Resistance, resilience, and patchiness of invertebrate assemblages in native tussock and pasture streams in New Zealand after a hydrological disturbance

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Abstract: We generated hydrological disturbances to investigate the role of disturbance in New Zealand streams in two land uses: native tussock grasslands and exotic pasture catchments. We tested whether physical differences in streambed structure confer higher resistance and resilience in tussock sites than in pasture sites. We also investigated changes in patchiness (at spatial scales larger than 0.06 m^2) caused by the disturbance. Invertebrate abundance decreased immediately after the disturbance. Species density remained unchanged, but species richness (rarefied) increased. Eight days after the disturbance event, abundance and species richness (rarefied) were similar to those of samples collected immediately before the disturbance. Resistance (measured as decrease in abundance) and resilience (measured as recovery within 8 days) did not differ significantly between the land uses. Patchiness increased in both stream types immediately after the disturbance but decreased to predisturbance levels after 8 days. Disturbance caused a redistribution of individuals among patches, some receiving individuals, others losing individuals, and some remaining unchanged. Our results conform with predictions of the patch dynamics concept and are consistent with results of studies of natural disturbance caused by floods.

Résumé : Nous avons produit expérimentalement des perturbations hydrologiques afin d'étudier le rôle de ces perturbations dans des cours d'eau de Nouvelle-Zélande dans des deux régions d'utilisation différente des terres, des bassins versants de prairies de tussack indigènes et de pâturages de plantes exotiques. Nous avons vérifié si des différences physiques dans la structure du lit des cours d'eau des prairies leur confèrent une résistance et une résilience plus grandes que les cours d'eau des pâturages. Nous avons aussi étudié les changements dans la structure en parcelles (aux échelles spatiales supérieures à 0,06 m^2) dus aux perturbations. L'abondance des invertébrés diminue immédiatement après la perturbation. La densité des espèces reste la même, mais la richesse en espèces (calculée par raréfaction) augmente. Huit jours après l'épisode de perturbation, l'abondance et la richesse en espèces (par raréfaction) sont semblables à ce qu'elles étaient dans les échantillons récoltés immédiatement avant la perturbation. La résistance (mesurée par la diminution de l'abondance) et la résilience (mesurée par la récupération au bout de 8 jours) ne diffèrent pas dans les deux bassins dont l'utilisation des terres est différente. La structure en parcelles augmente dans les deux types de cours d'eau immédiatement après la perturbation, mais elle retourne aux niveaux observés avant la perturbation après 8 jours. La perturbation cause une redistribution des individus parmi les parcelles, certaines perdant des individus, d'autres en acquérant, d'autres enfin restant inchangées. Nos résultats sont en accord avec les prédictions du concept de la dynamique des parcelles et sont compatibles avec les résultats d'études des perturbations naturelles causées par les crues.

[Traduit par la Rédaction]

Received 25 June 2002. Accepted 27 May 2003. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 18 July 2003.
J16961

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Introduction

Natural physical disturbance has been recognized by ecologists as an important factor determining the structure of communities (Sousa 1984; Resh et al. 1988). In streams, high discharge events are thought to be the main disturbance structuring invertebrate communities (Townsend 1989; Lake 2000), reducing abundances of most species (Scrimgeour et al. 1988; Hax and Golladay 1998), and redistributing individuals among habitats (Palmer et al. 1996). Recovery following a spate or flood is usually fast, and original abundances are generally regained within 10–120 days depending on disturbance intensity (Mackay 1992; Flecker and Feifarek 1994).

High discharge events can affect stream invertebrates directly in two ways: by detachment from the substrate or as a result of movement of stones with the potential to crush or bury individuals. The first mechanism is indicated by the dislodgement of increasing numbers of invertebrates as discharge in experimental channels is increased (Holomuzki and Biggs 1999) and by the concentration in hydraulic refuges, after floods, of species that are vulnerable to flow detachment (Lancaster 2000). The second mechanism is indicated by higher postflood densities on embedded stones than on loose stones (Matthaei et al. 2000), weak effects of floods in stream reaches with high sediment stability (Cobb et al. 1992), and high mortality in experimental channels containing large, mobile substrate particles (Holomuzki and Biggs 1999). Additionally, disturbance can differentially affect patches that differ in physical structure and stability (Downes et al. 1997), for example, sites with high physical heterogeneity offer a range of hydraulic refuges (dead zones).

Natural physical disturbance is known to induce patchiness in the distribution of organisms in terrestrial (Segura et al. 1998) and marine systems (Underwood 1998), but few studies have specifically addressed this issue in stream systems (Lake 2000). Lancaster and Hildrew (1993) showed that some insect species respond to floods by concentrating in patches where shear stress does not increase with an increase in discharge, whereas Palmer et al. (1995) observed that larval chironomids and copepods were redistributed among habitats following a disturbance. The patch dynamics concept of stream communities (Townsend 1989) suggests that disturbances cause a mosaic of patches, some losing individuals, some not affected, and some receiving individuals. Fast recolonization of depleted patches is possible due to the existence of nearby refuges. Given a long recurrence interval, communities would be expected to have greatest patchiness immediately following a disturbance and then tend toward a more even distribution of individuals among patches until a new disturbance resets the system. In the context of this study, patchiness is defined as aggregated distribution in which each unit (patch) is larger than 0.062 m^2 (the area included by our sampling device) and spaced at least 10 m from each other (the minimum distance between the sampled areas on each sampling occasion).

The study of physical disturbance in streams can be assisted by the use of manipulative experiments to simulate discharge disturbance (Matthaei et al. 1996). In contrast to previous studies, which were generally concerned with small-scale impacts (single stones up to 10 m^2) and located in a single stream (e.g., Douglas and Lake 1994; Matthaei et al. 1996), we applied a hydrological disturbance to reaches 60–90 m long in replicated stream sites. We examined resistance, resilience, and patchiness of macroinvertebrate assemblages following disturbance in streams draining exotic pasture or native tussock grassland. We hypothesized that tussock streams may have greater resistance and resilience than pasture streams because tussock sites are more heterogeneous, which could provide a greater range of hydraulic refuges.

Materials and methods

Study area

The study was carried out in second- and third-order tributaries of the Taieri and Waipori rivers (45°43′S, 169°51′E, total area encompassing all sites = 132 km^2) in the Otago Province of the South Island of New Zealand. Catchment areas ranged from 0.74 to 1.43 km^2 with the exception of Broad Stream (Table 1). Broad Stream had a larger catchment area, but much of the water upstream has been diverted from the catchment to a reservoir so the stream was comparable in size to the others. All study streams contained brown trout (*Salmo trutta* L.), an introduced species that can affect invertebrate behaviour and community composition (Townsend 1996).

The streambed at all sites was composed mainly of cobbles and gravels. Tussock streams had lower mean particle sizes than pasture streams because they had more small particles, sometimes beneath moss (Table 1). Streams in tussock catchments were partially shaded by overhanging grasses, especially species of *Chionochloa* and *Festuca*. Grazing by sheep occurred in tussock catchments historically, but only at low intensity and only during some periods of the year. Grazing had not occurred in our tussock catchments for at least 2 years. Streams in pasture catchments were unshaded, and grazing by sheep and cattle was intense but varied among streams. It is possible that such variation contributed to between-stream variation, but we were unable to address this question.

A large rainfall event occurred in our study area in September 2000, more than 5 months before our experimental disturbances. Our disturbances and sampling occurred during a prolonged dry period in late February and early March of 2001. The only substantial rainfall (12.5 mm) in this period, recorded at a nearby gauge 1 week before our experiment (P. Stevenson, Otago Regional Council, Private Bag 1954, Dunedin, 9001, New Zealand, unpublished data) did not cause increased flow and could not have affected invertebrate communities in our streams. During our study, we observed no sign in the riparian vegetation of a recent flood (such as flattened vegetation or dead leaves trapped in the vegetation). There was no significant rainfall while the experiment was being performed.

Physicochemical properties

Physical and chemical characteristics of the streams were determined following standard methods. Reach gradient was determined with a level and a stadia rod. Width, depth, velocity, and moss cover were determined at 10 cross-sections

Table 1. Physicochemical characteristics of stream sites.

	Tussock			Pasture		
	Anchor	Clarks	Stone	Broad	Bush	M. Road
Drainage area (km^2)	1.21	1.06	0.74	6.04	1.32	1.43
Elevation (m)	540	600	540	480	580	450
Reach gradient (%)	2.6	3.9	4.9	2.5	4.9	2.5
Velocity ($m \cdot s^{-1}$)	0.11	0.13	0.15	0.11	0.10	0.20
Width (m)	0.66	0.66	0.79	0.71	1.40	1.21
Depth (m)	0.32	0.22	0.22	0.28	0.20	0.13
Moss cover (%)	58	64	52	9	0	0
DRP ($\mu g \cdot L^{-1}$)	2.5	1.8	0.9	13.7	6.1	4.9
DIN ($\mu g \cdot L^{-1}$)	1.6	2.5	2.1	61.2	15.6	5.6
MPS (mm)	25	26	11	60	92	10
CV-PS (%)	128	120	161	106	90	73

Note: DRP, dissolved reactive phosphorus; DIN, dissolved inorganic nitrogen; MPS, median particle size of streambed substrates; CV-PS, the coefficient of variation for particle size. Values for width, depth, velocity, and moss cover are means obtained from measures at 10 cross-sections along each stream.

along each stream. Velocity was measured using a flowmeter (Marsh-McBirney Flo-Mate Model 2000; Marsh-McBirney Inc., Frederick, Md.). A Wolman pebble count of at least 100 particles was conducted to determine the median particle size of streambed substrates (Wolman 1954). Concentrations of dissolved reactive phosphorus (DRP) and dissolved inorganic nitrogen (DIN = NH_4^+ + NO_3^- + NO_2^-) were measured (two replicates on each of three visits to the sites) by colorimetric methods on an autoanalyzer.

Experimental design and the disturbance event

The experiments were done using a repeated-measures design. Samples collected immediately before the experimental disturbance were considered controls, whereas samples collected 2 h and 8 days after the disturbance were used to measure resistance and resilience of the invertebrate community, respectively. Three replicates of each stream type were used, totaling 18 samples. Each sample comprised four sampling units, collected at depths of 10–40 cm in similar riffle areas using a Surber sampler (area = 0.062 m^2).

An experimental hydrological disturbance was applied to the streams by means of a water compressor and hose to simulate the high velocities and shear stresses that occur during a flood. In each stream, we systematically hosed a 60- to 90-m reach for about 1 h. The operator moved downstream, "washing" the streambed and taking care to apply the water jet to all portions of the bed, including riffles, pools, and areas under overhanging vegetation and banks. The experimental disturbance was enough to turn the water completely turbid, move stones, and cause the detachment of portions of moss in tussock sites. As a measure of disturbance intensity, shear stress caused by the water jet was sufficient to move even the heaviest standard hemisphere developed by Statzner and Müller (1989) to measure shear stress.

Sampling units collected using the Surber sampler were preserved individually in the field. In the laboratory, we split each sampling unit into two halves and sorted all individuals from one-half (because of the large number of individuals). Invertebrates were identified to the lowest taxonomic level possible. In cases in which species identification was not possible, we separated individuals into morphospecies.

Analysis

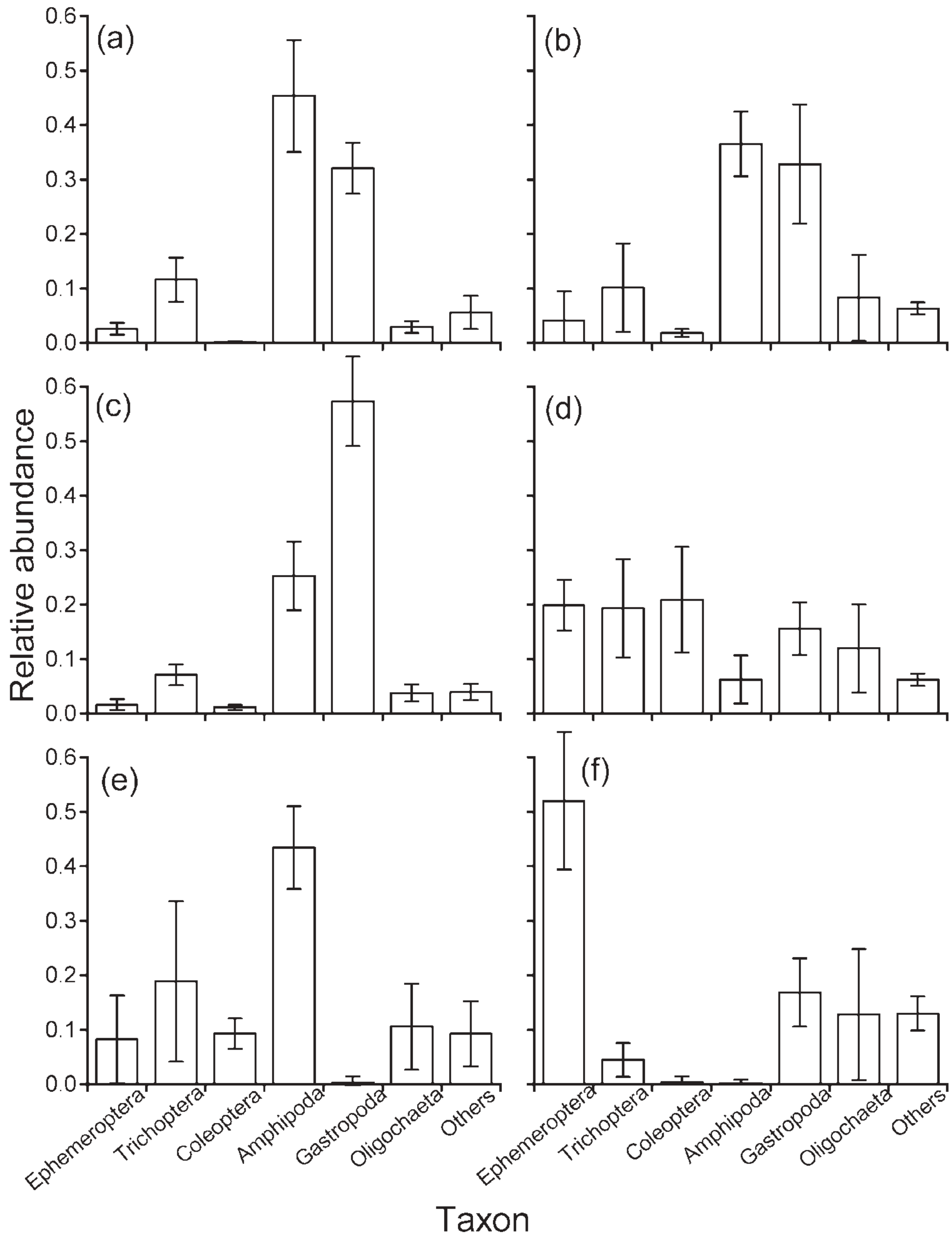
Resistance and resilience in pasture vs. tussock streams

Resistance and resilience of the invertebrate assemblages were assessed using a nested two-way repeated-measures analysis of variance (ANOVA), with land use (pasture, tussock) as the between-subjects factor and time (before, after, and 8 days after) as the within-subject factor. Data from sampling units (Surbers) were nested within streams, the subject of the analysis. Because of the nonindependent levels of the time factor and the consequent potential problems in the variance–covariance matrix, p values were corrected for time and interaction factors by the Huynh–Feldt method (Gurevitch and Chester 1986; Looney and Stanley 1989). We set two a priori comparisons in case the within-subjects factor (time) was significant: before vs. after and before vs. 8 days after sampling times. Analyses were carried out using NCSS software (Hintze 2001). Because of the low replication of streams possible in our large-scale experiment, the power of our analysis was generally relatively low and we set the significance level for α (alpha) at 0.10.

Three metrics were used in the ANOVA analysis: (1) $\log_{10}$ abundance, (2) species density (number of species in sampling units), and (3) species richness (expected values derived by rarefaction-like resampling; see Gotelli and Colwell 2001). Values of species richness were obtained using EcoSim software (Gotelli and Entsminger 2001). The lowest abundance value found in a Surber sampling unit over the three time periods was used in the rarefaction of the other 17 sampling units. The reason for including rarefaction estimates of species richness was the findings of McCabe and Gotelli (2000) that a decrease in species density in a small-scale disturbance experiment was a consequence of reduced abundance in disturbed treatments.

Although we have assessed statistically the differences among catchment types using the repeated-measures ANOVA analysis described above, we illustrate results of our experiment regarding abundance using indexes of resistance and resilience. Resistance was obtained as the total abundance (sum of four sampling units) found immediately after the disturbance divided by the total abundance before the distur-

Fig. 1. Main invertebrate groups found in the six streams studied (left column, tussock streams; right column, pasture streams): (*a*) Anchor; (*b*) Broad, (*c*) Clarks, (*d*) Bush, (*e*) Stone, and (*f*) M. Road. Most individuals of Ephemeroptera in Bush and M. Road belonged to *Deleatidium* spp. (Leptophlebiidae). Nearly all individuals of Gastropoda and Amphipoda collected were of the genera *Potamopyrgus* and *Paracalliope,* respectively. Data are from samples collected immediately before the disturbance event. Error bars indicate standard deviation calculated using four Surber sampling units.



bance event. Similarly, we computed resilience as the total abundance found 8 days after the disturbance divided by the total abundance before the disturbance event. Our original predictions were that tussock sites would have higher resistance and resilience than pasture sites, reflecting the availability of more refuges in the former.

Patchiness following the disturbance

We investigated changes in patchiness within a stream site in an exploratory way using a nonmetric multidimensional scaling (NMS) ordination of the four sampling units collected in each stream site and sampling time. We used Sørensen distances for $\log_{10}$-transformed abundances and performed the ordination in two dimensions. The analysis was carried out in PC-ORD software (version 4.10, MjM Software, Gleneden Beach, Oreg.) using all 72 sampling units (2 stream types × 3 replicated stream sites × 3 sampling times × 4 sampling units). However, we plotted results separately for each stream site because of the large number of sampling units. We expected that sampling units collected in the same site before the disturbance would be positioned close to each other in ordination space, reflecting high simi-

Fig. 2. Mean invertebrate (*a*) abundance, (*b*) species density, and (*c*) species richness (rarefied) in tussock (solid lines) and in pasture (dotted lines) stream sites for three sampling times. Standard errors are shown; n = 3 for each sampling time and catchment type.

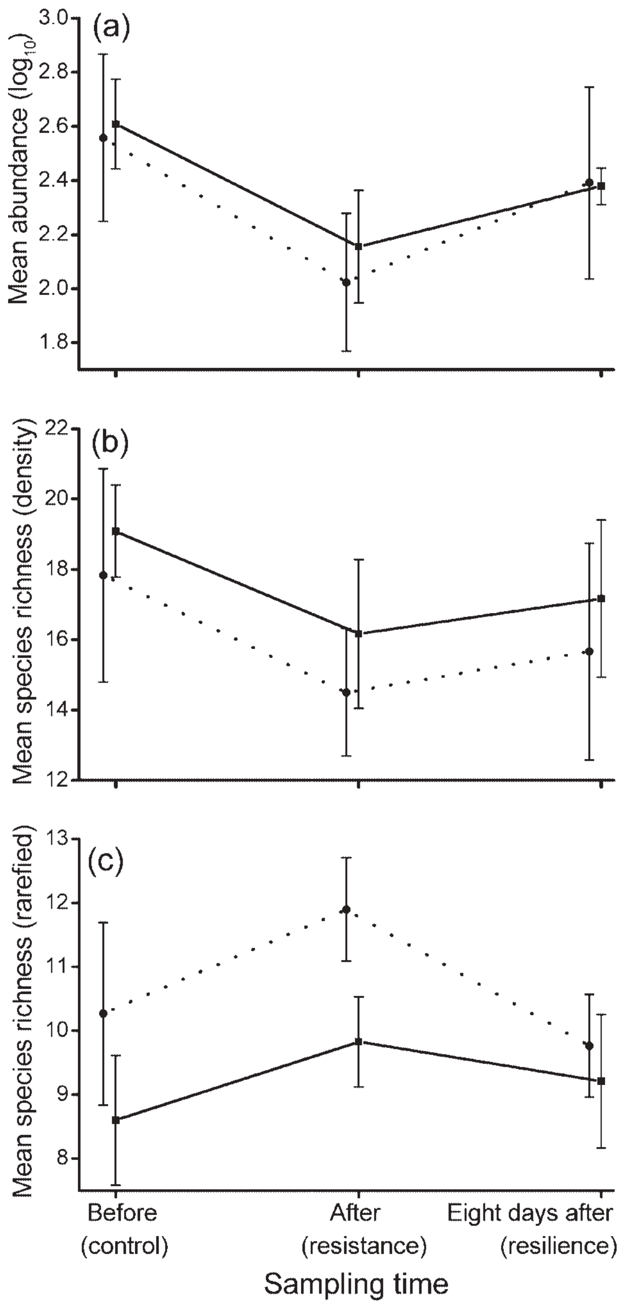


Table 2. Repeated-measures analysis of variance (ANOVA) of effects of land use (tussock vs. pasture) on (*a*) $\log_{10}$ abundance, (*b*) species density, and (*c*) species richness (rarefied).

	df	MS	*F*	*p*
(*a*) Log$_{10}$ abundance				
Between subjects				
LU	1	0.057	0.029	0.873
Streams(LU)	4	1.994		
Within subjects				
T	2	1.482	16.124	0.003
T × LU	2	0.031	0.339	0.693
T × Stream(LU)	8	0.092		
Residual	54	0.101		
(*b*) Species density				
Between subjects				
LU	1	39.014	0.265	0.634
Streams(LU)	4	147.306		
Within subjects				
T	2	60.43	2.334	0.159
T × LU	2	0.264	0.010	0.990
T × Stream(LU)	8	25.889		
Residual	54	10.134		
(*c*) Species richness (rarefied)				
Between subjects				
LU	1	36.871	1.250	0.326
Streams(LU)	4	29.487		
Within subjects				
T	2	15.745	5.012	0.039
T × LU	2	3.712	1.182	0.355
T × Stream(LU)	8	3.141		
Residual	54	2.514		

Note: *T*, time; LU, land use. Error term for the within-subject *F* tests was the interaction *T* × Stream(LU). *p*-values for within-subjects analysis were corrected using Huynh-Feldt method for repeated-measures ANOVA. Symbols "×" and "( )" indicate, respectively, crossing and nesting relationships among variables.

larity in assemblage composition and abundance. On the other hand, we expected that sampling units collected after the disturbance would be scored far from each other, reflecting low similarity among assemblages.

We also tested the hypothesis of increased patchiness (or heterogeneity) following the disturbance, and a subsequent decline, using a similar ANOVA design to that used in the analysis of resistance and resilience but without the nesting factor. The metric that we used was the mean of the squared Sørensen similarities (1 – Sørensen distance) from all six possible pairwise comparisons between the four sampling units collected at each stream site and sampling time. We did not nest the six similarity values within streams because each sampling unit would then be used more than once in the calculations, thus failing to meet the assumption of independence. Sørensen similarities were calculated using $\log_{10}$-transformed abundance. Our prediction was that similarity among sampling units would be high before the disturbance (low patchiness), decrease immediately after, and then increase toward original levels after 8 days.

Results

Physicochemical characteristics

Stream width, depth, velocity, and slope varied across sites within tussock and pasture land uses (Table 1). However, the range of values in the two land uses showed considerable overlap. Tussock streams had greater substrate heterogeneity, as indicated by a higher coefficient of variation for substrate particle size. Mosses were abundant at tussock sites, covering

Fig. 3. Average resistance and resilience of the macroinvertebrate assemblage in the face of a discharge disturbance in tussock (hatched bars) and pasture streams (open bars). Resistance was obtained as abundance immediately after the disturbance divided by abundance immediately before it. Resilience was obtained as abundance 8 days after the disturbance divided by abundance immediately before the disturbance. Standard errors are shown; n = 3 streams for each catchment type.

about half of the bed. Moss was present at only one pasture site, covering 9% of the bed. As would be expected, concentrations of dissolved reactive phosphorus and dissolved inorganic nitrogen were higher in pasture than in tussock streams.

Invertebrate assemblages

Invertebrate assemblages differed between streams in pasture and tussock catchments (Fig. 1). The most conspicuous difference was the high proportional abundance of mayflies (mostly *Deleatidium* spp.) in two of the three pasture sites. Invertebrate assemblages in streams in tussock catchments were dominated by *Potamopyrgus* snails and *Paracalliope* amphipods. One pasture site (Broad) had abundant snails and amphipods as well.

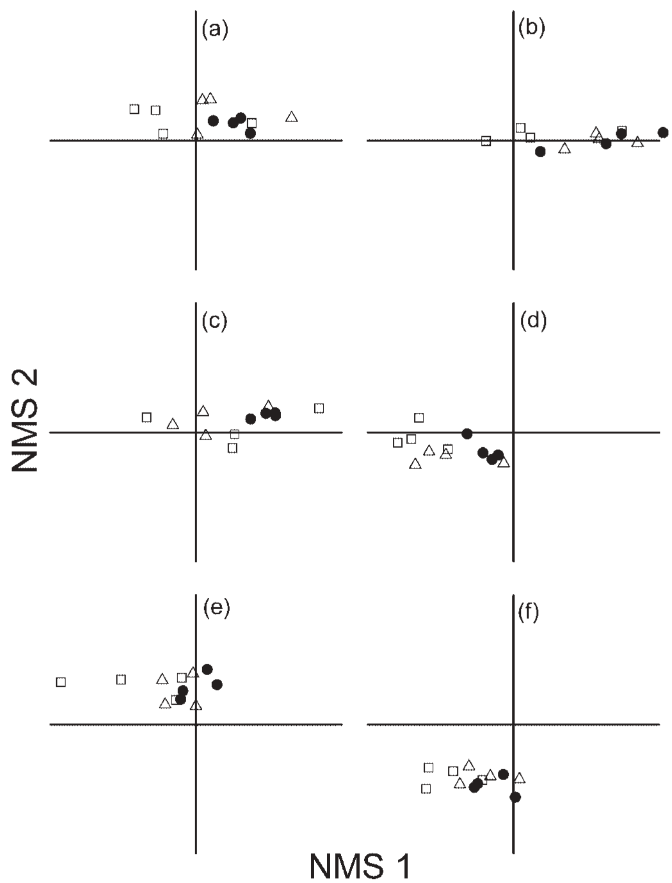
Resistance and resilience in tussock vs. pasture streams

Abundance decreased significantly in streams from both land uses immediately after the experimental disturbance (Fig. 2*a*; Table 2; a priori comparison before vs. after, $p < 0.001$). By 8 days after the disturbance, abundance of invertebrates had recovered to levels quite close to those of control samples (Fig. 2*a*; Table 2; a priori comparison before vs. 8 days after, $p = 0.053$). Resistance tended to be higher in the tussock streams, whereas resilience was similar for tussock and pasture streams (Fig. 3). However, overall there was no significant interaction between land use and time ($p = 0.693$; Table 2), indicating that the two stream types responded in a statistically indistinguishable manner to the disturbance.

There was no clear, consistent pattern in the response of species density by land use types. The effects of land use, time, and the interaction between them were not significant (for all cases, $p > 0.15$; Table 2). Species density did not change as a result of the disturbance, and the pattern was similar for the two land uses (Fig. 2*b*).

In contrast to abundance, which decreased after the disturbance, species richness (rarefied) increased significantly in streams from both land uses (Fig. 2*c*; Table 2; a priori comparison before vs. after, $p < 0.023$). Eight days after the disturbance, species richness had recovered to levels similar to those of the control samples (Fig. 2*c*; Table 2; a priori comparison before vs. 8 days after, $p = 0.917$). There was no significant interaction between land use and time ($p = 0.355$; Table 2), indicating that both stream types responded similarly to the disturbance.

Fig. 4. Nonmetric multidimensional scaling (NMS) ordination of all 72 sampling units collected immediately before (solid circles), immediately after (open squares), and 8 days after the experimental disturbance (open triangles). The analysis was performed once for all samples together but was plotted separately for each stream site. For both axes, lengths are the same and were scaled to the maximum score range of the 1st axis of the analysis. Stress value is 12.2%. Sites on the left are from tussock catchments and those on the right are from pasture catchments: (*a*) Anchor, (*b*) Broad, (*c*) Clarks, (*d*) Bush, (*e*) Stone, and (*f*) M. Road.



Patchiness following the disturbance

The first axis of the exploratory NMS ordination was strongly correlated with $\log_{10}$ abundance (Fig. 4; in all six cases, $r > 0.89$, $p < 0.0001$). The second axis reflected differences in community composition and separated the two land uses only partially, producing high scores for tussock sites and low scores for pasture sites along the second axis (Fig. 4). Sampling units collected before the disturbance were scored closer to each other than those collected immediately afterwards in all three tussock sites and, to a lesser extent, in one stream draining pasture (Bush Stream). With the exception of Broad Stream, sampling units collected 8 days after the disturbance tended to be scored along the first axis at po-

Table 3. Repeated-measures analysis of variance (ANOVA) of effects of land use (tussock vs. pasture) on mean Sørensen similarity among each of four sampling units collected at each stream site and sampling time.

	df	MS	*F*	*p*
Between subjects				
LU	1	0.0026	0.812	0.418
Streams(LU)	4	0.0032		
Within subjects				
T	2	0.0121	11.026	0.008
T × LU	2	0.0021	1.893	0.220
T × Stream(LU)	8	0.0011		

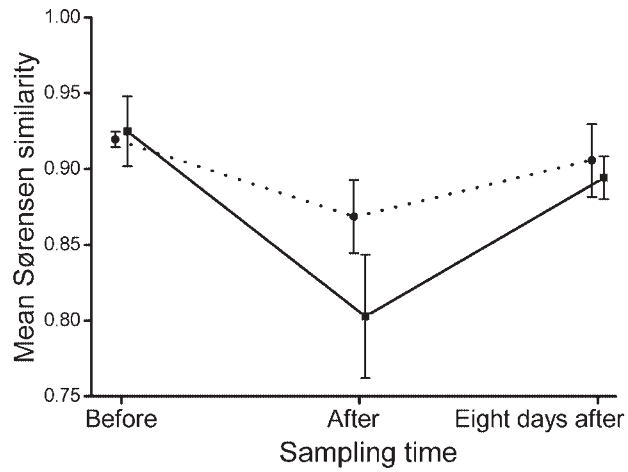
Note: *p* values for within-subjects analysis were corrected using the Huynh-Feldt method for repeated-measures ANOVA. Symbols "×" and "( )" indicate, respectively, crossing and nesting relationships among variables.

sitions intermediate to sampling units collected before and immediately after the disturbance.

Despite the significant overall reduction in abundance detected by the ANOVA analysis, some sampling units were not affected negatively by the disturbance. Except for Bush Stream, all streams had sampling units immediately after the disturbance with similar densities to those of control sampling units (scored close to the control sampling units in Fig. 4). In two streams (Anchor and Clarks), sampling units had abundances higher than the controls (scoring to the right of the reference units in the NMS), probably reflecting the accumulation of individuals dislodged from patches affected negatively by the disturbance. We checked whether sampling units with high abundance after the disturbance were located downstream in the study sites, in which case high abundance could just be an artificial consequence of colonisation by dislodged individuals from upstream, disturbed areas. All four sampling units at each site were collected in sequence starting downstream, and for each stream, the positions of the two highest scored units were 2 and 1, 3 and 2, 2 and 3, 4 and 2, 4 and 3, and 1 and 2, respectively, for Anchor, Clarks, Stone, Broad, Bush, and M. Road. These data show that density of invertebrates after the disturbance was unrelated to location in the stream reach.

Results of the ANOVA analysis of mean Sørensen similarities were similar to those obtained using abundance (Table 3). The interaction between land use and time was not significant ($p = 0.220$; Table 3). There was no difference between land uses ($p = 0.418$), but a significant difference was found among sampling times ($p = 0.008$). Mean similarity among sampling units was high before, decreased immediately after (a priori comparison before vs. after, $p = 0.002$), and recovered to original levels by 8 days after the disturbance (a priori comparison before vs. 8 days after, $p = 0.281$; Fig. 5).

Fig. 5. Mean Sørensen similarity in tussock (solid line) and in pasture (dotted line) stream sites for three sampling times. Data for each stream and sampling time were obtained by averaging the six pairwise comparisons among the four sampling units (Surbers). Standard errors are shown; $n = 3$ for each sampling time and catchment type.



Discussion

Several experimental studies have examined the effects of disturbance on stream invertebrate communities. However, these have generally been concerned with relatively small scales, such as individual stones (Lake and Schreiber 1991), artificial substrates (Malmqvist and Otto 1987; McCabe and Gotelli 2000), baskets filled with stones (Reice 1985; Death 1996), or small areas up to 9 m^2 (Matthaei et al. 1996, 1997). Furthermore, most of them were unreplicated (Mackay 1992; but see Death 1996). Although small-scale studies have shown some of the ways that disturbance can influence stream communities, it is likely that experiments incorporating large areas and replicated in a number of streams will produce more realistic and general results (but see discussion in Death 1996). For example, recovery in a stream patch is likely to be influenced by the surrounding patches. In studies in which the disturbance effect is applied to small patches, resilience is likely to be greater than would be observed in natural floods, where surrounding patches are generally also affected and fewer colonists are available (Brooks and Boulton 1991; but note the similarity in response of invertebrates to natural and experimental disturbance events described in Matthaei et al. (1997)).

Resistance and resilience in pasture and tussock sites

The reduction in invertebrate abundance that we found immediately after the disturbance is in accordance with previous studies of natural and experimental hydrological disturbances. We observed no changes in species density in our study, and this concurs with some previous experiments. McCabe and Gotelli (2000) listed 10 studies that evaluated disturbance effects on species density. There were reductions in species density in eight of them, whereas no change was observed in the studies of Englund (1991) and Reice (1984, 1985). In contrast to abundance, we found an increase in rarefied species richness after the disturbance event. The study of McCabe and Gotelli (2000) was the first to use rarefied species richness to measure changes in stream invertebrate diversity. They found an increase in species richness as a result of several disturbance treatments. Our experimental disturbance involved entire stream reaches, whereas those of McCabe and Gotelli (2000) were restricted to individual paving stones. The observation of increased species richness in two studies performed at contrasting spatial scales warrants the use of this metric in future disturbance research in streams.

Our original hypotheses that tussock streams would be more resistant and resilient in the face of a disturbance in terms of abundance, species density, and species richness was not supported, as revealed by the nonsignificance of the interaction factor in the ANOVA analyses. Compared with pasture sites, tussock sites had greater heterogeneity of substrates (coefficient of variation (CV) of particle size), which may indicate more hydraulic refuges. On the other hand, particle sizes were two to five times larger in two of the pasture streams than in tussock streams, which could confer high resistance to water flow (Downes et al. 1997). However, these habitat features were not significantly associated with higher resistance or resilience. This result partially disagrees with Death (1996), who found differences in species density, but not abundance, when comparing recovery in stable and unstable stream sites. In his study, recovery of species density in stable streams was faster than in unstable streams.

Although the lack of statistically significant differences between the land-use types in our study might represent the actual situation, we do not exclude completely the original hypothesis that assemblage structure in tussock streams would be more stable in the face of a disturbance. Our experimental disturbance was designed to mimic a natural flood. Indeed, except for one stream, abundance reductions in our study (59, 6, 51, 70, 71, and 57%, respectively, for Anchor, Clarks, Stone, Broad, Bush, and M. Road) were in the range generally found in other studies (e.g., Brooks and Boulton 1991; Matthaei et al. 1996). However, as in other experimental studies, this disturbance was not completely realistic. Although we believe that our experiment was more realistic than previous ones regarding spatial scale, we admit that it contained some differences to a real flood. Water velocities near the bed and shear stresses were probably artificially high for our chosen study streams. The water jet was able to move even the heaviest hemisphere used by Statzner and Müller (1989) to measure shear stress, indicating that shear stresses were much higher than usually recorded in floods. The experimental disturbance scoured large patches of moss in tussock sites (A.S. Melo and D.K. Niyogi, personal observations), which is unlikely to happen during real floods in these streams. An additional point is that discharge during our experimental procedure remained unchanged relative to before the experiment, perhaps preventing invertebrates from being flushed very far from the experimental area. Furthermore, rapid recovery of disturbed areas may have been in part due to drift from the undisturbed, upstream reaches (Townsend 1989).

Average resistance and, to a lesser extent, resilience were somewhat higher in tussock streams than in pasture streams, but these differences were not significant. A natural flood, large enough to cause movements of smaller stones but not detachment of moss, might have led to significant differences in resistance and resilience between pasture and tussock sites if greater substrate heterogeneity provided more refuges for invertebrates in tussock streams.

Nearly complete recovery was observed within 8 days in our study. This is in agreement with reports in the literature regarding natural spates and small-scale disturbance experiments (Brooks and Boulton 1991; Mackay 1992).

Disturbance generating patchiness

Our hypothesis that disturbance would cause a transient increase in patchiness was supported by the ANOVA analysis. Similarity among sampling units collected at a site was high before the disturbance, decreased immediately following the disturbance, and then recovered to original levels in 8 days. No differences between tussock and pasture sites were detected by the ANOVA analysis. However, the increase in patchiness following disturbance was more conspicuous for tussock than for pasture sites in the NMS analysis.

An increase in habitat heterogeneity after disturbance is predicted by the patch dynamics concept (Townsend 1989). Matthaei et al. (2000) found an increase in the number of invertebrates associated with embedded stable stones immediately after a spate and a corresponding decrease in abundance on loose, unstable stones. Similarly, spates may cause an accumulation of individuals in patches where shear stress does not increase during spates (Lancaster and Hildrew 1993). In both cases, increases in heterogeneity after the disturbance were clear, with two distinct patch types: refuges and nonrefuges. We collected all of our sampling units in similar areas in riffles; therefore, any (unmeasured) characteristic of the streambed responsible for the increase in heterogeneity is likely to be subtle.

Palmer et al. (1995, 1996) noted a redistribution of benthic copepods following disturbance, but among rather than within distinct stream habitats (sandy mid-channel, fine sediments around dams, coarse sediments around dams, and dam debris). Species found in specific habitats in the absence of disturbance were found in other habitats after a spate. As a consequence, heterogeneity among habitats was high before a disturbance (i.e., each habitat contained a specific pool of species) and tended to decrease after the disturbance. However, not all patches inside the habitats that acted as refuges (vegetation debris and fine sediments around dams) actually received individuals. Patch-specific characteristics (mainly near-bed flow and water flux) were important in determining whether or not a patch acted as a refuge during a flood.

The picture emerging from our results and previous studies is that floods cause a predictable redistribution of invertebrates. Some patches within habitats and some entire habitats lose individuals during spates, whereas some patches within habitats or entire habitats retain or receive individuals, acting as refuges.

Acknowledgements

We thank Chris Arbuckle for assistance in selecting study sites and providing the disturbance equipment. Dean Olsen and Ross Thompson helped identify the invertebrates and Rebekah Eyles helped in the field. We also thank Mark Koren, who assisted at all stages of this work. Claudio Froehlich and three anonymous referees provided useful suggestions to improve previous versions of this article. A.S.M. received a scholarship and travel funds from Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP; Proc. No. 98/00590-0) and thanks all members of the Otago University stream team for providing a very friendly environment during his visit to Dunedin.

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