

Recruitment rates exhibit high elasticity and high temporal variation in populations of a short-lived perennial herb

F. Xavier Picó, Pedro F. Quintana-Ascencio, Eric S. Menges and Fabiola López-Barrera

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Empirical studies for different life histories have shown an inverse relationship between elasticity (i.e. the proportional contribution to population growth rate) and temporal variation in vital rates. It is accepted that this relationship indicates the effect of selective pressures in reducing variation in those life-history traits with a major impact on fitness. In this paper, we sought to determine whether changes in environmental conditions affect the relationship between elasticity of vital rates and their temporal variation, and whether vital rates with simultaneously large elasticity and temporal variation might represent a characteristic life-history strategy. We used demographic data on 13 populations of the short-lived *Hypericum cumulicola* over 5–6 years, in three time-since-fire classes. For each population of each time-since-fire, we computed the mean matrix over years and its respective elasticity matrix, and the coefficients of variation in matrix entries over study years as an estimate of temporal variability. We found that mean elasticity negatively significantly correlated with temporal variation in vital rates in populations (overall eight out of 13) included in each time-since-fire. However, seedling recruitment exhibited both high elasticity and high temporal variation in almost all study populations. These results indicated that (1) the general relationship between elasticity and temporal variation in vital rates was not modified by environmental changes due to time-since-fire, and (2) high elasticity and high temporal variation in seedling recruitment in *H. cumulicola* is a particular trait of the species' life history. After seed survival in the soil seed bank, seedling recruitment represents the most important life-history trait influencing *H. cumulicola* population growth rate (and fitness). The high temporal variability in seedling recruitment suggests that this trait is determined by environmental cues, leading to an increase in population size and subsequent replenishment of the seed bank in favorable years.

F. X. Picó, Dept of Ecology, Univ. of Nijmegen, Toernooiveld 1, NL-6525 ED Nijmegen, The Netherlands (xavier.pico@sci.kun.nl). – P. F. Quintana-Ascencio, E. S. Menges and F. López-Barrera, Archbold Biological Station, PO Box 2057, Lake Placid, 33862 FL, USA. PFQ-A and FL-B, División de la Conservación de la Biodiversidad, El Colegio de la Frontera Sur, San Cristóbal de Las Casas, MX-29290 Chiapas, México.

Understanding the relationships between elasticity (i.e. the proportional contribution of vital rates to the population growth rate; de Kroon et al. 1986, 2000, Caswell 2001), variability in vital rates, and population growth is crucial to reveal patterns of species persistence and life-history evolution (Real 1978, Lacey et al. 1983, van Tienderen 1995, Benton and Grant 1996). A growing

number of empirical studies have shown an inverse relationship between elasticity and variation in vital rates, that is, vital rates with a major importance for population growth exhibit low levels of temporal variation and vice-versa (Lande 1988, Ehrlén and van Groenendael 1998, Gaillard et al. 1998, Pfister 1998, de Kroon et al. 2000, Picó 2000, Sæther and Bakke 2000,

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Zuidema and Franco 2001). This seems to be a common pattern shown by many organisms, which may indicate that selective pressures may alter life histories to reduce variation in those traits with a major impact on population growth rate, which is considered a surrogate for fitness (Pfister 1998, Benton and Grant 1999, de Kroon et al. 2000).

However, a few empirical studies have clearly indicated that, despite the general negative relationship between elasticity and variation in vital rates, some life histories can exhibit particular vital rates with both high elasticity and high temporal variation. For example, Wisdom et al. (2000) found that survival among juveniles of the prairie chicken (*Tympanuchus cupido pinnatus*) had the highest elasticity and the widest temporal variation, and Picó et al. (2002) found that early seedling recruitment of the sweet alyssum (*Lobularia maritima* [L.] Desv.) also exhibited both high elasticity and high temporal variation. These results suggest the following question: are vital rates with simultaneously large elasticity and temporal variation inconsistent with life history theory?

Two different arguments have been given to explain the existence of vital rates with high elasticity and high temporal variation. On the one hand, Wisdom et al. (2000) argued that this could be related to rapid human-induced environmental degradation altering the temporal pattern of variation in particular vital rates, so that anthropogenic environmental variation might mask the real relationship between elasticity and variance in vital rates. Furthermore, Wisdom et al. (2000) also argued that sampling error included in the temporal variation might also cloud the pattern of variation in vital rates. On the other hand, Picó et al. (2002) suggested that vital rates with high elasticity and high temporal variation might have also been under selection, as they contributed to population persistence in a variable environment through peaks of recruitment. Theoretical studies have shown that when life-history trait variance is associated with population fluctuations in response to disturbances, the evolutionary process does not result in the elimination of variation (Ekbohm et al. 1980, Benton and Grant 1996). Furthermore, there is empirical evidence indicating selection for vital rate variation, and demonstrating that variance, in addition to mean, can be an important determinant of fitness (Lacey et al. 1983, Real and Ellner 1992).

In this paper we identify vital rates with high elasticity and high temporal variation. We seek to determine to what extent the relationship between elasticity and temporal variation in vital rates is affected by changes in the environment, and whether vital rates with simultaneously large elasticity and temporal variation may represent a life history strategy. Our study species was the short-lived perennial herb *Hypericum cumulicola* (Small) P. Adams that grows in environments with recurrent fire. *H. cumulicola* population dynamics are

characterized by high population growth rates in recently burned patches. With time-since-fire, survival, fecundity, establishment, and consequent population growth rates decrease (Quintana-Ascencio et al. 2003). In this study, we analyzed the relationship between elasticity and temporal variation in vital rates in 13 *H. cumulicola* populations over 5–6 years in three time-since-fire habitats. For each population of study, we applied elasticity analysis to determine the importance of vital rates in contributing to population growth rate, and estimated the temporal variation in vital rates by calculating their coefficient of variation. We then plotted and analyzed the relationship between elasticity and temporal variation in vital rates of *H. cumulicola*.

Material and methods

Plant species and study site

Hypericum cumulicola is a small, iteroparous, short-lived perennial herb that flowers and fruits between June and September (Quintana-Ascencio and Morales-Hernández 1997). This endemic plant of central Florida forms a persistent seed bank that can survive burning, although fire generally kills all aboveground plants. *H. cumulicola* is practically restricted to open areas between shrubs in Florida rosemary scrub (Quintana-Ascencio and Morales-Hernández 1997). Fire and drainage are major factors shaping Florida rosemary scrub, an open plant community that occurs on sandy and well-drained soils on ridges and knolls in central and coastal Florida (Abrahamson et al. 1984, Menges and Kohfeldt 1995, Menges 1999). The study was carried out at Archbold Biological Station, Highlands County (Florida, USA), which comprises a mosaic of areas with different fire histories.

Population sampling and matrix analysis

We used demographic data from 13 *H. cumulicola* populations, chosen to represent a time-since-fire gradient. Available records of fire occurrence (1968-present; Main and Menges 1997) were used to determine fire history of each site. We selected three time-since-fire classes: 3–6 years after fire (recently burned patches), 9–14 years after fire (patches a decade post-fire), and > 20 years after fire (long-unburned patches). Data on *H. cumulicola* survival, growth, and fecundity for each population were collected from annual August–September censuses of marked individuals (overall 4029 individuals) conducted for six years (1994–1999; Quintana-Ascencio et al. 2003).

A total of 62 six-stage population-year matrices were constructed: 12 (3 populations × 4 years) in recently burned patches, 30 (6 populations × 5 years) in patches

a decade post-fire, and 20 (4 populations \times 5 years) matrices in long-unburned patches. The six stages were (I) seeds in the soil seed bank, (II) a single stage of first-year plants (seedlings), (III) a single vegetative stage, and three reproductive classes: (IV) small (12–33 cm tall), (V) medium (34–50 cm), and (VI) large flowering plants (> 50 cm). Details for field sampling, data collection and matrix model parameterization can be found elsewhere (Quintana-Ascencio et al. 2003). For each population, we calculated the coefficients of variation ($CV = 100 \times SD/mean$) in matrix entries over study years as an estimate of temporal variability. Elasticity ($e_{ij} = a_{ij}/\lambda \times s_{ij}$) provides a measure of the sensitivity of population growth rate λ (s_{ij}) to proportional changes in the matrix elements (a_{ij}) (de Kroon et al. 1986, 2000, Caswell 2001). For each population, we computed the mean matrix over years and its respective elasticity matrix with MATLAB (MathWorks 1997). We used mean matrices because theory suggests that the arithmetic average of vital rates determines greatly how sensitive a population will be to variability in those vital rates (Tuljapurkar 1982, Pfister 1998). We correlated elasticity of mean matrices and CV in matrix entries over study years by using Spearman rank order correlations.

Temporal variability of seed survival in the soil seed bank (i.e. the between-year variation in the proportion of ungerminated seeds that remain alive in the soil) was not available. In fact, this is one of the most difficult matrix entries to estimate accurately given the great number of ecological factors affecting seed survival (e.g. dormancy, predation, aging, overlapping generations; Baskin and Baskin 1998). However, the probability of ungerminated seeds to remain in the soil seed bank was recorded once for each population of study (see details in Quintana-Ascencio et al. 1998). Seed survival in the soil is the only mean matrix entry represented by a single value and not by the mean over years. Seed survival rates ranged between 57.1 and 89.9% with a CV across populations of 13.6%. Given the great difficulties to estimate accurately the between-year variation in this transition for each population of study, we used the observed between-population estimate of variability in seed survival in the soil in all the analyses. We did not use $1 -$ (seed germination rate) as an estimate of seed survival rate because this approximation ignores important factors in *H. cumulicola*, such as seed dormancy and its variability between overlapping seed generations, so that variability in seed survival in the soil seed bank would be overestimated.

Results

The relationship between elasticity and temporal variability in vital rates was significant in eight of 13 *H.*

cumulicola populations. There were two non-significant relationships in recently burned patches, two in patches a decade after fire, and one in long-unburned patches (Fig. 1). All significant relationships (and even non-significant ones) showed negative coefficients (Fig. 1), indicating that demographic traits with the lowest temporal variation had the highest effect on population growth rate. In general, seed survival in the soil seed bank exhibited a high elasticity and the low value of temporal variation computed for this transition fits well with the expected general pattern. When seed survival was dropped from the dataset and analyses performed again, results were totally consistent with those of Fig. 1 (P-values and correlation coefficients), indicating that the inverse relationship between elasticity and temporal variation in vital rates is a robust pattern and did not strictly depend on seed survival in the soil seed bank.

Independently of the significance of the relationship between elasticity and variability in vital rates, some transitions exhibited both high mean elasticity and high temporal variability. In particular, seedling recruitment, from the seed bank or from adult plants (i.e. the average number of seedlings produced per large adult plant and year), showed elasticity values higher than 10% and CVs higher than 100% in 10 out of 13 populations of study (Fig. 1). For many populations, seedling recruitment had the second highest elasticity value after seed survival in the soil seed bank, but with temporal variability estimates comparable to those showed by survival rates of juvenile and reproductive plants (Fig. 1).

Discussion

Previous findings indicated an inverse relationship between elasticity and temporal variation in vital rates: vital rates with a major impact on population growth often exhibited the lowest levels of variability and vice-versa (Lande 1988, Ehrlén and van Groenendael 1998, Gaillard et al. 1998, Pfister 1998, de Kroon et al. 2000, Picó 2000, Sæther and Bakke 2000, Zuidema and Franco 2001). Our results were also consistent with these empirical studies and showed that elasticity and temporal variation in vital rates of *Hypericum cumulicola* were negatively significantly correlated in eight of 13 populations of study across all three time-since-fire classes. Environmental differences between habitats due to time-since-fire did not affect the relationship between elasticity and temporal variation in vital rates. The lack of correlation between elasticity and variability in vital rates for some populations suggests that small-scale population characteristics may affect vital rates and their patterns of temporal variability. Ecological factors that may explain this variability include (1) allelopathic compounds released by certain shrubs and lichens that

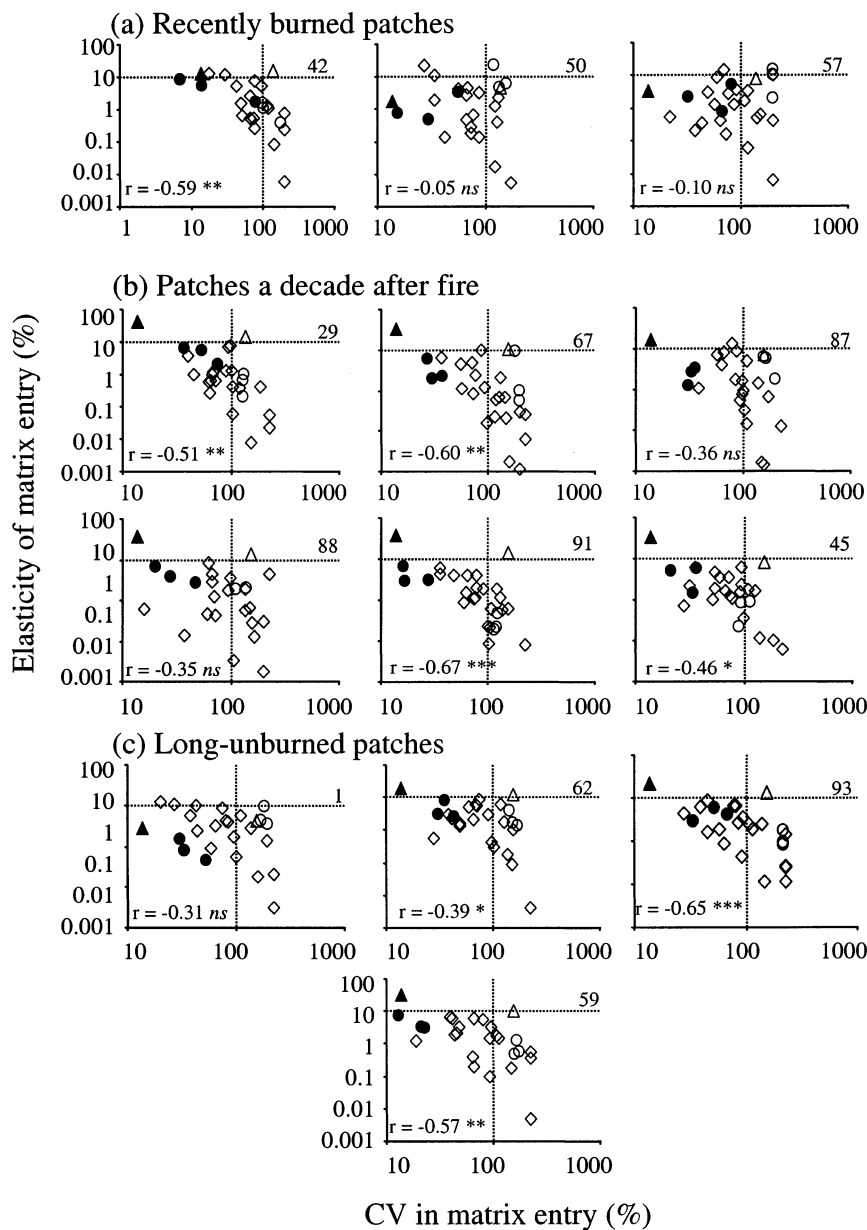


Fig. 1. Log-log plots of mean elasticity and coefficient of variation (CV) in matrix entries for each *H. cumulicola* population of study in each time-since-fire habitat. Demographic traits were grouped into five classes. Seed survival in the soil seed bank (filled triangles), seedling recruitment from seed bank (hollow triangles), seed production (filled circles), seedling production (hollow circles), and plant survival that includes survival, growth and retrogression of juvenile and reproductive plants (hollow diamonds). Dotted lines indicate elasticity values of 10% and CV of 100%. The population code within each time-since-fire is in the upper-right corner, and the r -value of Spearman rank order correlations is in the lower-left corner of each graph. Significance: ***, $P < 0.0001$; **, $P < 0.001$; *, $P < 0.05$; ns, non-significant.

may affect negatively seed germination, seedling growth and fecundity (Richardson and Williamson 1988), (2) mechanical obstruction of seedling recruitment and growth by lichens (Quintana-Ascencio and Menges 2000), and (3) belowground interference of shrubs constraining nutrient and water availability (Tyler 1996, Quintana-Ascencio and Menges 2000).

Some vital rates of *H. cumulicola* showed both high elasticity and high temporal variation. In particular, seedling recruitment from the seed bank and, to a lesser extent, seedling production exhibited such pattern in almost all populations in each time-since-fire, suggesting that this could be a specific life-history strategy of

H. cumulicola. After seed survival in the soil seed bank, seedling recruitment represents a critical life-history stage influencing *H. cumulicola* population growth rate and consequently fitness (Quintana-Ascencio et al. 2003). In fact, massive recruitment in favorable patches and years allows *H. cumulicola* populations to increase rapidly and/or replenish the soil seed bank. Similar population explosions are documented in other short-lived perennials (Picó et al. 2002) and annual plants with a seed bank (Kalisz and McPeck 1992), which are able to cope with high or unpredictable environmental variation. Hence, survival of *H. cumulicola* populations in fire-dependent habitats relies on persistent seed

banks, whereas seedling recruitment is regulated by environmental cues. As a result, seedling recruitment exhibits high elasticity, since population growth rate in short-lived plants is largely affected by recruitment, but also high temporal variability, since temporal variability in fecundity and germination is affected by changes in environmental conditions.

High elasticity and high temporal variation in seedling recruitment was also found in *Lobularia maritima*, another short-lived perennial herb (Picó et al. 2002). As occurs in *H. cumulicola*, seedling recruitment in *L. maritima* was not the vital rate with the highest elasticity, but seedling survival (seed survival in the soil seed bank in *H. cumulicola*). In the case of *L. maritima*, seedling survival showed the lowest temporal variability of all vital rates, which also occurs with seed survival in the soil in *H. cumulicola*, even though we used the observed between-population coefficient of variation in seed survival in the soil in our analyses. In other words, the most important vital rate for population growth might always show the lowest temporal variation, which would fit with life history predictions. For this reason, it is expected that the real temporal variation in seed survival in the soil seed bank of *H. cumulicola* should not be very high.

The interaction between life-history type and environmental variation may allow high levels of vital rate variation (Higgins et al. 2000). In particular, for life histories that allow the storage of reproductive potential across generations (such as seed banks, delayed germination, clonal growth, resprouting, etc), variance in recruitment rates can promote persistence (Higgins et al. 2000). In other words, populations with storage of reproductive potential between generations can benefit from occasional bumper recruitment events because they can persist long enough to benefit from erratic years with exceptionally high recruitment. The interaction between life-history type and vital rate variation becomes more evident when other plant life-history types are considered. Recently, elasticity and vital rate variation of six long-lived perennials have been analyzed and no vital rate showed both high elasticity and high temporal variation (Zuidema and Franco 2001). In long-lived organisms, recruitment contributes little to population growth rate, but has moderate/high temporal variability (Silvertown et al. 1992, 1993, Pfister 1998). Hence, only short-lived life histories in which recruitment, rather than survival of adult individuals, strongly contributes to population growth would show vital rates with simultaneously large elasticity and temporal variation.

Despite all these suggestive results, further comparative studies are needed to fully understand the relationships between contribution of vital rates to population growth and their variability across a wide range of animal and plant life histories. We stress the importance of re-analyzing demographic data sets by taking

into account multiple populations over a range of habitat variation and for several years to elucidate whether (1) the inverse relationship between elasticity and variation in vital rates holds under different environments, and (2) the existence of particular vital rates with both high elasticity and high temporal variation is a common trait of life histories in which recruitment importantly contributes to fitness.

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