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RESEARCH ARTICLE

Temperature dependency of litter decomposition is not demonstrated under reciprocal transplantation of tussock leaves along an altitudinal gradient

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Abstract

1. Decomposition rates are an important component of carbon sequestration rates in soils, potentially mitigating future climate change. Here we aim to better understand decomposition's relationship with temperature in natural conditions.
2. In snow-tussock grassland dominated by *Chionochloa rubra* on Mount Tongariro, Tongariro National Park, New Zealand, we measured decomposition of *Chionochloa* leaf litter along an ≈ 700 m altitudinal gradient, as a space-for-temperature experiment, representing 4.2°C of warming. We examined decomposition rates in a full reciprocal translocation of litter bags between eight plots as both the origin of eight litter types and the eight destinations of plating out of litter bags, over 4 years using six replicates, and modelled their relationships to environmental variates.
3. Litter decomposed progressively over time, but at the same rate along the altitudinal gradient. There was no home-field advantage. In terms of litter quality, decomposition rates were related only to litter lignin, or fibre or litter N. Only decomposition at Year 4, and that only when organised by litter destination, showed a relationship to mean annual temperature jointly with soil C, and this was only weak and implausible. When studied across the full reciprocal transplant, there were no significant interactions between Origin and Destination data with or without Years. Therefore litter from each plot decomposed at the same rate as other plots' litter at all altitudes, allowing for small, often irregular differences in litter quality and micro-environment.
4. Despite the few modelled differences, decomposition rates show no plausible trends in our altitude-for-temperature substitution. We suggest this may be a universal finding, except perhaps under different moisture regimes. Thus, under projected climate warming scenarios, changes in temperature will not directly affect decomposition rates, and cannot influence C sequestration in nature.

Kevin R. Tate Deceased.

Dedication: To Kevin Russel Tate (8 April 1943–22 January 2018) whose life and science continue to inspire.

KEYWORDS
bunch-grass, ecosystem, fibre, grassland, lignin, litter quality, nutrients, precipitation, temperature, Tongariro National Park, translocation, tussock

1 | INTRODUCTION

Global climatic warming caused by accelerated emissions of greenhouse gases, including carbon dioxide, is currently challenging humanity (Ripple et al., 2017). Sequestering surplus carbon (C) in terrestrial ecosystems is a desirable approach to mitigating anthropogenic emissions—thus the need to identify influential variates (e.g. Lal, 2004; Schlesinger & Amundson, 2019; Stockmann et al., 2013).

The common, if often unexpressed, operational definition of ecosystem-level C sequestration (e.g. Natali et al., 2012; Ross et al., 1996; Tate, Scott, Parshotam, et al., 2000) is a positive balance in the annualised ratio of the rates of C fixation via photosynthesis to C release via respiration and/or decomposition (Krna & Rapson, 2013). In natural systems, and excluding autotrophic belowground respiration (i.e. by plants; Tang et al., 2020), the major source of CO_2 release is from decomposition of plant litter, reported as soil heterotrophic respiration (Kirschbaum, 2006), or more commonly as loss of biomass of litter samples, although ignoring the CO_2 production of decomposers during that release (e.g. Aerts, 1997).

Decomposition (i.e. a rate) is primarily affected by the chemical composition of litter (quality; e.g. Bontti et al., 2009; Murphy et al., 1998). But for any given quality, type or species of litter, there are reports of strong, positive relationships of decomposition with temperature (e.g. Flanagan et al., 2013; Murphy et al., 1998; Petraglia et al., 2019), precipitation or soil moisture (e.g. Djukic et al., 2018; Wang et al., 2021) and soil nutrients (e.g. Molloy et al., 1978; Williams et al., 1978), as well as substrate supply, especially of labile C (McLauchlan & Hobbie, 2004; Stockmann et al., 2013; Xu et al., 2018). Of these temperature is often considered the most influential variate (e.g. Petraglia et al., 2019), sometimes interacting with soil moisture (e.g. Wang et al., 2021).

However recent work confounds this widespread perception of decomposition's relationship with temperature. In a meta-analysis, Giardina and Ryan (2000) found that decomposition rates of forest C in mineral soils were remarkably constant across a 20°C range of temperature. Bontti et al. (2009) showed that decomposition rates of litter as wooden dowels had no relationship with temperature. In a meta-analysis of warming experiments, Carey et al. (2016) noted no impact on decomposition in most biomes. Djukic et al. (2018) and Petraglia et al. (2019) reported no temperature sensitivity of decomposition of tea bags over periods of 3 months to 3 years. Moinet et al. (2020) found no evidence of temperature dependence in heterotrophic soil respiration, concluding it was constrained by the physicochemistry of soil organic matter. Nevertheless records of temperature dependence of decomposition in nature continue to be published (e.g. Bonanomi et al., 2021; Cui et al., 2021; Tan et al., 2021).

Which view is the more correct? The difficulty in answering this question comes from the many, often confounding, variates that might be involved. The experimental design which best accommodates this difficulty is the fully factorial reciprocal transplant, which generates and tests all possible combinations of comparisons (Figure 1). In the case of litter along a natural gradient, it uses all combinations of 'origin' (where the litter is sourced from) versus 'destination' (where it is placed to decompose). Essentially this design neutralises potential differences within these factors, mainly expressed in terms of litter quality (varying at different 'origins') and micro-environmental variability about a trend (occurring at different 'destinations'), by asking if there are any 'origin' types which respond differently to the other origin types in at least some of the 'destination' zones. This would be shown by the presence of a significant higher-order interaction. If there is no such interaction, then

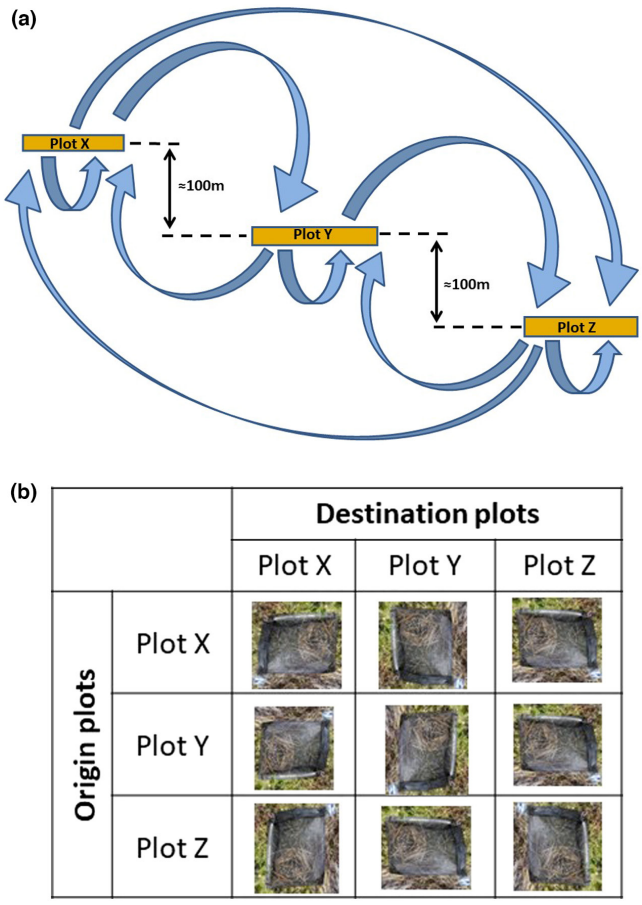

FIGURE 1 The reciprocal transplant design over three plots, with (a) the blue arrows showing the movement of litter bags from Origin to Destination sites, and (b) the grid of 3 × 3 samples. In reality we used eight plots with eight litter types and four harvests (yearly), replicated six times.

any apparent trends detected between destinations or between origins are due to small, effectively random differences in, respectively, litter quality or environment, which are cancelled out in the full analysis.

However, this reciprocal transplant approach has seldom been used in litter decomposition studies. Salinas et al. (2011) used a partial reciprocal transplant of litter from 15 species of tropical trees, across five sites on an altitudinal gradient, but did not test for interactions. Veen et al. (2015) used a fully factorial reciprocal transplant of three mixed litter types from and into three vegetation types across three source elevations on a 560 m elevational gradient. But, since they were studying home-field advantages, they did not comment on their higher-order interactions at all.

We employ the reciprocal transplant design to investigate the temperature dependence of litter decomposition in a fully controlled way. We operate along an altitudinal gradient which generates a space (or altitude)-for-temperature sequence (Faber et al., 2018), using a single dominant species to simplify issues re possible synergies in the decomposition of mixed litter types (Cornelissen et al., 2007; Gartner & Cardon, 2004), and a single vegetation type (giving a narrower range of environmental conditions and microbial floras; Bani et al., 2019; Yang et al., 2021). We drastically improve explanatory power in the design by adding more replicates and altitudinal steps, diluting random effects. We also increase the duration of the experiment, as we expect litter to be recalcitrant, showing slow decomposition rates (Rowland & Roberts, 1994; Tate, Scott, Parshotam, et al., 2000). This experiment is the first of its kind to have sufficient degrees of freedom to produce credible results for higher-order interactions when testing the temperature dependence of decomposition in nature.

Our chosen vegetation type, tussock grassland, occupies a 700 m altitudinal gradient on Mount Tongariro, New Zealand, 1 km west of Ketetahi Hot Springs (Figure 2), and forms the longest continuous altitudinal belt of a single herbaceous vegetation type we know. It is dominated by *Chionochloa rubra* ssp. *rubra* var. *rubra* (Connor, 1991; red tussock), a perennial bunch-grass to 80 cm tall, with leaves rolled into tubes of 3–4 mm diameter, and a life span of centuries (Mark, 1969). In a World Heritage Park it was not possible to sample roots, so we were restricted to leaf litter. Our aim is to examine whether decomposition rates are indeed higher at lower altitudes, as a proxy for warmer temperatures.

2 | MATERIALS AND METHODS

At Tongariro National Park (796 km^2), housing three active volcanoes, sampling was by permission of Department of Conservation and Ngati Rangi, Ngati Tuwharetoa and Ngati Tahu (National Permit Number: TT-29427-FLO). Prevailing winds are westerly to northwesterly, bringing rain or snow on at least half the days of the year (DoC, 2013). At the mountain village of Chateau Tongariro (13 km west of our site; 1119 m), mean annual temperature is 7.2°C, with a mean daily maximum for the warmest month (February) of 17.1°C, mean daily minimum for the coldest month (July) of −1.2°C and mean annual precipitation of 2838 mm (NZMS, 1983).

FIGURE 2 *Chionochloa rubra* at Plot 2, near the base of its altitudinal range, with tussock extending well upslope and into the snowy cap of volcanic Mount Tongariro, New Zealand. The highest field site sampled is near the peak, just under the shadow of the cloud. *Image*: Matthew A. Krna

On a northerly aspect of Mt Tongariro eight plots (15 × 30 m, elongated along the contour) were established, one every ≈100 m in elevation, in February 2011 from 1000 m (Plot 1) to 1700 m (Plot 8; Figure 3). Cover of *Chionochloa* per plot was estimated as that species' shadow at solar zenith (following Rapson, 2017; Table 1). Near each plot, precipitation was collected over the first 2 years of the experiment in two 1.5 L containers (containing 5 cm^3 of kerosene to prevent evaporation). Shaded air temperatures 10 cm above the soil surface were recorded bi-hourly with data loggers (HOBO model 8 K-UA-002-08) over the first 18 months of the experiment. Annualised data were derived, with some minor extrapolations for missing segments, although only winter data for 2013 were available for the lowest altitude plot. Additionally the mean daily maximum for the two warmest months (January and February) was extracted, and the mean daily minimum for the two coldest months (June and July).

Randomly placed soil cores (2.8 cm diameter; $n = 6–8$) were collected to 30 cm in depth (Allen et al., 1989) over two dry days in late summer 2013, divided into 10 cm segments and bagged. In the laboratory, soils were pooled across each depth for each plot, weighed, dried at 35°C for 7 days, re-weighed (giving soil moisture levels), sieved to 2 mm, and then finely ground. Analysis of C and N (nitrogen) content of soils was performed using flash combustion with a Leco furnace (Laboratory Equipment Corporation). Soil phosphorus (P; 0–30 cm) analysis followed the Kjeldahl wet oxidation method (Blakemore et al., 1987).

Over 5 dry days in mid-summer in 2011 we collected the youngest achlorophyllous (dying) leaves still attached to tillers of *C. rubra* plants adjacent to each plot, extracting as much sheath as possible. These leaves have very low moisture contents (<15%; Table 1). Each plot's pooled litter was cut into ≈5 cm segments for plating out (see below). Six subsamples were haphazardly extracted, placed

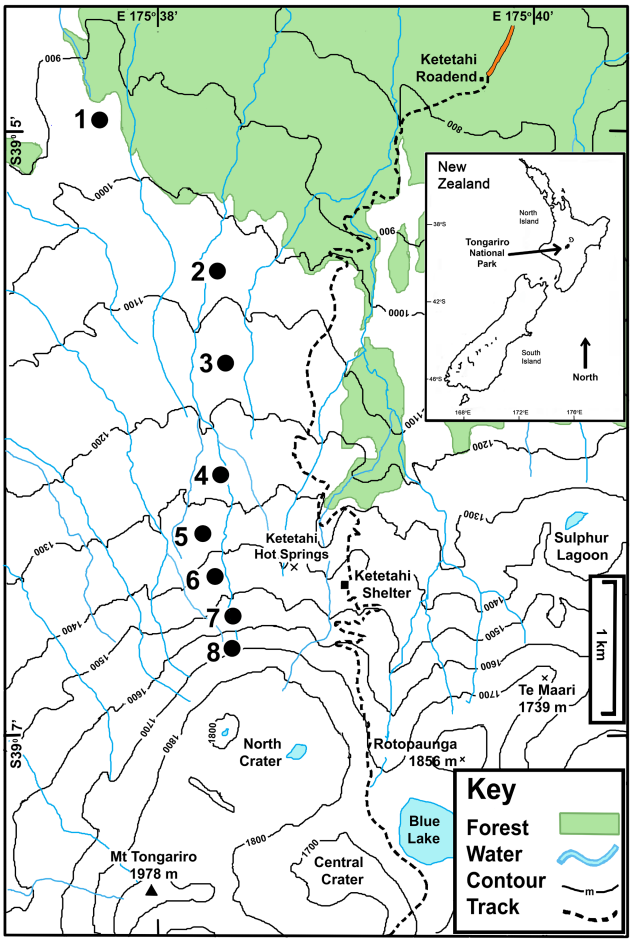

FIGURE 3 Topographic map depicting eight experimental plots spaced every ≈100 m in altitude on Mount Tongariro's north (sunny) face. Inset map of New Zealand shows location of Tongariro National Park.

in plastic bags prior to drying at 60°C for 72 h and weighing, with plot means of fresh/dry weight ratios used in calculations. Litter subsamples were analysed for C and N concentrations using a Leco TruMac Analyser® (Leco, 2003), and for P by the Kjeldahl method (Blakemore et al., 1987). Acid detergent fibre (AD-fibre), cellulose and lignin concentrations followed the methods of Rowland and Roberts (1994). Condensed tannins and total phenolics for Plots 1, 4 and 8 followed Broadhurst and Jones (1978) and Price and Butler (1977) respectively.

Litter decomposition was measured over 1460 days from February (summer) 2011. Litter decomposition bags, 20 cm × 25 cm in size and of black nylon rectangular mesh with a pore size of 2 mm, were filled in the field with a haphazard sample of 3.00 g fresh weight from each plot's pooled litter. 1536 bags were filled, for a full reciprocal translocation across the eight plots from where the litter had originated (i.e. 'Origin') to eight 'Destination' plots, giving a total of 64 grid-square comparisons, with four annual collection periods and six replicates of each (Figure 1). Bags were haphazardly pinned onto bare ground or ground-layer vegetation in intertussock spaces within each plot, and one quarter collected in March (autumn) of each of 2012–2015. Litter was then sorted to remove soil and ingrown species, dried and weighed as above, giving mass loss values over 1–4 years. Bag recovery was 91%.

For decomposition the half-life and decay rate coefficients (k from the litter decay curve, $y = a.\exp^{-k}$) over the 4 years were calculated following Sundarapandian and Swamy (1999) using treatment means. Home plot data (where Origin and Destination were the same) were also analysed separately.

The reciprocal transplant design, where all plots are 'copies' of all other plots, permits a three-way analysis of variance (ANOVA) on mass loss, which was used to determine significant effects and interactions of litter Origin, Destination and time (Years). Decomposition was also investigated separately for litter at its plot of origin (i.e. a 'home-field advantage'), using two-way ANOVA. Tukey's HSD (highest significant difference) post-hoc tests explored the plot differences using the *HSD.test* function in the AGRICOLAE package (de Mendiburu, 2012) in R (R Core Development Team, 2010). Although the plots are non-independent, the variances are relatively equal, and Tukey's is acceptably robust (Batista & Ferreira, 2020; Rogan et al., 1977).

We conducted >500 Akaike tests on correlates of expressions of decomposition, which however, revealed few significant, and even fewer interesting, results. Details are given in Supplementary Materials.

3 | RESULTS

Chionochloa had a mean of 12.8% cover at each plot, and plants were 74 cm tall, emergent above ground-level vegetation (Table 1), with a mean canopy diameter of 50 cm (data not presented).

Compared with the two lowest altitude plots, the two highest altitude plots had 32° steeper slopes and 237 cm more annual precipitation, while mean annual and summer temperatures were lower (by 1.7 and 3.3°C respectively; Table 1). Soil N, C, P and moisture were also lower at the two highest altitude plots (by <3.7, <1.5 and 0.15 mg g^{-1} and 3% respectively; Table 1), while the C:N ratios were higher (>9.5; data not presented).

Litter fresh:dry weight ratios differed significantly between plots ($p < 0.009$; $n = 6$), but showed only a very weak, nonsignificant trend of less dry biomass per unit fresh biomass with greater altitude (Table 1). Prior to decomposition, litter from higher-altitude plots contained higher concentrations of C and N, while P, phenolics, fibre and lignin were greater at lower altitudes ($r^2 > 0.77$ each; Table 1). Of the 112 Akaike tests on litter quality, 14% gave acceptable models for decomposition, and another 22% had parameters which were inseparable from null models (Table S1). Four measures of decomposition were successfully modelled (Table S1), with more litter N, lignin or fibre resulting in slower decomposition. However, relationships were weak and did not always depict the plots in strict altitudinal order (Table S2; Figure S1), weakening credibility.

For litter decomposing at its plot of origin (i.e. the Home plots' data), decomposition varied significantly only over Years (Table 2;

TABLE 1 Site environmental characteristics, *Chionochloa rubra* cover, soil nutrients at depth, chemical composition of leaf litter as achlorophyllous attached tissue and decomposition (as mass loss or k) at each of eight plots on a 700 m altitudinal gradient, along with variate means, slope of the regression of each variate against altitude (altitudinal multiplier), and coefficient of determination (r^2). Plot 1's temperatures are partially extrapolated. AD = Acid Detergent, C = Carbon, Dec. = Decomposition, k = decay rate, N = Nitrogen, P = Phosphorus.

Parameter	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Mean	Altitudinal multiplier	r^2
Site location											
Altitude (m)	986	1066	1162	1252	1368	1469	1565	1679	1318	1	1
Latitude (decimal degrees)	−39.08	−39.09	−39.1	−39.1	−39.11	−39.11	−39.11	−39.11	−39		
Longitude (decimal degrees)	175.63	175.64	175.64	175.64	175.64	175.64	175.64	175.64	176		
Site characteristics											
Chionochloa cover (% of plot)	25	20	15	6	15	4	16	2	12.9	−0.0242	0.524
Slope (°)	0	2	5	15	19	16	31	35	15	0.0509	0.932
Average annual precipitation (mm)	732	874	891	923	857	961	999	1082	915	0.3795	0.794
Mean annual temperature (°C)	8.5	8.4	8.6	8.3	7.8	7.4	7.3	6.2	7.8	−0.003	0.852
Mean daily maximum air temperature for the warmest 2 months (°C)	34.0	34.0	31.9	29.4	27.9	30.6	33.7	27.6	31.1	−0.006	0.307
Mean daily minimum air temperature for the coldest 2 months (°C)	−2.3	−2.1	−2.0	−1.1	−1.0	−1.9	−1.6	−1.2	−1.7	0.0012	0.353
Soil moisture (proportion by weight)	0.40	0.37	0.38	0.36	0.37	0.37	0.36	0.34	0.37	−0.00005	0.634
Soil nutrients											
C 0–9.9 cm (mg g^{-1})	67.5	61.3	55.7	55.7	64.1	70.2	55.4	36.6	58.3	−0.0231	0.295
C 10–19.9 cm (mg g^{-1})	40.2	39.1	47.0	42.4	42.3	42.9	33.3	38.5	40.7	−0.0065	0.159
C 20–30 cm (mg g^{-1})	30.6	37.8	49.6	35.8	30.9	36.2	28.1	22.8	34.0	−0.0184	0.317
N 0–9.9 cm (mg g^{-1})	4.25	3.97	2.83	2.13	2.63	2.93	1.90	1.67	2.79	−0.0032	0.725
N 10–19.9 cm (mg g^{-1})	2.95	3.38	2.86	1.71	1.79	1.87	1.46	1.79	2.23	−0.0024	0.684
N 20–30 cm (mg g^{-1})	3.16	3.22	2.54	1.70	1.37	1.39	1.22	1.23	1.98	−0.0032	0.841
P 0–30 cm (mg g^{-1})	0.39	0.27	0.30	0.19	0.22	0.19	0.18	0.18	0.24	−0.0003	0.709
Initial lamina litter contents											
Dry: fresh weight ratio	0.846	0.883	0.876	0.848	0.859	0.839	0.853	0.850	0.857	−0.0026	0.186
C (mg g^{-1})	467.0	470.0	470.0	472.2	472.7	474.7	476.7	476.5	472.5	0.0136	0.950
N (mg g^{-1})	2.05	2.63	2.59	2.61	2.85	2.79	3.23	3.05	2.73	0.0013	0.779
P (mg g^{-1})	0.097	0.072	0.058	0.062	0.063	0.06	0.066	0.069	0.068	−0.00002	0.232
Phenolics (mg g^{-1})	6.79			6.25				5.45	6.16	−0.0019	1.000
AD-Fibre (mg g^{-1})	430	426	411	417	410	409	407	399	414	−0.0359	0.807
Cellulose (mg g^{-1})	338	320	302	337	302	265	313	330	313	−0.0277	0.079
Lignin (mg g^{-1})	73.7	72.1	72.5	78.1	77.2	74.2	69.2	67.9	73.1	−0.0063	0.193
Decomposition											
Dec. at Home sites—Year 1 (g)	0.20	0.24	0.19	0.19	0.17	0.14	0.17	0.19	0.19	−0.00006	0.337
Dec. at Home sites—Year 4 (g)	0.55	0.52	0.55	0.51	0.59	0.62	0.61	0.60	0.57	0.0001	0.662
Dec. at Home sites—average (g)	0.37	0.38	0.35	0.36	0.38	0.37	0.39	0.42	0.38	0.00001	0.475
Dec. at Origin sites—Year 1 (g)	0.20	0.20	0.18	0.17	0.16	0.16	0.17	0.19	0.18	−0.00003	0.164
Dec. at Origin sites—Year 4 (g)	0.57	0.54	0.57	0.53	0.54	0.53	0.58	0.61	0.56	0.00004	0.148
Dec. at Origin sites—average (g)	0.40	0.38	0.37	0.35	0.36	0.35	0.38	0.41	0.38	0.00001	0.016
Dec. at Destination sites—Year 1 (g)	0.19	0.19	0.18	0.20	0.18	0.18	0.17	0.16	0.18	−0.00004	0.655
Dec. at Destination sites—Year 4 (g)	0.53	0.52	0.51	0.54	0.56	0.64	0.58	0.55	0.55	0.00009	0.286
Dec. at Destination sites—average (g)	0.36	0.36	0.35	0.39	0.38	0.41	0.38	0.37	0.37	0.00004	0.234
Dec. k at Home sites	0.19	0.18	0.19	0.18	0.22	0.23	0.23	0.24	0.21	0.00009	0.807
Dec. k at Origin sites	0.21	0.20	0.21	0.19	0.20	0.19	0.22	0.25	0.21	0.0034	0.217
Dec. k at Destination sites	0.19	0.19	0.18	0.21	0.22	0.25	0.22	0.21	0.21	0.0063	0.424
Litter half-life at Origin sites (year)	3.31	3.63	3.36	3.71	3.58	3.64	3.25	2.85	3.42	−0.0006	0.221
Litter half-life at Destination sites (year)	3.68	3.76	3.93	3.39	3.24	2.73	3.21	3.39	3.42	−0.0010	0.434

Figure 4a; *df* = 5.7). For the full reciprocal translocation, annual biomass losses were 18.0, 12.6, 16.7 and 13.2% over the 4 consecutive years (Table 3; Figure 4). Decomposition coefficient, k, was 0.218 over all eight plots with a half-life of 3.42 years (Table 1). Biomass loss was significant for data sorted by litter Origin and by Destination (Table 3), with both indicating faster decomposition at lower altitudes for Year 1 data, although trends were reversed for Year 4 and average data (Table 1; Figure 4b,c).

However, few Akaike models (4% of tests, i.e. fewer than the 5% acceptable probability level for Type II errors) gave acceptable results, and only another 7% gave models which were acceptable, but not significantly more so than null models (Tables S1 and S2). At Home sites, mean rate was *negatively* modelled by temperature (Table S2; Figure S1), although soil moisture was more influential at Year 4 (Table S2). Decomposition of Year 1 litter (examining labile C) at Home plots was not modelled by any variate, indicating no home-field advantage.

The only significant second-order interaction was between Destination and Year, developing at year 3, with Plots 1–3 having values averaging 13% lower than the other plots, while by year 4, Plot 6 had a value 18% greater than all other plots (Figure 4c).

There were no significant Origin × Destination interactions, with or without Years, so each litter type decomposed at the same rate as all others at each plot, regardless of any differences in micro-environment or litter quality between plots. Thus the very weak Origin and Destination effects described above do not persist when analysis of the full dataset is completed.

4 | DISCUSSION

In an altitude-for-temperature substitution we studied temperature sensitivity of litter decomposition rates in a fully factorial, replicated reciprocal translocation experiment. We used *Chionochloa rubra*, a long-lived, dominant bunch-grass of tussock grassland, investigating decomposition rates over eight plots covering 700 m in altitude on Mt Tongariro, New Zealand. Our gradient's length reflects a mean annual temperature range of 3.5°C by our short-term measurements (Table 1), or 4.2°C given the more reliable standard lapse rates (0.6°C 100 m^{-1}; Barringer, 1989; Hales & Roering, 2005).

We provide ecologically convincing evidence that decomposition of leaf litter does not vary with temperature at this site, and we assert, from other published evidence that the result applies globally. We evaluate our findings and their implications for decomposition research and for climate change.

4.1 | How well do our measurements capture the variates?

We were unable to measure root decomposition rates. Root production is 8%–33% of shoots in the *Chionochloa* genus (Lee et al., 2000; Meurk, 1978), with no consistent altitudinal trends (Williams et al., 1977). Occurrence of altitudinal differences in decomposition at our site would require rates of root decomposition to be at least three times that of shoots. Since the little evidence available suggests this is

TABLE 2 Analysis of variance table for annual mass loss of decomposing leaf litter of *Chionochloa rubra* at Home sites (eight plots) for each of 4 years (Year) of decomposition. Bolded *p* values are statistically significant.

	df	Sum of squares	Mean square	*F* value	*p* value
Home site	7	0.048	0.0069	1.187	0.314
Year	3	3.827	1.2758	220.447	**<0.0001**
Home site × Year	21	0.115	0.0055	0.950	0.528
Residuals	150	0.868	0.0058		

TABLE 3 Analysis of variance table for mass loss of decomposing leaf litter of *Chionochloa rubra* after reciprocal translocation from Origin (when the litter is sorted by the sites from which it originated) to Destination (when the litter is sorted by the sites into which it is plated out) for each of 4 years (Year) of decomposition. Bolded *p* values are statistically significant.

	df	Sum of squares	Mean square	*F* value	*p* value
Year	3	29.532	9.844	1949.912	**<0.0001**
Origin	7	0.483	0.069	13.677	**<0.0001**
Destination	7	0.513	0.073	14.539	**<0.0001**
Origin × Year	21	0.137	0.007	1.296	0.167
Destination × Year	21	0.506	0.024	4.775	**<0.0001**
Origin × Destination	49	0.284	0.006	1.146	0.230
Origin × Destination × Year	147	0.415	0.003	0.559	1.000
Residuals	1147	5.791	0.005		

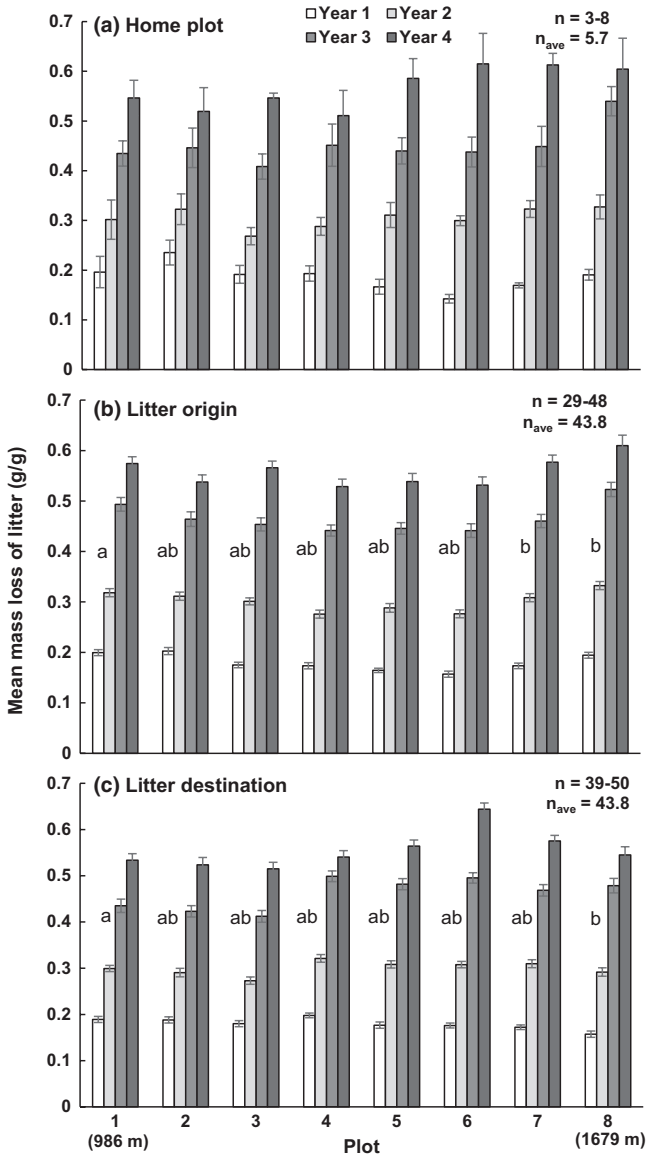

FIGURE 4 Mean ± S.E. mass loss of decomposing *Chionochloa rubra* litter across the eight plots after 1–4 years (white to dark grey) at Home plot (a), and by Origin (b) and Destination (c). 'Origin' refers to when the data are sorted by the sites from which litter originated, while 'Destination' refers to when the data are sorted by the sites into which litter is plated out. *n* values give range of sample numbers, and mean per datum point. Within a sub-figure, plots (i.e. with data organised by litter Origin or Destination, meaned over the 4 years of the study) with different letters differ significantly at the 5% level. Home plots are not significantly different from each other; nor was the Origin × Year interaction, despite the Tukey's tests, or the Destination × Year interaction, which is detailed in Results.

unlikely (Lin et al., 2020; McLaren & Turkington, 2010), including rates of root decomposition would probably not alter our findings much.

To represent litter soon to enter the decomposer cycle, we selected whole, attached, achlorophyllous leaves. Adding litter to a system constitutes priming (Kuzyakov et al., 2000), and using litter bags groups litter onto a horizontal plane instead of it being embedded as shards into the substrate (Boulton & Boon, 1991). Plated out on the ground, thus disturbing surrounding vegetation, our litter did become progressively embedded into the vegetation and substrate, but rates of decomposition may have slowed. However, these effects are equally impactful across our reciprocal transplant design, and so do not bias results.

4.2 | Is litter quality poorer at higher altitudes?

To ameliorate environmental stress, plants elevate production of lignin and phenolic compounds, and since these are recalcitrant (e.g. Murphy et al., 1998), decomposition rates are slowed (e.g. Bontti et al., 2009; Rowland & Roberts, 1994). Indeed the initial logic behind our experiment was that higher levels of recalcitrant compounds at higher altitudes would lead to even lower decomposition rates. However, our results do not support this hypothesis, which we abandoned.

Acceptable Akaike models indicate plausible differences in litter quality, but tannins are undetectable, and concentrations of phenolics, cellulose, fibre, lignin and phosphorus are all much lower at higher altitudes, the reverse of expected (Aerts, 1997; Murphy et al., 1998). When data are organised by litter Origin, which best reflects litter quality, the most influential variate is litter lignin (Figure S1). However, the fit may be merely coincidental, because lignin levels are extremely low throughout and actually greatest at mid-altitude plots (Table 1).

A home-field advantage, where litter decomposes fastest at its site of origin, has been explored in many studies (e.g. Ayres et al., 2009: Veen et al., 2015). However, there is only weak evidence of home-field advantage in our results (see Supplementary Materials), and that only appearing at Year 4. This delay is plausibly a response to the ongoing accumulation of small changes, due to the generally poor quality of *Chionochloa*'s litter (Hodges & Rapson, 2010), giving slow rates of decomposition. An experiment of longer duration may clarify the importance of home-field advantage here.

Liski et al. (1999) modelled some response of decomposition of labile C to warmer temperatures, but little for non-labile C. Readily released (Kirschbaum, 2006; Olson, 1963), labile C is experimentally measured over only very brief periods (<2 weeks; McLauchlan & Hobbie, 2004). Our decomposition rates for Home plot data in Year 1, are 1.4 times greater than for later years, largely attributable to labile C at 6% of initial dry weight in *Chionochloa* (Mark, 1994). But there are no signs of differences between plots in our study, and the modelled fit of Origin data to soil N and C had disappeared by Year 4.

4.3 | Are decomposition rates greater at lower altitudes?

While our decomposition rates differed significantly for litter sorted by either Origin or Destination (Table 3; Figure 4), the trends in positive temperature dependence for both are only weak, and rates are

≈ 3% faster at the two highest plots, the reverse of what is expected. For Destination data at Year 4, decomposition at Plot 6 was 16% faster than the trend, presumably a micro-site effect. Only data organised by Home or Destination fitted acceptable models, and these were indeed for mean annual temperature, with or without soil moisture (see Supplementary Materials). While directionally apposite, these relationships were weak (see Supplementary Materials), and occurred in a very low proportion of tests, below the threshold of occurrence of Type II errors, so their credibility is low.

A full reciprocal transplant allows all litter origins (largely reflecting litter quality) and all destinations of plating out of litter (i.e. exposure to micro-environmental variations about the trends) to be equally represented and equally influential, neutralising any differences within them, so that means can be confidently compared. In our study there were no altitudinal trends in decomposition rates for the Origin × Destination interactions. Allowing for differences in quality, all litters decompose at the same rate across the gradient, and all environments are equivalent in terms of favouring decomposition. Analysis of aspects of the data, basically of either the 'origin' or 'destination' type, can be modelled to litter quality or environmental variates with an apparently credible level of success, but this is inexorably negated by the failure of these trends to persist into higher-order interactions.

Few reciprocal transplant designs have been employed for decomposition studies, and none show higher-order interactions. In a small, but full reciprocal transplant, on a three-step altitudinal gradient over nearly 500 m in Sweden, Veen et al. (2015) also found no interactions. But they discussed their results on the dependence of decomposition on soil temperature only in the context of decomposers' communities, perhaps because their higher-order interactions had only modest explanatory power. Other relevant reciprocal transplants do not involve all local litters at all sampled destinations (e.g. Salinas et al., 2011), and so interactions are incompletely represented and confounding influences only partially neutralised. Thus decomposition rates do not appear to vary in any consistent way across altitudinal gradients despite any partial trends in litter quality, temperature and other environmental variates.

4.4 | How did such expectations of temperature dependence arise?

In laboratory experiments any physical or chemical reaction will show temperature sensitivity, because all other, potentially confounding, factors can be controlled (Kirschbaum, 1995). In nature, we are limited to operating within the temperature range where biological activity occurs. The scientific literature implies that temperature is widely considered a major correlate of decomposition, so that warmer temperatures, for example, at lower altitudes, accelerate decomposition (e.g. Cui et al., 2021; Petraglia et al., 2019; Tan et al., 2021; Veen et al., 2015; Wang et al., 2021). But this contradicts our results.

Kirschbaum (2006) says that "much of the current disagreement [about the temperature sensitivity of decomposition]… might disappear if different studies would ensure that they are all studying the same system attributes, and if confounding factors were always considered and, if possible, eliminated". These confounding factors are:

a. differing temperature sensitivities of decomposition of non-labile and labile C (Kirschbaum, 2006; Liski et al., 1999; Moinet et al., 2018);
b. differences in litter quality between sites (Bontti et al., 2009; Murphy et al., 1998);
c. use of different environments without adequate correction, hosting different decomposition rates (Djukic et al., 2018; Sundqvist et al., 2011), even of a standard litter type, such as tea bags (Elumeeva et al., 2018; Petraglia et al., 2019);
d. differences in the underlying microbial communities, which influence decomposition rates (Ayres et al., 2009; Lu et al., 2017; Sayer et al., 2017);
e. disturbance to the plant community, as often occurs in manipulative climate change experiments (e.g. Dale et al., 2015; Graham et al., 2014), with legacy effects lasting many years (Grime et al., 2008);
f. disturbance of the soil, such as excavating or sieving, which affects respiration rates by destabilising soil C, soil nutrients and the microbial community (Kirschbaum, 2006; Moinet et al., 2018).

Our experimental design avoided most of these issues as our labile C fraction is very small, our study site within a single vegetation type, our litter from a single species, and our study both long term and non-invasive, while both our off-plot litter collection and plating out of litter bags minimised disturbance, our altitude-for-temperature gradient avoided the impact of manipulations, and our reciprocal transplant cancelled out random micro-variations in both litter quality and environment.

4.5 | How credible are our findings?

Despite our long gradient (mean annual temperature range of 4.2°C), decomposition rates of leaf litter do not vary with altitude. Many reasons could (and indeed, will) be conceived to explain why our results might be wrong or misleading or atypical. It could be argued that real temperature differences along our gradient are incidentally cancelled out by other environmental factors. But the paucity of strong gradients in other environmental conditions along our gradient (Table 1) offers no alternative candidates for such juxtaposed cancellations, and in any case, the length of our gradient (700 m) makes accidental inverse monotonicity of even two variates unlikely. Furthermore, the coincident formation of our results by random variability, perhaps via a range of different variates, within all 64 separate sets of data (8 plots × 8 litter types; $n \approx 44$), while not impossible, is highly improbable. Our findings are credible.

New Zealand's grasslands may be atypical because they have evolved in the absence of mammalian herbivory (Antonelli et al., 2011), and its regular recycling of biomass. While insect

herbivores are common in New Zealand's montane grasslands, their consumption of biomass is low, and *Chionochloa* species are not preferred food (White, 1974), as they were for the formerly widespread swamphen, takahē (*Porphyrio*; Mills et al., 1991). However, there is no sign of an atypical level of feeding deterrents in our litter, or of high-quality litter such as would be preferentially browsed, or even of any herbivory.

It could be claimed that our species, *Chionochloa rubra*, is atypical. *Chionochloa* has very low growth rates (Lee et al., 2000; Mark, 1965; Williams, 1977), very low palatability (Hodges & Rapson, 2010), and a low proportion of labile C, except in post-fire regrowth (Mark, 1994). It may be acting more like a woody species being less decomposable than short-lived herbs (Rawlik et al., 2021). But the results of Veen et al. (2015) suggest lack of temperature dependence applies across vegetation types, in their case, as different as heathland, meadow and willow-dominated shrubland.

Our gradient may be atypical, as it is dominated by vulcanicity. Observation indicates tussocks are more silvery in colour close to active, sulphide-emitting vents, but impacts on vegetation types and also soil floras are unknown (c.f. Tortini et al., 2017).

A related argument may be that this lack of temperature dependence only occurs in montane environments. Our study area has a mean annual temperature of 8 °C, a low temperature, although extremes range from −2 to 34°C. Giardina and Ryan (2000) reported results were 'remarkably constant across a global-scale gradient' in a meta-analysis of both disturbed soils, and those incubated in the laboratory. They argued that the rate of supply of substrate to decomposers is more limiting than temperature. And the meta-analysis of warming experiments by Carey et al. (2016) indicates similar results to ours apply in most environments, with the possible exception of deserts and boreal forests.

So why are there so many reports of temperature dependence in the literature? The logical explanation for some, if not all of these reports, is that, when a study identifies temperature, it is as a correlated variate, not a causal one and a more robust type of experimental design, such as a reciprocal transplant, would have demonstrated this. Further analysis is required to disentangle this literature, and to identify any variates for which temperature is simply a proxy. It is also hoped our study will promote use of better-designed experiments, such as reciprocal transplants, in the future.

4.6 | Is there any variate on which decomposition rates are dependent?

In nature, many variates interact to create changes or gradients which can overlie and confound interpretations of anticipated trends (Kirschbaum, 1995). Discounting the role of temperature in decomposition, which was controlled in our experiment, a highly influential variate is soil moisture (Djukic et al., 2018; Petraglia et al., 2019; Wang et al., 2021). This influence is reinforced by the meta-analysis of Carey et al. (2016), where slight curvature in the response of decomposition to temperature was considered due to treatment-induced changes in soil moisture in all biomes (including deserts and boreal forests, where moisture is probably limiting anyway). In our study, soil moisture is actually positively correlated with temperature ($r^2 = 0.722$), but does not model for decomposition (except for Year 4 litter at Home sites), suggesting a weak home-field relationship. A longer-term experiment may have developed that relationship across the rest of our experiment as well.

5 | CONCLUSIONS

We have provided evidence that decomposition rates do not vary with temperature in our study and we suggest that this applies in all or most natural situations, as Kirschbaum (1995, 2006), Tate, Scott, Ross, et al. (2000) and colleagues (Giardina & Ryan, 2000; Liski et al., 1999; Moinet et al., 2018) have been saying for decades. Therefore temperature cannot affect C sequestration rates, even with climate warming. Any such apparent trends must come from differences in soil moisture, litter quality, the vegetation types or in the microbial communities, via interactions with the vegetation, and from associated changes in nutrient cycling and C dynamics (affecting litter quality), as well as from changes in productivity, as these are the factors influencing C sequestration rates (Krna & Rapson, 2013).

The big questions needing renewed focus are how to manage factors affecting C stabilisation in soils (e.g. Elumeeva et al., 2018), the impact of plant productivity rates on C sequestration, especially under climate change (Krna & Rapson, 2013), the role of moisture in controlling decomposition rates (e.g. Djukic et al., 2018; Petraglia et al., 2019; Wang et al., 2021), the transitions between ecosystems under warming regimes (e.g. Grime et al., 2008; Mayor et al., 2017), and the impacts of those transitions on C which is already sequestered (e.g. Cornelissen et al., 2007; Lal, 2019; Ward et al., 2014).

AUTHOR CONTRIBUTIONS

Matthew A. Krna and Gillian L. Rapson designed the study, Mathew A. Krna carried out the field work with assistance from Gillian L. Rapson and many others. Matthew A. Krna and Gillian L. Rapson analysed the results with input from Kevin R. Tate, Surinder Saggar and Hannah L. Buckley, while Mathew A. Krna wrote the thesis. Matthew A. Krna and Gillian L. Rapson wrote the manuscript with input from Kevin R. Tate, Surinder Saggar and Hannah L. Buckley. Matthew A. Krna and Gillian L. Rapson reanalysed and rewrote the manuscript. Gillian L. Rapson finalised the text multiple times.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to report.

DATA AVAILABILITY STATEMENT

Data upon which this study is based are available through the Dryad Digital Repository: https://doi.org/10.5061/dryad.612jm6475 (Krna & Rapson, 2023).

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SUPPORTING INFORMATION

Additional supporting information on "Akaike models of decomposition" can be found online in the Supporting Information section at the end of this article.

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