

Home and away: biogeographical comparison of species diversity in *Thymus vulgaris* communities

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Abstract We examined the effects of *Thymus vulgaris* (common thyme) on associated vegetation in both its native and introduced range. We compared local (within-community) and landscape (among-community) species richness and community composition between thyme-dominated communities in France (native range) and New Zealand (introduced range). From 7 native sites (France) and 10 introduced sites (New Zealand), all plant species present in 20 (New Zealand, 25 in France) randomly placed 100 cm × 50 cm quadrats were recorded. Local species richness was determined by calculating mean species richness/quadrat inside and outside thyme-

dominated plant communities and tested for significance with the factors of range and across sites. Landscape scale differences were determined by comparing total species richness inside and outside thyme communities across all sites from both ranges. Species differences between native and introduced thyme communities were analysed using similarity percentages. We found native range microenvironments with thyme harbour more species than microenvironments without thyme and this pattern was reversed in the introduced range with thyme decreasing local species richness. A higher percentage of shared species occurred both with and without thyme in the native range compared to the introduced range. In both ranges and across all sites (except for one) species composition of thyme-associated plant communities differed from communities without thyme. Native plant communities with thyme were more similar in species composition than plant communities without thyme, but in the introduced range species composition was most similar in plant communities without thyme. These results suggest thyme's ecosystem engineering consequences are context-dependent. Thyme may filter out competitive species that could negatively impact local species richness in its native range, but when introduced to a disturbed landscape in a novel biogeographic region, thyme reduces local species richness.

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Introduction

Invasive plants that reduce local species richness and abundance and homogenise biological communities can irrevocably alter ecosystem services (Pejchar and Mooney 2009; Winter et al. 2009; Pyšek et al. 2012). Some invasive introduced plant species occur at low densities in their native ranges but become dominant community members existing in higher densities in their introduced ranges (Day and Buckley 2011; Schaffner et al. 2011), but this pattern is not universal with many species displaying no differences in abundance between their home and introduced ranges (Firn et al. 2011; Parker et al. 2013).

A number of biogeographical comparisons have generated hypotheses for why native species that are not dominant in their native range become dominant in their introduced range [e.g. enemy release hypothesis (ERH), evolution of increased competitive ability (EICA), novel weapons hypothesis (NWH); reviewed by Inderjit 2005; Catford et al. 2009]. However, being able to predict which species will exhibit increased performances in their away ranges (and potentially become invasive), and which species will perform similarly between the home and away ranges continues to challenge ecologists. Investigating how dominant native species that function as ecosystem engineers in their native range modify plant communities when introduced to disturbed landscapes in a novel biogeographic region may increase our understanding of the complex effects of introduced species on plant community diversity.

The concept of ecosystem engineering comprises both the processes by which organisms modulate environmental conditions and resources (e.g. light, temperature, nutrients, carbon and water), and the context-dependent consequences of these abiotic changes for biota (Jones et al. 1994, 1997; Wright and Jones 2004; Jones and Gutiérrez 2007). One consequence of engineering processes is the enhancement of species richness at both local (“patch”) and landscape scales. This occurs firstly by ameliorating the local environment, and secondly by generating a mosaic of microhabitats that increase niche diversity (thereby increasing environmental heterogeneity) across a landscape (Schöb et al. 2012; Kikvidze et al. 2015).

One such engineer species is the Mediterranean aromatic shrub *Thymus vulgaris* L. (wild thyme)

which dominates species-rich garrigue vegetation. Wild thyme is comprised of several distinct chemical types (chemotypes) that are characterised by the dominant monoterpene (either phenolic or non-phenolic) in their essential oil (Gouyon et al. 1986; Keefover-Ring et al. 2009). Phenolic thyme dominates in areas with a typical Mediterranean climate where summers are hot and dry and winters are mild, compared to non-phenolic thyme which typically dominates in sites with stronger freezing temperatures in winters (Thompson et al. 2007). Monoterpenes enter the soil via leaf litter and are known to have direct allelopathic effects on other plants (e.g. Tarayre et al. 1995; Linhart and Thompson 1999; Linhart et al. 2015), and also to indirectly modify the availability of nutrients via their impact on the microbial soil community (White 1994; Paavola et al. 1998). Soil under thyme plants is richer in organic C and N than soil from microenvironments where thyme is absent (Ehlers and Thompson 2004), and the growth form of thyme as a small bush creates shade for small herbs. However, the phenolic and non-phenolic chemotypes differ in their allelopathic effects on associated organisms with the phenolic chemotypes being more toxic to microorganisms and more inhibiting to seed germination and plant growth than non-phenolic ones (Tarayre et al. 1995; Linhart and Thompson 1999; Linhart et al. 2015). In a recent study, Ehlers et al. (2014) showed that, despite the allelopathic effects of its monoterpenes, wild thyme in its native range had a positive effect on plant species richness, both at the local and landscape level. Not only was species richness higher in local microenvironments harbouring thyme, but species composition differed between micro-environments with and without thyme thus also increasing species richness among micro-environments across the entire landscape. Ehlers et al. (2014) also found that the impact of native thyme on local species richness differed among thyme chemotypes. For phenolic thyme plants, the positive effect of thyme on species richness was suggested to be via indirect facilitation such as “competitive exclusion”, as phenolic thyme reduced cover of an abundant and competitively strong grass.

Thymus vulgaris was likely introduced into New Zealand around the time of the 1860s gold rush in Central Otago (Thomson 1922). The invaded area has a complex history of human disturbance since the colonisation of New Zealand by European settlers in

the 1850s (Walker et al. 1995). Colonisation resulted in the regular occurrence of fires (to open up the land for pastoral use), sheep grazing, fluctuating rabbit populations (introduced in the 1870s) and the introduction of many exotic plant species. Much of the mid- to high elevations remain in pastoral use today (O'Connor 1986) and it is in these disturbed pastoral habitats that thyme has literally 'taken to the hills' and now densely covers several thousand hectares (Wilkinson et al. 1979; Morgan 1989; Nielsen et al. 2015b).

To date, only phenolic chemotypes (i.e. producing either carvacrol or thymol as the main monoterpene) of thyme have been reported in New Zealand populations (Morgan 1989; Nielsen et al. 2014a). Studies of phenolic chemotypes in New Zealand have found lower organic P and N in soil under thyme than outside thyme (Nielsen et al. 2014b), and similar to in its native environment, higher organic C in soil under thyme. However, unlike in its native range (Linhart et al. 2015), soil from under thyme had no effect on germination rates or seedling growth for either native or exotic grasses (Nielsen et al. 2015a) and species richness inside thyme-dominated communities is lower than outside (Nielsen et al. 2015a). Thus, in contrast to thyme's facilitative role in its native range, thyme decreases local species richness in its introduced range (Nielsen et al. 2015b).

Here we explore in more detail the differences in the impact of an ecosystem engineer on associated vegetation in its native and introduced range. By examining how thyme influences species richness and community diversity in both its native and introduced ranges, we may gain valuable insight into the sources of variation in the magnitude of engineering impacts across ecosystems useful for predicting the function of ecosystem engineers in nature. As only phenolic chemotypes are found in the introduced range, we restrict our comparison to native range communities dominated by thyme of a phenolic (i.e. either carvacrol or thymol) chemotype and include data from another three phenolic native range sites in addition to the four reported in Ehlers et al. (2014). Specifically we ask: (1) does thyme's impact on local (within-community) species richness vary between its native and introduced range? And (2) does thyme's influence on among-community species richness and plant community composition vary between its native and introduced range?

Materials and methods

Study sites

In France, seven sites were chosen within a 10 × 10 km region in the valley of St Martin de Londres approximately 25 km north of Montpellier where thyme dominates the low-growing, mainly herbaceous, species-rich vegetation known as "garrigue" (see Ehlers et al. 2014 for a detailed map of study region). Each site was typical of Mediterranean region thyme-dominated communities, where thyme produces a phenolic (thymol or carvacrol) chemotype (Thompson 2005). A subset of phenolic thyme community plot data for four of the seven French sites was re-used from a larger dataset containing both phenolic and non-phenolic thyme communities analysed in a related study (Ehlers et al. 2014). In New Zealand, ten sites from within the invaded region of Central Otago, southern South Island (168°47'–169°32'E and 44°59'–45°37'S) were selected to ensure the extent and geographic variability of thyme's habitat was representatively sampled (see Fig. S1 of Online Resource 1 in Supporting Information). The invaded areas are contained within an area approximately 60 km × 70 km and site selection process included visual reconnaissance, review of aerial photographs held by the Otago Regional Council, and consultation with private landowners. Each site contained clearly delineated thyme-invaded plant communities of at least 30 m × 20 m with distinct edges at the base of the slopes where plant community composition transitioned from being dominated by thyme to becoming a mix of mainly exotic grasses and herbs. Management history is not known in detail but the region has been burnt and heavily grazed in the past although current levels of both are much more lenient. (See Figs. S2, S3 of Online Resource 1 for photos of representative sites from both the native (France) and invaded (New Zealand) range).

Vegetation sampling

Sampling took place during summer for each location (May–June 2010 and May–June 2011 in Montpellier, and December 2009 in New Zealand). Twenty (New Zealand, 25 in France) 100 cm × 50 cm quadrats were randomly placed both inside and outside (at least 1 m from a thyme plant) of the thyme-dominated communities. All plant species present in each quadrat

were identified and recorded. Botanical nomenclature follows Edgar and Connor (2000).

Data analysis

Local species richness

Each data set included a large number of rare species, and because rare species may create a bias for presence/absence data, we compared analyses of reduced data sets that only included those species found in at least 10 quadrats to analyses of the full data set. Both sets of data produced similar results and thus we report the reduced data set here. There is some debate as to whether presence of species rather than their abundance drives community assembly in broad scale vegetation surveys (Bastow Wilson 2012; but see Firn et al. 2011). However, presence/absence data enabled the distribution of species and community assembly of multiple sites to be surveyed within the time constraints of the study.

We compared mean species richness/quadrat inside and outside thyme-dominated plant communities and tested if these differences were consistent with range and across sites with thyme presence treated as a factor. The experimental design consisted of 3 factors: range (R, 2 levels, fixed), site (S, 17 levels, nested within Range, random), thyme (T, 2 levels, fixed), and with $n = 20$ (NZ) and $n = 25$ (France) observations per combination of factor levels. The interaction terms of range \times thyme and site (range) \times thyme were included in the analyses. For the introduced range (New Zealand), comparisons were made based on the assumption that the species richness and species composition of uninvaded and invaded communities was similar prior to invasion (Vilà and Gimeno 2007) and this was corroborated by anecdotal information from landowners.

All tests were carried out using a permutational procedure (9999 permutations) as described for PERMANOVA below. Due to the unbalanced design ($n = 25$ for French sites, $n = 20$ for New Zealand sites), variance was partitioned using Type III for the calculation of the sum of squares (SS). This approach ensures complete orthogonality of all the data as it fits each factor to the ANOVA model only after taking into account all of the factors in the full model (Anderson et al. 2008). Where appropriate, significant terms were investigated with a posteriori pairwise

comparisons. Factorial univariate ANOVA tests of species richness were carried out using PRIMER v6 based on Euclidean distance. The F -ratios used for tests done this way are equivalent to those of traditional ANOVA (Anderson 2001).

Among-community diversity

We compared total species richness inside and outside thyme communities across all sites from both ranges. To test for differences in percent shared species between thyme and no-thyme communities in the native (French) range compared to the introduced range, we used the nonparametric Kruskal–Wallis test (JMP version 9, SAS Institute, Inc, Cary, NC). To compare thyme's impact on plant community diversity and to determine if these differences were consistent between ranges and across sites we carried out a distanced-based permutational multivariate ANOVA (PERMANOVA; McArdle and Anderson 2001) based on Simpson's measure of compositional dissimilarity generated using the software package Betapart (Baselga et al. 2013). The study design consisted of 3 factors: range (R, 2 levels, fixed), site (S, 17 levels, nested within Range, random), thyme (T, 2 levels, fixed), and with $n = 20$ (NZ) and $n = 25$ (France) observations per combination of factor levels. The interaction terms of range \times thyme and site (range) \times thyme were included in the analyses. Significant results for the influence of thyme were further analysed through pairwise comparisons. To further explore compositional differences between native and introduced thyme communities, similarity percentages (SIMPER) (Clarke 1993) analysis was used to identify the species that contributed most to differences inside and outside thyme-dominated communities between the introduced (New Zealand) and native (French) ranges.

Results

Biogeographical comparison of thyme's influence on local species richness

More species were identified in France than in New Zealand, both inside and outside of thyme with the difference being greater inside than outside thyme communities (Table 1).

Local species richness (mean species richness per quadrat) varied significantly between ranges ($F_{1,749} = 34.278$, $P < 0.0001$) and among sites ($F_{15,734} = 34.278$, $P < 0.0001$). The interaction terms indicated that thyme influences species richness differently across ranges ($\text{Range} \times \text{Thyme}$ $F_{1,747} = 16.935$, $P = 0.0006$) and among sites ($\text{Site} \times \text{Thyme}$ $F_{15,717} = 5.8698$, $P < 0.0001$). A posteriori pairwise t -tests revealed that for French sites, mean species richness per quadrat increased from outside (10.1 ± 0.44) to inside (12.8 ± 0.34) thyme-dominated communities ($P = 0.0318$) whereas for New Zealand sites, mean species richness per quadrat decreased from 4.0 ± 0.12 to 2.1 ± 0.10 ($P = 0.0011$) from outside to inside thyme-dominated communities (Figs. 1, S4).

Biogeographical comparison of thyme's influence on community diversity

The total number of plant species found inside all the quadrats with thyme was lower than for quadrats without thyme in three out of the seven sites in France and nine out of 10 New Zealand sites (Table 2). Across sites, there was a tendency for more shared species between thyme and no-thyme communities in the native range (French sites) relative to the introduced range [mean (+SE) shared % species French sites: 48.14 (4.8) and New Zealand sites: 36.4 (4.02), Kruskal–Wallis $Z = 1.91$, $P = 0.056$].

Species composition (Simpson's dissimilarity) varied significantly between ranges ($F_{1,749} = 5.5772$, $P < 0.0001$) and among sites ($F_{15,734} = 55.027$, $P < 0.0001$). The interaction terms indicated that the influence of thyme on species composition varied among sites ($\text{Site} \times \text{Thyme}$ $F_{15,717} = 12.677$, $P < 0.0001$) but not between ranges ($\text{Range} \times \text{Thyme}$ $F_{1,747} = 1.4758$, $P = 0.1826$). A posteriori pairwise

Table 1 Overall species richness across all sites in France and New Zealand

	France	New Zealand	% Difference
Total	248 (101)	63 (35)	−75 (−65)
With thyme	188 (98)	41 (29)	−78 (−70)
Outside thyme	203 (101)	57 (35)	−72 (−65)
Shared	139 (98)	29 (29)	−79 (−70)

Reduced data set in brackets

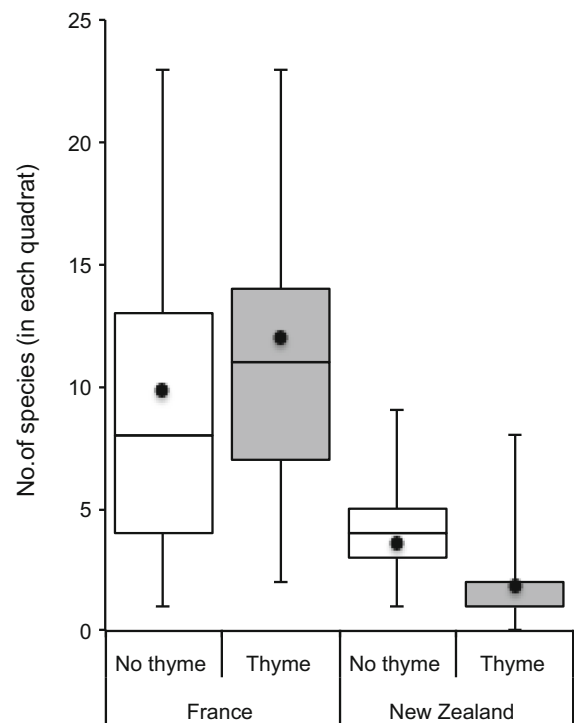


Fig. 1 Box plot showing the median (horizontal line) and mean value (black dot) of the number of plant species per quadrat (1 m \times 0.5 m) with and without *Thymus vulgaris* in France and New Zealand

t -tests of the site \times thyme interaction revealed that thyme altered community composition for all sites ($P < 0.05$) except for the French site T240 ($P = 0.1468$).

SIMPER analyses of presence/absence data showed that there was very little similarity (0.1%) in average species composition between sites in France and New Zealand (Table 3, Online Resource 1 Tables S1, S2). In France, communities with thyme were more similar in species composition than those without thyme, whereas the reverse occurred in New Zealand. Only four plant species (*Bromus hordeaceus*, *Echium vulgare*, *Rumex acetosella* and *Vicia sativa*) were found growing with thyme in both France and New Zealand, and outside thyme communities there were only eight shared plant species (*Bromus hordeaceus*, *Dactylis glomerata*, *Echium vulgare*, *Geranium molle*, *Plantago lanceolata*, *Rumex acetosella*, *Sedum acre*, *Vicia sativa*). *Dactylis glomerata* was not found growing inside thyme-dominated communities in New Zealand, but grows with thyme and outside of thyme in France. Similarly, *Poa pratensis* was not

Table 2 Overall species richness at 7 French and 10 New Zealand sites

Site	Range	Chemotype ^a	Total	T ^b	NT	Diff	Shared T-NT (%)
T240	France	T: 100%	90	68	67	1	45 (50)
T113	France	T: 91%, C: 9%	106	59	87	−28	40 (38)
C111	France	C: 83%, T: 17%	67	59	41	18	33 (49)
C279	France	C: 74%, T: 26%	76	54	64	−10	42 (55)
Cr	France	C: 90%, T: 10%	89	62	70	−8	43 (48)
Ct	France	C: 95%, T: 5%	55	45	37	8	27 (49)
Tgard	France	T: 87%, C: 13%	96	81	61	20	46 (48)
Alex	New Zealand	T: 80%, C: 20%	15	13	12	1	10 (67)
Chard	New Zealand	T: 100%	11	7	9	−2	5 (45)
Clyde	New Zealand	T: 80%, C: 20%	24	16	19	−3	11 (46)
Cromwell	New Zealand	T: 100%	8	6	5	1	3 (38)
Doolans Crk	New Zealand	T: 100%	16	5	14	−9	3 (19)
FTH	New Zealand	T: 100%	22	9	20	−11	7 (32)
Millers Flat	New Zealand	C: 80%, T: 20%	16	10	14	−4	8 (50)
Ophir	New Zealand	C: 80%, T: 20%	19	8	14	−6	3 (16)
Roxburgh	New Zealand	T: 100%	17	6	15	−9	4 (24)
Springvale	New Zealand	T: 80%, C: 20%	11	4	10	−6	3 (27)

^a Percentage of thyme plants at each site producing each chemotype: thymol (T), carvacrol (C)

^b Total number of species at each site found inside 25 (20 for New Zealand) quadrats with thyme (T) and without thyme (NT)

Table 3 Similarity of species composition inside and outside of thyme communities in France and New Zealand

	With thyme	Outside thyme	Combined
France (%)	18	13	15
New Zealand (%)	9	15	12
France–New Zealand (%)	0.1	1.1	0.6

found growing inside thyme-dominated communities in France, but grows with thyme and outside of thyme in New Zealand. (See supplementary material Tables S1 and S2 for the full list of discriminating species for dissimilarity inside and outside thyme-dominated plant communities in France and New Zealand).

Discussion

Examining how ecosystem engineering varies across habitats may help ecologists understand why some plant species reduce local species richness and diversity in their introduced but not their home range. Comparing species richness and composition inside and outside thyme-dominated plant assemblages showed several differences between native and introduced ranges. Notwithstanding that land management

history cannot be quantified as a factor, in the native range thyme-dominated microhabitats harboured more species than microenvironments without thyme. This pattern both reversed and increased in magnitude in the introduced range, where thyme was associated with decreased local species richness (Fig. 1). Furthermore, there was a strong tendency for more species to occur both with thyme and without thyme in the native than in the introduced range (Table 2, % shared species between thyme and no-thyme quadrats in France versus New Zealand, $P = 0.056$). While these results support the hypothesis of thyme filtering out competitive species that could negatively impact local species richness in its native range, they also clearly indicate that when introduced to a novel biogeographic region, thyme is associated with reduced local species richness. Although an important recent study by MacDougall et al. (2014) showed that anthropogenic factors rather than competition more

consistently influenced local (plot level) diversity in natural grasslands, we have to interpret our results within the context that the invaded region of New Zealand (the introduced range) has already been modified by being put into pastoral use.

In both ranges and across all sites (except for one), thyme-dominated community species composition differed from the species composition in communities without thyme. However, in the native range, plant communities with thyme were more similar in species composition than plant communities without thyme, but in the introduced range species composition was most similar in plant communities without thyme (Table 3). Although sampling over a greater area in New Zealand (60×70 km, compared to 10×10 km in France) could lead to less similarity among plant communities in New Zealand overall, given the identical sampling protocols for each range (proximity of thyme-dominated to outside thyme communities at each site (2–10 m), our results provide some evidence that thyme is influencing community composition differently between its introduced and native ranges.

Changes in growth habit, geographic differences in volatile chemical composition and range-specific local effects on herbivores, pollinators and physico-chemical soil properties may all contribute to thyme's change in role from a local environmental facilitator in its native range to a competitor that contributes to reduced resident community diversity in its introduced range. However, further studies are required to understand how thyme's impact in its introduced range has been affected by previous alterations to the invaded landscapes when they were put into pastoral use (i.e. burning, grazing, and the residential communities consisting of a limited number of exotic pastoral grasses and forbs).

Although recent studies looking at time since introduction have found that the initial dominance of an invasive plant species and its negative impact may lessen over time due to negative soil feedbacks and/or stabilising processes (Diez et al. 2010; Dostál et al. 2013), it is over 100 years since thyme was introduced to New Zealand, and our results together with comparisons of aerial and visual reconnaissance of the invaded area over the last 30 years have shown thyme is continuing to expand its habitat as it outcompetes resident exotic species in pastoral lands. Thus thyme's colonisation of already disturbed habitats may further exacerbate successional changes in community

composition by disrupting co-evolved interactions among resident communities.

Previous studies in its introduced range have found a negative correlation between local community species richness and the density of thyme populations which suggests the possibility of thyme's dense growth habit providing an advantage over other species competing for light, nutrients and moisture (Nielsen et al. 2015b). Others have also found that densely growing invasive shrubs or shrub-like species reduce species richness by outcompeting resident species in communities in the introduced range (Mason and French 2008). While anecdotal observations indicate that thyme's growth habit is much denser in its introduced range than its native range (Online Resource 1 Figs. S3, S4), Morgan (1989), these comparisons have not been made.

Similar contrasting effects on species richness between their native and introduced ranges have been reported for other allelochemical producing plant species (e.g. *Ageratina adenophora*, Inderjit et al. 2011; *Chromolaena odorata*, Xheng et al. 2015 and *Solidago canadensis*, Ledger et al. 2015). In particular, Inderjit et al. (2011) found quantitative differences in volatile chemical production between native and introduced populations of *A. adenophora* and suggested these differences may contribute to its successful invasion. Biogeographic differences in thyme's volatile monoterpene production may also contribute to our results demonstrating biogeographical differences in thyme's inhibitive (introduced range) or facilitative (native range) effects for any particular co-occurring species. Previous quantitative analyses of the mean dominant terpene percentage composition of the phenolic chemotype populations investigated in this study suggest that both thymol and carvacrol are present in lower and more variable levels in New Zealand. In their respective chemotype populations, Nielsen et al. (2014a) found mean thymol levels of $39 \pm 8\%$ compared to $53 \pm 1.4\%$ in France (Thompson et al. 2003), and mean carvacrol levels of $36 \pm 9\%$ compared to $57 \pm 1.3\%$ in France.

In its native range, the effects of thyme leaf litter on local soil nitrification processes may foster increased diversity by creating stable microenvironments that support nitrogen-source based niche differentiation (see White 1994; Paavola et al. 1998, for the effects of leaf leachate monoterpenes on soil ammonium:nitrate levels). The differences in chemical composition of New Zealand thyme leaf litter compared to French

thyme leaf litter may instead contribute to reduced local species richness in New Zealand. Previous studies have found decreased soil ammonium under thyme compared to no-thyme communities in its introduced range (Nielsen et al. 2014b) but further studies are required in order to tease out whether the decreased ammonium is due to thyme leaf litter leaching into the soil and altering the composition and function of soil microbial communities, whether thyme preferentially uses ammonium as a nitrogen source or whether thyme's larger standing biomass results in altered pools of other N cycle components because of an increased demand for N.

In conclusion, our detailed comparisons of species diversity inside and outside French and New Zealand thyme communities confirmed that there was very little overall similarity between the two ranges. The findings that French thyme community similarity was twice that of New Zealand's, and that French communities with thyme are more similar than French communities without thyme but that the reverse occurs in New Zealand, is likely indicative that French thyme sites are native-dominated communities that share a long co-evolutionary history. An important clue to our understanding how thyme influences community composition differently in its native and introduced ranges, may come from the finding that in the native range, several co-occurring species grow more abundantly in local thyme environments than identical species in the introduced range. For instance, the grass *Dactylis glomerata* co-occurs with thyme in France but not in New Zealand, another grass *Bromus hordeaceus* is found both inside and outside thyme communities in France but in New Zealand mostly outside of thyme communities, and a similar pattern was observed for the herb *Echium vulgare* (Tables S1, S2). We suggest reciprocal garden studies comparing the effects of local thyme populations on the performance of co-occurring species collected as seeds in the native and introduced ranges are an important next step towards understanding the ecological complexities of thyme's role in community engineering in its introduced and home ranges. Such studies may elucidate to what extent performance of co-occurring species in a thyme environment depends on species identity or population origin (and hence history of co-occurrence).

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Authors' contributions JN, BE, RMC and KJMD conceived the ideas; JN, EG and BE collected the data; JN and BE analysed the data; and JN and BE led the writing.

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