

Interpretation of Elasticity Matrices as an Aid to the Management of Plant Populations for Conservation

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Abstract: Population projection (Lefkovich) matrices are now a standard method for quantifying and analyzing the demography and population dynamics of plants. Elasticity analysis of such a matrix indicates the relative effect on the population growth rate (λ) of small changes to matrix elements representing different transitions in the life cycle. In a comparison of elasticity matrices for 84 species of plants we show that the relative importance of recruitment from seed (measured by composite elasticity F), stasis (measured by composite elasticity L), and growth (measured by composite elasticity G) varies systematically between the groups semelparous herbs, iteroparous herbs of open habitats, forest herbs, shrubs, and trees. We discuss how this result might be used to construct rules of thumb useful in plant conservation. By looking in detail at how λ covaries with the composite elasticities F, L, and G among 16 populations of the semelparous herb *Cirsium vulgare* and among 15 populations of the rare iteroparous herb *Pedicularis furbishiae*, we show that a naive interpretation of elasticities can give a misleading prescription for management. Instead, we show that elasticity analysis supports management prescriptions based upon the successional status of a species or upon its response to disturbance.

La interpretación de matrices de elasticidad como una ayuda para el manejo de la conservación de poblaciones de plantas

Resumen: Las matrices de proyección poblacionales (de Lefkovich), constituyen en la actualidad un método estándar para cuantificar y analizar la demografía y dinámica poblacional de las plantas. El análisis de elasticidad de dichas matrices indica el efecto relativo sobre la tasa de crecimiento poblacional (λ) de pequeños cambios en los elementos de la matriz, los cuales representan distintas transiciones en el ciclo de vida. En una comparación de las matrices de elasticidad de 84 especies de plantas, demostramos que la importancia relativa del reclutamiento de las semillas (medido por la elasticidad compuesta F), estás (medido por la elasticidad compuesta L), y crecimiento (medido por la elasticidad compuesta G), varían sistemáticamente entre los grupos de las hierbas semélparas, las hierbas iteróparas de hábitats abiertos, las hierbas de bosques, los arbustos y los árboles. Discutimos como estos resultados podrían ser usados para construir reglas generales útiles en la conservación de plantas. Estudiando en detalle como λ covaría con las elasticidades compuestas F, L y G entre 16 poblaciones de la hierba semélpara *Cirsium vulgare* y entre 15 poblaciones de la hierba rara iterópara *Pedicularis furbishiae*, demostramos que una interpretación ingénua de las elasticidades puede dar una prescripción para el manejo errónea. En cambio, demostramos que el análisis de elasticidad apoya las prescripciones de manejo basadas en el estado sucesional de una especie o en su respuesta a las perturbaciones.

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Introduction

Ecologists and conservationists face a dilemma in drawing up management plans for the maintenance and recovery of populations of wild plants. On one hand ecologists tend to favor an approach based upon detailed demographic research that demands a large investment of time and money (Schemske et al. 1994), but on the other hand conservationists generally have neither the time to wait for the results of a demographic study nor the money to pay for it. There is little argument that only demographic studies can provide definitive answers to such questions as how a population's growth rate may be increased, though some contend that such studies must include a genetic dimension as well (Falk & Holsinger 1991). Equally, there is no arguing with the urgency or the magnitude of the task facing plant conservationists; it has been conservatively estimated that about 10% of plant species are threatened with extinction (Smith et al. 1993). In the face of such a dilemma ecologists must come up with some rules of thumb to guide conservation management (Mace & Lande 1990).

Generalizing is notoriously difficult in ecology, and until recently ecologists have been conspicuously reluctant to risk it. Theorizing is more popular, but there is a well-recognized trade-off between generality and precision in theoretical models that limits the theoretician when asked for specific advice about a population with few known parameters. We explore one possible route to a set of rules of thumb for use in the conservation of plant populations. We apply a simple theoretical model, the population projection model (Caswell 1989), to 84 species of wild plants and then attempt to generalize from the results. This approach is a development from the previous work of two of us on comparative plant demography that employed somewhat smaller samples of species (Silvertown et al. 1992; Silvertown & Franco 1993; Silvertown et al. 1993).

Population projection matrices have become the model of choice in plant demographic studies because they are well suited to the range of complex life cycles typical of plants and because matrix analysis yields a number of informative statistics. The dominant eigenvalue of the matrix is equivalent to the finite rate of population increase (λ), and elasticity analysis can be used to measure the relative effect on λ of small changes to matrix elements that represent particular transitions in the life cycle (de Kroon et al. 1986; Caswell 1989). The elasticity e_{ij} of a matrix element a_{ij} is

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\delta \lambda}{\delta a_{ij}}$$

The elasticity values for the elements in a projection matrix possess the useful property that they sum to unity. This makes it possible not only to compare the ef-

fect on a population's rate of increase of altering one transition in the life cycle (say germination) with the effect of changing another (say fecundity), but it also allows comparison between populations and between species.

Silvertown et al. (1993) used elasticity analysis to compare 66 species of herbs and woody perennials representing plants with a wide range of life histories and occurring in a broad range of habitats. To facilitate comparison the elasticity matrix (derived from the projection matrix) for each species was divided into three regions, and elasticities were summed within each region (Fig. 1). The *G* region measured the combined effects on λ of changes to growth and clonal growth, the *L* region measured the combined effects of changes to stasis (individuals remaining in a size class) and retrogression (individuals shrinking), and the *F* region measured the combined effect of recruitment from dormant and nondormant seeds. The *G/L/F* ratios for the 66 species were compared by ordinating them on triangular plots that showed clear relationships between the relative values of *G/L/F* and four functional groups defined by plant life history and habitat. These relationships could potentially be useful as rules of thumb, indicating the likely demographic characteristics of species similar to those for which we have data. We discuss how the demographic triangle might be used in this way, and for that purpose

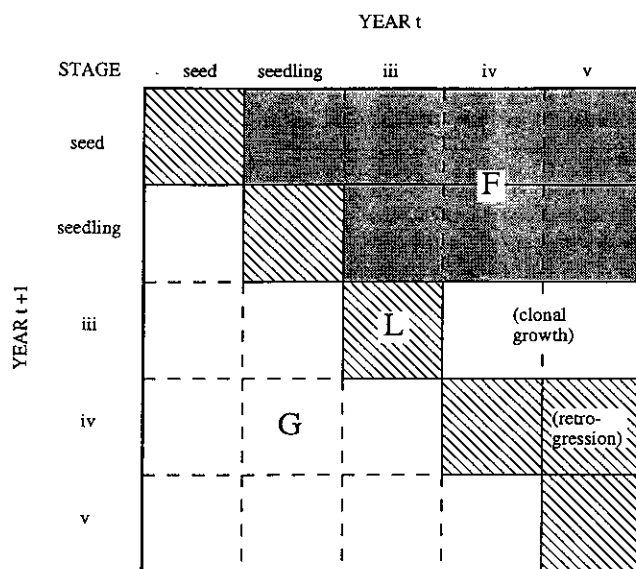


Figure 1. An ideal elasticity matrix divided into three regions, each containing life-history transitions associated with different components of the life cycle. Five life-history stages are shown: seed, seedling, and three size-classes (III-V) of adults. The composite elasticity values *G*, *L*, and *F* are the sums of the elements of the elasticity matrix in each region, as described in the text.

we repeat the ordination exercise for a larger sample of species.

Although elasticity indicates the relative sensitivity of λ to changes in a particular life-history transition, it does not indicate the relative sensitivity of those transitions to environmental perturbation. A large perturbation to a life-history transition with only a small elasticity value may have a greater impact on λ than a small perturbation to a life-history transition that has a larger elasticity value. For this reason it is unlikely that elasticities alone can be a completely reliable guide for conservation measures. The $G/L/F$ values also vary between different populations of the same species (Silvertown & Franco 1993), and this might make any rule of thumb unworkable. Therefore, as well as looking at variation in $G/L/F$ between species we also looked at variation in $G/L/F$ between populations. This was done for 16 populations of the semelparous perennial herb *Cirsium vulgare* and for 15 populations of the iteroparous perennial herb *Pedicularis furbishiae*.

Methods

An extensive literature search was conducted to identify plant demographic studies that either provided informa-

Table 1. Species and sources of data shown in Fig. 1 additional to the 66 listed by Silvertown et al. (1993).

Species	Source of data
Semelparous herb	
<i>Cirsium vulgare</i>	Bullock et al. 1994
Iteroparous herbs of open habitats	
<i>Andropogon semiberberis</i>	Silva et al. 1991
<i>Aristida bipartita</i>	O'Connor 1993 ^a
<i>Bothriochloa insculpta</i>	O'Connor 1993 ^a
<i>Digitaria eriantha</i>	O'Connor 1993 ^a
<i>Heteropogon contortus</i>	O'Connor 1993 ^a
<i>Pinguicula alpina</i>	Svennson 1993 ^a & pers comm.
<i>Pinguicula villosa</i>	Svennson 1993 ^a & pers comm.
<i>Pinguicula vulgaris</i>	Svennson 1993 ^a & pers comm.
<i>Setaria incrassata</i>	O'Connor 1993 ^a
<i>Themeda triandra</i>	O'Connor 1993 ^a
Iteroparous herbs of forest habitats	
<i>Allium tricoccum</i>	Nault & Gagnon 1993
<i>Cynoglossum virginianum</i>	Cippollini et al. 1993 ^b
<i>Cypripedium acaule</i>	Cochran & Ellner 1992 ^b
<i>Tolumnia variegata</i>	Calvo 1993
Woody plants	
<i>Cecropia obtusifolia</i>	Alvarez-Buylla 1994
<i>Fumana procumbens</i>	Bengtsson 1993
<i>Lindera benzoin</i>	Cippollini et al. 1994 ^b

^aData from this source averaged over 2 or more years.

^bMatrix from this source corrected or otherwise adjusted.

tion in the form of a population projection (Lefkovich) matrix or that reported data from which such a matrix could be compiled (Franco & Silvertown 1990). Silvertown et al. (1993) give further details of the 66 perennial species that formed our initial dataset, comprising nine semelparous herbs, 22 iteroparous herbs of open habitats (e.g., grasslands, dunes, deserts), 14 iteroparous herbs of forest habitats, and 21 woody plants. For the present analysis this sample was augmented by matrices for one semelparous perennial herb, 10 iteroparous perennial herbs of open habitats, four perennial forest herbs, and three woody species (Table 1). In most of the 84 cases there was no reliable information on seed banks. Elasticity analysis was carried out on each matrix, elements of the elasticity matrix were summed within the G , L , and F regions as already described, and the location of each species was plotted on the demographic triangle. Envelopes were drawn by eye around each of the four groups of species.

Very few plant demographic studies have been carried out on more than a handful of populations per species. One exception is the study of *Pedicularis furbishiae*, an iteroparous herb of riverbanks that is endemic to a 140-mile stretch of the St. John River in Northern Maine and adjacent New Brunswick (Menges 1990). The study described by Menges (1990) provided us with data on 15 populations of this species censused over a 2-year period. A single projection matrix was calculated for each population by averaging the two annual matrices.

Our second species for between-population comparison was the semelparous perennial herb *Cirsium vulgare*, which was studied by Bullock et al. (1994), who separately censused 16 populations of the plant over 1 year in the compartments of a sheep-grazing experiment near Oxford, England. *C. vulgare* is a thistle found as a widespread weed of pastures in northern Europe and North America (Klinkhamer & de Jong 1993). Elasticity analysis was performed on the 15 average matrices for *P. furbishiae* and on the 16 matrices for *C. vulgare*. The dominant eigenvalue (λ) of each matrix was calculated by the power method (Caswell 1989).

Results

The four groups of species in our dataset are shown plotted separately in Fig. 2. With the exception of a single outlier near the $F = 1$ vertex, semelparous herbs fell in the segment of the demographic triangle where growth is more important than fecundity or L (Fig. 2a). A minority (5/32) of iteroparous herbs of open habitats fell in this region; the majority occurred in a region stretching across the center of the triangle toward the $L = 1$ vertex (Fig. 2b). The forest herbs had a distribution similar to those of open habitats, though the importance of fecundity tended to be lower (Fig. 2c). The

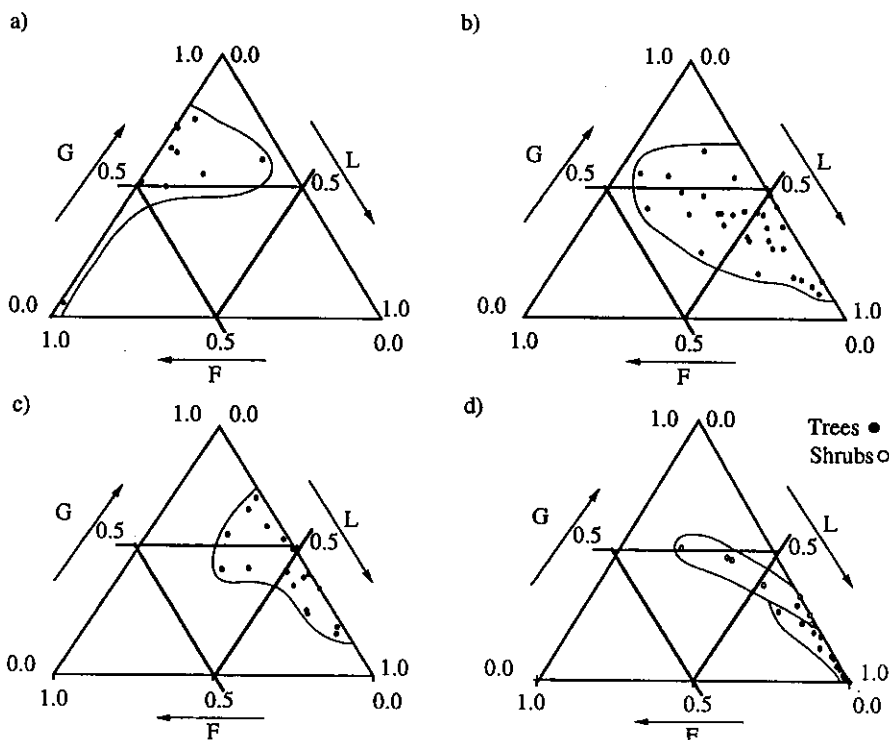


Figure 2. Triangular ordination of G/L/F elasticities for 84 species of wild plants: 10 semelparous perennial herbs (a); 32 iteroparous herbs of open habitats (b); 18 iteroparous herbs of forest habitats (c); 24 woody plants comprising eight shrubs (open symbols) and 16 trees (closed symbols) (d). Updated from Fig. 3 in Silvertown et al. 1993.

woody plants all fell within a remarkably narrow band joining the center of the demographic triangle with the $L = 1$ vertex, and trees and shrubs occurred toward opposite ends of this band (Fig. 2d). The importance of L in woody plants is to be expected because annual survivorship is high in these species. If average survivorship is, say, 98%, λ cannot be less than 0.98, even in the absence of growth or recruitment. This effect was stronger in trees than shrubs because shrubs tend to be short-lived.

Figure 3a shows the location in the demographic triangle of the 15 populations of *Pedicularis furbishiae* and the value of λ for each. All populations fell within a narrow band in the triangle; 14 of the 15 populations showed a systematic change in λ along the band from a maximum at $G = 0.39$, $L = 0.40$, $F = 0.21$ to a minimum at $G = 0.32$, $L = 0.62$, $F = 0.06$. One population with a low value of λ (0.80) was clearly below the gradient connecting the other populations.

With the exception of an outlier with a very low value for λ , the *Cirsium vulgare* populations shown in Fig. 3b were all located in the region of the demographic triangle where other semelparous perennials occur (Fig. 2a). Within this region the pattern of variation in λ among *C. vulgare* populations was very similar to that of *P. furbishiae*, with a clear gradient between maximum and minimum values along a narrow trajectory (Fig. 3b). Values of G varied little between *C. vulgare* populations, which differ mainly in the relative importance of L versus F . Populations with higher fecundity elasticities had higher values of λ .

Discussion

As we have reported previously for a smaller dataset (Silvertown et al. 1993), each of the four functional groups of species shown in Fig. 2 occupies a characteristic region of the demographic triangle. Among woody plants, shrubs and trees are clearly segregated. At first this may seem to suggest the broad generalization that efforts intended to increase a population's λ value should aim to increase growth and fecundity in the case of semelparous herbs, to increase survival and fecundity in the case of forest herbs, and to increase growth and survival for trees. The implications for iteroparous herbs of open habitats and for shrubs are less clear because these groups span large parts of the demographic triangle. Nevertheless, are the generalizations for the other groups a sound basis for management?

The between-population plots for *Cirsium vulgare* and for *Pedicularis furbishiae* suggest that they are not. Although in both cases different populations of the same species lie reasonably close to one another in the demographic triangle, it is clear from the gradients in λ that elasticity for a single population could be a poor guide to appropriate conservation measures. Take, for example, the population of *C. vulgare*, which has a very low value of λ (actually 0.18) that lies at the $L = 1$ vertex of the triangle in Fig. 3b. With a value of L far larger than the values for F and G , elasticity analysis of this population shows that its finite rate of increase would be most responsive to an increase in the survival of plants in

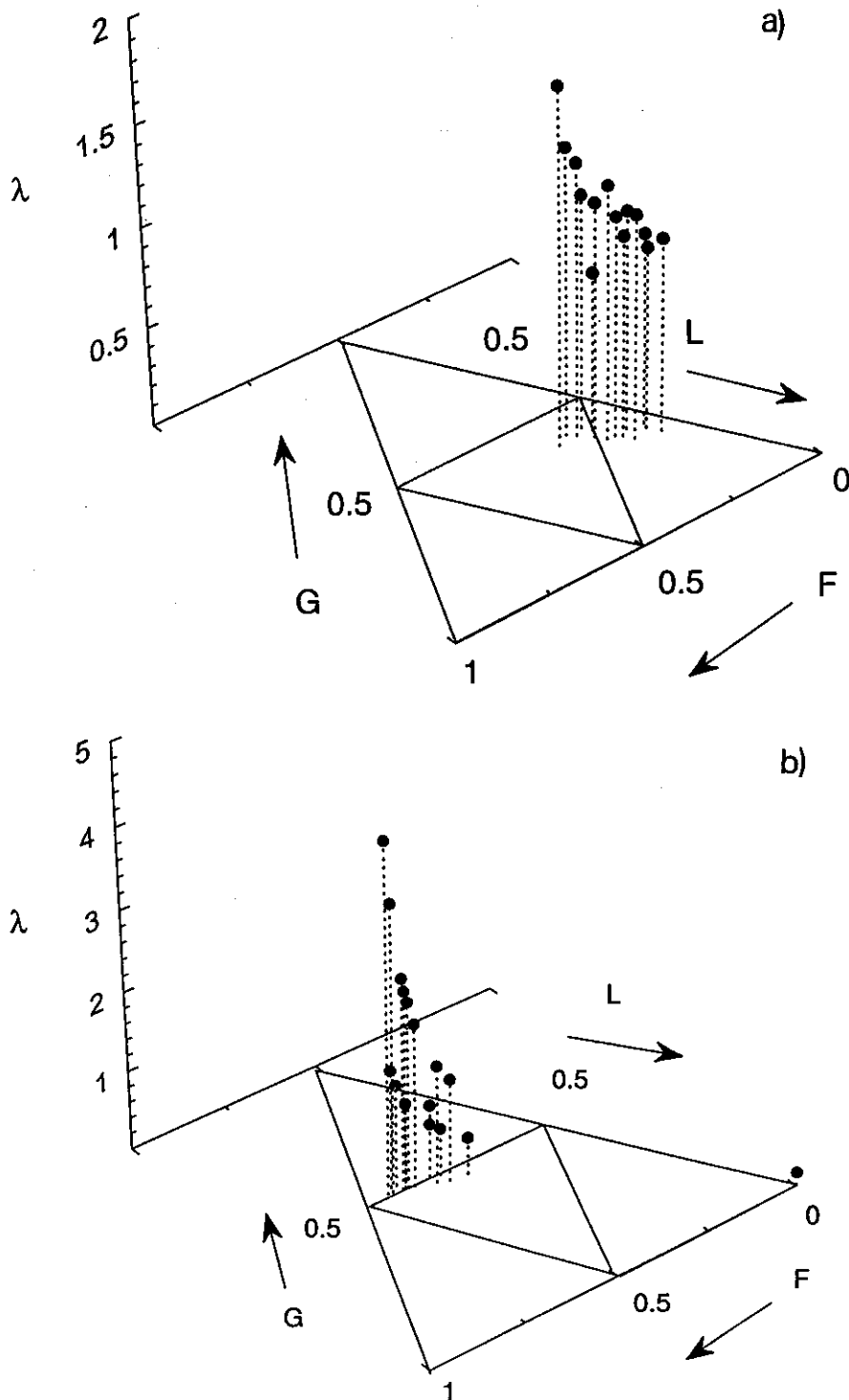


Figure 3. Triangular ordinations of G/L/F elasticities showing values of λ for 15 populations of *Pedicularis furbishiae* (a) and 16 populations of *Cirsium vulgare* (b).

their existing size classes. This finding is consistent with what one would expect in a rapidly declining population, but as a recipe for management it points in precisely the wrong direction. To prevent the extinction of this population we would want not only to prolong its decline but to reverse it. This outcome must involve raising the finite rate of population increase to a value larger than 1. But this can never be achieved simply by pro-

longing the life of individuals if there is no recruitment, as is often the case in declining populations, including this particular population of *Cirsium*. However long individuals live, to raise $\lambda > 1$ requires some recruitment. Prolonging life in a declining population may be useful in some circumstances, for example to buy time, but not as an end in itself, as elasticity analysis appears to suggest.

It is clear from a comparison of all 16 of the popula-

tions of *C. vulgare* in Fig. 3b that λ for this species increased with increasing F . This suggests that the correct form of intervention is not indicated by elasticities at a point in the triangle but by the direction of the λ gradient in the $G/L/F$ space. We have experimental verification of this point for *C. vulgare* because it has been shown that recruitment from seed is the chief factor influencing variation in λ between these 16 populations (Silvertown & Smith 1989).

In the 15 populations of *Pedicularis furbishiae*, there was a trend of increasing λ as L decreased and F and G increased (Fig. 3a). Evaluation of the environmental conditions for each population has shown that the value of elements in the G region of the matrix increased in sites with low percent cover of other plants. Populations for which percent cover was low and soil moisture high tended to have higher values of λ (Menges 1990). *P. furbishiae* occupies sites with disturbance frequencies intermediate between low frequencies that permit succession and the establishment of woody plants and high frequencies that destroy populations of the species.

Must we conclude that demographic studies of single populations are inadequate and that even more-intensive research is required before management recommendations can be made? We believe to the contrary because the λ gradients shown by the two herbs we studied in detail seem to have their counterpart in a larger pattern found in the demographic triangle as a whole. The distribution of functional groups across the triangle formed a pattern unmistakably like a successional trajectory. This trajectory started in the left-hand corner ($F = 1$) with short-lived (semelparous) herbs, arced toward longer-lived (iteroparous) herbs of open habitats in the uppermost segment of the triangle ($G > 0.5$), and descended via forest herbs and shrubs to trees in the bottom right-hand corner ($L = 1$) (Fig. 4a). When trajectories are used to indicate the downslope direction of λ gradients among populations of a species, such as for *C. vulgare* and *P. furbishiae*, they follow the between-species pattern to a remarkable degree (Fig. 4). Each species reaches its highest λ value in different parts of $G/L/F$ space, but the λ gradients follow trajectories that seem to follow a common pathway.

The interpretation of elasticities and the use of the demographic triangle is still in its early stages. Our sample of 84 species and 15 or 16 populations for two of them represents a significantly larger dataset than ever before analyzed and published, but it is still ludicrously small compared to the 250,000 species of plants estimated to exist. Because of this relatively small sample size we have not yet reduced the species in our dataset to a sample of phylogenetically independent taxa, though this will become a more practical priority as our dataset grows. Bearing these caveats in mind, we believe that it is possible to offer some rules of thumb based upon the demonstration in this paper that the demography of a

species is linked to its position in succession (Fig. 4). A conservation manager wishing to increase λ for a plant population should:

- (1) Identify the normal disturbance regime and successional sequence for sites where the species in question grows or is recorded as growing.
- (2) Identify the time since last disturbance, or the stage in the succession, where the species is most abun-

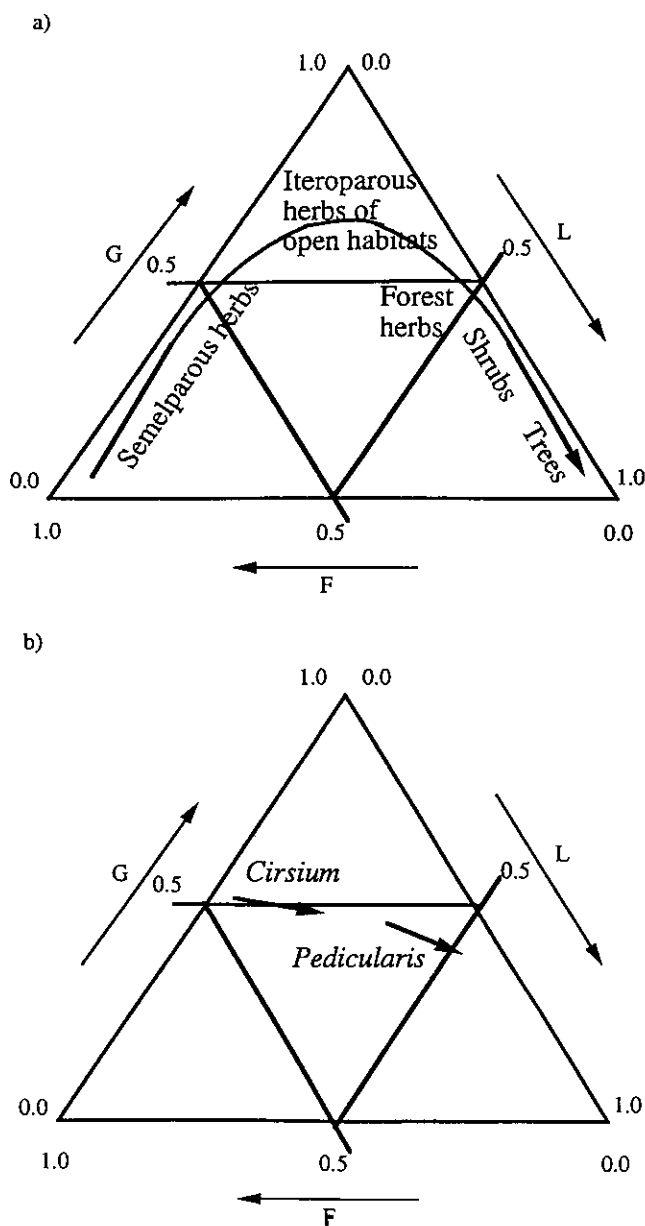


Figure 4. The hypothetical successional relationship of the functional plant groups shown in Fig. 2 (modified after Fig. 6 in Silvertown & Franco 1993) (a) and trajectories indicating the downslope gradient of λ for 15 populations of *Pedicularis furbishiae* and 16 populations of *Cirsium vulgare* (b).

dant; where this is not possible guess at this position based upon its life history (using Fig. 4a, for example).

- (3) Consider management of habitats or parts of habitats that will move these sites toward the optimum disturbance regime or successional phase for the species.
- (4) Monitor the effect of management treatments upon the species, and wherever possible conduct a designed experiment with controls (Travis & Sutter 1987).

Suggestions 1–3 involve considerably less time and effort than a full demographic study, but it is important that demographic studies be conducted where possible. Elasticity analysis of demographic data is useful, but as we have shown it must be interpreted carefully. In a growing population, elasticity analysis may indicate the life-history stages most important to sustaining that growth, but when $\lambda < 1$ (as may often be the case in populations that require conservation measures), it can be misleading as a prescription for management. In this situation it is important to compare populations either demographically (Fig. 3, for example) or using the quicker methodology suggested. The idea that conservation management is essentially a question of managing succession is of course not a new one, but we believe we have shown that this approach has a sound demographic basis for plants.

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