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## Negative associations can reveal interspecific competition and reversal of competitive hierarchies during succession

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Causes of interspecific associations are usually not discernible without properly designed experiments. Using relevant supplementary observational data, however, mechanisms of some associations can be explained. We found that the association between seedlings of *Arctostaphylos patula* (shrub) and two-year-old plants of *Cirsium vulgare* (introduced biennial herb) changes from neutral (2nd year), through negative (3rd year), to neutral (4th year), to negative again (5th and 6th year) during postlogging succession in the Sierra Nevada, California. Simultaneous analysis of the association between *A. patula* and one-year-old *C. vulgare* plants allowed us to interpret the observed pattern as successional reversal in the direction of competition. We explain the negative association between *A. patula* and mature *C. vulgare* plants in the 3rd year as a result of mortality of *A. patula* seedlings in the proximity of mature plants of *C. vulgare* (stronger competitor) and negative association in the 5th and 6th year as a result of mortality of *C. vulgare* in the proximity of *A. patula* (stronger competitor if more than four years old). Data on the year-to-year survival of the two species recorded in permanent plots concur with this explanation.

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It is difficult and often impossible to deduce the mechanisms structuring plant communities solely from observed patterns. Attempts to do so were common in the past. For example, the community organization was inferred from the structure of interspecific associations and conclusions about interactions among individuals were deduced from the observed intensity of spatial pattern in particular populations (see textbooks on quantitative ecology by Greig-Smith 1957 and Kershaw 1973). It is clear now, that the reliability of such deductions is very low and that analysis of spatial pattern by itself at a single point in time is not sufficient for understanding the underlying processes (Keddy 1989, Lepš 1990, Duncan 1991, Aguiar and Sala 1994). Repeated observations in time are more powerful and

manipulative experiments are often considered the only reliable tool for testing underlying mechanisms (Shipley and Keddy 1987, Hairston 1989, Aarssen and Epp 1990). Nevertheless, knowledge of spatial patterns (even for a single point in time) is important for generating hypotheses about mechanisms. Moreover, owing to constraints on manipulative field experiments (Diamond 1986), the use of non-experimental evidence is often the only evidence available.

Determination of interspecific association of a pair of species based on the co-occurrence of the species in sampling units and on subsequent analysis of a  $2 \times 2$  contingency table (species 1 present/absent vs species 2 present/absent) is one of the classical exercises of statistical ecology (Goodall 1953, Kershaw 1973). From the

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beginning, active and passive associations were distinguished, the active ones resulting from biotic interactions between investigated species and the passive ones resulting from concordant or discordant responses of the species to environmental variation within the study area. Generally, contingency tables do not provide information on causality. In this paper, however, we argue that under certain circumstances, causal mechanisms can be inferred if information on the the biology of the species involved is available.

Both *Cirsium vulgare* (Savi) Ten. (biennial herb) and *Arctostaphylos patula* E. Greene (shrub) are early successional species and important weeds in clearcuts and conifer plantations in the western U.S.A. (Rejmánek and Messina 1989, 1990, Randall and Rejmánek 1993). Our field observations suggested that there may be a negative association between *Arctostaphylos* and mature *Cirsium* plants, at least in some stages of postlogging succession. Clearcuts in submediterranean environments, however, represent relatively heterogeneous environments which more likely promote passive positive association between these two species, as both tend to germinate and establish in moist patches. The negative association, suggested by our observations, is more likely an active one, reflecting interspecific competition. Consequently, three questions were addressed in our research which was inspired by this line of reasoning: (1) Is there a significant negative association between *Arctostaphylos* and *Cirsium*?, (2) Does the strength of such an association change in the course of vegetation succession?, and (3) What is the underlying mechanism of the observed patterns?

## Methods

### Study site

The fieldwork was conducted in clearcuts/conifer plantations of the University of California Blodgett Forest Research Station in the central Sierra Nevada, El Dorado County, California, USA. The area has a sub-mediterranean climate, with hot, dry summers and cool, wet winters (Major 1988). Deep, well-drained soils belong to the Cohasset series developed from andesitic parent material. Analyzed plots were located in areas that had been clearcut and replanted 2, 3, 4, 5, and 6 yr earlier in compartments 620-South, 620-North, 371, 360, and 370, respectively. Each plot covered an area of 1500 m<sup>2</sup>, was at an elevation between 1260 and 1320 m and had slopes of less than 10%. None of the plots was grazed, physically weeded, or treated with herbicides. The two species described below comprised over 80% of the total cover in 94% of the quadrats studied.

### Species studied

*Cirsium vulgare* is a biennial species of the Compositae, native to Europe and Asia Minor. It was probably introduced to California at the end of the last century. It is now locally abundant throughout the Pacific states in waste places, pastures, mountain meadows, and forest plantations; <2300 m. In the Sierra Nevada, *C. vulgare* sets seeds in late summer through early autumn. The seeds are wind-dispersed. Germination occurs after the onset of autumn rains and in the spring after snow melt. An individual typically produces a rosette of spiny leaves in its first year, overwinters in this form, and then bolts and produces a flowering stalk 0.5–1.5 m high in its second year. The plants reproduce only by seed and die after setting seeds (Forcella and Randall 1994). The density of *Cirsium* usually increases during the first 3 or 4 yr of postlogging succession and declines later. Only very few plants can be found in undisturbed clearcuts/plantations older than 8 yr. "Rosette" will be used below to refer to plants that have not yet bolted, and "mature" or "adult" will be used for those that have.

*Arctostaphylos patula* is a shrub up to 2.2 m tall in the Ericaceae, native to Colorado, Utah, Nevada, Oregon, Arizona, California, and northern Baja California. It typically grows in open coniferous forests and clearcuts at elevations of 750–3350 m. Individuals begin to flower and fruit between the age of 8 to 10 years. The fruits are dispersed by birds and mammals from late summer until the following spring. The seeds germinate mainly after wildfires or after slash disposal fires done in site preparation for forest plantations (Berg 1974). There was virtually no new germination in plots which were older than 2 yr.

### Sampling

Sampling for determination of interspecific associations was carried out in the autumn of 1990. In each plot, 100 1 × 1 m quadrats were located randomly but always at least 1 m from the nearest conifer seedling/sapling. In each quadrat, numbers of *Arctostaphylos* plants, *Cirsium* rosettes, and mature plants of *Cirsium* were recorded. Only individuals rooting in quadrats were considered.

### Spatial pattern of a species

Lloyd's index of patchiness (Pielou 1977) was used to describe the spatial pattern of individuals. The index is defined as

$$L = 1 + (\text{variance}/\text{mean} - 1)/\text{mean},$$

where mean and variance refer to observed mean number of individuals per quadrat and its variance. Values close to one indicate randomness, values greater than one indicate clumping, and values smaller than one indicate some regularity (uniformity). The departure from randomness can be tested by virtue of the fact that the variance:mean ratio multiplied by the number of observations - 1 (=degrees of freedom) is approximately distributed as a chi-square variate (Pielou 1977: 125). As is notoriously known, most real populations do not follow the random spatial pattern. Consequently the null hypothesis of the random spatial pattern is highly unrealistic and could be expected to be false a priori. Therefore we used the Lloyd index as a descriptive tool only. It is important to realize that the value of Lloyd index of patchiness does not change when some of the population members are removed at random. Consequently, if the value of Lloyd's index decreases in the course of self-thinning of a population, we can conclude that individuals did not die randomly.

#### Interspecific associations: log-linear models

Contingency tables were constructed for the data on the presence/absence of species in quadrats. The relationships among the interspecific associations between *Arctostaphylos* and *Cirsium* in various stages were tested using three-dimensional contingency tables (Agresti 1990): factors are successional stage (categories 1 to 5), *Arctostaphylos* with two categories (present, absent) and *Cirsium* (present, absent). The fully saturated model contains first order interaction terms stage  $\times$  *Arctostaphylos*, stage  $\times$  *Cirsium* and *Arctostaphylos*  $\times$  *Cirsium* and a second order interaction term stage  $\times$  *Arctostaphylos*  $\times$  *Cirsium*. In this model, the interaction terms stage  $\times$  *Arctostaphylos* and stage  $\times$  *Cirsium* correspond to the differences in frequency of the two species in different successional stages, the term *Arctostaphylos*  $\times$  *Cirsium* corresponds to the interspecific association and the second order term corresponds to differences in the strength (and direction) of association in different stages. The three-dimensional contingency tables were completed and analyzed for both rosettes and adults of *Cirsium*.

#### Strength of interspecific associations

The strength of association between species in particular stages was evaluated using the ordinary  $2 \times 2$  tables for presence/absence data for pairs of species (rosettes and mature *Cirsium* plants were considered separately). The strength of association was measured using the  $V$  coefficient ( $V = (ad - bc) / \text{SQRT}(mnr s)$ ), where  $a$ ,  $b$ ,  $c$ , and  $d$  are frequencies in the  $2 \times 2$  table and  $m$ ,  $n$ ,  $r$ ,  $s$  are marginal totals (Pielou 1977).  $V$  could be rewritten as  $V = ((ad - bc) / \sqrt{ad - bc}) / \text{SQRT}((\text{chi-square}) / N)$ , where

$N$  is the total number of sampling units. As  $N = 100$  in all our cases, the "critical values" of  $V$  can be computed. Absolute values of  $V$  exceeding 0.20 and 0.26 indicate significant associations on 0.05 and 0.01 significance levels respectively.

The Pearson correlation coefficient ( $r$ ) calculated from the  $\log(\text{density} + 1)$  data was used as an alternative measure of interspecific association. As the data contain many zeroes, the critical value for  $|r|$  should be considered with caution (0.197 for 0.05 significance level). [Exclusion of quadrats with zeroes for both species (Myster and Pickett 1992) does not make the test more valid because the resulting sample is no longer random.]

#### Dependence of survival on the density of competitor

In two plots, 2 and 4 yr old, sets of 30 permanent quadrats  $1 \times 1$  m were established in August 1991. The individuals of both species were counted and their survival through August 1992 was determined. The regressions of the probability of survival on the density of both conspecific and heterospecific individuals were then calculated (after angular transformation of the estimated survival probability).

#### Results and discussion

Although the plots were selected to be as similar as possible and to differ only in the time from the clear cutting, some local differences in other factors (e.g. availability of diaspores) could occur. Consequently, not all the differences in plant populations can be attributed to a successional development; they always reflect conditions in particular plots in a given year to some extent. Nevertheless, the basic trend in the succession (confirmed by non-quantitative observations in other plots) is characterized by rapid increase in the cover of *Arctostaphylos* from  $<5\%$  to  $>60\%$ . The increase corresponds to the growth of individual shrubs, and is probably not particularly influenced either by the initial density of the shrubs, or by self-thinning. The other trend is the decrease of the ratio of the density of mature *Cirsium* plants to the density of rosettes with the age of the plot. This suggests increasing rosette mortality with time, probably due to increasing cover of *Arctostaphylos*.

#### Spatial pattern of populations

For *Arctostaphylos*, intensity of clumping decreases with clear-cut age (Fig. 1). Decrease in intensity of clumping and uniform pattern in older stages suggests intraspecific competition, i.e., decreased survival probability for individuals with very close neighbors.

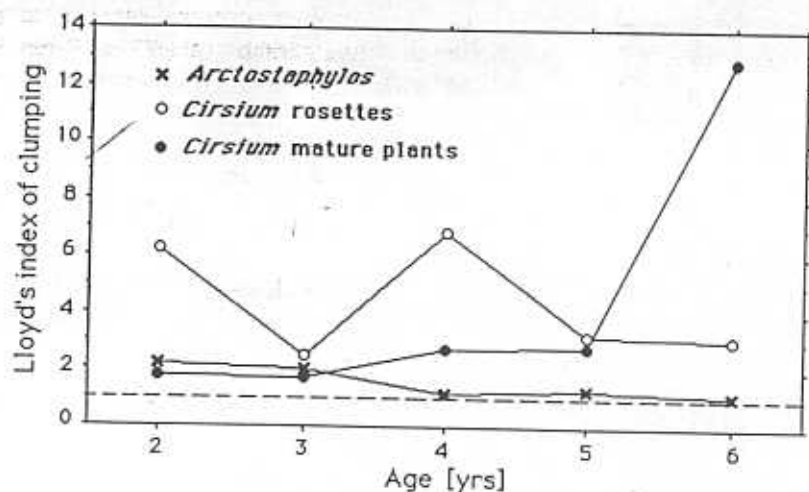


Fig. 1. Values of Lloyd's index of patchiness for *Arctostaphylos*, rosettes of *Cirsium* and mature plants of *Cirsium* in different successional stages.

There are two trends in the spatial pattern of *Cirsium* distribution. The intensity of clumping of mature plants increases with time and the rosettes are usually more clumped than the mature plants, particularly in the younger stages. The increasing patchiness of mature *Cirsium* is probably due to *Arctostaphylos* competition. Patches of increasing size occupied by dense *Arctostaphylos* shrubs are not suitable for the establishment or survival of *Cirsium*. The pronounced patchiness of rosettes is due to the type of dispersal (the capitula often fall to the ground before the seeds are released and then many seeds from the same capitulum germinate on the same spot) and it probably also reflects characteristics of a particular plot: it is why the patchiness of rosettes differs among particular plots without any pattern. There are also some places with higher probability of capturing of wind dispersed seeds. Some small shrubs, particularly the gooseberry (*Ribes roezlii* Regel) with spiny stems, typically capture many seeds. There is a significant positive association between gooseberry and *Cirsium* rosettes in the oldest plot where gooseberry is abundant ( $V=0.373$ ,  $P<0.01$ ). The lower intensity of clumping (Fig. 1) of mature *Cirsium* plants in the first four stages suggests the influence of intraspecific competition (self-thinning).

#### Interspecific associations

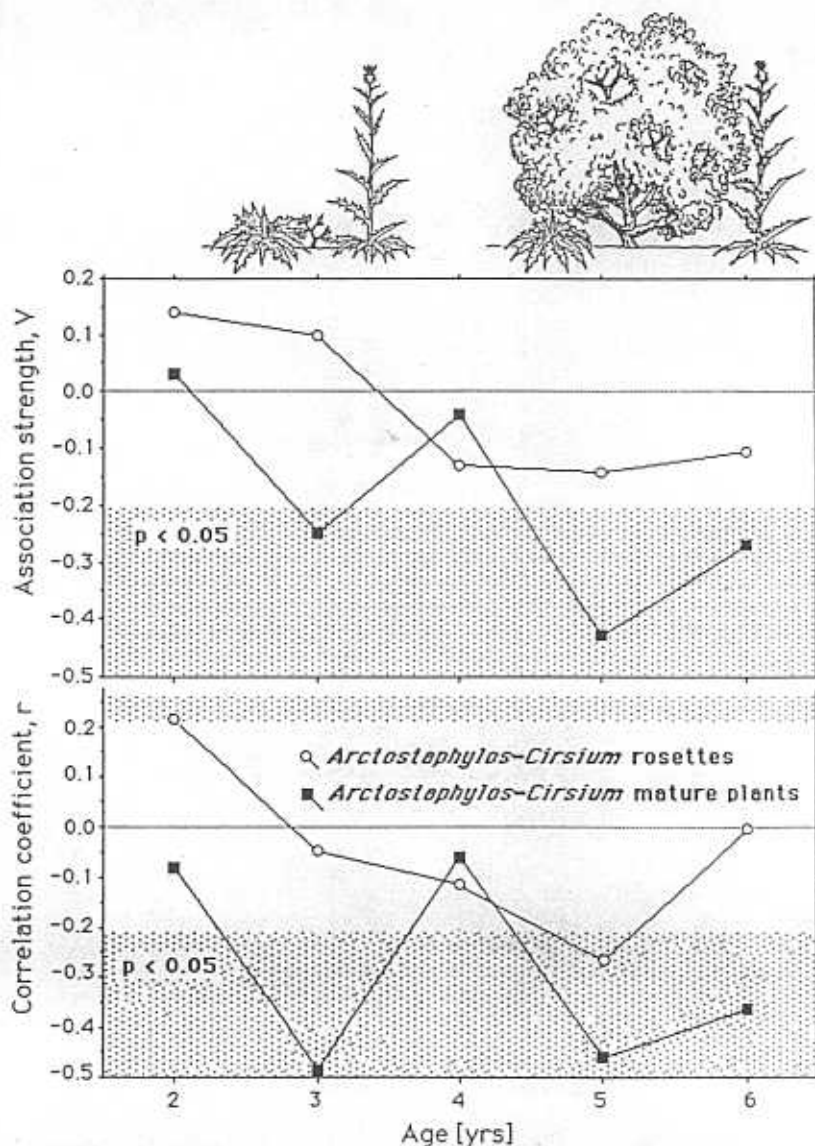
Analysis of three-dimensional contingency tables revealed that for mature *Cirsium* plants all the models simpler than the saturated model can be rejected ( $P<0.05$ ). This means that frequencies of both species change with time, there are significant associations between species and the strengths of the associations differ among successional stages. Consequently, it is meaningful to express the association strength ( $V$ ) in

each stage as shown in Fig. 2 in order to consider mechanisms responsible for the changes. The trend shown is consistent with the findings of Aarsen and Turkington (1985), i.e. associations stabilize in older communities (yr 5 and 6). For rosettes, a simpler model, including only interactions between *Cirsium* and stage, and *Arctostaphylos* and stage cannot be rejected. In this case, only differences in frequencies among stages were detected, and no significant associations (and obviously no significant differences in association strength; Fig. 2) were found. This difference between rosettes and mature *Cirsium* plants clearly points to the existence of active negative associations between *Arctostaphylos* and mature *Cirsium*. Successional changes of interspecific correlations follow the same pattern (Fig. 2). However, there seems to be a significant positive correlation between *Cirsium* rosettes and *Arctostaphylos* in the 2nd year of succession. In this case the positive correlation likely resulted from higher seedling survival of both species in favorable microsites but an active association between the species (e.g., buffering physical stresses; Carlsson and Callaghan 1991, Bertness and Hacker 1994) cannot be ruled out.

#### Survival of plants in permanent plots

In the two-year-old clearcut, the survival of *Arctostaphylos* was negatively influenced by the density of *Cirsium* plants, whereas *Cirsium* survival was not influenced by *Arctostaphylos* density (Fig. 3). Density of conspecific individuals did not significantly influence the survival of either species. On the contrary, in the four-year plot, *Arctostaphylos* survival was not influenced by *Cirsium* density, but the *Cirsium* survival decreased strongly with density of *Arctostaphylos* (Fig. 4). Nevertheless, in this plot, survival of both species

Fig. 2. Values of index of interspecific association ( $V$ ) and correlation coefficient ( $r$ ) between *Arctostaphylos* and rosettes of *Cirsium* and between *Arctostaphylos* and mature plants of *Cirsium*.



was negatively influenced by the density of conspecifics. For *Arctostaphylos*, the dependence was relatively weak ( $R^2 = 0.26$ ,  $P < 0.05$  for single regression). For *Cirsium*, the dependence was stronger: both regression coefficients in the multiple regression of arcsin SQRT(*Cirsium* survival) on log density of *Cirsium* (-31.3) and on log density of *Arctostaphylos* (-36.2) were highly significant ( $P < 0.001$ ; adjusted  $R^2$  for multiple regression = 0.74).

#### Underlying mechanisms

Knowing the biology of involved species and putting

the information from the one-point-in-time sampling (Figs 1 and 2) and from the permanent quadrats (Figs 3 and 4) together, we can conclude that early in the succession (going from the 2nd to 3rd year), the *Arctostaphylos* seedlings are still small and prone to the competition from *Cirsium*. At that time, they are not able to suppress the *Cirsium* plants. In the following year, the two species are about equivalent competitors. Later (5th year and later), only older, large individuals of *Arctostaphylos* are present. Their mortality is low, and is no longer influenced by *Cirsium* plants. At this time, most *Cirsium* plants die under the cover of *Arctostaphylos* shrubs. Therefore, the observed temporal

2nd → 3rd year

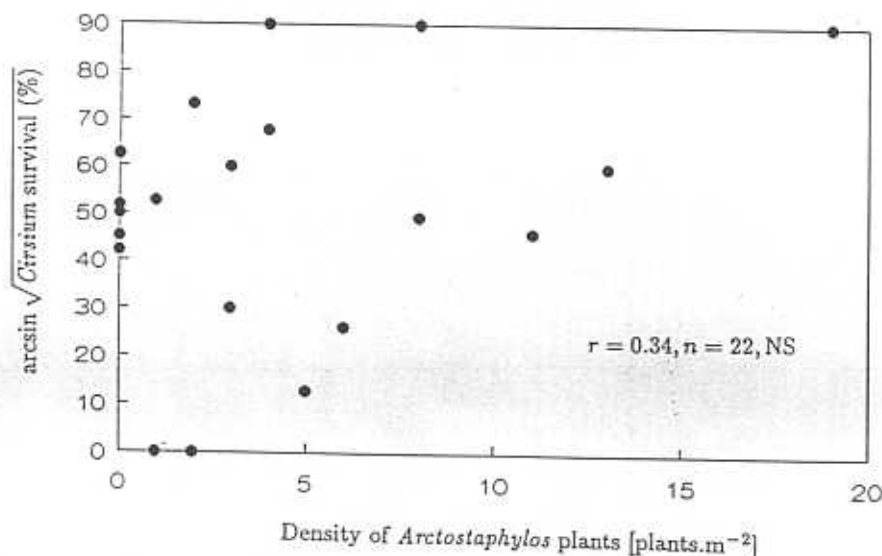
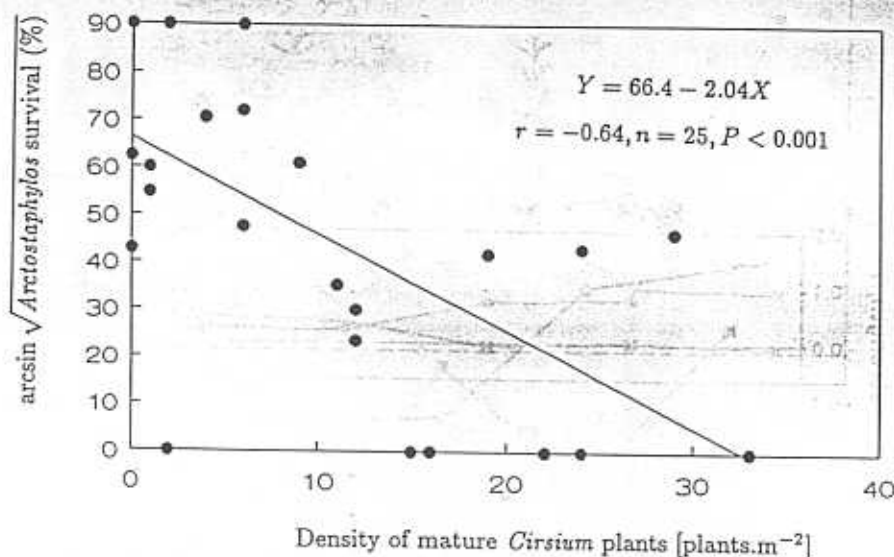


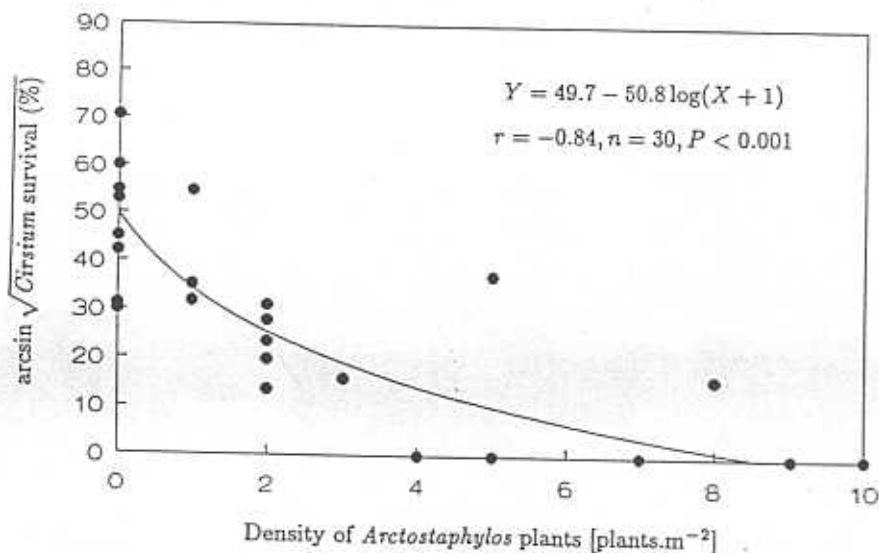
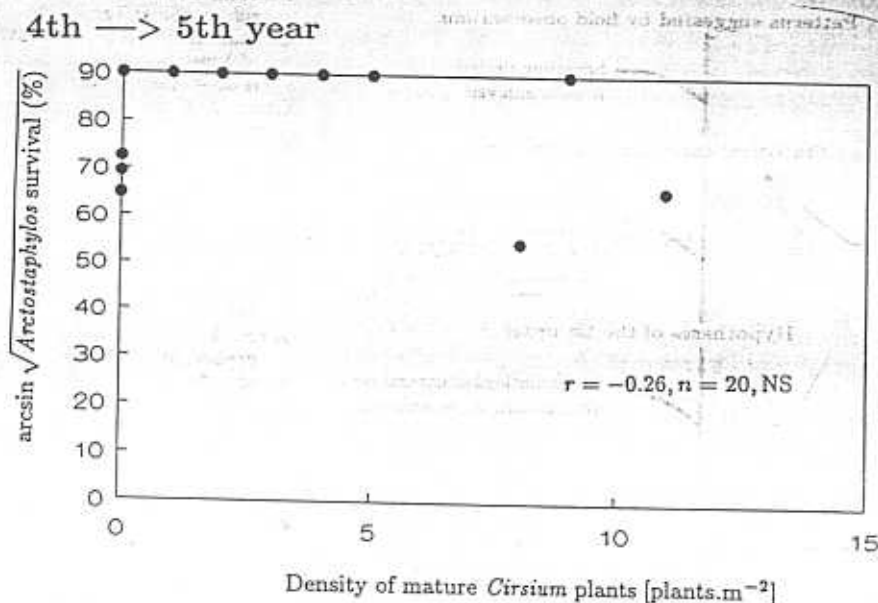
Fig. 3. Dependence of species survival between the 2nd and 3rd year on the abundance of the other species in the 3rd year.

fluctuation in the negative association between *Arctostaphylos* and mature *Cirsium* (Fig. 2) has a plausible causal explanation: successional reversal in the direction of real competition. This can be called an explanation of the 1st order (Fig. 5). Of course, we can now proceed to the higher order hypotheses, and ask questions about the mechanisms of interspecific competition. For example, is there any contribution of allelopathy? What is the relative contribution of shoot vs root competition? And if root competition dominates, is it mainly for soil moisture or for nutrients

(e.g., Yoder-Williams and Parker 1987, Wilson 1988, Rejmánek and Messina 1990, Caldwell et al. 1991)?

Competitive hierarchies between species are not necessarily constant (Jacquard 1968). It is well known that they can differ in different environments (Schmidt 1981, Rice and Menke 1985) and can change with the ontogenesis of involved individuals (Grace 1985). It is not surprising that the ranks of competitors can also change during vegetation succession and that this has consequences for spatial patterns of individual species, their associations, and succession itself.

Fig. 4. Dependence of species survival between the 4th and 5th year on the abundance of the other species in the 5th year.



Patterns suggested by field observations and proven significant via statistical analyses are important for the generation of hypotheses about mechanisms structuring biotic communities. There are currently no generally accepted criteria for satisfactory causal explanations (Shrader-Frechette and McCoy 1990, Lipton 1991, Pickett et al. 1994, Jones 1995). Nevertheless, we believe that the indirect causal analysis demonstrated in this study, represents a viable explanatory procedure for field ecology. There is not necessarily a sharp distinction between

manipulative experiments, natural experiments, and inference based on observed patterns. In the proper context, the quadrats of field ecologists can tell credible stories.

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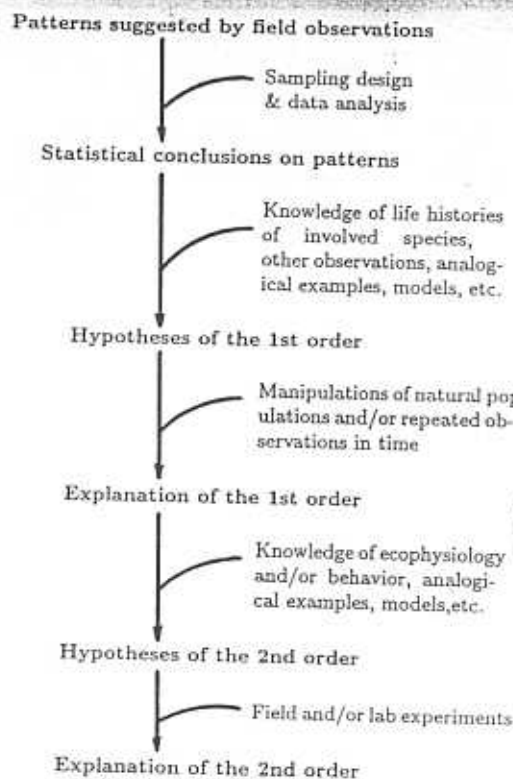


Fig. 5. A flow diagram of a hypothesis generation-explanation process in ecology.

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