

## **Pollination Niche Separation in a Winter Annual Community**

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**Summary.** Differences in major selective forces important in early and late successional communities should influence niche breadth and degree of overlap. Early successional species may not experience consistent, strong selection against competition and can be expected to have broader niches with more overlap than later successional species. This paper presents data from 2 early successional winter annuals that show clear niche separation under conditions in which coevolution is unlikely.

*Lactuca scariola* L. and *Erigeron annuus* (L.) Pers. flower in mid-summer and attract the same insect visitors. *Erigeron*, the more common species, begins to flower in mid-morning when insect visitors are quite active. *Lactuca* flowers open earlier in the morning and close just before *Erigeron* flowers open. The early morning hours are not optimum for *Lactuca* visitation, as most of the visits occur just before floral closing. Both species can self-fertilize without a vector, and *Lactuca* was introduced from Europe. It is, therefore, not possible that niche separation in flowering time and subsequent time of visit in *Erigeron* and *Lactuca* is a result of coevolutionary niche differentiation between the two species. This separation is likely to be a preadaptation resulting from coevolution with other species.

### **Introduction**

Much of current ecological theory about communities is based on MacArthur and Wilson's (1967) concept of an *r-K* selection continuum. In early successional communities of fugitive, *r*-selected species, competition is not considered to be as important in community organization as it is in mature communities composed of more strongly *K*-selected species. Accordingly, the differences in major selective forces in early and late successional communities should influence niche breadth and degree of overlap, with later communities having narrower niches and less overlap between species than earlier successional communities. Existing evidence from research comparing niche relationships of species of

fugitive and mature communities (Pianka, 1969; Parrish and Bazzaz, 1976, 1978; Werner and Platt, 1976) supports this hypothesis. Fugitive species do not appear to undergo as much selection for niche reduction as do species of more mature communities. Some species pairs of early succession do differ markedly in response to gradients to soil moisture (Pickett and Bazzaz, 1976, 1978), in rooting pattern (Parrish and Bazzaz, 1976) and in underlying physiology (Wieland and Bazzaz, 1975). However, overall community averages for proportional similarity are the same or higher than the average proportional similarities of computer-generated random communities with the same numbers of species and states (Parrish and Bazzaz, 1978). Therefore niche differentiation has not played a major role in early successional communities studied. In fact, strong directional selective pressures for broad physiological response may have resulted in similarities higher than random between early successional species (Pickett and Bazzaz, 1978).

If the importance of competition as a selective pressure increases with later successional position, species with enough of their resources unshared and those with a competitive advantage should replace other species. The threshold level of maximum niche overlap allowing coexistence should decrease as species co-occur over evolutionary time. As the importance of other organisms in the selective regime of a population increases with successional position, relationships such as that between a plant and its pollinators should become closer. There should be more similarity between early successional species in use of pollinators than late successional species due to decreased coadaptation of early species. The colonizer species of early succession are often autogamous (Allard, 1965; Baker, 1965, 1974; Mulligan and Findlay, 1970; Stebbins, 1970) and therefore do not rely on a pollen vector for seed set. However there are not many data on niche relationships from fugitive or early successional communities to compare with those from mature communities. Most of the work on plant-pollinator relationships has been done on species of mature plant communities, and close relationships have been interpreted as clear examples of coevolution (e.g. Kullenberg, 1961; Powell and Mackie, 1966; van der Pijl and Dodson, 1966; Galil and Eisekovitch, 1968; Macior, 1968; Levin and Berube, 1972). This is likely to be the case, but some counterintuitive data from an early successional winter annual community suggest other explanations that might be considered. This paper presents data from 2 early successional annuals that show clear niche separation under conditions in which coevolution is unlikely.

## Methods

A winter annual community dominated by *Erigeron annuus* (L.) Pers. (daisy fleabane) and *Lactuca scariola* L. (wild lettuce) in mid-summer was observed as part of a larger study (Parrish and Bazzaz, 1978). The study site near Woodson in Morgan County, Illinois, was under cultivation the previous year and had not been disturbed since harvest in October. Number of individuals flowering per m<sup>2</sup> was estimated from weekly counts of flowering stalks in 24 permanent 1 m<sup>2</sup> plots. Number of flowers per individual was estimated from counts on 10 marked individuals of each species. Number of flowers per m<sup>2</sup> was then estimated by multiplying the average number of individuals flowering at a given time of the season by the average number of flowers per individual at the same time of the season.

Heads of each species were observed at 15-min intervals throughout 3 typical summer days to determine daily timing of the floral display. Twenty heads of each species were bagged with dialysis tubing to determine if the flowers were dependent upon pollen vectors for seed set. Insect visits to individual plants were observed for consecutive periods of 15 min on sunny days throughout the peak of flowering. Several specimens of each type of visitor were collected throughout the display period of the flower for identification and pollen analysis. Insects were rubbed with or mounted on squares of glycerin fuchsin jelly (Beattie, 1971) to stain and preserve pollen for microscopic identification and quantification (Parrish and Bazzaz, 1978, for further detail on methods).

Niche breadths of the two species in seasonal time of flowering, daily time of floral opening and visitation, visitor identity, species of potential pollinator, and a two-dimensional measure of daily time of visitation and identity of visitor were calculated. Levins' (1968) formula for niche breadth ( $B$ ) was used:

$$B = 1 / \left( \sum_{h=1}^s p_h^2 \right) S$$

where  $p_h$  is the proportional response of a species in resource state  $h$  and  $S$  is the number of resource states or categories. A symmetrical measure of proportional similarity ( $PS$ ) of the two species,  $i$  and  $j$ , was calculated using the formula

$$PS_{ij} = 1 - 1/2 \sum_{h=1}^s |p_{ih} - p_{jh}|$$

where  $h$  is the resource state and  $S$  is the number of resource states. Proportional similarities were calculated for the same six parameters as niche breadths for the two species.

## Results

Autogamy (or often apomixis in *Erigeron*) of bagged inflorescences of both *Lactuca* and *Erigeron* resulted in seed set with no significant numerical difference from unbagged inflorescences, although unbagged inflorescences of both species were visited frequently by insects which transfer pollen. However, the potentially important effects of outbreeding on the overall fitness of offspring was not evaluated. *Lactuca* and *Erigeron* overlap broadly in flowering time in mid-summer (Fig. 1). The same species of potential cross-pollinators visit both plants, resulting in a high similarity in vector use (Table 1). Twenty-seven kinds of insects were observed to visit more than 1% of the flowers of either species, but only 8 were potential vectors (Table 2).

Though similarity in vector use is high, the daily timing of the visitation was quite different. *Lactuca* inflorescences opened, exposing about 17 flowers per head, around 0800 and closed permanently around 1000. *Erigeron* rays unfolded around 0900, but no stigmas were extruded until after 0930, with a peak in the early afternoon (Fig. 2a). There was very little overlap in diurnal floral display (Table 1), and even though most of *Lactuca's* visits occurred just before floral closing (Fig. 2b) there was little overlap in daily timing of insect visits. Analysis of pollen load revealed that the same individual insects collect pollen from both species within a day, visiting each species when it is available. *Halictus ligatus* Say, a common bee visiting flowers of both *Erigeron* and *Lactuca* (comprising 15% and 42% of the visits respectively) showed visitation characteristics typical of the generalist visitors observed. At the time when both *Erigeron* and *Lactuca* were closed (1000–1030), this opportunistic bee visited *Polygonum pensylvanicum* L. (Fig. 2c), the only summer annual that was important in the winter annual community. At the time of peak seasonal flowering for *Lactuca* and *Erigeron*, there was very little *Polygonum* in flower (Fig. 1).

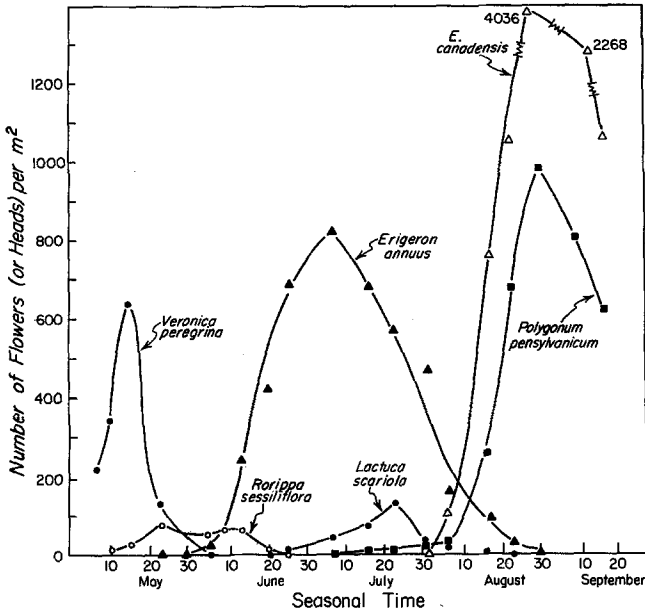


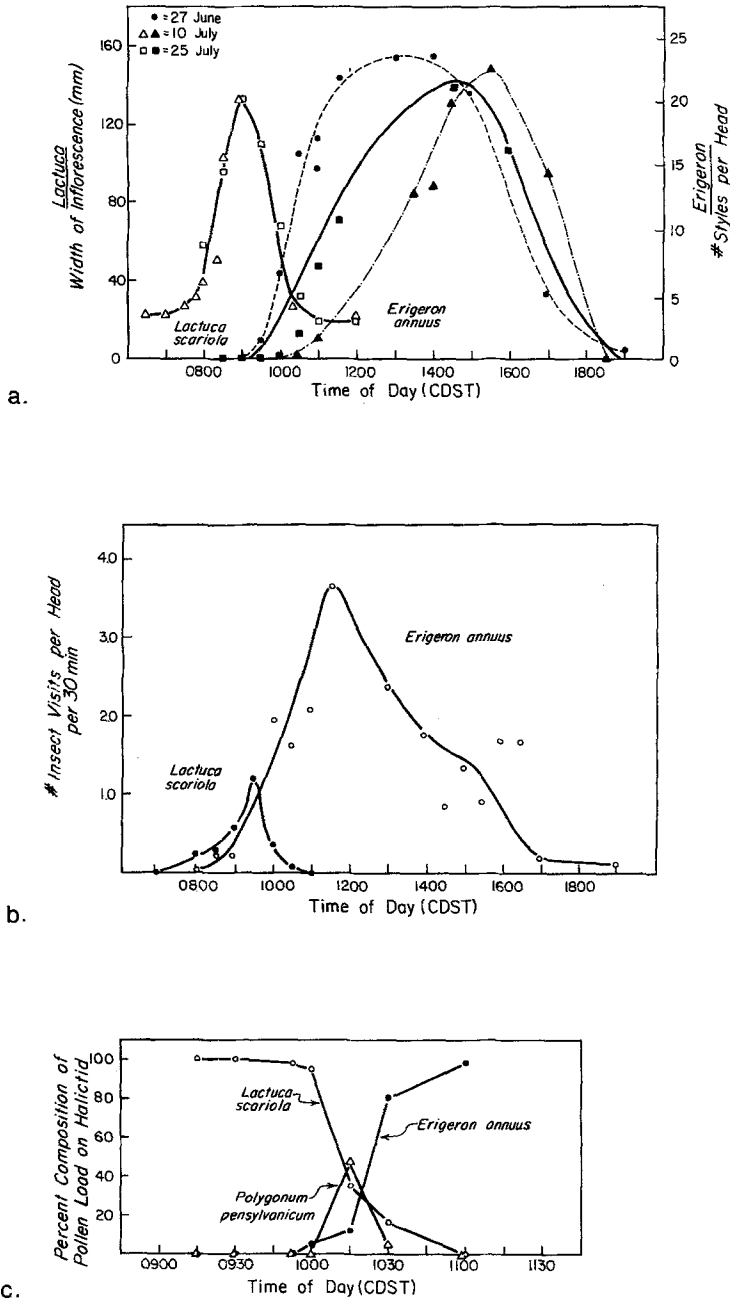
Fig. 1. Seasonal distribution of flowering in species of a winter annual community

Table 1. Proportional similarity (PS) of *Erigeron annuus* and *Lactuca scariola* along 6 parameters

Parameter	Data type	PS
Seasonal flowering time	# heads open/day of week	0.59
Time of visit	# visits/head/time period	0.17
Species of visitor	# visits/head/species of insect	0.57
Species of potential pollinator	# visits/head/species of insect	0.52
Daily floral opening	# stigmas/head/time- <i>Erigeron</i> ; width of head/time- <i>Lactuca</i>	0.05
2-D time of day, species of visitor	a) time PS $\times$ insect PS	0.10
	b) # visits/head/species insect/time	0.10

Table 2. Proportion of visits by eight potential pollinators

Insect	Family	<i>Erigeron</i>	<i>Lactuca</i>
<i>Mesograpta</i> spp.	Syrphidae	0.235	0.211
<i>Helophilolus</i> spp.	Syrphidae	0.053	0.039
<i>Sphaerophoria</i> spp.	Syrphidae	0.026	0
<i>Halictus confusus</i>	Halictidae	0.292	0.137
<i>Halictus rubicundus</i>	Halictidae	0.148	0.417
<i>Augochlorella</i> spp.	Halictidae	0.002	0
<i>Augochloropsis</i> spp.	Halictidae	0	0.067
<i>Melissodes bimaculata</i>	Anthophoridae	0.023	0.110



**Fig. 2.** a Diurnal flower availability on 3 days. Open symbols designate width of inflorescence for *Lactuca*. Closed symbols designate number of extruded stigmas for *Erigeron*. b Distribution of total number of insect visits per inflorescence over daily time. c Composition of pollen loads of seven individual *Halictus ligatus* collected throughout the morning of July 16, 1975

**Table 3.** Niche Breadths (*B*) of *Erigeron annuus* and *Lactuca scariola* on six parameters

Parameter	# Resource states	B	
		<i>Erigeron</i>	<i>Lactuca</i>
Seasonal flowering time	31	0.24	0.11
Time of visit	7	0.60	0.24
Species of visitor	75	0.21	0.14
Species of potential pollinator	8	0.39	0.35
Daily floral opening	26	0.56	0.23
2-D time of day, species of visitor	525	0.02	0.01

When the more abundant flowers of *Erigeron* became available after 1000, the generalist bee switched to *Erigeron*.

Niche breadths for *Lactuca* and *Erigeron* on the pollination parameters measured are presented in Table 3. *Erigeron*, the more abundant species at 19.6 flowering stems per m<sup>2</sup> compared to 2.2 flowering stems per m<sup>2</sup> for *Lactuca*, consistently had broader niches than did *Lactuca*. Seventy-seven percent of the visits to the more specialized *Lactuca* were made by potential pollinators compared to 59% of the visits to *Erigeron*.

## Discussion

*Lactuca* and *Erigeron* demonstrate some niche separation in number of visits by insect species. Differences in daily flowering time result in very little overlap in use of the renewable resource of pollinator time. This lack of overlap is expected in coevolved communities, especially on parameters directly related to reproduction. Separation in daily flowering has been demonstrated in other communities (Lindsley et al., 1964) and inspired Linneaus (1755) to suggest its use as a "flower clock" (Clauser, 1954). If one did not know the history of this winter annual community, it would be easy to develop a hypothesis to explain the daily flowering patterns based on recent coevolution. Competition for pollinators or selection to avoid interspecific transfer of pollen could have resulted in the compression of flowering time in *Lactuca*, the less abundant species. The more common species would be more likely to attract visitors, and the probability of transfer of pollen from *Erigeron* to *Lactuca* would be high if an insect did happen to visit *Lactuca*. Daily flowering time in *Lactuca* is not at an optimal time for insect visitation, as is evidenced by the high proportion of visits to *Lactuca* just before floral closing. However, the sharp differences in daily flowering pattern are not explainable in this way. These species are fugitives that are self-compatible. It is hard to imagine selective pressures being strong enough to result in such reduced overlap in pollinator use in *Erigeron* and *Lactuca*, even considering outcrossing to be very important in the maintenance of variability in potential selfers (Solbrig, 1972, 1976).

*Lactuca* was introduced from Europe. It is possible that the relationship between *Erigeron* and *Lactuca* is just a coincidence, the rare random event. However, *Lactuca* co-occurs with *Senecio* spp. and other plants similar to *Erigeron* in floral timing in Europe (Paul Poissonnet, pers. comm.). Coevolutionary niche separation between *Lactuca* and *Senecio* may have occurred, so *Lactuca* may have been pre-adapted to fit into the eastern United States winter annual community so neatly. In that case, selection to reduce competition for pollinators or selection to avoid interspecific pollen transfer may still have shaped flowering time in *Lactuca*'s previous community, though coevolution with *Erigeron* could not have. Many species in the Cichorieae tribe of the Compositae have daily flowering patterns similar to *Lactuca* (e.g. *Pyrrhopappus*, Estes and Thorp, 1975, *Cichorium*, *Taraxicum*). Thus *Lactuca* may be preadapted to fit into the winter annual community because of its long-inherited flowering characteristics.

This example of extreme niche separation between important species of a fugitive community in which coevolution could have had little organizing influence demonstrates that apparent coadaptation of species within communities could have other explanations. The relationships between *Lactuca* and *Erigeron* could be explained by: 1) Preadaptation through coevolution with species in other communities, 2) Preadaptation through characteristics common to a larger taxon, or 3) Chance. The separation of *Lactuca* and *Erigeron* emphasizes the necessity of obtaining baseline data from communities in which competition may play a relatively minor role in community organization before drawing conclusions about coevolution of species within communities.

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## References

- Allard, R.W.: Genetic systems associated with colonizing ability in predominantly self-pollinated species. In: Genetics of colonizing species (H.G. Baker, G.L. Stebbins, eds.), pp. 46-76. New York: Academic Press 1965
- Baker, H.G.: Characteristics and modes of origin of weeds. In: Genetics of colonizing species (H.G. Baker, G.L. Stebbins, eds.), pp. 147-168. New York: Academic Press 1965
- Baker, H.G.: The evolution of weeds. *Ann. Rev. Ecol. Syst.* **5**, 1-24 (1974)
- Beattie, A.J.: A technique for the study of insect-borne pollen. *The Pan-Pac. Ent.* **47**, 82 (1971)
- Clauser, G.: *Die Kopfur*. Stuttgart: Enke 1954
- Estes, J.R., Thorp, R.W.: Pollination ecology of *Pyrrhopappus carolinianus* (Compositae). *Am. J. Bot.* **62**, 148-159 (1975)
- Galil, J., Eisekovitch, D.: On the pollination ecology of *Ficus sycamorus* in East Africa. *Ecology* **49**, 259-269 (1968)
- Kullenberg, B.: Studies in *Ophrys* pollination. *Zool. Bidrag. Uppsala* **34**, 1-340 (1961)
- Levin, D.A., Berube, D.E.: *Phlox* and *Colias*: the efficiency of a pollination system. *Evolution* **26**, 242-250 (1972)
- Levins, R.: *Evolution in changing environments*, 120 pp. Princeton: Princeton Univ. Press 1968
- Linneaus, C.: *Somnus plantarum. Amoenitat. Acad.* **4**, 333 (1755)
- Macior, L.W.: Pollination adaptation in *Pedicularis groenlandica*. *Am. J. Bot.* **57**, 927-932 (1968)
- MacArthur, R.H., Wilson, E.O.: *The theory of island biogeography*, 203 pp. Princeton, N.J.: Princeton Univ. Press 1967

- Mulligan, G.A., Findlay, J.: Reproductive systems and colonization in Canadian weeds. *Can. J. Bot.* **48**, 859–860 (1970)
- Parrish, J.A.D., Bazzaz, F.A.: Niche separation in roots of successional plants. *Ecology* **57**, 1281–1288 (1976)
- Parrish, J.A.D., Bazzaz, F.A.:  $\alpha$ -niche relationships along a successional gradient. *Ecology* (submitted, 1978)
- Pianka, E.R.: Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* **50**, 1012–1030 (1969)
- Pickett, S.T.A., Bazzaz, F.A.: Divergence of two co-occurring successional annuals on a soil moisture gradient. *Ecology* **57**, 169–176 (1976)
- Pickett, S.T.A., Bazzaz, F.A.: Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology* (in press, 1978)
- Pijl, L. van der, Dodson, C.: Orchid flowers. Their pollination and evolution. Coral Gables: Univ. Miami Press 1966
- Powell, J.A., Mackie, R.A.: Biological interrelationships of moths and *Yucca whipplei*. *Univ. California Publ. Ent.* **42** (1966)
- Solbrig, O.T.: Breeding system and genetic variation in *Leavenworthia*. *Evolution* **26**, 155–160 (1972)
- Solbrig, O.T.: On the relative advantages of cross- and self-fertilization. *Ann. Mo. Bot. Gard.* **63**, 262–276 (1976)
- Stebbins, G.L.: Adaptive radiation and reproductive characteristics in Angiosperms, I: Pollination mechanisms. *Ann. Rev. Ecol.* **1**, 307–326 (1970)
- Werner, P.A., Platt, W.J.: Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *Am. Nat.* **110**, 959–971 (1976)
- Wieland, N.K., Bazzaz, F.A.: Physiological ecology of three codominant successional annuals. *Ecology* **56**, 681–688 (1975)

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