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Effects of the past and the present on species distribution: land-use history and demography of wintergreen

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Summary

1 Past land use can have long-term effects on plant species' distributional patterns if alterations in resources and environmental conditions have persistent effects on population demography (environmental change) and/or if plants are intrinsically limited in their colonization ability (historical factors).

2 We evaluated the role of environmental alteration vs. historical factors in controlling distributional patterns of *Gaultheria procumbens*, a woody, clonal understorey species with a pronounced restriction to areas that have never been ploughed, and near absence from adjoining areas that were ploughed in the 19th century. The demographic study was conducted in scrub oak and hardwood plant communities on an extensive sand plain, where it was possible to control for the effect of variation in environment prior to land use.

3 The observed demographic effects were contrary to the hypothesis that persistent environmental alteration depressed demographic performance and limited the distribution of *G. procumbens*. We observed no overall effect of land-use history on stem density, stem recruitment or flower production. In fact, some aspects of performance were enhanced in previously ploughed areas. Populations in previously ploughed areas exhibited less stem mortality in scrub oak transitions, an increase in germination, seedling longevity and proportion of potentially reproductive stems in both plant communities, a trend for slower observed rates of population decline in both plant communities, and a higher projected rate of population growth in the scrub oak transitions. Thus, particularly in scrub oak communities, the lower abundance of *G. procumbens* in formerly ploughed than in unploughed areas contrasted with its performance.

4 The limited occurrence of *G. procumbens* in formerly farmed areas was explained instead by its slow intrinsic growth rate, coupled with limited seedling establishment. Lateral population extension occurred exclusively through vegetative growth, allowing a maximum expansion of 43 cm year$^{-1.}$

5 We conclude that inherent limitations in the colonizing ability of some plant species may present a major obstacle in the restoration or recovery of plant communities on intensively disturbed sites, even in the absence of persistent environmental effects that depress population growth.

Key-words: clonal growth, demographic effects of land-use history, distributional restrictions, environmental alterations, *Gaultheria procumbens*, historical constraints on species distribution

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Introduction

The role of land-use history in determining the structure, composition and dynamics of modern plant communities is of fundamental importance to ecologists, conservation biologists and natural resource managers (Peterken & Game 1984; Motzkin *et al.* 1993). Like natural disturbances, human activities vary in size, intensity, longevity and pattern. The subsequent trajectory of vegetation recovery will depend on these characteristics, the extent to which the environment and resource availability are modified, and the inherent abilities of plant species either to survive the disturbance or to recolonize subsequently (Turner & Dale 1990).

Many parts of the world, including north-western Europe, eastern North America, the Caribbean and Latin America, have experienced major historical changes in the intensity of human land use. Sites that were previously cleared for agriculture have subsequently become reforested as farming has been discontinued (Glitzenstein *et al.* 1990; Foster 1993; Motzkin *et al.* 1996). Persistent patterns of species distributions and forest community composition are associated with variation in the intensity of past land use (Foster *et al.* 1992; Brunet 1993; Orwig & Abrams 1994; Motzkin *et al.* 1996) and may persist for many decades or centuries despite subsequent natural disturbance (Gomez-Pompa & Kaus 1992; Zimmerman *et al.* 1995; Motzkin *et al.* 1996). Prior studies in New England, USA, (Motzkin *et al.* 1996) have documented that some species are restricted to primary forests that have been wooded continually (although frequently logged throughout the historical period), that some species occur in greater abundance in secondary forest areas which were previously cleared for agriculture, and that other species occur in comparable abundance in areas of different history. These observations parallel findings in Britain (Peterken & Game 1981, 1984) and in Europe (Hermy 1994). In these landscapes, too, the effects of land-use history on plant community composition and species' distributional patterns are dramatic, variable and persistent.

Fewer studies have investigated what biological mechanisms might maintain such patterns. Restriction of species to continuously forested areas over long periods of time could be due to (i) persistent environmental effects of past land use that inhibit recolonization and subsequent population growth, and/or (ii) inherent limitations in species' dispersal, establishment and growth that impede the recolonization of sites from which species were previously removed by human activities. Such limitations to sexual propagules or to vegetative growth of rhizomatous plants could account historically for limited distributions, independently of current environmental conditions. Land managers and conservation biologists need to identify which of these possibilities is currently limiting ecological recovery. Species' abundance patterns alone are not sufficient to indicate whether current environmental conditions provide suitable habitat; a species may exhibit population growth in a particular habitat even if it is presently at low abundance. Assessments based on observations of distribution and abundance at one point in time may mistake the results of ongoing processes for those of stable conditions. It is therefore important to determine how extant environmental conditions interact with historical factors to determine patterns of distribution and abundance.

Most studies of land-use effects on community and species patterns are greatly complicated by the link between land-use patterns and underlying environmental variation. Consequently, although associations may exist between abundances of certain species and specific land-use patterns, these may reflect environmental differences that predated land use rather than land use itself. We focused on the distributional restriction of *Gaultheria procumbens* (L.), a clonal, woody understorey plant on the Montague sand plain. This plain is a flat, deltaic deposit in the Connecticut River Valley of Massachusetts, USA. *Gaultheria procumbens* exhibits a pronounced restriction to areas that have never been ploughed, and land use in this essentially homogeneous environment has varied as a consequence of ownership patterns and decisions rather than underlying patterns of environmental variation (Motzkin *et al.* 1996). We were therefore able to examine explicitly the effects of land use on plant distribution and demography while controlling for prior environmental variability.

We compared stem dynamics, stage structure, seed germination and establishment and rates of vegetative expansion of *G. procumbens* on sites that had never been ploughed with sites that had been formerly ploughed and subsequently abandoned. If the observed pattern of restriction is due to factors in the current biotic or abiotic environment that actively inhibit population growth in formerly ploughed areas, rather than the historical consequence of removing a species with limited colonization ability, we would expect populations growing in formerly ploughed areas to have demographic parameters that reduce population growth compared with populations growing in areas that have never been ploughed.

Methods

THE STUDY AREA

The Montague sand plain in central Massachusetts, USA, is a flat 775-ha delta that formed in glacial Lake Hitchcock which occupied the Connecticut River Valley. Land-use history of the area includes cutting on primary forest sites (referred to as 'unploughed' areas), and clearing, ploughing and natural reforestation on secondary forest sites (referred to as 'ploughed' areas). Historical land-use patterns were determined by land ownership rather than topography or variation in soils (Motzkin *et al.* 1996). Common plant assemblages on unploughed areas on the plain include a scrub oak community dominated by *Quercus ilicifolia* (Wangenh.) and *Q. prinoides* (Willd.), and a hardwood forest community comprising *Q. coccinea* (Muerch.), *Q. rubra* (L.) and *Acer rubrum* (L.). Boundaries between unploughed areas and adjoining areas that were previously ploughed are apparent as distinct changes in vegetation structure and composition within both plant communities (Motzkin *et al.* 1996). In scrub oak stands, the transition from unploughed areas is marked by an abrupt thinning of scrub oak cover, loss of a number of ericaceous plants and establishment of pitch pine forest with relatively little understorey and heavy needle litter. Overstorey transitions in hardwood forests are less apparent, but boundaries are easily identified by the dramatic loss of the dense huckleberry (*Gaylusaccia baccata* (Wang.)) understorey that is present on unploughed areas and limited pitch pine establishment on formerly ploughed areas in some of the sites.

SITE SELECTION

Five scrub oak transition sites and five hardwood transition sites were chosen for study. Each site comprised an unploughed area dominated by scrub oak or hardwood forest and an adjacent previously ploughed area. The exact locations of the land-use boundaries were determined from diagnostic soil characteristics (Motzkin *et al.* 1996): in previously ploughed areas a pronounced plough horizon (Ap) approximately 20–25 cm deep is apparent, whereas soils in unploughed areas are characterized by a shallow A horizon (< 10 cm) and gradual transition to the underlying B horizon. Each site was centred on a 100-m length of its plough boundary, and sampling extended up to 50 m into unploughed and previously ploughed areas.

STUDY ORGANISM

Gaultheria procumbens (wintergreen) is a woody ericaceous understorey plant that spreads clonally through rhizomes in the litter and organic soil horizons. Vertical stems, which are the visible ramets, occur at varying intervals along the rhizomes. Red aromatic berries are produced annually and, although some are dispersed by animals, many remain on the plant through the winter. On sand plains in the Connecticut River Valley, *G. procumbens* and other ericaceous species, including *Gaylusaccia baccata* (huckleberry), *Vaccinium angustifolium* (Ait.) and *V. vacillans* (Torr.) (blueberry), display pronounced restriction to areas that have been forested continually (Motzkin *et al.* 1996). A previous study has shown that *G. procumbens* occurs on 96% of the unploughed plots but on less than 5% of the previously ploughed plots sampled throughout the Montague sand plain (for a mapped distribution see Motzkin *et al.* 1996). It was one of the species that showed the greatest distributional restriction to areas that had never been ploughed. Thus, this study focuses on *G. procumbens* as a member of a group of species that display such a response to land-use history.

MAPPING SPECIES' DISTRIBUTIONS

In order to determine how the abundance of *G. procumbens* changes across the land-use boundary, transects were established perpendicular to the plough boundary at 20-m intervals within three scrub oak transition sites and three hardwood transition sites during the summer of 1995. Along each transect, quadrats ($1\,m^2$) were established at 5 m into the unploughed area, on the plough boundary itself, and at 5, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90 and 100 m into the previously ploughed areas. The number of *G. procumbens* stems (or vertical ramets) was counted in each quadrat.

DEMOGRAPHIC OBSERVATIONS

In order to compare demographic parameters of *G. procumbens* in areas of contrasting land-use history, replicate sampling plots were established within each of the five scrub oak and five hardwood transition sites in the summer of 1995. At 20-m intervals along the land-use boundary in each site, a 1-m^2 quadrat was established at a randomly chosen distance up to 50 m into the unploughed areas and up to the furthest distance at which *G. procumbens* occurred in formerly ploughed areas (always < 50 m).

Within each quadrat, we recorded the numbers of new stems, old stems with new growth, old stems, reproductive stems, flower buds, flowers and fruits. Up to 25 focal individuals were chosen arbitrarily and tagged within each quadrat. Age or stage (new, old with new growth or old), number of flower buds, flowers and fruits and survival over the growing season and over the following winter were recorded. These data permitted estimates of mortality over the course of one complete year. Collecting the same information for each quadrat and each tagged individual during a second year provided two seasons of data on standing stem density, stem recruitment, stem age or stage structure and reproductive success at the level of the individual and quadrat.

CLONAL AND BELOW-GROUND OBSERVATIONS

The clonal structure of *G. procumbens* makes it possible and important to determine whether characters of physiological individuals, as opposed to characters of individual above-ground stems, differ as a function of land-use history. Therefore, we excavated individuals on both sides of the land-use boundary at three scrub oak transition and three hardwood transition sites, following procedures similar to those in the demographic study to select the sampling location.

An individual was defined as a physically coherent structure, and no attempt was made to identify individuals as genotypes. Excavation proceeded along the entire rhizome of the randomly chosen shoot until either the growing tip or the necrotic end of the rhizome was reached. For each individual we recorded the total linear distance occupied, the number of new stems, old but living stems, and dead stems. The total number of stems of all types provides an estimate of the lifetime stem production by an individual, which when divided by the length of the rhizome gives an estimate of the average density of stems. This measure serves as a comparison with the standing stem density observable in 1 year, and allows density to be averaged over the average age of the rhizomes sampled. New stems grow only from the previous year's rhizome (K. Donohue, personal observation), and the distance from the growing tip of the rhizome (measured at the end of the growing season) to the last new stem therefore approximates the maximum distance of rhizome growth during the current year. Stem density and rates of vegetative expansion of rhizomes were compared between unploughed and previously ploughed areas within both scrub oak and hardwood transition areas.

SEED TRANSPLANTATIONS

In order to compare the effect of land-use history on germination and establishment of *G. procumbens* seeds, mature fruits were collected from unploughed and previously ploughed areas within one hardwood and one scrub oak transition site. Seeds were cleared from the fruits and placed into the field in autumn 1995 at random distances up to 50 m into unploughed and previously ploughed areas, at 10, 30, 50, 70 and 90 m along the plough boundaries of the same hardwood and scrub oak transition from which the seeds had been collected. In this study, locations in the previously ploughed areas were permitted to extend beyond the range at which *G. procumbens* occurred. Twenty seeds from each of the four habitat types (hardwood ploughed, hardwood unploughed, scrub oak ploughed, scrub oak unploughed) were selected randomly to be planted into each of the four habitat types, giving a total of 400 seeds. Equal numbers of seeds from each habitat type were assigned randomly to one of the five locations within each habitat type, and they were arranged randomly in 96-cell plug trays that had the bottom cut out to permit natural drainage. Each plug tray was buried so that its surface was level with the natural soil surface, and the trays were filled with soil native to the site into which they were placed. Seeds were placed on top of the soil, and natural litter was allowed to accumulate. Seeds overwintered in these locations.

The following growing season, the seed trays were visited at weekly intervals from spring into late autumn, and germination and mortality were recorded by lifting and then replacing the litter. This experiment was part of a larger experiment that included other species arranged randomly within the seed trays. Therefore, if a *G. procumbens* seedling was located within a cell in which a *G. procumbens* seed had been placed, it was assumed to be a seedling that germinated from an experimental seed rather from a naturally dispersed seed. In fact, natural seed germination of *G. procumbens* was so infrequent that all seedlings observed in the seed trays could be attributed to experimental seeds. These data provided information on germination and survival through one growing season in unploughed and previously ploughed areas within hardwood and scrub oak transitions. In addition, this experiment determined whether the habitat type from which the seed was collected had any effect on germination behaviour or survival in each of the areas.

STATISTICAL ANALYSIS

Effects of land-use history and plant community on demographic parameters were analysed with mixed model analysis of variance, with site as the random factor, nested within plant community (hardwood or scrub oak, fixed effect). Land use (ploughed or unploughed) was also a fixed effect, and its interaction with plant community was included in all models. Data from the demographic observation plots and the excavations were analysed with this model using restricted maximum likelihood (SAS Proc Mixed; SAS Institute 1990). The seed transplantation experiment was analysed with a fixed-factor analysis of variance (SAS GLM), with seed source, plant community germination location and land-use germination location as fixed factors. Two- and three-way interactions were included in the model. All analyses were based on type III sums of squares. Binomial variables, such as mortality, were analysed with logistic regression (Catmod in SAS) with site nested within plant community.

Demographic data based on the life cycle in Fig. 1 were used to derive transition matrices for each of

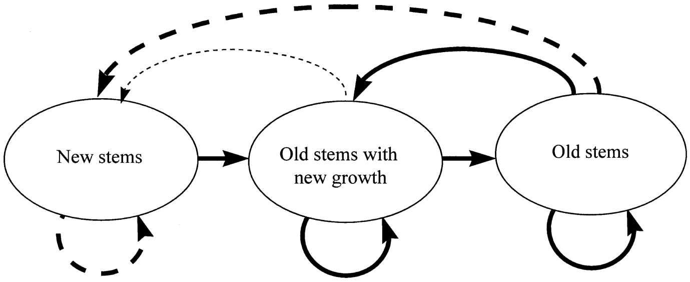

Fig. 1 Life cycle of *Gaultheria rocumbens*. Dotted lines indicate transitions to new stems through seeds or new rhizome growth. Old stems with new growth did not contribute to new stem recruitment in this sample, so that path is shown as a lighter line.

the four habitat types. Transition probabilities to new recruits were calculated as follows. We used information collected from the excavations (see below) to apportion the number of new recruits observed in the second season between the various stage classes that were likely to have produced them. The transition probability of each stage class to new recruits was then calculated as the total number of new recruits per quadrat in 1996 times the proportion associated with each stage class, divided by the number of each stage class per quadrat in 1995. Because seeds did not contribute to any life stage in this study (see the Results), their contribution to these transitions probabilities was zero. If seeds had germinated and grown into new recruits, their numbers would have been added to the transition probabilities of the first row of the matrix. The remaining transition probabilities were estimated from direct observations of the tagged plants. The transition probabilities denote the proportion of individuals of a particular stage class that became each stage class in the following year. Analyses of the transition matrices was performed using Mathematica 3.0 (Wolfram Research Inc., Champaign, IL, USA). Population growth rates were calculated from the dominant eigenvalues of the transition matrices. Stable stage distributions and relative reproductive values were calculated from the right and left eigenvectors of the transition matrices, respectively. Sensitivities and elasticities were calculated from these vectors following Caswell (1989). Projection of these matrices was performed for 100 generations.

Results

Gaultheria procumbens exhibited marked exclusion from previously ploughed areas, both in the hardwood and in the scrub oak transitions (Fig. 2). The average distance that *G. procumbens* extended into previously ploughed areas was 14.3 m (SE = 1.1) in the hardwood transitions and 10.4 m (SE = 0.8) in the scrub oak transitions, and this difference was not significant ($F = 0.88$, $P = 0.377$, d.f. = 1). Variation among sites was substantial (% variance explained = 41.2, $Z = 1.92$, $P = 0.054$). In no site did *G. procumbens* extend beyond 40 m into secondary forests, even though the sites were abandoned at least 50 years and in some cases more than 100 years previously. Furthermore, although the abundance of *G. procumbens* did not decrease monotonically with distance from the plough boundary, it never reappeared beyond the distance at which it reached zero abundance. Thus, where *G. procumbens* was present in previously ploughed areas it was completely contiguous to source populations in the

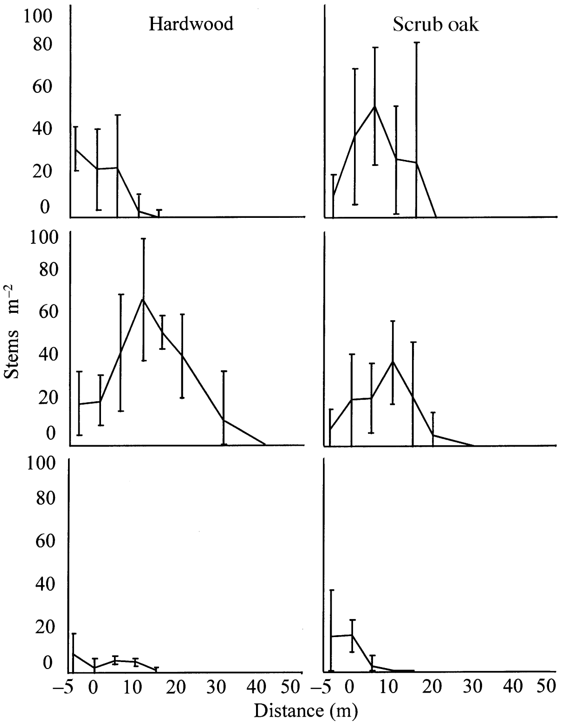

Fig. 2 Abundance of *Gaultheria procumbens* as a function of distance into previously ploughed areas from the plough boundary in three hardwood and three scrub oak sites. Standard deviation bars are shown. $n = 5$ quadrats at each distance per site.

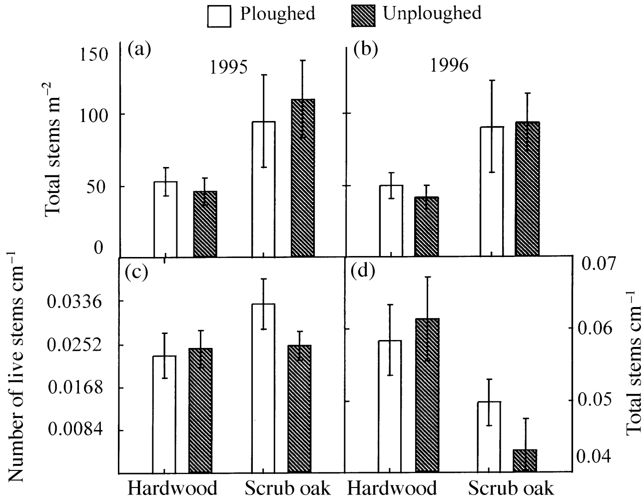

Fig. 3 Standing stem density per unit area in 1995 and 1996 (a and b); stem density along rhizome in 1995 (live stems, c; total stems, living + dead, d). Standard error bars are shown. $n = 25$ (a and b); $n = 9$ (c and d). Significant variation was observed for stem density per unit area among sites in 1995 (a; $F = 7.14$, $P = 0.0001$, d.f. = 8) and 1996 (b; $F = 7.10$, $P = 0.0001$, d.f. = 8) and for stem density per rhizome length between plant communities (d; $F = 8.07$, $P = 0.008$, d.f. = 1).

unploughed areas. These censuses provided no evidence that successful seedling establishment extended the distribution of this species into secondary forests. Moreover, in non-quantitative surveys up to 200 m beyond these study areas into previously ploughed land, not a single established clone of *G. procumbens* was observed that was not contiguous to the vegetatively expanding population. This is unlike other ericaceous species (*Vaccinium vacillans*, *V. angustifolium* and *Gaylusaccia baccata*), which show evidence of seedling establishment and subsequent vegetative expansion in the form of distinct circular clones that are physically disconnected from the advancing vegetative front of the source population. Stem abundance of *G. procumbens* often increased just inside the previously ploughed areas, suggesting that release from competitive conditions occurs as the ramets cross the plough boundary.

Standing stem density per unit area did not differ significantly between unploughed and previously ploughed areas in either year (Fig. 3a,b), but stem density varied greatly among sites in both years. The number of stems per centimetre of rhizome did not differ between unploughed and previously ploughed areas either (Fig. 3c,d). Thus, previous land use did not appear to influence stem density. Although stem density tended to be higher in the scrub oak community than in the hardwood community, this trend was not significant. However, individuals growing in the hardwood transitions grew significantly higher densities of stems on their rhizomes during their lifetime than those in the scrub oak transitions (Fig. 3d), although numbers alive at any one time were the same in the two communities (Fig. 3c). This suggests that stem recruitment and turnover may have occurred at a higher rate in the hardwood transitions in the past.

New stem recruitment per unit area and per centimetre of rhizome did not differ significantly among unploughed and previously ploughed areas, nor did it differ significantly among plant communities (Fig. 4). Variation among sites in stem recruitment was substantial in both years.

Significantly greater stem mortality occurred in the hardwood transitions, largely as a result of increased mortality during the winter (Fig. 5). More surprisingly, significantly greater mortality occurred in unploughed areas than in previously ploughed areas, particularly during the winter. During the growing season, only the scrub oak transitions had greater mortality in unploughed areas. Mortality also varied significantly across sites.

Reproductive activity per unit area did not differ with land-use history (Fig. 6a,b). Flowering per unit area in 1995 and flowering per stem in both years (Fig. 6c,d) were significantly higher in the scrub oak transitions. Again, variation in reproductive activity was substantial among sites.

Stage class parameters were affected by both plant community and land-use history (Table 1). Frequency distributions of the stages varied with land use (Table 1a). Specifically, the percentage of stems that were old with new growth was significantly greater in previously ploughed areas in both years, whereas the percentage of stems that were old with no new growth was significantly less. The percentage of stems that were new stems varied significantly across sites within plant communities in 1996, but not across land-use type or plant community.

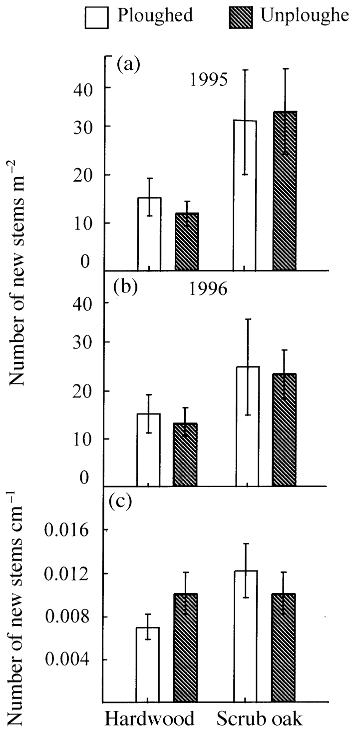

Fig. 4 New stem recruitment per unit area per year (a and b) and number of new stems per centimetre of rhizome in 1995 (c). Standard error bars are shown. $n = 25$ for each habitat type. Variation among sites was significant in 1995 ($F = 6.94$, $P = 0.0001$, d.f. = 8) and 1996 ($F = 7.28$, $P = 0.0001$, d.f. = 8).

Mixed model analysis of variance of flower production ($n = 1349$) showed significant variation among stage classes ($F = 9.13$, $P = 0.003$, d.f. = 2), sites (plant community) ($F = 11.34$, $P < 0.0001$, d.f. = 8), plant communities ($F = 51.07$, $P < 0.0001$, d.f. = 1) and land use ($F = 7.79$, $P = 0.004$, d.f. = 1), and a significant stage × plant community × land use interaction ($F = 4.46$, $P = 0.035$, d.f. = 1; Table 1b), indicating that stage-specific reproduction depended on the interaction between plant community and land use. These results also indicated that land use and plant community influenced flower production after controlling for stage structure. The number of flowers per new stem was significantly greater in scrub oak transitions than in hardwood transitions in both years, and the number was significantly greater in unploughed areas in 1995. It also varied across sites in both years. The number of flowers per old stem with new growth was greater in scrub oak transitions and varied across sites in both years, although the effects were significant in only one year.

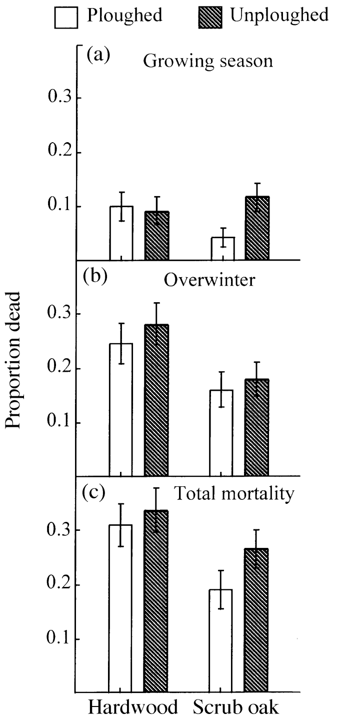

Fig. 5 Proportion stem mortality. Standard error bars are shown. $n = 2050$. Mortality during the growing season (a) showed significant effects of land use ($\chi^2 = 8.86$, $P = 0.003$, d.f. = 1), site ($\chi^2 = 53.49$, $P = 0.0001$, d.f. = 8), and land use × plant community ($\chi^2 = 12.65$, $P = 0.0004$, d.f. = 1). Overwinter mortality (b) showed significant effects of plant community ($\chi^2 = 24.36$, $P < 0.0001$, d.f. = 1), land use ($\chi^2 = 3.98$, $P = 0.046$, d.f. = 1) and site ($\chi^2 = 72.20$, $P < 0.0001$, d.f. = 8). Total mortality, which is the sum of mortality during the growing season and over the following winter (c), showed significant effects of plant community ($\chi^2 = 20.67$, $P < 0.0001$, d.f. = 1), land use ($\chi^2 = 10.80$, $P = 0.0001$, d.f. = 1) and site ($\chi^2 = 98.90$, $P < 0.0001$, d.f. = 8).

Although the proportion of new stems did not differ with respect to ploughing history or plant community (Table 1a), more old stems had new growth in previously ploughed areas than in unploughed areas during both years. Because sexual reproduction can only occur on new growth (K. Donohue, personal observation) this result implies that populations in previously ploughed areas have a greater proportion of potentially reproductive stems. However, new stems in unploughed areas had more flowers than those in previously ploughed areas (Table 1b), leading to no overall difference in reproductive activity between unploughed and previously ploughed areas.

Logistic regression of mortality probability ($n = 2028$) showed significant variation among stage classes ($\chi^2 = 108.60$, $P < 0.0001$, d.f. = 3), sites (plant community) ($\chi^2 = 106.03$, $P < 0.0001$, d.f. = 8), plant communities ($\chi^2 = 18.28$, $P < 0.0001$, d.f. = 1) and land use ($\chi^2 = 8.38$, $P = 0.004$; Table 1c). The lack of significant interaction terms indicates that stage-specific mortality did not depend on plant community or land-use history. However, the results indicate that land use and plant community influenced mortality independently of stage structure.

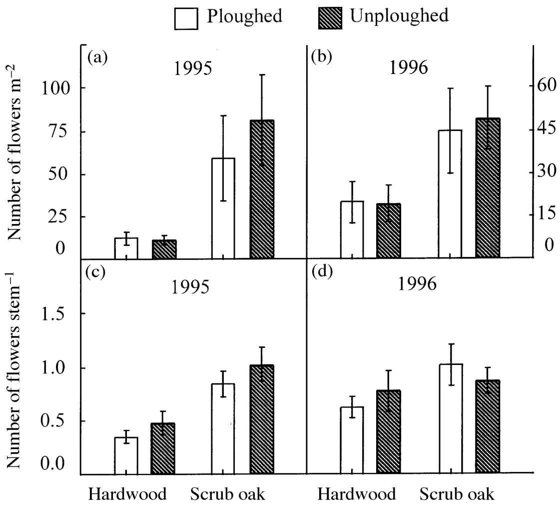

Fig. 6 Reproductive activity per unit area (a and b) and per stem (c and d). Standard error bars are shown. $n = 25$ for each habitat type. Reproductive activity per unit area differed among plant communities in 1995 ($F = 9.95$, $P = 0.002$, d.f. = 1) and varied among sites in 1995 ($F = 4.67$, $P = 0.0001$, d.f. = 8) and 1996 ($F = 8.18$, $P = 0.0001$, d.f. = 8). Reproduction per stem differed between plant communities in 1995 ($F = 26.86$, $P = 0.0001$, d.f. = 1) and 1996 ($F = 4.77$, $P = 0.032$, d.f. = 1) and varied among sites in 1995 ($F = 4.52$, $P = 0.0001$, d.f. = 8) and 1996 ($F = 4.50$, $P = 00001$, d.f. = 8).

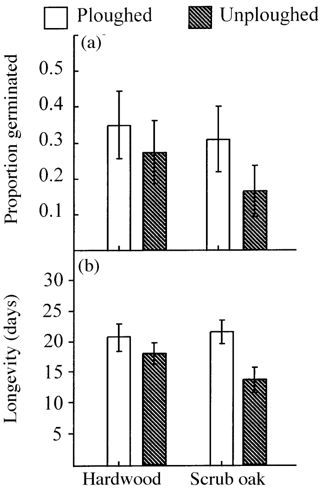

Fig. 7 Percentage seed germination and seedling longevity in different habitat types. Standard error bars are shown. $n = 100$ for each habitat type. Percentage germination differed among land use ($\chi^2 = 7.43$, $P = 0.006$, d.f. = 1), as did longevity ($\chi^2 = 4.39$, $P = 0.04$, d.f. = 1).

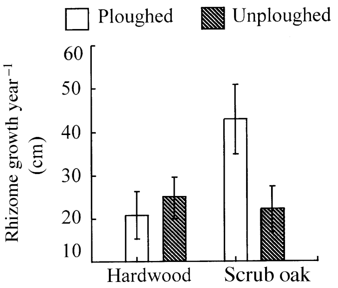

Fig. 8 Rates of rhizome growth. Standard error bars are shown. $n = 9$ for each habitat type. Land use × plant community had a significant effect ($F = 4.20$, $P = 0.05$, d.f. = 1). The difference in rhizome growth between ploughed and unploughed areas was nearly significant in the scrub oak transitions ($F = 3.44$, $P = 0.09$).

Germination occurred with significantly greater frequency in previously ploughed areas, and seedlings lived significantly longer in previously ploughed areas (Fig. 7). However, by the end of the growing season (early October) no seedlings were alive in either land-use type. No significant effects of seed source, plant community or any interaction (two-way and three-way) on either percentage germination or longevity were detected.

Rhizomes tended to grow a greater distance in previously ploughed areas than they did in unploughed areas in the scrub oak transitions (Fig. 8), but no significant difference in vegetative growth rate was found in the hardwood transitions.

Transition probabilities among stage classes are shown in Table 2 (see also Fig. 1). In all habitat types, the stage class that contributed most to new recruits was new recruits from the previous year (Table 2). Excavations revealed that most new recruits were connected by rhizomes to stems that had been new in the previous year, but that some were associated with old stems. Those rhizomes that maintained continuous uninterrupted growth from one year to the next tended to give rise to new stems from the previous year's rhizome, at the same time as showing new primary growth of this rhizome that would support new stems in the following season. This led to an association between new ramets formed in successive years. The proportions of new recruits associated with the previous year's new stems were 0.78 for scrub oak ploughed sites, 0.52 for scrub oak unploughed sites, 0.83 for hardwood ploughed sites and 0.59 for hardwood unploughed sites. The remaining proportion of new ramets grew from points where growth was interrupted by branching or as a result of damage. These were always associated with old stems rather than old stems with new growth (zero probability of the 1996 new recruits being associated with the intermediate stage class; Table 2), perhaps because re-initiation of growth after such interruptions precluded shoot production by an adjacent ramet. Consequently the proportion of 1996 new recruits associated with old stems of the previous generation is given by 1 minus the probability of being associated with new recruits

Table 1 Stage structure of *Gaultheria procumbens* as a function of plant community and land-use history showing frequency distribution (a), stage-dependent reproduction (b) and stage-dependent mortality (c). Standard errors are shown in parentheses. In cells with two rows, the first row shows results for 1995, and the second row shows results for 1996. Mixed model analysis of variance ($n = 100$) was performed on each stage separately ($n = 25$ for each habitat). Tests were conducted independently for the 2 years. Similar letter superscripts across habitats indicate no significant difference. *F*-ratios for significant stage-dependent effects are presented for each stage class. Primes (′) are used for the 1996 analysis. ΨNot significant with Bonferroni criterion. †$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Parameter	Habitat	New stems	Old stems with new growth	Old stems
(a) Frequency	Hardwood, ploughed	0.26 (0.03)^{a}	0.42 (0.03)^{a}	0.32 (0.03)^{a}
		0.27 (0.03)$^{a\prime}$	0.38 (0.03)$^{a\prime}$	0.35 (0.29)$^{a\prime}$
	Hardwood, unploughed	0.26 (0.03)^{a}	0.32 (0.03)^{b}	0.42 (0.03)^{b}
		0.28 (0.03)$^{a\prime}$	0.31 (0.02)$^{b\prime}$	0.41 (0.02)$^{b\prime}$
	Scrub oak, ploughed	0.28 (0.02)^{a}	0.37 (0.04)^{a}	0.35 (0.04)^{a}
		0.27 (0.26)$^{a\prime}$	0.34 (0.05)$^{a\prime}$	0.39 (0.04)$^{a\prime}$
	Scrub oak, unploughed	0.32 (0.02)^{a}	0.30 (0.02)^{b}	0.38 (0.02)^{b}
		0.24 (0.02)$^{a\prime}$	0.29 (0.02)$^{b\prime}$	0.47 (0.02)$^{b\prime}$
	Significant effects	Site′ = 2.90**	Land use = 8.66**	Land use = 4.50*Ψ
			Land use′ = 4.28*Ψ	Land use′ = 5.75*
(b) Reproduction (flowers/stem)	Hardwood, ploughed	0.18 (0.05)^{a}	0.47 (0.12)^{a}	0
		0.63 (0.15)$^{a\prime}$	0.62 (0.11)$^{a\prime}$	
	Hardwood, unploughed	0.47 (0.14)^{b}	0.41 (0.10)^{b}	0
		0.91 (0.28)$^{b\prime}$	0.65 (0.16)$^{a\prime}$	
	Scrub oak, ploughed	0.79 (0.16)^{a}	0.87 (0.14)^{a}	0
		1.15 (0.23)$^{a\prime}$	0.77 (0.14)$^{a\prime}$	
	Scrub oak, unploughed	1.01 (0.19)^{b}	1.01 (0.15)^{a}	0
		0.94 (0.14)$^{a\prime}$	0.91 (0.14)$^{a\prime}$	
	Significant effects	Community 26.83***	Community = 18.34***	
		Land use = 5.18*	Site = 1.96†	
		Site = 5.91***	Community′ = 3.21†	
		Community′ = 4.51*	Site′ = 3.33**	
		Site′ = 4.03***		
(c) % Mortality	Hardwood, ploughed	0.23 (0.007)^{a}	0.23 (0.004)^{a}	0.45 (0.005)^{a}
	Hardwood, unploughed	0.24 (0.007)^{a}	0.24 (0.005)^{a}	0.46 (0.005)^{b}
	Scrub oak, ploughed	0.11 (0.005)^{b}	0.14 (0.004)^{b}	0.29 (0.004)^{c}
	Scrub oak, unploughed	0.15 (0.004)^{c}	0.21 (0.004)^{c}	0.42 (0.005)^{d}

in the previous season. Although seeds were produced by the new stems (on average 23 per new stem in hardwood ploughed; 31 per new stem in hardwood unploughed; 68 per new stem in scrub oak ploughed; 69 per new stem in scrub oak unploughed), the germination study showed that no germinants survived. Therefore, seeds did not contribute to any stage class. In all habitat types, all stem types had a relatively low probability of producing new growth the following year.

The population growth rates estimated from stable stage distributions were close to one for all but the scrub oak unploughed habitat, where the lower value indicated population decline (Fig. 9). In hardwood transitions, populations growing in unploughed areas had a slightly faster projected rate

Table 2 Transition probabilities between life stages in four habitats. The matrix shows the probability that one life stage (that in the column) will become another life stage (that in the row) within 1 year

Habitat		New	Old with new growth	Old
Hardwood, ploughed	New	0.83	0	0.15
	Old with new growth	0.31	0.33	0.26
	Old	0.51	0.48	0.28
Hardwood, unploughed	New	0.67	0	0.27
	Old with new growth	0.27	0.27	0.19
	Old	0.54	0.55	0.34
Scrub oak, ploughed	New	0.63	0	0.15
	Old with new growth	0.30	0.37	0.22
	Old	0.60	0.52	0.49
Scrub oak, unploughed	New	0.36	0	0.25
	Old with new growth	0.28	0.25	0.16
	Old	0.60	0.59	0.42

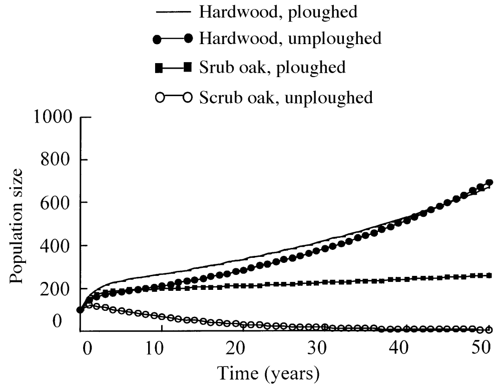

Fig. 9 Projected population growth in the four habitat types. Populations were started with 100 new recruits. Intrinsic rate of increase (r) and finite rate of increase (λ) were 0.02 and 1.02, respectively, for hardwood ploughed areas; 0.03 and 1.03 for hardwood unploughed areas; 0.01 and 1.01 for scrub oak ploughed areas; −0.07 and 0.93 for scrub oak unploughed areas.

of population growth than those in previously ploughed areas. Despite this difference in growth rate, it would 46 generations before unploughed areas had a larger population size, given the observed starting conditions. Thus, in hardwood transitions, unploughed areas would be expected to have the larger populations in the future only if the demographic parameters were to remain constant for approximately 50 years or longer. However, constancy of demographic parameters is unlikely in this successional system as environmental conditions that influence demography are expected to change substantially over time. A more conservative projection shows that after 10 years unploughed areas would have only 79% the number of stems present in ploughed areas in the hardwood transitions and 36% in the scrub oak transitions.

In all habitat types, the standing stem density was lower in 1996 than in 1995, indicating a population decline over the years studied. The unploughed areas had intrinsic rates of decrease that were at least twice as fast as those of the ploughed areas, based on the difference in standing stem density between years ($r = -0.06$ and $\lambda = 0.94$ for the hardwood ploughed habitat; $r = -0.12$ and $\lambda = 0.89$ for hardwood unploughed; $r = -0.05$ and $\lambda = 0.95$ for scrub oak ploughed; $r = -0.17$ and $\lambda = 0.84$ for scrub oak unploughed). However, the decline in stem density between years was only significant for the hardwood unploughed areas, based on paired t-tests of stem density across years (hardwood ploughed: $t = 1.16$, $P > 0.05$, d.f. = 24; hardwood unploughed: $t = 2.23$, $P < 0.05$, d.f. = 24; scrub oak ploughed: $t = 0.64$, $P > 0.05$, d.f. = 24; scrub oak unploughed: $t = 0.82$, $P > 0.05$, d.f. = 24). The difference between the observed and the projected rates of population growth were most likely to be due to the fact that these populations had not attained stable stage distributions. This may be because of recent disturbances or changing environmental conditions, including changing stem density. Quadrats with higher stem density had higher percentages of mortality (regression coefficient = 0.001, $t = 2.94$, $P < 0.005$), and the strength of the effect of density on mortality did not depend on habitat type or ploughing history, as indicated by their lack of significant interaction with stem density in a mixed-model analysis of variance.

According to the projections, the stable stage distribution was reached within 10 generations for all habitat types. The most abundant stage class in all habitat types was then the old stage class, and it was slightly more abundant in the scrub oak community than in the hardwood community (Table 3). New stems had the highest reproductive values in all habitats (Table 3). Sensitivities and elasticities revealed that population growth was most strongly influenced by new stem recruitment (Table 4). Although sensitivity coefficients showed that population growth rate was most sensitive to the contribution of the oldest stage class to new recruitment, the elasticity coefficient was highest for new stem recruitment from new stems in all habitats except the scrub oak unploughed habitat.

Discussion

If previous land use has persistent effects on the environment such that the current environment actively restricts species' distributions to sites that

Table 3 Stable stage distributions (upper) and reproductive values (lower) of the three stage classes in four habitats

Stage	Hardwood, ploughed	Hardwood, unploughed	Scrub oak, ploughed	Scrub oak, unploughed
Stable stage distribution				
New	0.31	0.33	0.21	0.24
Old with new growth	0.29	0.23	0.28	0.22
Old	0.40	0.44	0.52	0.54
Reproductive values				
New	1.00	1.00	1.00	1.00
Old with new growth	0.18	0.35	0.36	0.59
Old	0.27	0.49	0.45	0.68

Table 4 Sensitivity (left) and elasticity (right) coefficients of transition matrix elements

Habitat		New	Old with new growth	Old
Hardwood, ploughed	New	0.31/0.25	0.29/0.00	0.40/0.06
	Old with new growth	0.06/0.02	0.05/0.02	0.07/0.02
	Old	0.08/0.04	0.08/0.04	0.11/0.03
Hardwood, unploughed	New	0.33/0.21	0.23/0.00	0.44/0.12
	Old with new growth	0.12/0.03	0.08/0.02	0.15/0.03
	Old	0.16/0.08	0.11/0.06	0.22/0.07
Scrub oak, ploughed	New	0.21/0.13	0.28/0.00	0.52/0.08
	Old with new growth	0.08/0.02	0.10/0.04	0.19/0.04
	Old	0.09/0.05	0.13/0.07	0.23/0.11
Scrub oak, unploughed	New	0.24/0.09	0.22/0.00	0.54/0.15
	Old with new growth	0.14/0.04	0.13/0.03	0.32/0.06
	Old	0.16/0.10	0.15/0.10	0.37/0.17

were never ploughed, then extant populations should exhibit depressed growth in previously ploughed areas. Contrary to this prediction, our study demonstrated that previous land use had no overall effect on standing stem density, new stem recruitment or flower production of this highly restricted species. Furthermore, in previously ploughed areas there was unexpectedly (i) less stem mortality in the scrub oak sites; (ii) an increase in germination, longevity and proportion of potentially reproductive stems in both plant communities; and (iii) a trend for slower observed rates of population decline in both plant communities and a higher projected population growth rate in the scrub oak transitions. Rather than depressing demographic performance, previous ploughing allowed plants in the scrub oak transitions to perform better than those in the unploughed areas.

Although alteration of the environment accompanying historical land use cannot explain the distributional restriction of *G. procumbens*, land-use history nevertheless influences the environment currently experienced by this species, enhancing demographic performance in some areas. Because land-use history often affects changes in edaphic factors (Olmstead 1937; Wells *et al.* 1976) and plant community composition (Foster 1992), which can substantially alter the canopy structure and resulting light environment, it is not unexpected that demographic performance differs between populations growing in unploughed and previously ploughed areas. The age of the population of clonal species has also been shown to influence demographic parameters and the balance between older stems and new recruits (Nobel *et al.* 1979; Hartnett & Bazzaz 1985a; Wankhar & Tripathi 1993). Here, populations in previously ploughed areas are newer than their source population. Many disturbance-adapted species show a similar enhancement of growth, regeneration and relative abundance following disturbance (Little & Moore 1949; Buell & Cantlon 1950; Brown 1960; Putnam 1989; Matlack *et al.* 1993).

The persistence of the effects of land-use history depends on the site or population that was disturbed. On a regional scale, *G. procumbens* displays variation in the degree to which it is restricted to unploughed areas, and generally shows less distributional restriction in more mesic sites (G. Motzkin, unpublished data). In this study, land-use history often interacted with plant community such that effects of previous land use on mortality, germination, seedling longevity, rhizome growth rate and projected population growth rates were stronger in populations growing in the scrub oak transitions than in those in the hardwood transitions. The stronger effect of land use in the scrub oak transitions is not likely to be due to density-dependent processes. Although the density-dependent mortality observed within quadrats suggests density-dependent suppression of population growth, the same degree of density-dependent mortality would be expected in both plant communities as densities were comparable or even slightly lower in the hardwood transitions. Moreover, effects of land use on germination and seedling longevity cannot have been density-mediated because density was experimentally controlled. Thus effects of land use may operate primarily through changing abiotic factors or community structure.

It should be noted that environmental and demographic conditions measured at one point in time do not accurately reflect conditions experienced in the past nor those to be experienced in the future. This is particularly true for systems in which the environment is changing substantially due to successional processes. Therefore, although *G. procumbens* was shown to perform better on some formerly ploughed areas at the time of this study, this does not imply that it has done so since the beginning of agricultural abandonment. Only long-term studies can discover the actual trajectory of population recovery after disturbance.

Explanation of the current distributional restriction of *G. procumbens* requires evaluation of the demographic parameters that, in this study, predict slow rates of stem population increase or even a decrease in standing stem abundance over time. Although some of these estimates were based on only 1 year's worth of data, they strongly suggest that the *G. procumbens* populations sampled are not increasing rapidly in size. Enhancement of stem population growth, however, does not necessarily cause an increase in the spatial extent of vegetative expansion, as rhizomes can grow greater distances under poor conditions in a heterogeneous environment (Evans & Cain 1995). Sexual propagation is unlikely to contribute to the extension of the population because, although 32% of all seeds germinated within a single year, none of the seedlings survived one growing season. The conditions experienced by the experimental seeds were not identical to conditions experienced by naturally dispersed seeds. Nevertheless, as we also found no evidence of successful seedling establishment, the range of distribution in this system appears to be limited by vegetative expansion. Rhizomes grew only 20–43 cm year^{-1}, which, even if they grew exactly perpendicular to the plough boundary (for an accurate method for estimating vegetative growth rates see Cain 1990), would give an absolute maximum vegetative extension into a previously ploughed area of only 43 m in 100 years. Interestingly, this is consistent with our observation that *G. procumbens* did not extend beyond 40 m into any ploughed area after 50 to over 100 years since agricultural abandonment. If *G. procumbens* continued to expand at this rate in the absence of establishment from sexual propagules, it would take more than 1500 years to recolonize completely all formerly ploughed areas of the Montague sand plain.

The sensitivity and elasticity coefficients indicate that slow recruitment of new stems limits population growth of *G. procumbens* in this system, and reproductive values show that new stems contribute the most to future population growth. Sensitivity coefficients show that if new rhizomes were able to grow from old rhizome segments as a result of increased rhizome branching, rather than primarily from the continued linear growth of existing rhizomes, then new stem recruitment could increase and lead to higher population growth rates. However, because most new recruits come from the uninterrupted linear growth of rhizomes, a proportional increase in new recruits along existing rhizomes would lead to a greater proportional increase in population growth rate than a corresponding proportional increase in any other life stage, as indicated by the elasticity coefficients. The importance of new stem recruitment also suggests that if sexual propagules produced by the new reproductive stems were to increase their probability of survival to the new recruit stage, then population growth rate might increase substantially. Sexual reproduction results in a much greater number of potential recruits than vegetative reproduction from linearly growing rhizomes does, suggesting that even a small increase in the proportion of seed survival could strongly influence population growth rates.

Previous studies have suggested that dispersal limitation may be the primary factor limiting species' distributions after disturbance (Scanlan 1981; Primack & Miao 1992; Hermy *et al.* 1993; Matlack 1994a,b; Tilman 1997; Bossuyt *et al.* 1999). In addition, the ability of seeds to establish successfully may greatly affect spatial distributions. Although dispersal limitation may contribute to the severe distributional restriction of *G. procumbens*, this species did not establish well even when seeds were artificially dispersed. In species that recolonize primarily by vegetative expansion (Wankhar & Tripathi 1993; Bossuyt *et al.* 1999), particulars of its biology, including the degree of clonal integration (Hartnett & Bazzaz 1985b; Hara *et al.* 1993; Hara 1994; Suzuki 1994), the ability to forage effectively (Kelly 1994; Evans & Cain 1995) and biomass allocation (Tolvanen 1994), can influence rates of vegetative expansion.

This study of *G. procumbens* indicates that, in some instances, modern species' distributions result from historical factors in combination with the species' life-history limitations rather than from current environmental conditions. Even in the absence of severe or long-lasting environmental modification, disturbances, and in particular land use, may have persistent effects lasting decades or even centuries (Peterken & Game 1984). In this system, species abundance patterns did not predict habitat suitability accurately. In fact, abundance patterns predicted the opposite of what was observed; locations with the greatest abundance of *G. procumbens* had more depressed population demographic trajectories. This result has implications for biological impact assessments, because current abundance patterns may not predict the optimal habitat. Another important conservation implication is that, although sites may be restored, community composition, structure and species' distributions may remain significantly altered for long periods of time if recolonization only occurs as a result of natural processes. Slow colonizers such as *G. procumbens* may require an active programme of artificial propagation to restore their distribution to predisturbance levels.

In conclusion, historical land use does not cause persistent environmental changes that adversely influence the population demography of *G. procumbens*. Rather, a slow intrinsic growth rate coupled with limited seedling establishment accounts for this species' restriction, despite environmental changes that actually enhance population growth. This finding indicates that historical land use can have lasting effects on species' distributional patterns, even in the absence of persistent adverse alterations of the environment.

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