

Forest canopy affects stream macroinvertebrate assemblage structure but not trophic stability

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Abstract: Understanding the determinates of community structure and function is a central theme in community ecology. The form in which energy is supplied to food webs can strongly influence community structure and function. Trophic stability is also thought to be affected by the nature of food web energy pathways and whether they are external (allochthonous) or internal (autochthonous) to the ecosystem. In this study, we assessed whether stream invertebrate assemblages differ in taxonomic composition, energetic network structure, trophic network stability, and assemblage temporal variability based on whether the streams they occupy occur under forested canopies or in open grasslands. We assumed that forested sites would receive more allochthonous inputs, whereas grassland sites would rely more on autochthonous resources. We also tested whether food web stability (robustness, the conservation of energy flow) changed after simulated species extinctions. We found that the forest stream assemblages were dominated by filter feeders and shredders, whereas the grassland assemblages were dominated by grazers. In spite of these differences in assemblage composition, we found no significant differences in trophic network structure, stability, or temporal variability among different site types. Many stream systems, particularly in mountainous areas, such as New Zealand, are exposed to regular and large physical disturbance from flooding, which may result in assemblages with similarly generic diets irrespective of the energy source.

Key words: riparian, stability, macroinvertebrate, community, stream, land use, allochthonous, autochthonous, robustness, trophic network

The influence of energy supply on community structure and stability is a central theme in community ecology (McCann 2005, 2011, Ives 2007). Understanding how energy supply affects communities has become even more important as humans continue to deforest land and otherwise alter habitats, which can change the nature of energy supplies. Extensive research documents the effects of habitat alteration on species composition and, to a lesser extent, trophic structure (Ceballos et al. 2015, Peters et al. 2015). However, studies that simultaneously examine changes in energy sources, community stability, and energy flow pathways are rare (Saint-Béat et al. 2015, Mougi and Kondoh 2016). This lack of research is associated with both the difficulty of obtaining suitable quantitative data on trophic structure and the limited methods available for assessing stability (Rooney and McCann 2012, Saint-Béat et al. 2015).

Stability broadly describes a state in which community structure and function are constant (or at dynamic equilib-

rium) over time, in spite of disturbance (Costanza and Magueau 1999, Saint-Béat et al. 2015, Mougi and Kondoh 2016). Stability is a concept that includes the resistance, persistence, resilience, robustness, and dynamic equilibrium of species interactions within the community (Dunne et al. 2005). These metrics are difficult to measure; hence, the majority of food web stability studies have examined theoretical rather than empirical (based on real-world) webs (Saint-Béat et al. 2015). However, theoretical webs have been criticized for being unrealistic, randomly assembled, or bound by unjustifiable configuration rules (De Angelis 1975, McCann 2000, Rooney and McCann 2012). Furthermore, the empirical studies that have been conducted on community stability have generally examined binary webs and assess only topological robustness (Solé and Montoya 2001, Dunne et al. 2002). Inferences derived from simple binary webs may not be robust, however, because they ignore interaction strength and assume that trophic cascades occur solely from the bottom up, as

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species have been assumed extinct only once all prey are extinct, despite changes in higher trophic levels (Dunne et al. 2005, Fox 2006, Gilbert 2009, Canning and Death 2017). It is therefore unclear whether these approaches yield realistic predictions of natural communities.

A hybrid approach may provide robust insights regarding trophic interactions while being practically feasible. Specifically, quantitative (weighted) food webs can be used to test hypotheses regarding stream food web structure and function (Hall and Meyer 1998, Hall et al. 2000, Benke et al. 2010, Ledger et al. 2012). Weighted food webs support theoretical analyses while also allowing assessments of interaction strengths within complex food webs and more realistic network configurations. Ecological network analysis (ENA) provides a toolbox of metrics that can be used to assess and better conceptualize complex weighted food webs (Ulanowicz 2004, Latham 2006). In addition, ENA allows users to simulate disturbances to empirically derived weighted food webs and predict potentially new stable states (i.e., webs are rebalanced so that inflows are equal to outflows) (Allesina and Bondavalli 2003, Canning and Death 2017). Weighted food webs analyzed with ENA may therefore provide a more realistic assessment of trophic network stability. For example, weighted food webs are more sensitive to the loss of species with many direct and indirect effects than are binary food webs (Zhao et al. 2016). Furthermore, ENA shows that indirect flow intensity is a key factor controlling energy flow stability (Canning and Death 2017), which is consistent with theoretical analyses that show that weak flows stabilize webs (Rooney and McCann 2012, Saint-Béat et al. 2015, Mougi and Kondoh 2016). Hence, any process that affects the dominance or distribution of indirect flows within a food web may also influence its stability. Therefore, ENA provides a useful method for assessing and simulating changes in empirically derived weighted food webs that are more realistic than theoretically derived webs.

A primary way that humans change energy flows in stream ecosystems is through deforestation (Carpenter et al. 1992, Scanlon et al. 2007). Removing riparian forests reduces allochthonous litter input and increases periphyton growth (e.g., Duncan et al. 1989, Feminella et al. 1989, Naiman and Décamps 1997). Theoretical explorations of low-richness food webs suggest that low to moderate inputs of allochthonous material (relative to autochthonous material) can stabilize an autochthonous-based community (Huxel et al. 2002). Allochthonous inputs provide an alternative energy supply to temporally variable autochthonous production, which allows for the maintenance of greater population carrying capacities and the dampening of disruptive cascades (Huxel and McCann 1998, Jefferies 2000, Huxel et al. 2002). However, if allochthonous inputs are too high, then the community may be reliant on, and consequently sensitive to, the loss of the allochthonous inputs, resulting in reduced community resilience (Huxel and McCann 1998, Jefferies 2000,

Huxel et al. 2002). Furthermore, changing the balance of different energy types can change the invertebrate assemblages within a stream, which will further alter the dietary makeup of the assemblages and further affect trophic stability.

Mount Taranaki in New Zealand has streams that originate in a protected, forested national park, which then transitions into agricultural grasslands that were formerly forested. In the forested stream sections, allochthonous litter sources dominate, but in the grassland stream sections, autochthonous algal production dominates (Death and Zimmermann 2005). There is no difference in species richness between forested and grassland sites in 10 Taranaki streams, but grassland sites have greater evenness and higher densities of invertebrates than forested sites (Death and Zimmermann 2005). We postulate that grassland sites have smaller contributions of allochthonous energy inputs relative to autochthonous energy inputs than do forested sites. In turn, we hypothesized that the macroinvertebrate trophic networks at grassland sites will differ from those at forested sites, with forested sites having greater trophic network robustness and lower temporal variability.

METHODS

Study design and sites

We selected 10 streams located on Mount Taranaki, New Zealand, a dormant andesitic cone volcano, that share a similar geological origin. All 10 streams originated from the rimu–rata–kamahi forests of Egmont National Park and transition sharply to low-intensity agricultural grassland that has no forest starting at the park boundary. All streams are 400 to 500 m asl and have similar physicochemical characteristics, including substrate size composition (predominately large cobbles) (Death and Zimmermann 2005). We sampled each stream at two locations: at a forested site ~50 m upstream of the park boundary and at a site several hundred meters downstream of the boundary in the grassland (Fig. 1). We sampled each site monthly for periphyton and seasonally for macroinvertebrates between April 1999 and January 2000.

Periphyton sampling

We estimated periphyton biomass indirectly by measuring chlorophyll *a* (Chl *a*), which is generally correlated with primary production (Bott et al. 1978, Bott 1983, Morin et al. 1999). To estimate Chl *a* density, we collected 4 stones (maximum planar dimension <60 mm) monthly (between April 1999 and January 2000) from random locations in riffles at each site and subsequently froze them. In the laboratory we extracted pigments by soaking each stone in a known volume of 90% acetone at 5°C in the dark for 24 h. We then used a Varian Cary 50 UV-visible spectrophotometer to measure the absorbance of each solution and converted absorbance to pigment concentration (Steinman et al. 2017). We estimated pigment density ($\mu\text{g}/\text{cm}^2$) by dividing pigment

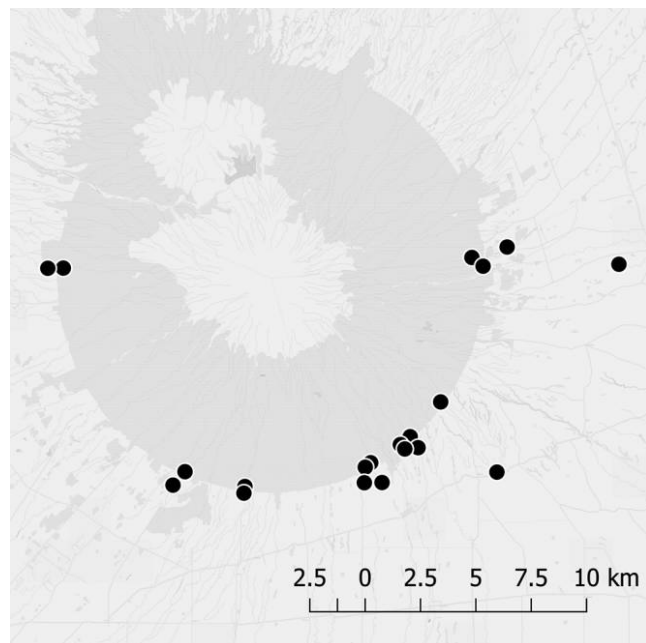


Figure 1. Twenty paired sample sites across 10 streams on New Zealand's Mount Taranaki ring-plain. Each stream had 2 sites, 1 within the forested national park and 1 within a downstream grassland.

concentration by half of the stone surface area; because periphyton is typically located only on the upper surface, the estimates for each stone were then averaged to give a global monthly estimate for each site.

Macroinvertebrate and POM sampling

We sampled benthic macroinvertebrates and particulate organic matter (POM) in riffles by taking 5 Surber samples (0.1-m^2 area with $250\text{-}\mu\text{m}$ mesh) at each site in April, July, and October 1999 and January 2000. We identified individual macroinvertebrates in each sample to the lowest taxonomic level possible based on available keys (Cowley 1978, Winterbourn et al. 1989, Towns and Peters 1996). Details regarding the characterization of the macroinvertebrate assemblages are available in Death and Zimmerman (2005). After removing the invertebrates, we dried the remaining sample residue at 80°C for 5 d, weighed it, and then ashed the samples at 600°C for 2 h. We then reweighed each sample and estimated organic matter mass per sample as the difference between post- and pre-ashed weights.

Data analysis of assemblage composition

Invertebrate densities (ind/m^2) were log transformed, and then nonmetric multidimensional scaling (NMDS) on a Bray–Curtis similarity matrix was used to visualize how macroinvertebrate assemblage composition (all seasons av-

eraged) varied between grassland and forested sites during the study period (*vegan* package, R Core Development Team 2012, version 3.0.3; Dixon et al. 2003, Oksanen et al. 2007). We then used analysis of similarities (ANOSIM) (Clarke 1993) with 999 permutations to assess whether observed differences between forested and grassland sites were significant and similarity percentage (SIMPER) analysis (Clarke 1993) to assess the contribution of each species to site type differences. SIMPER is sometimes criticized for being sensitive to abundant species, but prior log transformation reduces this impact. Furthermore, this study focused on global energy flows, which are primarily driven by the abundant species.

Trophic network construction

We assembled 20 trophic networks of macroinvertebrate energy flow based on the mean abundances of each species observed at each site (calculated across the 4 sample events) (Table 1). We obtained maximum individual lengths (typical for the Taranaki region) for each species from Moore (1998). We then estimated mean individual biomasses for each species based on published length–biomass regressions (Towers et al. 1994, Stoffels et al. 2003). We quantified energy stocks as megajoules per square meter (MJ/m^2) and flows as megajoules per square meter per year ($\text{MJ m}^{-2} \text{y}^{-1}$). We also estimated the total energy (measured in MJ) that each species (population density) contained from a mass-to-energy conversion database for aquatic organisms (Brey et al. 2010). We then estimated respiration/biomass (R/B) and production/biomass (P/B) ratios based on artificial neural network (ANN) models for aquatic benthic invertebrates (Brey 2010, 2012, respectively). Modeled, rather than measured, estimates of production and respiration were used because there is high error associated with estimating the production of populations with few individuals. Modeled data also have the advantage of removing the considerable ‘white noise’ that occurs with local one-off measures (Özkundakci et al. 2018). Furthermore, the models for R/B (Brey 2010) and P/B (Brey 2012) were built and cross-validated on very large global data sets (1252 and 22,920 respectively), accounting for a range of influential habitat and zoological factors, resulting in excellent-performing models with fits (R^2) of 0.801 and 0.847, respectively. A recent review of best-practice food-web modeling also recommends the use of Brey (2010, 2012).

We estimated dietary links between species based on literature reports of functional feeding group and diet (Table S1). In most cases we assumed that the dietary intake of each resource was proportional to the productivity of prey/basal taxa. However, in cases of a strong dietary preference, we used the proportions reported in the literature. We estimated the assimilation efficiency (assimilation/ingestion) of dietary components based on information in Benke et al. (2001). Given

Table 1. The location, altitude, stream order, distance between paired sites, particulate organic matter (POM, g/0.1 m²): chlorophyll *a* (Chl *a*, µg/cm²) ratio, and trophic network fragility for paired sites (one in upstream forest, the other in downstream grassland) at 10 Taranaki (New Zealand) ring-plain streams in the austral summer 2000.

Stream	Site	Coordinates (WPS 84)	Altitude (m)	Stream order	Distance between paired sites (m)	POM: Chl <i>a</i>	Dynamic stability
Waipuku Stream	F1	174°10'09" E 39°17'15" S	560	1	1650	1.08	79.71
	G1	174°11'15" E 39°17'00" S	480	1		0.00	72.77
Waipuku Tributary Stream	F2	174°10'30" E 39°17'28" S	529	1	400	1.36	78.97
	G2	174°14'46" E 39°17'25" S	520	1		0.51	81.82
Mangatoki Stream	F3	174°09'10" E 39°20'46" S	540	2	3800	5.03	81.09
	G3	174°10'56" E 39°22'29" S	400	5		0.95	74.03
Kaupokonui East Tributary Stream	F4	174°08'12" E 39°21'37" S	515	2	600	19.05	80.27
	G4	174°08'27" E 39°21'53" S	485	2		0.00	75.63
Kaupokonui East Stream	F5	174°07'53" E 39°21'49" S	505	2	300	4.17	81.40
	G5	174°08'02" E 39°21'55" S	490	2		2.94	79.05
Dunns Creek	F6	174°06'57" E 39°22'15" S	500	1	1000	2.67	82.32
	G6	174°07'19" E 39°22'44" S	455	1		0.56	79.98
Little Dunns Creek	F7	174°06'47" E 39°22'22" S	500	1	750	6.03	81.71
	G7	174°06'45" E 39°22'44" S	460	1		3.13	80.69
Ouri Stream	F8	174°03'00" E 39°22'50" S	450	3	225	2.33	82.45
	G8	174°02'58" E 39°23'00" S	435	3		0.82	81.19
Cold Stream	F9	174°01'07" E 39°22'28" S	400	1	900	9.81	80.27
	G9	174°00'44" E 39°22'48" S	370	1		0.00	76.56
Kapoiaia Stream	F10	173°57'17" E 39°17'30" S	410	3	750	7.73	77.38
	G10	173°56'47" E 39°17'31" S	380	3		1.26	82.77

that the networks were mass balanced, we assumed that the total consumption by a species was equal to the sum of the energy outputs due to production, respiration, and unassimilated food.

We used POM and periphyton measurements as basal nodes of the trophic network. POM and periphyton compartments were balanced to steady state by assuming that imports (i.e., upstream vegetation and detritus flowing into the reach or autotrophic growth) were equal to invertebrate consumption. We estimated imports as the energy assimilated by the food web, with the remainder assumed to be in dynamic equilibrium with outputs, because detrital input rates are variable and difficult to measure. The amount of energy leaving the system (exports) for each species was assumed to be equal to the estimated net population growth of that species, such that the networks are mass balanced with energy inputs equaling energy outputs. The energy exports could arise as consumption by higher trophic predators (such as fish), adult emergence, drifting downstream, death, and microbial decomposition.

Trophic network metric analysis

We used the *get.ns()* function within the *enaR* package (Borrett and Lau 2014, R Development Core Team 2012)

to calculate trophic network metrics at each site. Specifically, we estimated the number of nodes, relative ascendancy (Ulanowicz 1997), average path length (Finn 1976), indirect/direct flows (inputs) (Fath and Patten 1999, Borrett et al. 2006, Latham 2006), yearly consumptions of POM and periphyton, and total energetic exports.

We used one-way analysis of variance (ANOVA) to test for differences in each network metric between analyzed forested and grassland sites (R Development Core Team 2012). All calculated probabilities were corrected following the Holm–Bonferroni method (Holm 1979) with an α of 0.05.

Trophic stability analysis

One of the hypotheses tested was that small to moderate levels of allochthonous inputs (relative to autochthonous inputs) stabilize trophic networks. In testing this hypothesis, we used the ratio of POM: Chl *a* as an indicator of the relative levels of allochthonous inputs to autochthonous inputs. For each network we then derived estimates of dynamic trophic stability, which indicate how much of the total energy flow is conserved following species perturbation. We defined dynamic stability as the percent of the original, pre-perturbed network energy throughflow (the sum of all flows within a network) that remains at a new steady state after 25% of the taxa

are lost randomly (Canning and Death 2017). We then used the average (AVG) approach from Allesina and Bondavalli (2003) to simulate the networks to a new mass-balanced steady state. We used the enaR package with 20,000 iterations with taxa replacement to conduct these manipulations (Borrett and Lau 2014, R Core Development Team 2012). The AVG method averages the flows from the network brought to steady state via bottom-up (donor-control) dynamics equally with the flows from the network when brought to steady state via top-down (recipient-control) dynamics (Allesina and Bondavalli 2003). As a measure of temporal stability, we averaged the coefficients of variation for each species (population density) across the 4 sampling times at each site.

We used multiple ANCOVA (R Core Development Team 2012) to test whether dynamic stability and species population density variability differed between forested and grassland sites (categorical variable) across a range of POM:Chl *a* ratios. The POM:Chl *a* ratio is an independent variable representing the energetic contributions from allochthonous inputs relative to the autochthonous inputs (metric ~ riparian + POM:Chl *a*). This study was concerned only with changes in the POM:Chl *a* ratio (controlling for riparian cover), and as such, should the given metric differ significantly with differences in the values of riparian but not POM:Chl *a*, then the result was not explored.

RESULTS

Assemblage composition

Assemblage composition was significantly, though not markedly, different between forested and grassland sites (ANOSIM global $R = 0.2$, $p = 0.008$; Fig. 2). On average,

the forested sites had higher proportions of *Deleatidium* spp. (scraper), *Coloburiscus humeralis* (mayfly), and *Orthopsyche thomasi* (net-building caddisfly), whereas the grassland sites had higher proportions of *Orthocladinae* (chironomid midge), *Aphrophila neozelandica* (crane fly), and *Maoridiamesa* spp. (chironomid midge) (Table 2). Species that contributed the most to dissimilarity between the forested and grassland assemblages were *Deleatidium* spp. (28.5%), *Orthocladinae* (9.0%), *C. humeralis* (7.1%), *A. neozelandica* (6.8%), and *Maoridiamesa* spp. (6.5%) (Table 2).

Differences in basal energy supply arose from greater periphyton abundance at the grassland sites rather than from differences in POM. Average monthly Chl *a* density was approximately three times greater in grassland (21.0 mg/m²) than in forested (7.2 mg/m²) sites ($F_{1,18} = 21.2$, adj- $p < 0.01$; Fig. 3). POM did not differ significantly between forested (3.4 g/0.1 m²) and grassland (1.7 g/0.1 m²) sites ($F_{1,18} = 4.05$, adj- $p = 0.12$; Fig. 3). The POM:Chl *a* ratio was significantly greater at forested sites (4.9) than grassland sites (0.9) ($F_{1,18} = 11.6$, adj- $p < 0.01$).

Trophic network metrics

Of the 8 trophic metrics we measured, only 2 were significantly different between the forested and grassland sites (Table 3). The grassland assemblages were also estimated to consume an average of 70% more periphyton than forested assemblages (Fig. 4B, Table 3E). In addition, mean assemblage respiration in grasslands was over 50% higher than that for forest assemblages (Fig. 4D, Table 3H). Of marginal significance, mean energy exports from grassland assemblages were 40% greater than that in forested sites (Fig. 4C, Table 3G).

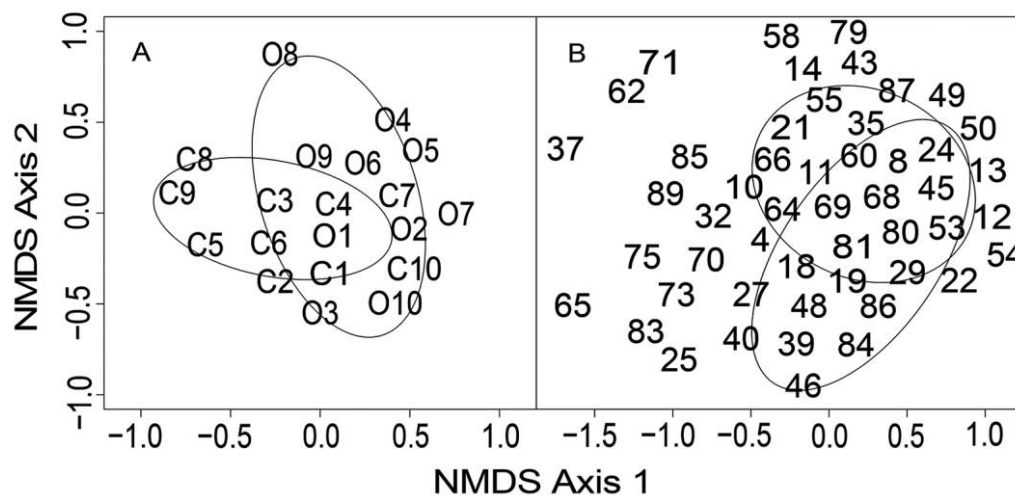


Figure 2. Nonmetric multidimensional scaling ordination (stress = 0.11) based on Bray-Curtis dissimilarity of macroinvertebrate assemblage composition at paired sites (upstream forested and downstream grassland) on 10 Taranaki (NZ) ring-plain streams. A.—Dispersion of sites in ordination space (C1-10 indicates forested sites, and O1-10 indicates grassland riparian sites). B.—Dispersion of species in ordination space (numbers represent taxa listed in Table S2).

Table 2. Similarity percentage (SIMPER) analysis comparing the dissimilarity of stream macroinvertebrate communities between paired sites on 10 Taranaki (NZ) ring-plain streams (1 in upstream forest and 1 in downstream grassland) sampled at 4 dates during 1999 and 2000.

Species	Average contribution to dissimilarity (%)	Standard deviation of contribution	Average abundance (forest)	Average proportion (forest, %)	Average abundance (grassland)	Average proportion (grassland, %)	Ordered cumulative contribution (%)
<i>Deleatidium</i> spp.	28.5	9.6	90.8	37.2	133.8	30.4	28.5
Orthocladinae	9.0	5.9	1.9	1.2	22.4	7.8	37.5
<i>Coloburiscus humeralis</i>	7.1	2.5	21.0	18.6	19.4	11.0	44.6
<i>Aphrophila neozelandica</i>	6.8	2.0	3.9	1.5	18.1	4.9	51.4
<i>Maoridiamesa</i> spp.	6.5	4.6	0.5	0.16	16.1	2.5	57.8
<i>Baeraeoptera roria</i>	5.5	3.4	2.7	7.5	12.6	19.4	63.3
<i>Zelandoperla decorata</i>	5.0	3.0	6.7	2.5	9.2	2.5	68.3
<i>Orthopsyche thomasi</i>	4.7	2.9	11.2	10.2	4.1	1.5	73.0
Elmidae	3.8	1.4	7.7	3.0	10.7	2.8	77.0
<i>Zelandobius</i> sp.	2.3	1.5	5.3	3.5	1.2	0.7	79.1

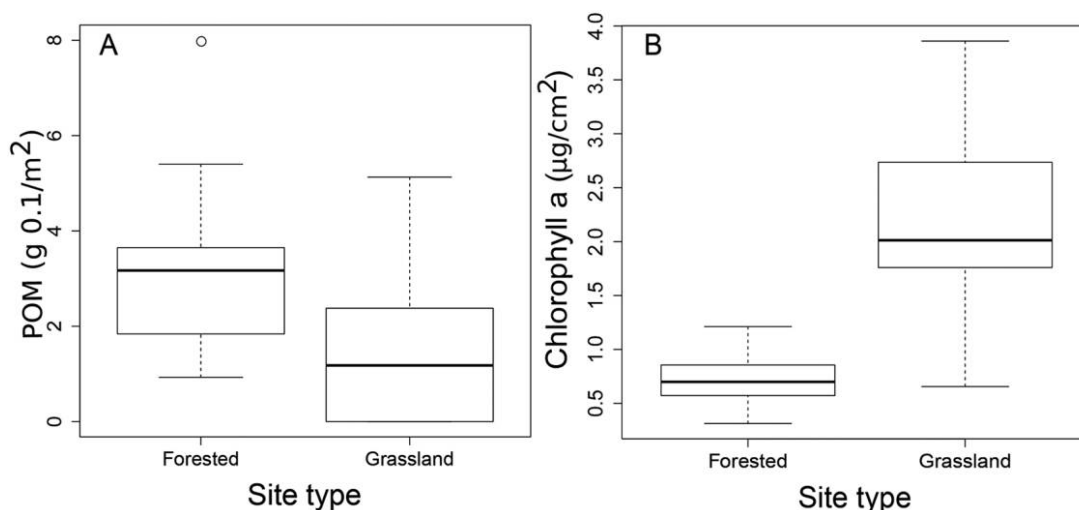


Figure 3. The particulate organic matter ($\text{g } 0.1/\text{m}^2$) (A) and chlorophyll *a* ($\mu\text{g}/\text{cm}^2$) (B) at paired sites (upstream forested and downstream grassland) on 10 Taranaki (NZ) ring-plain streams, sampled quarterly and monthly, respectively, over 1999–2000.

Trophic network stability

Dynamic stability at forested sites ranged between 77.4 and 82.6% (mean = 80.6%) and ranged between 72.8 and 82.8% (mean = 78.4%) at grassland sites. Dynamic stability was not different between these two site types when either only site type ($t = -1.09$, $p = 0.29$; Fig. 5A) ($t = 0.38$, $p = 0.71$ for POM:Chl *a*) or both site type and POM:Chl *a* were included ($r^2 = 0.05$, $F_{2,17} = 1.52$, $p = 0.25$).

The mean coefficient of variation at forested sites ranged between 102.8 and 122.8 (mean = 109.7) and at grassland sites between 104.9 and 127.6 (mean = 114.5). The mean coefficient of variation was not significantly different between site types ($t = 0.66$, $p = 0.52$; Fig. 5B), either with just POM:Chl *a* ratio ($t = -0.83$, $p = 0.41$) or with both factors included ($r^2 = 0.04$, $F_{2,17} = 1.48$, $p = 0.26$).

DISCUSSION

Deforestation, particularly of riparian zones, is one of the largest anthropogenic impacts on freshwater ecosystems (Carpenter et al. 1992, Scanlon et al. 2007). Riparian deforestation reduces allochthonous litter input and increases periphyton growth (e.g., Duncan et al. 1989, Feminella et al. 1989, Naiman and Décamps 1997). In New Zealand streams, native forested reaches are dominated by mayflies, stoneflies, and caddisflies, whereas reaches in pasture streams are dominated by chironomids and snails, and pine forest reaches have assemblages intermediate between these (Quinn et al. 1997a). It well known that riparian deforestation can alter macroinvertebrate assemblages, but the trophic consequences of assemblage changes on energy flows have seldom been explored. This study first examined whether forested and

Table 3. Mean metric values for stream macroinvertebrate trophic structure at paired sites on 10 Taranaki (NZ) ring-plain streams (1 in upstream forest and 1 in downstream grassland) sampled over 1999 and 2000. Adjusted *F*-test and *p*-values for ANOVAs comparing forested and grassland sites, $df = 1,18$. Metrics E–H are in megajoules per square meter per year ($\text{MJ m}^{-2} \text{y}^{-1}$).

Statistic	Mean forested canopy	Mean grassland canopy	<i>F</i> -test for differences between forested and grassland sites	Adjusted <i>p</i> -value for differences between forested and grassland sites
A Taxonomic groups	31	35	5.81	0.16
B Relative ascendancy	0.36	0.36	0.98	1
C Indirect/direct flows (inputs)	0.11	0.12	1.98	1
D Average path length	2.01	2.02	2.56	0.7
E Total consumption of periphyton	0.53	0.91	11.03	<0.01
F Total consumption of particulate organic matter	0.37	0.47	1.52	1
G Total macroinvertebrate exports	0.12	0.18	6.58	0.09
H Macroinvertebrate community respiration	0.78	1.2	8.69	<0.01

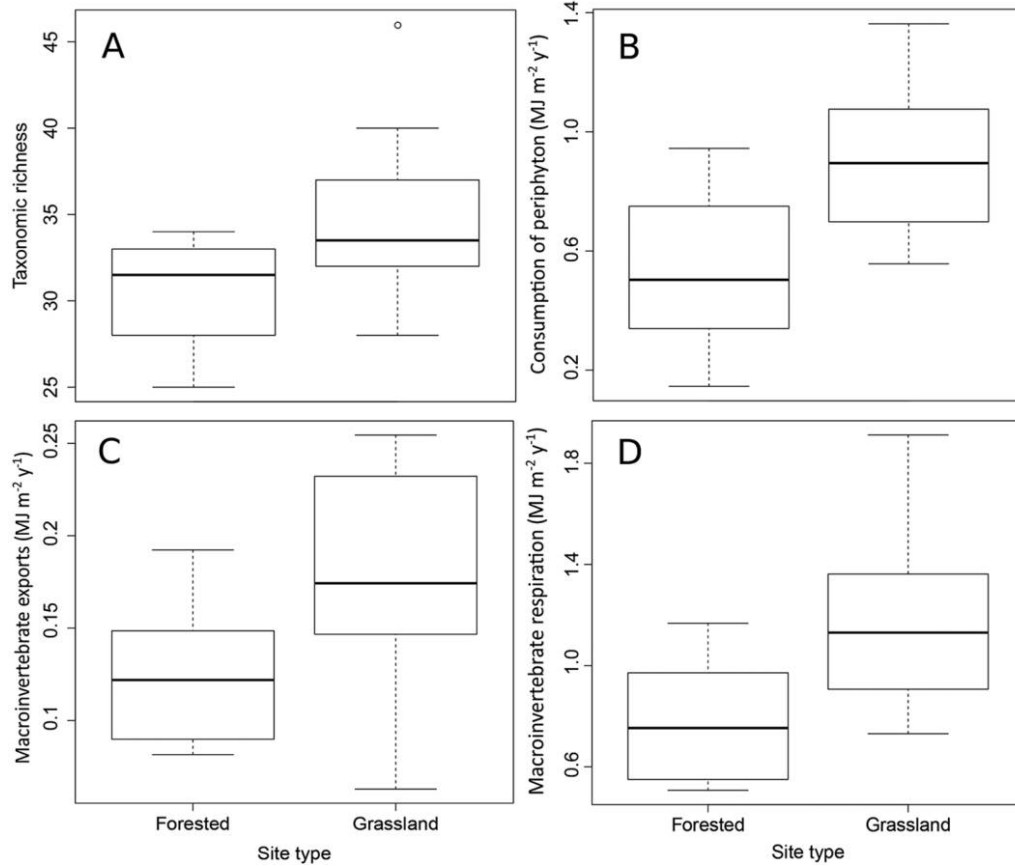


Figure 4. Significantly different are near-significant trophic network metrics between paired sites (upstream forested and downstream grassland) on 10 Taranaki (NZ) ring-plain streams: taxonomic richness (A); total consumption of periphyton ($\text{MJ m}^{-2} \text{y}^{-1}$) (B); total macroinvertebrate exports ($\text{MJ m}^{-2} \text{y}^{-1}$) (C); total macroinvertebrate respiration ($\text{MJ m}^{-2} \text{y}^{-1}$) (D).

grassland riparian cover alters macroinvertebrate assemblage composition and trophic flows. We then tested Huxel and McCann's (1998) hypothesis that small to moderate amounts of allochthonous matter (relative to autochthonous matter)

could stabilize a trophic network. We used the ratio of POM:Chl *a* (allochthonous:autochthonous indicator) and the trophic networks to empirically test the model-derived hypothesis. We did not find support for the hypothesis, even

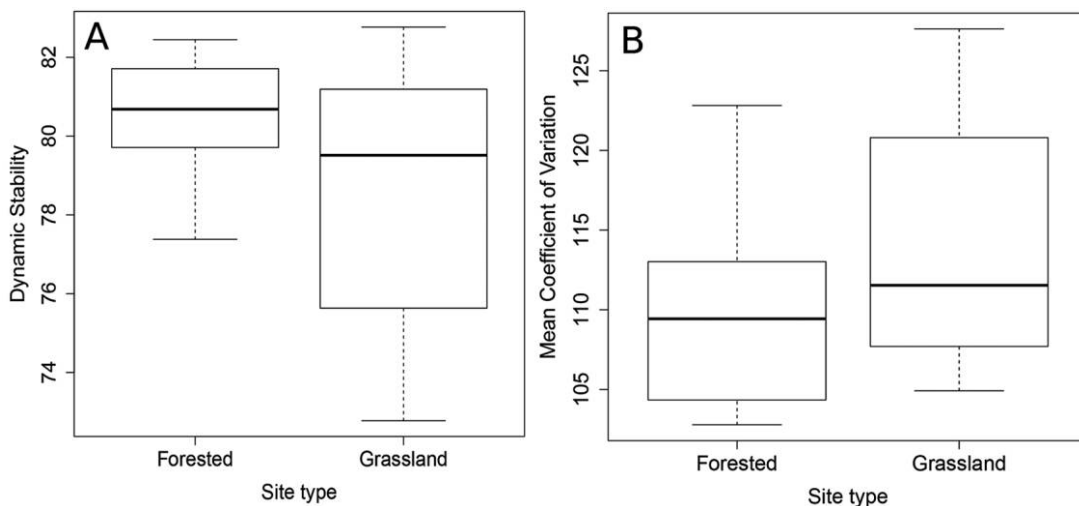


Figure 5. Differences in the dynamic stability (A) and mean macroinvertebrate coefficient of variation (B) between paired sites (upstream forested and downstream grassland) on 10 Taranaki (NZ) ring-plain streams.

though we found significant differences between the invertebrate assemblages in forested and grassland stream reaches.

Assemblage composition

Our findings are consistent with previous studies that found that mayflies, stoneflies, and caddisflies are dominant in forested streams, whereas chironomids and snails are dominant in pasture streams (Quinn et al. 1997a). All sites were dominated by *Deleatidium* spp., which feed primarily on diatoms and fine particulate organic matter (Winterbourn 1982, 2000, Towns and Peters 1996, Thompson and Townsend 2004). The forested sites were dominated by filter feeders that feed on POM in the water column. In contrast, the grassland sites were dominated by chironomid midges and crane flies, which both have life stages that feed primarily on diatoms and filamentous algae (Winterbourn et al. 1984, Winterbourn 2000, Thompson and Townsend 2004). Shade increases the relative level of filter feeding on fine POM and reduces grazers but was reported not to influence species feeding on coarse POM in artificial shading experiments in pasture streams (Towns 1981, Quinn et al. 1997b). Differences in assemblage composition in our study are therefore likely related to differences in food resource among POM-dominated forest streams and algae-dominated grassland streams.

Our Chl *a* estimates used only 4 stones, and given the spatial heterogeneity of periphyton in streams, the small sample size likely explains part of the large variation in Chl *a* at grassland sites. However, we still observed considerably large, and statistically significant, differences in Chl *a* between the forested and grassland sites.

Trophic network metrics

Differences in assemblage composition among grassland and forested sites drove greater estimated energetic (biomass) export and respiration. Greater basal energy supply at grassland sites supported greater macroinvertebrate growth, particularly in grazing invertebrates, which may have changed the relative abundance of functional groups, as has also been found in numerous other studies (e.g., Towns 1981, Hawkins et al. 1982, Rutherford et al. 1997, Zimmermann and Death 2002). Furthermore, algae have been shown to be a richer food source (i.e., leads to more efficient invertebrate growth) than detritus, primarily based on the nutrient stoichiometry (Cummins and Klug 1979, Bowen 1987, Elser et al. 2000), which may explain the greater invertebrate biomass at grassland sites. Thus, greater energetic exports from macroinvertebrates at grassland sites may support more predator (i.e., fish) biomass, resulting in greater growth of community biomass. However, although unshaded streams may provide more energy from macroinvertebrates to support higher trophic levels, observed responses of fish density to shading are mixed (Hawkins et al. 1983, Smokorowski and Pratt 2007, Kaylor and Warren 2017).

Contrary to expectations, greater macroinvertebrate biomass, predator presence, and total growth at the grassland sites did not lead to differences in average path length of the macroinvertebrate trophic networks among the site types. Thus, instead of the larger energy supply leading to a greater biomass of macroinvertebrate secondary consumers, it may have caused the macroinvertebrate trophic network to grow laterally such that macroinvertebrate primary consumer biomass increased. Alternatively, it is possible that most herbivores in our study shared predators, thus averaging out the influence of a few predators in the forested sites. The increased predicted macroinvertebrate exports in grassland sites may also influence the energetic flows of higher trophic levels beyond the macroinvertebrate assemblage, such as fish. Greater energy supply from macroinvertebrates could result in greater path lengths in the wider community (by supporting secondary consumers such as fish) if it is vertically assimilated locally, or it could support either downstream communities via drift or microbial communities through their decomposition. However, Canning et al. (2018) did not find longer food chains based on binary food webs that included fish (fish abundance data were not available for the present study) at grassland sites than at forested sites in this system. The increased energy may have increased the abundance of fish within a similar trophic level rather than promoting longer food chains.

Higher trophic levels may benefit from greater macroinvertebrate production, but that benefit comes at the potential cost of greater community respiration. Unless a river is well aerated, too much community respiration could result in oxygen depletion that may be stressful or lethal for the community (local examples in Clapcott and Young 2009, Wood et al. 2015). The macroinvertebrate communities at grassland sites had approximately 50% greater respiration than those at forested sites. Greater respiration at grassland sites is likely driven by the presence of twice as many invertebrates per square meter at those sites than at forested sites (Death and Zimmermann 2005). However, smaller-bodied invertebrates such as chironomids dominated the assemblage at the grassland sites, so the predicted metabolic demand of each individual was considerably less (Brey 2010). This lower metabolic demand could explain why doubled invertebrate density led to only 50% greater respiration rather than a doubling in community respiration. This idea is consistent with previous literature on allometric scaling relationships and metabolism, which shows small-bodied individuals to be more energetically efficient (e.g., Gillooly et al. 2001, Speakman 2005, Glazier 2010).

Trophic network stability

There was no difference in dynamic stability after random species loss, nor was there a significant difference in assemblage variability, despite some differences in energetic uptake and exports between the forested and grassland macroinver-

tebrate assemblages. Our findings are contrary to theoretical studies that suggest that low to moderate inputs of allochthonous material can stabilize autochthonous food webs by creating redundancy among resources, which should support greater carrying capacities and dampen disruptive oscillations (Huxel and McCann 1998, Huxel et al. 2002). However, high levels of allochthonous input may polarize aggregations of food resources, which could also destabilize the community if allochthonous inputs are perturbed (Jefferies 2000, Huxel et al. 2002).

These same theories predict that a steady stream of allochthonous inputs should support a community with low temporal variability (Huxel and McCann 1998). However, we found that neither dynamic stability nor variability significantly differed with relative levels of POM:periphyton in either forest or grassland streams. Previous studies of empirical trophic networks suggest that relative ascendancy, indirect/direct flows, and average path length can all also influence stability (Ulanowicz 2009, Ulanowicz et al. 2009, Rooney and McCann 2012, Saint-Béat et al. 2015, Canning and Death 2018, Canning et al. 2018). However, none of these metrics differed between forested and grassland streams, even though energy supply and assemblage composition differed (Death and Zimmermann 2005).

We suspect that food web stability may be similar between forested and grassland sites because of regular flood disturbances (Winterbourn 1997, Death 2008, 2010). Highly disturbed ecosystems have been found to have highly indeterminate energy pathways, short food chains, and weak interactions—all factors suggested to drive stability (Townsend et al. 1998, Post 2002, Ulanowicz 2009, McHugh et al. 2010, Sabo et al. 2010, Saint-Béat et al. 2015). Our study sites on each stream were in relatively close proximity to each other, so it is likely that they have similar flood frequencies. Frequent flooding is a disturbance that has been postulated to explain the highly flexible nature of feeding and life-history characteristics of New Zealand aquatic macroinvertebrates and many other mountainous areas around the world. It could also explain the stability of New Zealand riverine macroinvertebrate trophic networks (Winterbourn 1997, Townsend et al. 2003, Death 2008, 2010).

It is also plausible that the dietary links in our assembled food webs were too general to detect significant differences in stability. Diets inferred from functional feeding groups and the literature should account for all potential dietary links and therefore result in webs that are highly connected. Such webs may be relatively insensitive to species loss, which would make it difficult to observe differences among food webs. However, including the broad range of dietary links has the benefit of allowing dietary switching, as the webs assume that many or all those potential links already exist (Woodward et al. 2005, Woodward 2009). In contrast, food webs that are assembled based on gut content of local taxa instead of the literature can result in webs with artificially low connectance due to low sample size of gut contents of

the numerous species of interest (Woodward et al. 2005, Woodward 2009). We therefore maintain that accounting for all potentially dietary links provides a more realistic depiction of trophic stability by accounting for dietary switching.

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