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Adjacent land-use intensification facilitates plant invasions into indigenous shrubland fragments

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Abstract: Indigenous vegetation fragments in agricultural landscapes are vulnerable to creeping edge effects and stochastic extinctions on top of the effects of historic land use and disturbance which have already resulted in significant changes to baselines. Agricultural intensification can potentially increase these threats through spillover of nutrients, water, and weeds, especially in dryland ecosystems which are naturally low in nitrogen and soil moisture. We use plot-based vegetation data and soil measurements of stable isotopes of nitrogen to test whether adjacent agricultural intensification increases plant invasions into dryland shrubland fragments in Canterbury, New Zealand. Nitrogen spillover was only associated with edges adjacent to intensive agriculture. Animal effluent was the most likely source. Edges adjacent to intensive agriculture had higher dominance by exotic species, higher exotic graminoid cover, and depressed native bryophyte cover immediately adjacent to the agricultural boundary. Changes in exotic cover were due to weedy species that dominate in areas of high disturbance and nutrients rather than pasture species moving over the fenced boundary. Spillover created more abrupt environmental and vegetation gradients at the edge but didn't change the extent of the edge, which typically transitioned to the fragment core at about 40–50 m from the fragment boundary. Hence, the core vegetation remained little affected by adjacent intensification. Spatial buffers to manage fertiliser and irrigation spillover will help prevent further degradation of edge communities adjacent to intensive agriculture. However, the longer term threat to the ecological integrity of the core area of these spatially isolated fragments is likely to be random extinction and vegetation succession. The loss of spatial linkages between vegetation patches and the mosaic of vegetation at different developmental stages means that many of the species that once made up the regional species pool will be lost from this landscape without intervention.

Keywords: agricultural intensification, biodiversity, dryland shrubland, edaphic gradients, edge effects, invasion, spillover

Introduction

Vegetation clearance for agriculture has led to habitat fragmentation and biodiversity decline worldwide (Rand et al. 2006; Bell et al. 2022). Land left for conservation purposes is often small in size and highly influenced by stochastic species loss and edge effects, including spillover (Ewers & Didham 2006a). Spillover of agricultural inputs such as fertiliser and water (Wu et al. 2021), invasive shelter belt and plantation forest species (Ledgard 2001; van Etten et al. 2020), and other exotic weeds leads to a non-random loss of native species and ecotypes, often selecting for those which are pre-adapted to agricultural systems. This results in a loss of functional diversity and impacts ecosystem resilience (Bell & Tylianakis 2016). Agricultural intensification and the increased input of nutrients and water that this entails has the potential to make spillover worse. Understanding the nature, magnitude, and extent of spillover and the threats posed by exotic species planted in adjacent land enables the design and implementation of appropriate preventative measures such as buffers, clearance

rules and legal protections. While understanding of invasion and invasive species has advanced significantly (Mazia et al. 2019; van Etten et al. 2020), the biological impact of agricultural spillover remains poorly characterised, as does the threat that intensification poses to the stability of edges between indigenous vegetation and agricultural systems. With increasing intensification of agriculture (Rudel et al. 2009) there is a pressing need for better information to inform evidence-based regulatory frameworks.

Managing for edge effects is an important component of maintaining biodiversity in fragmented landscapes (Frost et al. 2015). The edge is a transition zone between the indigenous vegetation patches and the matrix vegetation, containing many species from either community, and sometimes edge specialist species that are found in neither community (Young & Mitchell 1994; Peyras et al. 2013; Burst et al. 2017). At edges between native dominated and non-native dominated vegetation communities, the edge is often highly asymmetric, with the native vegetation significantly invaded by agricultural species more adapted to the disturbance associated with

edges (Boutin & Jobin 1998). In small native reserves, the edge effect can severely compromise the ecological integrity of the indigenous vegetation (Ecroyd & Brockerhoff 2005; Didham & Ewers 2012), hence why minimum sizes are set where possible (Young & Mitchell 1994). Invasion can add considerably to the risk of species loss that occurs through stochastic extinction and isolation in the context of ongoing vegetation dynamics in fragments (Fahrig 2003).

The shape of the edge depends on the magnitude and steepness of the environmental gradient with flow-on effects for species distributions in response to the edge (Ewers & Didham 2006a). Large gradients over short distances produce sharp edges. Conversely, small gradients over large distances produce very graded edges. Patchily distributed disturbance and micro-sites make for diffuse edges, whereas very uniform gradients can result in sharp zonation such as on lakeshores (Harper et al. 2005). The manner in which different species are arrayed across the edge depends on their degree of specialisation with respect to the gradient (Ewers & Didham 2006b; Peyras et al. 2013). Species specialised to one or other of the abutting vegetation types may only minimally extend into the edge zone. Edge specialists may have a unimodal distribution, peaking somewhere in the edge zone, while generalists may show no clear distribution pattern at all.

Changes to the way agricultural lands are managed can directionally disrupt the environmental gradients maintaining the edge. Agricultural intensification increases the magnitude and reach of spillover into adjacent indigenous vegetation by modifying the edaphic gradient between the two (Murcia 1995; Boutin & Jobin 1998; Blitzer et al. 2012; Didham et al. 2015). The scale of these ecological impacts depends on the system and context: they can occur over a few metres for nitrogen in soil (Bowie et al. 2016) and over kilometres for windblown phosphate spillover (Duncan et al. 2008). The ecological impacts of such spillover may be particularly strong in low productivity systems, where nutrients and water are ordinarily too limiting for invasion by many common agricultural pasture and crop species (Piessens et al. 2006; Aavik & Liira 2010). Nutrient and water subsidies can encourage invasion from agricultural pasture and crop species (Boutin & Jobin 1998), change the abundance of edge specialists, and/or trigger community changes to the indigenous species that intergrade into the edge (Øien et al. 2018; Bell et al. 2022).

Past work has examined if there are links between intensification and nutrient spillover (Didham et al. 2015). Here, we examine how spillover from intensification modifies the depth and steepness of the edge. We ask how agricultural intensification modifies the plant species composition and extent of edges between agriculture and small reserves of native habitat. We focus our study on dryland shrubland conservation reserves in a matrix of intensive agriculture in Canterbury, New Zealand. These reserves, formerly part of grazing runs, and gazetted from 1970 through to 2019 as representative samples of the indigenous ecosystems, are the largest remnants of their kind (2.3–50 ha). Once a common vegetation association, most of the surrounding landscape has been converted to high intensity pasture for dairy (a process which began in the early 2000s). The reserves already contain significant exotic components, facilitated by a legacy of widespread grazing by domestic stock and feral lagomorphs, fertiliser addition, burning, and over-sowing (Molloy 1970; Molloy & Ives 1972; Ecroyd & Brockerhoff 2005; Bowie et al. 2016). While some exotic incursions are widespread, others are more localised around vehicle tracks, animal paths, or small-scale burns.

Detection of changes in the edge is therefore complicated by a significant baseline shift in the vegetation toward higher exotic dominance, coupled with ongoing vegetation succession and heterogeneous vegetation patterns. Edge effects must be measured against shifts in the baseline, including those from natural succession, which may be ongoing in ways unrelated to pressures around the edges (Fig. 1).

We used stable isotopes of nitrogen to measure the extent of fertiliser spillover into the remnants. The pattern of $\delta^{15}\text{N}$ enrichment with fertiliser addition depends on the fertiliser. In Canterbury dairy farms, cow manure collected from the cow sheds is often irrigated onto pastures, with the joint benefit of fertilisation of pastures and as a means of disposal (Saggar et al. 2004). Animal manures are enriched in $\delta^{15}\text{N}$ compared to air (Rogers 2008; isotopic differences ($\delta^{15}\text{N}$) between 2 to 11‰, with dairy manure measured at 4.5‰). Synthetic nitrogen fertilisers, by comparison, are synthesised using atmospheric nitrogen from air, and so are comparable to air (Rogers 2008; $\delta^{15}\text{N}$ between -2 and 2‰). Nitrogen compounds derived from soil nitrogen are in the middle of these two extremes and have $\delta^{15}\text{N}$ values in the range 2–5‰. We expected there to be a gradient in $\delta^{15}\text{N}$ from edge to interior for irrigated sites, and a lesser gradient or no gradient for unirrigated sites. This is because irrigation is also associated with extensive use of nitrogen fertilisers to promote grass growth. A positive gradient (i.e. increasing $\delta^{15}\text{N}$ with distance from the fence line) would indicate spillover of primarily synthetic fertilisers such as urea and ammonium nitrate, commonly used in high-intensity pasture farming systems. A negative $\delta^{15}\text{N}$ gradient with distance from fence line would indicate spillover from animal effluent, either over-sprayed or moving horizontally via runoff.

We predicted that, because the underlying natural environmental gradient is strongly water and nutrient limited, the plant species composition and extent of edges would be dependent on the degree of water and nutrient spillover. If spillover only partially extends into the edge zone, then there will be facilitation of invasion along the agricultural margin, but a steepening of the environmental gradient will result in the indigenous community margin being maintained in its current position (Fig. 1b and e). If nutrient and water spillover extend beyond the current indigenous community margin, then adjacent intensification will result in both a shortening of the edge vegetation gradient and a shift toward the interior of the fragment (Fig. 1c and f). We used Bayesian non-linear mixture models to test if agricultural intensification modifies the composition and extent of edges between agriculture and small reserves of native habitat, and if so, which *a priori* conceptual model best fits the observed patterns.

Methods

Study sites

We conducted our study at five shrubland fragments on public conservation land in the Canterbury Plains and Hurunui Basin, New Zealand (Fig. 2): (1) Bankside Scientific Reserve (2.8 ha; 100 by 260 m, gazetted 1970; irrigation present in 2009 imagery); (2) Culverden Scientific Reserve (c. 10 ha; c. 310 by 330 m; gazetted 1981; irrigation present in 2003 imagery); (3) Eyrewell Scientific Reserve (2.3 ha; 100 by 220 m; gazetted 1971; irrigation started between 2002 and 2009); (4) Medbury Scientific Reserve (c. 50 ha in total but c. 70% of shrubland has been lost to fire; area sampled: c. 300 by 350m; gazetted

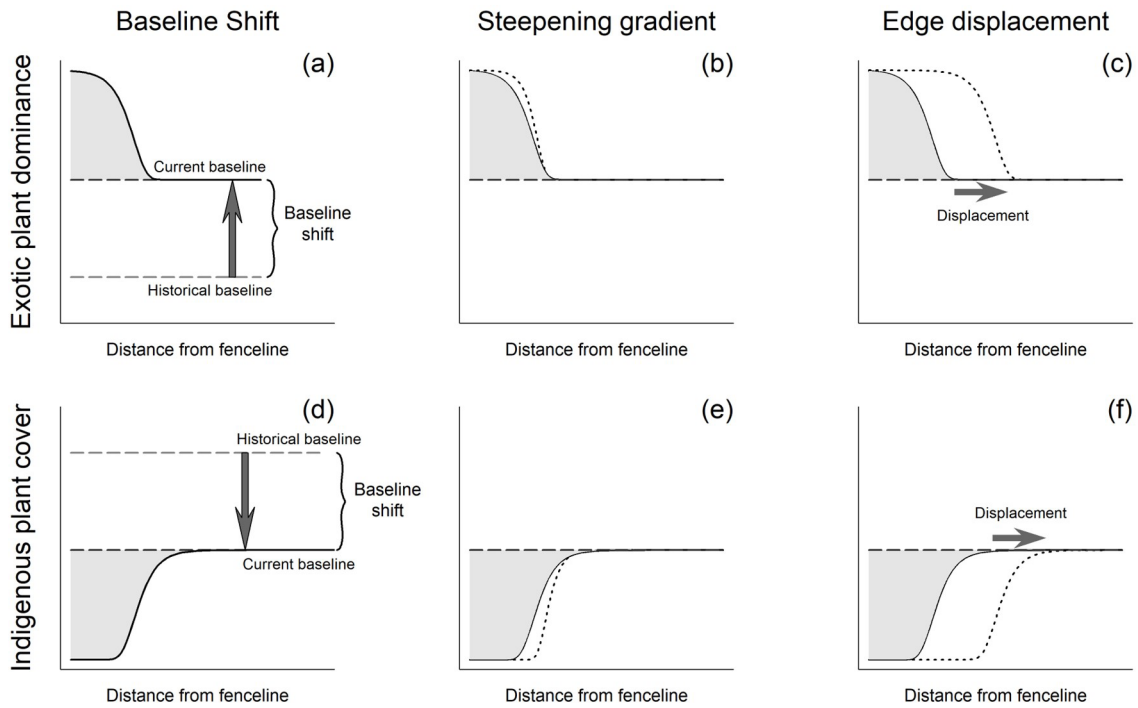


Figure 1. Conceptual model of changes in plant community structure in these dryland reserves. The solid line indicates exotic dominance (proportion of cover that is exotic; a–c) and indigenous plant cover (d–f) with distance from the fence line. Historical grazing and management has resulted in baseline shifts with mean exotic dominance in the reserve core increasing (a) and indigenous cover decreasing (d). Edge effects (grey shade) are additive to the baseline shift, with high exotic dominance nearest to edges and indigenous plant cover depressed. Dotted lines (b, c, e, and f) indicate potential shifts in exotic dominance or native cover due to increasing intensification in adjacent lands. We expected increasing intensification in adjacent lands to steepen the existing edge vegetation gradient (b and e) and/or displace the edge further into the reserves (c and f).

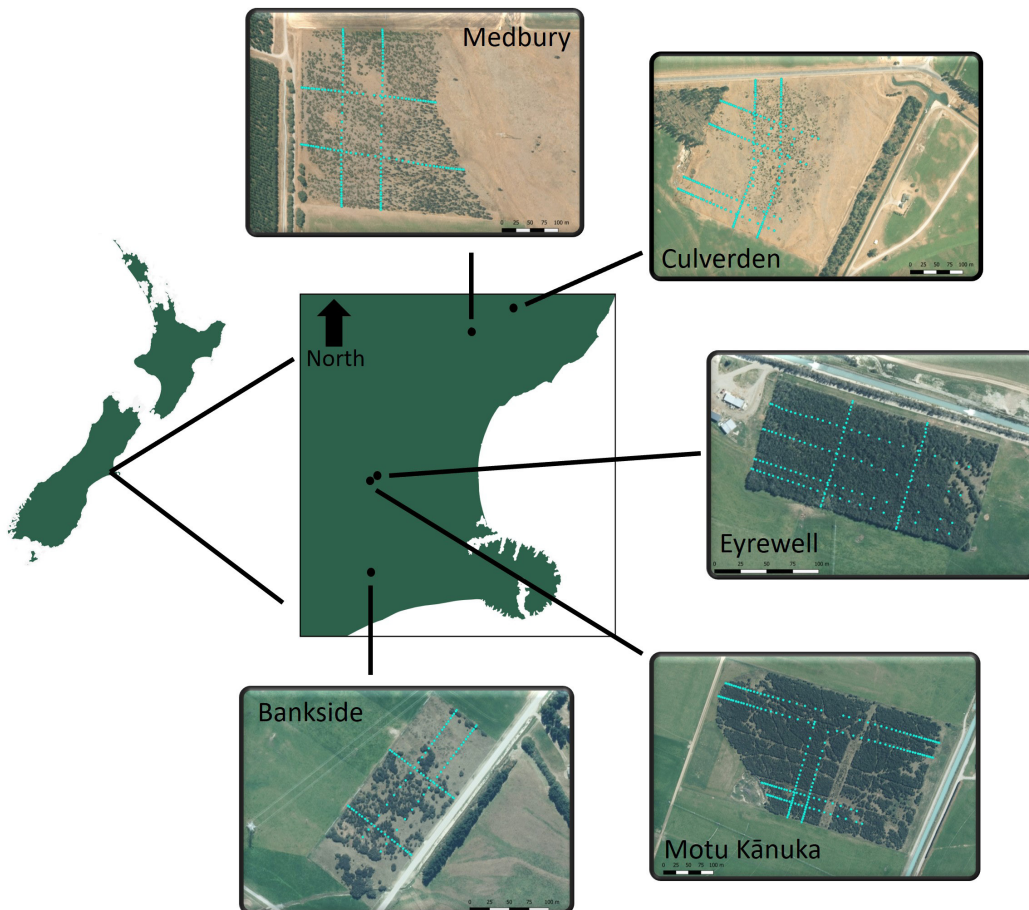


Figure 2. Location of the sites on the dry plains on the eastern side of South Island, New Zealand. The layout of the plots along transects at each site is shown (blue dots).

1997; irrigation started between 2003 and 2012); and (5) Motu Kānuka Scientific Reserve (12 ha; c. 270 by 400 m; gazetted 2019; irrigation present in 2002 imagery). All the reserves were historically grazed under dryland farming systems for over 100 years and locally impacted by burning, the provision of farm tracks, and an unknown level of fertiliser and over-sowing. Hence, the baseline vegetation had already shifted to include significant populations of exotic species prior to these blocks of land acquiring reserve status (Molloy 1970; Molloy & Ives 1972). Comparison with early records shows there has been a decline in native species richness since this time (e.g. Bowie et al. 2016). Since the early 2000s there has been a dramatic intensification of farming surrounding the reserves, with many farms being converted to dairy and installing irrigation systems, especially large centre pivot irrigators. The vegetation on these farms is usually a perennial ryegrass (*Lolium perenne*) dominated pasture, but fodder crops may also be planted. Around the margins adjacent to the fence, disturbance from vehicles and stock and the inability of direct drilling to go right up to the boundary sometimes results in a narrow band of exotic dominated sward of grasses and forbs.

Study design and sampling

Our experimental design utilised reserve boundaries with and without irrigation. Irrigated boundaries always abutted intensive pasture. For three of the five sites, irrigation had been established for at least 10 years prior to the date of vegetation sampling, and at the remaining two sites for 15 years prior to sampling. Non-irrigated boundaries abutted a mixture of ungrazed herbaceous road verges or herbfields, and in one case a grassy logged woodlot. We could not date the installation of irrigation accurately due to the timing of aerial imagery, so we did not include the length of time a boundary had been irrigated in the analysis. At each site, transects were established perpendicular to the boundaries from the edge to the interior. Transects were spread evenly across both downwind and upwind prevailing wind directions (Young & Mitchell 1994; Davies-Colley et al. 2000).

There were four transects per irrigation treatment (two upwind and two downwind) for each site, resulting in eight transects per site, except for Bankside where there were six transects due to site constraints. Transects were separated by no less than 10 m and randomly positioned along the boundary. In addition, they were no closer than 15 m to another boundary to avoid being confounded with strong effects from another edge.

To identify fine scale topographical variation, the transects were surveyed at 1 m intervals using a global navigation satellite system survey instrument. We made a simple classification of the topography into points that were higher than surrounding points (“tops”) and those that were not (“other”). We expected tops to be dryer than other microsites due to the combined effects of exposure to wind and drainage (Alexander et al. 2016).

Our expectation was that any edge effect changes in plant communities would be most rapid close to the boundary (Ries et al. 2004). To ensure that we adequately sampled those areas with high rates of community turnover, we sampled more intensively closer to the reserve boundaries than we did toward the centre. Our sampling distances were based on an exponential series and limited to a maximum of 200 m from the edge. When the opposite boundary of the fragment was less than 200 m, the transect was shortened to be no longer than the half-way point. The first 10 m of transect contained four plots. There were 12 plots in the first 50 m of each transect, compared with six from 50 to 100 m. From 100 to 200 m,

there were also six plots per transect. This design resulted in 836 plots across the five sites.

At each plot location we sampled the vegetation at two plot sizes. In the 1 × 1 m plot we recorded the percent cover of all vascular and non-vascular plant species up to 50 cm high, and percent cover of all vascular plants present from 50 cm to 2 m. In a 2 × 2 m plot centred on the middle of the 1 × 1 m plot we recorded percent cover of all species > 2 m.

Soil nutrient sampling was carried out in a quarter of the 1 m plots along each transect and such that the maximum number of distances were sampled across the two replicate transects (a total of 253 samples from across the five sites). The soil sample consisted of five 10 cm deep soil plugs taken from each plot using a 1 cm soil corer, after removing any vegetation and litter. These subsamples were pooled at the plot level and assayed for stable isotopes of nitrogen using standard methodologies by Isotracer Research, University of Otago.

Analysis

Spillover of nitrogen fertiliser

We modelled trends in total nitrogen and $\delta^{15}\text{N}$ using linear mixed effect models, with distance from the fence line log-transformed. Fixed effects included a full interaction model between distance to nearest fence line and irrigation. Transects nested within sites were included as random intercept terms.

Changes in community structure

We chose three response variables to model change in community structure: exotic dominance, exotic grass cover, and native non-vascular plant cover. Exotic dominance was defined as the sum of exotic plant cover across species divided by the sum of the cover of all plant species in the plot. Exotic grass cover and non-vascular cover were calculated as the sum cover of non-native graminoids and native non-vascular species respectively in the plot. Exotic dominance and exotic grass cover show the extent of invasion by non-native species. We chose non-vascular species because as a group, they are a key component of dryland ecosystems in Canterbury (both on the Canterbury Plains and in inland basins); non-vascular species were prevalent across all our sites, accounted for the majority of the native ground cover, and were likely to represent a high proportion of the native species present. Additionally, non-vascular species are known indicators of changes in soil moisture and nutrients (which are the main forms of spillover that we expected to be influencing the sites). For example, both mosses and lichens are often used as bioindicators for changes in nutrients (Duprè et al. 2010; Boltersdorf et al. 2014) and these species are often lost when soil nitrogen is increased (Stevens et al. 2004; Øien et al. 2018) due to both intolerance of high nitrogen and competition from faster growing herbaceous species.

We modelled exotic dominance, grass cover and non-vascular cover (measured in the 1 × 1 m groundcover plots) as a function of distance from the fence line using Gompertz functions (Tjørve & Tjørve 2017) fitted in a Bayesian modelling framework. These curves were selected to best fit our *a priori* conceptual model of edge effects at these sites (see Fig. 1). We expected that points in the reserves would be subject to effects from more than one edge because the reserves were so small. Hence, we modelled the edge effect using a Gaussian mixture model of the two closest edges. We can write a general probability statement for these models as:

$$p_Y(y|\theta, \mu, \sigma) = \sum_{z=1}^2 \theta_z N(y|\mu_z, \sigma_z) \quad (1)$$

Where y is our observed responses, and μ_z and σ_z are the mean and standard deviation of the z^{th} mixture component respectively. The θ_z are weight parameters to account for the contribution of the second edge to the response relative to the first edge, with $\theta_1 = 1 - \theta_2$. Here we assume $\sigma_1 = \sigma_2$.

We modelled the means of the mixture components using a Gompertz function. To simplify the models, we estimated a common asymptote of the curve at the outer (i.e. fence side) edge (a), and allowed the asymptote at the inner (i.e. side furthest from fence) edge to vary according to the characteristics of the site and the transect. This reflected our expectation that all outer edges adjacent to agriculture will be similarly dominated by exotics. The interior asymptote equates to an estimate of the current baseline state of the fragment's core and is assumed to be common to the two mixture components (i.e. the effects of irrigation are undetectable if far enough from the boundary). The Gompertz function for exotic dominance and exotic grass cover was modelled as:

$$\mu_{ijk} = b_{jk} + (a - b_{jk})\exp(-\exp(X\beta)) \quad (2)$$

where b_{jk} is the lower asymptote, a is the upper asymptote, and X is a matrix of predictors describing the lag and maximum slope of the Gompertz function which characterises the edge effect (shaded area in Fig. 1). The lag and maximum slope were modelled as a function of edge type (irrigated or not irrigated), distance from the edge, and their interaction with β , a vector of estimated parameters. For the non-vascular species model, the lower asymptote was common to all sites and the higher one was allowed to vary with characteristics of the site and transect. That is:

$$\mu_{ijk} = a + (b_{jk} - a)\exp(-\exp(X\beta)) \quad (3)$$

With the meaning of b_{jk} and a now reversed. The b_{jk} in both models was modelled as:

$$b_{jk} = V\gamma + \alpha_j + \alpha_k \quad (4)$$

where V is a matrix of predictors describing the effect of woody tree cover > 2 m (from the 2 m by 2 m plots) and topography (top of a swale vs. other) on the inner asymptote; γ is a vector of estimated parameters; and α_j and α_k are random intercept terms for the j^{th} transect and k^{th} site respectively. The transect and site random effects are assumed to be normally distributed with a mean of zero and estimated standard deviation of σ_{transect} and σ_{site} respectively. Finally, we weighted the mixture components for each subplot according to a logit function of the difference in the distances to the two nearest fence lines ($\Delta Dist_{ijk}$) for each plot:

$$\theta_{ijk} = 1/(1 + \exp(-\delta \times \Delta Dist_{ijk})) \quad (5)$$

with δ being an estimated parameter.

Models were fitted using Hamiltonian Monte Carlo Markov Chains (MCMC) in the package Stan, using the 'rstan' interface for R (Stan Development Team 2018). Exotic dominance and non-vascular cover were logit transformed prior to analysis. All predictors were standardised prior to fitting. Lags, slopes, and asymptote parameters assumed standard-normal priors. We constrained the main effect of slope to be either non-negative (non-vascular cover) or non-positive (exotic dominance and grass cover) for model identifiability. These constraints were based on our *a priori* expectations. In practice, the confidence limits on these parameters were

well differentiated from the boundary values, thus supporting our assumptions. We assumed Gamma priors on the standard deviations for the error distribution and the site and transect random effects. Convergence was assessed from six MCMC chains both graphically from trace plots and by determining if the Gelman-Rubin statistic \hat{R} was less than 1.05 (Gelman et al. 2004).

Estimating the extent of the edge effect

We used the method of Zurita et al. (2012) to define the extent of the edge effect as the upper and lower inflection points of the sigmoidal curves. We calculated the maximum and minimum values of the second derivative of the Gompertz function for a bootstrap sample of edge-effects curves from the posterior MCMC samples of our models to obtain 95% credible intervals for the extent. We randomly drew 10 000 samples of transects nested within sites. Within those transect samples we randomly selected one combination of topography type and tree cover. This combination of site, transect, topography type, and tree cover formed one replicate dataset. For each of these replicates we sampled from the posterior distribution of the model parameters and used the replicate dataset and parameter to describe an edge effect curve. The models account for nearby secondary edges when estimating the parameters; therefore, for the purposes of this simulation, we assume that transects were far enough away from secondary edges that this effect can be ignored. For each edge effect curve we numerically solved for the maximum and minimum of the second derivative using the parameter values that defined each curve. Each of these samples was used to calculate median and 95% credible intervals on the edge extents.

Individual species' responses to the gradient

To determine which species might be changing in the edge with adjacent irrigation, we fitted models to individual species' distributions along the gradient. We followed Peyras et al. (2013) in fitting five models. Model 1 assumed constant abundance with distance to fence line and implied a species that was unaffected by the edge. Model 2 assumed a linear trend, either increasing or decreasing, with distance from fence line, consistent with a species that was a specialist in either the agricultural or native communities. Model 3 assumed that trend was exponential. Model 4 assumed a sigmoidal function (four parameter Gompertz), acknowledging that abundance might change along the edge but remain more or less constant either side of it. Model 5 was a unimodal model, expected for an edge specialist whose abundance peaks somewhere in the edge. These models were also fitted using 'rstan' (Stan Development Team 2018), assuming Gaussian errors. Mixture models were numerically unstable for the individual species; therefore we used distance to the primary edge (i.e. the edge where the transect originated) as the distance to edge predictor. We allowed the intercept to be dependent on transect nested within site, with random intercept terms for transect and site. In practice, this meant that the effect of a second (usually parallel) edge was incorporated into the transect level random intercept anyway. We allowed the slope, intercept, and asymptotes (if any) of the relationship to depend on irrigation. As above, convergence was assessed graphically and using the Gelman-Rubin statistic \hat{R} (Gelman et al. 2004). We performed model selection between each of the five converged models for each species via leave-one-out cross validation using the R package 'loo' (Vehtari et al. 2022). We assessed the significance of any irrigation effect in the most parsimonious model for each

species by calculating 95% credible intervals for the relevant parameter estimates from the posterior samples.

Results

We found evidence of increased invasion by exotics on edges adjacent to irrigated pasture, which is associated with higher soil nitrogen in areas closest to the fence line. Spillover of nitrogen only extended into the edge areas, resulting in a steepening of the biological gradient within the edge rather than extending the edge further into the fragment. This is consistent with the conceptual model shown in Fig. 1b and 1e.

Nitrogen spillover

Total nitrogen significantly declined with distance from fence line in edges adjacent to irrigated pasture (Fig. 3, Table 1). A

similar, but stronger, gradient of decline with distance from fence line in edges adjacent to irrigated pasture was observed for $\delta^{15}\text{N}$ (Fig. 3; both positive main effect of distance and negative distance by irrigation interaction; Table 1). Mean values of $\delta^{15}\text{N}$ at the fence line boundary of irrigated edges were 2.05 ± 0.39 , similar to that of animal manure. From 50 m to 100 m, mean values of $\delta^{15}\text{N}$ for irrigated edges were 0.28 ± 0.31 , which is similar to levels in compounds derived from background soil nitrogen. For unirrigated edges there was no significant gradient in total nitrogen (parameter estimates [$\pm 95\%$ CI] for distance to edge main effect: $-0.02 [-0.04-0.01]$) or $\delta^{15}\text{N}$ ($-0.05 [-0.16-0.05]$).

Characterising edge communities

Of the 193 plant species we recorded across the five sites, 15% of vascular species were endemics, 36% were non-vascular species (mosses and lichens, all native except two species

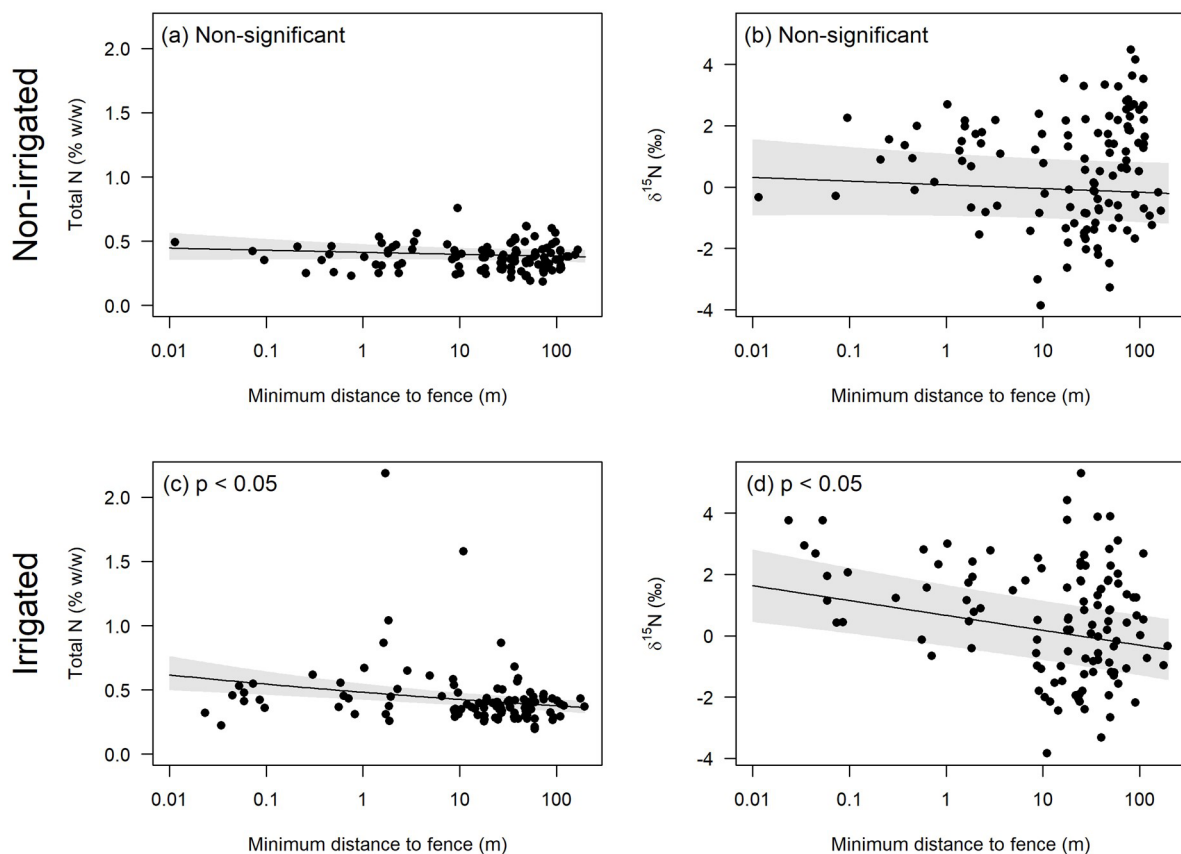


Figure 3. Total nitrogen and isotopic differences for nitrogen stable isotopes ($\delta^{15}\text{N}$) against minimum distance to an edge for non-irrigated (a, b) and irrigated (c, d) edges. Lines show the fitted relationships averaged over the other terms in the model, with 95% confidence interval shaded grey. Model r^2 : Total N = 24.1% and $\delta^{15}\text{N}$ = 70.0%.

Table 1. Parameter estimates for the models of total nitrogen and $\delta^{15}\text{N}$. Values are means [$\pm 95\%$ highest posterior density intervals]. Asterisks indicate 95% highest posterior density intervals that exclude zero.

Parameter	Total N	$\delta^{15}\text{N}$
Intercept	$-0.99 [-1.14-0.87]^*$	$0.79 [-0.19-1.80]$
log of distance to nearest edge	$-0.02 [-0.04-0.01]$	$-0.05 [-0.16-0.05]$
Irrigated edge	$0.15 [0.03-0.27]^*$	$0.59 [0.11-1.08]^*$
Log of kānuka cover.	$0.05 [0.02-0.08]^*$	$-0.31 [-0.41-0.21]^*$
Interaction between distance to edge and irrigation.	$-0.04 [-0.07-0.00]^*$	$-0.16 [-0.30-0.02]^*$

with unknown status), and 34% were exotic. Allowing for different sampling methodologies, the three sites for which we have past data have clearly shifted in composition in the last 40 years, losing much of the endemic component (Appendix S1 in Supplementary Materials). For example, 38 endemic plant species were recorded in 1970 at Bankside, but only six were recorded in 2017. At Eyrewell between the early 1970s and 2005 (comparing two comprehensive site surveys), the number of exotic species (as a percentage of the total species list) doubled, while the number of endemics halved (Table 2).

In addition to the longer-term shifts in species composition, we observed changes in composition that were attributable

to recent intensification. Increased invasion on edges with adjacent irrigation did not extend outside of existing edge margins; hence, the characteristics of the edge changed, but not any of the fragment core (Appendix S2). Exotic dominance (irrigation lag effect: 1.30 [0.13–2.44]), but not exotic grass cover (lag: 0.50 [−0.78–1.81]), was higher close to the boundary on edges with adjacent irrigation (Fig. 4). However significantly higher maximum slopes (distance by irrigation interaction; exotic dominance: 1.38 [0.37–2.36]; exotic grass cover: 0.52 [−0.59–1.66]) on irrigated boundaries meant that the inner margin to the edge was similar regardless of adjacent land use (Fig. 4).

Table 2. Comparison of number of exotic, endemic and native species recorded for sites at different time points.

Site	Year	Exotic	Endemic	Native	Reference	Notes
Bankside	1970	60 (44%)	38 (28%)	39 (28%)	Molloy (1970)	comprehensive survey
	2005	44 (66%)	9 (13%)	13 (19%)	Jenson & Shanks (unpubl. data)	one-day assessment
	2013	23 (50%)	7 (15%)	16 (34%)	Bowie et al. (2016)	transect survey
	2017	33 (61%)	6 (11%)	15 (27%)	Current study	
Culverden	2017	28 (59%)	9 (19%)	10 (21%)	Current study	
Eyrewell	1972	27 (28%)	39 (41%)	29 (30%)	Molloy & Ives (1972)	comprehensive survey
	1995	17 (37%)	16 (35%)	12 (26%)	Meurk et al. (1995)	botanical society visit
	2005	69 (60%)	26 (22%)	20 (17%)	Ecroyd & Brockerhoff (2005)	comprehensive survey
	2017	33 (53%)	10 (16%)	19 (30%)	Current study	
Medbury	1988	15 (35%)	13 (31%)	14 (33%)	Meurk (1988)	one-day assessment
	2017	29 (51%)	11 (19%)	16 (28%)	Current study	
Motu kānuka	2017	44 (48%)	14 (15%)	32 (35%)	Current study	

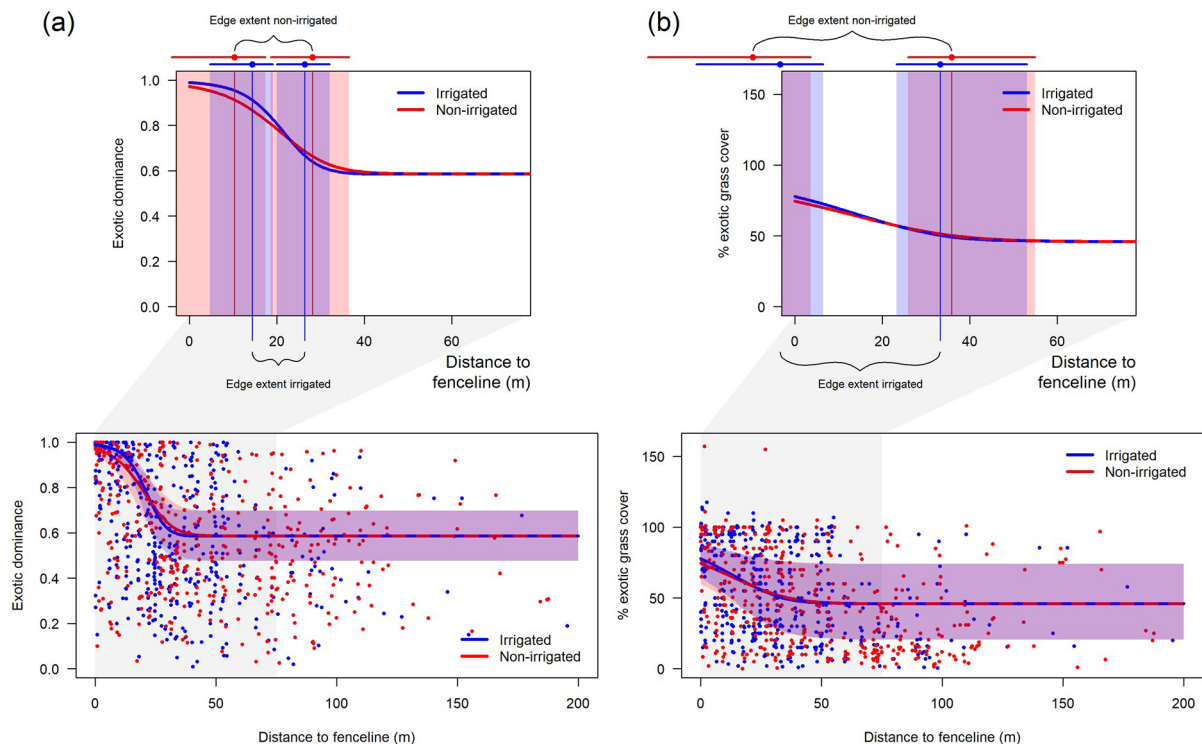


Figure 4. Exotic dominance (a) and exotic grass cover (b) declines with increasing distance from nearest fence line for irrigated and non-irrigated edges. Coloured curves (median) and shading (95% CI) show the fitted exotic dominance and grass cover relationships with the observations (lower row). The upper row focuses on the first 75 m from the fence line and shows the 95% CI for the location of the inner and outer extents of irrigated and non-irrigated edges (horizontal bars and shading). Points on the bars denote the median estimate of the location of the extent of the edge.

The impact of adjacent land use intensification on edge zone bryophyte cover was the opposite to that of exotic invasion (Appendix S2). Bryophyte cover on irrigated borders was initially lower for greater distances from the fence line than unirrigated borders (distance by irrigation interaction lag effect: -1.30 [-2.69 – -0.00]), but maximum rates of increase were higher (distance by irrigation interaction lag effect max slope effect: -1.31 [-2.47 – -0.16]), meaning that the inner boundary of the edge was similar regardless of intensification (Fig. 5).

Individual species

Individual species patterns in response to irrigation were more variable than the biotic groups analysed above. Pasture species (primarily ryegrass *Lolium perenne*) were mostly absent from the edge zone. Rather, the edge was comprised of a group of

disturbance/edge specialists grading into the dryland species of the interior shrubland. The exotic disturbance/edge specialists were generally higher in cover at the outer edge overall (*Dactylus glomerata*, *Bromus diandrus*, *Echium vulgare*), although *Festuca rubra* appeared not to be responding to the edge *per se* but was a localised invasive species in the edge zone. *Anthoxanthum odoratum* had its peak abundance within the edge. Of these edge species, only *D. glomerata* significantly benefited from adjacent irrigation. A further group of species was more common in the interior but graded into the ecotone toward the pasture boundary (*Pilosella officinarum*, *Racomitrium pruinosum*, *Rytidosperma clavatum*, *Hypnum cupressiforme*, *Leptinella pusilla*, and lichens as a group). Of these, *R. pruinosum* and *R. clavatum* were less abundant near irrigated edges. Kānuka (*Kunzea ericoides*) was also

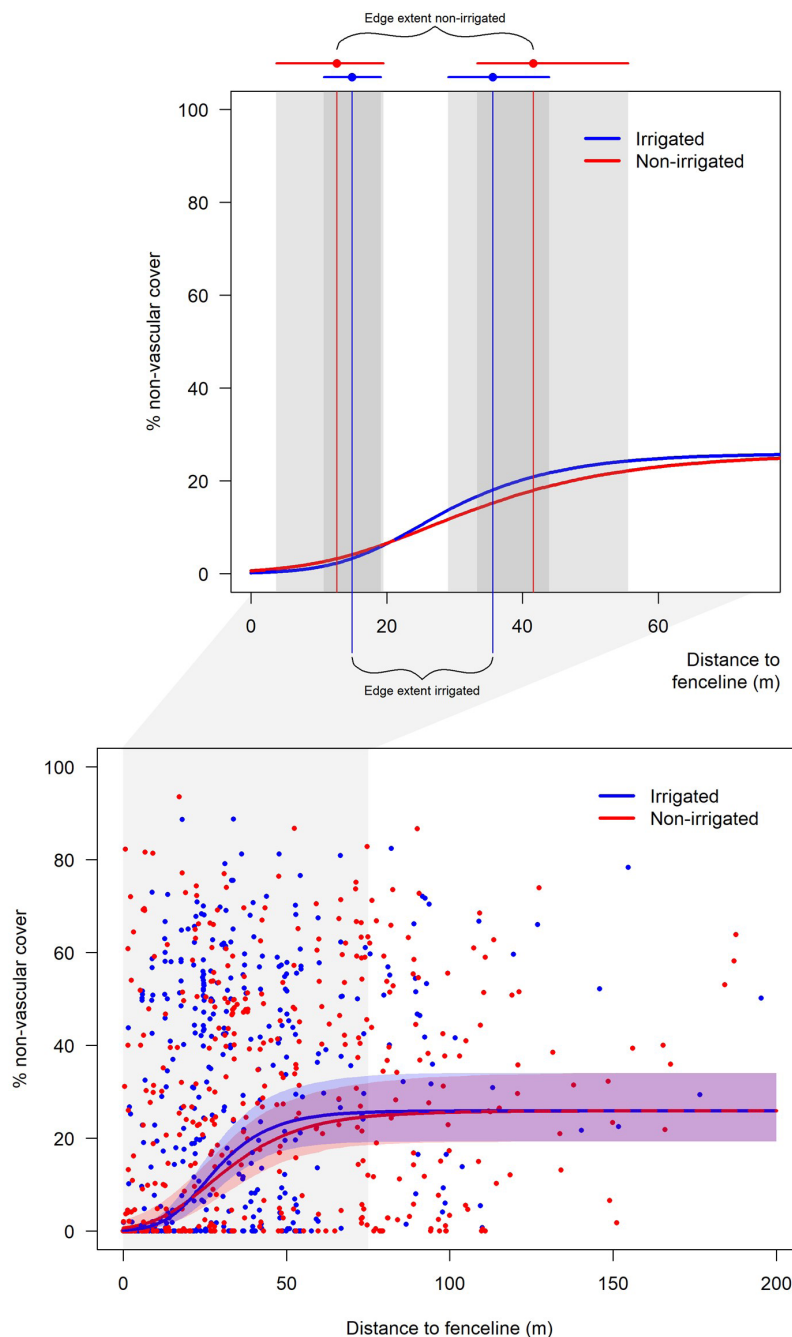


Figure 5. Non-vascular cover with distance from fence line for irrigated and non-irrigated edges. Coloured curves (median) and shading (95% CI) show the fitted non-vascular cover relationship (lower figure). The upper figure focuses on the first 75 m from the fence line and shows the 95% CI for the location of the inner and outer extents of irrigated and non-irrigated edges (horizontal bars and shading). Points on the bars denote the median estimate of the location of the extent of the edge.

significantly more common in the interior, however this likely reflects the design of the reserves because the shrubland is the focal point of the reserve. The fitted individual species models are shown in Appendix S3.

Discussion

Our results show that adjacent agricultural intensification steepened abiotic and vegetation composition gradients inside the edge of shrubland fragments, but appeared to have no additional effect on the vegetation in the core. We found increases in nitrogen and invasion by exotic species, and declines in indigenous non-vascular species within the edge zone, attributable to the additional effect of adjacent intensification compared to non-intensified edge effects on these fragments.

Nitrogen spillover

Detectable spillover of nitrogen from irrigated edges extended approximately 10 m into the fragments. At this distance, the values and spread of $\delta^{15}\text{N}$ and total nitrogen values appeared to be very similar to unirrigated edges. The $\delta^{15}\text{N}$ signature of the soil suggests that this is most likely the result of spillover from

irrigated animal manure because of the negative relationship with distance from fence line. Animal manure has higher $\delta^{15}\text{N}$ compared to soil, whereas synthetic nitrogen fertilisers, which are synthesised from atmospheric nitrogen, have lower $\delta^{15}\text{N}$ (Rogers 2008). Given that urea is commonly used in intensive farming, it is likely that the fertiliser signal contains urea, which would bring the $\delta^{15}\text{N}$ values down a little compared to a purely animal manure signal. On the North Island, New Zealand, both $\delta^{15}\text{N}$ nitrogen and soil nitrogen at fragment edges were positively correlated with farming intensity (Didham & Ewers 2012). At our sites, we think it is linked with overspray of irrigation/effluent because in these dryland environments lateral surface soil spread of manure directly deposited on the boundary by animals would be minimal.

While we do not directly measure water spillover in this study, it is likely that overspray from irrigators is also contributing to the changes we observed in irrigated edges. Aerial photos show green arcs consistent with the line of irrigators (Fig. 6), and the distribution and abundance within fragments of water demanding species such as *Holcus lanatus* appears to align with water spillover. The aerial images suggest that in some places observable irrigation spillover may extend up to 25 m, well beyond our detected nitrogen changes.

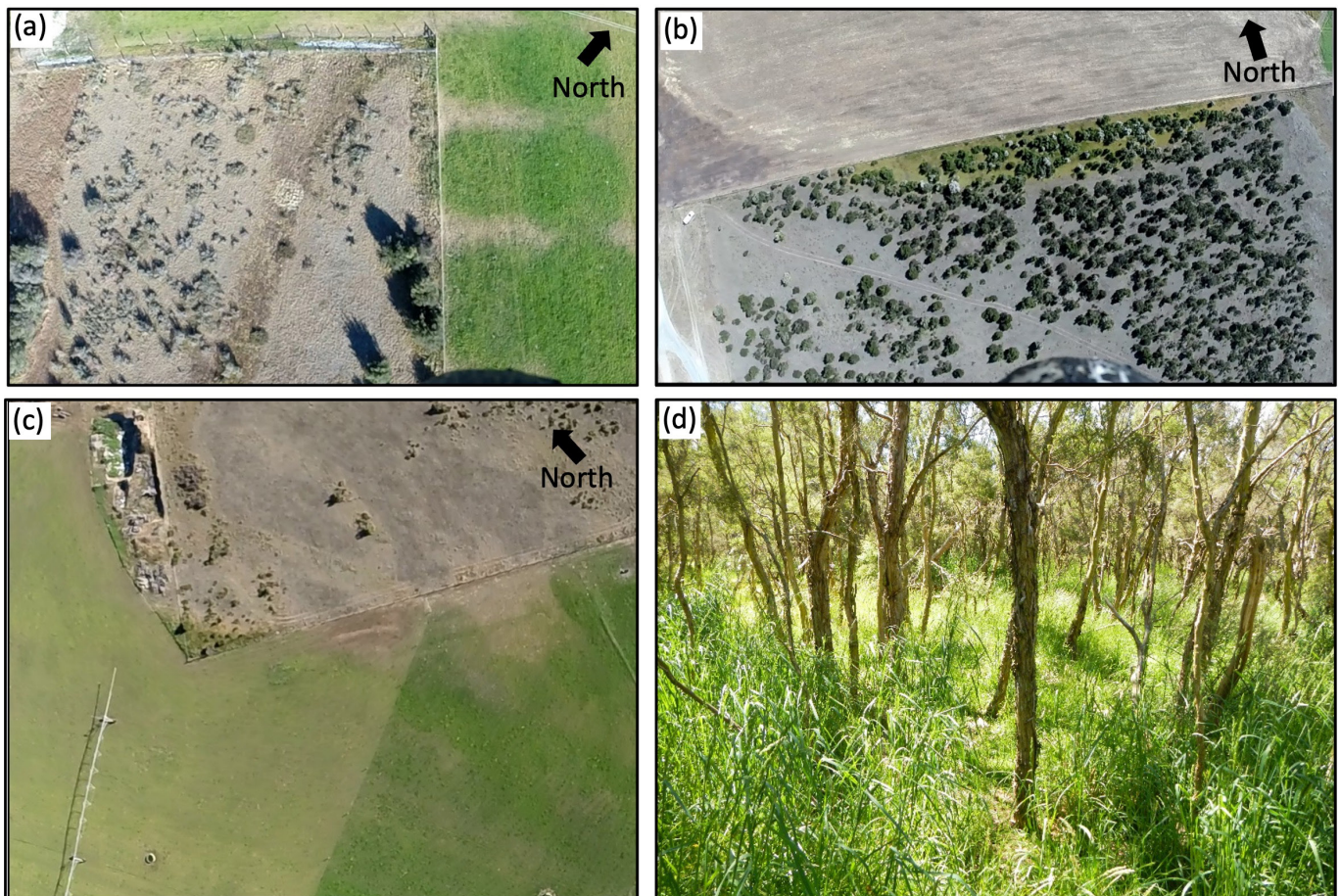


Figure 6. Images of four of the sites showing obvious effects of irrigation spillover into reserves. (a) Bankside showing overspray from k-line irrigation. (b) Arc of green extending 20 m into Medbury Scientific Reserve caused by an adjacent centre pivot irrigator. (c) A corner of overspray at Culverden Scientific Reserve. (d) Invasive Yorkshire fog (*Holcus lanatus*) established under indigenous kākūka (*Kunzea ericoides*) canopy along the main irrigated boundary at Eyrewell Scientific Reserve. Image credits (a)- (c): Nick Head; (d): Gretchen Brownstein.

Biological effects

Our analyses detected a clear edge zone that was consistent across measures of exotic dominance, exotic graminoid cover, and native non-vascular plant cover. This edge extended through to c. 40 m from the fence line using the method of Zurita et al. (2012), but through to c. 50–60 m if looking at where the fitted curves appeared to asymptote by eye. This zone comprised edge specialists grading into species that were more abundant in the core. Significantly, intensive pasture species were rare in the edge, despite ryegrass pasture often extending right up to the boundary fence. Ryegrass, the overwhelming dominant in the intensive pasture, was found in only 15 plots at two of the five sites. For plots greater than 10 m from the boundary, ryegrass cover was always less than 10% (mean of 3.25%), pointing to the inability of ryegrass to persist in this environment without the continual high inputs and maintenance found in an agricultural system (Jensen et al. 2001).

We found a steepening of the biological gradient (Fig. 1b and e) along irrigated edges that was consistent with the measured spillover of nitrogen. Only the first c.10 m of the edge were subject to nutrient spillover (and probably significant quantities of water), creating a steepening of the edaphic gradient. The biological response was an increase in exotic dominance at the outer edge, increasing exotic grass cover, and declining native bryophyte cover closer to fence line, resulting in a steepening of the edge vegetation gradient also. Significantly, in a pattern similar to that found by Boutin and Jobin (1998), we did not see an increase in the number of agricultural pasture species present. Rather we saw these nutrient subsidies change the abundance of edge specialists and reduce the abundance of native species in the edge (Øien et al. 2018; Bell et al. 2022). At similar sites, Dollery et al. (2022) found a pattern of lower bryophyte cover and higher exotic grass cover in the first 20 m from the edge, which they also link with spillover. Comparable to other low nutrient systems (Piessens et al. 2006), spillover from agricultural intensification has led to steeper edge effect gradients.

Our individual species analyses detected only one exotic species (*Dactylis glomerata*) that responded to the irrigated edges, despite exotics as a group collectively responding. Fast growing perennial exotic grasses are favoured in this environment of higher nitrogen and can outcompete low-statured or slow-growing species in what are naturally low nutrient habitats (Bakker & Berendse 1999). While *Dactylis glomerata* is drought tolerant, it also has higher growth rates than other common grassland species when growing in high soil moisture (Jensen et al. 2001).

The reasons for few detected individual species' responses to irrigation are two-fold. First, the patchiness of individual species' distributions means that there were high levels of noise in our individual species' data. It was probably no accident that the widespread and dominant species *D. glomerata* was the only species where change was detected. These spatially variable individual species' responses are smoothed out when exotic species are considered as a group. Species we might have expected to respond include the grasses *Bromus diandrus*, *Festuca rubra*, and *Anthoxanthum odoratum*, which all show increased growth responses to high soil nitrogen (Elberse & Berendse 1993). Second, not all edge and/or exotic species respond to nutrients and water (Blackshaw et al. 2004). Many of the edge species are disturbance specialists in dryland habitats, benefitting from the vehicle tracks, fires, and the prior history of disturbance found on the margins of the shrublands. Examples

include the forbs *Conium maculatum*, *Crepis capillaris*, and *Echium vulgare*.

The loss of non-vascular cover with spillover is likely a result of competition, with species able to grow faster (and hence shade out competitors; Øien et al. 2018) in response to spillover subsidies. In general, non-vascular species that grow in naturally low nutrient habitats such as these dryland shrublands are unable to respond with rapid growth to nutrient inputs (Bates 1994). For example, additional nitrogen reduced *Racomitrium* species' growth in the field, though other species (*Dicranum fuscescens*) did respond positively to nitrogen additions (van der Wal et al. 2005). Other *Racomitrium* and *Polytrichum* species do poorly under low light; 50% graminoid cover is enough to reduce light to the moss layer by roughly 50% (van der Wal et al. 2005). The loss of non-vascular species is important for these dryland systems as they are ecosystem engineers, regulating soil moisture and temperature and influencing germination and establishment of native plants (Dollery et al. 2022).

It is possible that we have not observed the full extent of vegetation change in response to spillover because edges continue to develop and change with age (Harper et al. 2005; Peyras et al. 2013; Bell et al. 2022). The shrubland fragments in our study have been adjacent to intensified agriculture for at least 10 years. However, if spillover continues in the same manner, we do not think it will drive weed expansion deeper into the fragments, as there is no mechanism to facilitate the edaphic changes that would support further expansion of the invasion front beyond the observed spillover zone. If spillover were removed, and weeds in the edges were managed, the native species might be able to re-establish in the edge zone. However, soil nitrogen levels would need to be reduced before species' diversity could be restored (Bakker & Berendse 1999).

Our data and analysis highlight the difficulty of measuring spillover effects in these highly fragmented dryland landscapes. These fragments have complex histories, having once been subject to low intensity agricultural practices. This, combined with fine scale variation due to local topography and its interaction with the dryland climate, means that the vegetation is complex and highly variable. Our models have been able to cut through this variation to give an objective and consistent assessment, regardless of metric, of the detectable extent of spillover and changes to the edge.

Implications for management

When trying to protect biodiversity in developing landscapes, often small habitat fragments are all that are available. Knowing that edge effects and spillover will be a concern, reserve boundaries should be set to encompass a buffer that is at least the distance of the edge (in our case 50–60 m) out from the boundary of the indigenous vegetation being protected. This would make the reserve less reliant on neighbouring landholders taking corrective actions to manage spillover. Further work would be required to assess how large buffers for irrigation and fertiliser spread should be to protect the edges themselves. We found evidence of nutrient spillover up to c. 10 m, but any assessment of buffers would also need to add the distance from the boundary of the source and a precautionary margin. The spillover distance from irrigation is likely more, and the observed vegetation changes on irrigated edges were more like 30–40 m.

Due to the small size of the reserves measured here, it is likely that even with buffers, active management of the edges would be required to maintain biodiversity in the fragments.

Our findings here echo those of other studies from New Zealand and around the world (Ewers & Didham 2006a; Rand et al. 2006; Bell et al. 2022), that edge effects and spillover have negative impacts on native biodiversity and need to be seriously considered when designing conservation reserves.

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Additional information and declarations

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Species lists for each site.

Appendix S2. Model parameter estimates.

Appendix S3. Observed data and fitted models of individual species cover as a function of distance to edge.

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