly in riparian forests, these relict and endemic species are remarkably rich (Jiang et al., 2002; Wei et al., 2009, 2010).

2.2. Field investigation and laboratory processing

We placed 18 *E. pleiospermum* quadrats in the riparian forests in the Shennongjia area. Quadrats ranged from $10\ m \times 20\ m$ to $50\ m \times 50\ m$ depending on local population patch size and were apart from each other between 0.06 and 3.86 km. In each quadrat, diameter at 1.3 m height (DBH hereafter, basal diameter if height <1.3 m) of each tree was recorded. For sprouted trees, the largest stem was deemed as seedling-origin stem, and the rest as sprout. In total, 3645 *E. pleiospermum* stems were registered with a mean density of 2014 ± 1410 stems/ha.

Cores were extracted from 109 *E. pleiospermum* trunks at the height of 1.3 m for determining the age-size relationship and evaluating growth rates through dendrochronological procedures. From 26 young *E. pleiospermum* stems slightly >1.3 m in height, basal and breast-height dices were truncated to estimate the time for a stem to be 1.3 m tall. Cores and discs were dried and polished until all annual ring boundaries were clearly visible. Ring width was measured to the nearest 0.001 mm with the WinDendro image-analysis system (TM2003b, Regent instruments Inc., Quebec, Canada). If any core did not meet the pith, number and width of those inner missing rings were estimated by the Duncan (1989) method which was incorporated into the WinDendro package.

Based on these dendrochronological procedures, the time for *E. pleiospermum* seedlings to reach 1.3 m in height was 2.5 ± 1.7 years ($n = 26$), and the age-radial growth relationship at 1.3 m height was $Y = 3.241DBH^{0.892}$ ($n = 109$, $r^2 = 0.8536$, $p < 0.001$).

2.3. Matrix model

All stems, regardless of seedling- or sprout-origin, were pooled and grouped into 7 stage classes. Stems lower than 1.3 m in height made up Class I, in which sprout- and seedling-origin stem were discriminated into two sub-classes: Ia and Ib, respectively. Class II consisted of stems with $\geqslant$1.3 m height and $\leqslant$2.5 cm DBH. DBH Intervals were 5 cm for Classes III through VI and Class VII included stems with >22.5 cm DBH.

The basic population growth equation is given by:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t)$ is the stage-structured population size at the time t in column vector, $\mathbf{n}(t+1)$ is the population vector at the next time step, and $\mathbf{A}$ is a population projection matrix (Lefkovitch, 1965) representing demographic transition rates such as probability of survival, recruitment and reproduction within a time interval. For this *E. pleiospermum* population, $\mathbf{A}$ is an $8 * 8$ matrix and $\mathbf{n}$ is a column vector with 8 elements.

Vital rates in each stage were estimated according to Caswell (1989) and Couralet et al. (2005). Stage-specific survival (σ_i) was calculated as:

$$\sigma_i = (n_{i+1}/n_i)^{(1/\Delta t)} \tag{2}$$