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# Ecological interactions between *Cepaea nemoralis* and *Cepaea hortensis*: competition, invasion but no niche displacement

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**Abstract.** The importance of coevolution in shaping communities is not clear. Experiments with shells marked with a paint which fades in the sun show that the land snail *Cepaea hortensis* (Müll.) is more exposed to daylight than is *Cepaea nemoralis* (L.), but that there is no change in this behaviour when snails are placed in mixed or single species populations and no evidence of an interspecific interaction that might be a precursor of coevolution and character displacement for this niche dimension. *C. hortensis* on the Marlborough Downs has invaded many *C. nemoralis* colonies and replaced others during the past 25 years, a range expansion that may reflect the competition between the two that has been observed in the laboratory. If the lack of interaction for the niche dimension studied here is typical, the relative abundance of *C. hortensis* and *C. nemoralis* may reflect a balance between invasion and extinction rather than coevolution.

*Key-words:* Competition, invasion, niche displacement, coevolution, behavioural thermoregulation, community structure, land snail, *Cepaea*

## Introduction

The disjunct geographical distributions of the land snails *Cepaea nemoralis* (L.) and *Cepaea hortensis* (Müll.) were among the first to be cited as evidence for interspecific competition in nature (Boycott, 1934; Diver, 1940). It is often claimed that such competition leads to coevolution and that the ensuing niche divergence is important in structuring biological communities. However, the evolutionary significance of competition is still

not clear (Connell, 1983; Roughgarden, 1983; Strong *et al.*, 1984) and it is particularly uncertain whether it can lead to character displacement, a genetic response by one species to the presence of another (Arthur, 1982a). Differences in the niche dimensions of coexisting species in a community (e.g. Fenchel, 1975; Schluter, Price & Grant, 1985; Roughgarden, 1979) might equally reflect repeated invasion and extinction, rather than coevolution (Harvey *et al.*, 1983; Roughgarden, 1983). Experiments on natural populations are essential before differences in the habitat preference of closely related and coexisting species can safely be ascribed to character displacement (Connell, 1980, 1983). Competition will not lead to displacement unless it is strong enough to overcome other evolutionary forces but sufficiently weak to allow the two species to coexist (Taper & Case, 1985); and unless the species differ in allopatric populations in any character liable to diverge, they interact in sympatry and the character is heritable (Slatkin, 1980).

*Cepaea nemoralis* and *C. hortensis* have many of these attributes. There is competition between them in the laboratory (Cameron & Carter, 1979), they differ in habitat preference in unmixed populations (Cameron, Carter & Palles-Clark, 1980; Harvey, 1973, 1974) and sometimes diverge for heritable shell patterns when present together (Clarke, 1962; Arthur, 1982b). *C. hortensis* extends further north than does *C. nemoralis*, prefers cooler habitats and is more active at low temperatures in the laboratory (Cameron, 1970a, b, c). The frequencies of some genes in each species are also influenced by thermal stress (Jones, Leith & Rawlings, 1977). On sunny days, *C. nemoralis* escapes from the layer of hotter air near the ground by climbing (Jaremovic & Rollo, 1979) and there are differences in the behaviour of various shell morphs of this species in sunlight (Jones, 1982). In other poikilotherms, thermoregulatory behaviour may be modified by interspecific competition (Huey, 1982). Differences in behaviour in sunshine between *C. nemoralis* and *C. hortensis*

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might therefore be useful as a tool for investigating habitat partitioning and niche displacement.

Here we investigate the interaction of *C. nemoralis* and *C. hortensis* by marking snails in field population cages containing one or both species with spots of a paint which fades at a known rate when exposed to the sun. In addition we examine temporal changes in their relative distribution.

## Materials and methods

The fading paint consists of the photolabile dye Benzyl Blue (Bayer Dyestuffs — Special BR Blue FFR 200) dissolved in monoethyleneglycol monoethylether and mixed with a yellow polyurethane paint (International Paint Group, series 101; Yellow 109) to give a green paint that fades to yellow as the blue dye loses its colour (Jones, 1982). A spot of paint was placed at the midline of the shell just behind the lip. Fading was measured by comparison with a scale produced from serial 3:1 dilutions of the green mixture with the yellow base paint.

The experiment was carried out in 60 cages in an open field in Oxford University's Wytham Wood Estate. Each cage was a covered cylinder 90 cm high and 90 cm in diameter, made of 6.4-mm 'Weldmesh' (British Reinforced Concrete Engineering Company, Stafford, UK). Cages were planted with nettles, *Urtica dioica* L., grasses and other plants growing naturally around the cages such as red and white dead nettle, *Lamium purpureum* L. and *Lamium album* L., thistle, *Cirsium arvense* (L.), groundsel, *Senecio vulgaris* L. and goosegrass, *Galium aparine* L. They developed a diverse flora that resembled that of habitats often occupied by *Cepaea*. Samples of 375 snails from each of four populations of pure *C. nemoralis* and four of pure *C. hortensis* were collected from paired locations (Fig. 1) on the Marlborough Downs in southern England on 26–30 May 1985. Shells were painted grey since this removes the behavioural differences that result from differences in the thermal relations of animals of different colour and banding pattern (Jones & Cowie, in preparation). Fifteen cages were established for each of the four pairs of populations, five containing 50 *C. nemoralis* alone, five with 50 *C. hortensis*, and five with 25 of each, and assigned within the array at random. Snails were placed in the cages on 7 June 1985 and removed 93 days later. More than 90% of them were found alive.

From 1983–85 we studied the distribution of *Cepaea* on the Marlborough Downs, a region of

rolling chalk downland, woods and arable land. We have compared our results with those from a survey carried out in 1960 and 1961 by Cain & Currey (1963).

## Results

### Cage experiments

Paint-fading scores (full details of which can be obtained from the authors on request; and which are summarized in Fig. 2) were analysed by three-way analysis of variance with replication (Sokal & Rohlf, 1981), using species (*C. nemoralis* or *C. hortensis*), cage type (single- or mixed-species) and population pair (A, B, C or D) as the three factors and with five replicates for each combination of these. Only 'species' made a significant contribution to the variance ( $P < 0.001$ ) and there were no significant first- or second-order interactions (Table 1). Because of the lack of independence of the mean scores for the two species in the mixed-species cages ( $r = 0.861$ ;  $P < 0.001$ ), a two-way analysis of variance was performed on the scores from single-species cages only, using species and population pair as the two factors and with five replicates of each combination. Again, only 'species' had a significant effect ( $P < 0.01$ ; Table 2).

Paired comparisons of the scores for the two species in mixed-species cages show that in all 20 cages the mean fading score for *C. nemoralis* was lower than that for *C. hortensis* (sign test  $P < 0.001$ ). The mean fading score over all 60 cages for *C. nemoralis* was  $6.225 \pm 0.128$  and for *C. hortensis*  $7.017 \pm 0.240$ . Hence, the two species showed marked divergence in niche components that manifest themselves through exposure to sunshine.

However, there is no evidence that this niche dimension in either species was significantly affected by the presence of the other. Mean fading for *C. nemoralis* is  $6.199 (\pm 0.357)$  in mixed populations, compared to  $6.250 (\pm 0.259)$  in unmixed; and for *C. hortensis*  $7.140 (\pm 0.331)$  in mixed populations compared to  $6.893 (\pm 0.347)$  in those containing this species alone (Fig. 2). A similar analysis of the variances of fading scores from each cage revealed no significant differences between 'species', 'cage type' or 'population pair' and there was no significant correlation between the variances for *C. nemoralis* and those for *C. hortensis* in mixed-species cages. This validates the use of analysis of variance on the mean scores.

**Table 1.** Three-way analysis of variance on the mean fading scores.

Source of variation	df	SS	MS	F	P
Pair	3	1.135	0.378	0.641	NS
Species	1	12.483	12.483	21.158	<0.001
Cage type	1	0.195	0.195	0.331	NS
Pair × species	3	0.095	0.032	0.054	NS
Pair × cage type	3	2.859	0.953	1.615	NS
Species × cage type	1	0.439	0.439	0.744	NS
Pair × species × cage type	3	0.158	0.053	0.090	NS
Within subgroups (error)	64	37.745	0.590		
Total	79	55.109			

**Table 2.** Two-way analysis of variance on the mean fading scores for single-species cages.

Source of variation	df	SS	MS	F	P
Pair	3	1.157	0.386	0.710	NS
Species	1	4.115	4.115	7.564	<0.01
Pair × species	3	0.016	0.005	0.010	NS
Within subgroups (error)	32	17.420	0.544		
Total	39	22.708			

### Distribution

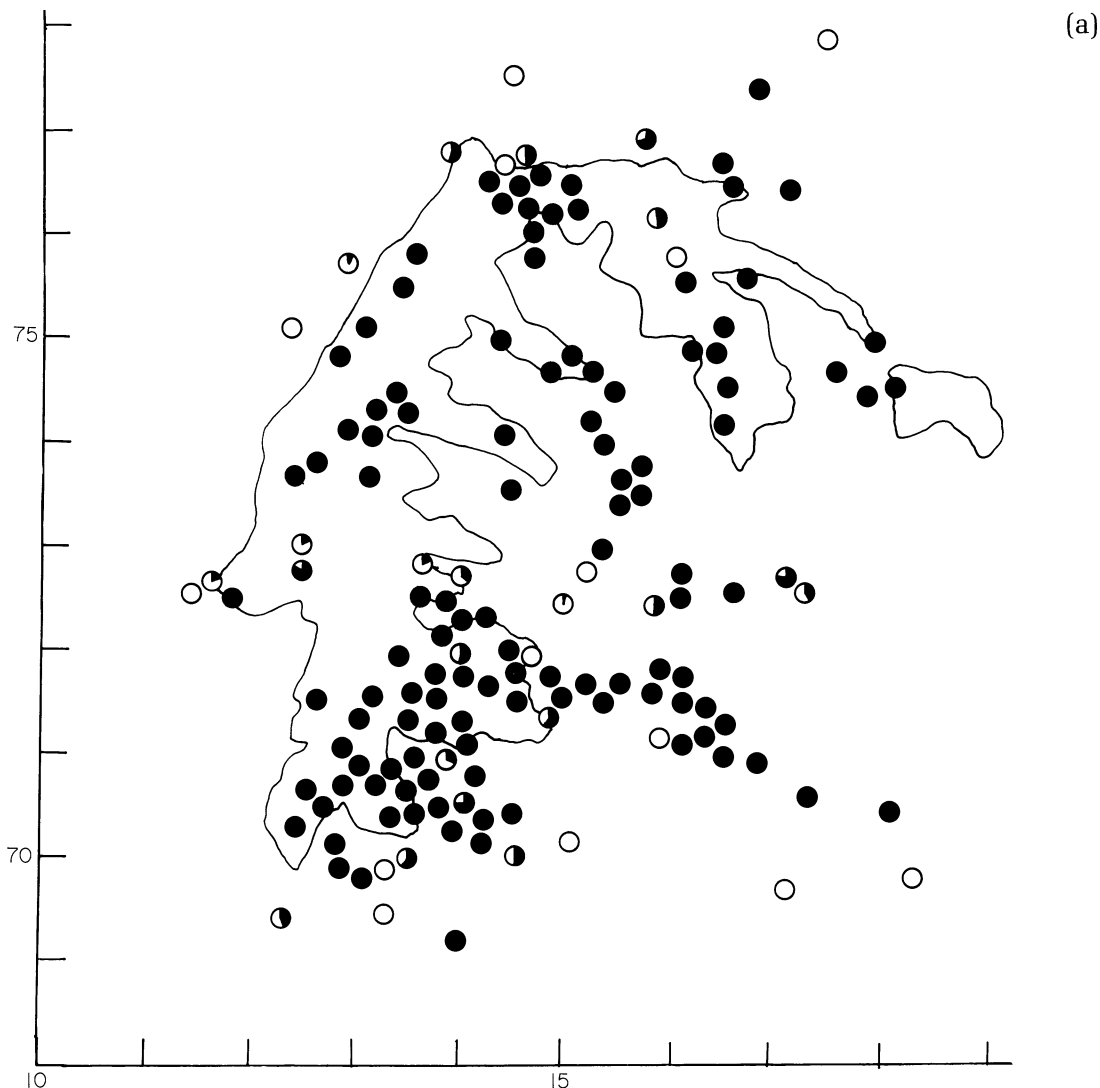
*C. hortensis* has greatly expanded its range on the Marlborough Downs at the expense of *C. nemoralis* (Fig. 1). Three sites that previously contained only *C. nemoralis* now contain only *C. hortensis* and 28 *C. nemoralis* sites now contain both species. Five of the 12 sites that were previously mixed now contain only *C. hortensis*. No sites have gained *C. nemoralis* at the expense of *C. hortensis* and the proportion of *C. hortensis* has increased in six of the seven sites containing both species on both sampling occasions. The main result to emerge from these observations is that, in spite of a marked interspecific divergence for a niche component and an invasion of the range of *C. nemoralis* by its sibling species, there is no evidence of any interaction between *C. nemoralis* and *C. hortensis* for this aspect of their niche when they are experimentally mixed.

### Discussion

The range of expansion of *C. hortensis* on the Downs has been accompanied by the disappearance of its sibling. There are a few deposits of fossil *Cepaea* in southern England and these show that there have been earlier phases of expansion of *C. hortensis* in this region during the past several thousand years (Currey & Cain, 1968; Cain, 1971). In contrast, *C. nemoralis* has increased its

range in comparison to that of *C. hortensis* in the Rhone valley since the last glaciation (Favre, 1927). The two species may fluctuate in relative range. Some of these fluctuations may be related to climate since *C. hortensis* is generally found in cooler places than is *C. nemoralis*. However, there has been no consistent trend in temperature on the Downs over the past 25 years; the mean temperature at Marlborough from May to October (the months during which *Cepaea* is active) in 1960 was 13.2°C, in 1965 12.1°C, in 1970 13.5°C, in 1975 13.4°C, in 1980 12.6°C and in 1985 12.7°C (Meteorological Office, unpublished). Much downland is now lost to *Cepaea* because of ploughing and parts of the Downs have become overgrown since the disappearance of rabbits after myxomatosis. This may favour *C. hortensis*, since it prefers longer and damper vegetation than that favoured by its sibling (Cameron, Carter & Palles-Clark, 1980). There has been a great decrease in the extent of predation in our samples compared to those of Cain & Currey (Cain, personal communication), but it is not clear why this should confer an advantage upon *C. hortensis*. The changes in the relative range of the two species might also reflect competition between them.

In spite of an overlap in food preference between *C. nemoralis* and *C. hortensis* there is no indication of interspecific resource competition (Carter, Jeffery & Williamson, 1979). However, there is strong evidence for interference compe-

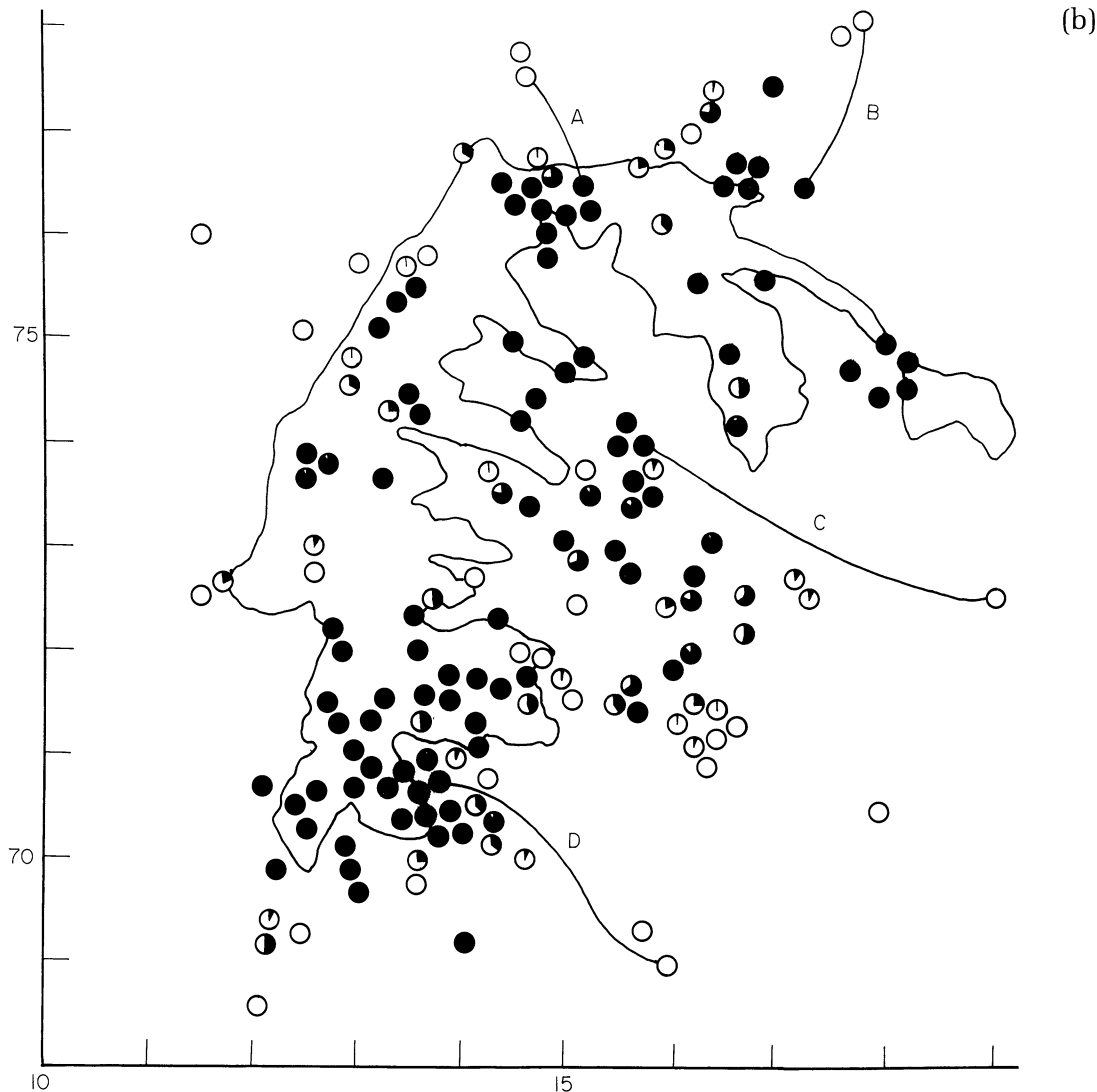


**Fig. 1.** The distribution of *Cepaea nemoralis* and *Cepaea hortensis* on the Marlborough Downs: (a) in 1960–61 (data from Cain & Currey, 1963) and (b) collected by ourselves in 1983–85. Our samples consisted of 179 collections, 107 of which were recollections of sites first sampled in the 1960s and located to within 50 m. We collected over 11 000 snails. Fewer than 200 of these had been broken by predators. The dark segment in each pie diagram represents the proportion of *C. nemoralis*; the continuous line is the 700 foot (225 m) contour. Pairs of samples, A, B, C and D were the donor

tition. In populations of *C. nemoralis* in field enclosures, an increase in population density decreases growth rate, adult size, longevity, clutch size and hatching success (Oosterhoff, 1977) and in natural populations an increase in density leads to a decrease in shell size and fecundity (Williamson, Cameron & Carter, 1977). Many of these effects are mediated by slime-trail pheromones, whose inhibitory action is almost as great between the two species as within each of them (Cameron & Carter, 1979). Also, in field population cages *C. nemoralis* and *C. hortensis* greatly influence each other's mortality (Tilling, 1985).

A snail's exposure to daylight is influenced by

time of activity and by the position taken up during the day. Temporal changes in activity are usually important in maintaining an optimal temperature in poikilotherms and may be complemented by choice of an appropriate position (Stevenson, 1985). In lizards, for example, inter-specific partitioning of the thermal niche usually involves differences in time and position of occupation of a favourable habitat (Roughgarden, 1979; Huey, 1982). The same is true in *Cepaea*. In field cages, *C. hortensis* chooses a higher aestivation site and is more diurnal than is *C. nemoralis* (Tilling, 1986). Both these behaviours accord with the relatively greater paint fading in the former.



populations for the cages. Grid references and sampling areas: *C. nemoralis* A = SU 148764, 20 × 30 m; B = 171764, 100 × 50 m; C = 154740, 30 × 15 m; D = 136706, 300 × 80 m; *C. hortensis* A = 145775, 55 × 20 m; B = 176780, 40 × 5 m; C = 196725, 80 × 10 m; D = 158690, 25 × 3 m. Numbers on axes represent grid references. Sample locations and scores can be obtained from the authors on request.

Such niche separation is often a direct indicator of interspecific competition. Some coexisting species of anoline lizards which partition their habitat by perching at different heights increase this niche difference in sympatry compared to allopatry (Roughgarden, Pacala & Rummel, 1984). In mixed populations of these species in enclosures, one of them perches higher, eats less, grows more slowly and lays fewer eggs than when it is the only species present. This is due primarily to interference between animals competing for a thermally optimal niche.

Although there is competition and habitat separation in *Cepaea*, we found no evidence of an

interspecific interaction in experimentally mixed populations of *C. nemoralis* and *C. hortensis* for components of behaviour manifest in paint fading that might precede the evolution of an increased divergence of this niche dimension in sympatry. It is probably not true that our experiment was too small to detect such an effect, as it involved a study of the behaviour of nearly 3000 individuals. Of course, competitive displacement might influence niche components that we have not identified and it is also possible that niche displacement takes place on occasions not encompassed by our experiment or in places or populations other than those used here (for example, see the work of Dunham

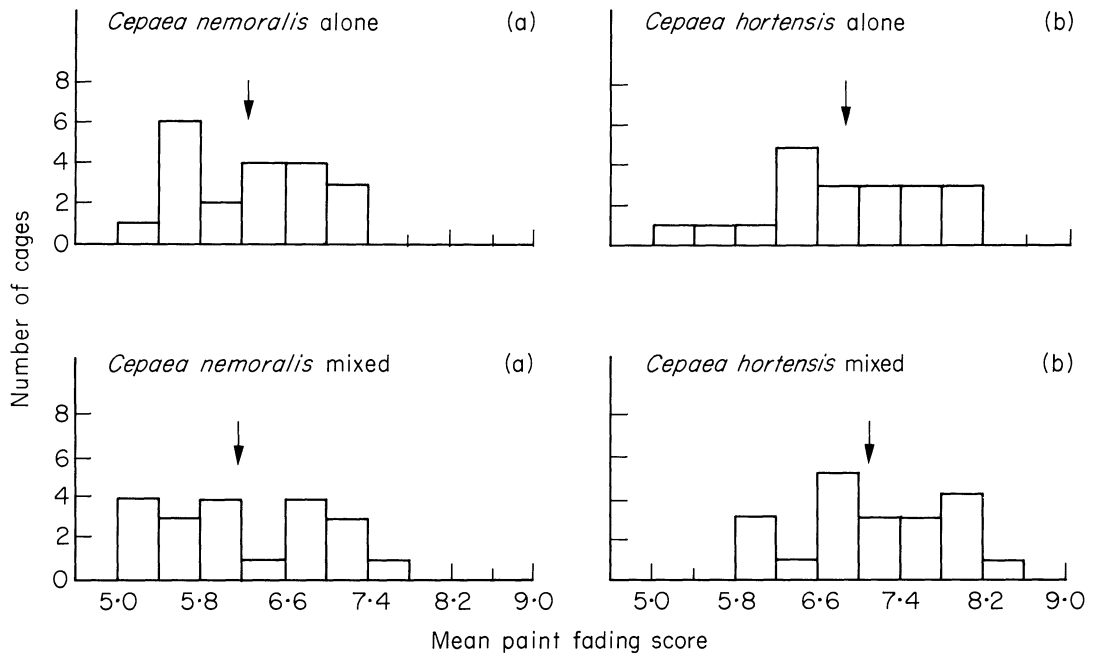


Fig. 2. Distribution of paint fading scores in experimental populations of *Cepaea nemoralis* and *Cepaea hortensis*. (a) *C. nemoralis* in single-species and mixed populations; (b) *C. hortensis* in single-species and mixed populations. The arrows show the mean fading score for each category.

[1980] on salamanders; and Hairston [1983] on lizards).

Interspecific interaction leading to character displacement is often invoked as a general mechanism that shapes natural communities. Our work on niche partitioning in *C. nemoralis* and *C. hortensis* began in the hope of studying character displacement in sympatric and allopatric populations. In the event we have found no evidence even of a response of one species to the other for the niche dimension studied. Hence, there is little opportunity for coevolution of the two species to promote their joint exploitation of the thermal environment. It is notoriously difficult to identify the 'ghost of competition past' (Connell, 1980). Nevertheless, Harvey & Ralls (1985) suggest that character displacement is now more or less bereft of reliable examples. The structure of many communities may be shaped as much by the invasion of competitors rendered more successful because of ecological change as by coevolution (Strong, 1983).

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