IMPACTS ON STREAM FOOD WEBS OF NATIVE AND EXOTIC FOREST: AN INTERCONTINENTAL COMPARISON

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Abstract. Native pine-forest streams from Maine and North Carolina, USA, and exotic pine-forest streams from New Zealand were compared to assess the effects of geographic location on three aspects of community structure: (1) taxonomic composition, (2) trophic structure (summarized in terms of functional feeding groups), and (3) food web structure (as connectivity food webs). In addition, pine-forest assemblages in New Zealand were compared to assemblages from New Zealand native forest and grassland streams. Taxonomic similarity was, as expected, low for invertebrates, but there were strong similarities in the algal assemblages in different geographic locations. Trophic structure analysis was unable to distinguish either geographic or land-use effects. Food web analysis revealed structural similarities between the pine-forest streams, regardless of location, but there were clear differences among land uses in New Zealand. Pine-forest streams were typified by food webs with few algal species, low internal connectance and a relatively square shape. Grassland food webs were more triangular in shape and exhibited high internal connectance, while native forest food webs had intermediate characteristics. The results show that the native stream biota, despite a distinct species composition, can adapt to a novel riparian vegetation type and produce trophic and food web structures that are difficult to distinguish from those in the country of origin.

Key words: biogeography; exotic vs. native forests; food web; invasions; Maine (USA); New Zealand; North Carolina (USA); streams.

INTRODUCTION

Invasions have always been a key force in structuring biological communities. In the natural case, invasions of new areas, geographical separation, and subsequent divergence from source stocks have contributed significantly to the evolution of diversity. In recent times, the rate of invasions has increased exponentially as a result of human activities (Vermeij 1991, Townsend 1996) and the mixing of biotas from widely separated landmasses has potentially severe negative consequences for biodiversity. The plight of island fauna subject to invasion by exotic predators has been well documented (Vermeij 1991, Atkinson 1996, Vitousek et al. 1997) as have the effects of exotic plants on terrestrial communities (e.g., Vitousek 1990). Invaders may have no discernible effects, may drive vulnerable competitors or prey to extinction or may have widespread consequences that resonate through the food web, such as the impacts of brown trout in New Zealand streams (Flecker and Townsend 1994, McIntosh and Townsend 1994, Huryn 1996). Invaders also have the potential to alter physical environments, chemical conditions, and biogeochemical cycles of the areas they colonize. The deliberate transplantation by humans of exotic flora and fauna into new locations provides ecol-

ogists with the opportunity to test the resilience of native communities to the arrival of invaders.

Invasions induced by humans extend beyond the introduction of a single species into an existing native setting, sometimes involving the transplantation of an entire exotic landscape. The planting of North American conifer species for timber production is widespread in Europe, South America, South Africa, and New Zealand (Le Maitre 1998). The ecosystem consequences of such conversions are often profound in terms of alteration to soil structure (Ormerod et al. 1993), water yields (Fahey and Jackson 1997), and biogeochemistry (Reynolds et al. 1995, Ventura and Harper 1996). Afforestation of riparian zones has also been shown to impact on stream productivity and benthic invertebrate communities (Edwards and Huryn 1995, Harding and Winterbourn 1995, Friberg et al. 1997, Clenaghan et al. 1998). This is partly a result of disturbance due to forest management, and partly due to changes in the natural disturbance regime (via impacts on hydrology) and in energy supply (as sunlight and as organic matter entering the stream).

Afforestation of New Zealand stream margins by Monterey Pine (*Pinus radiata* D. Don) has occurred as gully land, which is marginal for pastoral farming, has been converted to plantation forestry. New Zealand has no native riparian vegetation type equivalent to such a conifer monoculture. Conifers in New Zealand, such as kauri (*Agathis australis*, Salisbury), *Libocedrus* spp. (kawaka, pauhatea), the podocarps (miro, totara, matai,

TABLE 1. Locations and physico-chemical characteristics of the study sites.

Location	Catchment	Site	Vegetation	Longitude	Latitude	Alt (m a.s.l.)
Maine, USA	Martins	Troy	*Pinus strobus*	44°40′55″ N	69°07′39″ W	130
Maine, USA	Martins	Martins	*Pinus strobus*	44°40′52″ N	69°07′38″ W	128
North Carolina, USA	Coweeta	Herlzler	*Pinus strobus*	35°02′50″ N	83°26′10″ W	760
North Carolina, USA	Coweeta	Cooper	*Pinus strobus*	35°03′50″ N	83°25′55″ W	705
New Zealand	Mimihau	Venlaw	*Pinus radiata*	46°21′30″ S	169°05′10″ E	220
New Zealand	Meggat burn	Berwick	*Pinus radiata*	45°56′50″ S	170°01′45″ E	140
New Zealand	Silver	North col	native bush	45°46′00″ S	170°27′40″ E	300
New Zealand	Silver	Powder	native bush	45°47′45″ S	170°25′30″ E	120
New Zealand	Kye burn	Trib C	tussock	44°57′00″ S	170°21′00″ E	740
New Zealand	Sutton	Sutton	tussock	45°36′00″ S	169°55′00″ E	520

Notes: Abbreviations are: Alt, altitude (meters above sea level); Ctch, catchment area; Flow, velocity in meters per second; Depth, water depth; Width, active channel width; Biof, ash free dry mass of biofilm; Sest, organic seston; CPM, coarse particulate organic matter (>1 mm); FPM, fine particulate organic matter (0.25–1 mm). Results are shown as means with standard errors in brackets below.

kahikatea), and the *Dacrydium* species (rimu, loose-leaved *Dacrydium*), grow mainly in mixed forest and have scale-like leaves rather than true needles. Thus, the introduction of dense pine monocultures to the riparian margins of streams is imposed on a stream biota that is naïve to this sort of forest environment.

In addition to the lack of a common evolutionary history with conifer monocultures, the New Zealand stream fauna lacks a number of taxonomic groups that are widespread in streams in the native range of *Pinus*. These include the mayfly families Baetidae and Heptageniidae, gammarid amphipods, the trichopteran families Limnephilidae and Glossosomatidae, and a number of Plecopteran families (Winterbourn 1995). Many of these groups consist predominantly of ''shredders'' that feed on organic deposits such as leaf material. Winterbourn et al. (1981) hypothesized that the steepness of New Zealand's topography and the flashy nature of the streams contribute to low retention of organic matter and the relative paucity of shredder species. Given the lack of major taxonomic and trophic groups, it may be that New Zealand streams cannot assemble a community similar to those in pine streams in North America.

In this paper, we explore the impacts on New Zealand stream communities of the introduction of *Pinus* into riparian margins. Lövei (1997) colorfully refers to the ''Macdonaldization'' of the biosphere—the process whereby the breakdown of geographical barriers by humans results in the mixing of biota and a homogenization of the world's communities. We seek to explore the question of whether transplantation of exotic riparian vegetation can result in the development of communities that are similar to those at the point of origin of the vegetation. We address two main questions:

1) Has the planting of pine around streams in New Zealand acted to make New Zealand stream communities more similar to those in areas in which pine is native? Streams flowing through exotic pine (*Pinus radiata*) in New Zealand are compared to streams where native pine (*Pinus strobus*) occurs in natural tree monocultures in Maine, and to streams in North Carolina where pine (*Pinus strobus*) is native but grows in an induced monoculture. Our aim is to determine whether comparable ecological influences from riparian pines result in similar stream communities. Specifically, we determine the extent to which these stream communities (a) have species in common, (b) have similar trophic structure (representation of major functional feeding groups [Cummins 1973]), or (c) have similar food web structure (connectance, mean food chain length, etc.).

2) To what extent has afforestation by pine changed New Zealand stream communities? We compare species composition, trophic structure, and food web structure in New Zealand pine streams with nearby streams in native podocarp forest (bush) and native tall grassland (tussock).

METHODS

Study sites

The ten study sites, on second- or third-order streams, represent three land use types and three geographical locations (Table 1). All streams had cobble

TABLE 1. Extended.

Ctch (km²)	Flow (m/s)	Depth (cm)	Width (m)	Biof (g/m²)	Sest (mg/L)	CPM (g/m²)	FPM (g/m²)
1.4	1.56	16.40	1.73	1.51	2.06	591.40	8.29
	[0.29]	[2.44]	[0.10]	[0.27]	[1.06]	[140.70]	[1.81]
10.6	2.90	33.40	4.31	1.21	0.67	282.50	12.21
	[0.16]	[3.29]	[0.29]	[0.15]	[0.11]	[204.21]	[6.12]
1.3	0.19	2.95	1.36	0.68	0.06	98.56	5.61
	[0.05]	[0.60]	[0.39]	[0.07]	[0.06]	[38.69]	[1.41]
1.6	0.41	3.65	0.79	0.62	<0.01	118.27	6.28
	[0.02]	[0.40]	[0.14]	[0.08]		[55.90]	[1.98]
6.4	0.59	38.00	1.11	1.26	2.13	20.31	10.53
	[0.14]	[3.65]	[0.29]	[0.26]	[1.09]	[2.99]	[1.62]
1.3	0.25	9.58	1.26	2.03	2.65	312.69	17.51
	[0.10]	[4.55]	[0.21]	[0.29]	[0.31]	[200.12]	[4.42]
6.8	0.26	11.00	2.70	3.51	5.02	26.87	4.36
	[0.02]	[8.72]	[0.24]	[0.22]	[2.68]	[5.27]	[0.46]
9.9	6.16	10.10	3.67	9.14	1.16	34.35	4.46
	[0.07]	[5.92]	[0.16]	[1.54]	[0.22]	[0.11]	[0.67]
1.6	0.44	6.50	1.97	1.43	0.47	0.32	0.29
	[0.02]	[4.96]	[0.15]	[0.04]	[0.11]	[0.11]	[0.08]
15.2	0.70	11.60	2.40	1.16	0.94	3.81	0.33
	[0.02]	[7.43]	[0.11]	[0.01]	[0.13]	[1.95]	[0.09]

or pebble beds and flowed continuously through the year. Sites were chosen to avoid recent local human impacts (such as forest clearance or vehicle crossings). Aerial photos were used to ensure that upstream of each study site (1) the stream had a complete riparian zone of the desired vegetation type extending to the headwaters and (2) all of the catchment was dominated (>70% cover) by the desired vegetation type. Sampling occurred in summer (New Zealand, November–January; USA, June–July) of 1995 (New Zealand tussock and bush sites) and 1997/1998 (New Zealand and USA pine sites).

New Zealand.—The two native-forest (bush) sites are in the catchment of Silver Stream, a tributary of the Taieri River in the South Island of New Zealand. The study sites are in drainages of mixed broadleaf forest dominated by nondeciduous broadleaf species including *Griselinia littoralis* and *Pseudopanax* sp. A variety of understory species are present, including *Hebe* spp., several fern species, and the deciduous *Fuschia excorticata*. Unlike the New Zealand beech streams described in previous studies (Winterbourn et al. 1981), these trees produce litter that is likely to be palatable to invertebrate species and that breaks down quickly in the stream (Winterbourn 1995).

The two native-grassland sites are also on tributaries of the Taieri River, but occur at higher altitude than the bush sites (Table 1). They flow through riparian margins of native tall-tussock grasses (primarily *Chionocholoa rigida*), subject to light grazing by cattle and sheep.

The two New Zealand pine streams flow through catchments of mature (>30-yr-old) *Pinus radiata*. The trees are large (>30 m tall) and produce complete canopy closure along the length of the stream. The Berwick site is an unnamed tributary of the Meggat Burn in the Taieri River drainage. Prior to planting in the 1960s, the site was covered in low native scrub and native tussock grasses; it now has limited undergrowth, primarily exotic Himalayan honeysuckle (*Leycesteria formosa)*, native shrubs in the *Hebe* genus, and native crown ferns (*Blechnum* spp.) (see Plate 1). The Venlaw site is an unnamed tributary of Mimihau stream in the Southland region of the South Island. Land-use cover prior to planting in the 1960s was mixed podocarp–broadleaf forest, and the pine forest maintains a sparse undergrowth of these species.

United States of America.—The North American pine streams flow through catchments of white pine (*Pinus strobus*), a large tree that is closely related to *Pinus radiata* (Le Maitre 1998) and is the dominant canopy species in mid-to-high latitudes of the eastern United States and Canada. Although it forms occasional monoculture stands in the wild, *P. strobus* usually grows in association with hemlock and hardwood species (at more southerly latitudes) or spruces and firs (northerly latitudes).

The Maine sites are located near the town of Troy in Waldo County. The Martins site is on the main stem of Martins Stream, while the Troy site is a tributary of Martins Stream. Both sites are in woodlots composed of predominantly white pine and balsam fir (*Abies balsamea*) growing in mixed-age stands (see Plate 1). In the Martins site, but not the Troy site, there is a prolific understory of broadleaf species dominated by red maple (*Acer rubrum*). This forest is the product of natural regeneration of pastoral land retired ~60 yr ago and is minimally managed to encourage good timber species such as fir and pine. Areas immediately adjacent to the stream have not been harvested in the last 60 yr and contain large specimens of white pine that form a closed canopy over the stream.
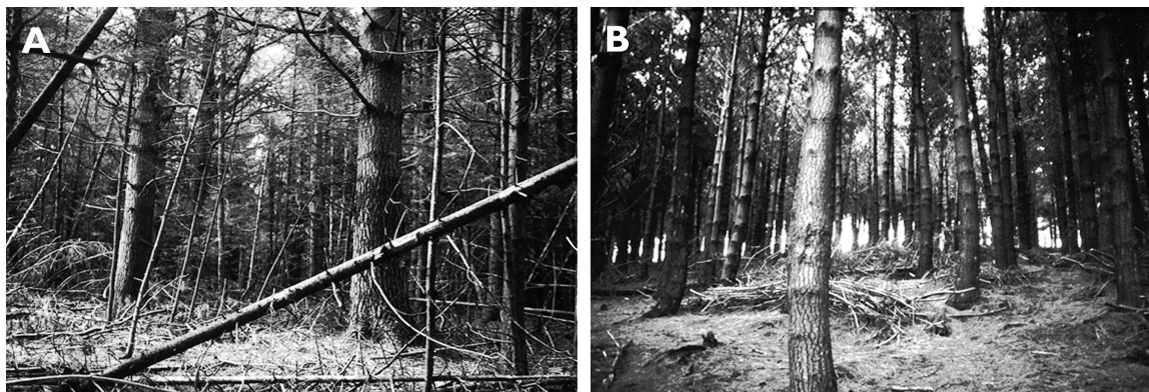
PLATE 1. View of pine forest in (A) Troy, Maine (USA) and (B) Berwick, Otago, New Zealand (Photos: R. Thompson).

The two North Carolina study sites are located in the Coweeta Hydrologic Laboratory (U.S. Forest Service) near the town of Otto in Macon County. Both sites are second order streams flowing through experimental monocultures of white pine, and have been described in detail elsewhere as catchments 1 (Cooper) and 17 (Herlzler; Woodall and Wallace 1972, Swank and Crossley 1988, Whiles and Wallace 1997). These sites were converted from native mixed hardwood–softwood forest (with a component of white pine) to white pine monocultures in 1956 (Herlzler) and 1957 (Cooper). The sites are intensively managed to maintain pine as the dominant species (Whiles and Wallace 1997), but exhibit a sparse undergrowth of rhododendron (*Rhododendron maximum*).

Physicochemical sampling

A suite of ecological variables was measured at each site to define physical and chemical parameters at base flow. Flow velocity at 40% of total depth was measured at 20 random locations along the site using a standard meter. Organic-matter standing crop and supply were measured using the methods of Jaarsma et al. (1998), as follows. Ten Surber samples (area 0.06 m², mesh size 250 μm) were placed at random locations along the stream. Organic matter derived from these samples was wet sieved into 250 μm–1 mm (fine particulate organic matter [FPOM]) and >1 mm (coarse particulate organic matter [CPOM]) fractions, weighed, ashed (at 550°C for 12 h), and reweighed to ascertain the amount of organic matter on the streambed. Two 500-mL water samples were filtered through preweighed Whatman GF-C filters, dried, weighed, ashed (at 550°C for 3 h), and reweighed to ascertain supply of organic matter as seston (at base flow).

Biofilm at each site was measured as ash free dry mass (AFDM) per square meter of substrate. Ten cobbles were gathered at random along the stream reach, and each was scrubbed clean of biofilm into a known volume of distilled water and allowed to settle for 12 h before blending in a commercial food blender. Samples of 15 mL were then filtered on to preweighed

Whatman GF-F filters (Whatman, Clifton, New Jersey), dried, weighed, ashed (at 550°C for 3 h), and reweighed to measure the amount of biofilm on each rock. A foil weight–area regression was used to estimate the surface area of each rock.

A multivariate analysis was used to test for significant differences in the physical nature of the sites. Analysis of similarities (ANOSIM; Clarke and Warwick 1994) with 10 000 iterations was used to test for any significant differences between locations and land uses. This procedure is analogous to analysis of variance in univariate statistics and uses a simple nonparametric permutation procedure (Faith et al. 1987, Clarke and Green 1988). The values for the different physical parameters (mean and standard deviation of flow velocity, depth, and width) were used to cluster the sites using hierarchical agglomerative clustering (Clarke and Warwick 1994). This technique generates a matrix of dissimilarity scores between sites. ANOSIM was used to analyze whether the dissimilarities within our a priori defined groupings (i.e., either location or land use) were higher than between groupings. The test statistic used is global rho, which equals 1 when all replicates within a group are more similar to each other than any replicate outside the group, and equals 0 when the dissimilarities between groups and within groups are the same on average. A similar analysis was carried out on the data for food resources (AFDW biofilm, organic seston, CPOM, and FPOM).

Algal sampling

Algal species composition was described based on rock scrubbings. Five 0.5-mL samples were taken from the rock scrubbings from each site and used to construct wet mounts. These were inspected under 200–400× magnification to identify algal species present using the texts of Patrick and Reimer (1966, 1975), Prescott (1973, 1981), Whitford and Schumacher (1973), Foged (1979), Bourelly (1981, 1985, 1988, 1990), Krammer and Lange-Bertalot (1986–1991), Cassie (1989), and an unpublished key (National Institute of Water and Atmospheric Research, Christchurch, New Zealand).

Algal taxonomy was checked by photographing species and sending the photographs to local experts to confirm identifications (see *Acknowledgments*).

Animal sampling

Ten randomly located Surber samples (area 0.06 m², mesh size 250 μm) were taken at each site to sample benthic macroinvertebrates and preserved in 5% formaldehyde for return to the laboratory. Where fish were present (New Zealand and Maine sites), these were sampled using electric fishing, and 10 of each species were euthanized and retained for gut analysis. Where aquatic amphibians were present (frogs and newts in Maine, salamanders in North Carolina) only wholly aquatic life stages were retained. Crayfish were sampled both by manually searching under rocks and by electric fishing.

Surber samples were searched under 10× magnification in the laboratory for invertebrates, excluding those <1.5 mm in length, terrestrial invertebrates, partial invertebrates, pupae, and empty insect cases. Such a procedure excludes meiofaunal species, but these were very rare in the gut contents (two occurrences) and so probably comprise a minor component of these food webs. It may also exclude some small instars of macro-invertebrates, but as these individuals often cannot be identified to species level, and we were unable to carry out gut analysis on them, these were excluded from the food webs. Pupae were rare (three occurrences) and were excluded as it was not possible to identify species reliably. Macroinvertebrates were measured and identified to the highest degree of taxonomic resolution possible. Winterbourn and Gregson (1989) was used for general identification of New Zealand invertebrates, with reference to specialist keys for hydraenid beetles (Ordish 1984) and rhyacophilid caddisflies (McFarlane 1951). Merritt and Cummins (1996) was used for general taxonomy of American invertebrates together with Pennak (1978), Brigham et al. (1982), Thorp and Covich (1991), and Wiggins (1996). Fish (Fish and Wildlife Unit, Department of Zoology, University of Maine, Orono, Maine, USA), crayfish (Pennak 1978), and salamanders (Conant 1975) were also identified to species level. Identification was carried out to species or genus level where keys existed, or to morphospecies where keys were incomplete or absent. Morphospecies are distinctive morphological groupings, usually based on external coloration and body form. They were later attributed species names where possible by sending to relevant experts. Of the 175 taxa identified in the 10 sites, 87% were identified to genera and 35% to species. Some taxonomic groups (e.g., Empididae, Muscidae, oligochaetes) are poorly described in New Zealand, and were left at a morphospecies level for both the New Zealand and USA samples to permit intercontinental comparisons (Appendix A).

Invertebrate lengths were used to estimate biomass using the length–biomass relationships (for the USA) of Benke et al. (1999) and (for New Zealand) of Towers et al. (1994). Where these were not sufficient, length–mass relationships were generated using individuals from samples or nearby sites. Crayfish were not included in biomass analyses as their occurrence was very patchy and a single individual in a sample had a disproportionate effect on the data.

Species composition

Species lists were formed for each site. For diatoms and invertebrates, these were simplified into simple measures of richness. For the invertebrates only, abundance data were also used to calculate a measure of equitability (Pielou's evenness). Similarities in species lists were calculated separately for diatoms and invertebrates using presence/absence data. Similarity percentages (Clarke and Warwick 1994) were calculated using the program Simper in the computer package Primer (Plymouth Marine Laboratory, Plymouth, UK). This procedure calculates the Bray-Curtis dissimilarity between groups of samples and the average similarity within a group of samples.

Effects of location (New Zealand, Maine, or North Carolina) and land use (pine, tussock, or bush) were analyzed separately using one-factor randomization tests (Manly 1997). Location analyses used the six pine sites and described differences in overall richness, invertebrate richness and evenness, and diatom richness. Land-use analyses compared the same measures between the New Zealand pine, bush, and tussock sites. A simple Excel macro (Microsoft, Redmond, Washington, USA) was designed that randomly assigned the sample labels 10 000 times, calculating each time the differences between randomized group means using the F statistic. The number of times that the randomized F statistics exceeded those from the correctly labeled data set was used to calculate a P value. It is important to note that, for randomization tests, F may be large but not significant, if a result as high occurs many times by chance alone. The resultant F is specific to each test, so a smaller F may be significant in one test, even if a larger value of F is not significant in another. Randomized t tests (1000 iterations) were used as post hoc tests for differences between pairs of locations and land uses. As power is low for this study, a flexible approach has been taken to hypothesis testing, alpha has been set at the 10% level and post hoc tests are considered for comparisons where nonadjusted P values exceed this level. In addition, in order to acknowledge the likely increased probability of Type I error due to multiple testing, a sequential Bonferroni adjustment procedure (Holm's procedure, Wright 1992) was used to generate critical values for the rejection of the relevant null hypotheses. Tests that remain significant under those criteria are indicated.

TABLE 2. Similarities in species composition for invertebrates (plain text) and algae (bold text) based on presence/absence data.

	Internal similarity	Maine	North Carolina	NZ pine	NZ bush	NZ tussock
Internal similarity		**48.10**%	**56.67**%	**56.67**%	**47.06**%	**68.52**%
Maine	49.68%		**47.85**%	**53.69**%	**46.32**%	**46.05**%
North Carolina	60.36%	24.88%		**48.15**%	**47.46**%	**43.69**%
NZ pine	46.74%	2.05%	0.36%		**54.29**%	**45.24**%
NZ bush	42.04%	4.68%	3.52%	44.14%		**36.41**%
NZ tussock	52.03%	5.37%	0.87%	34.14%	39.59%	

Note: Results are expressed as percentage similarity within groups and between locations.

Trophic structure

Invertebrate trophic structure was described using functional feeding groups. This technique groups species together based on similar feeding characteristics. The groups used in this analysis are based on those of Merritt and Cummins (1996). Species were divided into algal consumers, collector–filterers (filter material from the flow using constructed nets), collector–gatherers (feed on organic deposits on the stream bed), filter feeders (filter material from the flow using mouthparts), predators (feed on other invertebrates), and shredders (feed on coarse organic material, e.g., leaves, wood). Each species was attributed a functional feeding group based on the literature (USA, Merritt and Cummins 1996; New Zealand, Cowie 1983, Commonwealth Scientific and Industrial Research Organization 1991). Effects of location (New Zealand, Maine, or North Carolina) and land use (pine, tussock, or bush) were analyzed separately using one factor randomization tests (Manly 1997) as outlined above. Similarity percentages among pairs of stream sites were calculated for functional feeding group composition in terms both of representation of species and biomass in the groups. Differences in trophic structure were analyzed using analysis of similarities (ANOSIM) with 10 000 iterations (Clarke and Warwick 1994) on a similarity matrix generated using hierarchical agglomerative clustering. As replication in this study is low, it was not possible to carry out post hoc tests. The data are displayed using multidimensional scaling ordinations (Clarke and Warwick 1994).

Food web structure

Ten individuals of each animal taxon per stream were selected to represent the full size range present. These individuals were processed for gut analysis either separately (for large invertebrates) or in groups of up to five (for smaller invertebrates) as described elsewhere (Jaarsma et al. 1998, Townsend et al. 1998). Where 10 individuals were not available, as many individuals as possible were used. Invertebrates were gutted and the contents filtered on to 0.4-μm filters. These were mounted on permanent slides and then examined at 200–400$\times$ magnification. The species identity of gut contents was determined under a stereomicroscope, us-

ing a reference collection of invertebrate and algal taxa or relevant texts cited earlier. This technique allowed identification of most contents to either species or genus level for both animal and algal taxa. Algal taxa that were found in gut contents but not in rock scrubbings were added to the list of algal taxa present. Terrestrial invertebrates in the gut were grouped into a single basal category. Unidentifiable material was either classified as organic detritus and included as a single basal category, or as inorganic material and excluded from the food web. Although 10 individuals may be considered minimal, this represents a logistically challenging but achievable sample size for food webs as rich in species as those considered here. Woodward and Hildrew (2001) found that large numbers of individual guts (100+) need to be surveyed to detect all trophic links, but such an effort was not feasible. Instead we have taken the approach of standardizing effort across the different streams and taxonomic groups in order to make the food webs comparable (Thompson et al. 2001).

Food webs were compiled using identified taxa as row (gut contents) and column (feeding taxa) headings in a binary matrix (Cohen et al. 1990). Detection of a link was indicated in the body of the matrix by a ''1.'' Known suctorial species (Empididae and flatworms) that occurred in seven of the ten sites (Appendix A) were excluded, as it is not possible to identify their prey from gut analysis. Predatory taxa that contained nonpredatory invertebrate taxa in their guts were excluded from linking with algal taxa to avoid false detection of links due to prey within prey. This may obscure some omnivory, but predator guts with no invertebrate remains also lacked algae. Where species were found in gut contents, but not in field samples, they were attributed the trophic links of the most closely trophically and taxonomically related species (Jaarsma et al. 1998).

Food web attributes were calculated using a macro generated in Microsoft Excel. This used recursive programming to trace each food chain and so calculate the numbers of species, links, and food chains, as well as mean chain lengths and the numbers of top, intermediate, and basal species. Mean chain length was defined as the mean length of all chains that culminate in a top
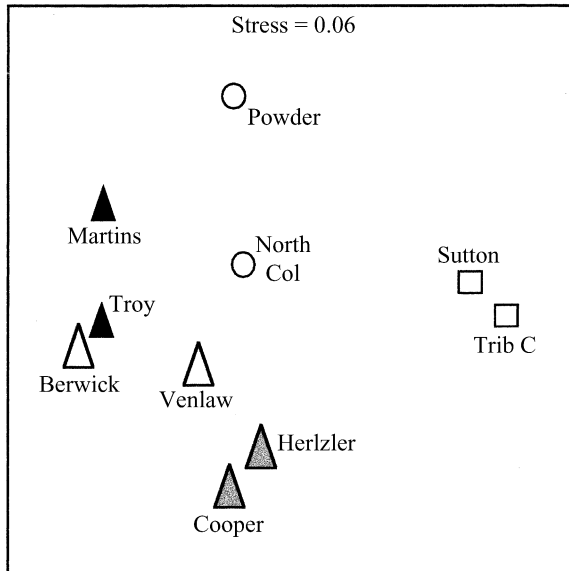
FIG. 1. Multidimensional scaling ordinations of sites using food resources data (Table 1). Sites were clustered using hierarchical agglomerative clustering (normalized Euclidean distances). Triangles indicate pine sites (black, Maine; gray, North Carolina; white, New Zealand); circles indicate native bush sites, and squares indicate tussock grassland sites.

species (Pimm 1982). These primary attributes were then used to calculate other food web attributes. Trophic connectance was estimated using the formula of Jaarsma et al. (1998):

$$C = \frac{L}{S^2 - ([\{pp + ba\}S] + [S - \{pp + ba\}] + [pr\{pp + ba\}])}$$

where C = connectance, S = number of trophic elements in the web, L = number of trophic links, pp = number of primary producers (algae and diatoms), ba = nonalgal basal elements (e.g., detritus), and pr = predators.

This modifies Warren's (1994) formula to allow for the fact that a large number of the taxa in our food web (i.e., algae) were nonfeeding. The first subtracted term removes links from algae and other basal categories from the equation, as these groups cannot feed. The second term removes all cannibalistic links. The third term removes the possible links of predators eating primary producers or basal categories. Connectance in these analyses is a measure of the proportion of links that occur divided by the number that could conceivably occur. A simple measure of prey:predator ratio ([percentage of basal + intermediate species]/[percentage of top + intermediate species]; Cohen 1977) was used to describe the shape of the food web (high values, more triangular; low values, a "square" food web).

Differences in food web structure between locations (pine sites only) and land use (New Zealand sites only) were analyzed using univariate and multivariate techniques. Differences in single attributes were analyzed using the one-factor randomization test outlined above for species richness measures. Holm's sequential Bonferroni procedure (Wright 1992) was used to generate adjusted P values for the rejection of null hypotheses, following the recommendation of Bender and Lange (2001). To test for overall differences in food web structure the attributes were analyzed collectively using ANOSIM in the same way as for trophic structure, and are displayed using multidimensional scaling ordinations.

RESULTS

Physical structure and food resources

Sites were chosen to control, as far as was feasible, for differences in bed structure and size of stream, but limitations of site availability resulted in differences in the physical characteristics of the streams. All were perennial and, to meet this requirement, the Maine

TABLE 3. Summary of food-web attributes for the 10 streams.

Site	Land use	S	AS	IS	IB	Pi	C	L	L/S	MC	T	I	B	P:P
Maine														
Troy	*P. strobus*	78	36	36	210.07	0.66	0.07	181	2.32	1.95	0.27	0.21	0.51	1.50
Martins	*P. strobus*	105	45	54	2062.36	0.71	0.07	343	3.27	3.13	0.31	0.23	0.46	1.28
North Carolina														
Herlzler	*P. strobus*	71	35	32	501.52	0.84	0.08	148	2.08	1.52	0.37	0.10	0.54	1.36
Cooper	*P. strobus*	58	25	29	304.87	0.78	0.08	126	2.17	2.04	0.48	0.17	0.35	0.79
New Zealand														
Venlaw	*P. radiata*	69	28	36	287.33	0.67	0.08	190	2.75	2.12	0.30	0.25	0.42	1.22
Berwick	*P. radiata*	79	32	43	178.27	0.64	0.10	284	3.59	1.68	0.44	0.14	0.39	0.91
North Col	bush	78	22	52	736.55	0.53	0.11	421	5.40	2.27	0.36	0.32	0.32	0.94
Powder	bush	78	29	45	999.61	0.60	0.08	268	3.44	2.24	0.31	0.28	0.41	1.17
Trib C	tussock	98	53	41	1068.19	0.65	0.18	626	6.42	2.35	0.16	0.25	0.59	2.05
Sutton	tussock	92	55	33	683.92	0.68	0.17	423	4.60	1.79	0.11	0.14	0.69	3.30

Notes: Attribute definitions are as follows: *S*, species richness; AS, algal *S*; IS, invertebrate *S*; IB, invertebrate biomass (mg ash-free dry mass per m^2); Pi, Pielou's evenness; *C*, connectance; *L*, number of trophic links; MC, mean chain length; *T*, proportion of species that are top; *I*, proportion that are intermediate; B, proportion that are basal; P:P, predator prey ratio. Land use: *P*, *Pinus*; bush, native bush.

TABLE 4. Analysis of location and land use effects on food-web attributes for the ten streams (for definitions of column headings see Table 3).

Effect	Parameter	Pairwise comparison	S	AS	IS	IB
Location (Pine only; Me vs. NC vs. NZ)	$F_{2,3}$			2.26	2.24	1.68	0.69
	P			0.18	0.27	0.20	0.71
	post hoc P value	Me vs. NC					
		Me vs. NZ					
		NC vs. NZ					
Land use (New Zealand only; P vs. B vs. T)	$F_{2,3}$		10.97	40.83	2.71	7.15
	P		0.12	**$\leq$0.01**	0.20	0.16
	post hoc P value	P vs. B		0.70		
		P vs. T		**0.09**		
		B vs. T		<u>**0.02**</u>		

Notes: Abbreviations for location: Me, Maine, USA; NC, North Carolina, USA; NZ, New Zeland. Abbreviations for land use: P, *Pinus*, B, native bush, T = tussock. Significant F values (10% level) for one-factor randomized ANOVA are in bold with post hoc values for pairwise comparisons below. Significant values after adjustment for multiple testing (Holm's adjustment) are underlined.

streams were considerably larger than those in North Carolina and New Zealand. The Maine streams were also characterized by higher mean velocities. Variation in altitude was evident, as pine-forest sites in North Carolina and tussock sites in New Zealand were only available at higher altitudes. These differences contributed to some evidence for an effect of geographical location on physical structure (ANOSIM, Global rho = 0.611, P = 0.07) although there was no difference between land uses (ANOSIM, Global rho = 0.139, P = 0.24).

An ordination of sites using food resource data (Fig. 1) showed significant land use effects (ANOSIM, Global rho = 0.466, P = 0.02), with a pine cluster in the lower left quadrant and a clustering of tussock sites to the right of the plot. Pine sites were mainly distinguished from tussock sites by large amounts of organic matter on the streambed (Table 1). Bush streams were characterized by large biomass of biofilm (Table 1). Among pine sites, there was no evidence of any differences due to location (ANOSIM, Global rho = 0.778, P = 0.13).

Species composition, biomass, and richness

Algal communities (Appendix B) at all sites had a common core of species, including *Gomphoneis herculeana*, *Cocconeis placentula*, and *Rhoicosphenia curvata*. As would be expected for a cosmopolitan group such as diatoms, there were no clear differences in algal species composition between geographical locations. Similarity percentages (Table 2) were quite high within and between pairs of sites in each land use/ location combination. The New Zealand tussock sites were the most distinctive, but still shared a mean of 43% of species with the other locations. New Zealand pine sites tended to share more algae with pine sites in North America than with nearby tussock sites. Some land use effects on algal communities were evident, with tussock sites having significantly more species than forested sites (Tables 3, 4). No particular genera

were associated with tussock sites, but the diversity of species within genera was much higher. Forested sites tended to have high intersite variation, with species compositions differing even within a particular locality, whereas tussock sites exhibited greater similarity to each other.

The New Zealand streams shared almost no invertebrate taxa with the North American streams (0.4–5.4%; Table 2). Even these figures are inflated because shared taxa were at the genus or morphospecies level (no named species occurred in both continents). Site-to-site variation within each pair of streams was quite high (42–60% shared). The Maine and North Carolina sites shared almost a quarter of their species, predominantly in the Coleoptera and Ephemeroptera. Maine sites were dominated by Chironomidae taxa, whereas North Carolina sites were distinguished by high richness of Trichoptera and Coleoptera taxa. In New Zealand pine streams, Ephemeroptera (primarily *Deleatidium* spp.) and Plecoptera (primarily *Zelandoperla* spp.) were dominant. Similarities between land-use types in New Zealand were low. New Zealand pine and bush sites shared 44% of species, the latter being defined by a distinctive chironomid and trichopteran community and by the grazing mollusc *Potamopyrgus antipodarum*. Similarity between pine and tussock sites was even lower (34%), while bush and tussock sites shared 40% of species. The shredders *Rhabdomastrix* and *Austroperla cyrene* typified the two groups of forested sites, whereas grassland sites were different from forested sites and from each other. A distinctive chironomid community distinguished Trib C, whereas *P. antipodarum* dominated Sutton Stream. All the New Zealand sites contained high densities of the generalist ephemeropteran grazer *Deleatidium* spp.

Invertebrate biomass was notably high in the Martins Stream site (Table 3). However, pine sites other than Martins Stream tended to have lower invertebrate biomass than bush and tussock sites. New Zealand pine sites had lower biomasses than bush or tussock sites

TABLE 4. Extended.

Pi	C	L	L/S	MC	T	I	B	P:P
11.59	3.00	1.48	2.08	1.08	1.66	1.32	0.49	0.87
0.10	**0.06**	0.27	0.20	0.51	0.33	0.42	0.58	0.41
0.09	0.32							
0.75	**<0.01**							
0.02	0.31							
5.43	19.50	3.43	2.09	0.74	7.84	1.71	13.94	6.10
0.06	0.11	0.11	0.31	0.48	0.15	0.20	**0.04**	0.14
0.09							0.84	
0.91							**0.09**	
0.02							**0.03**	

(Tables 3, 4). There were no marked differences in invertebrate species richness among locations or land uses; the Martins pine site in Maine and the North Col native bush site in New Zealand had the highest values for richness. The North Carolina sites had the highest values for Pielou's evenness. The majority of invertebrates in the Maine sites were from only six species, and the New Zealand streams also tended to have just a few species predominating. New Zealand bush sites displayed the least even distribution of individuals among species, largely due to the high abundance of the coleopteran *Hydora nitida* and the ephemeropteran *Deleatidium* spp.

Trophic structure

In terms of distribution of species among functional feeding groups (FFGs), similarity percentages were high for all intersite comparisons, ranging from 82% to 94% (Table 5). Lowest values for similarity were found when North Carolina sites were compared with any of the others. Predatory taxa and collector–gatherers (predominantly Chironomidae) tended to dominate in all locations and land uses (Fig. 2), with algal consumers present in lower but similar proportions everywhere. These common patterns accounted for the high levels of similarity. However, some differences were evident, both among locations (North Carolina sites were notable for the absence of any filter-feeding species, collector filterers were more prevalent in North Carolina than New Zealand while the reverse was the case for omnivores) and land uses (omnivores were more prevalent in New Zealand pine than tussock and shredders in New Zealand pine than bush; Table 6). Ordination of the sites clearly separates the North Carolina sites from the others (Fig. 3A). ANOSIM points to this location effect (Global rho = 0.722, P = 0.07) and also a land use effect (Global rho = 0.944, P = 0.07), in which bush sites can be discerned from tussock sites.

When comparison was based on distribution of biomass among the FFGs, similarity values were somewhat lower, ranging from 76% to 88% (Table 5), with North Carolina sites still the most distinctive. There was more variation in the FFGs that predominated in different locations and land uses (Fig. 4) but few statistically significant differences: omnivore biomass was higher in New Zealand than in North American sites, filter-feeder biomass was higher in New Zealand bush than pine sites, and omnivore biomass in bush sites was higher than in tussock sites (Table 6). Some other features worth noting are that New Zealand pine sites had a higher biomass of shredders than those in the USA, the Maine sites had particularly low biomasses of algal consumers, and the Martins Stream site had an exceptionally high biomass of predatory taxa (Fig. 4). A greater scatter in the biomass ordination reflects the more variable nature of FFG distribution by biomass compared to species (compare Fig. 3A with 3B). Nevertheless, analysis of similarities provides some evidence for clusters based on location (Global rho = 0.889, P = 0.07), with New Zealand pine sites clustering away from the American pine sites (largely due

TABLE 5. Similarities in invertebrate trophic structure in terms of percentage of species (bold text) and of total biomass (plain text) in different functional feeding groups.

	Internal similarity	Maine	North Carolina	NZ pine	NZ bush	NZ tussock
Internal similarity		**92.27**%	**89.69**%	**94.67**%	**97.41**%	**96.32**%
Maine	84.47%	...	**84.89**%	**91.36**%	**92.02**%	**92.09**%
North Carolina	90.33%	84.19%	...	81.25%	**82.37**%	**86.88**%
NZ pine	95.62%	78.32%	76.22%	...	**94.24**%	**90.17**%
NZ bush	89.14%	82.06%	77.92%	87.69%	...	**92.18**%
NZ tussock	86.34%	79.78%	77.77%	84.06%	81.79%	...

Note: Results are expressed as percentage similarity within groups and between locations.

TABLE 6. One-factor randomization tests on the percentage of species and invertebrate biomass in each functional feeding group.

Effect	Parameter	Pairwise comparison	Percentage of species			
			Ac	Cf	Cg	Ff
Location (Pine only, Me vs. NC vs. NZ)	$F_{2,3}$		0.85	0.98	1.45	30.60
	P		0.42	0.26	0.40	**0.01**
	post hoc P value	Me vs. NC				**0.10**
		Me vs. NZ				0.56
		NC vs. NZ				<**0.01**
Land use (New Zealand only, P vs. B vs. T)	$F_{2,3}$		2.53	0.58	1.69	2.64
	P		0.21	0.60	0.41	0.26
	post hoc P value	P vs. B				
		P vs. T				
		B vs. T				

Notes: Abbreviations are: Ac, algal consumers; Cf, collector-filterers; Cg, collector-gatherers; Ff, filter-feeders; O, omnivores; Pr, predators; Sh, shredders. Location: Me, Maine; NC, North Carolina; NZ, New Zealand. Land use: P, pine; B, bush; T, tussock. The F statistic and P values are shown with significant values (10% level) in bold, with results of post hoc pairwise comparisons (randomized t tests). Where P values remain significant after Holm's adjustment for multiple testing, they are underlined.

to the high biomass of predators in the American sites and the presence of omnivores in the New Zealand sites). Land use effects are not significant (ANOSIM, Global rho = 0.333, P = 0.20); however tussock sites may be separated on the basis of a paucity of shredders, and pine sites by high biomasses of filter feeders (Table 6). The Sutton Stream tussock site is distinguished from all other sites in the ordination by the dominance of algal consumers.

Food web analysis

Algal consumers at each site tended to have gut contents consisting of a single algal species, or a small group of species in which one dominated strongly. Shredders showed little evidence of feeding directly on pine litter, but in all pine sites a major component of the gut contents was pine pollen. Most predatory invertebrate species had diverse diets. Vertebrate species (fish and salamanders) also had diverse diets but high individual variation was present, with some guts only containing a small number of species.

Connectance ranged from 7% to 18%, with a tendency towards lower values in the North American sites, particularly in Maine (Tables 3 and 4); this difference was also reflected in the number of links per species with the four North American sites having lower values than all but one site (pine) in New Zealand. Tussock sites had the highest values for connectance (17% and 18%) and displayed high numbers of links per species (Table 3). There was no effect of location on any other food web attribute, but some land use effects were evident. The proportion of basal species (algae) was significantly higher in tussock than forested New Zealand streams (Tables 3, 4), a pattern that was mirrored by lower proportions of top species and reflected in particularly high prey:predator ratios. In contrast to the "square" forest food webs, tussock streams had more "triangular" (higher prey:predator ratio)

webs due to the presence of significantly more algal species.

When the attributes are considered collectively, there was no effect of location (ANOSIM, Global rho = −0.111, P = 0.87), and the ordination shows all pine sites clustering together (Fig. 5). All pine sites had simple food webs dominated by food chains of length 1 (a primary consumer feeding on a basal resource, often detritus). A land-use pattern is evident in the ordination, with tussock sites clustering away from all others. Overall, native bush sites were not significantly different from pine sites, although values for number of trophic links and number of links per species were intermediate between pine and tussock. Analysis of similarities did not show a strong effect of land use (Global rho = 0.611, P = 0.130) because of the similarity between bush and pine sites. However, an analysis comparing forested (bush and pine together) with tussock sites reveals a significant difference (ANOSIM, Global rho = 0.931, P = 0.02).

DISCUSSION

Comparison of native and exotic pine-forest streams

There was no overlap in macroinvertebrate species composition between the North American and New Zealand pine sites. The translocation of *Pinus* to New Zealand has not involved a simultaneous translocation of any stream fauna and no cosmopolitan invertebrates are available for community assembly in both native and exotic settings. The algal communities in the different streams shared many species, although this may reflect limitations in existing taxonomy rather than genuine cosmopolitan distributions. Recent work on New Zealand diatoms has suggested that a great deal of endemism may have been masked by dependence on taxonomic literature from the northern hemisphere (R. Lowe, *personal communication*). Even taking this into

TABLE 6. Extended.

	Percentage of species			Percentage of invertebrate biomass						
O	Pr	Sh	Ac	Cf	Cg	Ff	O	Pr	Sh
23.95	0.49	0.42	12.24	1.71	1.35	1.09	8.91	2.32	4.72
≤0.01	0.57	0.61	0.15	0.27	0.34	0.40	**0.05**	0.21	0.15
0.10							0.93		
0.56							**0.07**		
≤0.01							**≤0.01**		
3.93	0.77	8.25	1.23	0.49	0.08	49.80	4.92	1.23	3.58
<0.01	0.34	**0.09**	0.48	0.64	0.98	**0.05**	**≤0.01**	0.48	0.21
0.27		**0.03**				**≤0.01**	0.18		
≤0.01		**0.09**				0.32	0.62		
0.33		0.91				0.27	**≤0.01**		
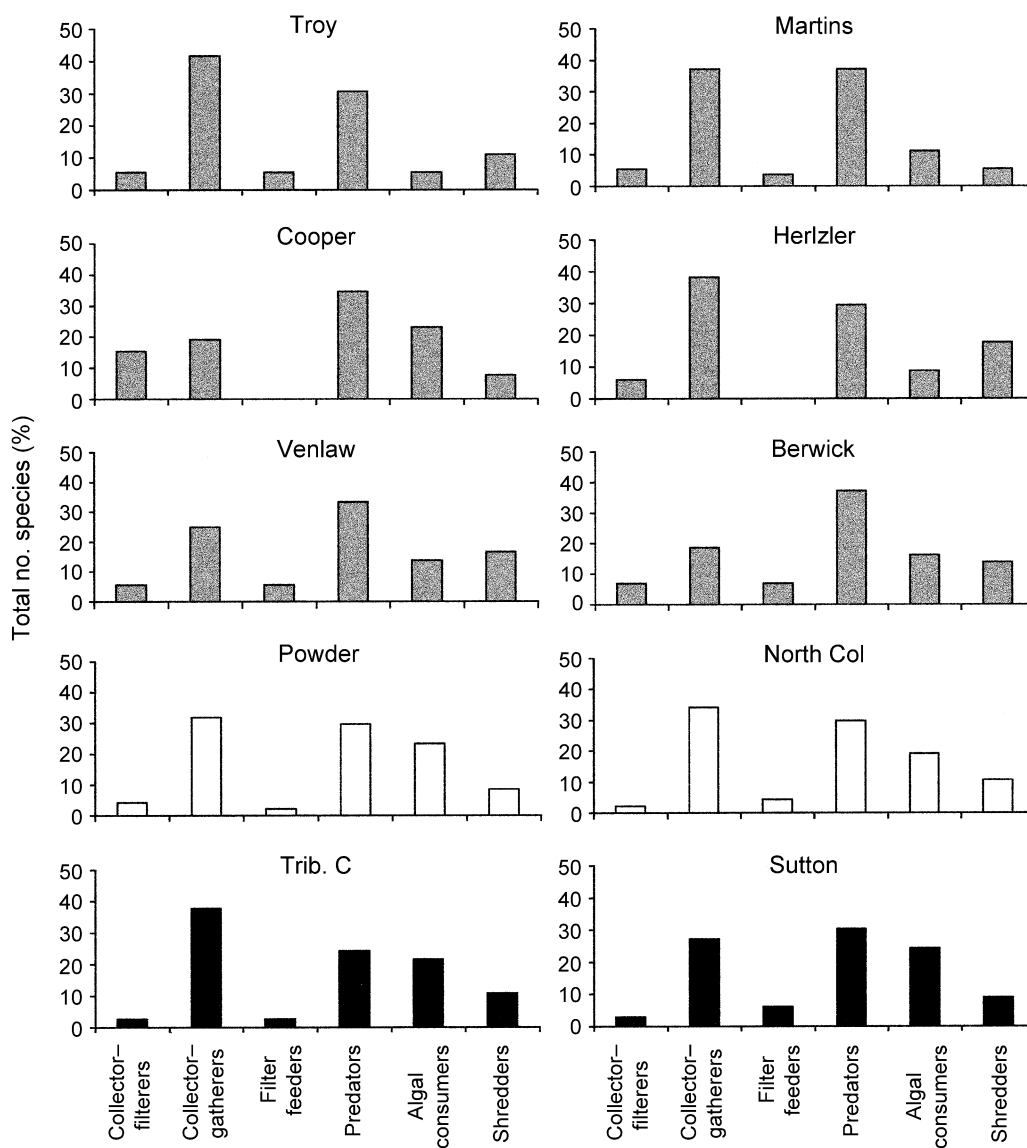
FIG. 2. Invertebrate species richness for each site separated into functional feeding groups. Gray bars indicate pine sites, white bars bush sites, and black bars tussock sites.
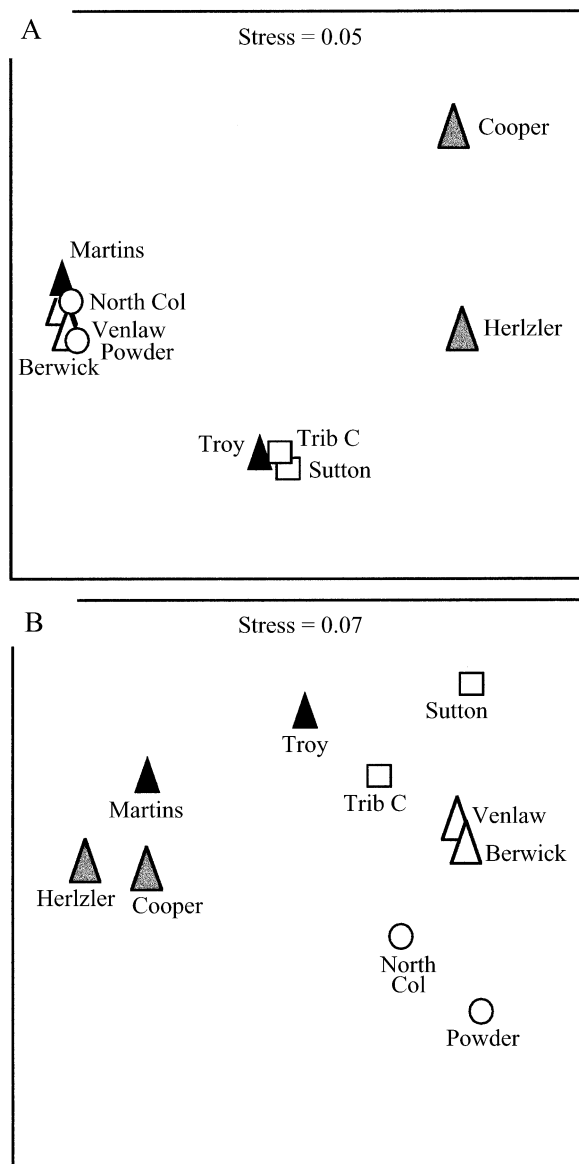
Fig. 3. Multidimensional scaling ordinations of sites using trophic structure (functional feeding groups). Sites are clustered based on the distribution of (A) species and (B) biomass across the functional feeding groups. Sites were clustered using hierarchical agglomerative clustering (Bray-Curtis similarities). Triangles indicate pine sites (black, Maine; gray, North Carolina; white, New Zealand); circles indicate native bush sites, and squares indicate tussock grassland sites.

account, it is notable that the diatom flora in New Zealand pine streams was more similar to North American sites than nearby native tussock or bush settings. All pine sites, regardless of location, were dominated by *Navicula avenacea*, *Rhoicosphenia curvata*, and *Cocconeis placentula*. This may reflect an ability of these species to survive physicochemical conditions resulting from riparian pines.

Despite profound differences in invertebrate species composition in native and exotic settings, in all pine streams comparable numbers of species were assembled into pine stream communities that were similar in terms of trophic structure. Some differences were observed in Functional Feeding Group (FFG) patterns with perhaps the most notable result that shredders were as important in New Zealand pine sites as in their North American counterparts. This was unexpected because New Zealand is regarded as having few specialist shredder species (Winterbourn 1995, Thompson and Townsend 2000a) and shredders have traditionally been thought to be relatively unimportant because many New Zealand streams have steep gradients and are poorly retentive of tree leaves (Winterbourn et al. 1981). This may apply to streams flowing through southern beech (*Nothofagus* spp.), which is the predominant remaining native forest type in the southern part of New Zealand and which yields a peculiar litter that is nonlabile and difficult to retain (Winterbourn et al. 1981); however we believe it may not be true of other forest types. In addition, the relative importance of New Zealand shredders may have been underplayed because of an ability of many generalist species to shred facultatively. New Zealand's fauna is relatively nonspecialist in nature and extreme flexibility of diet has been reported (Winterbourn et al. 1981). In the present study, we observed *Megaleptoperla grandis* (traditionally classified as predators) burrowing in pine wood and recorded wood and leaf material in these individuals' guts. In addition, eusirid amphipods (e.g., *Paracalliope* sp.) were important shredders in the New Zealand pine streams, apparently filling the role of gammarid amphipods elsewhere. Recent efforts to resolve Eusiridae taxonomy have revealed significant diversity (A. Chapman, *personal communication*) and this may act to redress the apparent lack of shredders in New Zealand systems.

Food web analysis goes a step beyond the FFG approach, dealing with actual feeding links rather than generalizations about the previously recorded feeding habits of particular species. Food web attributes define the trophic structure of a community in a much more detailed manner than assignment to FFGs. In addition, because they also elucidate patterns of energy flow, food webs provide a partial description of ecosystem functioning. Food web attributes of pine communities were almost indistinguishable in native and exotic settings. The only trend of note was that Maine sites tended to have slightly lower values for connectance than New Zealand pine sites.

The only other indicator of a distinction in ecosystem functioning among pine sites was the markedly high invertebrate biomass in Martins stream in Maine. Our observed biomasses in the North Carolina streams were lower than those observed by Whiles and Wallace (1997; 1000–1200 mg/m²) using a different sampling method, although patterns in the distribution of bio-
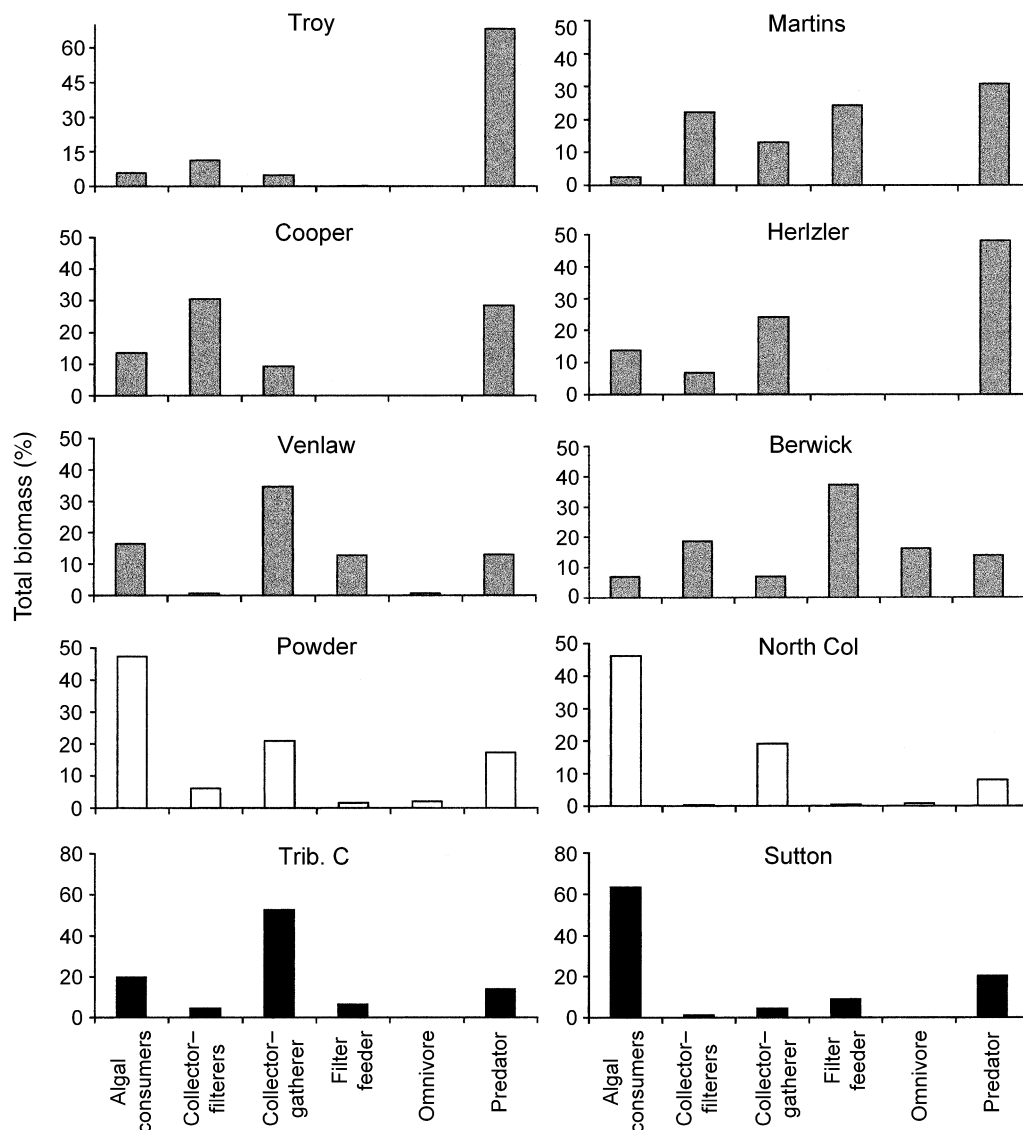
FIG. 4. Invertebrate biomass for each site separated into functional feeding groups. Gray bars indicate pine sites, white bars bush sites, and black bars tussock sites.

mass across trophic groupings were nearly identical. The lower invertebrate biomass in New Zealand and North Carolina sites could reflect their artificial nature as even-aged monocultures that are actively managed to maintain this state. The Troy site, essentially a natural pine monoculture with little undergrowth, was somewhat atypical of natural white pine forest, in that it had no forest gaps opened by senescence of trees. On the other hand, Martins Stream was dominated by pine, but with a large component of other trees, including spruce, fir, and maple, and an herbaceous layer maintained in canopy gaps that result from natural senescence of trees. The Troy, North Carolina, and New Zealand sites all receive allochthonous matter that is dominated by relatively homogeneous pine litter of poor quality (Whiles and Wallace 1997). The high in-

vertebrate biomass in Martins Stream could reflect the fact that it receives a large input of organic material that is more diverse in nature and includes high quality broadleaf litter.

Comparisons with food webs described using different techniques must be made with caution, due to the sensitivity of food web attributes to differences in taxonomic resolution (Martinez 1993, Thompson and Townsend 2000b) and effort expended (Martinez et al. 1999, Thompson et al. 2001). However, a highly resolved food web from a stream flowing through a mixed forest including *Pinus strobus* in Canada (Tavares-Cromar and Williams 1996) was also dominated by detritus and had similar values for connectance to the pine stream food webs in this study. However, diatoms were not identified to species level in Tavares-Cromar and
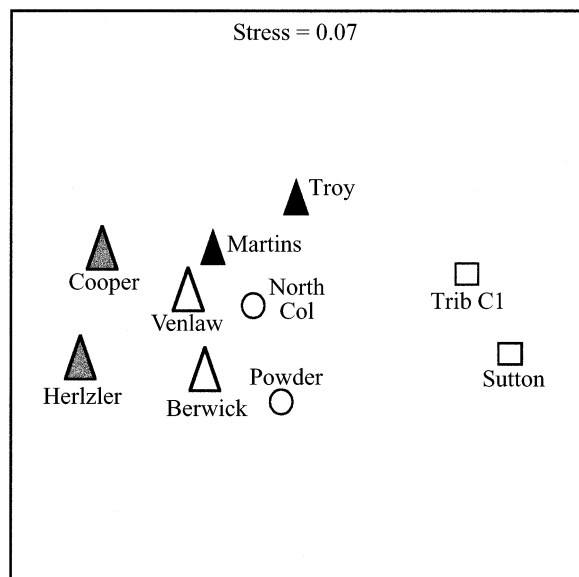
FIG. 5. Multidimensional scaling ordinations of sites using food web attributes (Table 2). Sites were clustered using hierarchical agglomerative clustering (Bray-Curtis similarity). Triangles indicate pine sites (black, Maine; gray, North Carolina; white, New Zealand); circles indicate native bush sites, and squares indicate tussock grassland sites.

Williams' (1996) study, and it is difficult to determine whether their food webs were a similar "shape" to our pine stream food webs. Detailed descriptions of food webs from streams in North American broadleaf forest are needed to determine which characteristics are attributable to the presence of pine, and which are derived from geographical location.

Comparison of streams in pine, bush, and tussock streams in New Zealand

Species richness of algae was significantly higher in tussock streams, while invertebrate richness did not differ among land use categories in New Zealand. Based on presence/absence data, both algal and invertebrate assemblages in New Zealand pine-forest streams were more similar to those of native-bush than native-tussock streams. However, two dominant shredders from bush sites, *Austroperla cyrene* (Plecoptera) and *Rhabdomastrix* spp. (Eriopterini), were rare in our pine sites (but note that Harding and Winterbourn 1995, observed high densities of *Austroperla* in other pine sites in New Zealand). Pine sites also had the lowest invertebrate biomasses of any land use in New Zealand. Our observations indicate that *A. cyrene* are less active and suffer higher mortality in the presence of pine litter (R. Thompson, *unpublished data*); at least in this respect, perhaps a lack of coevolutionary history affects ecosystem function in exotic pine streams. Winterbourn et al. (1981) claimed that a generalist core of New Zealand species tends to dominate all streams regardless of vegetation type. Our study identified a generalist

core of 10–15 species, but has also highlighted assemblages of species that are unique to forested, as opposed to tussock, streams. These assemblages have much in common with those identified in a previous land-use comparison (Townsend et al. 1997), but the greater age of the pine sites in the present study seems to have resulted in a greater distinction between tussock and pine assemblages.

Similarity in trophic structure according to FFG representation in the three land uses was high (90–94% in terms of species richness, 82–88% in terms of biomass). However, some differences were noted. When assessed on the basis of species richness, tussock sites clustered away from pine and bush streams, which clustered together in the ordination, mainly because of a lack of omnivores in tussock. When FFG representation
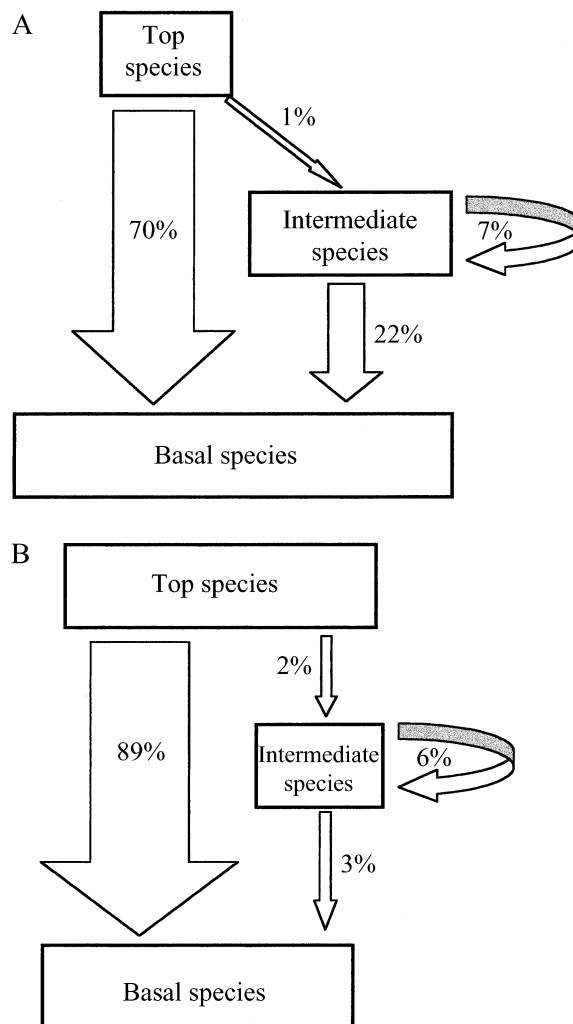

FIG. 6. Diagrammatic representations of food webs from (A) a New Zealand tussock grassland stream (Trib C) and (B) a New Zealand pine-forest stream (Berwick). The size of the boxes indicates the percentage of species in each level of the food web. The arrows indicate the percentage of links that occur between each of the levels.

was assessed on the basis of biomass distribution, three clusters were produced corresponding to the three land uses, as a result of a higher representation of filter feeders in pine and of omnivores in bush.

Finally, in terms of food web attributes, tussock sites formed a distinct cluster in the ordination that was furthest removed from pine, with bush sites occupying an intermediate position (but closer to pine). The bases for this pattern were the higher connectances, proportions of basal species and prey:predator ratios and lower proportions of top species in tussock streams and lower number of links per species in pine streams. In other words, the food webs in tussock sites were more structurally complex and were typified by a triangular shape while forested webs were very simple, with the vast majority of food chains composed of only a basal resource and a primary consumer (Fig. 6 generalizes the differences between forested and tussock settings). These differences in food web structure could be due to differences in energy supply to the different systems. Measuring the energy available to food webs from algal, bacterial, and fungal sources, and correlating these with food web attributes is likely to be a fruitful area of research.

The communities that have assembled in the exotic pine settings have species composition, trophic, and food web structures that are more similar to bush than tussock situations. This is despite the fact that the Berwick site was developed on land previously under tussock, although the Venlaw forest site used to be native bush. Rather than recent history determining stream community structure, it is the current physicochemical setting that matters.

Appraisal of the food web approach

Approaches to studying food webs have been criticized in the past on many grounds (e.g., Paine 1988, Closs 1991, Cohen et al. 1993), particularly in relation to the practice of collecting food webs using diverse methods and from diverse systems, and seeking generalities. This approach may work, but only if patterns are extremely robust (or artifacts of the way in which the food webs have been constructed!). The approach used here, and advocated by Townsend et al. (1998), consists of a rigorous standardization of methods to build food webs that are comparable within the study. The effort expended on gut analysis in terms of the number of guts surveyed and standardization of effort across taxonomic groups was identical in each case to allow direct comparisons between the food webs (Thompson et al. 2001). Although the effort used is unlikely to be sufficient to detect all trophic links (Woodward and Hildrew 2001), we believe this approach will detect most common trophic links while still making it feasible to generate replicate food webs. This study is also limited to a single-season comparison based on one sampling occasion. Seasonal variation is an important contributor to variation in food web struc-

ture (Tavares-Cromar and Williams 1996, Thompson and Townsend 1999) and sampling in these streams was carried out in the same season to avoid this problem. Nonetheless, it is important to realize that the differences found may not apply to other seasons.

The fundamental linkage between the stream and its catchment has long been a tenet of stream ecology theory (Hynes 1975, Junk et al. 1989). Our food web analyses provide a further example of the importance of land use in determining stream community patterns. In both areas where humans have induced pine monocultures, the systems seem less productive. Whiles and Wallace (1997) have also commented on the negative effect on ecosystem processes of pine conversion in the North Carolina sites. We are beginning to understand the role of diversity of species in maintaining ecosystem processes (Sterner et al. 1996). In the present case, it may be that diversity of food resources may also be an important and formerly unappreciated factor.

The translocations of species between continents represent accidental experiments of extraordinary proportions, providing opportunities for ecologists to gain insights into the processes that structure communities. Coupled with our analyses of species composition and representation of functional feeding groups, our food web results provide evidence of the homogenizing effects of interchange of vegetation among continents. The New Zealand pine sites displayed similarities to both the native pine forest sites of North America. There has been no catastrophic loss of species with the introduction of exotic pine; rather the existing stream biota has reassembled to match the novel conditions and has come to mimic communities on the other side of the world. In New Zealand, the relatively generalist nature of the stream fauna may facilitate appropriate reassembly. Where biotas are more specialized, transformation to exotic landscapes may give rise to more fundamental distinctions from the native case.

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APPENDIX A

A table presenting the invertebrate and vertebrate species present in stream sites in New Zealand and the United States of America is available in ESA's Electronic Data Archive: *Ecological Archives* E084-003-A1.

APPENDIX B

A table of algal species present in stream sites in New Zealand and the United States of America is available in ESA's Electornic Data Archive: *Ecological Archives* E084-003-A2.