Properties of ecotones: Evidence from five ecotones objectively determined from a coastal vegetation gradient

Walker, Susan[1,2]**; Wilson, J. Bastow**[1*]**; Steel, John B.**[1]**; Rapson, G.L.**[3]**;**
Smith, Benjamin[1,4]**; King, Warren McG.**[1,5] **& Cottam, Yvette H.**[6]

[1]*Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand;* [2]*Present address: Landcare Research, Private Bag 1930, Dunedin, N.Z.;* [3]*Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, N.Z.;* [4]*Present address: Climate Impact Group, Plant Ecology, Department of Ecology, Ekologihuset, Lund University, SE-223 62 Lund, Sweden;* [5]*Present address: CRC for Weed Management Systems, New South Wales Agriculture, Orange Agricultural Institute, Forest Road, Orange, NSW 2800, Australia;* [6]*Institute of Food, Nutrition and Human Health, Massey University, Palmerston North, N.Z.;* [*]*Corresponding author; Fax +6434797583; E-mail bastow@otago.ac.nz*

Abstract. Several properties have been suggested to be characteristic of ecotones, but their prevalence has rarely been tested. We sampled five ecotones to seek evidence on seven generalizations that are commonly made about ecotones: vegetational sharpness, physiognomic change, occurrence of a spatial community mosaic, many exotic species, ecotonal species, spatial mass effect, and species richness higher or lower than either side of the ecotone.

The ecotones were in a sequence from scattered mangroves, through salt marsh, rush-marsh, scrub, woodland, to pasture. We developed a method to objectively define, by rapid vegetational change, the position and depth of an ecotone, identifying five ecotones. Their positions were consistent across three sampling schemes and two spatial grain sizes. One ecotone is a switch ecotone, produced by positive feedback between community and environment. Another is anthropogenic, due to clearing for agriculture. Two others are probably environmental in cause, and one may be largely a relict environmental ecotone.

Sharp changes in species composition occurred. Three ecotones were associated with a change in plant physiognomy. In two, the ecotone was located just outside a woodland canopy, in the zone influenced by the canopy. Community mosaicity was evident at only one ecotone. There were few strictly ecotonal species; many species occurred more frequently within ecotones than in adjacent vegetation, but there were never significantly more ecotonal species than expected at random. There was little evidence for the spatial mass effect reducing ecotonal sharpness, or leading to higher species richness within ecotones. Species richness was higher than in the adjacent habitat in only one ecotone.

It seems that supposedly characteristic ecotone features depend on the particular ecological situation, and the ecology of the species present, rather than being intrinsic properties of ecotones.

Keywords: Boundary; Ecotonal species; Edge; Exotic species; Mangrove; Marsh; Mosaicity; Spatial mass effect; Species diversity; Salt marsh.

Nomenclature: Connor & Edgar (1987) and references therein, and Stace (1997), except where indicated.

Introduction

Ecotones – abrupt edges in vegetation – have long fascinated ecologists, and challenged them to find causes and resulting patterns. The existence of ecotones has been used to test between competing ecological theories, since some theories predict that most boundaries between communities will be abrupt (Odum 1983; Gilpin 1994), and others predict that abrupt boundaries will occur mainly when there are abrupt environmental changes (Wilson & Agnew 1992; Auerbach & Shmida 1993). Ecotones are a basic unit in landscape studies (Hansen et al. 1988; Wiens 1992), and may have significance for management in the face of climate change, since such effects are likely to be seen first at ecotones (Neilson 1991; Kupfer & Cairns 1996; Allen & Breshears 1998).

The term 'ecotone' was introduced by Clements (1905) as "The line that connects the points of accumulated or abrupt change in the symmetry. …Ecotones are well marked between formations, particularly when the medium changes: they are less distinct within formations". In spite of suggestions that, for etymological reasons, 'ecotone' should have implications of stress (van der Maarel 1990), most authors have followed Clements in defining it in terms of spatially-rapid vegetation change (e.g. Tansley & Chip 1926; Odum 1983; Gosz 1993). We use such a definition here: "A zone where directional spatial change in vegetation (i.e. qualitative and quantitative species composition) is more rapid than on either side of the zone" (Lloyd et al. 2000). We here develop a method for locating and delimiting ecotones, based on ordination scores.

Several features have been proposed as characteristic of ecotones, but there is little documentation. In this paper, we search for evidence of one defining feature of ecotones: a. the sharpness of vegetational transition, and six hypotheses ('b' to 'g'):

b. change in physiognomy (especially plant height);

c. community mosaicity (i.e. the occurrence of a spatial vegetational mosaic);

d. ecotonal species (i.e. the existence of species restricted to ecotones);

e. spatial mass effect (i.e. continued migration of propagules into an ecotone, and establishment of plants, of species not able to form self-sustaining populations there);

f. species richness (suggested to be higher or lower in ecotones than in the communities to either side); and

g. exotic species (being particularly common in ecotones).

We use vegetation data collected at a coastal site in northern New Zealand, that seemed to show discontinuities in the vegetation, and proved to contain a number of ecotones.

Methods

Sampling

We sampled a sequence of vegetation at Emauha Point in Northland, New Zealand (172°52' E, 34°33' S; mean annual temperature 15.8 °C; rainfall 1276 mm; precipitation deficit 106 mm; Leathwick et al. 2002). The sequence went from mangrove, through a rush community (primarily *Juncus krausii* var. *australiensis*,

marsh with shrubby trees of *Leptospermum scoparium* (manuka), woodland of *L. scoparium* and *Kunzea ericoides* (kanuka), to pasture. Because this is a tidal region, we expected that some of these would be environmental ecotones, i.e. ecotones caused by a sharp environmental change. The *Kunzea* to pasture ecotone is clearly anthropogenic, caused by clearing of the woodland for pasture.

All vegetation sampling was in 0.5 m × 0.5 m quadrats, recording the shoot presence of all vascular species. Seedlings were recorded separately, a seedling being defined as: (1) for a woody species: unbranched and less that 10 cm tall, or (2) for a grass or rosette herb: with three or fewer leaves, or (3) for other forbs: with five or fewer leaves. The height of the vegetation, and, where appropriate, the girth of the largest woody stem in each quadrat, were recorded.

There were three parts of the sequence from mangrove to pasture in which vegetation change seemed to be more rapid (Fig. 1a): a. mangrove to rush, b. rush to woodland, and c. woodland to pasture.

In each of these three parts, an intensively-sampled transect (Fig. 2a) was randomly located within a 150 m wide sector of the sequence. The transect was at right angles to the apparent ecotone, and extended into the apparently more uniform vegetation on either side. For the length of each intensive transect, sampling was in eight quadrats placed contiguously across the transect, and contiguously along it. Between the three intensive transects,
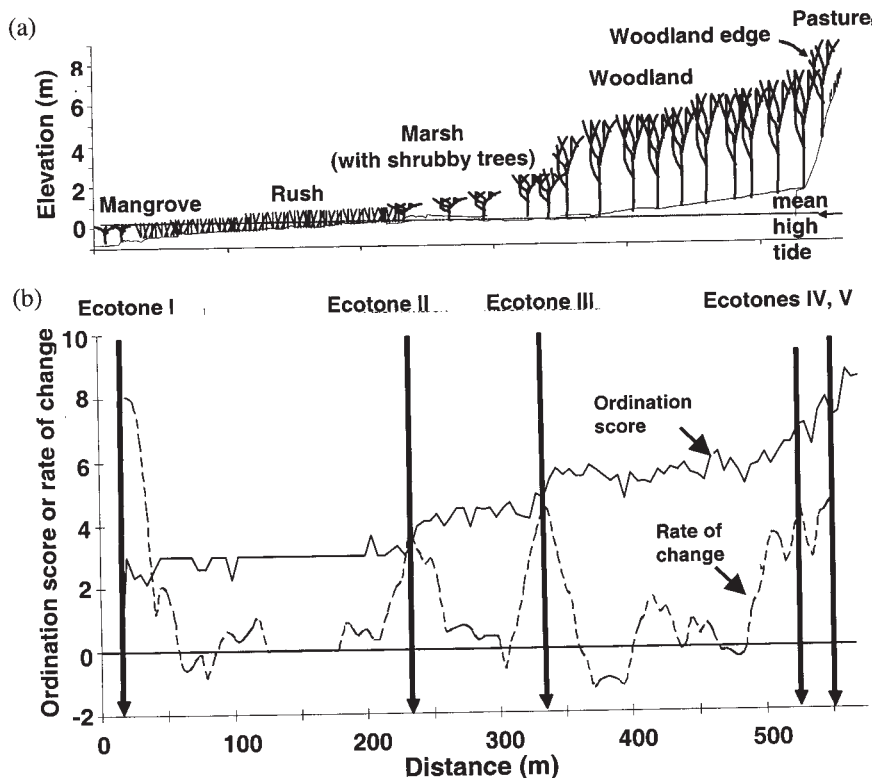

Fig. 1. (a) Profile through the Emauha Point study area from measured elevations and canopy heights, and **(b)** Ordination scores along the entire transect from the equally-weighted ordination, and the rate of change in ordination score with distance (i.e. the slope of the regression of ordination score on distance, i.e. its first derivative) within a window width of 25 m. Vertical arrows indicate the positions of the centre of the five ecotones (I to V) as identified by a peak in the rate of change.

lines of non-contiguous quadrats were placed at 5-m intervals. In total, 4092 quadrats were sampled. Trunk sections were taken from five of the largest trees at two points in the sequence where rapid physiognomic change was apparent, and their age estimated by ring counts. Elevations were recorded at each quadrat in each intensive transect using surveying equipment. The height of high tide was similarly recorded on seven days, and used to calibrate the elevations to mean tide level. Light intensity available to seedlings was measured at 50-cm height on a 1-m grid over the intensive transects (except in the mangrove-to-rush transect, where there was no tall vegetation) using a Licor quantum PAR sensor, and expressed as a percentage of the incident light level in the open, taken every four quadrat readings. In the mangrove-to-rush transect, the percentage of bare mud was estimated visually.

Tests of ecotone features

Analyses were performed at the sampled spatial grain of 0.5 m × 0.5 m, and, for the intensive transects, also by lumping square blocks of adjacent quadrats at grains of 1 m × 1 m, 1.5 m × 1.5 m and 2 m × 2 m.

a. Sharpness of vegetational transition (location and width of ecotones); b. Change in physiognomy:

The exact position of ecotones and their widths were determined from ordination scores. Three sets of ordinations were performed using Detrended Correspondence Analysis (Hill & Gauch 1980) of the species presence/absence data (excluding seedlings):

1. **Overall**: This used the entire data set of 4092 quadrats of 0.5 m × 0.5 m, and ensured that the areas selected for intensive sampling were indeed those where ecotones occurred.

2. **Equally-weighted**: Here we also used data from across the entire ecotone sequence, but selected one, of the eight 0.5 m × 0.5 m quadrats across a row diagonal to the transect, at random in each 5 m distance interval in each intensive transect. This was to check for the effect of differences in sampling intensity.

3. **Separate**: We performed separate ordinations for each intensive transect using all the quadrats from that transect. These were repeated at two different spatial grain sizes, 0.5 m × 0.5 m and 1 m × 1 m, because it has been suggested that vegetation spatial grain might be important in identifying changes at ecotones (Hansen et al. 1992). Coarser grain sizes than 1 m × 1 m were not analysed because the number of quadrats would have been too small.
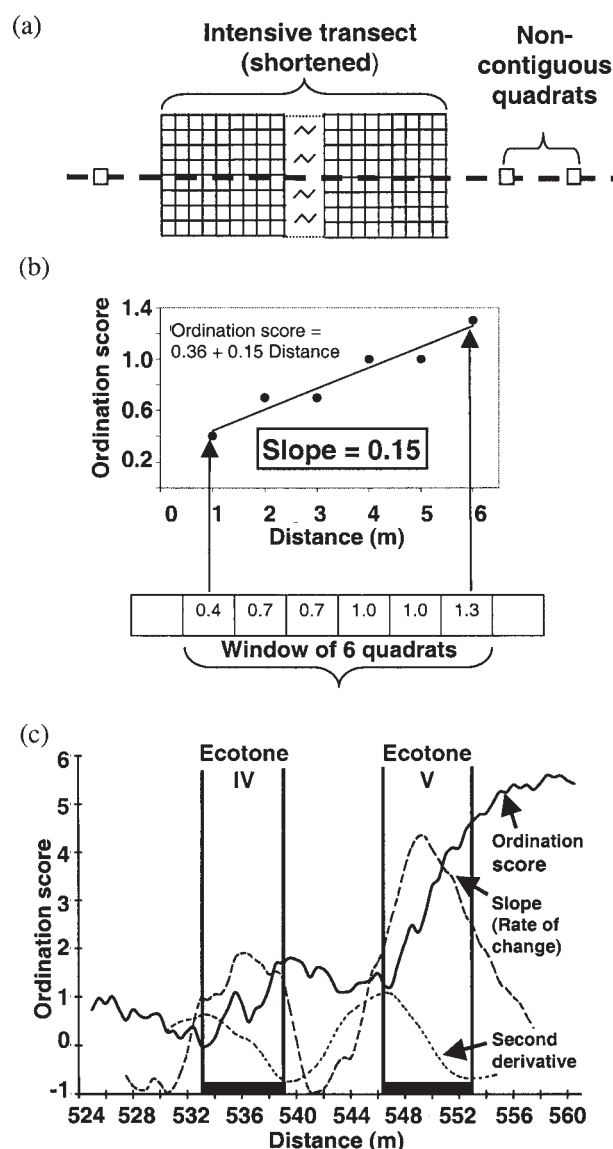

Fig. 2. (a) Detail of layout of an intensively-sampled transect, **(b)** Demonstration of method of calculating the rate of change in species composition using a moving window, and **(c)** as an example, the definition of the positions of Ecotones IV and V from the second derivative of the ordination scores.

To verify that the first ordination axis represented the sequence along the transect, we calculated the rank correlation of ordination score with distance along the sequence from mangrove to pasture.

To locate the exact position of ecotones, a moving-window regression method was developed, using the ordination scores, similar to those previously used to analyse two-phase patterns of vegetation (Whittaker & Naveh 1979; Whittaker et al. 1979). We represented species composition with Axis 1 ordination scores (averaged over the eight quadrats in a row within intensive transects), and calculated the rate of change in ordination

score with distance, as the linear least-squares regression slope within a window of n (see below) ordination scores along the vegetation sequence (Fig. 2b). The midpoint of an ecotone was identified as the position of maximum rate-of-change in ordination scores along the length of the transect. Therefore, it is seen as a peak in the regression slope (Fig. 2c; rate of change). To determine the width of an ecotone, a second moving-window regression was performed of the slopes (i.e. rates of change) produced by the first regression on distance. Points of inflection in the scores of the first regression (i.e. the second derivatives), are seen as maxima and minima in the scores of this second regression, and are interpreted as the boundaries of the ecotones (Fig. 2c; second derivative). These boundaries were used to divide the vegetation sequence into ecotones and non-ecotone zones.

In a moving-window regression method, a small window contains too much noise, whereas a wide window is liable to smooth over the vegetation change of interest. We therefore chose optimum window widths after performing preliminary analyses at a range of widths. A 25 m window was used for the Overall and Equally-weighted ordinations, and a 6 m window was used for the Separate ordinations.

c. Community mosaicity:

We developed indices of community mosaicity to test whether a small-scale spatial mosaic is characteristic of ecotones (Pound & Clements 1900; Gosz 1992; Neilson et al. 1992). We applied these to each row of eight contiguous 0.5 m × 0.5 m quadrats (i.e. a row transverse to the direction of the transect; Fig. 3) within each intensive transect. First, an 'adjacent' mosaicity index, M_A, was calculated by examining the spatial turnover in species occurrences (excluding seedlings) between adjacent pairs of quadrats (Fig. 3):

$$M_A = \sum_{s=1}^{S} \frac{N_P}{n-1} \tag{1}$$

where N_P = the tally, across the eight quadrats in a row of the transect, of pairwise differences, i.e. cases where the species occurs in one or other but not in both quadrats of the pair (**X-** or **-X**) (Fig. 3); n = the number of quadrats in a row (here $n = 8$, therefore there are $n - 1 = 7$ adjacent pairs); and S = number of species.

A drawback of M_A is that if the vegetation zonation is diagonal to the transect, some zonation would appear as mosaicity. Therefore, a second index, the 'trios' mosaicity index, M_T, was calculated from trios of quadrats (Fig. 3):

$$M_T = \sum_{s=1}^{S} \frac{N_T}{n-2} \tag{2}$$

where: N_T = the tally, across the eight quadrats in a row of the transect, of trio reversals, i.e. instances in which a species was present in both the first and third quadrats of a trio but not in the second (**X-X**), plus the number of instances in which a species was present in the second quadrat but not in the first or third quadrat (**-X-**) (Fig. 3). Indices M_A and M_T were calculated using the 0.5 m × 0.5 m and the 1 m × 1 m quadrats. A high value for either index would indicate a community mosaic.

d. Ecotonal species:

For each intensive transect, possible ecotonal species were noted as those (excluding seedlings) which occupied a higher proportion of quadrats in the ecotones than in the zones on either side. The expected proportion of quadrats occupied by a species in each zone was estimated as the average across the whole intensive transect. However some species would be expected to have their highest frequency in an ecotone, if they were distributed at random. Therefore, a null model was constructed in which a length of transect equal to the observed ecotone was placed at random along the transect (or in transects with two ecotones, the positions of both were randomized, with the restriction that they could not overlap), and the number of 'ecotonal' species was calculated. Significance was calculated as the proportion of 2000 randomizations in which the number of ecotonal species was equal to, or more extreme than, the number observed, multiplied by 2 to give a 2-tailed test.

e. Spatial mass effect:

For each species for which seedlings were recorded, the data were examined for the occurrence of seedlings beyond the range of adult plants, which would be evidence for the continued migration of propagules and establishment of plants in areas where the species was not able to form a self-sustaining population.

f. Species richness; g. Exotic species:

In each of the intensive transects, total species richness per quadrat, and the proportion of exotic species, were compared between each zone (ecotones, above and below ecotones), using Analysis of Variance with unequal replication, testing against within-zone variance.
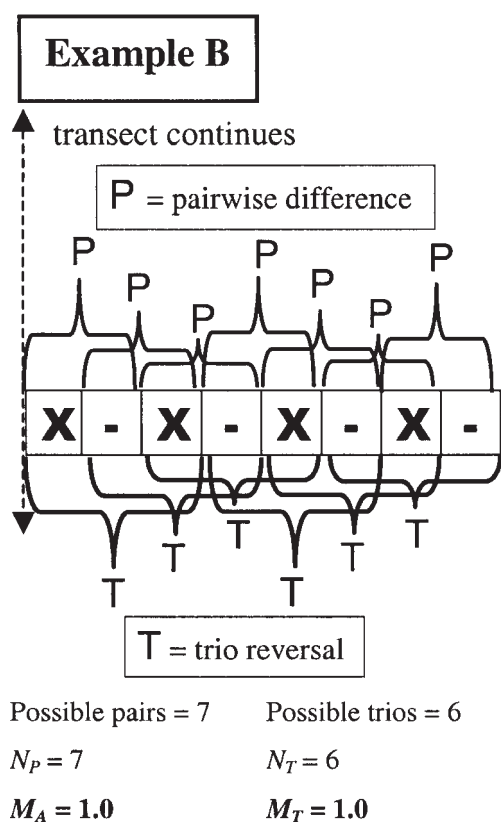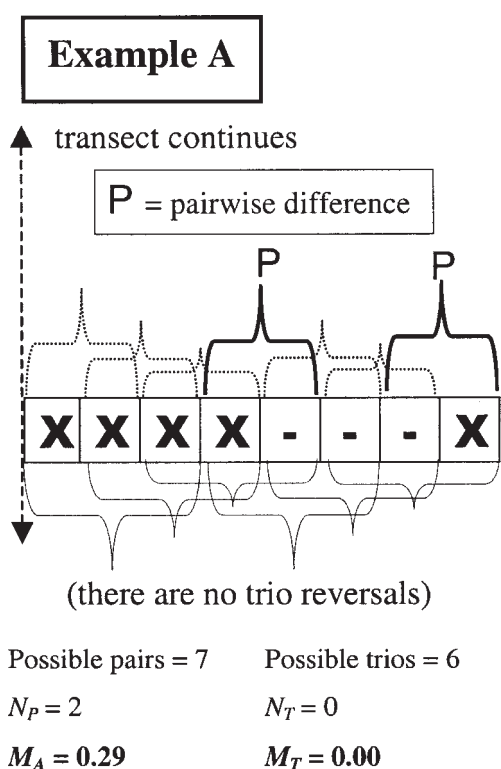
Example A

transect continues

P = pairwise difference

P   P

X X X X - - - X

(there are no trio reversals)

Possible pairs = 7   Possible trios = 6

$N_P = 2$ $N_T = 0$

$M_A = 0.29$ $M_T = 0.00$

Example B

transect continues

P = pairwise difference

P
P   P
P   P
X - X - X - X -
T
T   T   T
T   T
T   T

T = trio reversal

Possible pairs = 7   Possible trios = 6

$N_P = 7$ $N_T = 6$

$M_A = 1.0$ $M_T = 1.0$

Fig. 3. Calculation of M_a (adjacent) and M_t (trio) mosaicity for a single-species community.

Results

a. Sharpness of vegetational transition (location and width of the ecotones)

The first ordination axis represented well the sequence along the transect, with distance and ordination score having a rank correlation of 0.95. An ecotone (zone of rapid change in the vegetation) is shown by a high rate of change in ordination score (Fig. 2c). By this criterion, the Equally-weighted ordination showed five main ecotones over the area (Ecotones I to V; Fig. 1), all located within the three intensive transects:

Mangrove to rush transect:
    Mangrove/Rush (Ecotone I)

Rush to woodland transect:
    Rush/Marsh (Ecotone II)
    Marsh/Woodland (Ecotone III)

Woodland to pasture transect:
    Woodland/Woodland-edge (Ecotone IV)
    Woodland-edge/Pasture (Ecotone V)
    The three ecotones apparent in the Equally-weighted ordination at the uphill woodland edge (Fig. 1b) resolved into two in the finer scale analysis of that intensive transect (Fig. 2c). Otherwise, the positions of these ecotones, and the vegetation gradients identified, were almost identical in the Overall and Separate ordinations, and using spatial grains of 1 m × 1 m and 0.5 m × 0.5 m. Thus, the ecotone-location method seems to be robust against some variation in sampling intensity and spatial grain size. We use the most fine-grained information for further work.

Ecotone I: Mangrove/Rush:
    A sparse and dwarf monoculture of the mangrove *Avicennia marina* at the lowest elevation was replaced at Ecotone I (16.5 m) by a community dominated by *Juncus krausii*, with sporadic occurrence of salt marsh species such as *Sarcocornia* (≡ *Salicornia*) *quinqueflora* (Figs. 1a, 4a). The ecotone occurred at a 0.3 m high erosion clifflet, convoluted into a mosaic of creeks and islets.

Ecotone II: Rush/Marsh:
    At the lower end of this ecotone (230 m), very uniform *Juncus krausii* (rush) with sporadic occurrence of other salt tolerant species, was replaced at a rise in elevation, by marsh dominated by the upright-stem cyperad *Baumea juncea* and the exotic *Gladiolus undulatus*, with scattered *Leptospermum scoparium* shrubs (Fig. 4b).

Ecotone III: Marsh/Woodland:

Two maxima in the rate-of-change in species composition between 326 and 340 m indicate that Ecotone III comprised two transitions in rapid succession. *Sarcocornia quinqueflora* was not found above this ecotone, and only scattered *Juncus krausii* continued beyond the ecotone. Tall *Leptospermum scoparium* trees (those examined being 7, 11 and 15 yr old respectively) were recorded, for the first time along the vegetation sequence, just beyond Ecotone III. Ordination scores fluctuated in the woodland zone between 340 m and 533 m (especially in the ca. 70 m before Ecotone IV; Fig. 1b), with a gradual change to dominance by tall trees of *L. scoparium* and *Kunzea ericoides*, and shrubs of *Coprosma parviflora*, over a herbaceous layer (Fig. 4b).

Ecotone IV: Woodland/Woodland-edge:

Continuous woodland of *Leptospermum scoparium* and *Kunzea ericoides* extended across Ecotone IV at 533 - 540 m (Figs. 1a, 4c). However, understorey herbs which occurred in the marsh (especially rushes and cyperads) were largely replaced by species more typical of the pasture.

Ecotone V: Woodland-edge/Pasture:

The beginning of Ecotone V, at 546.5 m, was a transition from woodland with *Kunzea ericoides* trees up to 35 years old to a herbaceous pasture community dominated by exotic species: grasses *Anthoxanthum odoratum*, *Axonopus affinis* and *Vulpia bromoides*, forbs *Hypochaeris radicata* and *Lotus subbiflorus*, and the rush *Juncus dichotomus* (Figs. 1a, 4c). At the inland edge of the ecotone (553.0 m) exotic species became dominant, with the grasses *Pennisetum clandestinum* and *Poa trivialis* prominent.

b. Change in physiognomy

Vegetation canopy height doubled across Ecotone I (Mangrove/Rush: Fig. 4a), but showed no change in Ecotone II (Rush/Marsh). Trees of *Leptospermum scoparium* replaced shrubs a few metres above the end of Ecotone III (Marsh/Woodland; Fig. 4b). Canopy height did not change with the understorey transition of Ecotone IV (Woodland/Woodland-edge; Fig. 4c), but it decreased dramatically at Ecotone V as woodland gave way to pasture. The girths of *Leptospermum scoparium* and *Kunzea ericoides* trees were greatest immediately before Ecotone V, at the woodland edge (Fig. 4c).

c. Community mosaicity

At Ecotone I (Mangrove/Rush), average values of mosaicity indices M_A and M_T at the 0.5 m × 0.5 m grain
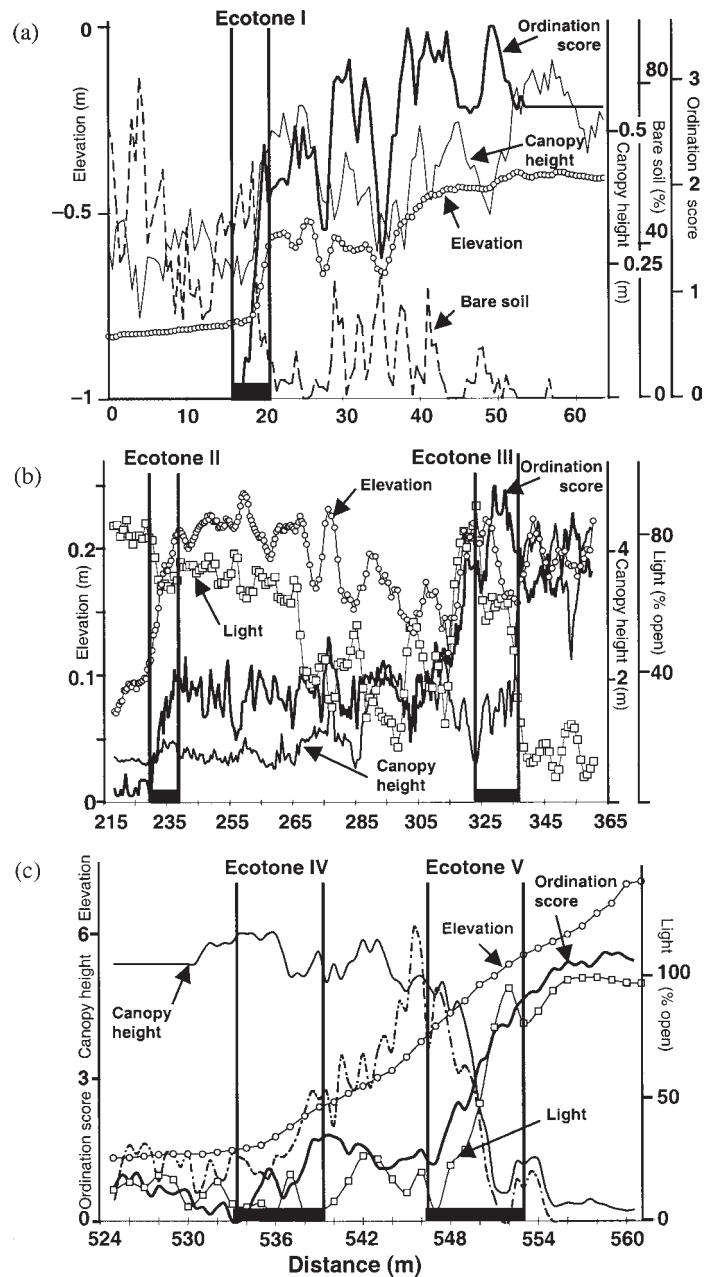

Fig. 4. Ordination scores and environment characteristics of the five ecotones: **a.** Mangrove/Rush (Ecotone I); **b.** Rush/Marsh (Ecotone II) and Marsh/Woodland (Ecotone III); **c.** Woodland/Woodland-edge (Ecotone IV) and Woodland-edge/Pasture (Ecotone V).

size were significantly greater in Ecotone I than in the communities at each side of the ecotone ($P < 0.001$ for both indices; Fig. 5a). At the coarser (1 m × 1 m) grain, community mosaicity was highest in the rush community above the ecotone. There was a general trend for community mosaicity to increase upshore across Ecotones II (Rush/Marsh) and III (Marsh/Woodland). M_T (at both grain sizes) and M_A (at 0.5 m × 0.5 m)
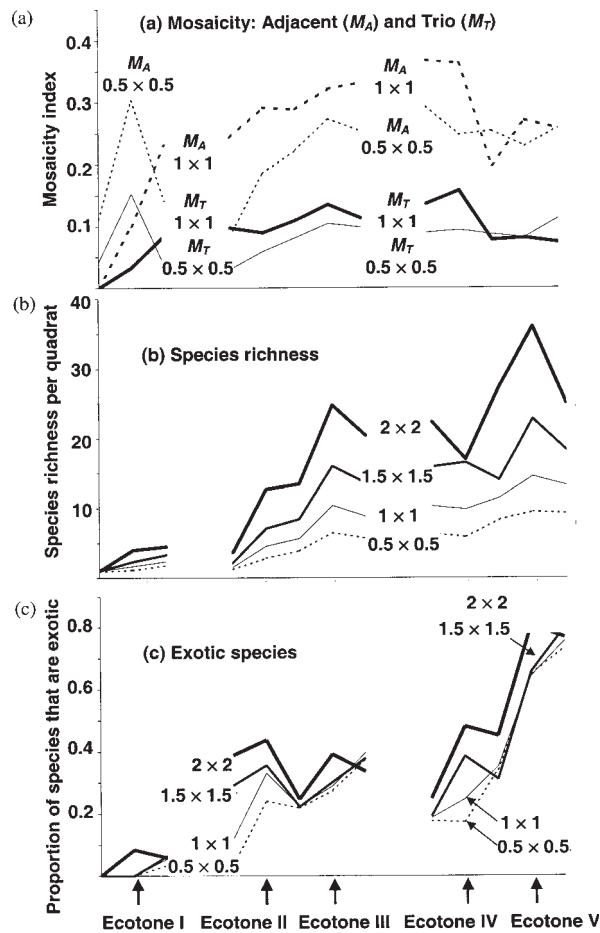
Fig. 5. a. Vegetation mosaicity, estimated by two indices ('Adjacent' index M_A and 'Trio' index M_T) at two spatial scales (dimensions shown in m) in five ecotones (I to V) and in the adjacent vegetation; **b.** Species richness in the same zones, at four spatial scales; **c.** Proportion of species that are exotic, at the same four scales.

reached local, though non-significant, maxima within Ecotone III (Fig. 5a). Neither of the two woodland ecotones (IV and V) was significantly different in community mosaicity from their adjacent communities.

d. Ecotonal species

In no ecotone was the number of species reaching their maximum in the ecotone greater than that expected at random (Table 1, 2). No species were found significantly more frequently in Ecotone I (Mangrove/Rush) than in either of the adjacent communities. All of the adult plants of *Anagallis arvensis* (exotic) and *Plagianthus divaricatus* recorded occurred within Ecotone II (Rush/Marsh; 10.7 and 14.7 × the number expected at random). *Sonchus oleraceus* was found more frequently within Ecotone II than in the marsh beyond (6.9 times

Table 1. Possible ecotone species for the five ecotones (I to V), as species more frequent in the ecotone than in the community above or below it, excluding cases where the ecotonal species occurs only one or two times. Entries are the percent frequency in each zone. Asterisks denote exotic species.

	Below	Ecotone	Above
Ecotone I: Mangrove/Rush			
No ecotonal species			
Ecotone II: Rush/Marsh			
Anagallis arvensis *	0.0	2.9	0.1
Baumea juncea	5.7	68.4	52.2
Lotus pedunculatus *	0.0	16.2	11.7
Plagianthus divaricatus	0.0	9.6	0.0
Sonchus oleraceus *	0.6	5.9	0.7
Ecotone III: Marsh/Woodland			
Baumea juncea	52.5	85.8	84.7
Briza minor *	0.0	3.0	0.0
Cotula coronopifolia	1.3	3.0	0.0
Holcus lanatus *	0.1	3.4	1.5
Isolepis reticularis	4.5	43.1	11.9
Isolepis sepulcralis	12.8	37.1	19.5
Juncus articulatus *	0.4	2.6	0.2
Juncus effusus *	0.4	4.3	0.2
Juncus pallidus	2.8	36.6	28.6
Juncus planifolius	1.3	9.9	3.6
Lobelia anceps	34.6	50.9	10.6
Lachnagrostis filiformis	8.5	47.4	3.2
Lolium perenne *	0.1	3.9	2.5
Pennisetum clandestinum *	0.6	8.2	1.7
Paspalum dilatatum *	0.3	78.4	49.2
Ecotone IV: Woodland/Woodland-edge			
Anthoxanthum odoratum *	83.6	91.2	59.1
Carex breviculmis	0.8	3.8	0.0
Cirsium vulgare *	0.0	5.0	0.0
Crepis capillaris *	0.8	3.8	0.0
Dactylis glomerata *	0.8	17.5	1.7
Geranium molle *	3.1	5.0	0.0
Holcus lanatus *	13.3	85.0	53.4
Hypochaeris radicata *	75.0	91.2	59.1
Juncus gregiflorus	3.1	5.0	0.0
Lotus pedunculatus *	1.6	87.5	62.5
Lolium perenne *	41.4	61.2	0.0
Trifoium repens *	18.8	56.2	0.0
Veronica arvensis *	2.3	6.2	0.0
Ecotone V: Woodland-edge/Pasture			
Carex breviculmis	0.0	7.7	0.0
Coprosma parviflora	46.0	65.4	32.5
Dichondra sp.	0.0	9.6	0.0
Juncus planifolius	0.6	4.8	2.5

the frequency of occurrences expected at random). In Ecotone III (Marsh/Woodland), *Briza minor* occurred 9.1 times more frequently than expected at random. Other species considerably more abundant in Ecotone III than expected at random included *Holcus lanatus* (5.2×), *Isolepis reticularus* (4.8×), *Juncus articulatus* (5.2×), *J. effusus* (6.2×), *J. planifolius* (4.5×), *Lachnagrostis filiformis* (4.5×), *Paspalum dilatatum* (4.5×), and *Pennisetum clandestinum* (5.5×). There were no true ecotonal species in Ecotone IV (Woodland/

Table 2. Number of ecotonal species, defined as having greater frequency in the ecotone than in the communities on either side: expected under a null model of random ecotone position, observed, and the significance of the difference. n.s. = $P > 0.05$.

Ecotone		No. of species		
		Expected	Observed	P
I	Mangrove/Marsh	1.9	1	n.s.
II	Rush/Marsh	7.3	7	n.s.
III	Marsh/Woodland	8.8	17	n.s.
IV	Woodland/Woodland-edge	14.7	16	n.s.
V	Woodland-edge/Pasture	8.4	5	n.s.

Woodland-edge), though all of the ten occurrences of the creeping herb *Dichondra* sp. found in the study were within Ecotone V (Woodland-edge/Pasture).

e. Spatial mass effect

The occurrence of seedlings in ecotones when adult plants were not present would be evidence for the spatial mass effect. We examined those species of which seedlings were found. In the Rush/Marsh ecotone (II), *Anagallis arvensis*, *Plagianthus divaricatus* and *Sonchus oleraceus*, which occurred in the ecotone, occurred as just one, two and three seedlings respectively beyond the range of adults, all above the ecotone. This is the opposite pattern from that proposed by theory: i.e. seedlings of ecotonal species were outside the ecotone. The other species for which seedlings were found all occurred as adults in the Marsh/Woodland (III) ecotone, and also in one or both of the adjacent communities. They therefore offer no evidence for the spatial mass effect.

f. Species richness

Species richness was low throughout Ecotone I (Mangrove/Rush), and was not significantly higher than in adjacent zones at either grain size. Species richness increased sharply at both Ecotones II (Rush/Marsh) and III (Marsh/Woodland) at all spatial grain sizes (Fig. 5b), but decreased again only after Ecotone III. Only at a grain size of 0.5 m × 0.5 m were differences between zones significant. Species richness in Ecotones IV (Woodland/Woodland-edge) and V (Woodland-edge/Pasture) was not significantly different to that in adjacent communities.

g. Exotic species

In no case was the proportion of exotics significantly higher in an ecotone than in the two adjoining communities at the grain size of 0.5 × 0.5 m (Fig. 5c).

The exotic proportion in Ecotone II (Rush/Marsh) was only slightly and non-significantly higher than above

the ecotone at the 0.5 m × 0.5 m grain size, though at coarser scale (1 m × 1 m) this was significant. The proportion of exotics in Ecotone III was generally intermediate between the values in the communities above and below it. The proportion of exotic species (mainly pasture species), rose across the transect as a whole, with a tendency to rise in the ecotones IV (Woodland/Woodland-edge) and V(Woodland-edge/Pasture), and reached its highest value in the pasture (Fig. 5c).

Discussion

Types of ecotone

Different types of ecotone can be distinguished on the basis of the cause of the community sharpness (Lloyd et al. 2000). The main types are (a) environmental, caused by a sharp environmental change, (b) switch, caused by a positive feedback between community and environment, (c) invasion, where there is invasion of a dominant species along a front, and (d) anthropogenic, caused directly by humans. The Mangrove/Rush ecotone (I) is probably a switch ecotone (Wilson & Agnew 1992), i.e., caused by a positive feedback switch. Where the sward is intact, the muddy substrate is held together by the plant roots. Once erosion starts at a point, the plants no longer hold the substrate together, and it is eroded further, causing more plant death. It is a characteristic of switches that they can produce an ecotone by sharpening an underlying gradient, and that they can create a mosaic (Wilson & Agnew 1992). Both effects are shown here, where there is a clifflet defining the edges of a mosaic.

The position of the Rush/Marsh ecotone (II) exactly correlates with an increase in substrate elevation, from only just above mean high tide level to about 0.2 m above. The profile suggests that this might be an old levee. Ecotone II is clearly an environmental ecotone. There is a small increase in substrate elevation at the start of Ecotone III (Marsh/Woodland), which probably represents an old marsh edge, a few decades old to judge from the tree ages, and the ecotone may be largely relictual.

As substrate elevation increases steeply, taking the plants beyond the reach of flooding, the Woodland/Woodland-edge ecotone (IV) exhibits a similar situation to that in Ecotone II. However, drainage is poor, allowing the occurrence of several marsh species. The ecotone is clearly environmental in cause.

The Woodland-edge/Pasture ecotone (V) is certainly anthropogenic, caused by felling of woodland up to this line, and subsequent grazing, probably with over-sowing of pasture species and fertilising. However, it occurs

close to the bottom of the slope, where moisture will accumulate (Fig. 1). This is probably a case of a switch based on human/stock activity sharpening an environmental gradient, as both humans and stock avoid the marshy area below (Wilson & King 1995).

Properties of ecotones

In very little ecotone work is the position of the ecotone determined objectively. Methods do exist for boundary detection (see Cornelius & Reynolds 1991) but ecological studies of ecotones have generally used subjective methods. Our method examines the rate of change, rather than the difference between two segments as in the moving-window method of Cornelius & Reynolds (1991). We suggest this is more appropriate for analysing ecotones, which are zones of rapid change rather than points of instantaneous change. We believe our method is also more appropriate for the purpose of identifying ecotones along a clear environmental gradient than the wombling method of Fortin & Drapeau (1995), which is intended for two-dimensional mapping.

The five ecotones that were identified ranged in width from 4 m to 14 m. Our method gave almost identical results for ecotone location and width with the two spatial grains (0.5 m × 0.5 m and 1 m × 1 m), suggesting that it is not critically dependent on the spatial grain at which the vegetation is examined (cf. Fortin 1999), though 5 m is too large. The Mangrove/Rush ecotone (I) was the narrowest, probably about 0.5 m at any one point, but with the mosaic covering 4 m. Clements (1905), originator of the ecotone concept, commented that: "Ecotones are rarely sharply defined". However, our results demonstrate that quite sharp boundaries can occur, with rapid replacements of suites of species (i.e. communities).

Gosz (1992) suggested that physiognomy (life form) will change across an ecotone, and such a change is explicit in the ecotone definitions of Tansley (1939) and Dice (1952). At our study site, changes in physiognomy occurred in three of the five ecotones (Mangrove/Rush; Marsh/Woodland, and Woodland-edge/Pasture). We initially chose the study area because of the changes in physiognomy, and chose the positions of the intensive transects by a combination of physiognomy and species composition, but the final positions of the ecotones were determined, and two extra ecotones were identified, by the objective regression method. The change in vegetation height in Ecotone I coincided with the position of the ecotone, as identified by species composition, but the physiognomic changes associated with Ecotones III and V were just outside the ecotones. The latter ecotones are in the zone just outside the tree canopy, but still influenced by it. It is often assumed that the intermediate community is just inside a forest (Schonewald-Cox & Bayless 1986), but our results indicate that the true ecotone, in terms of the most rapid change in species composition, can be just outside the tree canopy.

Towards an ecotone, conditions will become marginal for some of the species, and species occurrences will therefore become more sensitive to environmental heterogeneity, potentially resulting in a small-scale community mosaic in species composition (Neilson et al. 1992; Gosz 1992). Indeed, it has been recognized from the origin of the ecotone concept that there was likely to be "a mosaic, in which the various pieces now stand out sharply, and are now obscure" (Pound & Clements 1900). Obviously, mosaicity will depend on the spatial grain at which the system is viewed, but there is very little evidence in the literature for mosaics at ecotones. Mosaicity does not seem to be a necessary feature of ecotones. The only clear case of mosaicity in this study was at Ecotone I (Mangrove/Rush), where the mosaic element comes from channels of mud flat with islets of salt marsh. The mosaicity is not a direct result of the ecotone; instead both the ecotone and mosaicity are the results of the switch. The high mosaicity was not apparent at a spatial grain of 1 m × 1 m (Fig. 5a), because quadrats of this size included both mud flat and salt marsh. This emphasizes the scale-dependent nature of mosaics.

The literature contains the concept of ecotonal species, i.e. species that are restricted to the ecotone, and are absent from the two communities on each side of the ecotone (Clements & Shelford 1939; Hansen et al. 1988; Neilson et al. 1992). Species with such distribution patterns might occur if: (a) environmental conditions in ecotones were intermediate between those of the adjacent communities and there were species adapted to these conditions, or (b) if there were unique environmental conditions in the ecotone (Stoutjesdijk & Barkman 1992), or (c) because the species needed resources from both sides of the ecotone (such as climbers at a forest edge, requiring the light from outside, but the trees for support: Putz 1984). There have been few previous reports of ecotonal species, and in most cases the evidence has been doubtful (e.g. Anderson et al. 1980; Jose et al. 1996). In this study, we found several species which occurred considerably more frequently within ecotones than in the communities adjacent to the ecotone, though only three which were restricted entirely (within the studied area) to an ecotone, including some common species (e.g. *Isolepis reticularis* and *Lachnagrostis filiformis* in Ecotone III; Table 1). However, compared with a null model, we found that in no ecotone were there significantly more ecotonal species than expected. There are also species characteristic of

more than one ecotone (Table 1): *Carex breviculmis*, *Holcus lanatus*, *Juncus planifolius* and *Lolium perenne*. Of these, *C. breviculmis* occurred 12× in two ecotones and only once outside an ecotone. These are more convincing as ecotonal species.

The spatial mass effect is the repeated flux of propagules, from one ('source') habitat in which the species can reproduce and maintain a population, into another ('sink') habitat in which the species cannot maintain a population, even though plants can grow (Shmida & Ellner 1984; Pulliam 1988; Stevens 1992). It is very difficult to find evidence for the spatial mass effect (Wilson 1990). However, finding seedlings outside the range of adults, in a situation where active invasion is not occurring, is appropriate evidence. If the ecotones are sink habitats, this would explain the postulated high species richness there. In our study, seedlings were recorded beyond the ranges of adult plants for only a few species. All of these species occurred more commonly within ecotones than in communities adjacent to the ecotones. Therefore the seedling distribution did not lead to higher species richness within the ecotones, and no spatial mass effect of the type hypothesized is apparent.

Many ecologists have suggested that richness will be higher in ecotones than in adjacent communities (e.g. Leopold 1933; Odum 1983; Petts 1990), but van Leeuwen (1966) and van der Maarel (1976) suggested there will be environmental fluctuations at ecotones, making the environment unfavourable for plant growth, leading to low species richness. There is little empirical data relevant to this subject. There have been a few demonstrations of higher ecotonal richness, but none are very convincing (Shmida & Wilson 1985; Brothers 1993; Wolf 1993; Carter et al. 1994). Some reports show species richness in the ecotone to be no different from that in adjacent communities (Harper 1995; Luczaj & Sadowska 1997). In our study, species richness was intermediate between the richness of the two adjacent communities in two ecotones (I and II), but closer to the higher-richness community. One ecotone (IV) showed a slight, and non-significant, tendency to be less species-rich than either adjacent community. In the other two ecotones, richness was higher than on either side, though significantly so only in Ecotone III. It is clear that high species richness is not an intrinsic feature of ecotones.

Ecotones, both natural and anthropogenic, contain a relatively high proportion of exotic species (Norton 1992; Brothers & Spingarn 1992; Risser 1995). A few examples have also been reported of exotic species invading ecotones (Ewel 1986; Elias 1992; Puyravaud et al. 1994; Duggin & Gentle 1998). In our study area, more than half (21/38) of the species identified as possibly ecotonal were exotic, out of a total flora of 100 species. The proportion of exotic species in our study area showed a general increase with distance from the sea, but at a spatial grain of 2 m × 2 m, there was indication of a higher exotic representation in all five ecotones than in adjacent communities. The effect was consistent across spatial grain sizes only in Ecotone II, and even there significant only at a spatial grain of 1 m × 1 m. Thus, the evidence in our study for exotics being more frequent in ecotones is weak.

General conclusions

The literature contains many generalizations about ecotones. Situations can be found that conform to each, but none of the generalizations was true of all five of the ecotones that we investigated. Only one ecotone coincided precisely with a change in physiognomy. There was some evidence for the existence of ecotonal species, but little for the spatial mass effect. There was evidence for mosaicity, higher species richness and a higher frequency of exotic species in only one ecotone each, and the effects often varied with spatial grain size. We conclude that none of the hypothesized ecotone features that we examined are intrinsic properties of ecotones. All the effects result from the particular ecological conditions and the properties of the species present.

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