Litterfall, nutrient concentrations and decomposability of litter in a New Zealand temperate montane rain forest

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Abstract: Litterfall reflects forest productivity and is an important pathway of nutrient cycling in forests. We quantified litter quantity, nutrient concentrations, and decomposability for 22 permanently marked plots that included gradients of altitude (a range of 320–780 m), soil nutrients and past disturbance in a cool temperate evergreen montane rain forest in the western South Island of New Zealand. For each plot we quantified total fine litterfall and sorted it into components over a 2-year period, and for each of four widespread tree species in each plot (when present) we measured litter nitrogen (N) and phosphorus (P) concentrations, litter decomposability, and the release of litter N and P during decomposition. Total fine litterfall (mean 2.96 Mg ha^{-1} year^{-1}) was low compared with other similar montane forests in New Zealand and elsewhere, and it declined with altitude and increasing successional stage of the plots. However, litterfall of four widespread tree species was unrelated to successional stage and that of only one was related to altitude. Further, neither total fine litterfall nor that of these four species was related to soil N or P concentrations with one exception. For the four species we found substantial variation among plots in litter N and P concentrations (up to 16-fold for N, 57-fold for P), litter decomposability, and the release of N and P during decomposition. Despite this, these variables were only rarely correlated with altitude, successional status, or soil nutrient concentrations across plots. Our results suggest that within-species variability in litterfall, nutrient concentrations, and decomposability are likely to be substantial in systems that have a high level of spatial variability because of recurrent large disturbances, and this has potentially important implications for the cycling of carbon, N and P, at the landscape scale.

Keywords: altitude; forest succession; *Griselinia littoralis*; Kokatahi River valley; *Metrosideros umbellata*; *Pseudowintera colorata*; soil nutrients; *Weinmannia racemosa*

Introduction

Litterfall reflects forest productivity and is an important pathway of nutrient cycling in forests (Bray & Gorham 1964; Vitousek 1984; Lowman 1988), and both the quantity and quality of litterfall impact on nutrient cycling (Bray & Gorham 1964). Determinants of quantity and quality of litter include abiotic factors such as climate and soil fertility (Vitousek 1984; Tanner et al. 1998; Takyu et al. 2003), and the characteristics of the plant species present, such as their productivity, concentrations of nutrients, structural form, and defence compounds, all of which are highly variable among and sometimes within species (Hättenschwiler et al. 2005, 2008). Litter quality and quantity are also determined by the disturbance regime, because species composition and litterfall are influenced by time since disturbance and therefore successional stage (Ewel 1976; Connell 1978; Richardson et al. 2005; Zhou et al. 2007). Changes in climate, nutrient inputs, and disturbance regimes are affecting forests worldwide (Dale et al. 2001; Aber et al. 2003), so a better understanding is needed of how these factors impact on litterfall quantity and quality.

An emphasis on the functional traits of plants is aiding understanding of litter quality and its role in governing ecosystem processes such as decomposition and nutrient fluxes (Grime 1979; Díaz & Cabido 2001). Links have been established between soil nutrient availability, leaf chemistry and structure, and the decomposability of leaves (e.g. Cornwell et al. 2008; Ordoñez et al. 2009). Further, some studies have focused on how forest succession may impact upon foliar and litter traits (e.g. Mason et al. 2011), and therefore on plant litter decomposition (Wardle et al. 2009a). Most work has focused on characterising variability in foliar traits and litter decomposability among species, but there is growing recognition that there can be considerable variation in these properties within species (Wardle et al. 2009a; Sundqvist et al. 2011). Much remains unknown about the drivers of variation in litter traits both within and among species, in relation to some abiotic factors such as altitude, and some biotic factors such as the successional status of plant communities.

Most New Zealand data about litterfall derive from lowland forests (e.g. Cowan et al. 1985; Enright 1999), with only limited data from montane forests (Wardle 1984; Davis et al. 2004). We therefore have a restricted understanding of litter dynamics in montane forests of New Zealand relative to other forest types. In this study, we sampled total litterfall for 22 permanently marked plots that included gradients of altitude, soil nutrients, and past disturbance (and thus successional stage), in a cool temperate evergreen montane rain forest in the western South Island of New Zealand. We predicted that litterfall would decline with increasing altitude

and therefore declining net primary productivity (Kitayama & Aiba 2002), and that it would increase with increasing soil nutrient concentration (Paoli et al. 2005, but see Wardle et al. 2003). These forests are subject to disturbances that result in primary successions and forest development after death of canopy trees (Reif & Allen 1988), so we also predicted that total litterfall would be greatest in plots that contain young forests that have developed on primary seres (Wardle et al. 2003). We tested these predictions in relation to total litterfall. We then quantified the litter nutrient concentrations and decomposability for four common, coexisting tree species in each of these plots and the extent of intraspecific variability among the plots for each species, and determined whether this variability is related to differences among plots in altitude, soil fertility, and successional stage after previous disturbance.

Methods

Study site

The study site is c. 10 km^2 in the upper reaches of the Kokatahi River valley, Hokitika River catchment, western South Island, New Zealand (42°56–58´S, 171°12–15´E, 320–780 m a.s.l., with surrounding peaks 1600–2050 m a.s.l.). The main geological substrate of the valley is foliated schist, grading to semi-schist in the east. The area has a high rate of geological uplift (> 10 mm year^{-1}; Whitehouse 1988), with high rates of erosion and periodic large earthquakes (Wells et al. 2001). Rainfall is 7000–8000 mm year^{-1}, with much occurring as high-intensity events (Henderson & Thompson 1999). Mean average annual temperature is c. 10°C. Soil development in the valley occurs rapidly, with rapid nutrient loss; nutrient availability peaks in < 200 years, and podsols can form in as little as 500 years (Tonkin & Basher 2001). Humaquepts and endoaquepts are the predominant soils of the valley.

The dominant vegetation in the valley is cool temperate montane rain forests, and the most common trees are evergreen dicotyledons (*Griselinia littoralis*, Griseliniaceae; *Metrosideros umbellata*, Myrtaceae; *Pseudowintera colorata*, Winteraceae; *Quintinia acutifolia*, Paracryphiaceae, and *Weinmannia racemosa*, Cunoniaceae; hereafter referred to by genus; nomenclature follows http://nzflora.landcareresearch.co.nz/); conifers (principally *Podocarpus cunninghamii*, Podocarpaceae) are less common (Reif & Allen 1988). Landslides and floods are frequent and give rise to sites of primary successions, while widespread death of canopy trees has occurred throughout the valley since the 1940s followed by succession to shorter forests of different composition (Allen & Rose 1983; Bellingham & Lee 2006).

Field methods

We measured litterfall and stem biomass throughout the valley in 22 permanently marked plots (20 × 20 m) that were established systematically in 1972 along seven random compass lines (locations shown in Bellingham & Richardson (2006)). The origin of each line was located along a stream channel in a restricted random fashion, and plots were located at 100-m-contour intervals until subalpine shrub communities were reached. Each line had 2–5 plots (mean = 3 plots). Line origins ranged from 300 to 1200 m apart. The plots sampled an altitudinal range of 320–780 m (Appendix 1).

We measured litterfall in each plot for 2 years, using four regularly spaced circular litter traps per plot, 10 m apart from each other; each trap was positioned at a height of 1 m, sampling 0.28 m^2. We collected litter between February 2003 and February 2005, every 4 months throughout the year, i.e. in July (mid-winter), November (spring) and February (summer). Litter collections were pooled for each plot at each sampling date, and the samples were oven-dried (60°C, 96 h). We report on fine litterfall, which is the combined dry mass total of branchlets < 2 cm in diameter (twigs), fallen bryophytes, reproductive parts, and leaf litter. For leaf litter, leaves were sorted to species and weighed.

We collected freshly fallen litter from four widespread trees in February 1998 from each plot in which they were present: *Pseudowintera* (22 plots), *Griselinia* (21 plots), *Weinmannia* (14 plots), and *Metrosideros* (11 plots). We chose these four species because they are all angiosperms and are dominant across montane rain forests throughout the western South Island (Reif & Allen 1988), and because they occur in at least half the plots sampled. A subsample of each litter sample was oven-dried, ground, and analysed for total N and P (Kjeldahl method). The decomposability of each litter sample collected was assessed using a standardised laboratory bioassay (Wardle et al. 2002, 2009b). For litter from each species in each plot, three Petri dishes (9-cm diameter) were each two-thirds filled with a standardised humus substrate (26.9% C, 1.38% N, 0.142% P, pH = 6.8) collected from under mixed hardwood forest in Kaituna Valley, New Zealand (43°44´ S, 172°41´ E) and amended to 117% moisture (dry mass basis), which corresponds to 80% of water-holding capacity. For each dish, a disc of nylon mesh with 1-mm holes was placed on the surface of the humus, and litter (1 g, oven-dried; cut into 5-mm fragments) was placed on the surface of the mesh. The dish was then sealed with tape to minimise water loss and incubated for 90 days at c. 22°C. After this time, all remaining (undecomposed) litter was removed from each Petri dish and rinsed, oven-dried (60°C, 48 h), and its dry mass determined. Litter decomposition rate was determined as the percentage mass lost during incubation. Loss of N and P from the litter was calculated as the total mass × nutrient concentration prior to incubation minus that present after incubation (Wardle et al. 2002, 2009b). The loss of N and P was expressed both as a percentage of the total initial litter mass present at the start of the incubation and as a percentage of the total N and P present at the start of the incubation.

To measure tree biomass and biomass increments on each plot, all stems ≥ 3 cm at 1.35 m (dbh) within the plot were identified to species, tagged permanently, and diameters measured in 2002 and in 2010. We estimated live biomass of each stem at each census using allometric equations incorporating diameter, mean height of stems, and species' wood density (Hall et al. 2001; Coomes et al. 2002). Wood densities (mass per volume; air-dried basis) were determined separately for each species. Biomass values were summed for each plot, and annual biomass increment determined (mean census interval = 8.0 years). We computed a ratio of live to dead biomass on each plot as a surrogate for successional stages of each stand; this ratio is greatest during early stages of succession on primary surfaces and least during late succession and retrogression, especially after deaths of canopy trees (Allen & Rose 1983). We used values tabulated in Hilton et al. (2011) to compute this ratio.

Soils cored to 15 cm depth, including organic horizons, were obtained from four randomly selected subplots in each of the 22 plots in 2010. The soils were analysed for N (CHN analyser, LECO Corporation, St Joseph, MI, USA), and total P

(H_2SO_4-soluble component extracted after ignition; Blakemore et al. 1987; Appendix 1).

Analysis

We compared inter-annual variation in litterfall using paired *t*-tests. Among the four widespread species for which we evaluated litter quantity and quality, we compared differences among species by ANCOVA (plot as covariate). We used Pearson correlations to evaluate relationships between litterfall and altitude, stem biomass increment, live to dead biomass ratio, and soil nutrient concentrations. Similarly, we used Pearson correlations to quantify relationships between litter quantity and quality of four widespread species and altitude, live to dead biomass ratio, and soil nutrient concentrations. All percentage data were arcsine–square-root-transformed before analysis.

Results

Litterfall quantity, composition, and inter-annual differences

The total fine litterfall in these cool temperate montane rain forests was 2.96 Mg ha^{-1} year^{-1} (coefficient of variation (CV) = 0.20) across both years and across all plots (Fig. 1). The first year's litterfall was greater than the second year's (paired *t*-test, t_{21} = 4.91; $P < 0.001$). Despite this variability, there was no difference in mean monthly temperature or total monthly rainfall between years (paired *t*-tests, $P > 0.6$; climate data from Arthur's Pass at c. 750 m, 27 km east of the study site).

Leaf litterfall comprised 79% of the total fine litterfall on average. Winter–spring (November) had the lowest leaf litterfall in both years (Fig. 1). Dicotyledons comprised the great majority, 90.6%, of total leaf litterfall across the two years (2.11 Mg ha^{-1} year^{-1}; CV = 0.20). The four widespread tree species (*Griselinia*, *Metrosideros*, *Pseudowintera*, and *Weinmannia*) contributed cumulatively 16.9% of total leaf litterfall (Fig. 2a). Ferns, mostly tree ferns (commonly *Cyathea smithii* and rarely
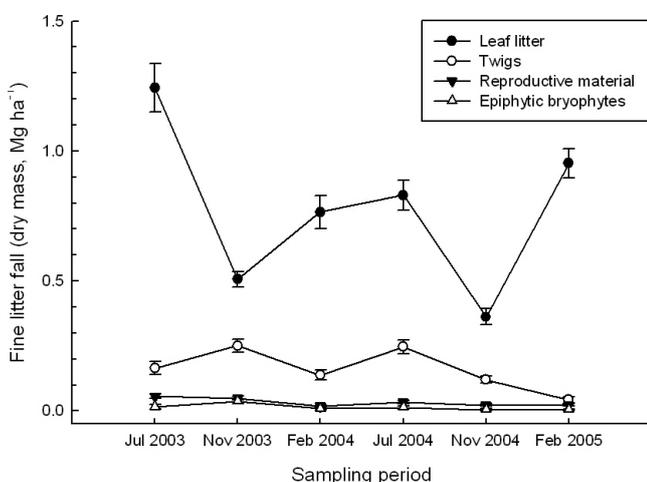
Dicksonia squarrosa), were the next most common component of leaf litterfall (8.6%; 0.20 Mg ha^{-1} year^{-1}; CV = 1.32), with conifers and monocotyledons contributing small amounts (both 0.01 Mg ha^{-1} year^{-1}). The non-leaf components of fine litterfall comprised twigs (on average 16% of fine litterfall), reproductive material (4%) and fallen bryophytes (1%, Fig. 1).

Litter chemistry and decomposition of four widespread tree species

Litter N and P concentrations and the release of N and P from decomposing litter were not different among four widespread tree species (Fig. 2), and there was also no difference for the N to P ratio (data not presented). However, there was considerable intraspecific variability in litter chemistry and release of N and P (Fig. 2). For example, litter N concentrations varied 7.6-fold among plots for *Pseudowintera*, 13.3-fold for *Metrosideros*, 15.1-fold for *Weinmannia*, and 15.5-fold for *Griselinia*, and litter P concentrations varied 17.4-fold for *Griselinia*, 19.5-fold for *Pseudowintera*, 27.6-fold for *Weinmannia*, and 57.0-fold for *Metrosideros*. The ex situ decomposition rates of *Griselinia* were double those of *Metrosideros*, *Pseudowintera*, and *Weinmannia*, which were not different from each other (Fig. 2d). Decomposition rates varied within species by a factor of 1.5 for *Metrosideros*, 1.8 for *Weinmannia*, 2.0 for *Pseudowintera*, and 2.2 for *Griselinia*.

Relationships with altitude, soil nutrient concentrations, stem biomass, and successional status

The mean annual total fine litterfall per plot (2003–2005) was negatively correlated with plot altitude ($r = -0.45$, $P = 0.03$). Fine litterfall per plot was unrelated to total soil N or P concentrations in plots ($r < 0.24$, $P = 0.29$). It was also unrelated to the live stem biomass in 2010 ($r = 0.32$, $P = 0.15$; Appendix 1), but was positively correlated with the change in biomass per plot between 2002 and 2010 (3.56 Mg ha^{-1} year^{-1}; CV = 3.47; $r = 0.42$, $P = 0.05$). Further, it was positively correlated with the ratio of live to dead biomass, i.e. it declined along a proxy gradient of succession ($r = 0.52$, $P = 0.02$).

Annual leaf litterfall of individual species was unrelated to soil N concentrations or live to dead biomass ratio (Table 1). Annual leaf litterfall of *Griselinia* was positively correlated with plot altitude, in contrast to total annual fine litterfall, and annual leaf litterfall of the other three species was unrelated to plot altitude (Table 1). Annual leaf litterfall of *Weinmannia*, but no other species, was positively correlated with soil P concentration (Table 1). Litter N and P concentrations (and litter N:P) and the release of N and P of all four species from individual plots were unrelated to plot altitude, soil N or P concentrations, or live to dead biomass ratio (i.e. successional stage). The decomposition rate of *Griselinia* litter was positively correlated with soil N concentrations in the plots whence its litter derived (Table 1), but decomposition rates of the other three species were unrelated to any soil nutrient concentrations. The ex situ decomposition rate of *Pseudowintera* litter was positively correlated with the live to dead biomass ratio on the same plot (i.e. declined along a proxy gradient of succession; Table 1), but this was not the case for the other three species.

Figure 1. Composition of fine litterfall at three collections annually over 2 years (2003–2005) (Jul = July, mid-winter; Nov = November, spring; Feb = February, summer); means and standard errors across 22 plots within a New Zealand cool temperate montane rain forest.

Discussion

There have been comparatively few measures of litterfall conducted in temperate evergreen montane rain forests. The
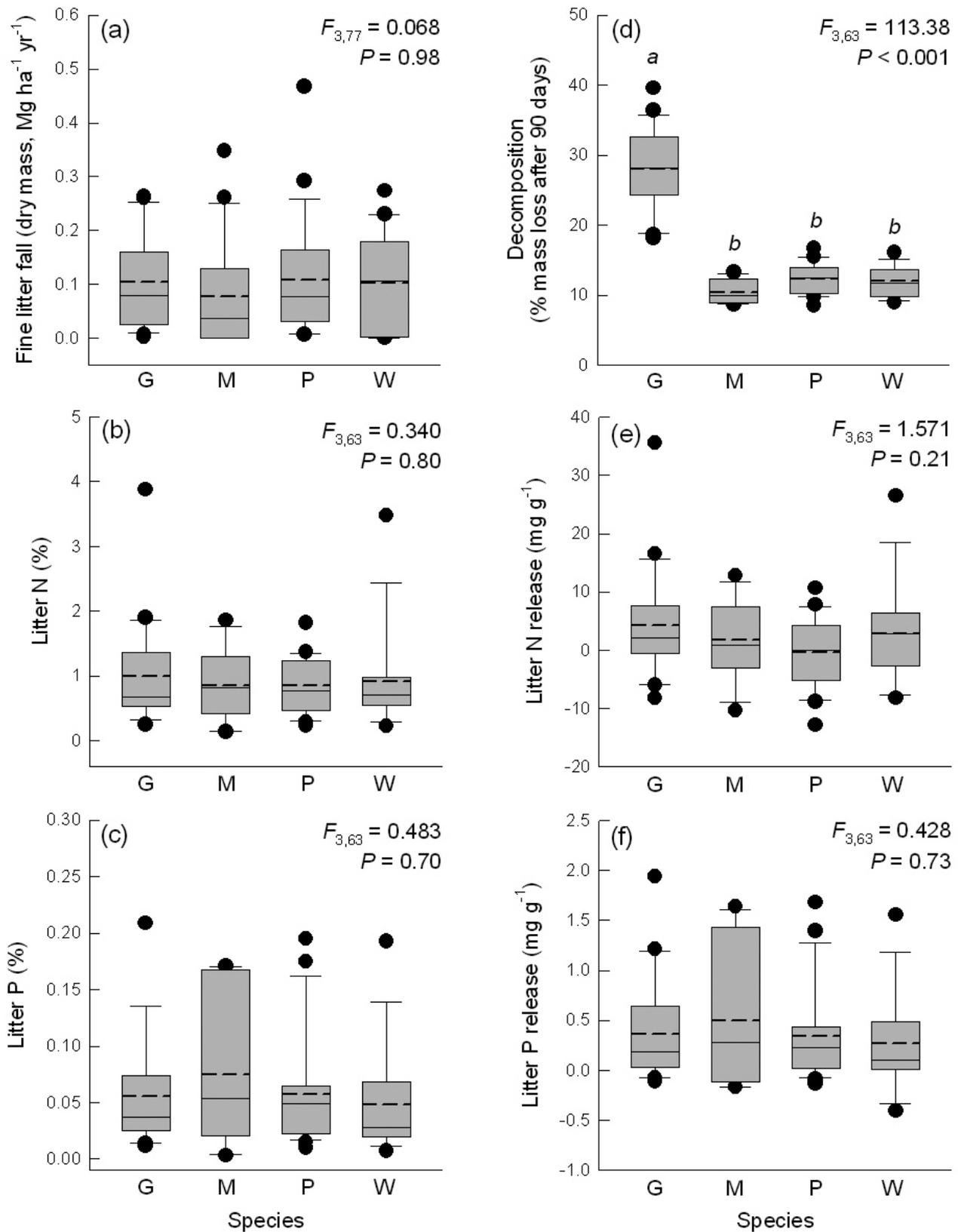
Figure 2. Litterfall, litter nitrogen (N) and phosphorus (P) concentrations, decomposition, and N and P release of four widespread tree species in plots in a New Zealand cool temperate montane rain forest: For litterfall per plot $n = 22$ plots for all species; for all other measurements $n = 21$ plots for *Griselinia littoralis* (G), 11 plots for *Metrosideros umbellata* (M), 22 plots for *Pseudowintera colorata* (P) and 14 plots for *Weinmannia racemosa* (W). The boxes indicate the 25th and 75th percentiles; within each box the solid bar and dashed bar represent the median and mean, respectively. Error bars indicate the 10th and 90th percentiles, with outliers denoted beyond. *F*-values are from ANCOVA (with plot as covariate) testing for differences among species, with *P*-values. Percentage data were arcsine–square-root-transformed for analyses. Boxes topped with different letters indicate significant ($P < 0.05$) differences among species (post-hoc Tukey tests).

Table 1. Pearson correlation coefficients of annual litterfall, litter nutrients and nutrient release, and ex situ decomposition rates from individual plots of four tree species, against plot altitude, soil nitrogen (N) and phosphorus (P) concentrations, and ratio of live to dead biomass, with each plot representing an independent data point. Percentage data were arcsine–square-root-transformed for analyses. * denotes significant ($P \leq 0.05$) correlations.

	Annual litterfall	Litter N	Litter P	Litter N release	Litter P release	Decomposition
Griselinia littoralis (*n* = 21)						
Altitude	0.50*	0.15	0.28	0.17	0.20	0.09
Soil N	0.16	0.18	0.15	0.16	0.03	0.50*
Soil P	−0.16	−0.16	−0.38	−0.18	−0.28	0.13
Live:dead biomass	−0.31	−0.13	−0.03	−0.11	0.04	0.20
Metrosideros umbellata (*n* = 11)						
Altitude	0.07	0.18	0.51	0.55	0.60	−0.17
Soil N	0.31	0.05	−0.13	−0.04	−0.02	0.38
Soil P	−0.30	0.18	−0.08	−0.13	−0.19	0.18
Live:dead biomass	0.45	0.23	0.14	0.34	0.24	0.11
Pseudowintera colorata (*n* = 22)						
Altitude	0.40	−0.26	−0.16	0.00	−0.08	−0.28
Soil N	−0.31	0.17	0.06	0.41	0.04	0.04
Soil P	0.09	0.38	0.22	−0.31	0.04	0.03
Live:dead biomass	−0.41	−0.30	0.06	−0.09	0.03	0.42*
Weinmannia racemosa (*n* = 14)						
Altitude	−0.46	−0.11	−0.10	−0.03	−0.01	−0.10
Soil N	0.07	0.14	0.08	0.27	0.13	0.16
Soil P	0.53*	0.31	0.24	0.14	0.29	−0.10
Live:dead biomass	0.03	0.08	0.37	−0.01	0.23	0.37

mass of total fine litterfall in the forest that we studied was 19% less than the average of eight other temperate montane forests, including three in New Zealand (Table 2). Leaf litterfall was 9% less than the average of seven other temperate montane forests, while total twig litterfall mass was 59% less than the average of six other forests (Table 2). Leaf litterfall in our study site formed a greater portion of total fine litterfall (79%) than the c. 70% average for montane forests internationally (Bray & Gorham 1964; O'Neill & DeAngelis 1981; Vitousek 1984). The leaf to twig ratio in fine litterfall from our site was nearly double that in other montane forests in New Zealand (data not shown). This could be because the other New Zealand montane forests are dominated by evergreen *Nothofagus* species, some of which exhibit strong seasonal peaks of twig loss (Wardle 1984), and these are absent from our study site (Reif & Allen 1988).

The mass of total leaf litterfall in the New Zealand montane forest was 57% less than the average across 21 tropical montane forests reviewed by Röderstein et al. (2005), and this is consistent with a decline in productivity further from the equator, even when climates are broadly similar (Bray & Gorham 1964; Hawkins et al. 2003). The physiognomic and floristic similarities between the temperate forests at our site and some tropical montane forests (Bellingham & Sparrow 2009) are therefore unimportant with respect to productivity.

In our study, litterfall peaked in autumn to mid-winter (July) or spring to summer (February) and was least in spring (November; Fig. 1) in both years, consistent with patterns observed in other cool temperate evergreen forests. For example, in other evergreen montane forests in New Zealand there are autumn peaks of leaf and twig litterfall for *Nothofagus solandri* var. *cliffortioides* and leaf litterfall for *N. menziesii* (Wardle 1984). In two montane rain forests in Chile at a similar latitude and altitude, litterfall peaks in summer and winter

and is least in spring (Pérez et al. 2003). Autumn leaf loss in evergreen species in cool temperate regions is likely to be because it is not advantageous to retain as many leaves during winter, when low temperatures result in low net assimilation by leaves, and when low soil temperatures cause diminished nutrient supply because of a reduction in the permeability of root cell membranes (Givnish 2002).

Relationships between litterfall, altitude, forest succession, and soil nutrients

Fine litterfall declined with increasing altitude in montane rain forests at our site, which is consistent with our predictions, and the same trend as for three other montane forests in New Zealand (Wardle 1984) and elsewhere (e.g. Garkoti & Singh 1995; Kitayama & Aiba 2002; Röderstein et al. 2005; Zhou et al. 2007; Girardin et al. 2010). This trend is likely to result from declining above-ground net primary productivity with altitude (Raich et al. 1997; Kitayama & Aiba 2002), most likely due to impairment of carbon fixation, decomposition processes and nutrient supply from the soil as temperature declines (Girardin et al. 2010; Sundqvist et al. 2011, 2012). High rates of natural disturbance in our study site result in a mosaic of vegetation of different ages on landslide surfaces and floodplains as well as widespread secondary succession after canopy tree mortality (Reif & Allen 1988). As a consequence, many tree species are widely distributed in the Kokatahi River valley and altitude is not a strong driver of vegetation composition (Allen et al. 1991). Therefore it is unlikely that declining litterfall with increasing altitude in our study site is much influenced by changes in tree species composition along the same gradient. The increase in annual leaf litterfall with altitude of an individual tree species, *Griselinia*, is probably because its biomass per plot increased ($r = 0.45$; $P = 0.04$) with altitude as well.

Table 2. Fine litterfall in temperate evergreen montane forests in New Zealand and internationally.

Location	Latitude	Altitude (m)	Fine litterfall (Mg ha⁻¹ year⁻¹)			Reference
			Leaf	Twig	Leaf + twig	
Kaweka Range, New Zealand	39°17′S	1040–1340	2.98	1.11	4.09	Wardle 1984 (mean of 3 sites)
Kokatahi Valley, New Zealand	42°57′S	320–780	2.33	0.48	2.81	This study
Craigieburn Range, New Zealand	43°15′S	550–1340	2.42	0.96	3.38	Wardle 1984 (mean of 5 sites)
Craigieburn Range, New Zealand	43°15′S	1015–1208	2.64	–	–	Davis et al. 2004 (mean of 2 stands)
Takitimu Mountains, New Zealand	45°43′S	576–886	2.98	1.05	4.03	Wardle 1984 (mean of 3 sites)
Nanda Devi Reserve, Uttarakhand, India	30°29′N	2750–3300	2.67	1.55	4.22	Garkoti & Singh 1995 (mean of 3 sites)
Chiloé National Park, Chile (conifers)	42°30′S	>600	–	–	2.04	Pérez et al. 2003
Chiloé National Park, Chile (mixed angiosperms)	42°30′S	500–600	–	–	3.33	Pérez et al. 2003
Findley Lake, Washington, USA	47°20′N	1200	2.08	0.94	3.02	Turner & Singer 1976
Olympic National Park, Washington, USA	47°50′N	342–714	2.17	1.43	3.60	Edmonds & Murray 2002 (upper catchment)

Fine litterfall has been shown to increase as total N and P concentrations in soils increase along some natural gradients (Paoli et al. 2005; Dent et al. 2006) but this is often not the case (e.g. Tanner 1980; Wardle et al. 2003; Hyodo et al. 2013), because plant-available forms of N and P can be in low amounts even when total amounts are high (Peltzer et al. 2010). Our results also show that, contrary to our predictions, litterfall is independent of concentrations of total soil N and P. Studies that have demonstrated links between soil nutrient concentrations and leaf litterfall in fertilisation experiments (e.g. Tanner et al. 1992; Vitousek et al. 1993; Davis et al. 2004; Kaspari et al. 2008) have either been conducted in old-growth stands or controlled for successional stage. In contrast, the plots in which we measured litterfall were randomly assigned across a catchment in which primary succession is common after landslides and floods (Reif & Allen 1988; Bellingham et al. 2001; Hilton et al. 2011), and in which some old-growth stands have died in situ followed by secondary succession (Allen & Rose 1983). There was a decline in litterfall along a gradient from primary succession to old-growth stands in which canopy trees have died (i.e. along a gradient of declining live to dead biomass ratio) and this is consistent both with our predictions and with patterns found along gradients of succession and retrogression elsewhere (Wardle et al. 2003; Köhler et al. 2008).

The weak correlation between fine litterfall and stem biomass productivity in our study is not unexpected because allocation to foliage and wood can differ substantially among species as well as in response to climate and soils (Shoo & VanDerWal 2008) and because the efficiency of converting leaf production to tree biomass growth can be strongly dependent on climate and soil nutrients (Paoli et al. 2005). For example, across a range of studies in tropical forests there was only a weak positive correlation between fine litterfall and stem biomass productivity (Shoo & VanDerWal 2008). Total fine litterfall was found to be a good predictor of net primary productivity compared with stem biomass increment in a meta-analysis of data from 35 tropical forests (Malhi et al. 2011).

Relationships between litter quality, altitude, forest succession, and soil nutrients

Variation in plant functional traits within species is increasingly recognised as a possible mechanism to explain community assembly and richness (Laughlin et al. 2012). Most recent attention on intraspecific trait variation has focused on foliar characteristics (e.g. Albert et al. 2010). Recent studies have also quantified intraspecific variation in litter chemistry, and shown it to be slight in lowland tropical rainforests in French Guiana (Hättenschwiler et al. 2008), but 2- to 3-fold in lowland temperate rainforest in New Zealand (Richardson et al. 2008). In our study, there was much greater variation in litter chemistry rates of all four widespread tree species; i.e. 8- to 57-fold variation in litter N and P concentrations.

The causes of such large intraspecific variation in litter chemistry of the four widespread tree species that we considered are unclear. There was no relationship of litter N or P concentrations for any of our four individual species with altitude. In comparison, litter N concentrations of all species combined declined with altitude in four tropical montane forests in Colombia, Costa Rica, Sabah, and Sarawak, whereas litter P concentrations showed no consistent trends (Tanner et al. 1998). While the quantity of litter (total annual litterfall) declined as succession proceeded (using live to dead biomass ratio as a proxy measure), quality, in terms of nutrient content and release of four widespread species, did not. The lack of relationship between litter N and P concentrations of four widespread trees in our study and soil N and P concentrations is consistent with some other studies (Ordoñez et al. 2009; He et al. 2010; Lagerström et al. 2013) and emerges because plant-available forms of N and P can be low even when total amounts are high.

In our study site there was c. 2-fold variation in plant litter decomposition rates for each of the four species across plots. While intraspecific variation in decomposition rates have not been explicitly quantified across plots in other studies, there is evidence of high within-species variability of decomposability of litter sourced from plots with contrasting environmental conditions (Crews et al. 1995; Wardle et al. 2009a, b). There is no obvious driver for the high level of intraspecific variation that we found across plots; decomposition rates of all four species were unrelated to altitude or succession and, among the four species, only decomposition rates of *Griselinia*, which were the most rapid, were related to soil chemistry, i.e. positively correlated with soil N concentrations.

Conclusions

Our work focused on a study system in which there is considerable heterogeneity in site conditions among plots resulting from steep topography, frequent landslide activity due to high rainfall, and high ongoing tectonic activity. This in turn leads to substantial spatial variation in litterfall, in litter N and P concentrations within each of the four dominant tree species among plots (up to 16-fold for N, 57-fold for P), and (to a lesser extent) in litter decomposability and N and P release. These results have several implications. First, there is considerable recent interest in the role of within-species variability as an ecological driver (Wardle et al. 2009a; Albert et al. 2010), and our results indicate that this role is likely to be especially significant in systems that have a high level of variability as a result of recurrent large disturbances. Second, our work highlights the complexities that exist when attempting to identify the precise drivers of litterfall, litter quality, and litter decomposition in areas that are geologically active and where multiple gradients (in this case, of altitude, soil fertility and successional stage) therefore coexist in the landscape. Third, the very high level of inter-plot spatial variability of both the quantity and quantity of litter inputs in these types of geologically active areas is likely to have important implications for the spatial heterogeneity of biogeochemical fluxes of nutrients, and the cycling of carbon, N and P, at the landscape scale.

Acknowledgements

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Appendix 1. Altitude, soil nutrient concentrations, live stem biomass and its increment, and the ratio of live to dead biomass for individual plots in cool temperate evergreen montane rain forest, Kokatahi River valley, western South Island, New Zealand.

Plot	Altitude (m)	Soil N (%)	Soil P (mg kg^{-1})	Live stem biomass 2010 (Mg ha^{-1})	Stem biomass increment 2002–2010 (Mg ha^{-1} year^{-1})	Live:dead biomass
62/1	470	0.29	698	66.05	4.81	0.02
62/2	590	0.64	674	460.12	8.54	5.67
62/3	750	0.52	359	406.93	−0.62	1.17
63/1	510	0.32	710	321.06	1.30	8.09
63/2	630	0.85	503	356.20	1.65	3.76
63/3	700	0.61	541	376.18	14.81	1.63
64/1	580	0.77	745	259.93	6.84	5.67
64/2	700	0.41	835	150.33	9.70	0.49
67/1	420	0.45	703	127.16	−1.29	3.76
67/2	500	0.87	676	190.10	4.92	3.76
67/3	610	0.90	597	237.83	7.22	0.82
68/1	610	0.51	742	119.20	3.44	2.13
68/2	710	0.61	668	63.55	3.92	0.10
69/1	460	0.37	753	191.94	7.10	1.50
69/2	580	0.41	727	300.01	7.94	4.56
69/3	700	0.70	584	756.89	8.55	13.29
69/4	780	0.35	580	190.85	8.78	0.37
70/1	320	0.22	660	95.38	5.77	15.67
70/2	420	0.16	726	91.56	3.43	1.70
70/3	560	0.45	646	182.69	6.41	0.12
70/4	690	0.32	628	74.48	3.95	0.09
70/5	740	0.30	653	70.71	3.85	5.67