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RESEARCH ARTICLE

Pasture production–diversity relationships in a kānuka silvopastoral system

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Abstract

1. Silvopastoral systems have great potential for forming multifunctional landscapes that provide a range of economic and environmental benefits to pastoral land. However, pasture production–diversity relationships in silvopastures require further exploration.
2. This study measures how pasture functional group production, pasture species diversity and pasture functional diversity (FD) are impacted by trees in a novel native silvopastoral system in New Zealand hill country with kānuka (*Kunzea* spp.).
3. Silvopastoral trees facilitated the growth of fast-growing competitor functional groups (*Lolium perenne*, *Dactylis glomerata* and high fertility annuals: *Bromus hordeaceus* and *Critesion murinum*), because of positive impacts on soil fertility, organic matter and porosity.
4. Shannon diversity, species richness and species evenness were significantly less in the more productive pastoral environment under the trees, but functional richness, functional evenness and functional dispersion were similar between kānuka pasture and open pasture.
5. These results show that silvopastures can increase pasture production by promoting the growth of competitive pasture functional groups, and that reduced species diversity under silvopastoral trees does not necessarily impact FD in the context of production. Moreover, species indices overestimated diversity reductions under the trees compared to functional indices. Thus, considering FD in silvopastoral systems is integral for not misinterpreting diversity outcomes.

KEYWORDS
agroforestry, alpha diversity, biodiversity, botanical composition, kanuka, mass ratio hypothesis, pasture stability, poplar silvopastures, tree-pasture

1 | INTRODUCTION

The mass ratio hypothesis suggests that the traits of dominant species drive ecosystem functionality, and that total production is relatively insensitive to species richness changes (Grime, 1998). Many studies have found evidence for this (Hooper & Vitousek, 1997; MacGillivray et al., 1995; Roscher et al., 2007; Sonkoly et al., 2019; Wardle et al., 1997). In silvopastoral research, past studies have generally reported reduced pasture species diversity under silvopastoral trees compared to treeless pasture (Alonso et al., 2020; Fernández-Moya et al., 2011; López-Carrasco et al., 2015; Marañon, 1986; Rossetti et al., 2015). Assessing whether this reduced pasture diversity impacts pasture functionality in terms of production is fundamental when evaluating silvopastoral systems as a land management practice.

Various studies have compared pasture production–diversity relationships in silvopastoral systems (Alonso et al., 2020; López-Carrasco et al., 2015; Marañón & Bartolome, 1994). All three of these studies reported reduced species richness under silvopastoral trees, although production–diversity relationships varied. Marañón and Bartolome (1994) reported reduced pasture production under California live oak *Quercus agrifolia* (Née) trees. López-Carrasco et al. (2015) reported a positive relationship between species richness and total dry matter (DM) production in two of the study years under holm oak *Quercus ilex* (L.) silvopastures in Spain, but not in the wetter third study year. Finally, Alonso et al. (2020) reported that grass biomass was statistically similar between *Nothofagus antarctica* (G.Forst.) Oerst. silvopastures and open pasture in Southern Chilean Patagonia. Clearly pasture production–diversity relationships are dependent on the system, and even yearly climatic variations.

These past studies, however, did not consider two important aspects. First, these studies (Alonso et al., 2020; López-Carrasco et al., 2015; Marañón & Bartolome, 1994), as well as others that have measured diversity changes in silvopastoral systems (Fernández-Moya et al., 2011; Marañon, 1986; Rossetti et al., 2015), did not calculate whether the loss of species diversity resulted in a loss in functional diversity (FD). When measuring diversity changes, it is important to consider FD because species diversity changes may not represent functional changes to the system if functional redundancy exists. Assessing FD in silvopastures is therefore important for quantifying the true impact of species loss on pasture functionality.

Second, the authors did not differentiate between the production of a full range of pasture functional groups that had been quantitively described based on functional response in the field (Alonso et al., 2020; López-Carrasco et al., 2015; Marañón & Bartolome, 1994). Learning why silvopastoral trees impact different pasture functional groups is integral for providing evidence as to the ecological mechanisms for how silvopastures impact pasture production. This knowledge can then be used to help design new silvopastoral systems that maximize the growth of more productive and desirable pasture functional groups.

The current study measures pasture production–diversity relationships in the context of functional ecology in New Zealand hill country. Hill country is an agricultural region defined as having steep or hilly land (>15°), being below 1000 m a.s.l. and having pastoral farming as its main land use (sheep, cattle and deer) (Dodd et al., 2016). Many areas of hill country have a low pasture production (López et al., 2003; Nicholas, 1999), with slope being one of the main drivers determining soil-water dynamics and the presence and abundance of pasture species and their performance (López et al., 2006; Nicholas, 1999). Trees may be a valuable way of improving the production of these sloped areas.

This study examines a silvopastoral system in New Zealand hill country with kānuka (*Kunzea* spp.; Mackay-Smith et al., 2021; Mackay-Smith et al., 2022a). Kānuka is a native genus that has 10 endemic species in New Zealand (de Lange, 2014). Kānuka has previously been reported to increase pasture production compared to open pasture positions by over 100% at two sites in New Zealand (Mackay-Smith et al., 2022a). This increase in pasture production was hypothesized to be because of the trees encouraging preferential livestock activity in the tree-pasture environment, in addition to the potential of litterfall adding organic matter to the soil (Mackay-Smith et al., 2022a). Because of these previously measured facilitative effects of kānuka trees on pasture production at these two sites, we hypothesize that (1) total pasture production is greater under kānuka compared to open pasture because the trees facilitated the growth of more competitive and fast-growing perennial species at both the sites, and (2) this will decrease species diversity, but not decrease FD, because of functional redundancy in the system.

2 | MATERIALS AND METHODS

2.1 | Site characteristics

Two sites were selected to study with similar climates, soil types and livestock operation. One site was in the Wairarapa region, ~10 km north of Martinborough (Wairarapa site) (41°08′41.3″S, 175°29′58.3″E, 122 m), and another in the Hawkes Bay region, ~20 km south of Waipukurau (Hawkes Bay site) (40°08′25.9″S, 176°23′39.1″E, 288 m). Permission was granted by both farmers to use their land for field sites. The Wairarapa site is underlain by sandstone, and the Hawkes Bay site is underlain by mudstone. The soil type at both sites is a Mottled Argillic Pallic Soil in the New Zealand classification (Hewitt, 2010), and a Ustalf in the USA soil classification (Hewitt, 2010). The topsoil type at both sites is a silt loam. The subsoil type (B horizon) at both sites is a silty clay loam.

The mean 30-year annual rainfall at Wairarapa was 903 mm (min: 548 mm; max: 1297 mm; Station 2631; 6.6 km from the site, elevation: 58 m; CliFlo, 2021), and 883 mm at Hawkes Bay (min: 527 mm; max: 1483 mm; Station 2523; 5.8 km from the site, elevation: 153 m; CliFlo, 2021). The mean 10-year annual temperature at Wairarapa was 18.3°C (min: 17.5°C; max: 19.0°C; station 21,938; 15.0 km from the site; CliFlo, 2021), and 16.7°C at Hawkes Bay (min: 15.8°C; max: 17.5°C; Station 25,820, 15.3 km from the site; CliFlo, 2021).

Both sites were in permanent and naturalized pasture on typical commercial sheep and beef farms of the region. Peak pasture growth occurs in spring and early summer (October–December), and slowest pasture growth is in winter (June–July; Li et al., 2011). The paddock topography at Wairarapa was moderately to severely steep (15–40°) and it was rolling to moderately steep (10–30°) at Hawkes Bay. The aspect of the site at Wairarapa was northeast, and it was northwest at Hawkes Bay. Individual *Kunzea robusta* de Lange et Toelken (kānuka) trees grew in the study site paddocks at densities that ranged from ~10 trees ha^{-1} to ~2000 trees ha^{-1}. The land was most likely cleared for grazing 100–200 years ago and after this the trees likely established as seedlings. The trees were not planted by either farmer and the pasture was likely to have been sown when the land was cleared in the early 1900s. Aerial imagery indicates that the fully grown kānuka trees studied at the Wairarapa site were at least 80 years old (Retrolens, 2021). Old aerial imagery could not be found for the Hawkes Bay site, but it is likely the trees were at least this age as the trees at this site were larger compared to the Wairarapa site.

Livestock were rotationally grazed at the Wairarapa site for 2–3 days at a time in all seasons and the grazing intensity was 9.1 Angus cows ha^{-1} day^{-1}, 3.4 Friesian bulls ha^{-1} day^{-1}, 40 lambs ha^{-1} day^{-1} and 57 ewes ha^{-1} day^{-1}. The paddock at Hawkes Bay was set stocked with pregnant ewes during lambing for about 1 month in spring and summer. Livestock were rotationally grazed in this paddock throughout the year by Angus cows at 0.8 ha^{-1} day^{-1} for about 1 week at a time. The fertilization rates at the Wairarapa site were 21.5 kg P ha^{-1} and 37 kg S ha^{-1}, which were annually surface applied in early summer. This was 25 kg N ha^{-1} and 28.75 kg S ha^{-1}, or 25.8 kg P ha^{-1} and 42 kg S ha^{-1} at the Hawkes Bay site, which was surface applied in winter. Fertilization did not happen every year at the Hawkes Bay site because of sufficiently high soil phosphorus (P) fertility as deemed by the farmer.

The study had two measurement positions replicated at each site. 'Kānuka pasture' silvopastoral measurement positions were under individually spaced kānuka tree canopies (half-way between the canopy edge and stem; Figure 1). 'Open pasture' measurement positions were in paired open pasture positions with similar slope position, slope gradient and characteristics at least 15 m from the nearest tree trunk. A 15 m distance from the tree trunk was chosen because there was a ~5 m distance between the trunk and the drip line (edge of canopy) for each studied tree, and Howlett et al. (2011) selected a distance of a three times the drip line for open pasture positions. All positions were on slope gradients between ~20° and ~25°. There were nine tree replicates in total (n = 9), four at the Wairarapa site and five at the Hawkes Bay site.

As 5–20 m long soil moisture sensors connected to a central data logger were to be installed permanently at both sites, trees in each paddock were selected based on there being open pasture and four or five individual kānuka trees in close proximity of each other. Moreover, in each study paddock, there were a few trees that had livestock camping spots on the downslope side of the trees. These were avoided as study trees during site selection.

Soil moisture, soil fertility and soil physical properties at the measurement positions in this study have been previously reported by Mackay-Smith et al. (2022a). Volumetric soil moisture (VSM) measured between 0–30 cm throughout the year (kānuka pasture: 23.0%; open pasture: 22.3%) and just in summer (kānuka pasture: 17.0%; open pasture: 15.9%) were statistically similar between kānuka pasture and open pasture. Olsen-P (kānuka pasture: 63.2 mg L^{-1}; open pasture: 29.3 mg L^{-1}), potassium (K) (kānuka pasture: 1.2 mg 100 g^{-1}; open pasture: 0.6 mg 100 g^{-1}), magnesium (Mg) (kānuka pasture: 2.8 mg 100 g^{-1}; open pasture: 2.1 mg 100 g^{-1}), sodium (Na) (kānuka pasture: 0.3 mg 100 g^{-1}; open pasture: 0.1 mg 100 g^{-1}) and porosity between 2 and 5 cm in the topsoil (kānuka pasture: 60.6%; open pasture: 55.7%) were all significantly greater in kānuka pasture. Total-nitrogen (N) (kānuka pasture: 0.5%; open pasture: 0.3%), pH (kānuka pasture: 5.6; open pasture: 5.6), sulphate–sulphate (S) (kānuka pasture: 12.1 mg kg^{-1}; open pasture: 55.7 mg kg^{-1}) and organic matter (kānuka pasture: 10.1%; open pasture: 6.8%) were statistically similar between kānuka pasture and open pasture, although there was a significant interaction for organic matter and total-N between site and position.

2.2 | Pasture measurements

Pasture measurements were undertaken from 12th December 2019 until 11th December 2021. The pre-trimmed exclusion technique was used to measure accumulated pasture production of

FIGURE 1 Some of the kānuka trees evaluated in the study. (a) Shows some of the evaluated trees at Hawkes Bay. (b) Shows some of the evaluated trees at Wairarapa. Both photographs were taken by the lead author.

each pasture species (Radcliffe et al., 1968). One pasture cage per position was used to measure pasture production at each position (n = 9 per position). Following pre-trimming to 1 cm using electric clippers within the pasture cage area, pasture was harvested after a ~2-month regrowth period (the regrowth period varied depending on the season; López et al., 2003). Pasture was harvested from a 25 cm × 50 cm quadrat within the pasture cage area after being cut to 1 cm in height. The cage was then placed in a new pre-trimmed pasture spot within the same position and rotated between three pasture cage spots within each position during the study. This allowed livestock grazing behaviour to continue within the sampling locations throughout the study. Different positions were used if there were obvious dung or urine deposits in a cage position. Each sample was oven-dried for 72 h at 70°C and weighed. Every season a subsample was taken, separated into individual species and dead matter, and all individual pasture species were identified. These individual pasture species groups and dead matter were also oven-dried for 72 h at 70°C and weighed. Each season, the proportions of each species and dead matter were used to calculate total green DM production (kg DM ha^{-1} $year^{-1}$) of individual pasture species and total production. Pasture species were then grouped into functional groups as described below.

2.3 | Soil and climatic measurements

Continuous measurements of VSM were taken during the study period using one time domain reflectometry soil moisture sensor in each position (n = 9 per position). The sensors measured VSM every 30 min between 0 and 30 cm, and were installed vertically (CS616 – sensor length 30 cm, Campbell Scientific). They were installed in the centre of each position. One VSM measurement per position was calculated by averaging all the VSM measurements over the period.

For the soil fertility analysis, 10 soil cores (0–7.5 cm) were systematically sampled from a pasture cage spot within each position in December 2019 and December 2021. After sampling the 10 soil cores, they were bulked to form one representative sample for each position and sent to a testing laboratory (Hills Laboratories, Hamilton; Certified NZS/ISO/IEC 17025:2005 by International Accreditation New Zealand). Samples were analysed for Olsen-P (30-min bicarbonate extraction followed by Molybdenum Blue Colorimetry; Olsen et al., 1954), soil organic matter (Dumas combustion was used to calculate total carbon and organic matter was 1.72 × total carbon; Nelson & Sommers, 1996) and K (1 M neutral ammonium acetate extraction followed by ICP-OES; Blakemore et al., 1987). The two time period measurements (December 2019 and December 2021) were averaged to form one measurement per position (n = 9 per position).

Particle density and bulk density were measured in September 2021 between 2 and 5 cm in the topsoil using 3 cm (height) by 4.8 cm (diameter) cores. In each position, four replicate cores were sampled 50 cm to left of the soil moisture sensor. The measurements for each of these replicate cores were averaged per position (n = 9 per position). One replicate per position was used to calculate particle density (see Gradwell & Birrell, 1979) for more details of the method). Particle density along with bulk density was used to calculate porosity.

2.4 | Statistical analysis

A multivariate canonical variate analysis (CVA) was undertaken to show how the production of individual pasture species responded to different soil conditions at the sites and positions (Jobson, 1996; Weihs, 1995). If pasture species responded in a similar way in the ordination, they were grouped into a functional group. Past literature was also used to differentiate between some of the species. For instance, López et al. (2006) also grouped pasture species into functional groups based on species production responses in different slope and fertility treatments. López et al. (2006) reported *Agrostis capillaris* and *Lolium perenne* as separate 'generalist' functional groups based on a cluster analysis because of their distinctive responses and high overall individual production. It is important to separate species into distinctive functional groups that have a large biomass because species with a large biomass have been shown to have a greater impact on ecosystem functionality than species with a smaller biomass (Norkko et al., 2013). Accordingly, this study also separated *Agrostis capillaris* and *Lolium perenne* into separate functional groups because of their high individual production, and the results of the cluster analysis reported by López et al. (2006). Although *Dactylis glomerata* was not recorded by López et al. (2006), because of the high individual production of this species in this study, and its distinctive morpho-physiological attributes, such as deep roots, drought tolerance and shade tolerance (Joshi, 2000; Koukoura & Kyriazopoulos, 2007; Mosquera-Losada et al., 2006), it was also considered in its own group. Any species that formed less than 1% of the species composition in all treatments were grouped in a low presence functional group because of their minimal impact on pasture functionality in the context of production.

A mixed-effect model with position (kānuka pasture and open pasture) as a fixed effect, and site as a random effect, was used to compare pasture functional groups between the positions (Crawley, 2013; Zuur et al., 2009). A significance level of 5% was used for the analyses. The models also calculated the position and site interactions. Models without data transformation were visually checked to see if they followed model assumption (Crawley, 2013; Zuur et al., 2009). Because they did not, total production and all the plant functional groups were square root transformed (Crawley, 2013).

Linear regression analysis was used to form the relationships between total production and the functional groups *L. perenne*, *A. capillaris*, LF, *Hypochaeris radicata*, *Plantago lanceolata* and other dicotyledons. *Dactylis glomerata* was modelled using a polynomial regression analysis. High fertility annual (HFA) grasses had two extreme values that were not deemed outliers so a relationship between total production and this functional group could not be modelled. A CVA was also used to discriminate which soil variables explained the functional group variation between the positions and sites. Organic matter as a variable was removed from this CVA analysis because when it was included it inverted the axis due to the interaction between kānuka pasture and open pasture reported by Mackay-Smith et al. (2022a).

Species richness was calculated by converting pasture species percentage composition data to presence/absence data, and species richness was the total number of species in each treatment. Shannon diversity was calculated in the 'Vegan' package in the statistical software R (Oksanen, 2020), and species evenness (Pielou's evenness) was calculated using (1) (Oksanen, 2020):

$$\text{Pielou's evenness} = \frac{\text{Shannon diversity}}{\log(\text{species richness})}. \quad (1)$$

To account for different aspects of FD, three FD indices were calculated (functional richness [FRic], functional evenness [FEve] and functional dispersion [FDis]), using the 'FD' package in R (Laliberté & Legendre, 2010; Sonkoly et al., 2019; Villéger et al., 2008). Species traits are inputted along with the relative abundance of each species in each community (Laliberté et al., 2015). As functional groups were based on response in the field, these functional groups were inputted as a single nominal trait. Total biomass production of each species in each community was used as the abundance data. FRic is the number of functional groups per community (Laliberté et al., 2015; Laliberté & Legendre, 2010), FEve accounts for the regularity of biomass growth for each of the functional groups in the communities (Mason et al., 2005; Tsianou & Kallimanis, 2020) and FDis is the mean distance of each functional group from a centroid calculated between the species, and thus the spread or dispersion of the community (Laliberté & Legendre, 2010). All calculated diversity indices were tested between the treatments also using mixed effect models with position as a fixed effect and site as a random effect. These diversity variables did not need data transformation (Crawley, 2013), and the position and site interactions were also calculated.

All the statistical analyses were done on R (v.4.1.1.) (R Core Team, 2021). The mixed-effect models were created using the LME4 package (Bates et al., 2015) and the CANDISC package was used to do the CVA analysis and create the biplot (Friendly, 2021).

3 | RESULTS

3.1 | Pasture functional groups

The pasture species CVA explained 98.8% of the total variation (Figure 2). The Wilks' lambda was significant ($p = 0.008$). Canonical 1 variate explained 93.2% of the variation ($p = 0.008$) and canonical 2 variate explained 5.6% of the variation ($p = 0.223$). Canonical 3 variate explained 1.2% of the variation ($p = 0.519$). Table 1 shows the functional groups formed following the analysis. *Dactylis glomerata* and *L. perenne* were separated into their own functional groups because of their contrasting responses on canonical 2 (CVA *y*-axis), and the high individual production of both these species (Table 2). *Bromus hordeaceus* and *Critesion murinum* were separated into a HFA grass functional group as both these annual species responded positively to the improved soil conditions in kānuka pasture. *Agrostis capillaris* was separated into its own functional group because of its high overall production (Table 2). *Vulpia bromoides*, *Anthoxanthum odoratum* and *Rytidosperma* spp. were put into a low fertility (LF) tolerant functional group because they responded similarly to the significant canonical 1 variate (CVA *x*-axis). *Hypochaeris radicata*, *P. lanceolata and* other dicotyledons were separated into their own functional groups as they all responded differently in the CVA plot (Figure 2).

3.2 | Pasture functional group comparison between positions

Lolium perenne and then *D. glomerata* were the most abundant group in kānuka pasture, and *A. capillaris* was the most abundant group in open pasture (Table 2). There was significantly more total production ($p < 0.001$), *L. perenne* ($p < 0.001$), *D. glomerata* ($p = 0.007$)

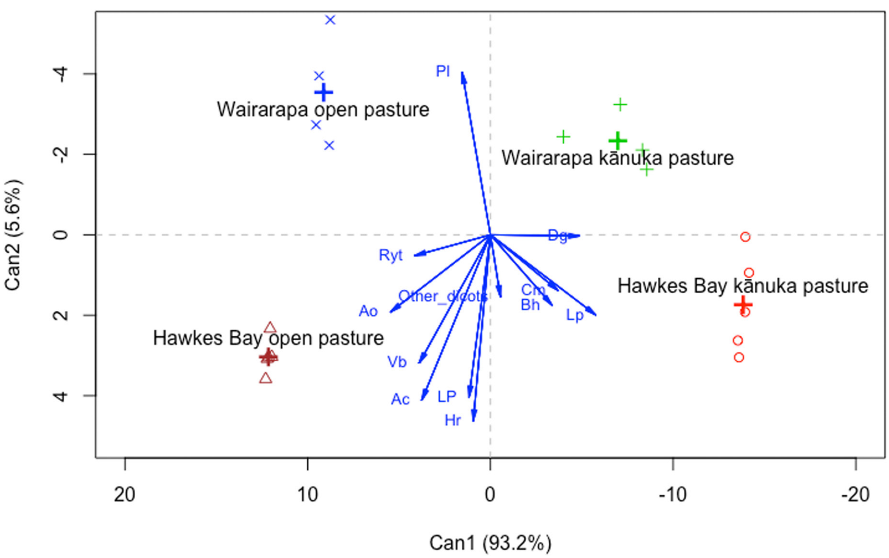

FIGURE 2 Canonical variate analysis showing how individual pasture species responded to the sites and positions. Lp = *Lolium perenne*. Dg = *Dactylis glomerata*. Ac = *Agrostis capillaris*. Bh = *Bromus hordeaceus*. Cm = *Critesion murinum*. Vb = *Vulpia bromoides*. Ao = *Anthoxanthum odoratum*. Ryt = *Rytidosperma* spp. Hr = *Hypochaeris radicata*. Pl = *Plantago lanceolata*. LP = low presence.

TABLE 1 Pasture functional groups used in the data analysis.

Functional group	Species Latin name	Species common name
Lolium perenne	*Lolium perenne* L.	Perennial ryegrass
Dactylis glomerata	*Dactylis glomerata* L.	Cocksfoot
Agrostis capillaris	*Agrostis capillaris* L.	Browntop
High fertility annual grasses (HFA)	*Bromus hordeaceus* L.	Soft brome
	Critesion murinum (L.) Á. Löve	Barley grass
Low fertility tolerant grasses (LF)	*Anthoxanthum odoratum* L.	Sweet vernal
	Rytidosperma spp.	Danthonia spp.
	Vulpia bromoides (L.) Gray	Vulpia hair grass
Hypochaeris radicata	*Hypochaeris radicata* L.	Catsear
Plantago lanceolata	*Plantago lanceolata* L.	Narrowleaf plantain
Other dicotyledons	Other dicotyledons	
Low presence species (LP)	*Carex* spp.	Sedges
	Cirsium arvense (L.) Scop.	Creeping thistle
	Crepis capillaris (L.) Wallr	Smooth hawksbeard
	Cynosurus cristatus L.	Crested dogstail
	Holcus lanatus L.	Yorkshire fog
	Juncus spp.	Rushes
	Lamium amplexicaule L.	Common henbit
	Sporobolus africanus (Poir.) Robyns & Tournay	Ratstail
	Trifolium dubium Sibth.	Suckling clover
	Trifolium glomeratum L.	Clustered clover
	Trifolium pratense L.	Red clover
	Trifolium repens L.	White clover
	Trifolium subterraneum L.	Subterranean clover

TABLE 2 Total production and the production of the pasture functional groups for each position averaged over the sites. All units are kg DM ha^{-1} $year^{-1}$. The standard error of the mean is given in brackets.

Variable	Kānuka pasture	Open pasture	Est.	SE	*df*	*t*-value	*p*-value
Total production	6222.8 (784.4)a	3680.6 (441.8)b	19.6	4.5	14	4.3	<0.001
Lolium perenne	2560.1 (482.1)a	348.3 (96.8)b	38.2	6.1	14	6.3	<0.001
Dactylis glomerata	1279.6 (238.7)a	134.0 (64.0)b	18.4	5.8	14	3.2	0.007
Agrostis capillaris	240.3 (53.5)b	716.8 (199.0)a	−16.1	4.5	14	−3.6	0.003
High fertility annual grasses (HFA)	528.2 (236.4)a	83.5 (26.1)b	17.9	6.1	14	2.9	0.011
Low fertility tolerant grasses (LF)	1.4 (1.0)b	221.3 (45.3)a	−15.9	2.1	14	−7.5	<0.001
Plantago lanceolata	62.6 (32.7)a	203.6 (101.1)a	−4.8	3.7	14	−1.3	0.211
Hypochaeris radicata	31.7 (21.4)a	51.2 (21.2)a	−3.1	2.6	14	−1.2	0.251
Other dicots	173.6 (79.0)a	160.1 (86.6)a	3.4	5.9	14	0.6	0.569
Low presence	10.2 (6.2)a	17.0 (5.2)a	−1.6	1.3	14	−1.3	0.231

Note: Different letters represent significant differences between the positions using a significance level of 0.05. Est. = Estimated coefficient value for the model, which is the average response variable change for a one-unit change in the predictor variable.

and HFA ($p = 0.011$) in kānuka pasture, and significantly more *A. capillaris* ($p = 0.003$) and LF ($p < 0.001$) in open pasture. Only *P. lanceolata* ($p = 0.002$) had a significant interaction between positions.

There was a significant relationship between total production and *L. perenne* ($R^2 = 0.7$, $p < 0.001$) and *D. glomerata* ($R^2 = 0.4$, $p = 0.004$; Figure 3).

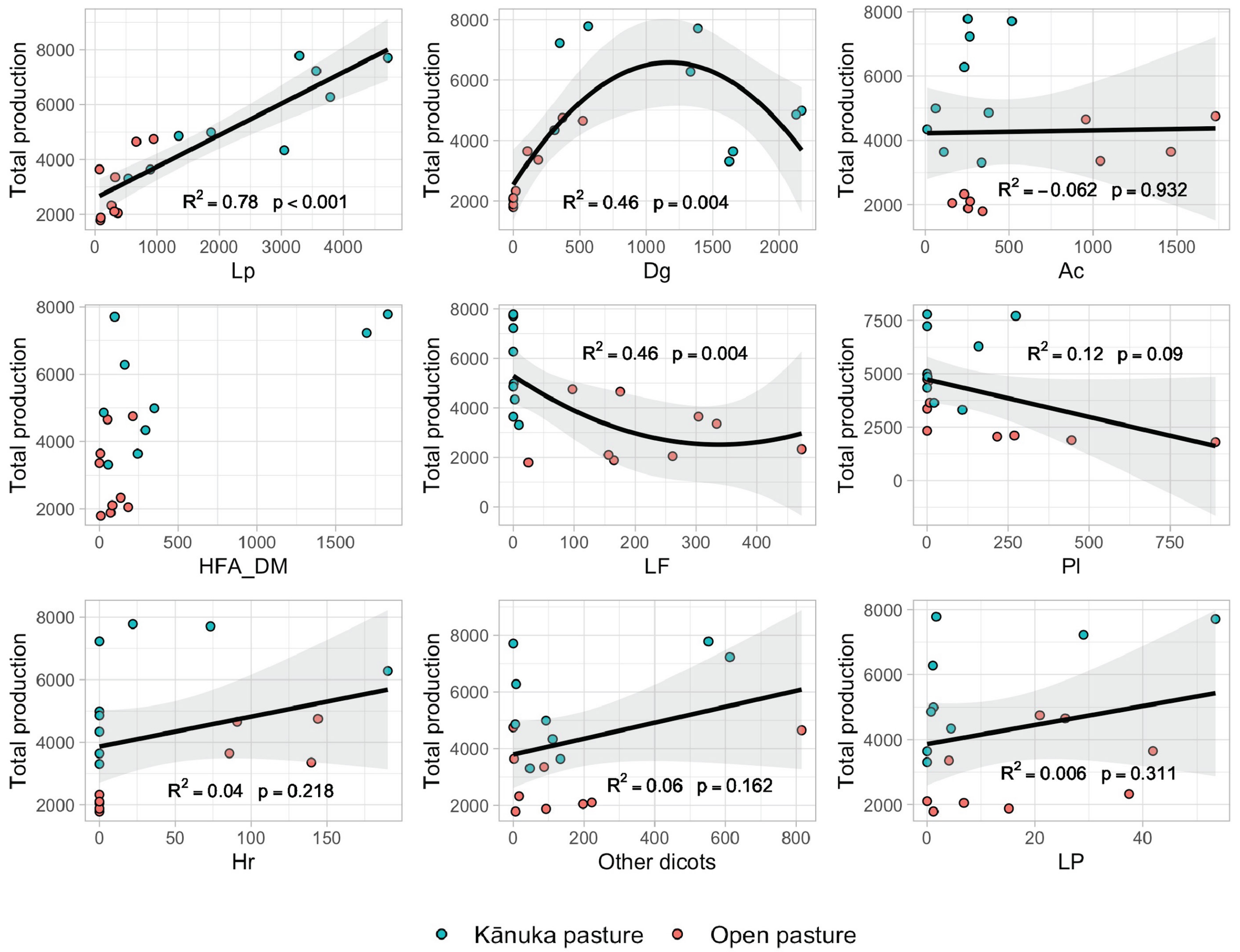

FIGURE 3 Relationships between total production and the pasture functional groups for all data. Data have been pooled for both sites (Wairarapa and Hawkes Bay) and for both positions (kānuka pasture and open pasture). All units are kg DM ha^{-1} $year^{-1}$. The shaded areas represent the 95% confidence interval. Lp = *Lolium perenne*. Dg = *Dactylis glomerata*. Ac = *Agrostis capillaris*. HFA = High fertility annual grasses. LF = low fertility tolerant grasses. Pl = *Plantago lanceolata*. Hr = *Hypochaeris radicata*. LP = low presence.

3.3 | Canonical variate analysis

The CVA for the pasture functional groups and soil variables explained 97.9% of the total variation (Figure 4). The Wilks' lambda was significant ($p = 0.022$). Canonical 1 variate explained 95.0% of the variation ($p = 0.022$) and Canonical 2 variate explained 3.3% of the variation ($p = 0.220$). Canonical 3 variate explained 1.7% of the variation ($p = 0.233$). Canonical variate 1 separated the data per position (kānuka and open pasture) (*x*-axis) and canonical variate 2 separated the data per site (Hawkes Bay and Wairarapa) (*y*-axis). The functional group *L. perenne* was most strongly positively related to the soil fertility variables (potassium and Olsen-P). *D. glomerata* was strongly positively related to porosity and Olsen-P. HFA was also positively related to improved soil conditions in kānuka pasture. *A. capillaris* and LF were the functional groups most strongly positively related to the poorer soil conditions in open pasture.

3.4 | Pasture species diversity

There was a significantly lower Shannon diversity ($p = 0.004$), species richness ($p < 0.001$) and species evenness ($p = 0.004$; Table 3) in kānuka pasture. There were no significant differences between any of the FD indices, and there were no interactions between the treatment and site for the diversity indices.

4 | DISCUSSION

4.1 | Functional groups and pasture production outcomes

The improved soil fertility and soil porosity results measured in kānuka pasture positions were suggested by Mackay-Smith et al. (2022a) to be a result of the trees encouraging livestock activity

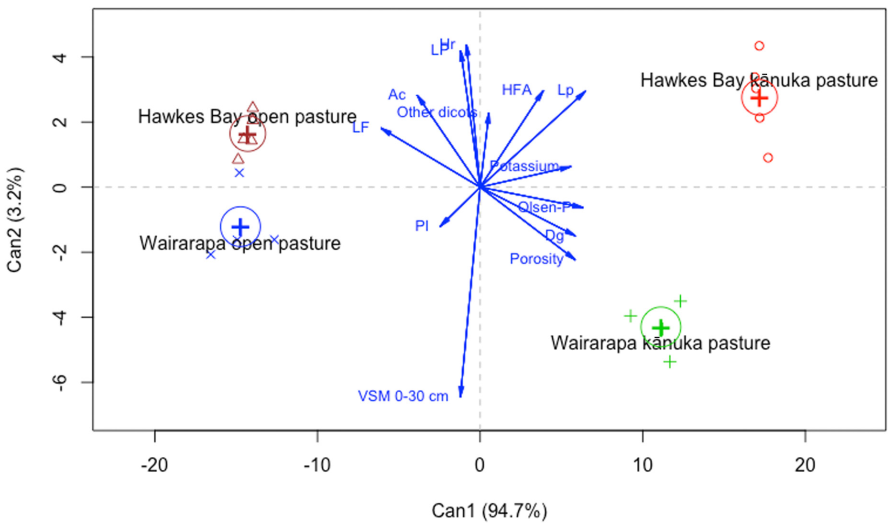

FIGURE 4 Canonical variate analysis showing which pasture functional groups and soil variables best explain treatment and site differences. Lp = *Lolium perenne*. Ac = *Agrostis capillaris*. Dg = *Dactylis glomerata*. HFA = high fertility annual grasses. LF = low fertility tolerant grasses. Hr = *Hypochaeris radicata*, Pl = *Plantago lanceolata*, LP = low presence. P = phosphorus. VSM = volumetric soil moisture.

TABLE 3 Shannon diversity, species richness, species evenness, functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis) for each position (kānuka pasture and open pasture) averaged over both sites. The standard error of the mean is given in brackets.

Variable	Kānuka pasture	Open pasture	Est.	SE	*df*	*t*-value	*p*-value
Shannon diversity	1.20 (0.06)b	1.81 (1.10)a	−0.55	0.16	14	−3.5	0.004
Species richness	7.33 (0.23)b	11.20 (0.74)a	−4.60	0.99	14	−4.7	<0.001
Species evenness	0.38 (0.02)b	0.58 (0.03)a	−0.18	0.05	14	−3.5	0.004
FRic	6.89 (0.20)a	7.33 (0.33)a	−0.80	0.49	14	−1.6	0.123
FEve	0.45 (0.05)a	0.46 (0.04)a	0.07	0.09	14	0.8	0.463
FDis	0.24 (0.01)a	0.28 (0.01)a	−0.03	0.02	14	−1.6	0.124

Note: Different letters represent significant differences between the positions using a significance level of 0.05. Est. = Estimated coefficient value for the model, which is the average response variable change for a one-unit change in the predictor variable.

under tree canopies, in addition to the potential of litterfall adding organic matter to the soil. Another study at just the Wairarapa site but in the same paddock provides evidence for livestock preferentially using the kānuka pasture area (Mackay-Smith et al., 2022). This was because the standing grass biomass (spot measurements of the amount of grass in each treatment and not annual pasture production measured using livestock exclusion cages) was significantly lower in the kānuka tree areas (Mackay-Smith et al., 2022), despite the rate of pasture growth being greater (Mackay-Smith et al., 2022a). This study highlights that the improved soil conditions under the kanuka trees resulted in the growth of more productive pasture functional groups such as *L. perenne*, *D. glomerata* and HFA (Table 2).

Poorer condition environments with less resources often select for 'slow trait' plants, which grow slower and have resource conservation strategies, whereas environments with more abundant resources have faster growing plants that have traits that can better utilize resources (Buckland & Grime, 2000; Reich, 2014). These faster growing species can be defined as competitor species, and these competitor species can outcompete 'slow trait' plants (Buckland & Grime, 2000; Gurevitch & Unnasch, 1989; Marañon, 1986). These competitor species are the mechanism for the mass effect hypothesis, with a few dominant species being the principal contributors to the total biomass growth of a community (Grime, 1998; Sonkoly et al., 2019). This study also found evidence of the mass effect hypothesis, with total production being associated with the growth of *L. perenne*, *D. glomerata* and HFA.

This study shows that when silvopastoral trees facilitate an increase in the availability of nutrients and improve soil structure, the growth of competitor species such as *D. glomerata* and *L. perenne* can result in more pasture production under silvopastoral trees. Marañon (1986) also presented similar results, because although the author did not measure pasture biomass, a greater percentage cover of *D. glomerata* was measured under oak trees (*Quercus* spp.) in a Spanish *dehesa* site dominated by annuals. The consistent findings between this study and Marañon (1986) indicate that trees could be an important management option for farmers attempting to increase the production of pastures because of their positive influence on fast growing and competitive functional groups. This management practice could be especially important in New Zealand hill country, because even though open pasture at both sites had a history of annual fertilization, *A. capillaris* and LF functional groups mainly grew in open pasture.

4.2 | Individual species interactions

In past New Zealand silvopastoral research when comparing tree-pasture environments with open pasture, the percentage composition of *L. perenne* has been shown to only decrease under radiata pine (*Pinus radiata* D. Don; Cossens & Hawke, 2000; Hawke, 1991; Percival & Hawke, 1985) and be similar (Douglas et al., 2006; Wall, 2006) or decrease (Crowe & McAdam, 1992; Guevara-Escobar et al., 2007) under poplar (*Populus* spp.). The results of this study show that soil conditions can improve under some silvopastoral trees in New Zealand and lead to an increase in the production of *L. perenne* when compared to open pasture.

In hill country without trees, López et al. (2006) reported low amounts of *D. glomerata*, even in high fertility microsites. Other studies that have measured pasture under trees in hill country have recorded *D. glomerata* (Cossens & Hawke, 2000; Douglas et al., 2006). Previous research indicates the potential of *D. glomerata* as a viable silvopastoral pasture species because of its tolerance to shade (Joshi, 2000; Kyriazopoulos et al., 2013; Mosquera-Losada et al., 2006; Peri et al., 2001).

Despite *D. glomerata* being a competitive species (Buckland & Grime, 2000; Gurevitch & Unnasch, 1989), the relationship with total production was unimodal (Figure 3). Moreover, *L. perenne* had a stronger positive relationship with soil fertility variables, and *D. glomerata* had a stronger positive relationship with porosity and organic matter (Figure 4). This reveals that *L. perenne* and *D. glomerata* function differently in the agroecological system and have distinctive functional strategies. This unimodal relationship could have been because of the mixed strategy functions of *D. glomerata*. In addition to its function as a competitor species, *D. glomerata* has been shown to have stress tolerator traits (in terms of light and water stress; Lin et al., 1999; Turner et al., 2012; Van Sambeek et al., 2007).

The other two abundant species in the kānuka pasture positions were the annuals *C. murinum* and *B. hordeaceus*, although the abundance of both these species was much less than *D. glomerata* and *L. perenne* (Tables 2 and 3). Both *C. murinum* and *B. hordeaceus* grow in nutrient-rich areas (Groves et al., 2003; Škornik et al., 2010), and *C. murinum* has been shown to compete with *L. perenne* and *D. glomerata* at high soil fertility levels (Groves et al., 2003). In this present study, the two positions with the greatest production overall also had the greatest production of high fertility annuals (Figure 2). Therefore, the growth of these annuals is likely a valuable support for maintaining pasture feed during spring.

A negative aspect of *C. murinum* is that their seed heads can penetrate sheep wool and skin, impacting sheep growth and their wool (Bourdôt et al., 2007; Ghanizadeh & Harrington, 2019). Because of this, it has also been identified as one of the most important agricultural weeds by farmers in a survey in New Zealand (Bourdôt et al., 2007). The potential benefits to production from the growth of *C. murinum* must be considered against this cost.

The LF species in this study responded in a similar way to the species studied by López et al. (2006) and Nicholas (1999), and had almost no production in better soil conditions, but were able to persist in the poorer soil conditions of open pasture. This indicates that these species are stress tolerators (Grime et al., 1988; Reich, 2014). The growth of these species in poorer soil conditions is still important for maintaining a good pasture cover in open pasture areas, with the higher standing grass biomass measurements in open pasture reported by Mackay-Smith et al. (2022) resulting in reduced surface runoff and associated sediment losses compared to higher fertility areas under kānuka trees.

4.3 | Pasture production–diversity relationships

This study found that the increased growth of more competitive species in kānuka pasture, such as *L. perenne*, *D. glomerata* and HFA, was related to reduced Shannon diversity, species richness and species evenness (Table 3). This result is similar to many other past studies in oak silvopastoral systems in southern Europe that have also found reduced pasture diversity under trees in presence/absence and percentage cover studies (Alonso et al., 2020; Fernández-Moya et al., 2011; López-Carrasco et al., 2015; Marañon, 1986; Rossetti et al., 2015). FRic, FEve and FDis were, however, similar between kānuka pasture and open pasture. This shows that despite reduced species diversity in kānuka pasture, the silvopastoral environment maintained a similar number of functional groups, growth evenness and spread of different functional groups throughout the year compared to open pasture. As these functional groups were formed using production data, these results provide evidence that reduced species diversity in silvopastoral systems do not necessarily result in FD reductions in the context of production functionality.

The statistically different species diversity, but the statistically similar FRic, FEve and FDis, between kānuka and open pasture, indicates that species diversity indices overestimated the impact of species diversity reductions on pasture functionaility in the context of production in kānuka pasture. This shows that it is integral to consider FD in future silvopastoral research to appropriately assess the impact diversity changes to system functioning.

Another aspect of pasture functionality that was not measured in this study was pasture stability. Pasture stability has also been shown to be related to the growth of plant with specific stress-tolerant traits (Sankaran & McNaughton, 1999; Tracy & Sanderson, 2004), and not necessarily total species diversity. As was explained in Section 4.2, the functional groups that were promoted in kānuka pasture had different survival strategies, with *D. glomerata* having stress tolerant traits, and the HFAs not growing through summer. Moreover, *D. glomerata* and *L. perenne* had different niches, with *D. glomerata* being positively associated with improvements to soil physical properties, and *L. perenne* being positively related to soil fertility variables (Figure 4). The promotion of these functional groups with a range of survival strategies in kānuka pasture could also be important for pasture stability, in addition to pasture production.

5 | CONCLUSIONS

This study investigated pasture production–diversity relationships in silvopastoral systems from a functional ecology perspective by comparing pasture functional group production, species diversity and FD under and away from kānuka trees in New Zealand hill country. This study highlights the potential of silvopastoralism to increase pasture production compared to treeless pasture by increasing the growth of fast-growing and competitive species, with *L. perenne*, *D. glomerata* and HFA (*B. hordeaceus* and *C. murinum*) having greater biomass in the kānuka environment because of improved soil fertility (Olsen-P and K) and porosity. The production of medium fertility and LF grasses were greater away from the trees in poorer soil conditions and were associated with increasing species diversity.

Despite reduced species diversity in kānuka pasture, FRic, FEve and FDis were similar between kānuka pasture and open pasture positions. This indicates that there was functional redundancy in the pasture under the kanuka trees, and that species diversity reductions did not translate to FD reductions in the context of production. Moreover, these results highlight that considering functional indices is integral for appropriately measuring the impact of diversity changes on the functionality of silvopastures.

AUTHOR CONTRIBUTIONS

Thomas H. Mackay-Smith, Ignacio F. López, Lucy L. Burkitt and Janet I. Reid conceived the ideas and designed the methodology; Thomas H. Mackay-Smith collected the data; Thomas H. Mackay-Smith analysed the data; Thomas H. Mackay-Smith led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

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DATA AVAILABILITY STATEMENT

Data available from the Zenodo Data Repository https://doi.org/10.5281/zenodo.7374528 (Mackay-Smith et al., 2022b).

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