Return to previous file: sfc265.pdf

TABLE 6. DIRECTION AND PERCENTAGE OF VARIATION EXPLAINED BY SINGLE FACTOR REGRESSIONS ON ORDINATION SCORE ON EACH OF THE FIRST FOUR AXES DCA ORDINATION AXES (AXES 1, 2, 3, AND 4).

FACTOR		AXIS1	AXIS2	AXIS3	AXIS4
Location	East latitude	3.9	0.0	-2.9	20.9
	Mataura catchment	0.0	-3.3	-4.2	5.6
	Oreti catchment	9.4	9.7	0.0	13.5
	Waiau catchment	-4.6	0.0	0.0	-22.8
Environment	LENZ L3.1a	3.7	-3.4	0.0	0.0
	LENZ L3.2a	-9.1	-6.1	0.0	0.0
	LENZ L5.1b	0.0	0.0	7.0	4.7
	LENZ Q4.1D	0.0	5.5	-8.2	-7.3
Habitat					
Predominant substrate type	Silt substrate	0.0	0.0	0.0	-8.6
	Gleyed soils	0.0	-15.9	0.0	0.0
	Peat substrate	-5.5	-4.2	0.0	0.0
Landform	Terrace	0.0	0.0	-5.6	0.0
	Swamp	0.0	-7.9	0.0	0.0
	Levee	0.0	12.8	8.8	0.0
	Backswamp	0.0	-11.5	0.0	0.0
Characteristics of the community					
Tiers	Presence of emergent tier	9.5	-17.3	-7.4	0.0
	Species in understorey tier	-6.8	5.9	0.0	0.0
	Presence of subcanopy tier	-10.3	0.0	-19.4	0.0
	Presence of epiphytes	-5.0	0.0	4.4	0.0
	Maximum height of emergent tier	0.0	-15.4	-5.6	0.0
	Minimum height of emergent tier	0.0	-13.2	-5.6	0.0
	Maximum height of canopy tier	-32.6	11.5	0.0	0.0
	Minimum height of canopy tier	-31.3	10.4	0.0	0.0
	Maximum height of subcanopy tier	-27.6	0.0	0.0	-3.8
	Minimum height of subcanopy tier	-21.2	3.1	0.0	0.0
	Maximum height of understorey tier	-20.3	0.0	-17.5	-4.0
	Minimum height of understorey tier	-18.5	0.0	-9.4	-2.9
	Tier complexity	0.0	-5.8	-5.4	0.0
Cover	Ground cover	7.7	0.0	10.7	0.0
	Litter cover	-5.6	0.0	-14.4	0.0
	Canopy tier cover	3.1	-9.5	0.0	0.0
	Ground tier cover	-9.9	-4.9	-12.0	-7.2
Richness	Species richness	0.0	-15.3	-14.6	0.0
	Species richness of epiphytes	-7.7	-5.1	0.0	-3.0
	Species richness of liane species	0.0	0.0	-5.8	0.0
	Species richness of emergent tier	8.4	-13.3	-7.3	0.0
	Species richness of canopy tier	19.4	-6.0	-3.2	0.0
	Species richness of subcanopy tier	-4.3	0.0	0.0	0.0
	Species richness of understorey tier	-12.3	-6.3	-21.3	-5.1
	Species richness of ground tier	0.0	-11.7	-9.8	0.0
Rarity	Number of rare species	6.3	0.0	-5.9	0.0
	Rare species in epiphyte tier	0.0	4.9	11.3	0.0
	Number of rare species in emergent tier	4.7	0.0	0.0	0.0
	Number of rare species in canopy tier	39.1	0.0	-5.6	0.0
	Number of rare species in subcanopy tier	6.1	0.0	0.0	0.0
	Number of rare species in understorey tier	0.0	0.0	-13.4	0.0
	Rare species in ground tier	0.0	0.0	-5.4	0.0
Invasion	Exotic species richness	5.8	16.3	3.8	17.1
	Number of exotic species in canopy tier	3.9	3.4	0.0	12.4
	Number of exotic species in subcanopy tier	0.0	8.6	0.0	22.4
	Number of exotic species in understorey tier	0.0	4.3	-4.3	5.2
	Exotic richness of ground tier	6.0	12.1	6.9	10.3

TABLE 6—*Continued.*

FACTOR		AXIS1	AXIS2	AXIS3	AXIS4
Indicators of fragmentation					
	Edge:area ratio of forest fragment*	0.0	7.2	0.0	4.5
	Spatial isolation of plot from forest*	0.0	13.1	18.5	0.0
	Percentage floodplain ecosystem loss	0.0	12.2	0.0	14.5
	Area of forest fragment (LCDB1)	–4.6	0.0	0.0	–5.0
	Area of scrub fragment (LCDB1)	0.0	–8.2	0.0	0.0
	Catchment deforestation	3.4	0.0	0.0	23.2
	Estim. deforestation of catchment	–4.8	6.7	0.0	8.9
	Distance of forest plot to forest edge	0.0	13.4	0.0	0.0
	Forest fragment has a pasture edge	3.0	5.2	8.7	0.0
	Artificial edge (e.g. pasture)	7.0	8.2	5.3	3.3
	Classified as indigenous forest (LCDB1)	–4.7	–9.8	0.0	0.0
	Plot in pasture	4.6	6.4	15.2	0.0
	Forest fragment has stream edge	6.8	–4.1	–3.5	0.0

* Indicates GIS-derived index.

Axis 1

The first axis distinguishes distinctive Back Valley *Pittosporum obcordatum* terrace forest communities, which lie at the right of the axis from all other vegetation types. This community is restricted to the low-lying, impounded, frequently flooded, frost-prone basin of Stinking Creek near Lake Manapouri. The most compositionally similar vegetation type to Community E is mixed manatu terrace forest (Community D), which occurs towards the middle of the first axis. The most dissimilar types (positioned at the far left of Axis 1) are the mountain beech (Community F) and kahikatea backswamp (Community H) forest types, both of which also occur in Back Valley. Communities A, B, C, and G all have intermediate scores on the first axis.

Axis 2

The second axis separates kahikatea backswamp forests (Community G) and kahikatea–silver beech levee forests (Community H) at its lower extreme from dry terrace forest types dominated by totara and/or matai with the highest scores (i.e. Community C and subtypes of Communities A or B). Most Community C plots (i.e. those sampled at Taylor’s Bush, Broadlands, and Swale Road) are not associated with the characteristic, regularly flooding, meandering streams of the floodplain ecosystem, and so are not true floodplain forest types. Nevertheless, they contain the rare species *Melicytus flexuosus* and *Coprosma obconica* and they are useful in determining the nature of this gradient.

Plots with high scores on Axis 2 typically contain numerous exotic species, particularly in the ground layer. They are typically situated in spatially isolated fragments that are distant from the nearest forest patch. Usually such fragments are on terrace or levee landforms, while much of the original ecosystem sequence has been removed. In contrast, plots with low scores on Axis 2 tend to be species-rich, particularly in the ground layer, and characterised by tall emergent (kahikatea or pokaka) trees, and occur largely in backswamp habitats on gley soils.

We interpret this principally as a gradient in substrate/ecosystem characteristics. However, we note that this gradient is also associated with increasing fragmentation, which may be partly a consequence of the greater agricultural potential of drier terrace landforms, which tend to have higher Axis 2 scores.

Axis 3

The third and fourth axes are also correlated with community types and fragmentation indices. However, these may also be confounded by environmental components.

The third axis separates terrace forest fragments on older, more leached soils (totara, kohuhu, and manuka are typical components of plots at Broadlands, Taylor's, and Swale Road in the Waiau) from young, regularly disturbed, unleached levee forest (plots dominated by manatu, kowhai, and—where

TABLE 7. NUMBER AND PERCENTAGE OF PLOTS SAMPLED THAT CONTAINED THREATENED PLANTS IN REMNANTS AND CATCHMENTS OF SOUTHLAND.

A. Number of plots sampled that contained the six, target, threatened plants in remnants and catchments of the Southland Plains. (Numbers in parentheses indicate the number of plots in which seedlings were recorded.)

CATCHMENT	REMNANT	*Coprosma obconica*	*Coprosma pedicellata*	*Coprosma wallii*	*Melicytus flexuosus*	*Olearia hectorii*	*Pittosporum obcordatum*
Waiau	Back Valley		6 (3)		6 (3)		6 (3)
	Broadlands – Motu Road	2 (1)					
	Mouat's	5 (5)	12 (8)	15 (5)	8 (5)		3 (1)
	Quinn's	8 (6)	6 (5)	1	2 (1)		
	Swale Road				2 (1)		
	Taylor's/McLee's				2 (1)		
Oreti	Cowie Road						
	Dunsdale		1	12 (2)	6 (6)	1	
	Harris Road		1			1	
	Mabel Bush				4 (3)	2	1
	Otapiri			1			
	Swale's Bush				1		
	Taringatura				1 (1)	1	
	Turnbull's	2	8 (2)	8 (1)	9 (3)	1	2
Mataura	Glendenning		2				
	Gorge Road		1 (1)				
Toi	Titiroa		1 (1)				
Waihopai	Waihopai		1				
Waituna	Cook Road		3 (1)				
Total		17 (12)	42 (21)	37 (8)	41 (24)	6 (0)	12 (4)

B. Percentage of plots containing threatened plants that also supported seedlings of that threatened plant at Back Valley (the most intact study area), in remaining study areas in the Waiau catchment, in the Oreti Catchment, and in remaining catchments (Mataura, Waituna, Waihopai, Toi).

CATCHMENT GROUP	*Coprosma obconica*	*Coprosma pedicellata*	*Coprosma wallii*	*Melicytus flexuosus*	*Olearia hectorii*	*Pittosporum obcordatum*
Back Valley	–	50.0	–	50.0	–	50.0
Other Waiau study areas	80.0	72.2	31.3	57.1	–	33.3
Oreti fragments	0.0	20.0	14.3	61.9	0.0	0.0
Other	–	38.0	–	–	–	–

modified—willow or gorse at Quinn's, Cowie Road, and Otapiri). Often, the acidic terrace forests have richer understoreys than the younger levee forest plots, which tend to be in small fragments within developed pasture.

Axis 4

The fourth axis separates eastern sites (with high scores) from western sites (with low scores), and tends to be correlated with increasing forest fragmentation from west to east across the Southland Plains, and the associated presence of exotic species (especially pasture grasses and the woody species hawthorn, crack willow, gorse and elderberry). However, west-to-east transition is also associated with an increasingly dry and frosty climate, and the effects of this environmental gradient are probably confounded with those of fragmentation.

Table 7 also shows differences in the number and percentage of plots with rare plant seedlings across different sites and catchments.

Table 8 suggests that many target rare plants (with the exception of the rarely recorded *Olearia hectorii*) have preferential biases, but are not strictly confined to one or a small number of physiographic habitat types and plant communities. Of the target plants, *Coprosma obconica* is clearly one of the most generalist, occurring in six of the eight community types and on substrates ranging from deep peat to dry platform soils. *Melicytus flexuosus* was recorded in seven of the eight communities, but shows a distinct preference for dry platform habitats. *Pittosporum obcordatum* was recorded in only two forest community types, but across all of the four habitat types. *Coprosma pedicellata* was recorded in a wide range of community and habitat types, but showed a clear preference for Kahikatea backswamp forest type, and for backswamp habitats, or small winter-wet hollows or depressions within platform habitats.

2.3.3 Effects of fragmentation

Effects of fragmentation on the plant community

Correlations between major vegetation gradients and selected community characteristics and possible indicators of fragmentation are shown in Tables 8 and 9.

All of the four major vegetation gradients show some correlation with different indicators of fragmentation, and all of the potential indicators are correlated with one or more gradients. This suggests complex relationships between the vegetation pattern and different types of fragmentation processes and their effects. However, the relationships are not strong, i.e. individual fragmentation indicators account for small proportions of the overall vegetation variation.

Four biological characteristics that showed significant relationships with the possible indicators of fragmentation are shown in Table 10.

Species richness. Species richness (i.e. native + exotic) of plots in forest fragments decreased with ecosystem loss, and with spatial isolation of the forest fragment, where plots are in pasture and where there are artificial (incl. pasture) edges. This was seen most clearly in the lower (i.e. ground and understorey) tiers. The emergent tier was often absent where fragmentation was well advanced, and therefore its richness is also negatively correlated with ecosystem loss, spatial isolation, and artificial (including pasture) edges.

Exotic species richness. This strongest predictor of exotic species richness was the nature of the edge; plots in fragments nearest to artificial forest edges contained more exotic species, particularly in the ground layer. Since the majority of artificial forest edges were boundaries between forest and pasture,

TABLE 8. NUMBER OF RARE PLANT RECORDS BY FOREST COMMUNITY AND HABITAT TYPE.
(Percentage frequencies of rare plants by ecosystem type are in parentheses.)

COMMUNITY		*Coprosma obconica*	*Coprosma pedicellata*	*Coprosma wallii*	*Melicytus flexuosus*	*Olearia hectorii*	*Pittosporum obcordatum*
A	Matai–kowhai–manatu levee forest	5	7	16	20	5	6
B	Silver beech–pokaka terrace forest	2		3	2		
C	Totara–matai terrace forest	2			3		
D	Mixed manatu levee–terrace forest	2	2	12	7	1	
E	Back Valley *Pittosporum obcordatum* forest				6		6
F	Mountain beech forest		5				
G	Kahikatea backswamp forest	1	22	6	2		
H	Kahikatea –silver beech levee/backswamp forest	5	6		1		
Number of communities		6	5	4	7	2	2
HABITAT TYPE							
	Levee	7 (37)	8 (19)	11 (30)	8 (18)	3 (43)	2 (14)
	Platform	7 (37)	12 (29)	17 (46)	30 (68)	3 (43)	8 (57)
	Backswamp	3 (16)	16 (38)	8 (22)	3 (7)	0 (0)	2 (14)
	Swamp	2 (11)	6 (14)	1 (3)	3 (7)	1 (14)	2 (14)
	No. records	17	42	37	41	6	12

TABLE 9. CORRELATIONS (DIRECTION: – = NEGATIVE) AND STRENGTH (% VARIATION EXPLAINED) BETWEEN THE MAIN GRADIENTS OF VEGETATION VARIATION (ORDINATION AXES 1 TO 4) AND MEASURED INDICATORS OF THE DEGREE OF FRAGMENTATION OR INTACTNESS.

INDICATORS	AXIS1	AXIS2	AXIS3	AXIS4
Catchment loss (field estimate)	–4.8	6.7		8.9
Catchment deforestation*	3.4			23.2
Percentage floodplain ecosystem loss		12.2		14.5
Plot in indigenous forest	–4.7	–9.8		
Spatial isolation of plot from forest*		13.1	18.5	
Area of forest fragment*	–4.6		3.1	–5.0
Distance of forest plot to forest edge		13.4	3.0	
Edge:area ratio of forest fragment*		7.2		4.5
Forest fragment has natural edge (e.g. stream, forest flat)				
Artificial edge (e.g. pasture)	7.0	8.2	5.3	3.3
Plot in pasture	4.6	6.4	15.2	
Forest fragment has a pasture edge	3.0	5.2	8.7	

Indicators are arranged in approximate order from a landscape to a local scale.

* Indicates GIS-derived index.

the correlations also show that plots in forest fragments surrounded by or adjacent to pasture contained high numbers of exotic plant species. Both catchment deforestation and ecosystem loss were also strongly correlated with exotic species richness, but in this case, particularly with exotic invasion of woody tiers (canopy, subcanopy, and understorey), rather than the ground tier.

Number of rare plants per plot. The number of different rare plant species recorded in a plot decreases with the area of the forest fragment, with deforestation of catchment and with ecosystem loss, and where plots are in pasture. This trend was seen most clearly among rare plants occupying the lowest (i.e. ground) tier, in other words, juvenile size classes. An interesting trend is the overall increase in the number of threatened plant species present per plot in smaller fragments, although there was a negative correlation with plots in pasture.

Tier complexity. Forest fragments with natural edges tended to have more complex tier structures, while low tier complexity was associated with artificial forest edges, and in particular, with forests adjacent to or in pasture. Tier complexity was typically lower in eastern catchments that were more deforested. As tier complexity decreases, lianes are typically the first structural component to disappear from a fragmented forest, followed by emergents and epiphytes.

Effects of fragmentation on rare plants

We use the presence or absence of seedlings as a simple surrogate for demographic trends in each of our target rare species in our plots. Many of the rare plants and their seedlings showed negative relationships with our

TABLE 10. CORRELATIONS (DIRECTION: – = NEGATIVE) AND STRENGTH (% VARIATION EXPLAINED) BETWEEN LIKELY BIOLOGICAL INDICATORS OF FOREST FRAGMENTATION.*
Indicators are arranged in approximate order from a landscape to a local scale.

INDICATORS	TOTAL SPECIES RICHNESS	EXOTIC SPECIES RICHNESS	NO. RARE PLANT SPECIES PER PLOT	TIER COMPLEXITY
Catchment deforestation (field estimate)	–11.7	5.6	–8.0	–8.8
Catchment deforestation†		16.5		
Percentage floodplain ecosystem loss	–7.9	14.6	–6.1	–6.7
Plot in indigenous forest†		–5.2		
Spatial isolation of plot from forest†	–9.0	3.3		
Area of forest fragment†		–5.6	–5.6	
Distance of forest plot to forest edge	–4.0			
Edge:area ratio of forest fragment†		3.5		
Forest fragment has natural edge (e.g. stream, forest flat)	3.2	–9.9		5.8
Artificial edge (e.g. pasture)	–8.2	27.4		–7.0
Plot in pasture	–14.8	21.5	–2.9	–11.7
Forest fragment has a pasture edge	–5.0	23.8		–5.1

* That is: native and exotic species richness, number of rare plant species per plot and tier complexity (number of tiers present), and measured indicators of the degree of fragmentation or intactness.

† Indicates measure derived from LCDB1 in GIS.

indicators of fragmentation of the floodplain ecosystem and its biological consequences (Table 11).

Apart from two plots at Turnbull's Bush (which did not contain seedlings), *Coprosma obconica* was recorded exclusively in native-species-rich forest plots in the least deforested Waiau catchment. Plots with seedlings as well as adult plants contained significantly fewer exotic species than those without seedlings.

Coprosma pedicellata showed relationships with several factors, indicating that fragmentation has negative consequences for its persistence and viability. Most *Coprosma pedicellata* plants were recorded in the comparatively intact western Waiau catchment, and within indigenous forest rather than in a pasture matrix, and those forest fragments with *C. pedicellata* tended to have natural (e.g. stream or swamp) edges rather than artificial edges. Forest fragments with *C. pedicellata* tended to have relatively high tier complexity and negative species richness, and be little invaded by exotic species. Seedlings were recorded in half or more of plots with adult *C. pedicellata* plants in the most intact study area (Back Valley) and elsewhere in the Waiau catchment, but in lower proportions of plots elsewhere. Seedlings tended not to accompany adult plants of *C. pedicellata* in sites with high numbers of exotic species.

Coprosma wallii showed a rather different association with indicators of fragmentation and its biotic consequences. Adult plants were associated with

TABLE 11. SIGNIFICANT DIFFERENCES (BY *T*-TESTS WITH UNEQUAL REPLICATION) IN LIKELY BIOLOGICAL CONSEQUENCES OF FRAGMENTATION (RICHNESS OF NATIVE AND EXOTIC PLANTS, AND TIER COMPLEXITY) AND MEASURED INDICATORS OF THE DEGREE OF FRAGMENTATION OR INTACTNESS AT PLOTS WHERE TARGET RARE PLANT SPECIES ARE PRESENT OR ABSENT.

	Coprosma obconica	*Coprosma pedicellata*	*Coprosma wallii*	*Melicytus flexuosus*	*Olearia hectorii*	*Pittosporum obcordatum*
No. plots	17	42	37	41	6	12
(No. plots with seedlings)	(12)	(21)	(8)	(24)	(0)	(4)
Native species richness	$+^{**}$	$+^{**}$				
Exotic species richness	$-^{*}$	$-^{*}$	$+^{*}$	$(-^{**})$	$+^{*}$	
	$(-^{***})$	$(-^{***})$				
Tier complexity		$+^{*}$				
Catchment deforestation (field estimate)						$-^{**}$
Catchment deforestation	$-^{*}$	$(-^{**})$			$+^{*}$	
	$(-^{***})$					
Percentage floodplain ecosystem loss (field estimate)						$-^{**}$
Plot in indigenous forest		$+^{*}$	$(+^{**})$			
Area of forest fragment			$-^{*}$	$-^{*}$		
Edge:area ratio of forest fragment*				$(-^{**})$		
Forest fragment has natural edge (e.g. stream, forest flat)				$(+^{***})$	$-^{*}$	
Artificial edge (e.g. pasture)		$-^{**}$	$+^{*}$			
Plot in pasture	$-^{*}$	$-^{*}$	$+^{*}$	$-^{*}$	$+^{*}$	
Forest fragment has a pasture edge				$(-^{**})$		

Results of comparisons: + = higher, – = lower.
$^{*} = P < 0.05$; $^{**} = P < 0.01$; $^{***} = P < 0.001$.

smaller forest fragments, and those with artificial edges, and with pasture, as well as with relatively high exotic species richness. Seedlings of *C. wallii* were recorded in relatively few (8/37) of the plots that contained adult plants. Seedlings were recorded in a higher proportion of those plots in the Waiau catchment (i.e. those on Mouat's property) than those at Dunsdale and Turnbull's in the Oreti. Notably, those plots with *C. wallii* seedlings were exclusively within forest, rather than in pasture.

Like *C. wallii, Melicytus flexuosus* is associated with smaller rather than larger forest fragments. However, it was negatively, rather than positively associated with pasture. More than half of the sites with *M. flexuosus* contained seedlings, which occurred largely in those fragments with lower edge-to-area ratios, natural rather than pasture edges, and which contained few exotic species.

Olearia hectorii was recorded in a very few sites in our sampling of the Southland floodplain ecosystem. All sites were east of the Waiau in more deforested catchments, and either in pasture or highly modified fragments with high exotic species richness. No seedlings were recorded. This distribution is consistent with populations originating around the time of first land clearance, before exotic grass swards became a widespread impediment to recruitment as suggested by Rogers (1996).

Pittosporum obcordatum was also recorded rarely in our study. In five of the six plots recording *P. obcordatum* outside the large Back Valley population (several 100 plants), a single individual adult plant was recorded, and two individuals were recorded in the sixth plot. Seedlings were recorded in one of these plots (on a fragmented forest edge on Mouat's property in Dean Burn) but later in the year a follow-up inspection found no live seedlings remained as a result of cattle trampling and browsing.

2.4 DISCUSSION

2.4.1 Regional vegetation patterns

The broad compositional characteristics of Southland's floodplain forest communities show some geographic influences; e.g. two of our vegetation types were entirely confined to Back Valley and a third largely confined to forest remnants at Dunsdale. These regional distinctions probably result from biogeographic history, including factors affecting Holocene forest recolonisation (especially the slow invasion of beech forest from the west) as well as differences in the physical characteristics of floodplain ecosystems (e.g. geology, hydrological regime) and their landscape history. Both factors may have been important large-scale drivers of plant compositional patterns within the original floodplain ecosystem. However, biogeographic patterns are now confounded by, and difficult to distinguish computationally from, the non-random large-scale patterns of fragmentation across the Southland Plains.

Despite some underlying compositional variability, the floodplain ecosystem is distinctive in its composition, rare plant components, and habitat features, and examples were located and sampled across the entire Southland study area (examples are also known in the Catlins, outside the area of our study). This suggests that although locally confined by specific habitat conditions, the ecosystem was formerly widespread across Southland.

2.4.2 Habitat specificity

The floodplain ecosystem contains a wide range of habitat types, and habitat changes within the ecosystem occur with very subtle alterations in topography, and often within distances of one to a few metres. Sampling forest vegetation and recording habitat characteristics in an ecosystem with such high, complex local habitat turnover inevitably entailed some compromises.

Our sampling design represents a compromise between the practical need to record characteristics of a forest plant community (in which the canopy area of an individual tree is large) within regular plots, and the precise determination of the habitat within a plot. It was frequently not possible to position vegetation sampling plots within uniform areas of each habitat type even though our vegetation sampling plots of 10 × 10 m are only 25% of the size of a standard RECCE forest plot of 20 × 20 m (Wraight 1962). Therefore, it is not uncommon for from one to three different habitat types to be represented within a plot. For example, between the characteristic silty levee and the more-distant and larger backswamp depression (typically a cut-off meander or oxbow with gleyed silt loam soil in our physiographic classification) small (1–5 m diameter) hollows and depressions with gleyed and mottled soils were often scattered across the broad floodplain platform, characterised by a dry, crumbly loam soil that was heavily exploited by the surface roots of the canopy trees. A plot placed on this platform would typically contain species specific to the hollows and depressions (e.g. *C. pedicellata*) and those that occur exclusively on the dry platform soils (e.g. *Melicytus flexuosus*).

Where the ecosystem has undergone a high degree of fragmentation, its more subtle features are obliterated. For example, small 1–5 m diameter hollows and depressions with gleyed and mottled soils (described above) typically disappear following clearance of the forest canopy, alteration of the flooding regime, and the establishment of pasture. Consistent recording of habitat in the field necessitated the use of habitat categories that were readily recognisable by the non-expert observer in the field, in fragmented situations. Therefore, we chose to record a limited number of simplified habitat categories (levee, platform, backswamp) rather than attempting a higher level of physiographic discernment.

Despite these limitations, the wide variation in community composition resulting from diverse fragmentation processes, and the fact that fine-scale habitat heterogeneity was indiscernible in more fragmented sites, our results show broadly consistent patterns of vegetation and occurrences of target rare plants across floodplain ecosystem habitat types. The typical vegetation transition is from light-canopied kowhai–manatu communities on levees (associated with the target plants *Coprosma obconica, C. wallii* and *Olearia hectorii*) to denser-canopied forests of matai (and, in western catchments, beech) on platforms (associated with *Melicytus flexuosus, Coprosma obconica, C. wallii* and *Olearia hectorii*, with *C. pedicellata* on the margin of minor gleyed hollows and depressions), and then to distinctive kahikatea-dominated communities in the winter-wet backswamps (the typical habitat of *Coprosma* *pedicellata* and *Pittosporum obcordatum* outside Back Valley, embracing flood channel, cut-off meander and oxbow, and depression or hollow habitats of Table 2). A transition to predominantly open (shrubland or restiad-dominated) peat bog vegetation occurs some distance away from the stream. Large populations of *C. obconica* were recorded on deep peat in the Dean Burn catchment, supporting the observation of Wilson & Galloway (1993) that it is characteristic of both 'poorly drained and sharply drained sites'. Other target rare plants were recorded in narrow transition zones between habitats (e.g. *Coprosma pedicellata* on the margin of gleyed oxbow habitats and peat swamp). The high habitat turnover on the primary and youngest terraces (the floodplain ecosystem of our study) is replaced by more homogeneous vegetation types on more uniform, well-drained terrace surfaces further away from the stream or river channels (see Appendix 1: Waiau River).

2.4.3 Rare plant strategies for recruitment and persistence

We suggest that our rare target plants are both stress-tolerators and disturbance exploiters in their survival strategies, and that the different species show different narrow specialisations for stressed sites in the floodplain ecosystem. Broadly, all are predominantly stress-tolerators, with lower stature and apparently somewhat slower growth rates than their taller forest-tree competitors. Evidence for narrowly prescribed habitat tolerances is provided by the high allopatric separation at a small (i.e. habitat) scale despite their broadly sympatric distributions at the larger scale of the floodplain ecosystem as a whole. Precise habitat preference is likely to be an evolutionary consequence of stress tolerance, as suggested by Drury (1974) and applied to *Pittosporum obcordatum* by Clarkson & Clarkson (1994).

The propagule dispersal (and in some cases vegetative reproduction) strategies of the target plants reinforce our perception that they are both stress-tolerators and disturbance exploiters. For example, we suggest that given narrowly provisioned, stressed habitats it would be important to seed-saturate the local environment (e.g. using gravity, invertebrate, and/or lizard dispersal mechanisms), as well as to foster bird and water dispersal to exploit distant regeneration opportunities that are spatially and temporally relatively unpredictable or discontinuous (e.g. dieback induced by an extended flooding event). Little is known about the reproduction and dispersal strategies of our target plants. Bird transport of fleshy fruits (of *Melicytus* spp., *Pittosporum obcordatum* and *Coprosma* spp.), and wind (in the case of *Olearia hectorii*) are likely to be the main propagule dispersal mechanisms today. *Olearia hectorii* regenerates through annual production of abundant, light-weight, wind-dispersed seed. This enables it to exploit a shifting mosaic of streambank and levee disturbance along its linear floodplain habitat. However, with the onset of senescence in the absence of disturbance, *O. hectorii* invests in epicormic resprout or vegetative persistence. *Coprosma pedicellata* also invests in long-term clonal persistence to complement disturbance-exploiting long-distance dispersal.

Juveniles of *Melicytus flexuosus* are scattered through the understorey of Southland's terrace podocarp and hardwood forests in an apparently random manner, sometimes associated with reproducing adults, which are largely confined to edges and light gaps. Many older adults beneath more closed canopies have etiolated growth forms that indicate a rapid vertical extension as the canopy has closed around the plants. For this species, we infer high shade tolerance for juveniles that persist long term to exploit an unpredictable provision of light gaps from treefalls or from temporary provision of edges. Additionally, a closely related species, *M. drucei*, exhibits basal resprout in response to herbivory and it is possible that *M. flexuosus* also has this capability.

Seedlings, but less so saplings, are relatively frequent with adults in *Coprosma obconica* populations in less fragmented forest habitats. Saplings of this species may have less shade persistence within tall forest than those of *M. flexuosus* and it appears to require light-dappled understorey conditions for growth to approximately 4 m and subsequent reproduction.

A perplexing, general lack of seedlings and saplings of *Coprosma wallii* makes interpretation of its regeneration strategy difficult. This species grows to a relatively large size (c. 10 m tall) and forms the canopy of even-aged stands on terraces in the Dean Burn and in Dunsdale (as if a massed recruitment response to catastrophic flooding or other forest clearance has taken place at some time in the past) and others where it forms a dense subcanopy beneath centuries-old canopy trees (suggesting that recruitment followed a flood event perturbing ground and understorey tiers, but not the canopy or emergents). Thus it is not clear whether direct light is required to stimulate regeneration or for growth to maturity. We suggest three different strategies that may enable it to exploit the vicissitudes of disturbance and stressed sites with forest. Firstly, durable testas may ensure persistent seed banks that respond to infrequent creation of light gaps following cohort senescence. Secondly, gravity- or water-dispersed seed could exploit local disturbances or fresh, silty sediment. Thirdly, birds could transport the fleshy fruits to distant stressed or disturbed sites. *C. wallii* is associated more strongly with artificially modified edges and pasture situation than most other target plants, but no seedlings are detected in these situations; in this it resembles *Olearia hectorii*. We suggest that, like *O. hectorii*, many of these edge and pasture specimens originated before the consolidation of pasture grasses. The strategies of *Coprosma wallii* (durable testas to ensure persistent seed banks, and gravity- or water-dispersed seed) might also be characteristic of *Pittosporum obcordatum* and *Coprosma pedicellata*.

2.4.4 Rare plant responses to fragmentation

Our correlation analyses (Tables 9 and 10) reveal general, significant decreases in rare plants (both threatened plants in general, and our six target rare plants and their seedlings) with a wide range of indicators of forest fragmentation. Within this broad trend, however, each of our target rare plant species shows a different set of relationships with the suite of fragmentation indicators. This result is consistent with the subtly different adaptations and strategies of the different target species.

Those adaptations that the target rare plants have evolved for persistence in a natural, intact floodplain ecosystem (where canopy gaps are largely created by dieback consequent upon flooding or frost) may have allowed the rare plants to regenerate and persist to a limited extent in fragmented habitats. For example, it is not uncommon to find adult shrubs of *Coprosma pedicellata, C. wallii* and *Melicytus flexuosus* along recent artificially created edges that either intersect or lie just outside the floodplain ecosystem. The frequency of occurrences of *C. wallii* and *Melicytus flexuosus* on forest fragment edges is expressed in the negative relationship between recorded occurrences and fragment size. The apparently even-aged population structures of shrubs on artificial edges suggest that chance, temporally discontinuous recruitment has occurred in response to idiosyncratic disturbance events.

We suggest that clearance and fragmentation of forest in Southland from human arrival c. 800 years ago created high-light, high-nutrient habitats with reduced competition from taller canopy trees, and this probably stimulated irregular pulses of recruitment in many of our target rare plant species. However, it appears that little recruitment of target plants follows the ingress and consolidation of pasture grasses, and where grazing and browsing animals are present (e.g. Clarkson & Clarkson 1994). Thus, it seems reasonable to suggest that a window of opportunity for recruitment opened by initial clearance of forest (either in Polynesian or early European times) has been closed more recently by the spread of pasture grasses and high stocking levels (Rogers 1996). Idiosyncratic opportunities for recruitment still occur (e.g. illustrated by our observation of several tens of *Pittosporum obcordatum* seedlings in an almost-bare, cattle-trampled ground layer in Dean Burn in the spring), but we suggest that the odds are stacked more heavily against survival (no *P. obcordatum* seedlings survived trampling by cattle over the summer). Recent alterations of flooding regimes (e.g. through drainage and channel straightening works) have reduced the frequency and intensity of flood-induced stress that limited competition and enabled the persistence of the stress-tolerant floodplain flora.

2.5 CONCLUSIONS FROM THE VEGETATION STUDY

The floodplain ecosystem is a product of fine-scale hydrological variations that occur as a result of subtle changes in relief. These subtle variations are not captured in current environmental GIS databases.

The distinctive floodplain forest communities and our target rare plant species components appear to be maintained by conditions of reduced competition that arise through natural disturbance events (primarily periodic severe frost and waterlogging floods) that impose periods of extreme stress within the floodplain ecosystem. Before human settlement, the ecosystem was probably locally confined by specific habitat conditions, but regionally widespread across Southland.

Since human settlement, chance artificial disturbances associated with forest clearance and other agents of fragmentation (e.g. stock trampling, earthworks) may have provided opportunities for the reproduction of certain of our target species, which are adapted to capitalise on conditions of temporarily reduced competition. The spread of sward grasses following European settlement is likely to have decreased these opportunities.

Individual indicators of fragmentation were of limited use in predicting specific effects on the vegetation and species of the floodplain ecosystem. Typically, the percentage of variation explained by each of the different indices was low.

Nevertheless, our regression analyses show associations between a broad range of fragmentation indicators and a general increase in exotic species richness and a simplification of the tier structure—in particular an early loss of liane, emergent, and epiphyte tiers. Species richness and the number of rare plants in the ground and understorey tiers also decrease significantly. Our results indicate decreased occurrence and recruitment of most of our target rare plants with increasing fragmentation of their ecosystem. These symptoms of fragmentation (increased exotic and reduced native richness, tier simplification, and rarity) appear to be common to all floodplain habitats.

We demonstrate negative correlations between seedling establishment and exotic species-rich understoreys and/or pasture environments, suggesting limited ability to compete with introduced ruderal species. Exotic species invasion (especially ingress of sward grasses) that accompanies fragmentation is likely to be an important factor in the decline of threatened plant species.

We conclude that, with fragmentation of floodplain ecosystems, the natural disturbance regime (primarily periodic severe frost and waterlogging floods that impose periods of extreme stress within the fertile floodplain ecosystem leading to canopy dieback) is altered to a regime of high fertility and high light (a greater extent of edge habitat) with a reduced frequency and duration of stress-inducing low-velocity flooding and water ponding. These conditions tend to favour ruderal and competitive plant strategies over the slow-growing stress-tolerant adaptations of natural floodplain plant communities.

3. Effects on floodplain forest invertebrates

3.1 INTRODUCTION

3.1.1 Invertebrates in plant communities

Invertebrates make up the bulk of biodiversity, and affect all other forms of life by sheer weight of numbers. Invertebrates are essential for maintaining the function of ecosystems for many reasons. They form integral parts of food webs, recycle organic matter, and make up the bulk of parasite species. Little is known about the diversity of invertebrates, and many species are yet to be identified. Much work is needed to better understand their ecological roles, and so to create a more-sound scientific basis for conservation and resource management initiatives to protect invertebrate diversity.

New Zealand has an extremely distinctive invertebrate fauna. There is a very high degree of species endemism (> 90%), with extremely high levels in the

Lepidoptera (> 94%), Orthoptera (> 95%), Coleoptera (96%), and 100% in the Phasmatodea, Ephemeroptera and Trichoptera.

In general, invertebrates form highly specific relationships with plant species and are assumed to be characteristic of particular plant communities. However, invertebrates may also exert influences on the composition of the plant communities, for example, as a consequence of their grazing habits, such as where polyphagous larvae (particularly beetles and moths) eliminate incoming seeds of weedy species from relatively intact habitat (Patrick 1994a).

3.1.2 Invertebrates as potential environmental indicators

Invertebrates utilise many habitats for all or part of their life cycles, including all stages of dead wood, bare ground and rock surfaces, river shingle, tidal wood and dead algae (e.g. Patrick 1994a). Assessment of native invertebrate biodiversity may provide useful information for biodiversity monitoring and the assessment of ecosystem state or condition.

Fragmentation of terrestrial ecosystems is likely to influence the availability of many different resources that are critical to invertebrates (such as mates or food; Yahner & Mahan 1997). The effects of fragmentation may be positive for some invertebrate species (e.g. some butterflies can benefit from human-modified landscapes providing more wildflowers; Yahner & Mahan 2002), and negative for others.

There is evidence to suggest that the more specialised taxa may be affected more by forest fragmentation either directly or indirectly than are generalist taxa, which are not dependent on a particular host or prey (Didham et al. 1996; Harrison & Bruna 1999; Laurance et al. 2002). The ability of the generalist taxa to utilise different hosts allows greater flexibility to persist within a changing environment (Didham et al. 1996). Thus, a switch from specialist to generalist invertebrates may be indicative of increasing fragmentation (i.e. declining condition). The presence of a threatened invertebrate species may be associated with (i.e. an 'indicator' species for) other rare natural heritage features (see Hutcheson et al. 1999).

3.1.3 Problems and approaches in invertebrate community studies

The ecology of invertebrates is poorly understood relative to that of vertebrates and plants. This is allied to inherent difficulties in studying invertebrate communities, which impose many limitations. Full invertebrate community studies are generally impracticable, because these communities are often very complex, and current knowledge of all the various taxa and their relationships is incomplete. Moreover, a large volume of work is involved with identifying all taxa to species level. Incomplete community inventory is often unsatisfactory; for example, obtaining a species count gives no indication of composition, and measuring richness gives no indication of turnover and may favour widespread common species, giving a misleading impression of increased richness or high biodiversity (Davies & Margules 1998). When studying invertebrate communities, pragmatic approaches are often adopted that do not require full taxonomic inventory to species level, including inventory to higher taxonomic levels, functional groups (Didham et al. 1996), or different trophic levels

(Didham 1998) rather than individual species. Studies of the invertebrate fauna of Southland's floodplain ecosystem reported here adopted such pragmatic approaches.

3.1.4 Invertebrate studies in the Southland floodplain ecosystem

The findings of three separate pilot studies of the invertebrate biodiversity and ecology of the Southland floodplain ecosystem are reported below.

Study 1—Beetle assemblages of fragmented and intact floodplain habitats

This study used pitfall and Malaise traps positioned along local habitat sequences and gradients of forest degradation in a replicated design to sample the invertebrate fauna. Malaise traps are a tent-like structure. Insects fly into a vertical side mesh and fly or walk upward (as is their natural tendency) along the sloping tent roof and are guided into a collection container that holds preservative. Pitfall traps collect ground-dwelling invertebrates (largely beetles, spiders, amphipods, ants, springtails, mites, grasshoppers, crickets, isopods, harvestmen and centipedes). They have a small container (usually containing preservative if left for long periods) that is sunk into the ground with its lip level with the ground surface. They often have a wooden cover to exclude rain and litter.

The data from this pilot study are used to examine the effects of fragmentation and habitat type on the composition and characteristics (richness, abundance, diversity) of a single selected focal invertebrate group (Coleoptera; beetles). Beetles were chosen since they make up a high proportion of the New Zealand insect fauna, their taxonomy is relatively well known, and they are well represented in collections (Klimaszewski & Watt 1977; Larochelle & Larivière 2001). Beetle ecology is also comparatively well studied overseas, where particular groups are used as environmental indicator species.

The data are also used to examine the assumption that vegetation communities can act as surrogates for invertebrate assemblages (in this case, beetle assemblages). This assumption has seldom been formally tested, but is a major issue for invertebrate conservation, because if vegetation communities and invertebrate assemblages are strongly correlated, the conservation of a representation of vegetation communities should protect invertebrates as well (an umbrella or focal species concept). There are a number of studies that support opposing views on this idea, although it is often difficult to separate the effects of different taxa, sampling methods, and habitats examined.

Malaise and pitfall traps typically catch a high proportion of the species associated with an area of habitat, as well as transient species passing though the area. However, they do not necessarily catch those invertebrate species that are closely associated with particular species or vegetation types. Any links between vegetation and invertebrates are more likely to be revealed if the vegetation itself is directly sampled, using methods that collect invertebrates directly off vegetation (e.g. beating or sweeping).

Studies 2 and 3—Invertebrates on Coprosma *species and* Sophora microphylla

The remaining studies reported below examine invertebrates on individual plant species. Two plant genera (*Coprosma*—Study 2 and *Sophora*—Study 3) were chosen for these studies, because they are common in the Southland floodplain ecosystem, and are known to be important hosts for native invertebrates elsewhere in New Zealand (Patrick 1994b; Derraik et al. 2001, 2003). Both of these studies used beating methods to dislodge invertebrates from plants onto collecting traps. This method typically catches high proportions of spiders, beetles, true bugs (Hemiptera), flies, wasps, butterflies/moths, cockroaches, mantids and stick insects.

Study 2 focused on invertebrate populations found on four shrubs and small trees of the genus *Coprosma*. The aims were:

- To compare and contrast invertebrate loads and compositional patterns among rare and common species of *Coprosma.*

We expected that rare *Coprosma* species could harbour higher numbers of specialist invertebrates than common *Coprosma* species. In this case, it would be expected that rare *Coprosma* fauna might be most sensitive to changes across a fragmentation gradient. This comparison also explores how rarity of habitat (in this case a shrub species) might influence species' responses to habitat fragmentation.

- To examine the influence of decreasing forest area size on *Coprosma* invertebrate loads and composition.

Coprosma shrubs in larger patches of forest were expected to harbour higher levels of invertebrate loading and diversity, while shrubs in the smaller patches were expected to harbour lower diversity.

- To determine whether isolated *Coprosma* shrubs existing in degraded riparian habitat had different invertebrate loadings and composition to *Coprosma* shrubs still embedded within nearby structurally intact forest areas.

We expected that *Coprosma* shrubs located within structurally intact forest areas would have higher invertebrate loads and diversity than shrubs in highly degraded riparian habitats. Accordingly, two of the species of *Coprosma* selected for this study are rare target plants (*C. wallii, C. pedicellata*) while the other two are common (*C. rotundifolia* and *C. propinqua*).

In this second study, a two-tiered approach was used for invertebrate taxonomic determinations. All true bug (Heteroptera) and moth (Lepidoptera) adults and juveniles were separated and sent to specialists for examination and species-level identification. These two groups were chosen because juveniles are well represented in beaten shrub samples (Derraik et al. 2001); moreover, these are groups known to frequently evolve specialised relationships with host plants, and therefore are most likely to be influenced by host plant distribution. All the remaining invertebrates were separated into higher taxonomic groupings (i.e. mites, spiders, pseudoscorpions, harvestmen, booklice, plant bugs, flies, wasps, beetles and weevils, springtails, mayflies, stoneflies, caddis flies, lacewings, weta, and damselflies) and numbers of individuals per grouping were counted.

Study 3 used Lepidoptera (moths) as a group. These form a large group in New Zealand, with easily identifiable adults and a known tendency to be host-specific. They are relatively easy to rear, and have a strong amateur following, who can provide valuable information on distribution and biology. They have been used in overseas studies to illustrate effects of land use on indigenous biodiversity.

Because few studies have been done on the effects of fragmentation on invertebrates in New Zealand, it is advantageous to use a taxonomically well-known key functional invertebrate group, with a known set of generalist and specialist taxa, as noted in Crosby & Dugdale (1996). It is also desirable to examine the effects of fragmentation by focusing on a single host plant species that is present across a wide fragmentation gradient (i.e. from low to extreme degrees of forest degradation and fragmentation). *Sophora microphylla* (kowhai tree) was selected as a good candidate host plant species for this study because it is widespread in Southland across the entire spectrum of fragmentation states, and present in core forest areas, relatively intact remnants, small remnants, and as single individuals in pasture.

The various plant communities on the Southland Plains are known to host a wide range of moth fauna in terms of diversity, special features, and affinities (Patrick 1994b). The presence of a threatened moth species indicates a high probability of there being other natural history elements with high conservation value (Patrick & Dugdale 2000); such species are often referred to as 'indicator' species (see Hutcheson et al. 1999).

Most herbivorous Lepidoptera species are specialists on specific host plants, so many are prone to extinction because of habitat degradation or loss (Jermy 1984). In principle, this makes the Lepidoptera ideal study subjects to focus on as part of a fragmentation study—they should respond to major vegetation disturbances, such as fragmentation, and further changes in community composition are likely to be reflected in the associated Lepidoptera. For this study, we chose Lepidoptera as representative members of a particular trophic level based on herbivory, with members that have a specialist life cycle based around the kowhai tree. *Sophora microphylla* is an ideal host tree because it supports indigenous Lepidoptera specialists (Spiller & Wise 1982; B. Patrick, pers. comm. 2003) and generalists (B. Patrick, pers. comm. 2003).

The study addressed the following specific questions regarding the role of Lepidoptera on *Sophora microphylla*:

- Is there a difference in Lepidoptera taxon diversity, and relative abundance on *S. microphylla* trees, between forest fragments of different sizes?
- Is there a difference in Lepidoptera taxon diversity and relative abundance on *S. microphylla* trees between core areas and nearby riparian vegetation remnants?
- Does the degree of individual *S. microphylla* tree isolation from its conspecifics affect the associated Lepidoptera taxon diversity and abundance?

We expected that Lepidoptera loading and diversity would be higher in larger fragments and in core areas, and lower in smaller fragments and in riparian remnants. We expected that the isolation of trees from their conspecifics would have a negative effect on Lepidoptera diversity and abundance.

For clarity, we report the methods, results, and discussion specific to each study in turn, and then draw these results and conclusions together in a joint general discussion.

3.2 STUDY 1—BEETLE ASSEMBLAGES OF FLOODPLAIN HABITATS

3.2.1 Methods

Sampling design

This study was located entirely within the catchment of the Dean Burn, with study sites established on the properties of the Mouat and Quinn families. Therefore, only a portion of the regional fragmentation gradient is represented, and the effects of fragmentation are local rather than regional. Three habitat types were selected for sampling (levee, platform, and backswamp), and examples of each were located in intact forest (the forest was continuous from the stream into the adjacent hillslope or peat vegetation) and in fragmented forest (where the forest was cleared from landforms adjacent to the floodplain ecosystem). There were three replicates of each habitat-fragmentation combination (i.e. a total of 18 sites). The sites were split between Quinn's property (6 sites) and Mouat's property (12 sites). At each site, five pitfall traps and one Malaise trap were installed and sampled. Sampling containers were installed and then collected from each of the 90 pitfall and 18 Malaise traps at the beginning and end, respectively, of each of four sampling periods: 14 November–13 December 2001 (Spring Year 1), 14 February–14 March 2002 (Autumn Year 1), 12 November–12 December 2002 (Spring Year 2), and 14 February–14 March 2003 (Autumn Year 1).

It was not possible to ensure uniform vegetation at each replicate of the six habitat-fragmentation combinations. A vegetation sampling plot was recorded at each study site simultaneously, or soon after the establishment of the traps. The a posteriori classification of these plots identified the following vegetation types:

- Intact levee (Subcommunities A5, A5, A2)
- Intact platform (Subcommunities A2, B2, G3)
- Intact backswamp (Subcommunities F1, G1, G4)
- Fragmented levee (Subcommunities A5, F1, F1)
- Fragmented platform (Subcommunities A1, A5, A5)
- Fragmented backswamp (Subcommunities A2, G1, G2)

Once collected, each sample assemblage was washed under water and debris removed. Samples were sieved (500 µm) and the contents placed in Petri dishes. Specimens were separated using a low-power binocular microscope. For the first sampling period, specimens were sorted to ordinal level. For the other sampling periods, only beetles were separated from the bulk invertebrate material. A large part of this work was completed by Landcare Research technicians and also by participants in several workshops associated with learning procedures for KOIORA-BIOASSIST™.

Beetles were separated into recognisable taxonomic units (RTUs) using external morphological characters (e.g. size, shape, colour). Images of each RTU morphotype were taken using the AutoMontage facility, and these images were used to assist in the identification of specimens to RTU level, and for cross-referencing. The BIOTA database was used to manage specimen and locality information. Beetle RTUs were identified to species level by Andre Larochelle (Carabidae; Landcare Research Honorary Staff member) and Stephen Thorpe (Auckland Museum), using the New Zealand Arthropod Collection (NZAC) as a reference source.

Data analysis

Pitfall and Malaise trap data were analysed separately. In sampling periods 2 and 3, a number of Malaise traps fell over or were otherwise damaged due to extreme weather conditions, so that several sites were not sampled. This resulted in bias in the data that makes comparisons difficult. Unless otherwise stated, most of the results reported here utilise data from all four periods combined for pitfall traps, and combining data from sampling periods 1 and 4 only for Malaise traps.

Species richness, abundance, and species diversity were calculated for each site. Analysis of variance was used to compare these variates between fragmented and intact sites, extracting the variance due to landform and the landform–fragmentation interaction.

Two different multivariate analyses were used to investigate differences in faunal composition between sites and treatments. These were: principal components analysis in Golliwog, and non-metric multi-dimensional scaling (nMDS) in the PRIMER software package (Clarke 1993). Ordination scores should be more similar for more similar beetle assemblages. PRIMER software was used to compare nMDS scores simultaneously across all axes of variation. The SIMPER program within PRIMER was used to identify taxa that contributed most to the compositional differences between treatments.

Knowledge of functional roles at lower taxonomic levels is usually poor, and often inferred or extrapolated from related taxonomic groups. Therefore, the family level is currently judged to be the most suitable taxonomic level at which to undertake functional analysis. We divided beetles into five functional groups based on published literature sources (Klimaszewski & Watt 1977; Hammond 1990). These are: fungivores, herbivores, predators, saprophages, and xylophages (wood feeders). The proportions of different functional groups (i.e. numbers of species and individuals) were compared between fragmented and intact sites for each habitat type using chi-squared tests.

3.2.2 Results

Richness and diversity of beetles

Overall 4644 beetles were collected, representing 271 species. From pitfall traps 66% of specimens could be identified to genus and 21% to species. From Malaise traps, 71% could be identified to genus and 32% to species. All species are listed in Appendix 2.

From pitfall trapping, 1587 specimens of ground-dwelling beetles were collected, representing 29 families and 118 species. There were 44 species (37%) that were only represented by one specimen (i.e. singletons).

In the first year, 695 specimens of beetles were collected, representing 22 families and 77 species. In the second year, 892 specimens of beetles were collected, representing 26 families and 92 species. The difference in the abundance between years was primarily due to one family, the Carabidae (ground beetles). Seven families of beetles were collected in year two that were not collected in year one, and three families were collected in year one that were not collected in year two. However, these families represented less common families, and the abundance of the specimens contributed < 1% of the total abundance from each year.

From Malaise trapping, 3057 specimens of beetles were collected, representing 42 families and 222 species. There were 66 species (30%) that were only represented by one specimen (i.e. singletons).

In the first year, 1715 specimens of beetles were collected, representing 35 families and 171 species. In the second year, 1342 specimens of beetles were collected, representing 38 families and 163 species. The difference in the abundance between years was primarily due to Scirtidae and Clambidae. Seven families of beetles were collected in year two that were not collected in year one, and five families were collected in year one that were not collected in year two. However, these families represented less common families and the abundance of the specimens contributed < 1% of each year's catch.

Species richness and total abundance of beetles were higher in spring (November) than in autumn (February), both in pitfall and Malaise traps. However, diversity showed no consistent seasonal trend (Table 12).

Species accumulation curves for beetles

Species accumulation curves representing numbers of beetles collected at the 72 sites over the four sampling periods (Fig. 3) show no asymptotes. These data suggest that more beetle species could still be caught in pitfall and Malaise traps at these sites.

Differences in beetle assemblages between fragmented and intact forest

The richness and abundance of ground-dwelling beetles (i.e. caught in pitfall traps) was significantly higher in fragmented than in intact sites (Table 13). However, the richness and abundance of beetles caught in Malaise traps were not significantly different between fragmented and intact sites. The diversity of beetle assemblages was higher in intact habitat than in fragmented habitat (in both pitfall and Malaise-trapped faunas).

Species richness, abundance and diversity showed inconsistent patterns among habitats and between sites (Fig. 4).

The composition of beetles caught in pitfall and Malaise traps tended to be distinct between fragmented and intact sites (Fig. 5). The program SIMPER within PRIMER identified taxa that contribute most to the compositional

Figure 3. Smoothed accumulation curves for the number of beetles collected by pitfall and Malaise traps at sites across four sampling periods.

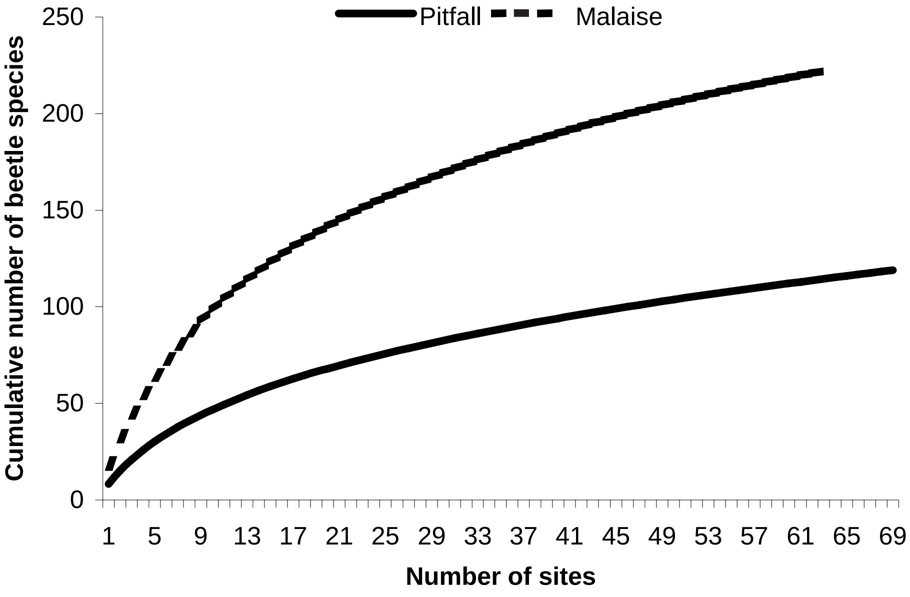

TABLE 12. BEETLES COLLECTED BY PITFALL AND MALAISE TRAPS FOR THE FOUR SAMPLING PERIODS: TOTAL ABUNDANCE AND SPECIES RICHNESS, AND AVERAGE DIVERSITY PER PLOT.

	YEAR 1		YEAR 2	
	SPRING (NOV. 2001)	AUTUMN (FEB. 2002)	SPRING (NOV. 2002)	AUTUMN (FEB. 2003)
Pitfall traps				
Abundance	427	268	581	311
Richness	65	40	74	50
Diversity	0.78	0.77	0.79	0.85
Malaise traps				
Abundance	1270	445	790	552
Richness	135	86	125	93
Diversity	0.85	0.87	0.91	0.86

TABLE 13. AVERAGE RICHNESS, ABUNDANCE, AND DIVERSITY OF BEETLES (PITFALL AND MALAISE TRAPS) AT SITES ACROSS FOUR SAMPLING PERIODS.

	PITFALL TRAPS (all periods)			MALAISE TRAPS (periods 1 and 4)		
CHARACTERISTICS	INTACT	FRAGMENTED	*F*	INTACT	FRAGMENTED	*F*
Richness	7.5	9.4	4.5 *	20.1	14.9	2.7 ns
Abundance	15.7	29.7	13.5 ***	49.7	47.3	0.1 ns
Diversity	0.85	0.75	8.3 **	0.91	0.84	4.4 *

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

differences between intact and fragmented sites (Table 14). Several species of Carabidae (ground beetles) and Staphylinidae (rove beetles) contribute strongly to differences.

We found a predominance of predators in pitfall traps (both in terms of species richness and abundance), and a greater evenness of functional groups in Malaise traps (Tables 14 and 15).

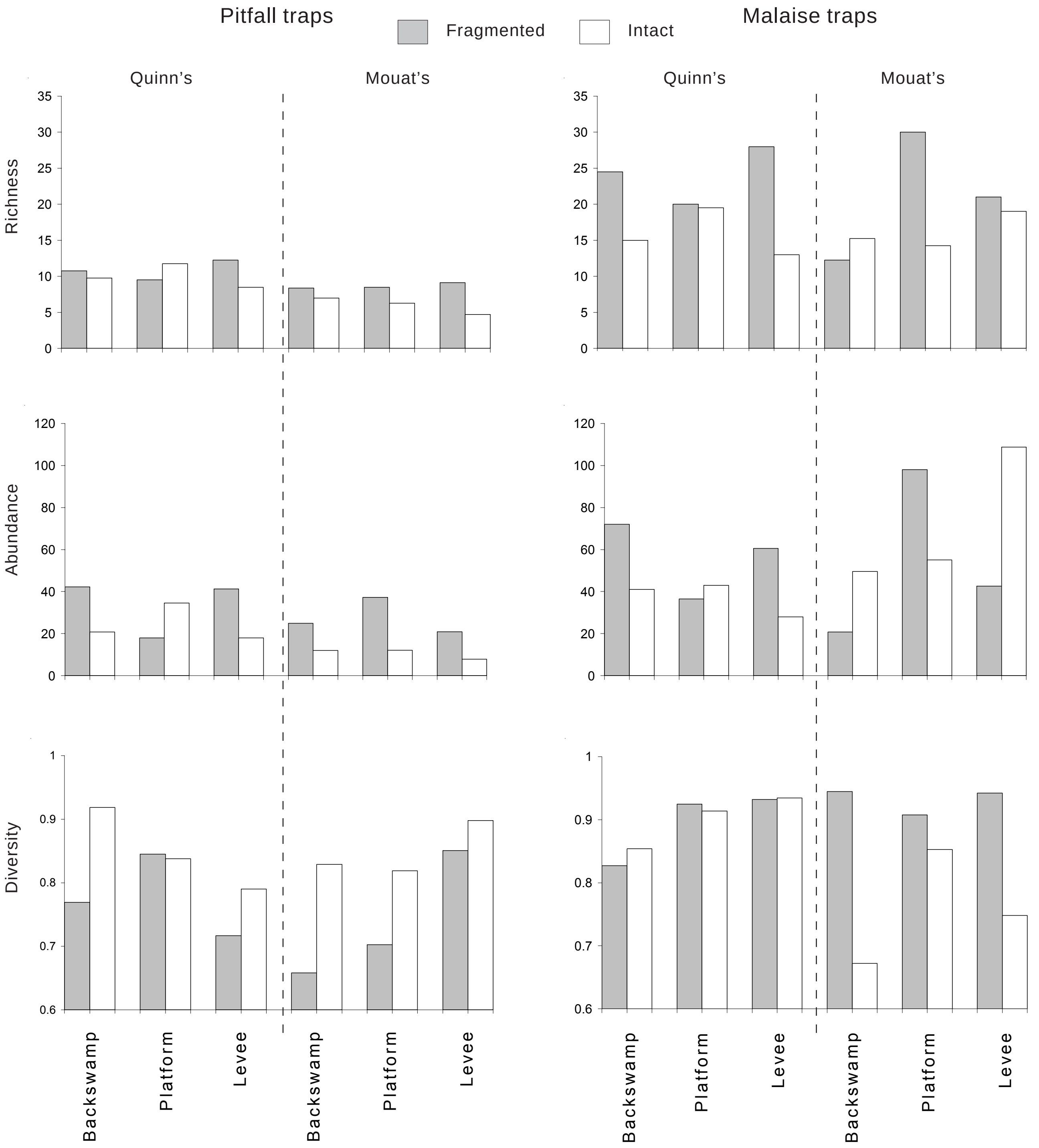

Figure 4. Average species richness, abundance, and diversity of beetles collected in pitfall and Malaise traps in different properties, habitats, and fragmentation states within the Dean Burn. For pitfall traps, statistics average across all four sampling times, while Malaise trap statistics are the averages for periods 1 and 4 (see text for explanation).

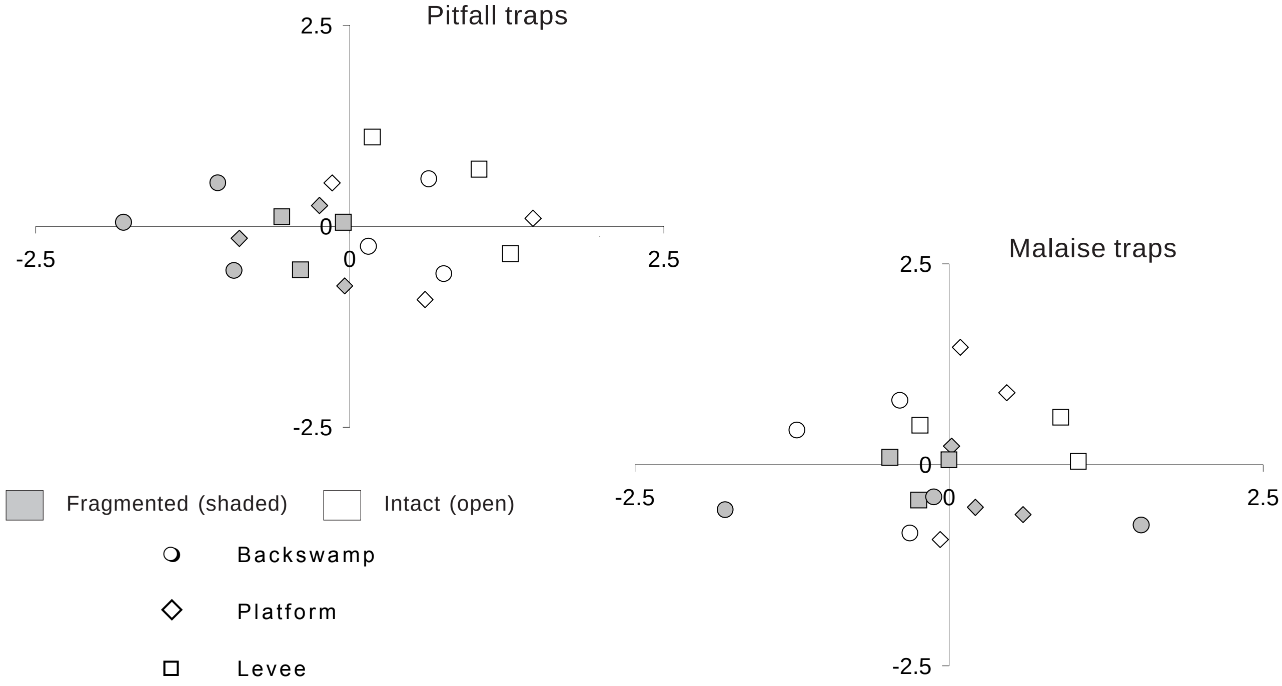

Figure 5. Multivariate analysis of composition of beetles collected in pitfall and Malaise traps in different habitats and fragmentation states in the Dean Burn: ordination scores from non-metric multi-dimensional scaling for beetle assemblages at the 18 sampling sites. For pitfall traps, statistics average across all four sampling times, while Malaise trap statistics are the averages for periods 1 and 4 (see text for explanation).

TABLE 14. AVERAGE ABUNDANCE OF BEETLE SPECIES CAUGHT IN PITFALL AND MALAISE TRAPS AT INTACT AND FRAGMENTED SITES.

Species are listed in decreasing order of their ability to consistently discriminate between intact and fragmented sites.

				AVERAGE ABUNDANCE	
CODE	FAMILY	FOOD GROUP	SPECIES	INTACT	FRAGMENTED
PITFALL TRAPS					
Colanchmacr	Carabidae	Predator	*Anchomenus macrocoelis*	6.78	30.89
col(omal)sp02	Staphylinidae	Predator	(Omaliinae) sp. 02	0.67	25.78
Colmegasand	Carabidae	Predator	*Megadromus sandageri*	11.89	6.44
Colnotaneof	Carabidae	Predator	*Notagonum neoferedayi*	0.22	5.11
col(aleo)sp07	Staphylinidae	Predator	(Aleocharinae) sp. 07	1.33	6.67
coltripsp01	Mycetophagidae	Fungivore	*Triphyllus* sp. 01	0.11	4.00
Colooptirid	Carabidae	Predator	*Oopterus iridescens*	3.56	0.11
Colholcimpi	Carabidae	Predator	*Holcaspis impigra*	4.67	3.56
col(crypt)sp02	Curculionidae	Herbivore	(Cryptorhynchini) sp. 02	1.33	2.44
col(trop)sp03	Curculionidae	Herbivore	(Tropiphorini) sp. 03	0.78	1.56
MALAISE TRAPS					
col(scir)sp05	Scirtidae	Saprophyte	(Scirtidae) sp. 05	45.22	18.00
col(clam)sp01	Clambidae	Fungivore	(Clambidae) sp. 01	12.44	1.89
col(trop)sp01	Curculionidae	Herbivore	(Tropiphorini) sp. 01	4.44	6.78
colpraosp03	Curculionidae	Herbivore	*Praolepra* sp. 03	4.56	3.78
colneomfulv	Curculionidae	Herbivore	*Neomycta fulva*	6.33	1.44
col(aleo)sp07	Staphylinidae	Predator	(Aleocharinae) sp. 07	3.00	8.44
colperisp02	Curculionidae	Herbivore	*Peristoreus* sp. 02	3.67	4.44
colaridbifa	Latridiidae	Fungivore	*Aridius bifasciatus*	1.89	5.56
col(scir)sp01	Scirtidae	Saprophyte	(Scirtidae) sp. 01	4.89	1.89
col?adosp01	Coccinellidae	Predator	?*Adoxellus* sp. 01	2.56	5.78

Functional group proportions differed significantly between fragmented and intact sites in terms of abundance, but less so in terms of species richness (Table 15). For example, significantly more predator beetles were caught in pitfall traps in fragmented sites than in intact sites (Table 15). It is not surprising, then, that the composition distinction between intact and fragmented sites among ground beetle assemblages was largely due to differences in species of predatory beetles, particularly *Anchomenus macrocoelis* and '(Omaliinae) sp. 02' (Table 14). Notably, the Staphylinid

TABLE 15. NUMBER (AND PERCENTAGE) OF BEETLES IN DIFFERENT FUNCTIONAL GROUPS IN INDIVIDUALS COLLECTED IN PITFALL TRAPS AT DIFFERENT HABITAT TYPES IN FRAGMENTED AND INTACT FOREST IN THE DEAN BURN.
The chi-squared test compares counts of species and individuals between fragmented and intact habitat.

	FRAGMENTED			INTACT		
	LEVEE	PLATFORM	BACKSWAMP	LEVEE	PLATFORM	BACKSWAMP
PITFALL TRAPS—**Number**						
Fungivores	10 (19)	8 (20)	14 (25)	8 (20)	9 (18)	10 (22)
Herbivores	8 (15)	7 (17)	9 (16)	5 (12)	10 (20)	6 (13)
Predators	28 (54)	21 (51)	24 (43)	21 (51)	26 (52)	25 (56)
Saprophages	5 (10)	5 (12)	5 (9)	5 (12)	3 (6)	4 (9)
Xylophages	1 (2)	0 (0)	4 (7)	2 (5)	2 (4)	0 (0)
χ^2 Habitat type (8df)			5.63			4.41
χ^2 Fragmented versus Intact (4 df)	0.96	2.76	4.25	Overall (all habitats) χ^2 Fragmented versus Intact (4 df) = 0.48		
—Abundance						
Fungivores	28 (8)	24 (6)	34 (9)	14 (11)	21 (9)	23 (14)
Herbivores	26 (8)	12 (3)	17 (5)	6 (5)	23 (10)	10 (6)
Predators	253 (76)	308 (83)	306 (83)	97 (76)	174 (78)	126 (75)
Saprophages	24 (7)	26 (7)	6 (2)	7 (6)	3 (1)	8 (5)
Xylophages	1 (0)	0 (0)	5 (1)	3 (2)	2 (1)	0 (0)
χ^2 Habitat type (8df)			31.26***			15.28
χ^2 Fragmented versus Intact (4 df)	6.82	26.33***	10.14*	Overall (all habitats) χ^2 Fragmented v. Intact (4 df) = 11.19*		
MALAISE TRAPS—**Number**						
Fungivores	23 (22)	28 (23)	23 (22)	18 (22)	21 (23)	22 (25)
Herbivores	23 (22)	26 (21)	24 (23)	17 (21)	26 (28)	23 (26)
Predators	22 (21)	27 (22)	25 (24)	22 (27)	22 (24)	21 (24)
Saprophages	23 (22)	27 (22)	24 (23)	23 (28)	22 (24)	20 (23)
Xylophages	14 (13)	16 (13)	10 (9)	2 (2)	1 (1)	2 (2)
χ^2 Habitat type (8df)			1.12			2.43
χ^2 Fragmented versus Intact (4 df)	1.83	3.69	3.72	Overall (sum of three habitats) χ^2 Fragmented versus Intact (4 df) = 21.39***		
—Abundance						
Fungivores	109 (24)	156 (22)	88 (23)	84 (13)	166 (39)	116 (27)
Herbivores	112 (25)	173 (25)	102 (26)	34 (5)	86 (20)	180 (41)
Predators	94 (21)	156 (22)	100 (26)	76 (12)	78 (18)	49 (11)
Saprophages	111 (25)	185 (26)	70 (18)	458 (70)	92 (22)	86 (20)
Xylophages	26 (6)	34 (5)	26 (7)	4 (1)	1 (0)	5 (1)
χ^2 Habitat type (8df)			12.20			476.06***
χ^2 Fragmented versus Intact (4 df)	214.43***	20.11***	5.65	Overall (sum of three habitats) χ^2 Fragmented versus Intact (4 df) = 83.03***		

[*] Asterisks denote probability of non- significance (* = $P < 0.05$; *** = $P < 0.001$).

predator ‘(Aleocharinae) sp. 07’ was caught in both Malaise and pitfall traps far more frequently in fragmented than in intact sites.

In Malaise traps, saprophagous beetles were more abundant in intact sites, particularly ‘(Scirtidae) sp. 05’ (see Table 14) than in fragmented sites. Conversely, fragmented habitats had larger proportions of xylophagous beetles caught in Malaise traps (both species richness, and the total abundance of species, largely represented by Zopheridae and Cerambycidae) than intact sites. In Malaise traps, a wider range of functional groups differentiated beetle assemblages of intact and fragmented sites. Here, the major differentiating species were fungivorous (e.g. (Clambidae) sp. 01 was more abundant in fragmented sites), herbivorous (e.g. *Praolepra* sp. 03 and *Neomycta fulva* were more abundant in intact sites), and saprophagous species as well as predators. Several species of Curculionidae (weevils) caught in Malaise traps contributed strongly to compositional differences between fragmented and intact sites (see Table 14).

A number of species were identified as making a major contribution towards faunal differences between intact and fragmented sites. These species could potentially be used to monitor sites as indicator species. Five of the ‘top ten’ species most able to discriminate between intact and fragmented sites for pitfall trapping were ground beetles. These were also among the largest species collected and identified relatively by non-specialists from KOIORA-BIOASSIST™ images.

Differences in beetle assemblages between habitat types

Few generalisations can be made about observed differences in the richness, abundance, diversity and composition of beetle assemblages between the different habitat types trapped along the ecosystem sequence from levee to platform to backwamp. This is because there were large differences between beetle assemblages on different properties, between the sites on those properties (e.g. between the two intact transects at Mouat’s), between the four sampling periods, and in the assemblage patterns derived from the two different trap types. For example, there were significant compositional differences between the three habitat types (levees versus floodplain terraces versus backswamps) in some fragmented transects and in some intact transects, on one or other of the properties (Quinn’s or Mouat’s), and in some seasons, but not in others. Consistent habitat differences could not generally be discerned against this background variation. We note that while traps were placed in habitat types, precise environmental conditions associated with these habitat types show considerable variation, as did the plant community composition.

There were some differences between habitat types in the proportions of functional groups caught (Table 15). Most notably, at intact levee sites, the abundance of saprophagous beetles caught in Malaise traps was skewed by a large catch of Scirtidae sp. 05 (and less so by sp. 01 and sp. 03 species). In fragmented sites, ground beetle assemblages of levees were less heavily dominated by predators than those of platforms and backswamps, while comparatively few sapropageous beetles were caught in pitfall traps in backswamp habitats.

3.2.3 Conclusions from Study 1

Only a relatively small percentage of beetles could be identified to species (20–30%) and genera (c. 70%) level. This is fairly typical for a New Zealand situation.

Even in fragmented sites, sampling yielded high numbers of species, especially in the spring (i.e. November–December) sampling period. The December period has previously been suggested as the best time for sampling beetles by Malaise trapping in the North Island (Hutcheson 1990), and the results of pitfall sampling in this study suggest a similar seasonal pattern.

There were clear differences in beetle assemblages across the local fragmentation gradients. This was evident in higher species richness and abundance, but lower diversity of assemblages at fragmented sites.

Several beetle species are identified as the main contributors to compositional differences between fragmented and intact sites. These are potential indicators of degradation.

Functional group proportions differed significantly between fragmented and intact sites. In particular, predators were considerably more common in the ground beetle assemblages at fragmented sites than at intact sites.

Consistent differences in beetle assemblages between habitat types could not be discerned. This may suggest that habitat differences are more subtle than those induced by fragmentation. However, we prefer the explanation that the habitat ‘replicates’ were in fact considerably different from one another, as indicated by the vegetation classification, and that differences between habitat types were not discernable against the within-habitat variability.

The results suggest that beetle assemblages show high spatial turnover.

3.3 STUDY 2—INVERTEBRATES ON *Coprosma* SPECIES

3.3.1 Methods

Sampling design

Four study areas (Mouat’s, Turnbull’s, Harris Road, and Otapiri) were selected to represent the regional-scale gradient of habitat degradation across the Southland study area. Therefore, the study examines the effects of fragmentation across the west–east gradient.

Within the four different study areas (Table 16), local fragmentation effects were distinguished by selecting representatives of spatially isolated and core fragments. Core fragments at any of the four study areas are associated with varying degrees of catchment deforestation and ecosystem loss, but are not spatially isolated because the forest canopy across the local ecosystem sequence remains intact. At Mouat’s, Turnbull’s and Harris Road, riparian forest fragments radiate out from core forest areas along meandering streambeds. These riparian forest fragments consist of scattered individuals and small groups of native trees and shrubs. These are spatially isolated sites, representing parts of the floodplain ecosystem sequence from which the forest canopy has not been lost. Plots were selected to represent forest core and riparian forest habitats at three of the study areas (Mouat's, Turnbull's, and Harris Road) and from the riparian strip only at Otapiri (since no core area remains here).

Target shrub species

The *Coprosma* species chosen for the study provided a comparable type of structural habitat for shrub-dwelling invertebrates, since they share similar plant architecture, i.e. small leaves and divaricating branches.

To enable invertebrate comparisons to be made between rare and common *Coprosma*, we made an a priori selection of 10 × 10 m study plots that had been sampled in the vegetation study. A plot was selected if it contained at least one common and one rare *Coprosma* species, and where possible, all four of the target *Coprosma* species. Within each plot, a total of three individual plants representing each *Coprosma* species were selected for sampling. The height of all sampled *Coprosma* was standardised to above 2 m, and their location was recorded using GPS.

Because of the limited extent of floodplain habitat remaining, and the scattered distribution of rare plants within the remaining fragments, a fully replicated sampling design was not achieved. Only the most extensive and intact site, Mouat's, was found to contain all four target *Coprosma* species at the required abundance of three plants per species in both core area and riparian strip habitats (Table 17). Further along the degradation gradient at Turnbull's, all target shrub species were present in the core area, but their abundance declined markedly in the riparian strips, where *C. pedicellata* was absent, *C. propinqua* difficult to locate, and *C. wallii* represented by only three plants in c. 3 km of surveyed riparian habitat (Table 17). The degree of isolation of spatially isolated shrubs was considerably greater in riparian strips at Turnbull's than at Mouat's. Harris Road contained all four of the target shrub species, but in very low numbers (< 6 plants collectively), and the riparian strip associated with the Harris Road core area did not contain any of the target shrub species. At Otapiri, the riparian strip contained three of the target shrub species, but *C. wallii* was represented by only a single plant, and *C. propinqua* was difficult to locate, so that only *C. rotundifolia* could be found in the required abundance (Table 17). In total, invertebrates were collected from 60 *Coprosma* plants distributed among the four study sites.

TABLE 16. APPROXIMATE DIRECT DISTANCES BETWEEN THE STUDY SITES.

	MOUAT'S	TURNBULL'S	HARRIS ROAD
Mouat's	–		
Turnbull's	75 km	–	
Harris Road	55 km	25 km	–
Otapiri	62 km	15 km	10 km

Detailed descriptions of some of these sites are given in Rance & Simpson (2000).

Invertebrate sampling

Invertebrates on *Coprosma* shrubs were sampled using the non-quantitative beating technique (New 1998), following specific procedures outlined by Derraik et al. (2001). A clear polythene sheet measuring 1.0 × 1.3 m in size was placed on the ground below each shrub. Ten downward strokes were made on an accessible area of shrub foliage using a 1.5-m-long pole operated by the same person throughout the study. Only a proportion of the available foliage was beaten for each shrub, given the size restrictions of the collection sheet. A record was kept for the estimated area of sampled shrub foliage in relation to the area of total foliage (measured as the two longest axes in cross-section respectively). Attempts were made to keep the area of sampled foliage relatively consistent between different shrubs, i.e. approx. 1.5 × 2.0 m.

Material collected on the beating sheet (plant matter and invertebrates) was immediately transferred to a plastic container, which was stored in the freezer as soon as possible to both kill and preserve invertebrate specimens. Invertebrates were sampled between 6 February and 15 March 2003 during daylight hours (0800–1700 hours). Samples from the same site and habitat type (core area or riparian strip) were collected closely together to keep effects of temporal variation to a minimum. Wind and damp vegetation can greatly influence the efficiency of the beating technique, so samples were taken on dry and still days.

Invertebrate sorting and taxonomy

Invertebrates were segregated from the plant material by hand using a low-power binocular microscope. The same person sorted through all of the samples, and the dry weight of leftover plant material in each sample was

TABLE 17. DISTRIBUTION OF TARGET *Coprosma* SPECIES, AND MEAN (SE) VALUES FOR PARAMETERS CHARACTERISING HABITAT DEGRADATION AND SHRUB ISOLATION, AT FOUR STUDY SITES IN SOUTHLAND.

	MOUAT'S		TURNBULL'S		HARRIS ROAD		OTAPIRI	
TOTAL*	24		20		10		6	
	CORE	ISOLATED	CORE	ISOLATED	CORE	ISOLATED	CORE	ISOLATED
C. rotundifolia	3	3	3	3	3	0	0	3
C. propinqua	3	3	3	2	3	0	0	2
C. wallii	3	3	3	3	1	0	0	1
C. pedicellata	3	3	3	0	3	0	0	0
Core area size	c. 3200 ha		47 ha		< 1 ha		n/a	
OTHER *Coprosma*								
Foliage touching†	2.33 (0.33)		1.42 (0.34)		1.60 (0.31)		0	
Number of plants‡	48.82 (4.27)		64.0 (13.40)		6.30 (0.87)		4.83 (1.78)	
OTHER NATIVE PLANTS								
Woody richness§	12.00 (1.50)		9.58 (0.61)		3.40 (0.43)		4.33 (1.12)	

* Number of located shrubs at each site.

† Foliage touching = mean number of other *Coprosma* shrubs touching the foliage of sampled shrubs.

‡ Number of plants = mean number of *Coprosma* shrubs (all species) over 1 m height in 10 × 10 m plots containing sampled shrubs.

§ Woody richness = mean number of native woody plant species (including *Coprosma*) over 1 m height in 10 × 10 m plots containing sampled shrubs.

recorded. As with most collection techniques, beating collects some invertebrate groups more efficiently than others. Therefore, a two-tiered approach was used for invertebrate taxonomic determinations. For species-level identifications, all true bug (Heteroptera) and moth (Lepidoptera) adults and juveniles were separated and sent to specialists for examination. Juveniles of these two groups were well represented in beaten shrub samples. All of the remaining invertebrates were separated into higher taxonomic groupings and counted. Voucher specimens were deposited in the New Zealand Arthropod Collection (NZAC) in Auckland.

Data analysis

The invertebrate diversity associated with each shrub sample was characterised in two ways. Invertebrate load values were calculated as the number of individuals in each taxonomic group. Although loading calculations provide limited information regarding the richness and origin of component species, they allow for the broad taxonomic and functional composition of the (collected) invertebrate community to be assessed relatively quickly. Loading values are a simple method of assessing whether invertebrates are using certain habitat units and, if so, the relative extent of use.

A second and finer assessment of invertebrate diversity was made using the species-level data obtained from two focal groups (true bugs and moths). Each species from these groups was identified on each shrub and numbers of individuals were recorded for each life history stage.

Without species-level data for all of the invertebrates, a detailed assessment of the community functional composition was not possible, therefore, invertebrates were divided into two broad functional groups: predators and herbivores.

The invertebrate parameters above were correlated against measurements of the beaten foliage area to determine a possible sampling effect. However, we found little evidence for a sampling area effect, so loading and richness measures were retained as count values, rather than converted to density values (i.e. count per unit area). Invertebrate parameters were also correlated against the dry weight of collected plant material to assess the influence of this association on habitat distribution patterns.

Differences in invertebrate load and composition between individual *Coprosma* species, forest patch sizes, and core versus isolated shrubs were investigated using *t*-tests, analysis of variance, and Tukey's tests.

3.3.2 Results

Differences in invertebrate loads among Coprosma *species*

A total of 12 940 individual invertebrates were counted. These were clearly dominated by Arachnids, with very high mite loadings (9535; 74% of overall individuals) followed by spiders (1348; 10%). Pseudoscorpions and harvestmen were also represented but their numbers were low overall (24; < 1%) A range of insect orders were present, with booklice dominant (583; 5%), followed by plant bugs (374; 3%), flies (283; 2%), wasps (237; 2%), beetles/weevils (236; 2%), true bugs (146; 1%) and moths (95; < 1%). Springtails, mayflies, stoneflies, caddis flies, lacewings, weta, and damselflies were present in very low numbers.

The average invertebrate load per shrub was 215.7 (SE 24.3), which was reduced to 66.00 (SE 6.6) when mites were omitted. Orders that dominated community loads (e.g. mites and booklice) were patchily distributed among individual shrubs (indicated by standard error values in Table 18), while less abundant orders (e.g. beetles and flies) were more evenly distributed. Twelve invertebrate orders were found on all four *Coprosma* species.

The weights of plant material in samples and invertebrate loads were correlated (Pearson's $r < 0.50$), but applying a weight correction to loads had little influence on patterns of distribution of invertebrates among different *Coprosma* species so raw data are presented here.

Invertebrate loads clearly differed between common and rare shrub species. Common shrubs had higher average loadings than the rare shrubs (Table 18), largely due to higher mite loads on the two common species. When mites were

TABLE 18. DISTRIBUTION OF INVERTEBRATE LOADS AMONG FOUR DIFFERENT *Coprosma* SPECIES IN SOUTHLAND FORESTS.
Values in plain text indicate mean (and SE). Values in *italics* are sum totals of individuals.

	C. rotundifolia (n = 18)*	*C. propinqua* (n = 16)	*C. wallii* (n = 14)	*C. pedicellata* (n = 12)
Weight of plant material (g)	15.1 (2.2)	9.9 (1.3)	9.5 (1.2)	12.2 (3.6)
Acari	171.7 (34.9)	193.6 (52.2)	138.8 (35.6)	117.1 (31.4)
Mites	*3090*	*3097*	*1943*	*1405*
Araneae	27.3 (4.3)	23.1 (2.9)	21.9 (5.6)	15.0 (3.1)
Spiders	*491*	*370*	*307*	*180*
Other Arachnids†	0.7 (0.3)	0.25 (0.11)	0.3 (0.2)	0.2 (0.1)
	14	*4*	*4*	*2*
Gastropoda	1.7 (0.7)	0.75 (0.44)	0.7 (0.5)	1.8 (1.0)
Snails	*30*	*12*	*10*	*22*
Coleoptera	7.4 (1.5)	7.00 (1.5)	3.6 (0.8)	3.3 (0.8)
Beetles/weevils	*133*	*112*	*51*	*40*
Diptera	4.9 (0.9)	5.3 (1.7)	4.9 (1.2)	3.4 (1.3)
Flies	*89*	*85*	*68*	*41*
Homoptera	3.3 (0.8)	3.6 (0.9)	13.9 (7.3)	5.3 (3.1)
Plant bugs	*60*	*57*	*194*	*63*
Heteroptera	2.6 (1.0)	2.9 (1.0)	3.4 (0.9)	0.3 (0.2)
True bugs	*47*	*47*	*48*	*4*
Hymenoptera	5.4 (1.5)	4.0 (1.1)	2.9 (0.8)	2.9 (1.0)
Wasps	*97*	*64*	*41*	*35*
Lepidoptera	2.3 (0.5)	1.1 (0.3)	1.2 (0.4)	1.4 (0.5)
Moths	*44*	*17*	*17*	*17*
Psocoptera	10.9 (7.2)	2.2 (0.9)	19.1 (8.1)	7.0 (3.4)
Booklice	*197*	*35*	*267*	*84*
Other Insecta‡	2.6 (0.7)	2.1 (1.2)	1.5 (0.6)	6.4 (4.1)
	46	*33*	*21*	*77*
Total number	244.9 (42.7)	234.0 (56.4)	211.8 (49.1)	151.9 (44.8)
	4408	*3744*	*2695*	*1823*
Without Acari	73.2 (11.0)	65.9 (13.1)	73.0 (17.8)	47.1 (9.6)
	1318	*1055*	*1022*	*565*

* n = represents the number of individual shrubs examined.

† Includes pseudoscorpions and harvestmen.

‡ Includes springtails, mayflies, stoneflies, caddis flies, lacewings, weta, thrips, and damselflies.

omitted, *Coprosma wallii* had a similar invertebrate load to the common shrubs but loads on *C. pedicellata* were substantially lower (Table 18).

Only a few invertebrate orders had higher loadings on certain *Coprosma* species. For example, beetle/weevil loads were significantly higher ($P < 0.05$ by analysis of variance) on both of the common *Coprosma* species than on the rare *Coprosma* species. Plant bug and booklice loads were particularly high on *C. wallii* (Table 18; $P < 0.05$ by analysis of variance).

Relatively few true bugs and moths, collected to provide an indication of host-plant differences, were found on a single shrub (a maximum of 16 and 5 individuals respectively). True bugs were collected from 66% and moths from 74% of the shrubs examined. These loads were lowest on *C. pedicellata* (only four individuals were collected) and highest on *C. wallii*, whereas moth loads were highest on *C. rotundifolia* and similar among other species (Table 18).

The level of taxonomic determination in this study did not allow us to assess functional groups within the multi-trophic invertebrate orders of beetles and flies, and these were excluded from calculations. Taxa represented by only a few individuals were also omitted to reduce the influence of spurious observations. The mite trophic guild containing morphospecies known to feed on microbes and/or dead remains of higher plants clearly dominated the functional community, and were also excluded from predator/herbivore calculations. Remaining invertebrates were assigned to herbivore and predator functional groups.

Predator loads (represented by Arachnids and wasps) were more constant than herbivore loads (represented by non-predatory bugs, moths and booklice) among the different *Coprosma* species. Predator loads exceeded those of herbivores on all species except *C. wallii* (Table 19). Rare shrubs supported somewhat higher herbivore-to-predator ratios than common shrubs (Table 19) but differences between all species and between rare and common *Coprosma* species were not significant.

Differences in Coprosma *invertebrate loads along fragmentation gradients*

Effect of core area size—Loadings of invertebrates in three different-sized core forest areas were examined by pooling samples from all *Coprosma* species found in each area. Shrub-dwelling invertebrate community loads did not decline with decreasing habitat area (Table 20). Shrubs at Turnbull's Bush (the medium-sized core area) had significantly higher mite loads than other core

TABLE 19. AVERAGE (SE) PREDATOR AND HERBIVORE INVERTEBRATE LOADS AMONG FOUR DIFFERENT *Coprosma* SPECIES.

	C. rotundifolia (n = 18)	*C. propinqua* (n = 16)	*C. wallii* (n = 14)	*C. pedicellata* (n = 12)
Herbivores	18.1 (7.8)	8.1 (1.3)	35.1 (14.1)	13.8 (5.0)
Predators	33.4 (5.3)	27.4 (3.8)	25.1 (5.6)	18.1 (3.0)
Herbivore:predator ratio	0.69	0.33	1.4	0.75
Mites	171.7 (34.9)	193.6 (52.2)	138.8 (35.6)	117.1 (31.4)
Mite:other ratio	2.39	3.40	2.26	3.00

areas ($P < 0.05$ by Tukey's test), but similar non-mite loads. Invertebrate orders also showed few consistent patterns with core area size (Table 20). The collective load of 'other insects' increased successively from each core area size, and micro-snails were caught considerably more frequently in the larger core areas than the smallest area. However, loads of other orders showed no significant differences between core areas of different size.

Predator loads were higher than herbivore loads in all three core areas. The herbivore-to-predator ratio showed no trend in relation to core area size, but herbivore numbers were highest and predator numbers lowest in the medium-sized core area, producing a herbivore-to-predator ratio twice as high as in the other core areas (Table 21). The absence of *Coprosma wallii* in the smallest core area may have influenced this result, given that this species is associated with relatively high numbers of herbivores (Table 20).

The species-level data assembled for the true bugs and moth groups indicated distinct species assemblages in different core areas. Two true bug species were shared by all of the core areas (i.e. *Romna scotti* and *Bipuncticoris lineatus*, both in the Miridae family). The large and medium core areas shared two other species (the Miridid *Chinamiris guttatus* and an undescribed Phylinid species), while the smallest core area had two species not collected from either of the larger core areas (a new Deraeocorid species and an Anthocorid species, see appendix 2 in Walker et al. 2004). The moth fauna appeared to be even more distinct, with only one species (*Austrocidaria similata*) shared by all core areas. Two other moth species were collected only from the smallest core area, three from the medium, and four from largest respectively. There were no significant differences between areas in the number of individuals collected.

These data suggest that there are landscape-scale biogeographic differences in the invertebrate fauna.

TABLE 20. DISTRIBUTION OF MEAN (SE) INVERTEBRATE LOADS FOR INDIVIDUAL INVERTEBRATE ORDERS AMONG THREE DIFFERENT-SIZED CORE FOREST AREAS IN SOUTHLAND.

INVERTEBRATE ORDER	MOUAT'S (Large) (n = 12)*	TURNBULL'S (Medium) (n = 12)	HARRIS ROAD (Small) (n =10)
Acari (mites)	79.0 (33.7)	208.1(46.9)	56.1 (8.9)
Araneae (spiders)	24.5 (6.8)	15.3 (1.7)	21.6 (5.1)
Other Arachnids†	0.8 (0.3)	0.5 (0.4)	0.3 (0.2)
Gastropoda (snails)	2.0 (0.9)	2.1 (0.8)	0.1 (0.1)
Coleoptera (beetles)	4.0 (0.8)	3.8 (0.7)	8.1 (2.9)
Diptera (flies)	3.5 (1.2)	4.8 (1.3)	2.4(0.8)
Homoptera (plant bugs)	2.8 (1.4)	5.3 (1.9)	1.4 (0.5)
Heteroptera (true bugs)	1.1 (0.6)	1.4 (0.4)	1.0 (0.4)
Hymenoptera (wasps)	0.8 (0.3)	2.6 (0.9)	6.9 (2.3)
Lepidoptera (moths)	0.8 (0.5)	1.7(0.4)	0.7 (0.2)
Psocoptera (booklice)	3.4 (1.7)	4.1 (2.1)	3.5 (1.1)
Other Insecta‡	4.0 (1.7)	0.9 (0.3)	0.6 (0.3)

* n = number of shrubs examined per core area.

† Includes pseudoscorpions and harvestmen.

‡ Includes springtails, mayflies, stoneflies, caddis flies, lacewings, weta, thrips and damselflies.

Effects of spatial isolation—Loadings of invertebrates were compared between shrubs in isolated and core areas at two scales: across all sites using data pooled for all *Coprosma* species sampled in each fragmentation type, and within sites, pooling data for all isolated and all core shrubs within Mouat's and Turnbull's study areas.

Shrub-dwelling invertebrate community loads were greater on isolated shrubs than on those in core areas across all sites, and within Mouat's and Turnbull's study areas (Table 22). We note that *Coprosma pedicellata* had particularly low invertebrate loads, and was seldom sampled as an isolated shrub. Nevertheless, excluding *C. pedicellata* from analyses, and correcting loadings for material weight did not alter the direction of the result.

Predator loads were more even between core and isolated shrubs than were herbivore loads. Herbivore loads tended to be higher and predator loads lower on isolated shrubs than on shrubs in core forest areas at both the landscape and local scales, although these differences were not significant (Table 22). Consequently, herbivore-to-predator ratios were higher on isolated shrubs, although predators tended to dominate the community on both types of shrubs (Table 22). Notably, the herbivore-to-predator ratio was found to be much higher (2.51) at the most fragmented Otapiri site, which held only isolated shrubs.

TABLE 21. AVERAGE (SE) PREDATOR AND HERBIVORE INVERTEBRATE LOADS AMONG THREE DIFFERENT-SIZED CORE FOREST AREAS IN SOUTHLAND.

	MOUAT'S (Large) (*n* = 12)*	TURNBULL'S (Medium) (*n* = 12)	HARRIS ROAD (Small) (*n* =10)
Herbivores	8.3 (3.0)	11.4 (3.4)	6.3 (1.5)
Predators	26.1 (7.0)	18.4 (1.8)	28.8 (7.3)
Herbivore:predator ratio	0.36	0.63	0.23

* *n* = number of individual shrubs examined per core area.

TABLE 22. AVERAGE (SE) PREDATOR AND HERBIVORE INVERTEBRATE LOADS ON CORE AND ISOLATED *Coprosma* SHRUBS AT LANDSCAPE AND LOCAL SCALES.

	LANDSCAPE SCALE		LOCAL SCALE			
	TURNBULL'S + MOUAT'S		TURNBULL'S		MOUAT'S	
	Core (*n* = 34)*	Isolated (*n* = 26)	Core (*n* = 12)	Isolated (*n* = 8)	Core (*n* = 12)	Isolated (*n* = 12)
Herbivores	8.8 (1.6)	31.2 (9.2)	11.4 (3.4)	20.6 (12.7)	8.3 (3.0)	19.7 (5.3)
Predators	24.2 (3.3)	30.2 (3.5)	18.4 (1.8)	23.4 (4.5)	26.1 (7.0)	30.2 (6.1)
Herbivore:predator ratio	0.42	1.24	0.63	0.89	0.36	0.85

* *n* = number of individual shrubs examined per core area.

Both the true bug and moth loads tended to be higher on isolated shrubs than on core shrubs, although the differences between moth loads were relatively subtle. Six out of the nine species of true bug nymphs were collected off remnant shrubs, indicating host dependence on relict plants. However, different species appeared to respond variably to the spatial configuration of their habitat. For example, *Romna scotti* nymphs were collected in higher numbers on isolated shrubs (a pattern that was apparent at both the landscape and local scale), whereas *Chinamiris guttatus* was more strongly associated with core shrubs. A third species, an undescribed Phylinid, was relatively evenly distributed on core and isolated shrubs. Other true bug species were too scarce for analysis, although we note that nymphs from two of these species were found only on isolated shrubs. The landscape-scale results were strongly influenced by collections made at Otapiri Stream, where the six sampled shrubs had the most diverse (6/9 species) and abundant true bug faunas despite the small number of shrubs sampled.

Caterpillars of nine out of 20 moth species were collected off isolated shrubs, suggesting some host dependence on relict shrubs.

The species richness of the moth fauna was greater on isolated than on core shrubs at both study sites, and particularly at Mouat's Bush. Only five of the 20 moth species were shared by core and isolated shrubs, which included the most commonly encountered moth genus *Austrocidaria*. It is possible that some adult moth species could move between core and isolated shrubs within a site. Therefore, unlike the caterpillars, it is not clear to what extent adults used shrubs in the different habitat types, and whether or not they are affected by local gradients of habitat degradation. The data also suggest some separation between moth faunas of isolated and core shrubs, even within a single area. However, considerably more sampling would be required to confirm this observation.

3.3.3 Conclusions from Study 2

There was little evidence that invertebrates were specialists on particular species within the genus *Coprosma* (including true bug and moth species that are thought to be specialists of the *Coprosma* genus). Only a few invertebrates showed a preference for a particular species of *Coprosma*. In the case of *C. wallii* this might be explained by trophic links with secondary food sources hosted by (but not confined to) that particular *Coprosma* species, rather than the plants per se.

The rare species *C. pedicellata* did not host as many invertebrates as the three other *Coprosma* species (the common species *C. propinqua, C. rotundifolia* and the rare *C. wallii*).

Biogeographic differences appear to underlie observed differences in invertebrate composition between different-sized patches of remnant forest.

Coprosma shrubs that were isolated from forest patches in an extensive pasture matrix were well used by native invertebrates. In fact, community loads were significantly higher than in intact sites, providing strong evidence for a 'crowding effect' on these isolated shrubs.

3.4 STUDY 3—LEPIDOPTERA ON *Sophora microphylla*

3.4.1 Methods

Sampling design

This study used the same areas as the *Coprosma* study (above) except that the Harris Road Bush was not sampled.

Sophora microphylla (kowhai) trees were selected for sampling at each of three of the sites. Ten core and ten isolated trees were sampled at Mouat's and Turnbull's, and ten isolated trees were sampled at Otapiri (50 trees in total). Criteria for selection were accessibility, a consistent foliage area available for sampling, minimal signs of dieback, and positioning less than 10 m into the forest from the edge. Davies-Colley et al. (2000) suggested that microclimate edge effects extend at least 40 m into native New Zealand rainforest, but changes are abrupt up to 10 m, and reduce past that distance. Sampling within this distance ensured that all the sampled trees occurred as part of the 'edge' community, and not part of a community influenced more by the environmental conditions found further towards the interior of larger remnants. In the sense of Davies-Colley et al. (2000) and Young & Mitchell (1994), the Otapiri site and riparian sampling areas at Turnbull's Bush and Mouat's Bush have no interior conditions present (i.e. there were no forest areas more than 10 m across or more than 1 ha in area). For each tree, we recorded estimates of height, diameter at breast height (1.5 m), distance to nearest conspecific, distance from the nearest creek or river, and GPS grid reference.

Invertebrate sampling

Sampling was carried out twice over 3-day periods, in late autumn (8–10 May 2003) and late spring (4–6 December 2003); this was because some native invertebrate species are known to be active in autumn and spring, and relatively inactive in winter. Weather conditions during sampling were relatively stable, with little or no wind.

Trees were sampled by beating. Ten blows of equal force and direction were delivered to three separate areas of foliage on each tree, with blows aimed at secondary branches within patches of foliage rather than at foliage. The foliage beaten was 2–5 m above ground level and sampling volumes were estimated by eye to be 0.5–1.0 m^3 per sampling effort (i.e. 1.5–3.0 m^3 per tree). Samples were collected using an upturned umbrella, which was suspended under foliage between 2 m and 5 m above ground level using a 2.5 m length of dowel with a hook attached at one end. Another 2.5 m length of dowel was used to deliver the strikes.

Material was aggregated to a single sample for each tree. Most coarse material, such as twigs or large clumps of vegetation, that fell into the umbrella was immediately shaken several times and discarded. The remaining material was put into plastic containers and labelled for reference.

Invertebrate sorting and taxonomy

The collected material was manually sorted and Lepidoptera larvae were segregated into containers separating visual morphospecies. These larvae were reared to adulthood for identification by B.H. Patrick at the Otago Museum. Remaining vegetation was then put into a heat extractor for 24 hours, and all collected invertebrates where preserved in alcohol and examined. Any remaining Lepidoptera larvae were removed and counted.

Data analyses

Numbers of replicate samples available for statistical tests are low due to a limited study time frame. In addition, invertebrate distributions are notoriously patchy. This can undermine the reliability and assumptions of classic tests of mean differences between groups when sample replication is low. Consequently, this report highlights key patterns in the raw data rather than statistical significance in results.

Differences between sites and states (isolated and core areas) in total generalist and specialist Lepidoptera richness and abundance, as well as individual species distributions and habitat parameters, were compared using analysis of variance. Relationships between assemblages and habitat parameters were examined using simple regressions. Differences between trees in isolated and core areas were compared at two scales: (1) across all sites using data pooled for all isolated and all core trees sampled; and (2) within sites, pooling data for all isolated and all core shrubs within Mouat's and Turnbull's study areas.

3.4.2 Results

Lepidoptera recorded on kowhai

In total, 11 species were reared, with three common to both collection times (Table 23). They included six generalist species that feed on plants other than *Sophora microphylla*, and five specialist species that are known only from *S. microphylla* (Spiller & Wise 1982; B.H. Patrick, pers. comm. 2004). Dugdale (1988) warns that the definition of the subfamily Tortricinae needs revision and the members of this grouping may or may not be closely related.

Autumn sampling yielded far more Lepidoptera caterpillars (192), but fewer species (six) on kowhai trees than spring (31 individuals from eight species). We present analyses of the combined (both seasons) data here.

Sampled trees at Mouat's were significantly taller than at other sites, and those at Turnbull's were shorter. Trees at Otapiri had the greatest average girth (Table 24), and isolated trees sampled at all three sites had greater average girths than those in core areas at Mouat's and Turnbull's sites. We found no significant relationship between tree characteristics (estimated height and girth) or of isolation (distance to the nearest kowhai) and Lepidoptera composition or abundance. However, the specialist *Uresiphita maorialis* was only recorded on some of the tallest trees sampled.

When taxa are examined individually, the specialists *Uresiphita maorialis* and *Chalastra ochrea* were all recorded from trees where the nearest conspecific was within 10 m. However, numbers reared for these taxa was low. The majority of *Meterana decorata* individuals (32/44, or 73%) were on trees with conspecifics within 10 m and all but one were from trees within 30 m of the nearest *S. microphylla* neighbour.

Effects of fragmentation

There were no significant differences between sites in the number of species or the total abundance of Lepidoptera, or in the representation of specialist and generalist groups. Therefore, no significant trends in Lepidoptera composition

TABLE 23. LEPIDOPTERA COLLECTED AND REARED FROM *Sophora microphylla* (KOWHAI) TREES IN AUTUMN AND SPRING.

	MOUAT'S		TURNBULL'S		OTAPIRI
SPECIES	CORE	ISOLATED	CORE	ISOLATED	ISOLATED
AUTUMN†					
Cleora scriptaria	16	16	6	6	38
Ctenopseustis obliquana	8	5	28	14	6
*Meterana decorata**	13	12	4		5
Liothula omnivora		3	1	2	1
*Uresiphita maorialis**			1	2	2
*Stigmella sophorae**			1	1	
Total individuals autumn	37	36	41	25	52
No. species autumn	3	4	6	5	5
SPRING‡					
*Chalastra ochrea**		1			
Cleora scriptaria		2	3	1	3
Ctenopseustis obliquana			4	1	
Meterana decorata	2	1	4		3
*Stathmopoda aposema**				1	1
Harmologa amplexana			1		
Planotortrix excessana		2			
Harmologa scoliastes	1	1			
Total individuals spring	3	7	12	3	7
No. species spring	2	5	4	3	3
BOTH SEASONS					
*Chalastra ochrea**		1			
Cleora scriptaria	16	18	9	7	41
Ctenopseustis obliquana	8	5	32	15	6
Harmologa amplexana			1		
Harmologa scoliastes	1	1			
Liothula omnivora		3	1	2	1
*Meterana decorata**	15	13	8		8
Planotortrix excessana		2			
*Stathmopoda aposema**				1	1
*Stigmella sophorae**			1	1	
*Uresiphita maorialis**			1	2	2
Individuals (No. spp.)	40 (4)	43 (7)	53 (7)	28 (6)	59 (6)
Generalists (No. spp.)	25 (3)	29 (5)	43 (4)	24 (3)	48 (3)
*Specialists (No. spp.)	15 (1)	14 (2)	10 (3)	4 (3)	11 (3)

* Indicates kowhai specialists, illustrated in Crosby & Dugdale (1996).

† In autumn, 192 individuals were reared from 230 field-collected larvae (16.5% loss). Eight parasite cocoons were counted, of which one was an Ichneumonid wasp.

‡ In spring, 31 individuals were reared from 67 field-collected larvae (a loss of 46.3%); 32 parasite cocoons were counted, of which one was a parasitic fly, *Pales* sp. (Tachinidae).

TABLE 24. AVERAGES ACROSS THE TEN KOWHAI (*Sophora microphylla*) TREES AT THE STUDY SITES (DATA FROM AUTUMN AND SPRING COLLECTIONS COMBINED) FOR LEPIDOPTERA COMMUNITY AND HABITAT PARAMETERS.

	MOUAT'S		TURNBULL'S		OTAPIRI
SPECIES	CORE	ISOLATED	CORE	ISOLATED	ISOLATED
No. species	1.4	2.1	2.3	1.7	1.7
No. individuals	4.0	4.3	5.3	2.8	5.9
No. of generalist species	0.9	1.6	1.5	1.4	1.1
Abundance of generalist species	2.5	2.9	4.3	2.4	4.8
No. of specialist species	0.5	0.5	0.8	0.3	0.6
Abundance of specialist species	1.5	1.4	1.0	0.4	1.1
KOWHAI TREES					
Estimated height (m)	9.9	10.1	7.1	6.6	9.7
Girth at 1.5 m (m)	0.9	1.0	0.5	1.1	1.4
Nearest kowhai (m)	4.5	9.9	17.7	16.0	13.0
Metres to river	8.4	7.8	32.4	3.6	21.8

could be linked to the west–east regional gradient of fragmentation and consequent differences in the size of the forest core areas. There were significant differences between sites in the abundance of two species only: the generalist *Cleora scriptaria* was most abundant at Otapiri, while another generalist (*Ctenopseustis obliquana*) was most abundant in Turnbull's core sites.

Certain of the less commonly collected species were recorded in one or two study areas only. The specialist species *Chalastra ochrea*, and the generalists *Planotortrix excessana* and *Harmologa scoliastes* were recorded in small numbers only at Mouat's, while other 'rare' species (the specialists *Stathmopoda aposema*, *Stigmella sophorae*, and *Uresiphita maorialis*) were only found at Turnbull's Bush and at Otapiri. While this may indicate biogeographic differences across the regions, numbers collected are too low to be certain of this.

There were no significant differences between isolated and core trees in the number of species or the total abundance of Lepidoptera, or in the representation of specialist and generalist groups. Only one species (the generalist *Ctenopseustis obliquana*) was significantly more abundant on kowhai in core forest areas than on isolated trees.

3.4.3 Conclusions from Study 3

There was a large seasonal difference (between late autumn and late spring) in the abundance and composition of Lepidoptera larvae found on kowhai (*Sophora microphylla*).

Lepidoptera abundance and diversity found on individual *S. microphylla* trees within smaller degraded habitats was similar to that on trees within remaining core forest habitats.

There were uncommon native Lepidoptera present on individual *S. microphylla* trees within smaller degraded habitat remnants, and in remnant riparian areas.

3.5 DISCUSSION OF STUDY FINDINGS

In this discussion, we attempt to draw general conclusions from the three very different invertebrate pilot studies above.

3.5.1 Effects of fragmentation on invertebrate biodiversity

The beetle study examined a local gradient of fragmentation, and showed clear differences in beetle assemblages, i.e. between intact and fragmented sites within a single study area. This was evident in higher species richness and abundance in fragmented sites, and higher diversity in intact sites. These differences were more evident in ground beetle assemblages (i.e. those caught in pitfall traps) than in beetles caught in Malaise traps. It may be that the plant-dwelling invertebrate fauna has the potential to be more distinct than the ground-dwelling fauna in habitat fragments, given that the former typically operate at smaller spatial scales than the latter, which not only could lead to greater isolation effects, but also greater resilience in restricted areas of habitat. Compositional differences in the ground-dwelling fauna were largely driven by an abundant predator functional group in fragmented sites, while Malaise traps caught fewer saprophageous and more xylophageous beetles in fragmented sites than in intact sites.

How does the habitat area affect invertebrates? Our studies of individual *Coprosma* and kowhai plants suggest that there was little effect of forest patch size on invertebrate faunas. An exception was found in loading patterns for a group of more minor insect orders on *Coprosma*, which suggests that larger areas of habitat may provide larger insect species pools. However, local isolation of shrubs in degraded riparian strips or pasture were shown to have a positive effect on the magnitude of invertebrate loadings, and on the species richness and abundance of the hosted invertebrate faunas on *Coprosma*.

From these studies, it appears that fragmentation (at least at a local scale) may have a positive effect on invertebrate richness and/or number (though not necessarily on diversity). In other studies where similar effects of fragmentation on invertebrate richness and/or number have been recorded, this has been attributed to intact sites having a more specialised and natural fauna. In other words, while fragmented sites retain elements of the natural fauna, they may also contain many generalist species from the surrounding agricultural landscape.

Do the data from our studies support this proposition? In the Dean Burn beetle study, we did not attempt to classify the beetle fauna into generalist and specialist species, but we expect that the Carabid and Staphylinid predators *Anchomenus macrocoelis* and (Omaliinae) sp.02 that dominated the ground-dwelling fauna of fragmented sites in the Dean Burn are generalists. Moreover, lower beetle diversity in fragmented sites suggests that the higher richness and abundance was due to the addition of a few dominant species that are well able to exploit the disturbed habitat.

Although there were striking differences in herbivore : predator ratios between core and isolated *Coprosma* shrubs, species-level data for true bugs and moths on *Coprosma* shrubs indicate that native invertebrates dominated shrub faunas both within core areas and the more abundant fauna on isolated shrubs. This result does not suggest that exotic generalist species are the source of the greater abundance of invertebrates on isolated shrubs. Native species also dominated shrubs in a secondary fragmented shrubland studied by Derraik et al. (2001) in Otago.

The idea that greater richness and/or abundance in fragmented sites is due to the addition of generalist species to a specialised and natural invertebrate fauna is also given only equivocal support by our study of Lepidoptera on kowhai. In the Dean Burn, isolated kowhai supported on average a greater diversity of generalist moth species. However, at a second site (Turnbull's), isolated shrubs supported a significantly lower abundance of generalist species than those in core areas. Overall, that study showed no significant differences in generalist/specialist proportions across either regional or local fragmentation gradients.

3.5.2 Relict shrubs and trees as reservoirs of indigenous biodiversity

An initial expectation of the study was that invertebrates would have preferred shrubs in more intact forest areas, and consequently would have retreated to these core areas. Ecological models generally predict a decline in the diversity of resident species following fragmentation because of increasing disruptions to colonisation and extinction events in relation to decreasing habitat size and increasing spatial and temporal isolation (MacArthur & Wilson 1967; Hanski 1998).

Instead, invertebrates appeared to 'crowd' isolated shrubs and trees in fragmented floodplain ecosystem remnants, so that numbers of individuals and species were higher than on shrubs in core habitat. On *Coprosma* species high numbers of invertebrates were consistently collected off isolated shrubs growing in a pasture-dominated matrix. Moreover, our study of Lepidoptera on individual *S. microphylla* trees showed that small, degraded habitat areas contained some uncommon native Lepidoptera taxa, and had high abundances of the same native taxa present in the larger more intact habitats. Kowhai trees in the most isolated riparian sample site (Otapiri) held a similar or greater diversity and abundance of Lepidoptera than the more intact larger areas.

A 'crowding effect' of invertebrates in isolated habitats with low connectivity has been documented before (Kareiva 1987; Collinge & Forman 1998). Lovejoy et al. (1986) suggested that the effect is a function of the number of animals displaced (by fragmentation and loss of habitat) and the area of intact habitat available to absorb them. Shrubs in core forest areas, therefore, represent a fauna that is more diffusely distributed because of the availability of considerably more suitable habitat.

The Lepidoptera and *Coprosma* studies both illustrate that native plant species present in the small remnant patches of vegetation are important for the maintenance of biodiversity in these modified landscapes. Invertebrates may be persisting in the remnant areas as either declining or self-sustaining populations. Collinge & Forman (1998) have cautioned that the persistence of species in crowded and isolated habitats may be threatened because of negative density-dependent effects. It is also likely that invertebrates occupying core areas may be better cushioned against effects of stochastic events than invertebrates on isolated shrubs. In Southland, recruitment of native woody species is either slow or absent within a pasture matrix, and long-term persistence and replacement is unlikely. Consequently, remnant native plants probably act as biodiversity reservoirs in modified environments over relatively short periods. However, irrespective of decline, adult invertebrates on remnant plants are potential source populations for other areas through dispersal.

Mechanisms for the persistence of native invertebrates in highly modified habitats are still largely unknown. However, this may be complex and highly variable among invertebrate species. Certainly, some species have been found to 'switch' to exotic plant hosts (Patrick & Green 1991) or to have a degree of native host plant flexibility (Alan Eyles, pers. comm. 2003), both strategies that would undoubtedly assist with survival in changing habitats.

3.5.3 Spatial turnover and biogeographic differences in invertebrate communities

In addition to differences between intact and fragment sites, all three invertebrate studies showed differences between the sampling locations that suggest a high degree of spatial turnover in invertebrate biodiversity. The beetle study indicates particularly high spatial turnover over short geographic distances (i.e. within the Dean Burn). The study of invertebrates on *Coprosma* showed disparities between different study areas that may have a biogeographic basis; in particular a number of moth and true bug species appeared to be restricted to certain patches of forest. Lepidoptera on kowhai also showed geographic patterns in a few specialist species. A high degree of invertebrate spatial turnover has been shown before in New Zealand. For example, Lövei & Cartellieri (2000) found that smaller forest fragments shared only a sub-set of ground beetle species with the largest fragment, over separation distances similar to those in the current study. Spatial turnover may be reinforced by fragmentation. For example, Turner & Corlett (1998) have suggested that a combination of fragmentation processes and invertebrate dispersal limitations can result in unique communities within different fragments.

3.5.4 Determinants of invertebrate patterns

An intact dynamic floodplain ecosystem would have highly spatially variable plant and invertebrate communities, representing a variety of stages of recovery from different intensities and types of disturbance (e.g. frost, flooding) as well as habitat variation across the catena. However, all the areas that were sampled for invertebrates in this study on the Southland Plains have been fragmented by anthropogenic agents (e.g. logging, stock, deer, possums, rodents, flood mitigation, drainage) to some extent, and the mode, intensity, duration, and timing of these different artificial disturbances have also been highly spatially variable. It is not surprising, therefore, that invertebrate beetle assemblages in the Dean Burn are highly spatially variable, and that purely environmental habitat patterns (e.g. differences between levee, platform, and backswamp sites) were not distinguishable in our study.

More detailed work may, however, reveal habitat patterns among invertebrate assemblages. For example, specialist beetle species (i.e. those more strongly associated with particular species or types of vegetation) may well have shown different responses to habitat and community variations than generalist beetle species, or the combination of both generalists and specialists presented in this pilot study, which did not attempt to separate specialist and generalist species. Species associated with intact habitats in the Dean Burn (e.g. the ground-dwelling carabids *Megadromus sandageri*, *Oopterus iridescens*, and *Holcaspis impigra*) may be a starting point for these investigations.

Because beetle assemblages did not show strong associations with either habitat types or plant communities, it appears that fragmentation is currently the most overriding determinant of beetle assemblages in the Dean Burn. The study of invertebrates on *Coprosma* species also showed that fragmentation was the overriding influence on composition. Our results, therefore, do not support the idea that vegetation communities will act as surrogates for invertebrate assemblages (an umbrella, or focal species concept), at least at the level at which habitats and community types were discerned in this study. It follows that the conservation of representative vegetation communities in the Southland floodplain ecosystem may not necessarily protect the full range of invertebrate assemblages as well.

3.5.5 Host specificity

The study of invertebrates on *Coprosma* species indicated that invertebrates did not distinguish to a significant extent between different host plant species. This implies that the decline or loss of a rare plant species (e.g. *Coprosma pedicellata*) may not necessarily result in a concomitant loss of rare, host-specific invertebrates. Instead, the loss of rare *Coprosma* species may not negatively affect the invertebrate fauna as long as common *Coprosma* species remain. However, a comparison of the Lepidoptera faunas of *Sophora* and *Coprosma* shows no overlap, which suggests that there is host specificity at the genus level. Thus, invertebrates may be habitat-specific at the level of genera, rather than species; plant diversity at the genus level may be a better surrogate for invertebrate diversity than species richness.

4. General discussion

4.1 DEFINING CHARACTERISTICS OF THE FLOODPLAIN ECOSYSTEM

The forest communities and their rare-plant components studied exhibit a high degree of specificity to the narrow confines of the floodplain ecosystem, which is typically associated with the sinuous courses of narrow meandering streams. Although our sampling design did not formally compare the floodplain ecosystem with those forests that remain in the wider landscape (i.e. outside the narrow, spatially restricted floodplain ecosystem), combined field experience of the authors and comparisons with published and unpublished descriptions suggests that the vegetation types and target plants occur rarely, if at all, outside the floodplain ecosystem. However, because current knowledge of the invertebrate communities of Southland is far more limited, we have less information on the distinctiveness, or otherwise, of the floodplain invertebrate fauna.

We also found relatively high degrees of micro-habitat-specific assemblages within the floodplain ecosystem, at least in terms of plants and vegetation types. Beetle communities studied in the Dean Burn showed considerable variation between the three 'replicates' of the different habitat types. We suggest that the variability among the limited number of replicates of each habitat type (indicated by differences in the plant communities) overwhelmed common features of the habitats. An important conclusion from the invertebrate studies is that this component of the biota shows exceptionally high rates of spatial turnover within the ecosystem.

What are the characteristics of this floodplain ecosystem that give rise to such a distinctive vegetation and flora? We suggest that in their natural state, large, high-velocity floods are probably infrequent events in these ecosystems, and the meandering streams characteristically exhibit frequent but low-velocity flooding. Following bank overflow, this type of flooding flushes the understorey and deposits light veneers of sediment. This regular, low-velocity hydrological disturbance imparts high fertility, but does not cause catastrophic physical alteration of the forest light regime. Instead, high fertility is combined with intermittent conditions that impart high physiological stress on the forest community—namely, temporarily anoxic soil conditions associated with extended water ponding, and intermittent severe frosts (e.g. the 1995 frost that killed high numbers of mature matai trees). These conditions of high physiological stress would tend to lead to local dieback or exclusion of less flood- or frost-tolerant species. This distinguishes the floodplain ecosystem of our study from the floodplains associated with Southland's broad braided rivers (e.g. the Waiau, Oreti, Mataura on the Southland Plains), which typically experience catastrophic, high-velocity floods—a regime of very different disturbances and stresses, favouring a very different suite of adaptive characteristics.

The ecosystem is narrow in local extent (although regionally widespread), determined by subtle and local habitat features, and not easily identified and located using currently available GIS databases. These are features shared with several other ecosystem types (e.g. limestone outcrops, cliffs, and bluffs) that hold high numbers of threatened plant species in New Zealand (Rogers & Walker 2002).

4.2 FRAGMENTATION OF THE FLOODPLAIN ECOSYSTEM

Our study shows that fragmentation affects many aspects of the ecological integrity of the ecosystem. We show profound alteration of properties (weed invasion, diversity of native species, reduced structural complexity, and loss of rare elements) and, in particular, consequences for the specialist plant species restricted within the floodplain ecosystem. There is also substantial alteration of the invertebrate biota, even at local scales. Nevertheless, the study shows that scattered remnants can make a large contribution to invertebrate biodiversity, albeit for a limited time, since remnants may not regenerate in a pasture grass sward.

We suggest that the floodplain ecosystem forest communities and their rare-plants components are strongly dependent on the natural hydrological regimes. In our study, we did not measure hydrology directly or relate estimates of this to the measures of forest fragmentation we devised. However, the hydrological regime of the floodplain ecosystem has been vastly altered in the last century, with virtually all the meander channels of the secondary streams having been straightened by drainage earthworks. Additional drainage earthworks have lowered watertables across most low-lying depressions of the floodplain. Small sections of meandering streams remain water-filled, but channel relocation and straightening has isolated them from stream flow except in instances of peak flow. This disruption of natural hydrological regimes has undoubtedly had a profound effect on community composition, and negative consequences for the persistence of its rare-plant components.

4.3 LOWLAND BIODIVERSITY LOSS AND FRAGMENT VIABILITY

The extent of indigenous vegetation loss across the Southland Plains is on a par with the worst regions of New Zealand (including the Canterbury Plains, Western Bay of Plenty, Waipaoa River Plains (Gisborne), Wairarapa District, the Taranaki ring plain, and lowland Central Otago). The floodplain ecosystem was previously widespread, and is a prime example of rarity induced by human activity (> 99% of the original ecosystem has been lost across Southland).

The New Zealand Biodiversity Strategy (DOC & MfE 2000: 41) Objective 1, ‘first Priority Action, Biodiversity on land’, defines priorities for protection as those habitats and ecosystems that are: (a) not represented within the existing protected area network, and (b) at significant risk of irreversible loss or decline. The floodplain ecosystem in Southland clearly meets both criteria. Even small, highly modified, remnants of the floodplain ecosystem still contain several nationally threatened and at-risk plant species. Further, although fragmentation substantially modifies invertebrate communities, high invertebrate loadings are associated with individual isolated shrubs, even in the most highly fragmented floodplain ecosystem remnants (e.g. Otapiri).

One of the major objectives of this study was to assess the viability of the remaining fragments of floodplain forest on the Southland Plains, and to develop methods to assess their viability elsewhere in New Zealand. If, as we suggest above, the floodplain ecosystem forest communities and their rare-plant components are strongly dependent on the maintenance of natural hydrological regimes, it follows that systematic channel straightening and watertable lowering for agriculture (primarily to reduce property damage by periodic flooding) is the major long-term threat to the long-term persistence (i.e. viability) of the floodplain ecosystem.

Is it appropriate to simply declare fragments of floodplain habitat ‘inviable’ where hydrological regimes have been altered? Regardless of their state of fragmentation, all extant remnants of the floodplain ecosystem are significant for the maintenance of indigenous biodiversity, since further loss of remnants of the ecosystem and its rare-plant components will remove a high proportion of the small fraction of the ecosystem (and its associated biodiversity) that now remains across its former natural range. This suggests that floodplain ecosystem fragments have high conservation value across the full spectrum of fragmentation and modification states. Below, we outline a framework that may assist with the formulation of appropriate conservation goals for different situations, based on the concept of ecological integrity.

4.4 CONSERVATION GOALS FOR REMNANTS OF THE ECOSYSTEM

4.4.1 Components of ecological integrity

The concept of ecological integrity flows from Goal 3 of the New Zealand Biodiversity Strategy (DOC & MfE 2000: 18):

> ‘*Halt the decline in New Zealand’s indigenous biodiversity*
>
> Maintain and restore the full range of remaining natural habitats and ecosystems to a healthy functioning state, enhance critically scarce habitats and sustain the more modified ecosystems in production and urban environments; and do what else is necessary to maintain and restore viable populations of all indigenous species and subspecies across their natural range and maintain their genetic diversity’

To fulfil this goal, it is necessary to define a ‘healthy functioning state’ and what it means to ‘enhance’ a critically scarce habitat, and to ‘sustain’ a more modified ecosystem. Ecological integrity encapsulates the desired outcome of ecosystem maintenance and restoration, and has two components relevant to fragments of floodplain ecosystem:

- Indigenous dominance (including self-regeneration)
- Potential occupancy

In the alluvial floodplain ecosystem, indigenous dominance has two main aspects: the structural dominance of the indigenous forest canopy, and the dominance of natural (i.e. indigenous) ecological processes. The self-regeneration aspect of indigenous dominance means that natural population processes (e.g. recruitment, dispersal) occur without conservation intervention. Potential occupancy is simply a measure of the extent to which the full suite of species that naturally occur within an ecosystem are present.

Although the ideal healthy functioning state has all of the above components of ecological integrity (indigenous structural dominance, dominance of indigenous processes, self-regeneration, and full potential occupancy), this is clearly no longer achievable in many or even most remaining fragments of floodplain ecosystems in New Zealand. Nevertheless, we suggest that the components of ecological integrity provide a useful framework to direct realistic conservation goals and priority setting.

4.4.2 Larger tracts with intact hydrological regimes

A high degree of ecological integrity remains today only in larger tracts of floodplain forest that have fundamentally intact hydrological regimes (e.g. those in the Dean Burn). These fragments represent the very last, largely functioning examples of a once widespread, but now critically reduced ecosystem. In these few examples, conservation goals will be primarily focused on maintenance of ecological integrity, rather than on restoration. Specifically, it will be important to avoid future forest canopy clearance and/or installation of drainage and flood mitigation works, through the application of appropriate protection mechanisms (e.g. formal public protection or private covenant status, District Plan provisions). Maintenance of ecological integrity will also require implementation of fencing and control of feral herbivores and predators. Our study has focused on plants and invertebrates. However, we note briefly that native birds are critical components of the ecological integrity of the floodplain ecosystem; for example, their roles in dispersal and pollination drive the regeneration of many native tree and shrub species. Selective weed control (e.g. stem cutting and herbicide application to reduce the native vine pohuehue (*Muehlenbeckia australis*) and spot control of exotic grasses) may also be needed to maintain native species viability, particularly on artificial edges.

In Southland, floodplain ecosystem remnants that have fundamentally intact hydrological regimes are typically a mixture of continuous, compact core areas of forest, and narrower riparian strips or small fragments. Conservation managers will need to determine whether it is feasible to establish restoration areas outside the core areas, and, if so, their optimum location. For example, fencing and supplementary planting to extend and link remaining fragments would reduce edge effects on core and isolated/riparian areas in the short to medium term, and in the long term these areas would serve to extend the area of floodplain ecosystem.

4.4.3 Smaller fragments with intact or restorable hydrological regimes

Remnants of Southland’s floodplain ecosystem east of the Dean Burn are typically smaller and more isolated, with varying degrees of hydrological alteration. These eastern fragments typically contain more exotic species and fewer native species and rare plants, and have simpler tier structures. This suggests that fragmentation leads to a general decline in ecological integrity. We expect that these trends are ongoing (i.e. ecological integrity is continuing to decline overall), and that they are most rapid in the smallest fragments due to lack of buffering. The overall goal of conservation management for these smaller ecosystem fragments would be to enhance ecological integrity where possible, and elsewhere to merely halt its decline.

In some situations (e.g. Turnbull's, Mabel Bush) it may be possible to divert water from local artificial flood channels to recreate more natural flooding regimes. Here, ecological integrity would be enhanced by restoring the natural dominant ecological processes (i.e. flooding). Restoring a more natural flooding regime should have flow-on effects to other components of ecological integrity. For example, anoxic soil conditions associated with renewed flooding and water ponding may discourage exotic woody species and hence increase indigenous species dominance. Furthermore, self-regeneration of characteristic floodplain species may be stimulated, and the forest fragment may be able to support a greater suite of potential species occupants. As in larger, more intact fragments, the need to control feral and domestic herbivores and predators should be assessed and met. Because edge effects are likely to be more significant in smaller fragments, the protection and re-afforestation of linking and fringing buffer zones may be important, and should be undertaken in tandem with the restoration of flooding regimes.

4.4.4 Small fragments with modified hydrological regimes

As elsewhere in New Zealand, the hydrological alteration of catchments in Southland has been driven by economic forces and associated current land use practices, and is likely to be reversible only in certain situations. What then are appropriate conservation goals for smaller floodplain forest fragments where hydrological regimes have been profoundly altered and there is no prospect of ever restoring these?

Here, we suggest that there should be two primary goals: to maintain or restore structural indigenous dominance and self-regeneration of the common indigenous canopy trees, and to maintain, through active intervention, at least small populations of the floodplain-specialist flora (i.e. our target threatened plants) within or on the margins of these fragments. The rationale is that such forest fragments would retain at least the structural indigenous dominance component of ecological integrity and, therefore, potential for the restoration of higher levels of ecological integrity in the future (e.g. it may be possible to restore hyrological regimes to some extent should land-use practices change). Further, populations of our target rare plants would be maintained across a greater part of their natural range, thus retaining elements of the potential occupancy component of ecological integrity, and the genetic diversity of the rare plant species themselves.

4.5 FUTURE WORK

4.5.1 Hydrological alteration and reversal

To determine goals and prioritise conservation work among individual floodplain remnants, more detailed work may be needed to assess the level of upstream hydrological alteration and the feasibility of reversing this. In Southland, for example, hydrology at the Dunsdale site is largely unmodified by drainage and channel diversion, but natural flows may be affected by plantation forestry in the catchment. At Turnbull's and Mabel Bush, channel diversion and drainage works upstream and in the immediate vicinity have markedly affected the hydrology, but partial restoration of the hydrological regime may be feasible.

4.5.2 Restoration strategies and techniques

Active restoration interventions will be needed in many situations, to stimulate the re-establishment of forest canopies (e.g. to link fragments and mitigate edge effects) and/or to ensure the persistence of target threatened plants where natural ecosystem processes have been altered. Restoration strategies and techniques that are appropriate for the floodplain ecosystem may need to be developed and refined.

In section 2, we discussed the adaptations of the six rare target plants that may have enabled them to persist in fragmented sites, at least in the short and medium term. We also note that the windows of opportunity that arise fortuitously in the process of fragmentation may be closing progressively, with the alteration of the key stress-inducing flooding regimes and the consolidation of exotic grass swards. However, there may be ways in which their adaptations to human disturbance may be exploited for restoration purposes. For example, there is potential to explore a variety of artificial disturbance techniques to encourage recruitment of the target plants on edges (e.g. infrequent spraying with herbicide).

4.5.3 Autecological work

There is scope to improve understanding of the autecology of the six microhabitat-specific target threatened plant species, beyond the information compiled in this report and previous publications. In particular, their long-term security may be improved through a better understanding of their regeneration requirements, coupled with development of techniques to enhance recruitment and subsequent survival.

4.5.4 Advocacy and inter-agency co-operation

Persistence of the floodplain ecosystem in the long term ultimately depends on the maintenance of the required ecological processes at a catchment scale. In other words, if the goal is to maintain and restore the ecological integrity of remaining fragments of floodplain ecosystems, the requirements for this extend well beyond the current boundaries of those fragments, to the maintenance and restoration of hydrological regimes of whole catchments. Therefore, the engagement and co-operative efforts of a number of agencies and industries will be needed if the floodplain ecosystem is to persist in Southland into the future. This will only be achieved with much greater public and agency appreciation and understanding.

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