RESEARCH ARTICLE

Community-level flammability declines over 25 years of plant invasion in grasslands

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Abstract

1. Exotic plant invasions can alter fire regimes in plant communities. Invaders often possess traits that differ from native plants in the community, resulting in increases or declines in community-level flammability, changing fire regimes and potentially causing long-term modifications to plant community composition. Although considering traits of multiple invaders and native species together is useful to better understand how invasions change community-level flammability, few studies have done this.

2. We measured morphological and flammability traits of 51 native and exotic plant species common in tussock grasslands in New Zealand's south-eastern South Island to examine relationships between morphology and whole-plant and shoot-level flammability. Plant community data from 103 permanent transects in this region measured over a 25-year period (c. 1982–2007) were used to determine how flammability changed with increasing levels of plant invasion.

3. Invasion by exotic plants has led to reduced community-level flammability due to shifts from native tussock grasses with high flammability and high fuel loads to mat-forming exotic forbs with low flammability and little fuel. These changes will likely lead to considerable alterations to the fire regime, resulting in lower intensity fires that burn more patchily and for shorter amounts of time, potentially causing further changes in floristic composition. We found considerable differences in flammability across the wide range of species and growth forms that we studied, emphasising the importance of quantifying species-level flammability and the need to avoid treating grasslands as homogenous in terms of their flammability. Total biomass, leaf length and leaf area were the traits most positively correlated with flammability in these tussock grasslands.

4. *Synthesis*. We show how plant invasions over decadal time-scales have reduced the community-level flammability of tussock grasslands and, for the first time, demonstrate how this can be driven by exotic forbs. The total biomass of constituent species is a useful surrogate for community flammability across a wide range of species and growth forms in both temperate grasslands and savanna ecosystems and should be used in dynamic global vegetation models to assess how flammability varies under various global change scenarios.

1 | INTRODUCTION

Plant invasions can change fire regimes (D'Antonio & Vitousek, 1992) and, in turn, induce dramatic and potentially irreversible changes to an entire ecosystem (reviewed by Brooks et al., 2004). For example, an altered fire regime can change plant community composition, suppress regeneration of maladapted native species and reduce native wildlife habitat (Brooks et al., 2004). Exotic invasive species (hereafter exotic species) can alter community-level flammability in two main ways. First, the exotic species may possess functional traits, such as substantially different moisture content, volatile organic compounds or retention of dead material, which make it either more or less flammable than the native species in the recipient community, therefore changing community-level flammability (Brooks et al., 2004; Gorgone-Barbosa et al., 2015; Livingston & Varner, 2016; McGranahan, Engle, Miller, & Debinski, 2013). Second, invaders can increase, decrease or change the distribution and continuity of fuel loads (Berry, Wevill, & Curran, 2011; Brooks, 2008; Gorgone-Barbosa et al., 2015; McGranahan et al., 2013). Most examples of invasion-induced changes to fire regimes have focussed on the effect of a single invading species and have shown that the invader has increased the flammability of the community (D'Antonio & Vitousek, 1992); but invaders can also reduce plant community flammability (Brooks et al., 2004; Gorgone-Barbosa et al., 2015; Livingston & Varner, 2016; McGranahan et al., 2013). Furthermore, studies of the effects of invasion on fire typically compare the flammability of one invasive species with the community being invaded and generally do so at one point in time. Hence, there is a need to consider community-level changes in flammability associated with multiple invaders and also to assess how this changes over time.

The need to predict ecosystem responses to global change, such as changing fire regimes, has prompted researchers to link species-specific measurements and landscape-level characteristics of vegetation (Cornwell et al., 2008; Lavorel & Garnier, 2002; Lavorel, McIntyre, Landsberg, & Forbes, 1997). Scaling species response traits, effect traits and abundances up to the community level is likely to greatly improve predictions concerning the magnitude and direction of global change (Suding et al., 2008). One approach to understanding the specific links between temporal changes in plant composition due to invasions and community-level flammability is to examine functional traits of native and exotic species in communities (Funk, Cleland, Suding, & Zavaleta, 2008; Lavorel & Garnier, 2002; Tecco, Díaz, Cabido, & Urcelay, 2010). Schwilk and Caprio (2011) and Zylstra et al. (2016) have both demonstrated that leaf traits can predict fire severity at the landscape scale; however, to our knowledge, no study has explicitly investigated the flammability at the whole plant or shoot scale and used these data to scale-up to the community level.

Flammability is a property of both individual plants and ecosystems. As a trait of an individual, flammability can also be scaled up to represent a property of a species and a community. Flammability consists of four quantifiable components (Anderson, 1970; Martin et al., 1994): (1) ignitability, how easily a plant catches fire; (2) combustibility, the intensity of burning; (3) sustainability, the maintenance of flaming combustion; and (4) consumability, how much of a sample is burnt. A variety of methods are used to measure these properties (e.g. Anderson, 1970; Etlinger & Beall, 2005; Gill & Zylstra, 2005; Jaureguiberry, Bertone, & Díaz, 2011; Martin et al., 1994; White & Zipperer, 2010). Traditionally, in community-level approaches to flammability, grasses and other herbaceous plants have been reduced to just a few fuel-classes in terms of fire behaviour, due to the widespread belief that they have similar levels of flammability (e.g. Anderson, 1982). However, recent studies of savanna grasses (Simpson et al., 2016), and changes in grassland community-level flammability as a result of invasion by exotic species (Rossiter, Setterfield, Douglas, & Hutley, 2003), show there can be considerable interspecific variation in grass flammability. Therefore, there is a need to better understand the effects of interspecific variability on flammability at the community level.

New Zealand's native flora evolved with relatively localised and infrequent fire activity and generally lacks fire-adapted traits (Perry, Wilmshurst, & McGlone, 2014). Widespread burning by Māori and European settlers beginning *c.* 740 years ago led to tussock grasslands becoming abundant across the landscape below tree line, particularly in the South Island (McGlone, Duncan, & Heenan, 2001; Perry et al., 2014; Rogers, Walker, Basher, & Lee, 2007). Invasion of New Zealand's tussock grasslands by multiple exotic species is well-documented (e.g. Rose & Frampton, 2007; Treskonova, 1991), but it is unclear how they may have impacted flammability of these communities. Anticipated increases in fire severity due to climate change in New Zealand (Pearce et al., 2011) could interact with invasion-driven changes in community-level flammability, leading to an altered fire regime that would feedback to plant community composition.

To test the effects of species' traits on community flammability, we measured morphological and flammability traits of 51 common, native and exotic tussock grassland plant species in New Zealand's south-eastern South Island. We up-scaled these individual-level flammability measures to the community level using spatial and temporal variation in species frequencies and abundances from 103 permanent transects measured three times over 25 years (*c.* 1982–2007). These grassland transects vary in both the number of exotic species and the changes over time in many of these species, including invasive grasses and the mat-forming rosette forbs known as hawkweeds (*Hieracium* spp. and *Pilosella* spp.; Day & Buckley, 2011, 2013; Duncan, Webster, & Jensen, 2001). Both composition and invasion in these communities are strongly linked to environmental gradients, such as altitude (Day

& Buckley, 2011, 2013). Specifically, we ask how 25 years of plant invasion have affected plant community flammability across this region, and which traits most influence flammability. Plant traits influencing flammability have been studied in a number of fire-prone taxa (e.g. Ganteaume, Jappiot, Lampin, Guijarro, & Hernando, 2013; Schwilk & Caprio, 2011). However, few studies have empirically measured the influence of easy-to-measure morphological traits on the flammability of grasses and forbs (but see Fill, Moule, Varner, & Mousseau, 2016; Simpson et al., 2016), and none have done this for a large set of the most common dominant species of an entire grassland ecosystem.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Between 1982 and 2007, plant species presence was recorded in 125 permanently marked transects in grasslands across Canterbury and Otago in the South Island of New Zealand (Figure S1; Buckley & Freckleton, 2010; Day & Buckley, 2013; Duncan et al., 2001). Transects were measured three times: 1982–1986, 1993–1998 and 2005–2007. Plant species presence was recorded in 50 quadrats (0.5 × 0.5 m) spaced 2 m apart along all transects. In the 1990s and 2000s measurements, percentage cover of each species was recorded as one of six cover classes in each quadrat (<1%, 2%–5%, 6%–25%, 26%–50%, 51%–75% and 76%–100%).

We used the 103 transects that were classified as tussock grasslands (dominated by either *Chionochloa* spp. or *Festuca novae-zelandiae*; Day & Buckley, 2013) and measured functional traits on the 51 most frequent species in the 2000s out of the total of 334 species. Nomenclature follows the Landcare Plant Names Database (www. landcareresearch.co.nz/resources/data/nzplants). In December 2015 and January 2016, 11 of the 103 transects that contained most of those dominant species and represented the geographic spread of the community were revisited to collect samples for measuring flammability and morphological traits (Figure S1; Day & Buckley, 2013). For each species, one sample from each of eight haphazardly selected, healthy adult individuals was collected. For grasses and forbs shorter than 70 cm, we followed the methods employed by Jaureguiberry et al. (2011), which involved collecting the entire individual. Where it was not possible to collect an entire single individual, canopy architecture was preserved by collecting a distinct ramet and any detached litter from the same plant that was loosely held in the canopy. Forbs and grasses taller than 70 cm were tip-pruned, retaining only the material between 0 and 70 cm above the ground for the flammability experiments. For shrubs, a terminal branch 70 cm long was collected (Jaureguiberry et al., 2011; Wyse et al., 2016). For shrubs, grasses and tussocks exceeding the capacity of the flammability device (Figure S2), i.e. *Aciphylla aurea*, *Chionochloa macra*, *Chionochloa rigida* and *Dracophyllum acerosum*, we also used a vertical cylinder (radius = 5.5 cm; height = 70 cm) starting from the bottom centre of the plant to collect dead plant biomass and all other branches and stems partially included in the volume (Figure S3). In a separate methods test, we concluded that using this vertical cylinder to reconstitute the fuel

arrangement was a more realistic representation of the contribution of these species towards community-level flammability. For each individual sample, we measured sample height (maximum vertical spread), width (maximum horizontal spread) and length (maximum horizontal spread perpendicular to width). Samples were stored in sealed plastic bags in a covered trailer cooled with ice and transported to a refrigerator (4°C–8°C) within 4 days, where they were stored for less than 1 week prior to burning.

2.2 | Morphological trait measurements

The 51 species measured here represented an average of 86.6 ± 13.8% of the total cover of the transects and so encompassed the dominant species of this community (Table S1). By measuring flammability of up to 70 cm portions of plants, 46 of the 51 species (90%) had their flammability measured at the whole plant or ramet scale.

We measured four leaf-scale and five shoot-scale morphological traits for each species on the fresh samples (see Supporting Information for details on the rationale for morphological traits selection). Leaf traits included leaf length, leaf area, leaf thickness and specific leaf area (SLA). Measurements were taken on healthy, fully expanded leaves following Pérez-Harguindeguy et al. (2013) and the reported values are the mean of at least four replicate individuals per species (Table S2). Leaf area was measured on digital images using the computer program ImageJ 1.50b (Abràmoff, Magalhãs, & Ram, 2004). Leaf thickness at the middle of the leaf, excluding the midrib, was measured using a digital, outside micrometre, accurate to 0.001 mm (Insize, Suzhou, China).

For shoot traits, each fresh sample was weighed to obtain its total biomass. We visually estimated the proportion of dead material and calculated fuel bulk density as the ratio of total biomass to length × width × height of each shoot sample. Subsamples were taken from each fresh sample and weighed to determine their fresh mass at the time of collection (i.e. when removed from the cold storage) and 24 hr later at the time of burning. They were then oven-dried at 65°C for 48 hr to determine their dry mass. Moisture content at the time of burning (hereafter only "moisture content") and moisture loss when air-dried for 24 hr were subsequently calculated following (Behm, Duryea, Long, & Zipperer, 2004) (see Supporting Information for equations).

2.3 | Flammability trait measurements

Flammability traits of each plant sample were measured using an apparatus described by Jaureguiberry et al. (2011) and modified by Wyse et al. (2016) (Figure S2; Table S3), with adjustments for larger plants (the vertical cylinder described above). All samples were stored air-dry at room temperature for 24 hr before burning (Wyse et al., 2016) to ensure that the moisture content of the samples matched the ignition source (Wyse, Perry, & Curran, 2017). The burners were turned on until the grill reached *c.* 150°C and left on throughout the whole experiment to allow plant samples to be preheated, as would happen in a natural fire approaching vegetation (Burger & Bond, 2015). Each

sample was placed horizontally on the grill in the best position to fa-vour ignition and fire spread and exposed to preheating for 2 min. The blowtorch was turned on for 10 s to ignite the sample (Jaureguiberry et al., 2011).

Ignitability was visually estimated and ranged between 0.5 to 10 s. This variable was then inversely rescaled to give higher values (a maximum of 9.5) to those species that ignited quicker (0.5 s), and lower values (a minimum of 2) to those species that took the longest to ignite (8 s). Samples that did not ignite were given a zero value. Combustibility, the maximum temperature reached by the burning sample, was measured with a handheld infrared thermometer (Fluke 572; Fluke Corp., Everett, WA, USA). Samples that did not sustain a fire after the blowtorch was turned off were assigned values of 150°C for combustibility, which represents the average temperature of the grill. Sustainability was measured as the length of time the sample burned for after the blowtorch was extinguished. Consumability, the percent-age of the original biomass that had burned, was visually estimated by two people (Burger & Bond, 2015; Wyse et al., 2016). Samples that did not burn without the blowtorch were assigned zeros for consumability and sustainability.

2.4 | Data analysis

2.4.1 | Relationships between morphological and flammability traits

We used principal component analysis (PCA) to investigate varia-tion in flammability traits. First, a "Species Flammability Traits PCA" was performed on the flammability traits ignitability, combustibility, sustainability and consumability at the species level (n = 51), using mean values from the different individuals of the same species. The Species Flammability Traits PCA was used in further community-level analysis (see below). Second, to explore associations among all mor-phological and flammability traits at the species level, we performed a "Species Flammability and Morphological Traits PCA" with all flam-mability traits (ignitability, combustibility, sustainability, consumabil-ity) and morphological traits (leaf length, leaf area, leaf thickness, SLA, total biomass, dead biomass, bulk density, moisture loss and moisture content). Furthermore, we calculated Pearson correlation coefficients across the set of 51 species to further evaluate whether PCA axes from the Species Flammability Traits PCA and the flammability traits were associated with plant morphological traits at the species level; these correlations were performed using the mean trait values for species for all flammability and morphological traits. PCAs were im-plemented using the "PCA" function from the "FactoMiner" R package (v 1.28) (Lê, Josse, & Husson, 2008) on centred and standardised data.

2.4.2 | Predictors of change in community-level flammability

We combined the results from PC1 and PC2 of the Species Flammability Traits PCA with previously collected, long-term data in tussock grasslands to investigate changes in community-level

flammability over time. Only results for changes in PC1 are shown in Results (see Supporting Information for details on changes in PC2). Taxa recorded only at the genus level in the floristic surveys were given the PC loadings of congeners for which we measured flamma-bility. For example, we measured flammability of *Epilobium alsinioides*, and its PCA loadings were assigned to all *Epilobium* spp. Similarly, *Chionochloa* spp. flammability was calculated as the mean value of the loadings of *Chionochloa macra* and *C. rigida*, for which we had values (Table S4). To estimate flammability of species and genera for which we did not make flammability measurements (n = 283), we substituted PCA loadings from taxa with similar morphology and/or growth form as determined using independent, published data. To do this we clas-sified all 334 species in 14 different groups based on (1) their growth form following Pérez-Harguindeguy et al. (2013), and (2) their average foliage height following the Flora of New Zealand (http://nzflora.info; Table S4). Species in each growth form group were given a flammabil-ity trait value equal to the mean of those measured species in that group (see Figure S4). The strong relationships between the flamma-bility traits and morphological traits (see Section 3) supported these substitutions. As a result, a species × trait matrix was obtained and values rescaled following the min-to-max method to avoid negative scores (McCune, 2015). This matrix was multiplied by each sam-ple unit × species matrix using abundance-weighted trait averages (McCune, 2015) to generate five sample unit × flammability matri-ces (three measurement times with changes in frequencies, and two measurement times with changes in abundances). As a result, a single vector giving the community flammability for each of the 103 tran-sects was obtained for each time period. It was then divided by the row totals in the community matrix to get weighted averages. Finally, we calculated change in community-level flammability as the differ-ence between all combinations of measurement times considering species' abundance and frequency separately, e.g. 1990s flammability minus 1980s flammability (Figure S5). Change in species frequency was calculated as the difference in the number of quadrats each spe-cies occupied on each transect at each measurement. Change in spe-cies abundance was based on total area covered by each species on each transect at each measurement from the cover estimates in the 1990s and 2000s. To calculate this we first estimated the per cent quadrat cover of each species on each transect at each time using the midpoint of the cover score (0.5, 3.5, 15.5, 38, 63, 88). These val-ues were multiplied by the area of each quadrat (0.25 m^2) and then summed to obtain total area occupied by each species in each transect at each time.

We selected five environmental variables that we a priori predicted would be related to patterns of change in community-level flamma-bility: elevation, mean monthly temperature (30-year average), mean monthly precipitation (30-year average), solar radiation and change in exotics' frequency or abundance. For more details of data collection, see Day and Buckley (2011, 2013). Change in exotic species abun-dance was used only for models of change in flammability between 1990s and 2000s, whereas change in exotic frequency was used in the models for all time periods. Precipitation was log-transformed and all predictors were standardised and centred before being introduced to

TABLE 1 Candidate models used to assess the relative effects of environmental variables on change in flammability across 103 vegetation transects measured three times: 1980s, 1990s, 2000s. Change in exotic species abundance was used only for models of change in flammability between 1990s and 2000s, whereas change in exotic frequency was used in the models for all other time periods. Interactions among variables are represented with "*" symbol

Model name	Explanatory variables included	Effects represented
M1 Intercept-only	None	None
M2 Exotics	Change in exotics (abundance or frequency)	Variation in exotics
M3 Elevation	Elevation	Altitudinal gradient (temperature, management, species composition)
M4 Precipitation	Precipitation	Precipitation
M5 Exotics and elevation	Change in exotics * elevation	Change in exotics along an altitudinal (climatic) gradient
M6 Exotics and precipitation	Change in exotics * precipitation	Change in exotics along a rainfall gradient
M7 Climatic	Elevation, precipitation and solar radiation	Climatic conditions
M8 Full	Elevation, precipitation, solar radiation and change in exotics	As described above
Full (with interactions)	Elevation * precipitation * solar radiation * change in exotics	As described above

the model so that the coefficient values were comparable (Zuur, Leno, & Smith, 2007). Multicollinearity was assessed using the variance inflation factor (VIF) with function "vif" in the ʀ package "usdm" (v 1.1-15) (Naimi, 2015). Temperature was highly correlated with elevation ($r = -.94$) and was removed from all following analysis. Pearson correlations and VIF values indicated low multicollinearity ($-.3 < r < .30$ and VIF < 2 respectively) among the other predictors.

Change in community-level flammability was modelled as a function of explanatory variables using a set of nine candidate linear mixed-effect models (Table 1) implemented using the function "lme" in the ʀ package "nlme" (v 3.1-128) (Pinheiro & Bates, 2000). We calculated the AIC_c (the small-sample-size-corrected Akaike's information criterion; Anderson, 2008) values of each candidate model set and ranked them by their Akaike weights by means of the ʀ package "AICcmodavg" (v 2.0-4) (Mazerolle, 2017). The function "modavgPred" in the same package was used to compute the model-averaged predictions (Mazerolle, 2017), which is the natural average and reduces concerns about bias away from zero (Cade, 2015). In all models, the random effect of "property" was included to account for the clustering of transects within the 31 landholdings. Two outlying transects that showed extremely large values for community-level flammability variation between the 1980s and 1990s due to targeted control of exotic species by land managers were removed from the analysis because they significantly biased the results.

Some fire properties, such as flame speed or time to extinction at the community level (van Altena, van Logtestijn, Cornwell, & Cornelissen, 2012) or ignitability and maximum temperature reached at the shoot level (Wyse et al., 2017), might be determined by the most flammable species in the mixture. Consequently, the effect of lower flammability plants would be over-estimated by using their abundance values. We therefore repeated the analysis with the candidate models by considering only the 51 species for which we had trait measurements, which represented more than 86% of the total abundance in the 1990s and 2000s. We present only the results from the full community because they do not differ from the results using only the 51 species (see Tables S5 and S6). All statistical analyses were conducted using ʀ version 3.2.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Plant sample flammability

The 51 tussock grassland species we assessed showed variation in their flammability responses to experimental burning (Figure 1a; Table S4). The first axis (PC1) from the Species Flammability Traits Principal Component Analysis (PCA) explained 82.2% of the variation in the flammability of species and was positively associated with all four flammability variables: ignitability (loading = 0.52), combustibility (0.54), sustainability (0.41) and consumability (0.52). The second axis (PC2) explained 16.1% of the variation among species and was positively associated with sustainability (0.84) and weakly with combustibility (0.10), and negatively with both ignitability (−0.38) and consumability (−0.38). Ranking all 51 species by their loadings on PC1 and PC2, the most flammable species were *Chionochloa rigida*, *Dracophyllum acerosum*, *C. macra*, *Aciphylla aurea* and *Festuca novae-zelandiae* in both flammability dimensions (Figures S6 and S7). The first four of these species were characterised by long sustainability, as reflected by their high loadings on PC2. We also observed a large group of low-flammability species represented by small rosette forbs that were both native, such as *Brachyscome longiscapa*, *Lagenifera cuneta*, *Leptinella pectinata* and *Wahlenbergia albomarginata*, and exotic, such as *Crepis capillaris*, *Pilosella officinarum*, *Pilosella piloselloides* and *Hypochaeris radicata*.

3.2 | Relationships between morphological and flammability traits

Morphological traits were strongly correlated with flammability traits. PC1 of the Species Flammability Traits PCA (Figure 1a; Figure S8)
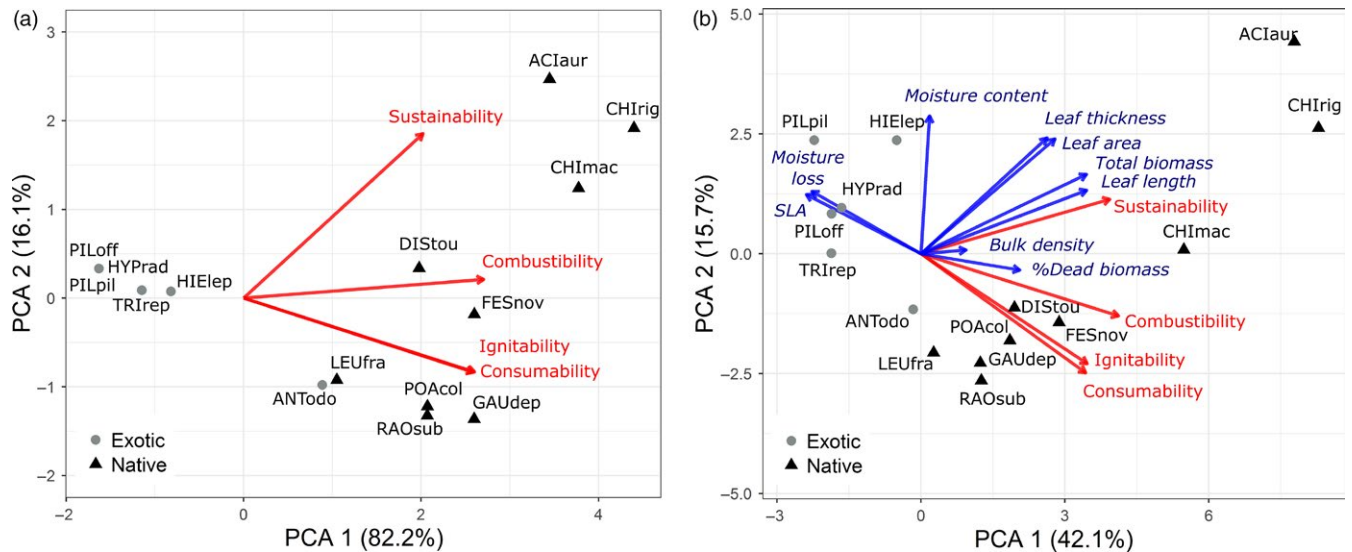
FIGURE 1 Principal component analysis (PCA) of (a) the four measured flammability traits (red arrows; ignitability (inverse ranking of "time to ignition"), maximum temperature, burning time and burnt biomass) alone (Species Flammability Traits PCA) and (b) in combination with other morphological traits (blue arrows, labels in italics; Species Flammability and Morphological Traits PCA). The 15 most dominant species in terms of abundance in the 2000s along the 103 transects are presented (see Figures S8 and S9 for all 51 species). Plant names abbreviations for selected species shown are as follows: ACIaur (*Aciphylla aurea*), ANTodo (*Anthoxanthum odoratum*), CHImac (*Chionochloa macra*), CHIrig (*Chionochloa rigida*), DIStou (*Discaria toumatou*), FESnov (*Festuca novae-zelandiae*), GAUdep (*Gaultheria depressa*), HIElep (*Hieracium lepidulum*), HYPrad (*Hypochaeris radicata*), LEUfra (*Leucopogon fraseri*), PILoff (*Pilosella officinarum*), PILpil (*Pilosella piloselloides*), POAcol (*Poa colensoi*), RAOsub (*Raoulia subsericea*) and TRIrep (*Trifolium repens*). Points indicate the mean scores for each species based on measurements of individuals (see Section 2 and Figures S4 and S5)

was positively correlated with individual-level total biomass and the proportion of dead biomass and negatively correlated with moisture loss (Table 2). PC2 was correlated with total biomass and weakly with moisture content (Table 2). The strongest correlation between traits was observed between sustainability and total biomass, although total biomass was also correlated with maximum temperature and to a lesser extent to ignitability and consumability (Table 2). Moisture loss was also correlated with ignitability, combustibility and consumability (Table 2). Bulk density and moisture content were not correlated with any of the flammability components.

PC1 of the Species Flammability Traits PCA was positively correlated with leaf length, leaf area and leaf thickness, and negatively correlated with specific leaf area (SLA) (Table 2). Positive significant correlations were also observed among leaf length, leaf area and leaf thickness, and combustibility and sustainability (Table 2). SLA was negatively correlated with combustibility and sustainability. The second principal component was also positively correlated with leaf area and leaf length and thickness (Table 2). Ignitability and consumability were only positively correlated with leaf length and negatively correlated with SLA (Table 2). In this case, the strongest correlation was observed between leaf length and sustainability (Table 2).

PC1 and PC2 of Species Flammability and Morphological Traits PCA accounted for 57.8% of the total variance (Figure 1b; Figure S9). All flammability traits were positively associated with the first PCA component (ignitability loading = 0.32, consumability = 0.39, sustainability = 0.37 and combustibility = 0.33), while total biomass (0.33) and leaf length (0.33), followed by leaf area (0.27) and leaf thickness (0.25),

were also positively loaded most heavily on this component, and SLA (−0.23) and moisture loss (−0.22) were loaded in the opposite direction. Only bulk density (0.09), the percentage of dead biomass (0.20) and moisture content (virtually orthogonal; loading = 0.02) were not strongly associated with the first component. All flammability traits, with the exception of sustainability (0.18), had negative loadings on the second component (ignitability = −0.38, combustibility = −0.20, consumability = −0.35). In contrast, all morphological traits, excluding percentage of dead biomass (−0.05), had positive loadings on the second component, with higher loadings for moisture content (0.44), leaf thickness (0.37), leaf area (0.37) and total biomass (0.26).

3.3 | Predictors of change in community-level flammability

Of our candidate models, the best model for change in community-level flammability for our data was that which contained the interaction between change in exotics (in terms of species abundance and frequency) and elevation (Table 3). This held for all time periods and also when modelling changes in flammability based on both species frequencies and abundance. These explanatory variables, combined with the random effect of property, explained between 27 and 65% of the variability in change in flammability as measured by PC1 (model weights ranged from 0.32 to 1.00). For the change in flammability as measured by PC1, change in exotics and elevation were both significant (model-averaged confidence intervals did not overlap zero) in all models except for Frequency 1980s–1990s (Figure 2; Table S7).

TABLE 2 Pearson correlations between morphological traits at the shoot and leaf levels and flammability traits

	Shoot traits					Leaf traits			
	Biomass (g)	Dead biomass (%)	Bulk density (Kg/cm³)	Moisture loss (%/day)	Moisture content (%)	Leaf thickness (mm)	Leaf length (mm)	Leaf area (mm²)	SLA (mm²/mg)
Flammability (PC1)	0.56***	0.33*	0.14	−0.48***	−0.08	0.34*	0.57***	0.38**	−0.51***
Flammability (PC2)	0.60***	0.12	0.09	0.05	0.29*	0.44**	0.44**	0.52***	−0.04
Ignitability	0.35*	0.29*	0.10	−0.48***	−0.17	0.18	0.38**	0.17	−0.45**
Combustibility (°C)	0.62***	0.32*	0.19	−0.47***	−0.08	0.37**	0.56***	0.39***	−0.52***
Sustainability (s)	0.80***	0.33*	0.15	−0.32*	0.14	0.55***	0.73***	0.64***	−0.40**
Consumability (%)	0.31*	0.26	0.08	−0.44**	−0.14	0.20	0.44**	0.25	−0.48**

*, **, *** Significant at $p \leq .05$, .01 and .001, respectively.

Since high loadings on PC1 indicated high flammability, a significant negative relationship indicates that community-level flammability declined over time. In all cases, transects that decreased most in flammability increased in the abundance and/or frequency of exotic species (Figure 2a–c; Table S7). This decrease in flammability was also associated with higher elevation, except for frequency 1980s–1990s (Figure 2d–f; Figure S10). The greatest increases in exotics were typically at mid elevations for abundance and frequency 1990s–2000s, but at mid-high elevation for frequency 1990s–2000s (Figure 2).

4 | DISCUSSION

We sought to examine changes in community-level flammability over decadal time-scales with increasing levels of exotic plant invasion by multiple species. Many of our transects in tussock grasslands, particularly those at low elevations, had large increases in the abundance of exotic species (Day & Buckley, 2011). By measuring the whole-plant and shoot flammability of the dominant species, we show that invasion by exotic plants has led to reduced community-level flammability over 25 years at a landscape level in tussock grasslands of New Zealand's South Island. These changes in flammability are linked to a shift from highly flammable native tussock grasses, which have high biomass and hence high fuel loads, to a suite of mat-forming exotic forbs that have low tissue flammability and low fuel loads. Our study also shows the importance of quantifying the flammability of many species within a plant community, as species and growth forms varied widely in their flammability.

We found that total biomass (as represented by fresh mass) shows promise as an easy-to-measure surrogate for flammability for all growth forms in grasslands, although leaf length and leaf area were also highly correlated with flammability. Total biomass has been shown to positively influence individual plant flammability in South African savanna grasses (Simpson et al., 2016) and greater fire intensity and fire spread rate in invaded savannas in northern Australia (Rossiter et al., 2003). Our study suggests that this easy-to-measure surrogate for flammability in temperate grasslands could be usefully tested in dynamic global vegetation models predicting grassland flammability under different global change scenarios, although other traits, such as fuel moisture content (Payton & Pearce, 2009), should also be included.

4.1 | Changes in community-level flammability

This study is one of few that have demonstrated a decrease in community-level flammability following herbaceous plant invasion (Brooks, 2008), and the first to empirically show how this can be driven by invasive forbs (here rosette-leaved hawkweeds). Community-level flammability declined over a c. 10-year time period (between the second and the third measurement), showing that the decrease in community-level flammability caused by exotic plant invasion was rapid, particularly given that the native component of these grasslands is dominated by perennial and long-lived species (Day & Buckley, 2011).

TABLE 3 Results from candidate models for changes in community-level flammability from plant abundance between 1990s and 2000s and plant frequency between 1980s and 1990s, 1990s and 2000s, and 1980s and 2000s. For each model, the number of parameters (*K*), the change in small-sample-size-corrected Akaike's information relative to the best model (ΔAIC$_c$), the model weight (*w$_i$*), the log-likelihood (Log(*L*)), the marginal *R*-squared (Marg. *R*²) and the conditional *R*-squared (Cond. *R*²) are given. Only the top four models are presented, whereas models within two AIC$_c$ points of the top model are shown in bold (see Tables S5 and S6 for complete results on change in flammability as measured by PC1 and PC2, respectively). Full = Model including elevation, precipitation, solar radiation and change in exotics. With int. = With interactions

Dependent variable	Model	*K*	ΔAIC$_c$	*w$_i$*	Log(*L*)	Marg. *R*²	Cond. *R*²
Abundance 1990s–2000s	**Exotics × elevation**	**6**	**0**	**0.64**	**150.02**	**0.35**	**0.50**
	Full	**7**	**1.18**	**0.36**	**150.59**	**0.35**	**0.49**
	Full (with int.)	18	11.05	0.00	160.36	0.45	0.60
	Exotics	4	14.43	0.00	140.55	0.20	0.38
Frequency 1980s–1990s	**Exotics × elevation**	**6**	**0**	**0.45**	**209.45**	**0.10**	**0.27**
	Intercept-only	**3**	**1.75**	**0.19**	**205.25**	**0.00**	**0.15**
	Elevation	4	2.86	0.11	205.78	0.01	0.16
	Exotics × precipitation	6	3.31	0.09	207.80	0.05	0.20
Frequency 1990s–2000s	**Exotics × elevation**	**6**	**0**	**0.68**	**219.75**	**0.36**	**0.65**
	Full	**7**	**1.53**	**0.32**	**220.14**	**0.36**	**0.67**
	Exotics × precipitation	6	12.87	0.00	213.32	0.30	0.63
	Full (with int.)	18	16.10	0.00	227.34	0.43	0.69
Frequency 1980s–2000s	**Exotics × elevation**	**6**	**0**	**1.00**	**195.31**	**0.29**	**0.42**
	Exotics	4	12.20	0.00	186.98	0.15	0.28
	Exotics × precipitation	6	13.90	0.00	188.36	0.18	0.32
	Full	7	15.91	0.00	188.51	0.17	0.29
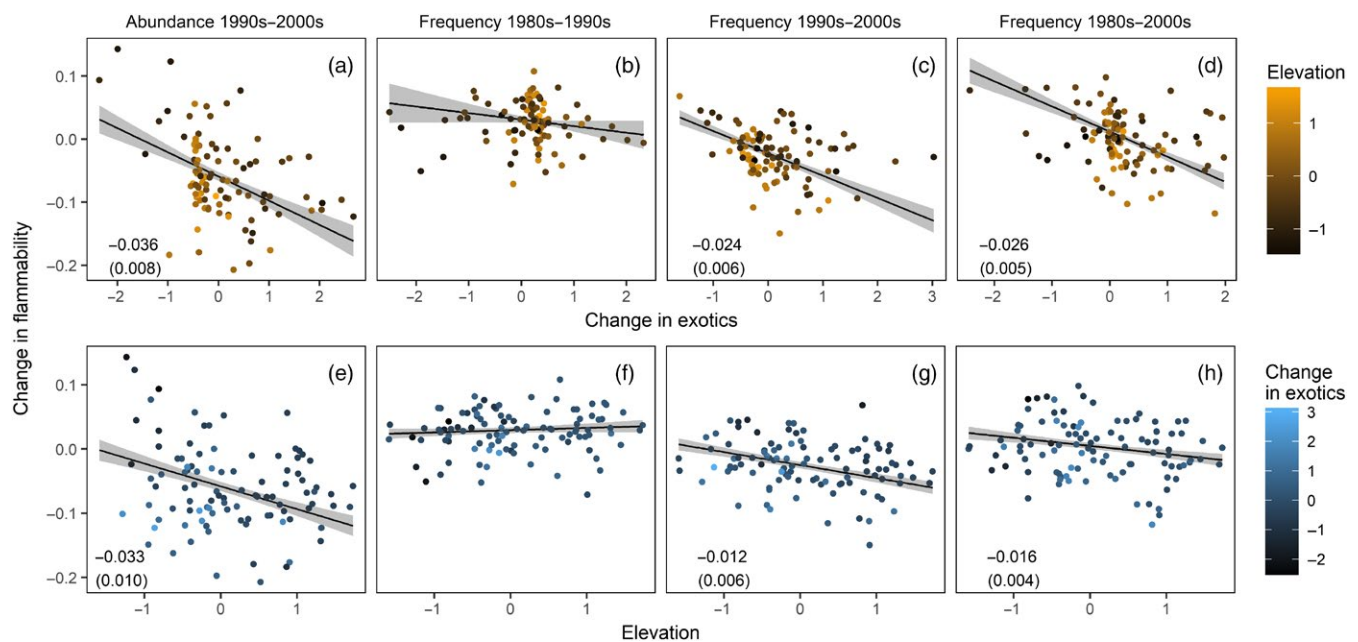
FIGURE 2 Relationships between changes in community-level flammability (model-averaged predictions; PC1 of the Species Flammability Traits PCA) and change in exotics (a–d) and elevation (e–h) at different measurement times. Points are coloured according to elevation (a–d) or change in exotics (e–h). Grey areas indicate confidence intervals (95%) based on the entire candidate model set. All variables were standardised and centred. Model-averaged coefficients and standard errors (in brackets) are given for variables for which the confidence intervals do not overlap zero. Full models are presented in Tables S7

Elevation was also an important predictor of changes in flammability. Elevation was positively correlated with soil alkalinity, strongly negatively related to temperature and strongly influences species composition (Day & Buckley, 2013). If exotic invasions in these grasslands are currently limited by low temperatures at higher elevations, then these species could invade higher elevations given

the significantly warmer temperatures predicted for these regions (Hennessy et al., 2007). Hence, we would expect more of these tussock grasslands to experience reductions in flammability in the future, due to increased invasion.

In disturbed tall tussock (*Chionochloa* spp.) grasslands, the spread of hawkweeds can be a reflection of past management practices and opening up of closed-canopied communities, often through burning and grazing (Rose & Frampton, 1999; Treskonova, 1991). However, previous studies have shown that changes in pastoral management in short tussock (*Festuca novae-zelandiae*) grasslands, such as exclusion of grazing and oversowing, have not necessarily reduced the net increase of hawkweeds (Day & Buckley, 2011; Rose & Frampton, 2007). The rapid spread of hawkweed species in both grazed and ungrazed short tussock grasslands probably reflects the communities' low resistance to invasive plants (Rose & Frampton, 1999, 2007). Consequently, future changes in community flammability derived from plant invasions in the absence of grazing might be expected.

One important caveat to our community-weighted mean approach to assessing community flammability is the underlying assumption that changes in flammability are additive. Recent shoot-level experiments on species mixtures of trees and shrubs in New Zealand suggest that this is the case for certain components of flammability, such as sustainability and consumability (Wyse et al., 2017). This could have important biological consequences as sustainability will affect fire residence time, a key driver of fire-based plant mortality (Keeley, 2009; Whelan, 1995). However, these same shoot-level experiments suggest that other flammability components (e.g. combustibility and ignitability) are determined by the most flammable species in a mixture, and that this influence can be disproportionately large compared to their relative biomass (Wyse et al., 2017). Field-based experimental burns would help resolve the role of particular species in suppressing or promoting fire and more broadly test the applicability of a community-weighted mean approach to assessing community flammability in these systems.

4.2 | Species effects on changes in community-level flammability

The most flammable species were tall tussocks and woody shrubs characterised by large amounts of biomass and long, thick leaves, variables all highly correlated with overall flammability. The low flammability end of the spectrum in our study comprised a group of species characterised by small, low growing forbs or rosettes. These species rarely carried a fire during the flammability testing, emphasising their low flammability, which was due to traits such as low total biomass, high moisture content, high specific leaf area (SLA) and low percentages of retained dead material. While many of these were native species, four key exotic species that are abundant in these communities also had low flammability. Most notably, *Pilosella officinarum* and *P. piloselloides* had low flammability and had also increased in frequency, abundance and cover on these transects over the 25-year period, and are in high local frequencies and abundances (Day & Buckley, 2011, 2013). These highly abundant exotic species have an important

influence on the relationship between the invasion and reduction in flammability. Although other rosette forbs occur in the native community, these were usually low in abundance and would have little influence on community-level flammability. However, when forbs form dense mats, or are found in very high abundance, as in the case for the invasive hawkweeds in this community (Figure 3; Day & Buckley, 2013), they will drastically reduce fuel loads, fuel continuity, fire residence time and plant flammability, likely causing reductions in fire frequency, intensity, severity and extent (Brooks, 2008).

We can use our data to make predictions on how plant invasions would likely influence the fire regime and floristic composition of these tussock grasslands. First, there are stark differences in the tissue flammability of some of the dominant native species (such as the large snow tussocks, *Chionochloa* spp., which have very high flammability) and the invasive exotics (e.g. *Pilosella* spp.), which rarely burned during testing. Second, there are considerable differences in fuel loads between many of the dominant natives (the snow tussocks are >1.2 m in height and grow in large clumps 1.3 by 1.5 m) and the mat-forming exotic rosettes, which are typically <0.2 m in height. This represents a shift from highly flammable native grasses with relatively large fuel loads that burn for a long duration, towards less flammable exotics (especially the mat-forming rosettes) with little fuel. These exotics would disrupt both horizontal and vertical fuel continuity (Figure 3). The likely consequences of this reduction in tissue flammability and fuel loads are less-intense fires, which burn much more patchily and with a reduced extent (Brooks, 2008). Importantly, the shift away from species which burn for a long duration will lead to reduced fire residence times, which will likely reduce plant mortality (Keeley, 2009; Whelan, 1995). If the low-flammable invasive species are favoured by changes in fire regimes to the detriment of native species, then this could trigger a positive feedback cycle (invasion and fire suppression and further invasion) that leads to permanent shifts in community composition.

We found substantial interspecific variation in flammability between our study species that encompassed a wide range of growth forms, including woody shrubs, subshrubs, prostrate shrubs, graminoids, cushion plants, rhizomatous plants and rosette forbs. This concurs with Simpson et al.'s (2016) work on grasses and further demonstrates that interspecific variation (including in key traits, such as biomass) must be accounted for when examining community-level flammability. We also show that interspecific differences in flammability are underpinned by differences in plant morphological traits.

4.3 | Trait–flammability relationships

Total biomass (as represented by fresh mass) was the key shoot trait influencing total flammability, as well as sustainability and combustibility. Simpson et al. (2016) also found this pattern, but we have expanded this relationship to an entire community encompassing a variety of plant growth forms. Hence, plant biomass could be used as a surrogate for flammability in grassland communities, potentially world-wide. The importance of total biomass in increasing flammability of fuel loads of tall tussocks at the community-level has been
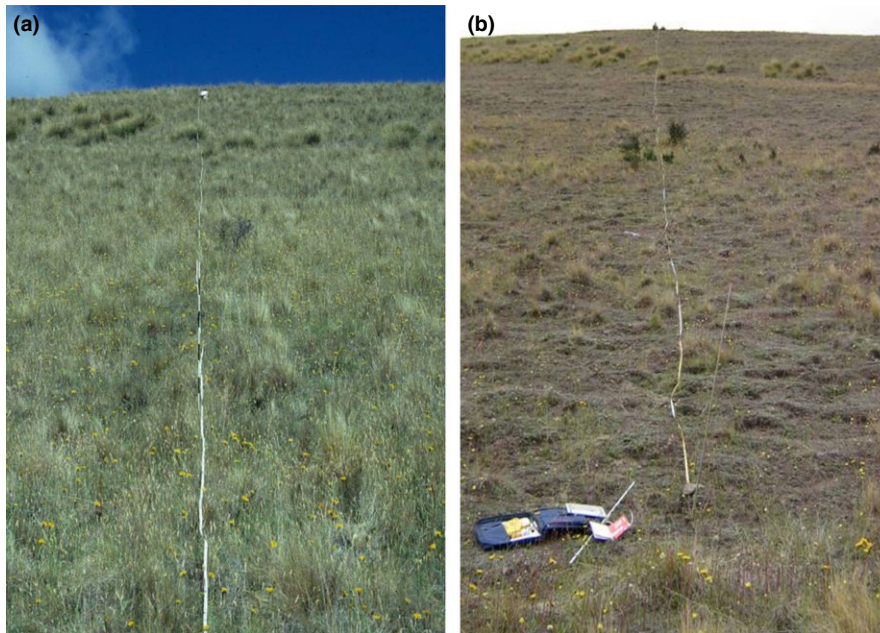
FIGURE 3 Example of transect where exotic species most increased in abundance over the time period (January 1986 (a) and January 2007 (b)). Invasion of exotic mat-forming forbs in (b) decreased total plant biomass and reduced fuel continuity. See Figure S11 for the relationship between community flammability and per cent abundance of exotic species

acknowledged by Payton and Pearce (2009) in their field-based experiments. We found that moisture content measured at the time of burning was not correlated with any of the flammability components in our study. Species that were both high (*Chionochloa rigida*, *Aciphylla aurea*) and low (*Pilosella piloselloides*) in flammability had the highest moisture content in our study. These high-flammability species also had the highest proportion of retained dead material, suggesting that the combination of these traits was more important than one trait alone.

To our knowledge, no previous studies have tested the relative effect of moisture loss on flammability, although Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013) both suggested that that twig drying time is correlated with flammability, with more rapid drying time resulting in more flammable plants. We found species exposed to drying conditions can lose water quickly and thus be more susceptible to fire. This is of major importance for tussock grassland recovery after fire events, because the vulnerability of tussocks to fire is determined by two major factors: the timing of the burns and the dryness of the grasslands (Payton & Pearce, 2009). Greater moisture losses are usually associated with smaller leaves because they have higher surface-to-volume ratio (Bowman, French, & Prior, 2014; Murray, Hardstaff, & Phillips, 2013; Pérez-Harguindeguy et al., 2013), but this relationship was not observed in our study. Furthermore, bulk density of samples did not influence flammability in our tests, unlike other studies, such as for dried grasses collected throughout Australia (Prior et al., 2017).

The correlations found between leaf traits and the measured flammability components in our study further demonstrate the possibility of using easy-to-measure traits to estimate plant flammability. For instance, leaf length was more important than total biomass in explaining overall flammability and consumability. Nonetheless, contradictory results have been observed when relating leaf length to flammability (Murray et al., 2013; Schwilk & Caprio, 2011), suggesting that these effects are context-dependent. The same applies

when examining our positive correlations among leaf area and leaf thickness with combustibility and sustainability. As with Murray et al. (2013), we found no correlation between leaf thickness and ignitability, despite the extensive literature reporting correlations between both parameters (Bowman et al., 2014; Gill & Moore, 1996; Saura-Mas, Paula, Pausas, & Lloret, 2010). SLA was negatively correlated with all flammability components and was the best correlate with consumability. However, other studies have found SLA to be positively correlated with ignitability (Bowman et al., 2014; Grootemaat, Wright, van Bodegom, Cornelissen, & Cornwell, 2015; Murray et al., 2013).

5 | CONCLUSIONS

We have shown how the invasion of multiple species (especially a suite of low-flammability forbs) has reduced community flammability in temperate grasslands over recent decades. We predict that this will lead to considerable changes to the fire regime, resulting in patchy, low-intensity fires with short residence time. In turn, this may set in train positive feedbacks whereby the new fire regime fosters increased invasion, further suppressing fire and repeating this fire-invasion cycle. Future work comparing species-based estimates of community-level flammability with field-based measures derived using experimental burns of grasslands is essential to link flammability traits with fire behaviour. If such a link is demonstrated, the community-weighted mean approach to estimating flammability will be a powerful tool to predict how invasions alter fire regimes.

AUTHORS' CONTRIBUTIONS

This study was conceived by T.J.C. and H.L.B. and designed by T.J.C., H.L.B., J.P.C. and N.J.D. J.P.C., R.P. and N.J.D. collected the data and J.P.C., H.L.B. and N.J.D. ran the analyses. J.P.C., T.J.C., H.L.B. and N.J.D. contributed to writing and revising the manuscript.

DATA ACCESSIBILITY

Raw data for morphological and flammability traits are available in Dryad Digital Repository: https://doi.org/10.5061/dryad.6qg43 (Padullés Cubino, Buckley, Day, Pieper, and Curran, 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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