

Plant Demography and Habitat: A Comparative Approach

JONATHAN SILVERTOWN¹⁾ and MIGUEL FRANCO²⁾

¹⁾ Department of Biology, Open University, Milton Keynes, MK7 6AA, U.K.

²⁾ Centro de Ecología, Universidad Nacional Autónoma de México, Apdo. Postal 70-275, 04510 México D.F., México

Abstract Progress in plant demography will depend upon being able to synthesize a large body of data and this requires a means of comparing populations between sites and species. We have employed a comparative technique using elasticity analysis of stage-projection matrices to partition the contributions of fecundity (F), survival (L) and growth (G) to the finite rate of increase λ . Ordination of populations of 77 perennial herbs and trees in G-L-F space has shown that species segregate in this triangular space according to their life history and habitat. In the present paper we use the correspondence between demographic parameters and habitat revealed by this method to predict how succession and a variety of environmental factors such as grazing and fire are likely to alter the demography of populations and ultimately to change the composition of communities.

Key words: elasticity, matrix analysis, plant demography, succession.

The comparative approach has been used in plant demographic studies from its very inception. Sarukhán and Harper's (1973) study of the demography of *Ranunculus* compared three species in the genus, and Harper and White's (1974) review of plant demography nearly twenty years ago was comparative in approach. Nevertheless, the subsequent development of the subject has lacked synthesis. The chief reason for this is possibly the difficulty of comparing studies done on species with a wide diversity of life histories in a wide variety of habitats. When we systematically surveyed the plant demographic literature three years ago we found studies of 580 species belonging to 99 families occurring in nine classes of habitat (Franco and Silvertown, 1990). Progress in the subject now depends on being able to draw together the results of this substantial body of data.

The methodology to compare species that we came up with was based upon using stage-projection matrices to summarize and describe the demography of populations (Caswell, 1989), and then to use elasticity analysis (de Kroon et al., 1986) to calculate the sensitivity of the finite rate of population increase λ to perturbations of different life-history transitions (Silvertown et al., 1993). Projection matrices for 66 perennial plant species were compiled or extracted from the literature covering herbs, shrubs and trees in a variety of habitats. Each matrix was divided into six regions representing the following transitions:

1. Recruitment of seeds to the seed pool.
2. Recruitment of seedlings or juveniles from current

seed production.

3. Clonal growth.

4. Retrogression due to plants decreasing in size during the year or reverting from a flowering state to a vegetative one or becoming dormant.

5. Stasis, or survival from one year to the next in the same stage class.

6. Progression to later stage classes.

In an ideal matrix these transitions are found in the regions shown in Fig. 1. In practice not all matrices contained all six components and transitions in published

		YEAR t				
		seed	seedling	iii	iv	v
YEAR t+1	seed	1				
	seedling		2			
	iii			3	4	5
	iv				6	7
	v					8

Fig. 1. An ideal stage projection matrix illustrating the six regions representing (1) recruitment of seeds, (2) recruitment of seedlings, (3) clonal growth, (4) retrogression, (5) stasis, and (6) progression. (From Silvertown et al., 1993).

matrices are not always in the positions shown.

Elasticities (e_{ij}) were summed within each of the six regions to give totals for each life-history process that were termed E_1 – E_6 respectively. To simplify comparisons between species we further reduced the number of variables to three, namely the relative importance of:

$$\begin{aligned} \text{Growth } G &= E_3 + E_6, \\ \text{Survival } L &= E_4 + E_5, \\ \text{Fecundity } F &= E_1 + E_2. \end{aligned}$$

All the elasticities in a matrix sum to unity and so $G + L + F = 1$. Triangular ordination of the 66 species in G-L-F

space showed that semelparous perennials, iteroparous herbs of open habitats, forest herbs and woody plants each occupied distinct regions of the demographic triangle (Fig. 2). Since compiling the original dataset we have acquired data for an additional eleven species whose locations are also shown in Fig. 2. The distribution of these species in the demographic triangle confirms the original pattern.

In this paper we demonstrate that the demographic triangle may be used to predict how the demography of populations changes with the successional status of the habitat.

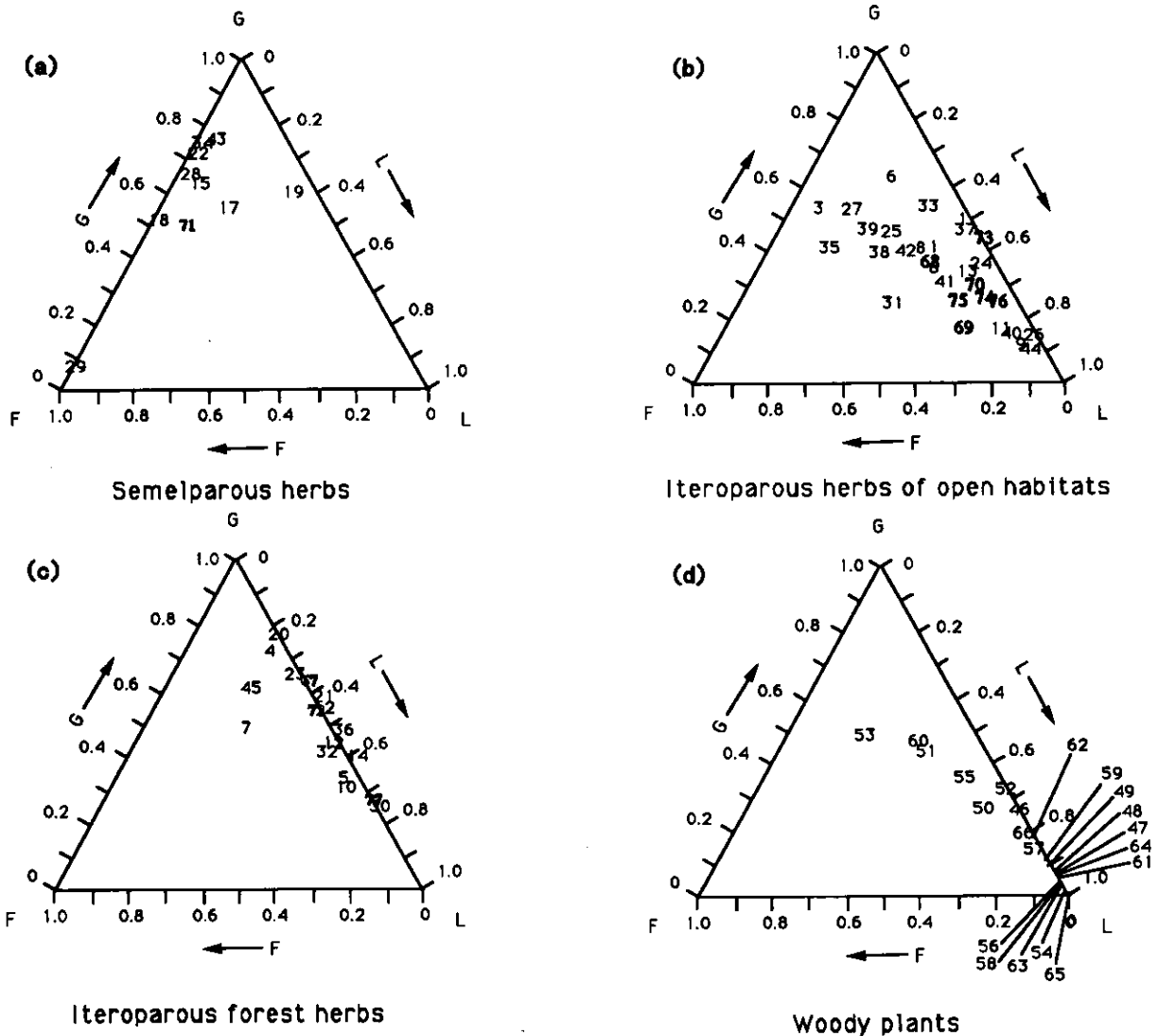


Fig. 2. Distribution of 66 perennial species in G-L-F space; (a) semelparous herbs, (b) iteroparous herbs of open habitats, (c) iteroparous forest herbs, (d) woody plants. Numbers 1–66 refer to species listed in Silvertown et al 1993. Numbers 67–77 are eleven additional species detailed in Table 1.

Table 1. Additional species and sources of data shown in Fig. 2. All species are perennial herbs.

Species	Habitat and life history	Source of data	No. in Fig. 2.
<i>Allium tricoccum</i>	bulbous forest herb	Nault and Gagnon, 1993	67
<i>Andropogon semiberberis</i>	savanna grass	Silva et al., 1991	68
<i>Aristida bipartita</i> (Ab)	savanna bunchgrass reproducing only by seed.	O'Connor, 1993 ¹	69
<i>Bothriochloa insculpta</i> (Bi)	savanna bunchgrass reproducing by seed, with limited stoloniferous growth.	O'Connor, 1993 ¹	70
<i>Cirsium vulgare</i>	semelparous thistle	Bullock et al., 1994	71
<i>Cypripedium acaule</i>	terrestrial woodland orchid	Cochran and Ellner, 1992	72
<i>Digitaria eriantha</i> (De)	savanna, stoloniferous grass, rarely reproducing by seed.	O'Connor, 1993 ¹	73
<i>Heteropogon contortus</i> (Hc)	savanna bunchgrass reproducing only by seed.	O'Connor, 1993 ¹	74
<i>Setaria incrassata</i> (Si)	savanna, rhizomatous grass also reproducing by seed.	O'Connor, 1993 ¹	75
<i>Themeda triandra</i> (Tt)	savanna bunchgrass reproducing only by seed.	O'Connor, 1993 ¹	76
<i>Tolumnia variegata</i>	epiphytic orchid	Calvo, 1993	77

¹ Data from this source averaged over two or more years.

Population Responses to Habitat Change

1. Grassland Herbs

Our first example is taken from a study of the semelparous perennial thistle *Cirsium vulgare* by Bullock, Clear Hill and Silvertown (1994). Sixteen natural populations of this species were censused in the compartments of a sheep grazing experiment at Little Wittenham, near Oxford, England. Eight grazing treatments were represented in the experiment, each

replicated twice. Matrices for each population were compiled, elasticity analyses were performed and then an average elasticity matrix was calculated for each treatment. All eight mean populations, although they received different grazing treatments, fall within the region of the demographic triangle where other semelparous herbs are concentrated (Fig. 3). When we look more closely at this region, we find that the eight populations lie along a line, with those in treatments receiving least grazing pressure having relatively low values of F and relatively high values of L , while those

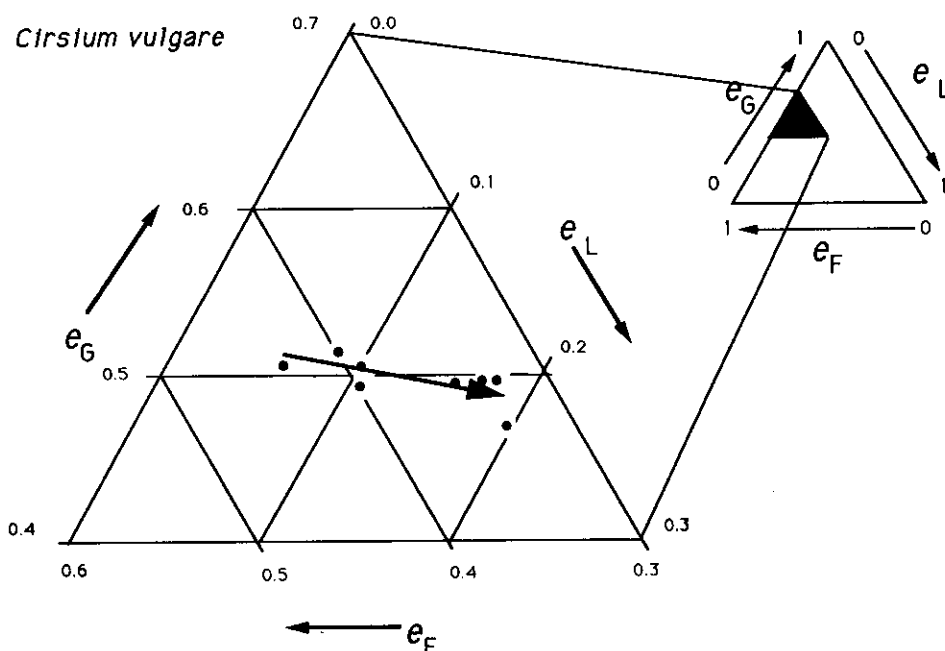


Fig. 3. Location in the demographic triangle of populations of *Cirsium vulgare* in grassland swards receiving eight different grazing treatments. The arrow indicates increasing grazing intensity. Modified from Bullock et al. (1994).

in heavier grazing treatments have lower values of L and higher values of F (Fig. 3). *Cirsium vulgare* is not itself grazed, but depends upon vegetation gaps created by grazing for recruitment. The finite rate of population increase λ rises with grazing intensity, hence the increased importance of F in these conditions.

It is interesting that growth was of little importance in altering the demography of *C. vulgare* under grazing, and that effects on fecundity and survival were all-important. This compares with the situation in six species of savanna grass studied by O'Connor (1993) in Southern Africa. O'Connor censused populations of the six species in plots with contrasting grazing pressures over a period of four years. We calculated average matrices for each species in each treatment, performed elasticity analysis on each of the mean matrices and then plotted the species in the demographic triangle (Fig. 4). All the species fall in the same region (Fig. 4), where some other grassland herbs are also found (Fig. 2). Closer inspection of the effect of grazing on the populations shows that in most cases a reduction in grazing pressure increases the importance of L and decreases the importance of F and G. In the case of *Bothriochloa insculpta* (Bi in Fig. 4) G was entirely unchanged by grazing, while in the case of the stoloniferous species *Digitaria eriantha* (De in Fig. 4) G changed, but not F.

Another species of savanna grass was studied by Silva et al. (1991) in Venezuela. Figure 5 compares a population exposed to annual burning with one protected from fire. The two populations both fall in a region of the triangle occupied by other species of open, fire-prone habitats (e.g. the shrub *Banksia ericifolia*, #51 in Fig. 2). Burning had an effect on *A. semiberberis* similar to the effect of grazing on *C. vulgare* and the African savanna grasses. In fact the unburnt population of *A. semiberberis* had a λ value < 1 , and could not have survived in this state (Silva et al., 1991).

2. Succession

Succession transforms open habitats to forest, with a corresponding shift in the life histories of the predominant species. These changes can be represented by a parabolic trajectory in the demographic triangle that goes from the F vertex to the L vertex. In the demographic triangle as a whole there is a clear tendency for species to segregate according to different life histories (Fig. 2). The arrangement of the life history groups from short-lived herbs on the left, through herbs and shrubs of open habitats towards the G vertex, to long-lived forest trees on the right is reminiscent of a successional sequence (Fig. 6).

The effects of grazing and burning on the grassland species we have looked at above shows that these

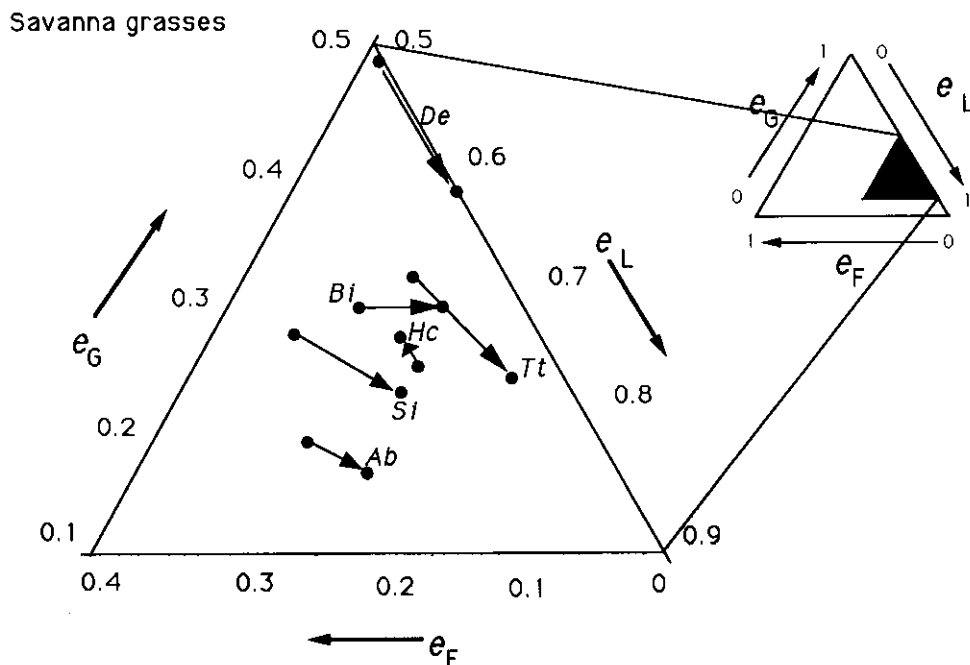


Fig. 4. Location in the demographic triangle of populations of six species of savanna grasses. Species are identified by the initials of the species in Table 1 that were studied by O'Connor (1993). For each species, an arrow points from the population experiencing high grazing intensity to the population experiencing lower grazing intensity.

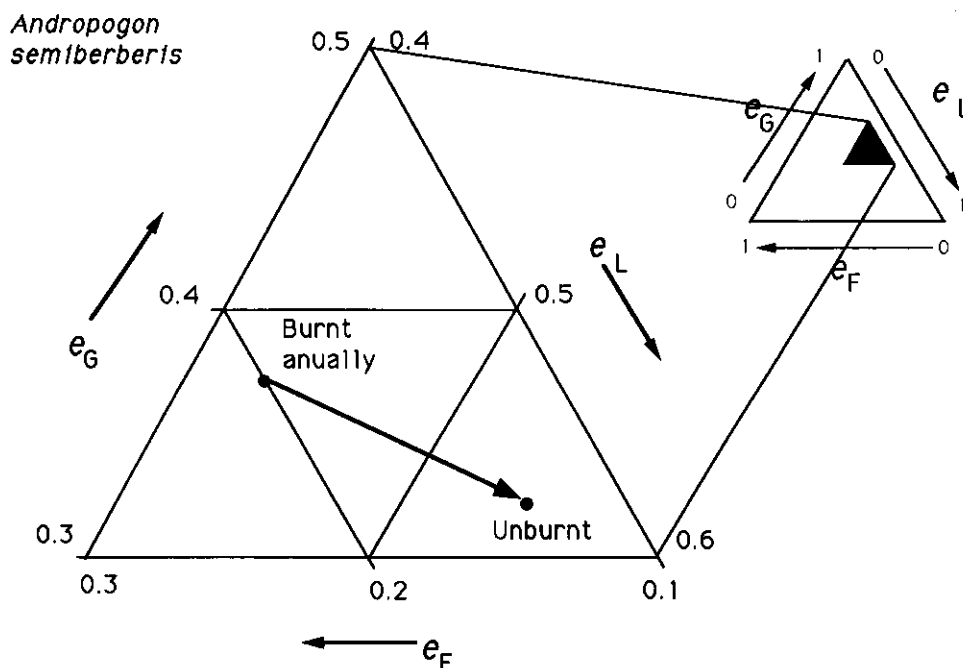


Fig. 5. *Andropogon semiberberis* in burned and unburned sites. (data from Silva et al., 1991).

forces push grassland populations in the direction of earlier successional states, as one would expect them to. Trajectories showing the effect of these changes in the successional status of the habitat on the location of populations in the demographic triangle are illustrated in Fig. 7. The fourth trajectory in this graph is for a demographic study of the palm *Pseudophoenix sargentii* by Durán (1992). Durán studied six populations of *P.*

sargentii in the Yucatan peninsula, Mexico, along a habitat sequence from sand dune to forest. This sequence can be thought of as a spatial analogue of succession. All six populations fell in the bottom right hand corner of the demographic triangle, within the "tree region". However, within this region of the triangle the six populations fell on a clear successional trajectory, as shown in Fig. 7, from the dune population with relatively high F and G and relatively low L , to the population of closed, evergreen forest with relatively low G and F and very high L (Durán, 1992).

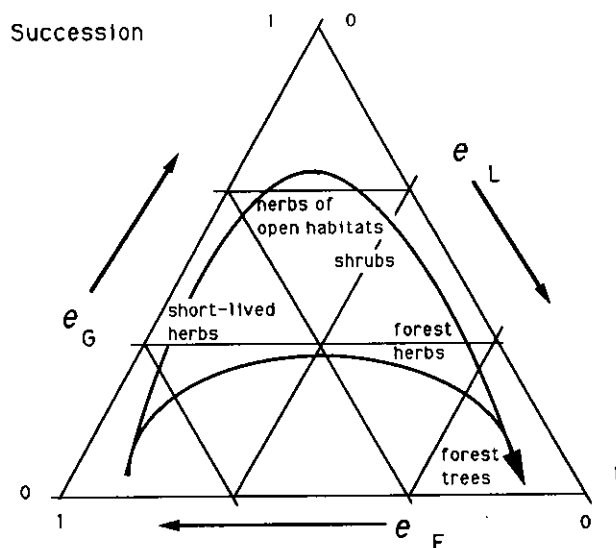


Fig. 6. Hypothetical successional sequence superimposed on the demographic triangle.

Although we have found no correspondence between the demographic triangle and Grime's C-S-R triangle when comparing individual herb species (Silverton et al., 1992), Grime has proposed that succession follows a parabolic trajectory in the C-S-R triangle (Grime, 1979) that is analogous to the trajectory in Fig. 6.

Conclusions

We draw four practical conclusions from the relationships between G-L-F trajectories and habitat successional status:

1. As succession proceeds, we expect populations with high F to be replaced by populations with high G and then these to be replaced in their turn by populations with high L .
2. Forces such as fire and grazing that arrest or

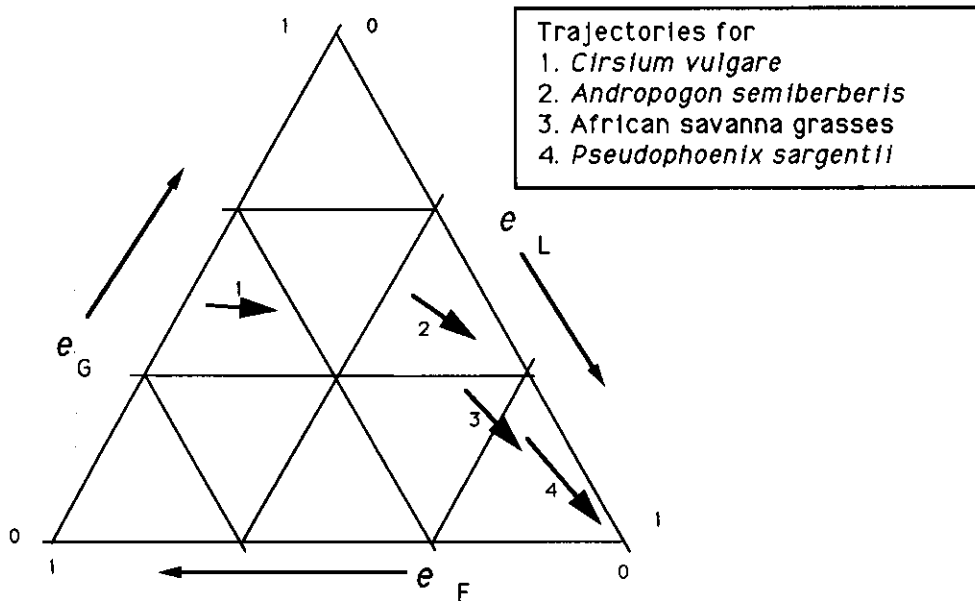


Fig. 7. Trajectories showing the effect of changes in the successional status of the habitat on the location in the demographic triangle of populations discussed in the text.

reverse the successional status of a habitat will have corresponding effects on values of G, L and F in populations found in them.

3. The same habitat factors (grazing, fire etc.) may drive populations in *different* directions in G-L-F space, depending on where populations are located in the triangle in the first place (Fig. 7).

4. The fact that species with particular life histories are found in particular habitats and are limited to particular regions of G-L-F space suggests that forces that push a population to the boundaries of a region may push the population to extinction. These boundaries can be mapped by plotting the region of the triangle within which $\lambda > 1$ for any particular species. This information may be useful for managing plant populations for conservation or harvesting.

Finally, we note that the demographic triangle shows the property of self-similarity. Patterns seen in the distribution of species at the larger scale also appear at the smaller scale in comparisons between populations of individual species. This makes the triangle an extremely robust tool for describing, comparing and predicting how changes to a habitat may alter the demography of plant species it contains.

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