

How does woody succession affect population densities of passerine birds in New Zealand drylands?

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Abstract: The density of shrubs is increasing in many dry grassland ecosystems worldwide. In the dry interior of the South Island, New Zealand, secondary succession generates novel woody communities, as shrubs colonise anthropogenic grasslands where fire frequency has decreased. The avifauna of this dry region is also novel, with many indigenous birds extinct, extirpated or uncommon, and exotic species predominant. We studied how succession from grassland to shrubland habitats affects the abundance of dryland birds, by estimating population densities of nine common exotic and indigenous passerine bird species in dryland habitats in grassland, mixed grassland–shrubland and shrubland, at three sites in Central Otago, South Island. We used distance sampling along line transects to estimate densities. Generally, succession from grassland to forest leads to decreased numbers of granivorous birds and feeding generalists, and increased numbers of insectivores. We therefore predicted that density of birds in five guilds would change as follows during succession to woodier habitats: (1) granivores: decrease, (2) a primarily ground-nesting, ground-feeding granivore–insectivore: decrease; (3) a tree- and shrub-nesting granivore–insectivore: increase; (4) ground-feeding insectivores: increase; (5) indigenous insectivores: increase. Our predictions were supported for only one guild. Yellowhammer (*Emberiza citronella*) (exotic primarily ground-nesting, ground-feeding granivore–insectivore that prefers open country) declined in density as woody-species frequency increased. Exotic European goldfinch (*Carduelis carduelis*) and common redpoll (*C. flammea*) (granivores) were most abundant at intermediate woodiness. Densities of other guilds did not vary consistently with woodiness. We conclude that continued succession to shrubland in Central Otago will have little effect on densities of many common exotic passerine birds, but may lead to local declines in yellowhammer, and ultimately goldfinch and redpoll. Our density estimates for silveryeye (*Zosterops lateralis*) and grey warbler (*Gerygone igata*) were lower than densities reported in forests; therefore later stages of succession may benefit these widespread indigenous insectivores.

Keywords: *Carduelis chloris*; *Fringilla coelebs*; habitat restoration; *Prunella modularis*; shrub encroachment; shrubland; *Turdus merula*

Introduction

The total population density of birds and the diversity of bird species are expected to increase during succession from grassland to woodland (Wiens 1989; Schwab & Sinclair 1994) because taller, more structurally complex woody vegetation provides more plentiful and varied food and shelter (MacArthur & MacArthur 1961; Mills et al. 1991). These patterns are not necessarily monotonic, and in some successional sequences, bird densities are higher in shrubby, intermediate-aged stands than in either grassland or mature forest (reviewed by Wiens 1989). Secondary succession from grassland to shrubland is occurring in many dry ecosystems worldwide owing to altered land use, herbivory, fire management and climate (Brown et al. 1997; Peñuelas & Boada 2003). Recent studies in these dry successional systems have demonstrated population declines in bird species of open habitats, including obligate ground-feeders or ground-nesters and granivores reliant on grass seeds, but population increases in many other species (Suárez-Seoane et al. 2002; Sirami et al. 2009; Kutt & Martin 2010).

In the dry interior of the South Island, New Zealand, secondary succession generates novel woody communities as indigenous and exotic shrubs colonise anthropogenic grasslands where fire is controlled (Walker et al. 2009, 2014a). Forests and shrublands once dominated this ‘dryland’ zone

(sensu Rogers et al. 2005), but were transformed into grasslands by fires following human colonisation in c. AD 1280 (McGlone 2001; McWethy et al. 2010). The avifauna of this region is also novel, with many indigenous species lost owing to habitat destruction, hunting, and predation by invasive introduced mammals (Worthy & Holdaway 2002; Wood 2007). Exotic European bird species and self-introduced Australasian birds are now dominant (Robertson et al. 2007). Ground-dwelling birds are under-represented in the present avifauna, compared with the prehuman assemblage (Wood 2007), and most of the common species are tree- and shrub-nesting passerines (Walker et al. 2014b). Most extant indigenous passerines are ‘forest’ birds, whose populations are thought to be limited primarily by habitat availability in this deforested region (Innes et al. 2010).

The population density of a bird species in a particular habitat may be determined by food supply, nest-sites, competition, and predation, superimposed on the species’ intrinsic demography and behaviour (Newton 1998). Species–habitat relationships arising from these interacting effects are difficult to predict and may vary geographically (Wiens 1989; Fuller 2002). However, predictable changes in the density of some feeding guilds of birds along successional forest sequences have been recognised (Wiens 1989; Helle & Mönkkönen 1990). In particular, granivores and feeding generalists often dominate early-successional habitats characterised by grasses, shrubs and

saplings, whereas specialised insectivores tend to increase in density during succession to taller, woodier vegetation (May 1982; Helle & Mönkkönen 1990). Bird population densities have been quantified in only a few New Zealand dryland environments (Gill 1980; MacLeod et al. 2005, 2009).

The common passerine birds that we identified in New Zealand drylands (Walker et al. 2014b) form five guilds defined by diet and ground-feeding or ground-nesting behaviours (based broadly on May (1982) and Helle & Mönkkönen (1990)). The first four guilds comprise European species that are often associated with modified habitats resembling those in their native ranges (MacLeod et al. 2009). (1) Granivores (European goldfinch *Carduelis carduelis*, 'goldfinch'; European greenfinch *C. chloris*, 'greenfinch'; common redpoll *C. flammea*, 'redpoll') exploit a range of habitats including farmland, scrub, and forest margins (Heather & Robertson 2000), travelling extensively between habitats to forage (Newton 1967). These cardueline finches are primarily granivorous but also feed on invertebrates in the breeding season (Newton 1967). (2) A primarily ground-nesting, ground-feeding granivore–insectivore, yellowhammer (*Emberiza citrinella*) is the most obligately open-country species of the birds we studied. It usually nests on the ground or in hedgerows (Stoate et al. 1998; MacLeod et al. 2005) and is seen most often in open farmland, orchards, and indigenous tussock grasslands (Heather & Robertson 2000; MacLeod et al. 2005). (3) A tree- and shrub-nesting granivore–insectivore (common chaffinch *Fringilla coelebs*, 'chaffinch') uses farmland, orchards and forests (Heather & Robertson 2000). In the breeding season, it is usually associated with trees and is primarily insectivorous (Newton 1967; Heather & Robertson 2000). (4) Ground-feeding insectivores (Eurasian blackbird *Turdus merula*, 'blackbird'; dunnock *Prunella modularis*) are widespread in habitats with a mixture of dense cover and open spaces, including gardens, scrub, and forest (Greenwood & Harvey 1978; Fuller 2002; Heather & Robertson 2000). (5) Indigenous insectivores (grey warbler *Gerygone igata* and silvereye *Zosterops lateralis*, also a frugivore–nectarivore) are widely distributed species able to utilise habitats dominated by exotic vegetation, during at least part of the year (Gill 1982; Robertson et al. 2007; van Heezik et al. 2008). The endemic grey warbler is the most specialised of the birds we studied, feeding primarily by gleaning invertebrates from foliage (Gill 1980). The self-introduced silvereye, in contrast, can use a wide variety of food sources and habitats and is also found in Australia and the Pacific Islands (Moed 1979; Heather & Robertson 2000).

In a study of effects of secondary woody succession on dryland bird fauna, we found (from observed numbers by species) that assemblages of native birds but not of exotic birds varied as a function of vegetation woodiness, with more indigenous bird species present in shrubland than in grassland at large scales (Walker et al. 2014b). We did not estimate bird population densities in that study because we had too few observations to do so for most of the 22 species recorded. Here, using data from that study, we estimate the population density of the nine most abundant exotic and indigenous passerine species, and test for variation in densities as a function of woody succession. We predicted that as vegetation woodiness increased, the population densities of five passerine guilds would change as follows: (1) granivores: decrease, (2) primarily ground-nesting, ground-feeding granivore–insectivore: decrease; (3) tree- and shrub-nesting granivore–insectivore: increase; (4) ground-feeding insectivores: increase; and (5) indigenous insectivores: increase.

Methods

Study sites

We sampled three sites (Bendigo, Blackstone Hill and Cambrian) in Central Otago in the southern South Island dryland zone (maps and detailed site descriptions are in Walker et al. (2014a)). All sites were on sloping faces of north-east- to south-west-trending mountain ranges. We chose sites where we could identify three blocks of at least 1 km² along a gradient of vegetation woodiness but with similar slope, aspect, and elevation. At each site we established a 'grassland' block in predominantly non-woody vegetation, an 'intermediate' block with a mosaic of shrubs and grasses, and a 'shrubland' block dominated by woody vegetation (shrubs and small trees). Blocks at Bendigo and Blackstone Hill were square (1 × 1 km) and oriented parallel to the major slope (due north at Bendigo, north-west at Blackstone Hill). At Cambrian, blocks were polygons narrower than long, but >500 m wide at their narrowest point. Here, each block spanned a creek, and block orientation varied from east to south-east.

Shrubland blocks were dominated by indigenous *Kunzea ericoides* (kānuka) shrubs at Bendigo, indigenous *Discaria toumatou* (matagouri) and exotic *Rosa rubiginosa* (sweet briar) shrubs at Blackstone Hill, and by indigenous matagouri and *Coprosma propinqua* shrubs and several lianes at Cambrian (Walker et al. 2014a). Grassland blocks were dominated by exotic annual and perennial herbs and grasses at Bendigo, by perennial exotic grasses, the forbs *Trifolium* spp. and indigenous tussock grasses of *Festuca novae-zelandiae*, *Poa cita* (silver tussock) and *P. colensoi* at Blackstone Hill, and by snow tussock grass (*Chionochloa rigida*) at Cambrian. Vegetation in intermediate blocks was patchy, and broadly intermediate to the grassland and shrubland blocks in plant species composition.

Bird surveys

We estimated the population density of birds by distance sampling along line transects (Buckland et al. 2001). This method was chosen instead of simple counts of birds in order to avoid bias resulting from expected variation in detectability of birds in different vegetation types and heights, in addition to other sources of heterogeneity (MacLeod et al. 2012c; Weller 2012). In each sampling block we established 3–6 transects 260–667 m long and 200–300 m apart, totalling 2000 m per block. Owing to unsuitable weather conditions, only two of three transects were sampled in each of the Bendigo intermediate and woody blocks (1334 m per block), and only four of six were sampled in the Cambrian woody block (1329 m).

Birds were surveyed three times on each transect, on different days and by different observers, during 11–13 March 2007 (Bendigo), 7–9 December 2007 (Blackstone) and 8–11 February 2008 (Cambrian), between 0800 and 1200 hours. Observers were trained by listening to recorded bird song and practising identification together in the field. Each observer walked slowly along a transect looking and listening for birds. The horizontal distance to each bird (or group of birds) detected was measured with a laser rangefinder (Leica Rangemaster 900); distances < 10 m were too close to use a rangefinder and were estimated. Binoculars (Swarovski SLC 8×30 NEU) were used to aid identification as needed. The compass bearing to the bird, number of individuals (group size), and whether heard or seen were also recorded. Distances were

not recorded if the location of a bird that was only heard was uncertain (this rule was not established at Bendigo, our first study site), but for flying birds the distance to a nearby object was recorded. Observers could leave the transect to confirm a species identification after recording other information. Surveys were not done in rain, strong winds or poor visibility.

Distance analysis

We were able to estimate the population densities of nine bird species, each with 49–325 observations at the three sites combined; Buckland et al. (2001) suggest a minimum of 60–80 observations. Mean densities were calculated for each woodiness level (sites combined) and also for each woodiness level at each site, using stratification and post-stratification facilities in program Distance version 6.1 (Thomas et al. 2010).

Fitting detection functions and model selection

We fitted detection functions based on half-normal and hazard-rate key functions (which define a basic curve shape), with 0 and 1 adjustment terms based on a cosine series (which make the shape more flexible; Buckland et al. 2001). Detection functions were accepted or rejected on the basis of fit and shape, according to goodness-of-fit tests and visual examination, after right-truncation (deleting observations at distances beyond which estimated detection probability was below approximately 0.15) and grouping observations into distance classes if necessary to improve fit (Buckland et al. 2001).

For each species, the model with the lowest AIC_c score (Burnham & Anderson 2002) was chosen from the set of acceptable models, after discarding models with cosine adjustments if the detection curve was clearly over-fitted to variation in the data, or if the unadjusted model had similar AIC_c but much lower model variance. Covariates were then added sequentially to these top models (Buckland et al. 2004) and retained if they lowered AIC_c . Covariates were (1) woodiness level, (2) site, (3) observer, (4) whether the bird was seen or only heard, (5) time of day (minutes past sunrise at the start of each observation period), and (6) mean vegetation height on each transect. Covariate models were discarded if fewer than 10 data points per estimated parameter meant that results might be unreliable, or if estimated detection probability of the species was small for many observed covariate values, leading to biased density estimates (Buckland et al. 2004).

Density estimates were calculated on the basis of the resulting best model (lowest AIC_c). In order to account for increased detectability of larger groups of birds, density calculations used either (1) expected flock size based on regression of observed flock size (\log_e -transformed) on distance from the transect, if this was statistically significant ($P \leq 0.15$), or (2) mean flock size when $P > 0.15$ (Buckland et al. 2001). For comparison with best-model estimates, we also calculated density by averaging models (in Microsoft Excel) after excluding those with $\Delta AIC_c \geq 4$ compared with the best model ($\Delta AIC_c = 0$). We also omitted any model obtained when a variable was added to a simpler model without improving its fit ('pretending variable'; Anderson 2008); in each case the two models had equal likelihoods and the simpler model had lower AIC by two units. Relationships between density estimates from the top models and those from model averaging were examined with linear models in program R (R Development Core Team 2013).

Vegetation measurements

Vegetation was sampled at 8-m intervals along each transect (Walker et al. 2014a). We used a modified Scott height-frequency method (Scott 1965) to record the presence of plant species in $10 \times 10 \times 10$ cm vertically contiguous cubes to the maximum height of the vegetation at each 10×10 cm sampling 'point'. Woody-species frequency, a measure of relative abundance, was calculated as the summed presence of woody plants on each transect, expressed as a percentage of the number of sampled points. Relative frequency can exceed 100% where woody species are present, on average, in more than one vertically contiguous sampling cube per point.

Testing for effects of woodiness and site on bird density

We tested for relationships between bird density and woodiness, at guild and species levels, by fitting quadratic models (to test for a humped pattern with peak density at intermediate woodiness) and linear models (to test for a monotonic increase or decrease in density). We used separate multivariate models (Wang et al. 2012) for each of granivores, ground-feeding insectivores, and indigenous insectivores, and separate univariate models for the ground-nesting granivore–insectivore (yellowhammer) and the tree- and shrub-nesting granivore–insectivore (chaffinch). Response variables were species-specific bird densities in each woodiness level at each site ($N = 9$ density estimates per species) and the predictor variable in all analyses was mean woody-species frequency on transects where birds were surveyed. We also tested for site differences with a categorical site predictor variable (three levels), fitted as a fixed effect because a minimum of six levels is recommended for estimating random effects (Bates 2010). Models had Gaussian error variances and densities were square-root-transformed (as suggested for data with an underlying Poisson process; Crawley 2002), to normalise and homogenise residuals. We used functions `manyglm` (package `mvabund` version 3.7.7; Wang et al. 2012), `lm` and `poly` in program R (R Development Core Team 2013).

Statistical significance ($P < 0.05$) of terms in each model was tested by comparing the model with a simpler model without that term (sequential analysis of variance). If the quadratic coefficient was not significant ($P > 0.1$) it was dropped and the linear term was then tested. Multivariate tests accounted for any correlation between species in the calculation of F statistics and P -values (the latter calculated by resampling from the data) (Wang et al. 2012). If a multivariate test was significant, we then examined corresponding univariate statistics, adjusted for multiple testing, for each species within the guild.

Results

Fitted detection functions

Line-transect detection functions in the best models were based on the half-normal key function, except in the case of blackbird, for which the hazard-rate key function was chosen (Appendices 1 and 2). Cosine adjustments tended to over-fit detection curves to the data, and were used for only two species (Appendix 2). One or two covariates – site (5 species), woodiness level (3 species), whether the bird was seen (2 species), or observer (2 species) – were included in top models for all species (Appendix 2). For blackbird, chaffinch, redpoll, silvereeye, and yellowhammer, detectability was higher

at Bendigo than at Blackstone Hill or Cambrian. The effect of woodiness level on detectability varied with species. For chaffinch, detectability was lowest in shrubland habitats and similar in grassland and intermediate habitats; for goldfinch, detectability was highest in grassland habitats and similar in intermediate and shrubland habitats; and for greenfinch, detectability was lowest in grassland habitats and similar in intermediate and shrubland habitats. Dunnock and grey warbler were more detectable when heard than when seen.

Bird density in relation to woody succession and site

Bird population density was strongly related to woody-species frequency only for granivores and the ground-nesting granivore–insectivore (Table 1). In the multivariate granivore model, both the quadratic ($P=0.028$) and site ($P=0.022$) terms were statistically significant (Table 1; $R^2 = 0.84$). Univariate models showed that the quadratic effect was due to humped patterns in goldfinch ($P = 0.037$) and redpoll ($P = 0.053$) densities, which were greatest at intermediate vegetation woodiness (Table 1; Fig. 1). Site differences were apparent only for goldfinch, with density highest at Bendigo and lowest at Blackstone Hill, after accounting for the effect of woodiness (Fig. 1). Density of the ground-nesting granivore–insectivore, yellowhammer, declined with increasing vegetation woodiness, and was highest at Blackstone Hill and lowest at Bendigo after accounting for woodiness (Fig. 1; $R^2 = 0.96$). Both the linear ($P = 0.001$) and site terms ($P=0.005$) were statistically significant for yellowhammer, and the quadratic term was not retained (Table 1). For other guilds, site effects were not significant (Table 1).

Woody-species frequency was strongly correlated with mean vegetation height on transects ($r_{29} = 0.96$), and therefore

appeared to be a useful indicator of successional changes thought to be important for birds. The gradient in vegetation woodiness between blocks (woodiness levels) was strongest at Bendigo and weakest at Blackstone Hill (Table 2). At Cambrian, the grassland block had a substantial, though short-statured, subshrub cover among tall *Chionochloa rigida* tussocks, and hence mean woody-species frequency was slightly higher than in the intermediate block along the transects we measured for birds (Table 2). However, when woodiness was considered across all transects and plots measured within the blocks (Walker et al. 2014a), the Cambrian intermediate block was slightly more woody overall (weighted mean woody species frequency 178%) than the Cambrian grassland block (161%).

Bird density estimates and precision

Estimated bird population densities in each woodiness level for all sites combined ranged from 2.7 per hectare (redpolls in grassland habitat) to 0.1 per hectare (blackbirds in grassland and shrubland habitat) (Table 3). Because the woody-species frequencies on each block differed between sites (Fig. 1) some patterns described above, e.g. greater redpoll densities at intermediate woody-species frequency, are not apparent in these woodiness-level estimates. Precision, calculated as coefficient of variation ($CV = SE \div Estimate$), was reasonably good (15–30%) for 52% of estimates, but poor (>40%) for 37% of estimates. Density estimates calculated for each site–habitat combination (Fig. 1) were more variable and less precise than the combined-sites estimates (Table 3). There were several high, relatively imprecise estimates for goldfinch, greenfinch, and redpoll in the grassland and intermediate blocks at Bendigo (Fig. 1), probably because many small flocks were recorded at this site. Density estimates and percentage CVs from the

Table 1. Results of tests of statistical significance of quadratic and linear terms in models relating bird $\sqrt{density}$ to woody-species frequency at three sites in Central Otago. For each species, $N = 9$ estimates (3 per site). Multivariate (MV) tests for multi-species guilds, and adjusted univariate (UV) tests for individual species done after significant MV tests, used F statistics with P calculated by resampling from the data (Wang et al. 2012); therefore sample sizes are relevant but degrees of freedom (d.f.) are not shown. Univariate (UV) tests for single-species guilds were traditional F -tests. In each case, results of sequential analysis of variance are shown, comparing fits of models with and without individual terms. The linear term was not tested if the quadratic term was retained. R^2 for each resulting quadratic or linear model is also shown. Bold and italic text shows statistical significance at the 0.05 and 0.1 level, respectively.

Guild	Species ¹	Number of species	MV or UV	Term	F	d.f.	P	R^2
Granivores	Goldfinch, greenfinch, redpoll	3	MV	Quadratic	30.4		0.028	0.84
				Site	28.3	0.022		
	Goldfinch	Adjusted UV	Quadratic	19.3	0.037			
			Site	26.4	0.026			
	Greenfinch	Adjusted UV	Quadratic	0.43	0.55			
			Site	1.67	0.49			
Redpoll	Adjusted UV	Quadratic	10.7	<i>0.053</i>				
		Site	0.25	0.79				
Ground-nesting granivore–insectivore	Yellowhammer	1	UV	Quadratic	0.11	1,4	0.75	
				Linear	55.9	1,5	0.001	0.96
				Site	17.9	2,5	0.005	
Tree- and shrub-nesting granivore–insectivore	Chaffinch	1	UV	Quadratic	0.31	1,4	0.61	
				Linear	0.27	1,5	0.62	0.49
				Site	2.41	2,5	0.18	
Ground-feeding insectivores	Blackbird, dunnock	2	MV	Quadratic	2.29		0.44	
				Linear	1.51		0.53	0.47
				Site	4.01		0.20	
Indigenous insectivores	Grey warbler, silvereye	2	MV	Quadratic	0.13		0.92	
				Linear	4.11		0.24	0.64
				Site	7.85		0.12	

¹See Table 3 for scientific names and full common names.

best models were very similar to model-averaged estimates (Table 3); the linear models relating them had $R^2 > 0.99$, slope approximately 1, and intercept approximately 0.

Discussion

Bird population densities in relation to woody-species frequency

Only one of our predicted relationships between the density of bird guilds and vegetation woodiness was supported.

Density of the primarily ground-nesting, ground-feeding granivore–insectivore, yellowhammer, declined as a function of woodiness. Density of granivores peaked at intermediate vegetation woodiness, a result that we had not predicted. Within the granivore guild, this humped pattern was apparent in goldfinch and redpoll, but not in greenfinch. Contrary to our predictions, densities of a tree- and shrub-nesting granivore–insectivore (chaffinch), ground-feeding insectivores (blackbird and dunnock) and indigenous insectivores (grey warbler and silvereye) did not increase significantly in relation to woody succession.

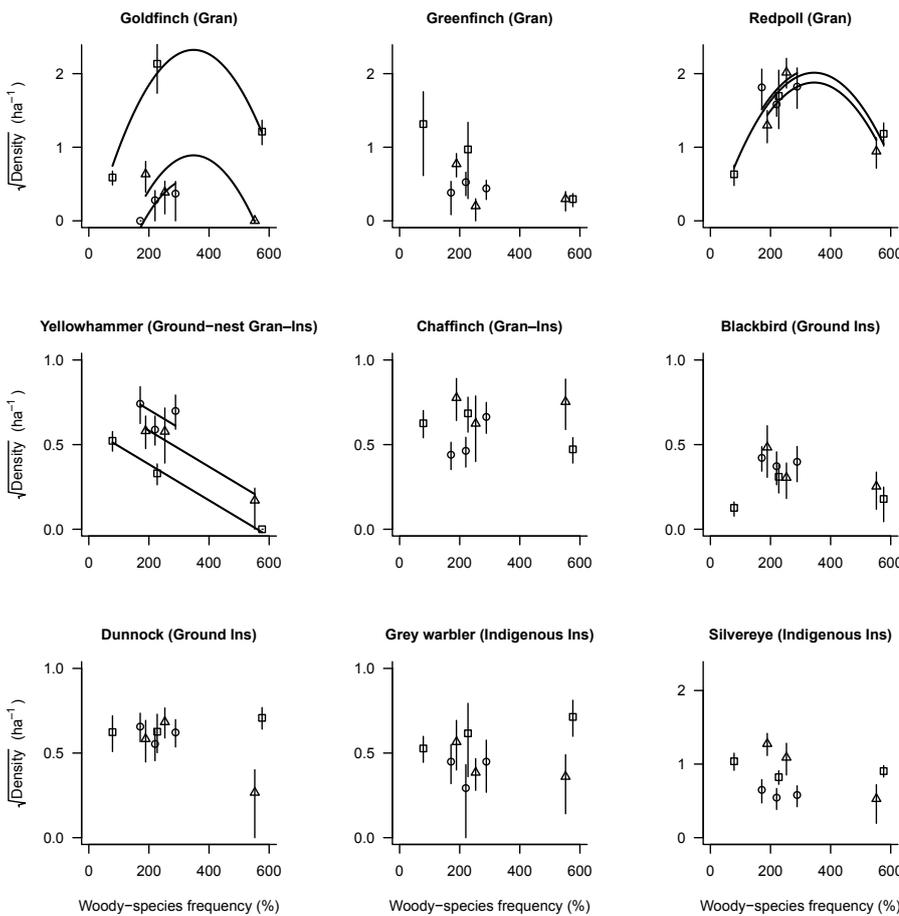


Figure 1. Square-root of density of nine bird species, in relation to mean woody-species frequency measured on transects, at each of three study sites (□ Bendigo, ○ Blackstone Hill, △ Cambrian) in Central Otago in summer. For goldfinch and redpoll, the fitted quadratic models are shown, and for yellowhammer the fitted linear model, with separate curves or lines for each site. Species guilds are Gran: granivore, Ground-nest Gran-Ins: ground-nesting granivore–insectivore, Gran-Ins: granivore–insectivore, Ground Ins: ground-feeding insectivore, Indigenous Ins: indigenous insectivore. Error bars show standard errors. Note variable vertical-axis scales. See Table 3 for scientific and full common names.

Table 2. Woody-species frequency and vegetation height on transects where birds were surveyed in grassland, intermediate, and shrubland blocks at three study sites in Central Otago. CV (coefficient of variation) = Standard deviation÷Mean; means and standard deviations are weighted by transect lengths. N is number of transects.

Site	Woodiness level	Woody-species frequency (%)			Vegetation height (m)			N
		Range	Mean	CV(%)	Range	Mean	CV(%)	
Bendigo	Grassland	27–120	79	61	0.16–0.19	0.17	7	3
	Intermediate	173–278	226	33	0.35–0.50	0.42	25	2
	Shrubland	309–844	576	66	0.80–1.73	1.26	52	2
Blackstone Hill	Grassland	81–243	171	48	0.19–0.36	0.30	32	3
	Intermediate	133–295	222	37	0.24–0.49	0.37	33	3
	Shrubland	184–459	289	52	0.38–0.75	0.52	39	3
Cambrian	Grassland	156–441	253	43	0.43–0.77	0.51	27	5
	Intermediate	22–412	189	86	0.22–0.63	0.39	44	4
	Shrubland	402–824	552	34	0.55–1.39	0.89	40	4

Table 3. Density estimates from best models and model-averaged estimates, for each woodiness level with all sites combined. CV (coefficient of variation) = $SE \div \text{Estimate}$.

Species	Woodiness level	Estimates from best models		Model-averaged estimates	
		Density (ha^{-1})	CV (%)	Density (ha^{-1})	CV (%)
Eurasian blackbird (<i>Turdus merula</i>)	Grassland	0.10	33	0.10	33
	Intermediate	0.14	32	0.14	32
	Shrubland	0.09	41	0.09	41
Common chaffinch (<i>Fringilla coelebs</i>)	Grassland	0.32	28	0.31	28
	Intermediate	0.43	23	0.44	23
	Shrubland	0.41	20	0.42	20
Dunnock (<i>Prunella modularis</i>)	Grassland	0.44	16	0.43	15
	Intermediate	0.34	23	0.35	23
	Shrubland	0.33	26	0.33	26
European goldfinch (<i>Carduelis carduelis</i>)	Grassland	0.16	50	0.16	51
	Intermediate	1.39	55	1.40	55
	Shrubland	0.48	50	0.48	50
European greenfinch (<i>Carduelis chloris</i>)	Grassland	0.46	67	0.51	68
	Intermediate	0.59	47	0.58	46
	Shrubland	0.13	42	0.14	41
Grey warbler (<i>Gerygone igata</i>)	Grassland	0.22	28	0.21	28
	Intermediate	0.25	40	0.25	40
	Shrubland	0.27	44	0.28	44
Common redpoll (<i>Carduelis flammea</i>)	Grassland	2.65	21	2.64	21
	Intermediate	2.16	20	2.15	19
	Shrubland	1.99	22	2.03	24
Silvereye (<i>Zosterops lateralis</i>)	Grassland	0.88	26	0.84	26
	Intermediate	0.82	27	0.85	27
	Shrubland	0.45	41	0.46	41
Yellowhammer (<i>Emberiza citrinella</i>)	Grassland	0.39	19	0.39	20
	Intermediate	0.29	22	0.28	22
	Shrubland	0.21	48	0.21	51

Exotic guilds

The dominance of yellowhammer in open habitats was consistent with successional studies in Europe (Fuller 1982; Winkler 2005). There, yellowhammer did not colonise open grassland until some shrubs had established (Fuller 1982); in our study also, shrubs were present in all of the grassland blocks. Yellowhammer forages in open habitats but requires cover for nesting, such as herbaceous or woody vegetation at the margins of cultivated fields (Stoate et al. 1998; MacLeod et al. 2005).

In highly modified environments in their native ranges, the granivores appear to select habitats primarily according to food availability (Newton 1967). Perhaps as a consequence, successional patterns of goldfinch and greenfinch abundance in Europe vary between studies. In predominantly agricultural landscapes, both species were most numerous on cultivated land (Southwood et al. 1986; Suárez-Seoane et al. 2002), but in managed forests they were more abundant in shrubland and young forest than in recent clearings (Winkler 2005). Redpoll also feeds on cultivated land in Europe, but is most often associated with shrubland, woodland or plantation forest (Newton 1967; Southwood et al. 1986). In a previous study in their introduced New Zealand range, goldfinch and redpoll preferred early-successional, open dry forest to taller dry forest (Gill 1980). Our results suggest that the patchy mixed grassland–shrubland habitats of Central Otago may furnish combined resources of seeds, insects and also shelter, which meet the breeding requirements of these mobile, opportunistic species.

In their natural European ranges, chaffinch, blackbird, and dunnock are associated with intermediate and later successional stages described as moderately dense shrubland to woodland and forest (Fuller 1982; Southwood et al. 1986; Suárez-Seoane et al. 2002; Winkler 2005). It is therefore possible that the lack of tall forest in our dryland successional sequences was the reason that we did not detect effects of woodiness on densities of the granivore–insectivore and ground-feeding insectivore guilds. However, studies in their introduced New Zealand range found that chaffinch densities in shrubland and forest were similar (MacLeod et al. 2012d) and that all three species preferred forest habitats that were relatively open, disturbed or near edges, compared with dense native forest (Gill 1980; Wilson et al. 1988). Other New Zealand density estimates for chaffinch in shrubland and forest (MacLeod et al. 2012a, d) and for blackbird in forest (MacLeod et al. 2012a) are similar to our estimates. These comparisons suggest that chaffinch and blackbird densities in New Zealand forest may not generally exceed those in shrubland. However, because we lack comparative New Zealand density estimates for dunnock, and for chaffinch and blackbird in dry forest, we cannot draw conclusions about the likely effects of continued succession to tall forest on the densities of these exotic species in drylands.

The European exotic birds we studied, except for blackbird, are much more abundant in New Zealand farmland than in comparable habitats in their native range, which may be due to unknown differences in food resources, predation, disease, or exposure to extreme weather events (MacLeod et al. 2005, 2009). For most of these species, our density estimates in

dryland habitats were generally similar to other New Zealand measurements (MacLeod et al. 2005, 2009, 2012a, c, d; Weller 2012). For goldfinch and greenfinch, however, most of our estimates were lower than published values (0.9–3 per hectare; MacLeod et al. 2009, 2011). The latter studies took place in dry cropland on the Canterbury Plains, and sheep and beef farms elsewhere in the South Island. Compared with our dry non-cropland sites, these agricultural environments may supply more plentiful seed resources as food for granivores.

Indigenous insectivores

Grey warbler and silvereye are habitat-generalist forest species (Innes et al. 2010) that are not classified as threatened (Miskelly et al. 2008). In the deforested dryland regions, populations of indigenous forest birds are thought to be limited first by habitat availability and second by predation by introduced mammals (Innes et al. 2010). For grey warbler, our dryland density estimates were lower than in dry forest (2.4–4.3 per hectare; Gill 1980) and other shrubland and forest locations (1–2 per hectare; MacLeod et al. 2012a, d), but higher than in non-woody alpine habitats and low-productivity grasslands (<0.1 per hectare; MacLeod et al. 2012d). For silvereye, in contrast, our density estimates were similar to densities in other New Zealand shrubland locations and intact dry Australian woodland, and were intermediate between estimates from forests and open habitats (New Zealand: 1.5–2.5 per hectare in forest, 0.5 in shrubland, <0.1 in non-woody habitats; Australia: 0.4–0.9 per hectare in relatively intact dry woodland, and 0.03 in open, degraded woodland; Ford & Bell 1981; MacLeod et al. 2012a, d). Collectively, these comparisons imply that both of these indigenous insectivores are most abundant in forest and least abundant in open, non-woody environments. Although grey warbler and silvereye can persist in shrubland, these dry shrublands may be suboptimal for the leaf-gleaning grey warbler, which is the most specialised feeder in our study. As we concluded for chaffinch, blackbird, and dunnoek, the absence of tall forest may explain why grey warbler and silvereye density did not increase along the successional gradient we studied.

Potential sources of bias and recommendations for density estimation

It is difficult to design studies that yield unbiased estimates for multiple bird species, because the strategy and effort that observers use to detect each species depend on its conspicuousness and behaviour (Buckland et al. 2001). However, as our main objective was to compare densities between different habitats, some bias was acceptable if these comparisons remained valid. Although sampling dates, observers, and one method differed between our study sites, we concluded that these differences did not introduce large biases, since for most species site effects were not important in models relating bird densities to woodiness. The method that differed between sites was either estimating distance to a bird whose location was uncertain, or not recording a distance at all. This decision traded off accuracy and sample size because sightings without distance measurements cannot be used in density estimation. A solution in hindsight would have been to record a distance band when unsure of the exact location, and group the data into distance intervals for analysis (as recommended in MacLeod et al. (2012d)).

Two sources of bias may remain. First, observers found it difficult to identify and record birds while navigating transect lines in dense shrubs or challenging terrain, and point transects

may therefore have been more suitable than line transects for this study (Buckland et al. 2001; MacLeod et al. 2012d). These problems may have led to incomplete detection of birds that were 0 m from a transect line, violating a key assumption of distance sampling and leading to density underestimation (Buckland et al. 2001) in the woodiest habitats. Such underestimation at high woodiness levels could potentially obscure any increases in density as a function of woodiness. Second, observations of animals that are fast-moving relative to the observer's speed can bias density estimates upwards (Buckland et al. 2001). This source of bias may have contributed to our high density estimates of goldfinch, greenfinch and redpoll at Bendigo, where these species were often flying in small groups. Any significant overestimation of goldfinch density on the intermediate block at Bendigo could have led to over-statement of the curved relationship between density of this species and vegetation woodiness. The post-breeding-season flocking behaviour (Heather & Robertson 2000) would have been avoided by sampling earlier in summer at Bendigo. Finally, the precision of our estimates could have been improved by using more and shorter line transects per block, compared with our design, or many points in a point-transect survey (Buckland et al. 2001).

Implications of continued shrubland succession for dryland passerines

Habitat restoration is a necessary precursor to the re-establishment of native forest birds where most forest has been lost (Innes et al. 2010). The same is likely to apply to Central Otago dryland ecosystems, where secondary shrubland supported indigenous bird species additional to those present in grassland (Walker et al. 2014b). Many forest birds are relatively specialised in their feeding requirements (Wiens 1989), and may face reduced availability of nest sites and increased exposure to predation and extreme weather at more-open sites (Ford & Bell 1981). Development of secondary woody plant communities may therefore allow some forest passerines to return to the Central Otago dryland landscape. Our prediction that densities of grey warbler and silvereye would increase during succession from grassland to shrubland was not supported across the habitat gradients we measured. However, dry forest may support larger populations of these indigenous species, based on comparison of our density estimates with published densities in other New Zealand forest ecosystems (Gill 1980; MacLeod et al. 2012a, d). Therefore, we predict that continued unassisted secondary woody succession to taller forest in drylands will increase not only the number of indigenous bird species (Walker et al. 2014b), but also the population densities of grey warbler and silvereye.

For common exotic passerines, our results show that the consequences of dryland woody succession are likely to vary between guilds. The composition of the exotic bird community, during the breeding season, is therefore also expected to change along the successional gradient. For the ground-nesting yellowhammer, woody succession may lead to local declines. Granivorous finches may become initially more abundant during a change from predominantly grassland to mixed grassland–shrubland, and then less abundant if shrubland becomes dominant. Our results predict little effect of shrubland succession on chaffinch, blackbird, and dunnoek in the breeding season. Although in Europe these species are often most abundant in tall woodland and forest (Southwood et al. 1986; Suárez-Seoane et al. 2002; Winkler 2005), we lack comparative density data from New Zealand dry forests to be

able to predict whether they will become more numerous in these later successional stages.

These conclusions are consistent with findings in other arid environments that woody succession is beneficial or neutral for most bird species (Suárez-Seoane et al. 2002; Sirami et al. 2009; Kutt & Martin 2010). They also support New Zealand studies in agricultural lands that found positive associations between non-crop woody vegetation and the abundance of indigenous birds and of many exotic species (Moller et al. 2008; MacLeod et al. 2012b). Although shrub encroachment may cause population declines in obligate open-habitat birds, losses may be offset as habitat area increases elsewhere owing to land clearance (Kutt & Martin 2010), and this may be true of exotic yellowhammer and granivorous birds in New Zealand drylands. Because no extant indigenous birds rely on dry grassland habitats, none will be negatively affected by succession from grassland to shrubland.

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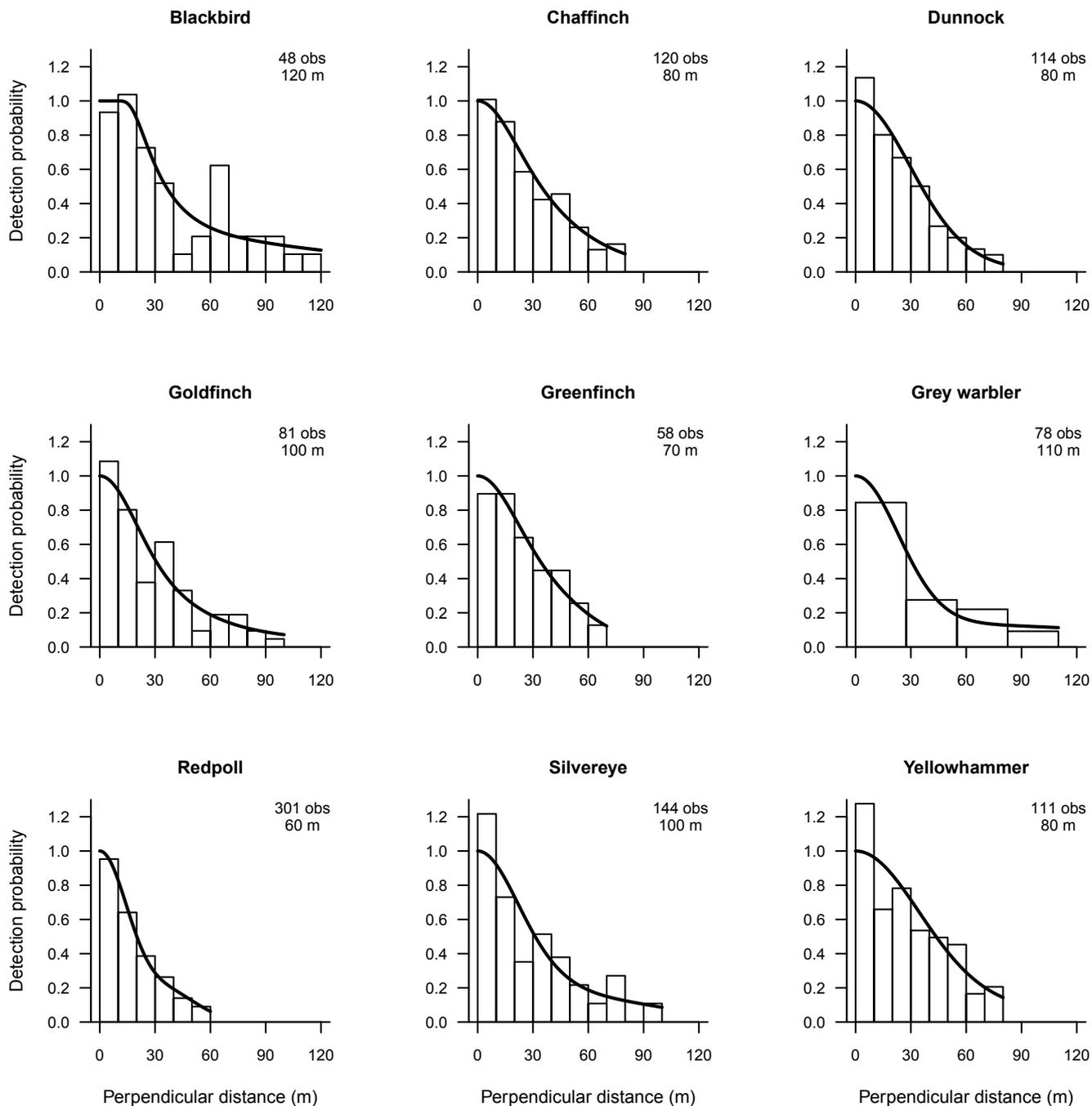
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Appendix 1. Detection functions (curves) fitted to observations (histograms) of nine common bird species sampled on line transects along a gradient of woody dominance (woodiness) at Bendigo (March 2007), Blackstone Hill (December 2007) and Cambrian (February 2008). The top-right corner of each graph gives the number of observations (obs) of that species (both single birds and groups) within the distance (m) at which the data were right-truncated for analysis. Data for grey warbler were grouped into distance classes for analysis, as shown in the histogram. Detection functions shown are best models based on AIC_c, averaged over all covariates. See Table 3 for scientific and full common names.



Appendix 2. Key functions, number of cosine adjustment terms, covariates, and the direction of covariate effects (where relevant) in the best-model detection functions (Appendix 1) for nine common bird species sampled on line transects at Bendigo, Blackstone Hill and Cambrian. ‘Seen’ means whether the bird was seen or only heard. A – or + indicates whether detectability decreased or increased, respectively, as a function of the covariate ‘woodiness’. For all species where ‘site’ was a covariate, detectability was higher at Bendigo than at Blackstone or Cambrian.

Species ¹	Key function	Cosine adjustment terms	Covariates	Direction
Blackbird	Hazard rate	0	Site	
Chaffinch	Half-normal	0	Site, Woodiness	Woodiness –
Dunnock	Half-normal	0	Seen	Heard > Seen
Goldfinch	Half-normal	0	Woodiness, Observer	Woodiness –
Greenfinch	Half-normal	0	Woodiness	+
Grey warbler	Half-normal	0	Seen	Heard > Seen
Redpoll	Half-normal	1	Site	
Silvereye	Half-normal	1	Site, Observer	
Yellowhammer	Half-normal	0	Site	

¹See Table 3 for scientific names and full common names.