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Shoot-Level Flammability of Species Mixtures is Driven by the Most Flammable Species: Implications for Vegetation-Fire Feedbacks Favouring Invasive Species

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ABSTRACT

Invasive species can cause shifts in vegetation composition and fire regimes by initiating positive vegetation-fire feedbacks. To understand the mechanisms underpinning these shifts, we need to determine how invasive species interact with other species when burned in combination and thus how they may influence net flammability in the communities they invade. Previous studies using litter and ground fuels suggest that flammability of a species mixture is nonadditive and is driven largely by the more-flammable species. However, this nonadditivity has not been investigated in the context of plant invasions nor for canopy fuels. Using whole shoots, we measured the flammability of indigenous-invasive species pairs for six New Zealand indigenous and four globally invasive plant species, along with single-species control burns. Our integrated measure of flammability was clearly nonadditive, and the more-flammable species per pairing had the stronger influence on flammability in 83% of combinations. The degree of nonadditivity was significantly positively correlated with the flammability difference between the species in a pairing. The strength of nonadditivity differed among individual flammability components. Ignitability and combustibility were strongly determined by the more-flammable species per pair, yet both species contributed more equally to consumability and sustainability. Our results suggest mechanisms by which invasive species entrain positive vegetation-fire feedbacks that alter ecosystem flammability, enhancing their invasion. Of the species tested, *Hakea sericea* and *Ulex europaeus* are those most likely to increase the flammability of New Zealand ecosystems and should be priorities for management.

Key words: *Cytisus scoparius* (Scotch broom); ecosystem engineers; fire behaviour; *Hakea sericea* (prickly hakea); invasive species; New Zealand; nonadditive; *Pinus radiata* (Monterey pine); *Ulex europaeus* (gorse).

Author Contributions SW, GP, and TC developed the research question and designed the experiment; SW and TC collected the data; SW analysed the data; SW led the writing with the assistance of GP and TC.

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INTRODUCTION

Biological invasions pose an ever-increasing threat to terrestrial ecosystems worldwide (Pysek and Richardson 2010). Some invasive species change only the composition of the communities they invade, but those that are 'ecosystem engineers' (sensu Jones and others 1994) can affect the structure and functioning of entire ecosystems (Crooks 2002; Gaertner and others 2014; Levine and others 2003). Such high-impact invasive species drive environmental change through feedbacks that enhance their own success (Gaertner and others 2014). For invasive plant species, reinforcing feedback mechanisms include the alteration of fire regimes, nutrient cycling and nitrogen fixation, soil biota, and seed bank composition (Brooks and others 2004; Gaertner and others 2014; Reinhart and Callaway 2006; Stevens and Beckage 2009; Vinton and Goergen 2006).

Among the most significant ecosystem-altering invasive plants are those that alter fire regimes (Brooks and others 2004; Gaertner and others 2014), a process that has been documented in a variety of ecosystems (Downey and Smith 2000; Fuentes-Ramirez and others 2016; Rossiter and others 2003; Van Wilgen and Richardson 1985). The most common examples involve plant invasions that increase fire frequency and severity, but invaders may also modify ecosystem processes by suppressing fire activity (Brooks and others 2004; Crooks 2002). Invasive species can modify the fire regime by altering the inherent flammability of the available fuel in a system by, for example, changing the relative proportion of live and dead material, as well as the amount and arrangement of fuel loads (Berry and others 2011; Brooks and others 2004; D'Antonio and Vitousek 1992).

The flammability of a plant or plant part can be quantified using a variety of techniques, and numerous studies have measured the flammability of individual species at scales ranging from single leaves to whole plants (for example, Schwilk 2015; Varner and others 2015; White and Zipperer 2010). However, few studies have examined the interactions of species flammability traits when multiple species are burned in combination, yet such studies consistently demonstrate nonadditive effects of the component species on the overall ('net') flammability of a species mixture, driven by the most flammable species (de Magalhaes and Schwilk 2012; van Altena and others 2012). Such nonadditivity may help to explain how some invasive species increase the flammability of the ecosystems they invade and insight into this phenomenon could greatly enhance our understanding of fire regime-altering plant invasions, as well as informing management practices. However, despite the global significance of fire regime-altering invasive plants, the potential nonadditive effect of invasive species on flammability has not been studied. In addition, all previous experimental work burning species mixtures has focussed on leaf litter or other ground fuels (Blauw and others 2015; de Magalhaes and Schwilk 2012; van Altena and others 2012; Varner and others 2017; Zhao and others 2016), and these findings may not be applicable in situations where fires are driven by elevated canopy fuels, such as in invaded shrublands and early successional forest.

One country where plant invasions of early successional forests and shrublands have changed fire regimes is Aotearoa-New Zealand (NZ). Indeed, the relatively recent and dramatic changes to fire regimes that have occurred since human colonisation, and the successes of exotic pyrophyllic plants (Perry and others 2014), make NZ an ideal context to study potential fire feedbacks associated with plant invasions. Prior to human settlement (c. 1280 AD; Wilmshurst and others 2008), NZ's forests experienced low fire frequencies, with recurrence times in the order of centuries to millennia (Ogden and others 1998), yet today wildfires are comparatively frequent, with approximately 3000 wildfires burning around 6000 ha of land annually (Anderson and others 2008). Of these fires, 40% were shrubland (scrub) fires, 54% were grass, and 6% were in mature forest. Shrubland fires can burn with high spread rates, are driven by elevated canopy fuels, and will consume entire plants (Anderson and Anderson 2010). The flammability of New Zealand's native forests largely follows a hump-backed or declining relationship with forest age, peaking in early succession 50–100 years following forest disturbance as shrubland communities, which are typically dominated by flammable Myrtaceous species such as *Kunzea robusta* and *Leptospermum scoparium* (Perry and others 2014; Wyse and others 2016). This relationship is driven by changes to the structure and composition of the available vegetative fuel, and accompanying microclimatic changes, rather than alterations to fuel load (that is, biomass) (Perry and others 2014; Tepley and others 2016). This hump-backed relationship generates the potential for a positive vegetation-fire feedback, whereby changes to species composition that alter the fire regime, particularly fire frequency, can become self-reinforcing, especially when plant invasions have occurred (Kitzberger and others 2016).

Invasive plants, including *Hakea* spp., *Pinus* spp., and *Ulex europaeus,* can rapidly colonise recently burned areas through regenerative adaptations such as serotinous aerial seedbanks or resprouting, traits largely absent from NZ's indigenous flora (Kitzberger and others 2016; Perry and others 2014; Sullivan and others 2007). These invasive species may also increase the flammability of the early successional shrubland communities they invade (Perry and others 2014), as species such as *Hakea sericea* and *U. europaeus* are among the most flammable species assessed to date in NZ (Wyse and others 2016). Fire-adapted invasive species will, therefore, be favoured by recurrent fire, which, in turn, enhances their invasion and may even act to stall succession as dense stands become self-sustaining (Perry and others 2014). These dynamics can be exacerbated by the effects of invasive mammals (Perry and others 2015; Richardson and others 2014) and other edaphic controls, both of which interact with fire. For example, browsing pressure by introduced mammals such as red deer (*Cervus elaphus*) on palatable mature-forest canopy trees can lead to arrested successions that maintain communities in the more-flammable early successional states (Richardson and others 2014). Edaphic effects are evident in areas such as Great Barrier Island (northern NZ), where invasive fire-tolerant taxa such as *H. sericea, Hakea gibbosa, Erica lusitanica,* and *Pinus radiata* have captured denuded sites on recurrently burned ridges, whereas in neighbouring gullies post-fire succession towards native forest has proceeded more rapidly (Perry and others 2010). A similar dynamic is exhibited by *Hakea salicifolia* in Abel Tasman National Park (northern South Island, NZ), which performs well on degraded soils and is likely to be favoured by future fire (Williams 1992). Analogous patterns involving similar invasive plant species have been observed in other parts of the world where fire has not been a common natural disturbance agent, including in Chile (Kitzberger and others 2016) and Hawaii (Smith and Tunison 1992).

To predict how invasive species will influence the flammability of the communities they invade, we need to understand how they interact with other species to affect community-level flammability. In this study, we burned two-species mixtures of 70-cm terminal shoots from six NZ indigenous and four invasive species that collectively span the range of flammability as determined by Wyse and others (2016). The method we used is explicitly designed to account for shoot architecture (Jaureguiberry and others 2011) and correlates well with observed vegetation flammability in the field

(Wyse and others 2016). The invasive species we consider are all common invaders of ecosystems within and beyond NZ. Based on previous studies of mixed-species flammability that used different plant components to the present study, we hypothesised that the most flammable species in any mixture will determine the net flammability of the species pairs. Thus, we expect that the net flammability of species in combination will be nonadditive. If net flammability is additive, the measured flammability variables for a species combination will be the mean of the component species when burned individually. All other outcomes would represent nonadditive (either subadditive or super-additive) flammability. Our study aims to provide insights into the mechanisms by which pyrophyllic exotic species affect the flammability of the ecosystems they invade. These results will enhance our understanding of the impact of invasive species on ecosystem fire dynamics and as such should help inform management practices and the development of predictive and conceptual models.

MATERIALS AND METHODS

Sample Collection

We collected samples from six NZ indigenous (*Coprosma robusta, Dodonaea viscosa, Kunzea robusta, Leptospermum scoparium, Melicytus ramiflorus,* and *Pomaderris kumeraho*) and four invasive exotic plant species (*Cytisus scoparius, H. sericea, P. radiata,* and *U. europaeus*), with the species selected to span a range of flammability levels according to Wyse and others (2016) (Table 1). All 10 species are woody trees and shrubs common in early successional shrubland communities in NZ (Wardle 1991; Williams 2011). The four exotic species are also all invasive species in other regions of the world, including: Australia (*C. scoparius, P. radiata, U. europaeus*); Canada (*C. scoparius, U. europaeus*); Chile (*C. scoparius, P. radiata, U. europaeus*); Portugal (*H. sericea*); South Africa (*C. scoparius, H. sericea, P. radiata, U. europaeus*); and the USA (*C. scoparius, U. europaeus*) (Becerra and Montenegro 2013; Brunel and others 2010; Richardson and Rejmanek 2011).

The samples that we used in the flammability trials consisted of a 70-cm-long terminal branch representative of the individual from which it was collected (following Jaureguiberry and others 2011; Wyse and others 2016). One sample was taken per individual, with 36 samples collected per species for the indigenous species and 48 samples collected per species for the invasive species. The

Table 1. Plant Species Included in This Study

Species	Species code	Family	Origin	Flammability category
Cytisus scoparius (L.) Link	CYTsco	Fabaceae	Exotic	Moderate/high
Hakea sericea Schrad. & J.C.Wendl.	HAKser	Proteaceae	Exotic	High
Pinus radiata D.Don	PINrad	Pinaceae	Exotic	Moderate
Ulex europaeus L.	ULEeur	Fabaceae	Exotic	Very high
Coprosma robusta Raoul	COProb	Rubiaceae	Indigenous	Low
Dodonaea viscosa Jacq.	DODvis	Sapindaceae	Indigenous	Moderate
Kunzea robusta de Lange & Toelken	KUNrob	Myrtaceae	Indigenous	Moderate/high[a]
Leptospermum scoparium J.R.Forst. & G.Forst.	LEPsco	Myrtaceae	Indigenous	High
Melicytus ramiflorus J.R.Forst. & G.Forst.	MELram	Violaceae	Indigenous	Low/moderate
Pomaderris kumeraho A.Cunn.	POMkum	Rhamnaceae	Indigenous	High

Taxonomy and indigenous range follows the New Zealand Plant Conservation Network (see: http://www.nzpcn.org.nz). Flammability category determined by Wyse and others (2016).
[a]*Wyse and others (2016) collected these samples prior to recent taxonomic revision of the K. ericoides species complex (de Lange 2014), and as such they were referred to under the previous nomenclature (Kunzea ericoides (A.Rich) Joy Thomps.). We cannot determine if this was the same, or a different species to that burned in the present study; however, K. robusta is the most abundant and widespread of the revised taxa.*

sampled individuals were all healthy, not visibly water-stressed at the time of sampling, and reproductively mature as evidenced by the presence of reproductive structures. Samples were stored for between 1 day and 2 weeks in sealed plastic bags at 8°C prior to burning. The duration of storage was randomised among samples and species, and no relationships were found between sample water content and storage time for any species ($R^2 < 0.06$, $P > 0.05$ in all cases) nor did any samples develop mould while in storage.

Flammability Measurements

Thirty-four different species combinations were burned, with each trial consisting of two samples. Six replicates were burned for each combination, following Jaureguiberry and others (2011). Ten of the combinations were control burns for each species and consisted of two samples of the same species. We used two samples to ensure that a similar amount of biomass was used for the single-species controls and the two-species mixes. The remaining 24 combinations were all possible indigenous-invasive species pairs. These combinations of indigenous and invasive species all occur in NZ ecosystems.

To measure shoot flammability, we largely followed the methods described by Jaureguiberry and others (2011) and Wyse and others (2016), who used a custom-built portable device constructed from a 85 × 60 cm barrel cut in half and arranged horizontally on four metal legs. We used the same device as Wyse and others (2016), which was built following the specifications of Jaureguiberry and others (2011), adjusted to meet NZ safety standards

(see Wyse and others (2016) for further details). This method was advocated by Perez-Harguindeguy and others (2013) in the most recent plant functional trait 'handbook' and was promoted by Schwilk (2015) as a rapid means of quantifying the crown flammability of many species, albeit with less precision than other laboratory methods. To date, the method has been used by Burger and Bond (2015), Calitz and others (2015), Wyse and others (2016), and Battersby and others (2017) to measure the flammability of many species burned singly. Wyse and others (2016) found a strong correlation between flammability rankings obtained using this method and rankings derived from the expert opinion of fire managers based on their observations of plant flammability in the field (Fogarty 2001); nevertheless, the method is still laboratory rather than field-based and the results should be interpreted with this in mind.

Following the protocol developed by Wyse and others (2016), all samples were air-dried at room temperature for 24 h, in order to match the ignition source to the moisture content of the material being tested (White and Zipperer 2010). As discussed by Wyse and others (2016), pilot burning trials showed that only the most flammable species consistently ignited on our device when burned immediately after collection, which meant that we could only measure relative differences in flammability for those few most flammable species. Thus, all samples were air-dried at room temperature for 24 h prior to burning to enable a wider range of species to be ignited by the blowtorch, and so allow a representative assessment of their comparative flammability; an extended discussion of this method is provided in Appendix 1. Sam-

ples were not completely dried prior to burning because between-species differences in fuel moisture content is an important component of the inherent differences in species relative flammability (Perez-Harguindeguy and others 2013). The burner heated the grill to a temperature of approximately 150°C and remained on for the duration of the experiment. Grill temperatures ranged between 100 and 160°C during the experiments. Wyse and others (2016) described a similar temperature range and found no relationships between grill temperature and any of the measured flammability variables or their overall flammability index across the 60 species they assessed.

Prior to burning, each individual sample was measured (maximum length, width, height) and weighed, using a spring balance (precision: 1 g); dimensional measurements and weight were used to calculate bulk density, and weight was used to determine the relative biomass contributions of each sample to the total burn biomass. Samples were placed on the grill horizontally and preheated for 2 min, following Jaureguiberry *and others* (2011) and Wyse and others (2016), to mimic the radiative preheating effect ahead of a fire front (Burger and Bond 2015; Jaureguiberry and others 2011), albeit at a lower heat than a wildfire. Following study of the arrangement of neighbouring plants in the field, we determined that the best method to mimic natural shoot arrangements was to place the two samples in each trial adjacent to each other on the grill (Figure 1). This arrangement provided both samples with an equal opportunity to ignite. Once arranged on the grill, the maximum length, width, and height of the combined samples were measured to enable calculation of gross sample volume and thus bulk density for the combined

Figure 1. Samples of *Hakea sericea* and *Kunzea robusta* arranged on the grill. The gas burner beneath the grill is preheating the samples prior to ignition of the blowtorch.

samples per trial. Following the preheating period, the blowtorch was turned on for 10 s to ignite the samples. Ignition speed (ignitability) was recorded as the time at which the first sample in each trial started flaming. Ignition speed ranged from 1 to 10 s, but, regardless of ignition speed, the blowtorch remained on for the full 10 s for all burns. Measurements of other flammability variables followed Wyse and others (2016) and started immediately after the blowtorch was turned off. These variables were the length of time the sample burned (sustainability), the maximum temperature reached by the burning sample (combustibility), and, once burning was complete, a visual estimation of the percentage of the original total biomass that was consumed during the burn (consumability). We inverted ignition speed such that a value of ten denoted the fastest time to ignition and one the slowest. Where both samples failed to maintain flaming ignition once the blowtorch was turned off, they were considered to have not ignited. These non-ignitions provide valuable information about the flammability of the relevant species and combinations, and as such the burns that failed to ignite were included in the statistical analyses, using values of zero for all four variables.

Subsamples were taken from each sample and fresh mass (FM) at the time of burning measured. The subsamples were then oven-dried at 65°C for 48 h to determine dry mass (DM). Moisture content (MC; %) on a dry mass basis of the subsamples at the time of burning was calculated following Behm and others (2004). Moisture content per burn was then calculated as the weighted average of the moisture content of the two samples, based on their pre-burn weights.

Bulk density (BD; $kg\,m^{-3}$) was calculated by dividing total dry biomass (kg) by gross volume (m^3), with sample volume calculated following the equation for a cone with an ellipse as its base (equation 1). Dry biomass per sample was calculated from the pre-burn weight using the subsample's moisture content as a calibration factor to convert fresh sample biomass to its approximated dry biomass. Bulk density was calculated per sample and per trial.

$$BD = 12 \times \frac{drybiomass}{\pi \times width \ \times height \times length} \quad (1)$$

Statistical Analyses

We used principal components analysis (PCA) to synthesise flammability patterns among species and species combinations using burn time, maximum

temperature, ignition speed, and burnt biomass for every sample. Correlation vectors for bulk density, dry biomass, and moisture content (measured per burn) were projected onto the PCA ordination space to investigate correlations between these explanatory variables and overall flammability (envfit command in the vegan R library version 2.4-2 [Oksanen and others 2017], with significance assessed using permutation tests). We used position on PCA axis one (which captured 71% of the variance) as an overall index of flammability for the species and combinations tested.

We assessed the relative contributions of each species to the mixed-burn results by examining the two-dimensional relationships in ordination space among the flammability of mixed-species burns and their component single-species burns, similar to the approach of Varner and others (2017). By extension, this enabled us to assess the nonadditivity of the net flammability of the species combinations. For each species combination, we calculated the Euclidean distances between: (1) the mean ordination coordinates (that is, PCA scores) of the mixed-species burns and those of their component single-species burns, and (2) the two single-species burns themselves. For each species pairing, we identified the more and less-flammable species in the pair based on the control burn results. We quantified the mean degree of nonadditivity in the mixed-species results for each species combination by subtracting the Euclidean distance in ordination space between the mixed-species burn and the more-flammable single-species burn from this same ordination distance for the less-flammable species (Figure 2). If the net flammability of a mixed-species burn was additive, these values should be approximately zero, whereas if it was nonadditive and more strongly influenced by the more-flammable species (super-additive), then the values should be positive (and vice versa for a sub-additive effect; Figure 2). A t test was performed on these values from the 24 species pairings to test whether they were collectively significantly above zero, and thus, the hypothesis that flammability of a mixed-species pairing is driven by the more-flammable species of the pair. We then used a linear model to assess the relationship between the degree of nonadditivity in a mixed-species burn and the Euclidean distance between the component single species, thereby testing whether the degree of flammability difference between species affects the relative influence of each species on the net flammability of a species combination.

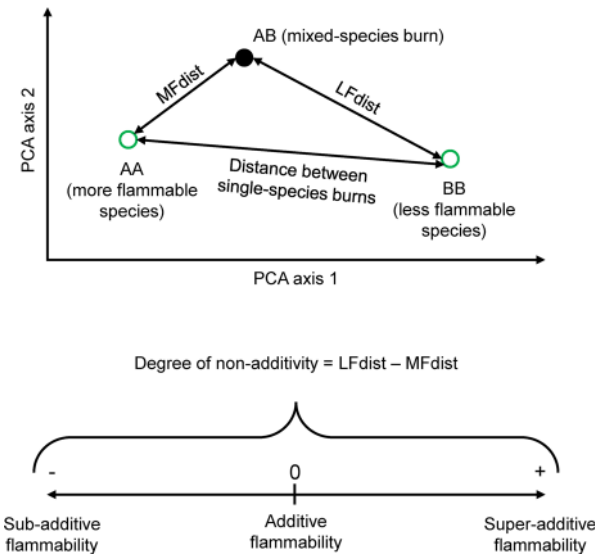We also investigated the contributions of each species to the mixed-burn results with a series of

Figure 2. Schematic overview showing how the degree of nonadditivity in the mixed-species burn results was determined from the mean locations of mixed- and single-species combinations in ordination space. MFdist = the distance between the more-flammable single-species and the mixed-species burn results, LFdist = the distance between the less-flammable single-species and the mixed-species burn results.

linear regression models, which included a term to account for potential effects of different species relative biomass (Quinn and Keough 2002). Regressions (of the form AB $\sim$ AA + BB + biomass proportion [A in AB]; for species A and B when burned as single- and mixed-species sample pairings) were performed for each of the four flammability components, as well as the scores for PCA axis one (that is, overall flammability index). For each flammability component, we modelled the mixed-burn results against the results of the respective single-species control burns, with each species per pair identified as either the most or least flammable species in the pair, based on the control burn results for that flammability component. We evaluated seven regression models for each response variable, encompassing all possible combinations of the three predictor variables. We then used the Akaike Information Criterion (AICc) to rank the models in terms of explanatory power and parsimony (Anderson 2008). All statistical analyses were conducted using R v. 3.1.2 (R Development Core Team 2014).

RESULTS

The species combinations varied considerably in their flammability (Figures 3, 4). The first PCA axis

explained 71% of the variation in the data and was negatively associated with all flammability components (Figure 3). As such, this axis provides an index of overall flammability integrating the four flammability components. The loadings of the four flammability variables were approximately equal on axis one (maximum temperature = -0.51, burn time = -0.44, burnt biomass = -0.53, ignition speed = -0.51). The second PCA axis explained 14% of the variation and had a strong positive correlation with burn time (loading = 0.89) and was weakly negatively correlated with maximum temperature, burnt biomass, and ignition speed (loadings = -0.22, -0.16, and -0.38, respectively; Figure 3). Average moisture content of the samples per burn was significantly correlated with the ordination (envfit: $R^2 = 0.487$, $P < 0.001$) and was positively correlated with the first PCA axis: samples with higher moisture contents were found to
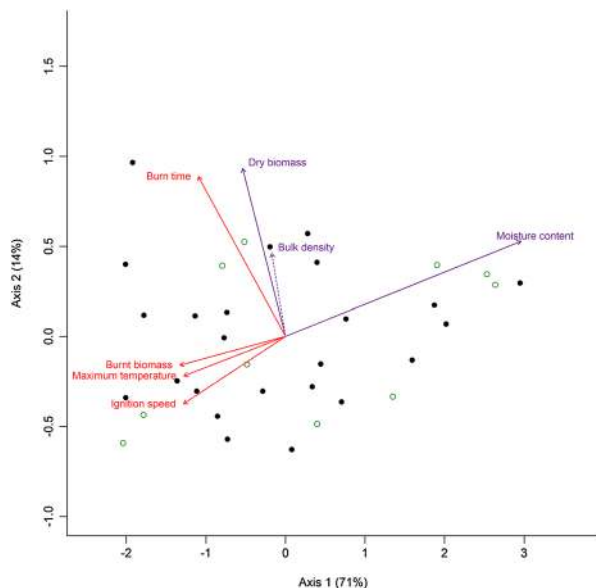

Figure 3. Principal components analysis (PCA) of the four measured flammability traits (maximum temperature, burn time, ignition speed, and burnt biomass). Points indicate the mean scores per species or species combination. Single-species control burns are shown with green, open points; mixed two-species burns are shown with black, closed points. Red vectors (burn time, burnt biomass, maximum temperature, and ignition speed) show the variables used to construct the PCA, purple vectors show three potential explanatory variables (bulk density, dry biomass, and moisture content) fitted on to the PCA scores by the function envfit (R vegan package). For these vectors, a solid line indicates a significant correlation between the variable and the ordination ($P < 0.05$), a dashed line indicates a nonsignificant variable. See Figure 4 for identification of the species and combinations.

have lower flammability. Specifically, moisture content showed a negative relationship with the flammability components burnt biomass, maximum temperature, and ignition speed, which were all closely aligned (Figure 3). In contrast, bulk density and dry biomass per burn were more strongly associated with the second PCA axis and the burn time flammability component (Figure 3); however, these variables explained little of the variation in the ordination (bulk density $R^2 = 0.013$, $P = 0.272$; dry biomass $R^2 = 0.063$, $P = 0.003$). Moisture showed an order-of-magnitude variation across the species (Figure S1a), but there was little interspecific variation in bulk density (Figure S1b). *Melicytus ramiflorus* had the highest average moisture content, followed by *P. radiata*, while *L. scoparium* and *K. robusta* had similarly low moisture contents. Using the position on PCA axis one as an index of flammability, the single-species control burns indicate that *L. scoparium* and *K. robusta* were the most flammable species burned in this study (Figure 4). The least flammable species burned were *M. ramiflorus* and *P. radiata*. Unexpectedly, *U. europaeus*, a species previously recorded as having "very high" flammability (Table 1), showed only intermediate levels of flammability when burned here, ranking fifth in overall relative flammability of the 10 species we assessed (Figure 4).

For the majority of species combinations (20/24; 83.3%), the PCA results suggest that the flammability of a species mixture departs from what would be expected if net flammability were additive. The location in ordination space of a mixed-species combination was consistently closer to the more-flammable species of the pairing (Figures 4, 5). When considering the mean location of each mixed-species burn relative to its component single-species burns (Figure 5), there is clear evidence that the flammability of the mixed-species burns was nonadditive and was driven by the more-flammable species of the pairing ($t = 4.476$, $df = 23$, $P < 0.0001$). There was a strong, positive correlation between the relative influence of the more-flammable species on the mixed-burn results and the magnitude of the disparity in flammability between the two species in the pairing (Figure 5; $R^2 = 0.612$, $P < 0.0001$): that is, the nonadditive effect increases with the difference in flammability between the species being burnt.

There were strong and significant correlations between the flammability variables for the mixed-species burns and the corresponding single-species burns (Table 2). The strongest correlations were for PCA axis one (that is, overall flammability index),
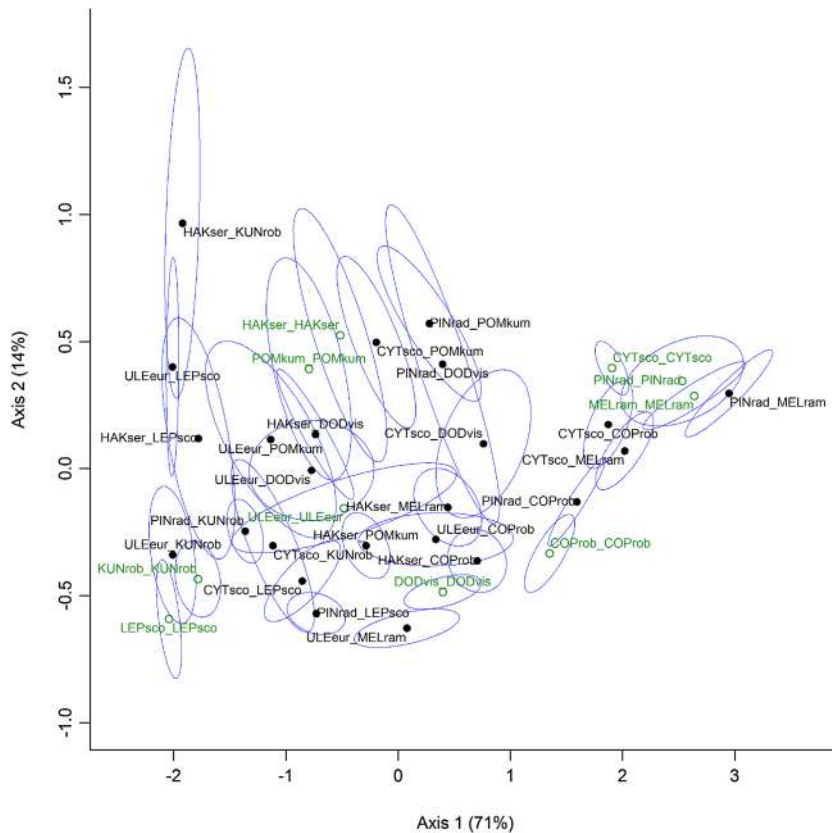
Figure 4. Principal components analysis (PCA) of the four measured flammability traits (maximum temperature, burn time, ignition speed, and burnt biomass). Points indicate the mean scores per species or species combination; ellipses indicate the standard error of the mean. Single-species control burns are shown with green, open points; mixed two-species burns are shown with black, closed points. See Table 1 for definitions of species codes.

burnt biomass, and ignition speed. The more-flammable species per burn was a predictor variable in the top-ranked regression models for all response variables except for burn time, and, when used as the sole predictor variable, explained more than twice the variation in the mixed-burn results than did the less-flammable species for PCA axis one, ignition speed, and maximum temperature (Table 2; Figure 6). The less-flammable species was included in the top-ranked models for burnt biomass, burn time, and PCA axis one. For burn time, both species explained a similar amount of variation in the mixed-burn results when used as sole predictor variables, with the less-flammable species the stronger predictor (Table 2; Figure 6). The fraction of the biomass in the mixed-species burn comprised of the more-flammable species was a predictor in the top-ranked model for burn time only (Table 2).

DISCUSSION

Patterns of Flammability in Species Mixtures

Our results show that the shoot-level flammability of a species mixture is not additive, with the most flammable component driving the net flammability of the combined samples. This outcome is consistent with previous studies based on leaf litter and other ground fuels (de Magalhaes and Schwilk 2012; van Altena and others 2012; Zhao and others 2016). The growing body of work demonstrating this pattern, now across multiple sample types, provides strong evidence for the nonadditive flammability effect and suggests that it is likely to apply in other contexts, such as combinations of entire plants, and potentially even entire plant communities. Our results are, however, laboratory-based: future field-based research should examine the potential for such patterns to scale up to plant communities. We also observed a strong relationship between the size of the nonadditive effect and the flammability difference between the species in the mixture. Zhao and others (2016) hypothesised this relationship, although they attempted to use phylogenetic difference as a proxy for difference in flammability traits, which they did not find to adequately describe inherent flammability differences at the species level. Here, we have shown that as the component species in a mixture become more dissimilar in their flammability, the relative influence of the more-flammable species on the net flammability of the species combination increases.
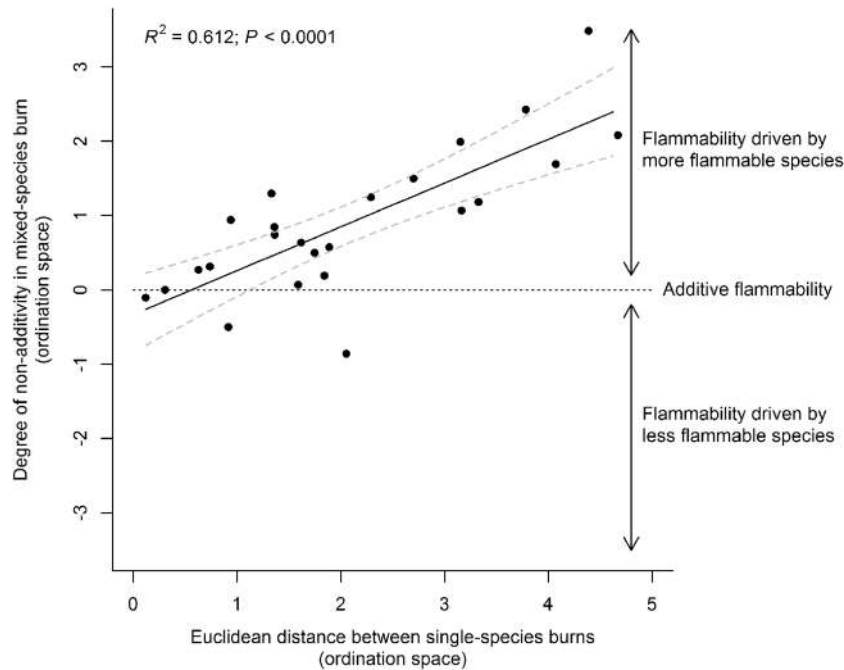
Figure 5. Relationship between the degree of nonadditivity in mixed-species burns and the Euclidean distances in ordination space between the mean coordinates of the two corresponding single-species burns. The degree of nonadditivity was calculated by subtracting the ordination distance between the mixed-species burn and the more-flammable single-species burn from this same ordination distance for the less-flammable species. If net flammability were additive, these two distances would be equal and thus the degree of nonadditivity would approximate zero (black dotted line), while anything else would represent nonadditive flammability. Positive values indicate nonadditive flammability driven by the more-flammable species in each pair; negative values indicate nonadditive flammability driven by the less-flammable species per pairing. Solid black line is a linear model fitted for these two variables, grey dashed lines represent the upper and lower 95% confidence bounds.

However, despite the clear, dominant influence of the more-flammable species in a pair on the overall flammability of a species combination, the relative contributions of the more and less-flammable species per pair differed for the four flammability components that we measured. Examining the relationships between the single- and mixed-species burns for these individual flammability components can help to elucidate the mechanisms causing the observed nonadditivity in the mixed-species burns. That the different individual flammability components behaved in different ways suggests that the interactions among species flammability characteristics are complex. Such an outcome supports the arguments of Pausas and others (2017), Prior and others (2017) and Varner and others (2015) that flammability should not be viewed as a single trait, but rather that its components should be viewed separately as they are not necessarily correlated and there are potentially inherent trade-offs between them. The various flammability components are also con-trolled by different plant traits, and, importantly, have differing ecological impacts. It follows, therefore, that the interactions between the species in a pairing may also differ among flammability components, and that these differences are likely to be ecologically meaningful. Our results indicate that the less-flammable species in a pair does not reduce the ease with which the more-flammable species ignites nor the temperature at which it burns, but it may act to extinguish a fire more quickly than where the more-flammable species was burned in isolation. The more-flammable species of a pairing drives the ignitability and combustibility of the combined samples and has an influence on these flammability components that is disproportionate to its biomass. These results have important implications for plant invasions and, if they hold in field experiments, provide empirical support for conceptual models describing how pyrophyllic invasive plants cause functional and compositional shifts in ecosystems that they invade by altering fire behaviour.

Table 2. Linear Regression Models Investigating Relationships Between Single- and Mixed-Species Burns

Model rank	Predictor variables	Δ_i	w_i	R^2
Burnt biomass (*consumability*)				
1	MF + LF	0.0	0.81	0.896
2	MF + LF + B	2.9	0.19	0.897
3	MF	20.3	0.00	0.724
4	MF + B	20.6	0.00	0.753
5	LF	32.6	0.00	0.541
6	LF + B	35.1	0.00	0.548
7	B	47.8	0.00	0.133
Maximum temperature (*combustibility*)				
1	MF	0.0	0.61	0.704
2	MF + LF	2.5	0.18	0.709
3	MF + B	2.6	0.17	0.708
4	MF + LF + B	5.1	0.05	0.716
5	LF + B	20.7	0.00	0.379
6	LF	23.6	0.00	0.208
7	B	25.1	0.00	0.157
Burn time (*sustainability*)				
1	LF + B	0.0	0.58	0.682
2	MF + LF + B	0.8	0.40	0.713
3	MF + LF	6.7	0.02	0.580
4	LF	9.3	0.01	0.471
5	MF	12.4	0.00	0.399
6	MF + B	13.1	0.00	0.451
7	B	20.8	0.00	0.147
Ignition speed (*ignitability*)				
1	MF	0.0	0.37	0.845
2	MF + B	0.2	0.33	0.861
3	MF + LF	1.1	0.21	0.856
4	MF + LF + B	3.0	0.08	0.864
5	LF + B	35.6	0.00	0.394
6	LF	37.6	0.00	0.256
7	B	42.9	0.00	0.070
PCA axis one				
1	MF + LF	0.0	0.83	0.929
2	MF + LF + B	3.2	0.17	0.929
3	MF	12.5	0.00	0.865
4	MF + B	15.1	0.00	0.867
5	LF + B	46.7	0.00	0.504
6	LF	47.0	0.00	0.431
7	B	59.2	0.00	0.053

Models are ranked according to Akaike Information Criterion (AICc). The mixed two-species burn results were predicted using the respective single-species control burns (MF and LF) and the proportion of the total mixed-burn biomass made up by the more-flammable species (B). The more (MF) and less-flammable (LF) species per pair were determined separately for each component on the basis of the control burn results. PCA axis one represents the overall flammability combining all four components and explained 71% of the variation in the flammability data. The model R^2 values, the differences in AICc from the best model (Δ_i), and Akaike weights (w_i) are shown for each model.

Implications for Plant Invasions

Invasive plants can modify fire regimes and can also be favoured by such changes (for example, Brooks and others 2004; D'Antonio and Vitousek 1992; Levine and others 2003; Mandle and others 2011; Pauchard and others 2008); for example, field studies have demonstrated increases in fire intensity as a result of invasions by grasses (for

example, D'Antonio and Vitousek 1992) and also by shrubs such as *Eupatorium adenophorum* in Chinese forests (Wang and Niu 2016) and *Chromolaena odorata* in South African woodland (te Beest and others 2012). The outcomes of our experiments suggest that where a more-flammable species invades a community composed of less-flammable vegetation the flammable invader is likely to in-
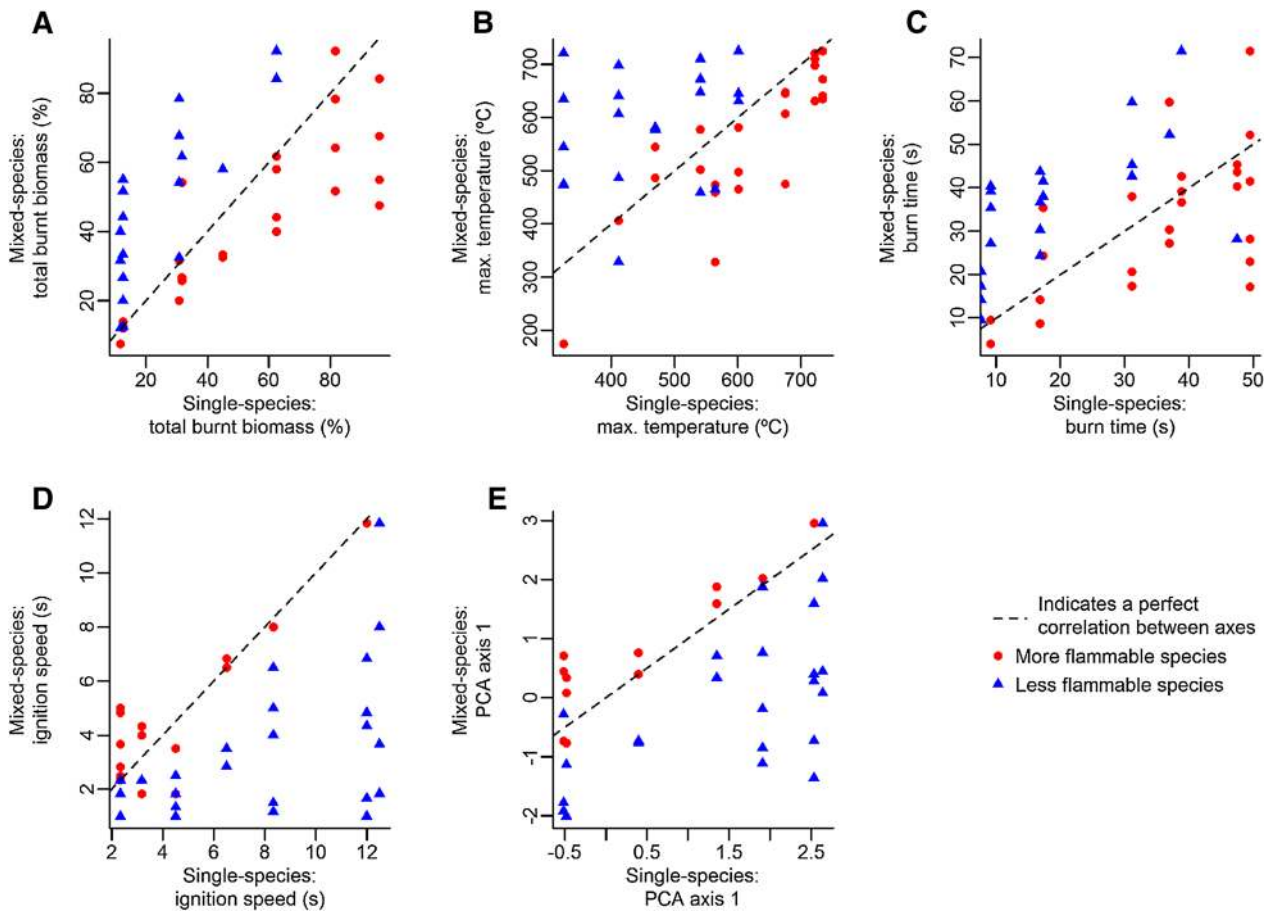
Figure 6. Relationships between the mixed two-species burns and their two associated single-species burns (as presented in Table 2) for the flammability components: **A** total burnt biomass, **B** maximum temperature, **C** burn time, **D** ignition speed, and **E** PCA axis 1. PCA axis one represents the overall flammability combining all four components and explained 71% of the variation in the flammability data. The more and less-flammable species per pair were determined separately for each flammability component based on the control burn results. The dashed line indicates where points would lie in a perfect correlation between the single-species and mixed-species results. An equal contribution of both the more and less-flammable species to the mixed-species results (that is, additivity) would result in this line to falling centrally between the two sets of points (for example, as in part **A**). A close fit between the line and one set of points would indicate nonadditivity, with that set of species (either the more or less-flammable species per pairing) driving the net flammability of mixed-species burns (for example, as in part **D**).

crease the ignitability of the combined vegetation and therefore enhance the likelihood of a fire. Thus, we provide mechanistic insight into fire-vegetation feedbacks during plant invasions. Additionally, our results indicate that a flammable invader may exert the strongest influence on the temperature at which the fire burns, thereby increasing fire intensity over what could be expected if the less-flammable vegetation was burning in isolation. Given the correlation between fire temperature and fire intensity and thus plant mortality (Keeley 2009; Michaletz and Johnson 2007), fires fuelled by pyrophyllic invaders may therefore be more damaging for native plant com-

munities than fires in corresponding non-invaded systems. Through these effects, flammable invasive species may act as ecosystem engineers as discussed by Crooks (2002), driving ecosystem change. In turn, the effects of these species on ecosystem properties may facilitate further plant invasions. Conversely, and highlighting the multifaceted nature of flammability, our results indicate that the less-flammable species of a mixture is the main driver of burn time, albeit with less dominance than the influence of the more-flammable species on ignition speed and fire temperature. This result has implications for fire residence time, suggesting that the relative flammability of resident species in

a given ecosystem might influence fire residence time following the invasion of a highly flammable species, reducing it from that expected if the invader were burning in isolation. Fire residence time is an important predictor of plant mortality from fire, as mortality results from the integration of time and heat flux; thus, slow, cooler, fires can be more lethal than fast, hot ones (Michaletz and Johnson 2007). Field-based experimentation is required to understand how the confounding effects of the more-flammable species on fire temperature and the less-flammable species on fire residence time interact to influence patterns of plant mortality.

For New Zealand ecosystems, we now have empirical, laboratory-scale, evidence supporting the hypothesis that pyrophyllic invasive species could cause shifts in vegetation composition and fire regime by reinforcing vegetation-fire feedbacks (Kitzberger and others 2016; Perry and others 2014). Of the invasive species included in our experiments, those most likely to trigger shifts in the fire regime are *U. europaeus* and *H. sericea*: these species were the most flammable invasive species measured in this study and among the most flammable species measured by Wyse and others (2016). *Ulex europaeus* and *H. sericea* may increase the flammability components of ignitability and combustibility in less-flammable ecosystems, such as those dominated by *Coprosma* spp. or *Dodonaea viscosa*, thereby changing the nature of wildfires in these communities. Thus, in such ecosystems, *U. europaeus* and *H. sericea* may be active drivers of community change. The direct effects of fire may also interact with other effects of these invasive species such as the influence of *U. europaeus* on nitrogen cycling (Magesan and others 2012), and on patterns of seed dispersal by birds (Sullivan and others 2007). These findings may extend to other settings where these species invade other less-flammable communities and may also be directly applicable wherever they invade communities containing the widespread species *D. viscosa*. Conversely, where *U. europaeus* and *H. sericea* co-occur in NZ with the most flammable indigenous species, *Leptospermum scoparium* and *Kunzea robusta*, our results suggest that they do not amplify the flammability of the vegetation. In such situations, pyrophyllic invasive species may simply benefit from recurrent fire, outperforming indigenous species at the regeneration stage and thereby more passively altering successional pathways and contributing to community change. This passive ('passenger'; MacDougall and Turkington 2005) dynamic has been observed in invasions of these

species in fire-prone ecosystems, such as *H. sericea* invasion of the South African Fynbos (Moodley and others 2014) and *U. europaeus* in California, USA (Keeley 2001).

In contrast to these flammable invasive species, and despite suggestions to the contrary (Mandle and others 2011), we have no evidence that live *C. scoparius* will increase community-level flammability when it co-occurs with the common indigenous early successional species we investigated. Although regeneration of *C. scoparius* is likely to be favoured by fire relative to many NZ native species, due to its resprouting capability and extensive and long-lived soil seed bank (Bossard and Rejmanek 1994), other feedback mechanisms, such as soil nutrient cycling, may be more important in facilitating the invasion process for this species (Haubensak and Parket 2004). Further research in the field may provide greater understanding of the mechanisms of invasion in this species and the role of fire.

Our results for *P. radiata* were similar to those for *C. scoparius*: *P. radiata* is adapted to recurrent and predictable crown fires (He and others 2012; Stephens and others 2004), yet our results do not suggest that it is likely to drive a vegetation-fire feedback dynamic in early successional shrubland. Consistent with Wyse and others (2016), shoots of *P. radiata* were among the least flammable species that we burned. However, Franzese and Raffaele (2017) found fire to be a key driver of serotinous *Pinus* invasions (such as *P. radiata*) in the Southern Hemisphere, and *Pinus* species are known to promote fire in other ecosystems (Cobar-Carranza and others 2014; Taylor and others 2017). It may be that it is the accumulation of flammable leaf litter and other dead material (Berry and others 2011), rather than the flammability of live shoots, that hold the potential to entrain a positive fire-vegetation feedback. Alternatively, in NZ *P. radiata* often occurs as one of a suite of invaders that enter an ecosystem following fire and then persist through recurrent burning (for example, as described by Perry and others 2010). In such situations, more-flammable invaders such as *H. sericea* and *U. europaeus* may facilitate the *P. radiata* invasion through their influence on the fire regime (that is, it is a 'passenger' invader; sensu MacDougall and Turkington 2005). Further research under field conditions should be undertaken to test these hypotheses and predictions.

Finally, our results demonstrate that not only does the more-flammable species drive the net flammability of a species mixture, but also that the influence of this species is disproportionate to its

relative sample biomass. These results suggest that even at comparatively low biomasses highly flammable invaders may influence vegetation flammability, particularly ignitability. This increased ignitability is likely to be particularly important in the early stages of an invasion: the biomass of a pyrophyllic invasive species could be relatively low and yet still have sufficient influence to trigger a shift in fire regime and vegetation composition. At later stages of an invasion, however, this effect will likely be eclipsed by the high biomass of the invasive species in an ecosystem, and the resultant influence of changes in fuel loads on fire dynamics (Brooks and others 2004; Mandle and others 2011). Although this hypothesis requires empirical testing in the field, it does emphasise the importance of controlling flammable invasive species even in the early stages of invasion when their biomass is comparatively low.

CONCLUSIONS

Our study demonstrates that, at the shoot level, flammability is not additive and that the most flammable species determines the overall flammability of a combination of samples, independent of sample biomass. Additionally, the strength of nonadditivity in a mixed-species burn was positively correlated with the difference in flammability between the two component species. However, not all flammability components behaved in the same manner. Ignitability (ignition speed) and combustibility (maximum temperature) were both strongly determined by the more-flammable species per pair, but both species contributed equally to consumability (burnt biomass) and sustainability (burn time). Our findings help to explain the mechanisms by which some invasive species alter ecosystem flammability and generate positive vegetation-fire feedback loops that enhance their success. In the context of invasive plants in New Zealand, we have demonstrated that, in terms of shoot flammability, *H. sericea* and *U. europaeus* are likely to increase the flammability of ecosystems they invade, whereas *C. scoparius* and *P. radiata* are less likely to do so. Despite fire being a factor enhancing the regeneration of all four of these species, we only have evidence to suggest that reinforcing fire feedbacks driven directly by shifts in flammability are likely to occur for *H. sericea* and *U. europaeus*. However, further research at the scale of whole plants under field conditions, and incorporating the leaf litter and other dead material that accumulates beneath some of these species, is required to evaluate these hypotheses.

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