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Contrasting responses of native ant communities to invasion by an ant invader, *Linepithema humile*

Adam J. M. Devenish · Rosemary J. Newton · Jon R. Bridle · Crisanto Gomez · Jeremy J. Midgley · Seirian Sumner

Abstract Invasive alien species pose a serious threat to the integrity and function of natural ecosystems. Understanding how these invaders alter natural communities is therefore an important aspect in predicting the likely future outcomes of biological invasions. Many studies have documented the consequences of invasive alien species on native community structure, through the displacement and local extinction of native species. However, sampling methods and intensities are rarely standardised across such studies, meaning that it is not clear whether differences in response among native communities to the same invader species are due to biological differences between the invaded regions, or differences in the methodologies used. Here we use a matched sampling methodology to compare the effects of the Argentine ant (*Linepithema humile* Mayr) on native ant community assemblages in two distinct biogeographical regions that share similar ecologies: Girona (Spain) and Jonkershoek Nature Reserve (South Africa). We found a strong negative association between *L. humile* presence and native ant species richness within both geographic regions. However, the effects differed between the two study regions: in Girona, a single native ant species (*Plagiolepis pygmaea*) persisted in invaded sites; by contrast, substantially more native ant species persisted at invaded sites in Jonkershoek Nature Reserve. In addition, in Jonkershoek Nature Reserve, the abundance of certain native species appeared to increase in the presence of *L. humile*. This study therefore demonstrates the potential variable effects of an invasive species in contrasting locations within different biogeographical regions. Future work should explore the causes of this differential resistance among communities and expand standardised sampling approaches to more invaded zones to further explore how local biotic or abiotic conditions of a

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region determine the nature and extent of impact of *L. humile* invasion on native ant communities.

Keywords Argentine ant · Biological invasions · Cape floristic region · Community structure · Competitive displacement · Field experiment · Formicidae · Iberian peninsula · *Linepithema humile*

Introduction

Invasive alien species (IAS) pose a serious threat to the structure and function of native communities. The frequency of IAS introductions has increased worldwide, with more than a third of all introductions occurring over the last 45 years (Seebens et al. 2018). Displacement of native species as a result of invasion is widely recognised as one of the leading drivers of global biodiversity loss (Clavero and García-Berthou 2005; Simberloff et al. 2013; Bellard et al. 2016). The presence of an IAS within a region is often associated with a number of negative impacts on resident communities, such as the reduction in the abundance and diversity of native species (Vilà et al. 2011). Cascading effects on the structure, function and resilience of native communities and ecosystems (Sanders et al. 2003; Sax and Gaines 2008) following IAS introductions can, in turn, have severe negative impacts on the economy and human health (Essl et al. 2011; Carpenter et al. 2013; Bradshaw et al. 2016). Understanding, predicting, and mitigating the impact of invasive species on biodiversity and human livelihoods therefore remains a key priority for the global community. In order to prioritise when and where an intervention is applied, one needs a clear understanding of which ecosystems are more vulnerable to invasion.

Our ability to predict the impacts of IAS largely comes from knowledge of prior invasion histories. Increasingly, more sophisticated tools and methods are being used to detect future invaders, and to identify where future invasions are likely to occur (Fournier et al. 2019). Nevertheless, predicting the direction and/or magnitude of the impact of IAS remains challenging (Jarić et al. 2019). This is because these predictions often assume the impact measured in one location or geographic region is likely to be representative of the potential impact in another location or geographic

region. In reality the impacts of IAS are heterogeneous, and seldom unidirectional (Vilà et al. 2011). Variable responses of different native communities to the same IAS may be due to the innate differences in the abiotic (e.g. temperature, rainfall) and/or biotic (e.g. population size, taxonomic diversity, functional diversity) conditions of the environment (Sofaer et al. 2018). Understanding what these differential responses tell us more broadly about community organisation and resilience requires not only a large source pool of studies, but also greater consistency in the approaches used. This is necessary to ensure findings are comparable across studies and/or geographic regions, so that they are representative of geographic and taxonomic differences, rather than differences in study design.

Invasive ants are among the worst and the most pervasive of IAS. As with other IAS, ants have benefited from the breakdown of geographical barriers and increase in globalisation, so much so that today invasive ant species can be found on every continent except Antarctica (Bertelsmeier et al. 2017). Many ant invasions go unnoticed until they are already well established; however, once present, these invaders not only displace native species, but also cause a rapid shift in the native ant community structure (Sanders et al. 2003; Wittman 2014). Some areas in which they are found show up to a 90% reduction in resident ant species richness, which can significantly alter the phylogenetic structure of native ant communities (Holway et al. 2002; Lessard et al. 2009). Ants, therefore, represent an excellent study system with which to explicitly test for different responses of native communities across different continents and communities.

Five invasive ant species (*Anoplolepis gracilipes; Linepithema humile; Pheidole megacephala; Solenopsis invicta; Wasmannia auropunctata*) are recognised as being among the '100 of the worst' invaders in the world (Global Invasive Species Database 2020). Of these species, one of the most well-known is the Argentine ant (*Linepithema humile* Mayr; subfamily Dolichoderinae). Originating from South America, *L. humile* can now be found across six continents and several oceanic islands (Suarez et al. 2001; Wetterer et al. 2009). It is particularly common in regions with a Mediterranean or subtropical climate (Tsutsui et al. 2000). Once present, it can quickly overwhelm the resident community, leading to

declines in species richness and abundance of both native ants (Suarez et al. 1998; Human and Gordon 1999; Sanders et al. 2003) and other invertebrates (Human and Gordon 1997). Whilst this species is generally associated with human-modified and disturbed habitats (Holway et al. 2002), it is also found in more 'natural' and undisturbed habitats (De Kock and Giliomee 1989; Christian 2001; Gomez and Oliveras 2003; Holway and Suarez 2006; Luruli 2007; Roura-Pascual et al. 2010; Mothapo 2013). Despite the almost ubiquitous nature of *L. humile*, assessing its impact across native communities remains difficult because different studies have used different sampling methods or have chosen different temporal periods over which to measure its impact on native ant community structure. Globally, of the regions that *L. humile* has invaded, the South African Cape Floristic Region is arguably one of the least studied areas, despite being recognised as a biodiversity hotspot and having a relatively long invasion history (Mothapo and Wossler 2011).

In this study, we apply identical sampling methodologies to two sites (Girona and Jonkershoek Nature Reserve) with a long invasion history, within two distinct biogeographical regions with a Mediterranean climate—South Africa and North-eastern Spain—to compare the effects of *L. humile* invasions on native ant community structure. We test whether patterns in co-existence of native ant species differ between regions, in order to understand whether these detected differences are due to the innate resilience of the local environments, rather than sampling design and methodology.

Materials and methods

Study area

We conducted our study within two distinct geographic regions, Girona (Spain; see Devenish et al. 2018) and Jonkershoek Nature Reserve (South Africa; Fig. 1). Both regions have a comparatively similar Mediterranean climates (Godoy 2019), with a prior invasion history spanning as far back as the turn of the twentieth century (Suarez et al. 2001).

Spain

Linepithema humile was first recorded in the Iberian Peninsula at the beginning of the nineteenth century (Espadaler and Gómez 2003). Since then its population has expanded considerably in Northern Spain, particularly in coastal regions at an estimated rate of 7.94 ($\pm$ 2.99) metres per year (Roura-Pascual et al. 2010). The study in Spain was conducted across eight sites (four control and four invaded; Fig. 1a) in and around Girona (North-eastern Spain) (Devenish et al. 2018). Four of the selected sites were previously known to be invaded by *L. humile*; two were near University of Girona Montilivi Campus (41°58′59.20"N, 02°49′29.75"E) and two near Castell d'Aro (30 km away) (41°49′04.61"N, 03°04′00.68"E). Sites were selected on the basis that they had been previously sampled for studies on the impact of *L. humile* on myrmecochorous seed dispersal processes (Espadaler and Gómez 1997; Gómez and Oliveras 2003; Bas et al. 2009) and therefore had a long prior invasion history (> 10 years).

To compare the effects of invasion on native communities, the other four sites were regions known to be free of *L. humile* invasions (control); two of these were near the University of Girona Montilivi Campus (41°58′59.20"N, 02°49′29.75"E) (providing a paired comparison with two of the invaded sites) and two near Santuari dels Angels (15 km away) (41°58′31.18"N, 02°54′34.02"E). Sites were at least 500 m apart. The vegetation at all sites is a combination of open cork-oak secondary forest, dominated by *Quercus* and *Pinus* tree species, with herbaceous myrmecochorous plant species in the clearings. The climate of this region is considered Mediterranean sub-humid, with an annual rainfall of 749 mm, and a minimum monthly average temperature in January (7.9 °C) and a maximum in July (23.5 °C). Sampling was carried out during the summer months of June–July 2014, when both native and invasive ant species were active.

South Africa

Similar to Spain, *L. humile* has been recorded in a number of otherwise 'natural' and undisturbed nature reserves within South Africa (Bond and Slingsby 1984; De Kock and Giliomee 1989) and was first detected in Jonkershoek in the 1980s, within the

Fig. 1 Map of sites used in this study. Location of invaded (red circles) and non-invaded (black triangles) transect/sites from two distinct regions: **a** Spain and **b** South Africa
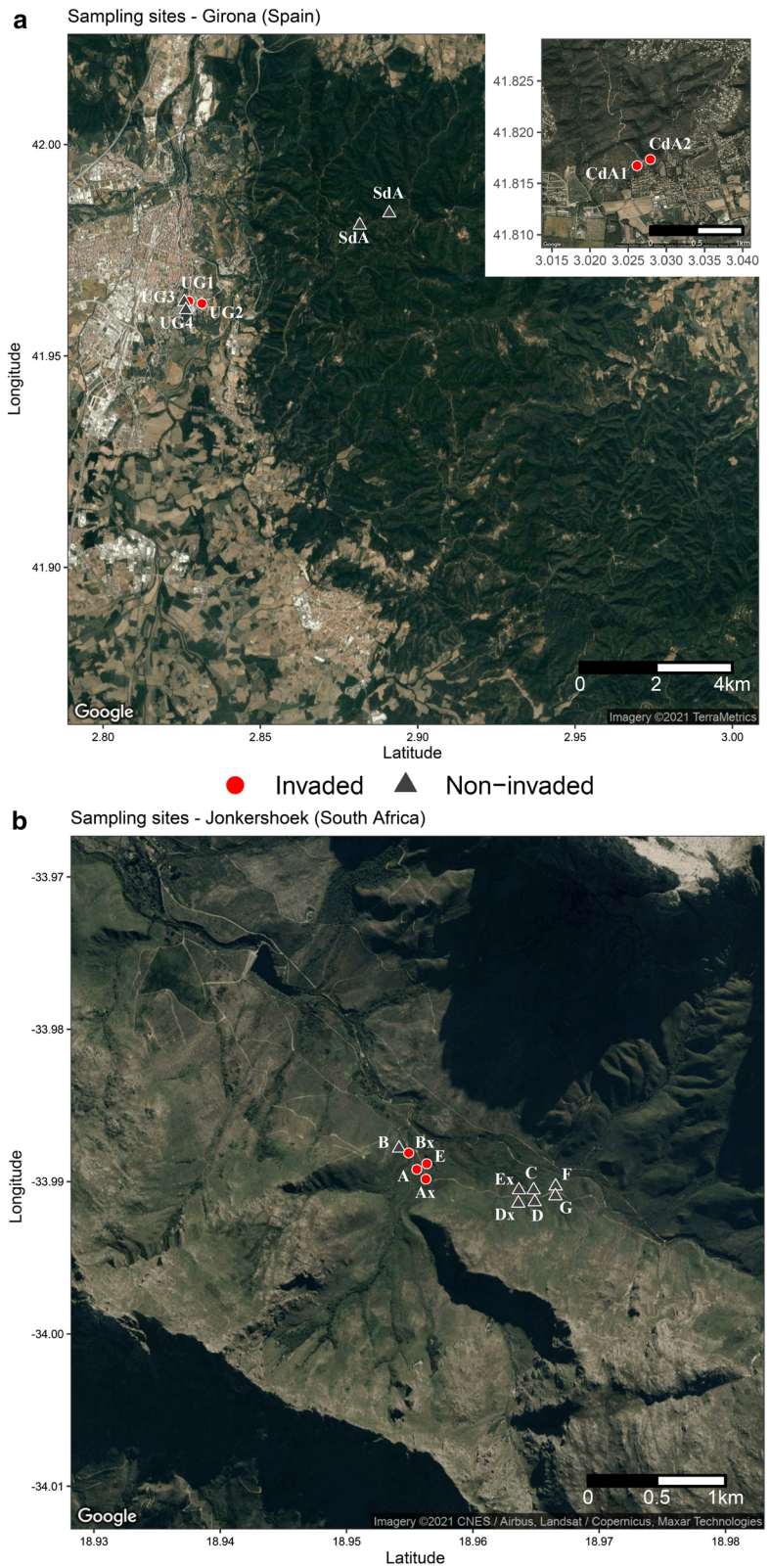
Swartboskloof region (De Kock and Giliomee 1989). Jonkershoek Nature Reserve forms part of the Boland Mountain Complex and contains several endemic vegetation types, including Kogelberg Sandstone Fynbos, Cape Winelands Shale Fynbos and Boland Granite Fynbos. The study in South Africa was conducted at 11 sites (Fig. 1b) within the Jonkershoek Nature Reserve (33°55′51′′S, 18°51′16′′E). Five sites were within the recognised *L. humile* invasion zone, first identified by De Kock and Giliomee (1989). These invaded sites were paired with six sites that were outside the invasion zone, but between 0.5 and 1.5 km away from the invasion front. This meant that the invaded and non-invaded sites were of a similar local biome and plant community, providing the closest possible option to a paired experimental design comparing ant community structure in the presence or absence of *L. humile*. All sites were near ($\pm$ 50 m) the road running through Jonkershoek Nature Reserve. The vegetation at all sites is endemic mountain fynbos, dominated by *Protea repens* and *P. neriifolia*, as well as various endemic Restionaceae and Ericaceae. The climate of this region is Mediterranean humid-subtropical, with an annual rainfall of 802 mm, and a minimum monthly average temperature in July (11.6 °C) and a maximum in January (21.1 °C). Sampling was carried out during the summer months of November–December 2014, when both native and invasive ant species were active.

Sampling design

Within each site a randomly positioned 100 m transect was set up. Two commonly-used methods (Agosti et al. 2000) were then employed to determine the spatial and temporal distribution of invasive and native ant species. Pitfall traps (e.g. Rodriguez-Cabal et al. 2012), for sampling active epigeous (above-ground foraging) ant species, were used to determine abundance and community composition of both invaded and non-invaded ant communities. Baiting traps (e.g. Albrecht and Gotelli 2001) were used to detect temporal (diurnal) partitioning of ant activity within each ant community.

Pitfall trap sampling

Twenty pitfall traps were placed at 5 m intervals along each 100 m transect in each of the sites to sample the ant community structure. Each pitfall trap consisted of a 150 ml beaker, which was buried into the ground, flush with the surface of the soil, into which 50 ml of propylene glycol was added. The pitfall traps were left out for 72 h (duration found to be sufficient for appraising ant assemblages in other Mediterranean habitats, such as Australia Agosti et al. 2000; Borgelt and New 2005), after which time all ants were collected separately by pitfall trap and stored in 70% alcohol for later species identification.

Baiting trap sampling

Ten baiting traps were placed along each 100 m transect at 10 m intervals to monitor diurnal activity (in terms of presence/absence) of species and consequently detect temporal variation in ant community structure during the day. A distance of 10 m is typical for such sampling methods, as it ensures each baiting station is effectively independent (Holway 1998; Andersen et al. 2002; Parr et al. 2004; King and Porter 2005). Each baiting trap consisted of 5 g of ant bait (five to one mix of tuna and honey) placed on a 10 cm² white laminated card. Baiting traps were set at 08h00 (morning), 12h00 (midday) and 16h00 (afternoon). An additional survey at 20h00 (evening) was done in Spain.

While widely used, this method favours detection of dominant ant species; therefore, the temporal activity of some subordinate ant species may not be accurately recorded (Ward 1987; Porter and Savignano 1990). After 1 h, species (rather than individual) occurrence was recorded by collecting ants from each baiting trap and storing them in 70% alcohol for later species identification. Additionally, soil temperature was recorded (at each baiting trap) at the time of collection using an electronic infrared soil probe (model: Fisherbrand—Traceable Infrared Thermometer Gun) to simply distinguish between diurnal periods. Soil temperature is recognised as a good predictor for foraging patterns in ants and other invertebrates (Porter and Tschinkel 1987).

Data analysis

Ants were identified to species level (where possible), using keys from Fisher and Bolton (2016) for South Africa and Gomez and Espadaler (2007) for Spain. Only ant workers were recorded, as alates (winged

sexuals) collected in pitfall traps do not accurately indicate the presence of an established colony (Fisher 1998). Sites within each country were then grouped and compared according the presence/absence of *L. humile* and classified as either invaded or non-invaded. Subsequent analyses were conducted on invaded and non-invaded sites within each region. All analyses were performed in R (version 3.6.3, RStudio Team 2020).

Ant diversity and abundance

Species accumulation curves were calculated for 999 permutations (mean ± SD) using the *specaccum* function in *vegan* (version 2.4.4, Oksanen et al. 2017) for each site, to explore the relationship between species richness and number of pitfall traps sampled. Ant diversity, evenness and abundance was calculated (where appropriate) for each site, using a range of widely used ecological metrics (Morris et al. 2014), including: Species richness $[N]$, Simpson's index $[D = \sum (n/N)^2]$, Shannon-Weiner index $[H = -\sum_{i=1}^{s} P_i ln P_i]$, Pielou's evenness index $[J = \frac{H}{H_{max}}]$ and Fisher's alpha index $[\alpha = N(1 - x/x)]$.

We also tested for spatial autocorrelation between sites using the Moran's I statistic (Moran 1950) using the *Moran.I* function in *ape* (version 5.3, Paradis et al. 2004). No evidence for spatial autocorrelation was found for the Spanish dataset ($I = 0.08$, $p = 0.21$); however, a significant effect of spatial autocorrelation was detected for the South African dataset ($I = 0.20$, $p < 0.01$).

In order to control for any potential spatial autocorrelation in the South African dataset, we used a Generalised Least Square (GLS) regression model (Dormann et al. 2007), with a distance-based exponential covariance function, to test for the effects of invasion status (invaded vs. non-invaded) on ant species diversity (across a range of metrics). This method was chosen as it directly models spatial structure (based on GPS latitude and longitude coordinates) in the residual's distribution, and was done using the *gls* function in *nlme* (version 3.1.1, Pinheiro et al. 2018).

Composition of ant communities

Native ant community structure (in terms of abundance of species collected in pitfall traps) of invaded and non-invaded sites were compared with a Bray–Curtis dissimilarity index (Bray and Curtis 1957) on log-transformed pitfall trap data using the *vegdist* function in *vegan* (version 2.4.4, Oksanen et al. 2017). Records of *L. humile* were excluded from this analysis. Furthermore, to achieve data normality and reduce heteroscedasticity, all data were log-transformed prior to analysis. Non-metric multidimensional scaling (NMDS) ordination (on all samples) and hierarchical clustering analysis (pooled samples) methods were used to test the effects of *L. humile* invasion on native ant community structure. The significance of this difference (i.e. ant species abundance) was determined by using an Analysis of Similarities (ANOSIM) and Similarity Percentage (SIMPER) test. These tests were done using the *anosim* and *simper* functions in *vegan* (version 2.4.4, Oksanen et al. 2017). Additionally, a Mantel test using the *mantel.test* function in *ape* (version 5.3, Paradis et al. 2004) was performed to check for potential effects of spatial autocorrelation on native ant community structure between sites (Mantel and Valand 1970).

Diurnal ant activity

Diurnal temporal differences (in terms of presence/absence of species collected at tuna and honey baits) between, and within, invaded and non-invaded ant communities were compared with a Sørensen-Dice coefficient (Dice 1945) using the *vegdist* function in *vegan* (version 2.4.4, Oksanen et al. 2017). Hierarchical clustering analysis (samples pooled by sampling period) was performed on presence/absence data collected from baits, with baits where no ant activity was recorded being excluded (following methods described in Magurran 2004). The significance of this difference (in terms of native species presence/absence) was determined by using a non-parametric ANOSIM test. Where appropriate, we used a parametric ANOVA and a Generalised Linear Model (GLM) with a Poisson error distribution to analyse the effects of temperature/diurnal period on species presence/absence at tuna and honey baits.

Results

A total of 25,622 ants were collected across 19 sites in the two distinct regions (Fig. 1). In Girona (Spain), 16,456 ants were collected in the 160 pitfall traps across eight sites (averaging 2057 [± SE 388] ants collected per site), belonging to 31 species, from 15 genera (Table 1; Devenish et al. 2018). In Jonkershoek Nature Reserve (South Africa), 9,166 ants were collected in the 220 pitfall traps across 11 sites (averaging 833 [± SE 194] ants collected per site), belonging to 41 species, from 22 genera (Table 2). In Jonkershoek Nature Reserve, *L. humile* was not recorded at one of the sites within the invasion zone (Fig. 1b); this site was therefore included with the non-invaded sites, generating a total of $n = 7$ for non-invaded and $n = 4$ for invaded in this region. Irrespective of the difference in the total number of species, all sites in Girona ($n = 8$) and Jonkershoek Nature Reserve ($n = 11$) appeared to reach an asymptote (Fig. 2; Supplementary Fig. S1), thereby indicating that 20 pitfall traps were enough to capture most of the local epigeous ant species richness in both regions.

Presence of *L. humile* affects native ant community abundance and diversity

The presence of *L. humile* influenced the number of native ant species in both countries, but with some important differences. Of the 30 native ant species recorded in Girona sites, 29 were found exclusively in non-invaded sites ($n = 4$). Only one native ant species (*Plagiolepis pygmaea*) was found within invaded sites ($n = 4$; Table 1). For the Jonkershoek Nature Reserve sites, in total 38 native ant species were recorded within non-invaded sites ($n = 7$), and 28 native ant species within invaded sites ($n = 4$; Table 2). This difference in species richness in both countries is further reflected in the species accumulation curves, as pitfall traps sampled in invaded sites approached an asymptote far more rapidly than those sampled in non-invaded sites (Fig. 2).

The presence of *L. humile* influenced overall ant abundance and diversity. In Girona sites, more ants were collected in pitfall traps in invaded sites than non-invaded sites (Fig. 3a; Table 1). This high abundance of *L. humile* in Girona sites is further reflected by the fact that invaded sites scored significantly lower in terms of species richness (GLS: *Beta* = 15.50,

$p < 0.001$, $n = 8$; Fig. 3c), diversity (GLS: *Beta* = 0.60, $p < 0.001$, $n = 8$; Fig. 3e, g), and evenness (GLS: *Beta* = 0.43, $p < 0.001$, $n = 8$; Fig. 3i), when compared with non-invaded sites (Fig. 3; Supplementary Table S1). Of the 30 native species found in non-invaded sites, *Pheidole pallidula* was the most abundant (accounting for 63% of all individuals collected in pitfall traps; Table 1).

By contrast, in Jonkershoek Nature Reserve sites *L. humile* formed a smaller portion of the total number of ants collected in invaded sites (Fig. 3b; Table 2). Despite this difference in the recorded numbers of *L. humile* between Girona and Jonkershoek Nature Reserve sites, non-invaded sites in Jonkershoek Nature Reserve were still significantly more species rich than invaded sites (GLS: *Beta* = 7.21, $p < 0.001$, n = 11; Fig. 3d). By contrast to the Girona populations, invasion appeared not to have a significant negative effect on overall species diversity in Jonkershoek Nature Reserve (GLS: *Beta* = − 0.07, $p = 0.151$, $n = 11$; Fig. 3f, h). However, invaded sites did score higher in terms of both species' evenness (GLS: *Beta* = − 0.14, $p = 0.048$, $n = 11$; Fig. 3j) and Fisher's α diversity (GLS: *Beta* = 0.68, $p = 0.046$, $n = 11$; Fig. 3k) than non-invaded sites (Fig. 3; Supplementary Table S1).

Presence of *L. humile* affects native ant community structure

The presence of *L. humile* was associated with a significant change in native ant community structure in both Girona and Jonkershoek Nature Reserve populations (Fig. 4). In Girona sites, native ant community composition (measured in terms of species abundance) differed significantly between invaded and non-invaded sites (*ANOSIM*: permutations 999, $r = 1.00$, $p = 0.032$; Fig. 4a). This difference was further reflected in the NMDS analysis which shows that pitfall traps sampled in invaded sites clustered separately from those placed in non-invaded sites (Fig. 4b). Further tests for spatial autocorrelation revealed that sampling site was not a sufficient predictor of these differences in native ant community structure (Mantel test: $r = − 0.12$, $p = 0.714$). In addition, SIMPER analysis revealed that seven ant species (*Aphaenogaster subterranea, Cataglyphis piliscapa, Lasius grandis, Myrmica* sp., *Pheidole pallidula, Tetramorium caespitum* gr., and

Table 1 Ant species collected from pitfall traps ($n = 160$) in *L. humile* invaded and non-invaded sites during June–July 2014. Sites coded according to geographic location (*UG* University of Girona, Montilivi Campus; *CdA* Castell d'Aro; *SdA* Santuari dels Angels) and transect number

Ant species	Status	Invaded				Non-invaded			
		UG1	UG2	CdA1	CdA2	SdA1	SdA2	UG3	UG4
Dolichoderinae									
Linepithema humile Mayr[a]	Invasive	**2105**	**3166**	**3490**	**2377**	**0**	**0**	**0**	**0**
Tapinoma madeirense Forel[a]	Native	0	0	0	0	6	13	7	0
Formicinae									
Camponotus aethiops Latreille[a]	Native	0	0	0	0	0	0	1	6
Camponotus cruentatus Latreille[a]	Native	0	0	0	0	0	0	1	182
Camponotus lateralis Olivier[a]	Native	0	0	0	0	1	0	0	0
Camponotus pilicornis Roger	Native	0	0	0	0	0	0	0	6
Camponotus piceus Leach	Native	0	0	0	0	0	4	1	0
Camponotus truncatus Spinola	Native	0	0	0	0	1	0	0	0
Cataglyphis piliscapa Forel[a]	Native	0	0	0	0	0	28	33	4
Formica cunicularia Latreille[a]	Native	0	0	0	0	0	3	0	0
Formica gagates Latreille	Native	0	0	0	0	1	5	5	2
Formica gerardi Bondroit[a]	Native	0	0	0	0	6	0	1	2
Lasius emarginatus Olivier[a]	Native	0	0	0	0	18	0	1	0
Lasius grandis Forel[a]	Native	0	0	0	0	20	0	86	1
Plagiolepis pygmaea Latreille[a]	Native	23	27	30	34	0	45	85	74
Myrmicinae									
Aphaenogaster subterranea Latreille[a]	Native	0	0	0	0	40	0	29	31
Crematogaster auberti Emery	Native	0	0	0	0	3	0	0	1
Crematogaster scutellaris Olivier[a]	Native	0	0	0	0	12	1	8	1
Diplorhoptrum sp.	Native	0	0	0	0	0	5	4	23
Messor barbarus Linnaeus[a]	Native	0	0	0	0	0	3	0	2
Messor capitatus Latreille	Native	0	0	0	0	0	150	0	0
Messor structor Latreille[a]	Native	0	0	0	0	2	24	0	0
Myrmica sp.[a]	Native	0	0	0	0	2	7	74	10
Pheidole pallidula Nylander[a]	Native	0	0	0	0	97	511	597	2081
Solenopsis sp.	Native	0	0	0	0	0	0	0	3
Temnothorax racovitzai Bondroit	Native	0	0	0	0	2	0	0	0
Temnothorax unifasicatus Latreille	Native	0	0	0	0	2	0	0	0
Tetramorium caespitum Linnaeus[a]	Native	0	0	0	0	2	391	224	26
Tetramorium semilaeve Andre[a]	Native	0	0	0	0	2	0	9	22
Tetramorium sp.[a]	Native	0	0	0	0	0	106	46	0
Ponerinae									
Hypoponera eduardi Forel	Native	0	0	0	0	1	0	1	0
Total number of ants		2128	3193	3520	2411	218	1296	1213	2477
Species richness		2	2	2	2	18	15	19	18
Simpson's Index		0.02	0.02	0.02	0.03	0.75	0.73	0.71	0.29
Shannon-Weiner Diversity index		0.06	0.05	0.05	0.07	1.87	1.62	1.69	0.73
Pielou's evenness index		0.09	0.07	0.07	0.11	0.65	0.60	0.57	0.25

[a] Identified in both pitfall and baiting traps

The bold was just to highlight the focal species of this study *L. humile*

Table 2 Ant species collected from pitfall traps (n = 220) in *L. humile* invaded and non-invaded sites during November 2014 in Jonkershoek Nature Reserve, South Africa. Sites denoted by letters A to G
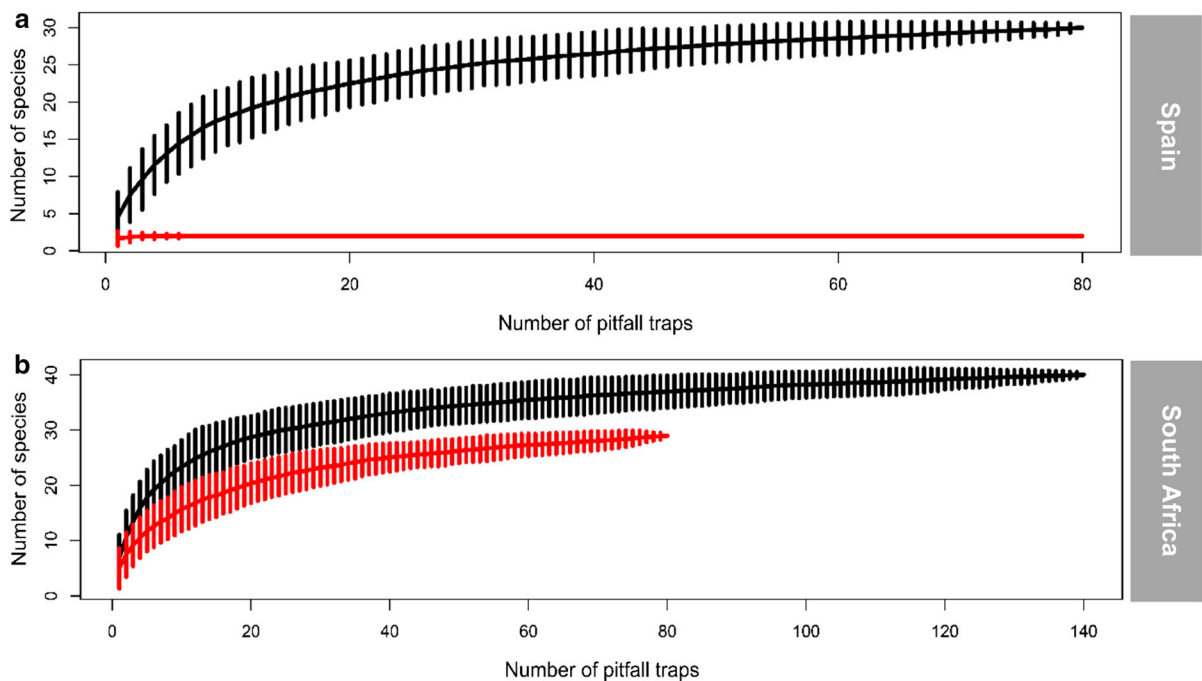
Ant species	Status	Invaded				Non-Invaded						
		A	Ax	Bx	E	B	C	D	Dx	Ex	F	G
Dolichoderinae												
*Axinidris lignicola*Snelling	Native	0	0	1	0	0	0	0	0	0	0	0
Linepithema humile Mayr[a]	Invasive	89	128	47	88	0	0	0	0	0	0	0
Dorylinae												
Dorylus sp.	Native	0	0	0	0	1	0	0	0	0	0	0
Formicinae												
Anoplolepis custodiens Smith[a]	Native	0	0	0	0	0	4	11	0	238	138	802
Anoplolepis steingroeveri Forel[a]	Native	0	0	0	0	0	0	461	43	88	197	42
Anoplolepis sp.	Native	0	0	0	0	0	2	2	0	7	10	22
Acropyga arnoldi Santschi	Native	0	0	0	0	0	0	0	0	0	2	0
Camponotus baynei Arnold	Native	0	0	0	0	3	0	0	0	0	0	2
Camponotus cuneiscapus Forel	Native	0	5	0	0	0	2	3	0	1	6	1
Camponotus havilandi Arnold	Native	0	2	0	1	0	3	2	0	4	0	0
Camponotus maculatus Fabricius	Native	33	1	4	4	10	4	4	4	8	0	2
Camponotus niveosetosus Mayr[a]	Native	3	0	1	0	3	4	0	1	2	2	5
Camponotus vestitus Smith[a]	Native	2	1	1	0	2	4	2	0	4	0	4
Camponotus werthi Forel[a]	Native	0	1	10	0	8	2	2	3	11	0	0
Lepisiota capensis Mayr[a]	Native	0	1	1	0	41	462	1207	12	109	63	146
Lepisiota sp.	Native	0	0	0	0	2	17	9	0	2	3	10
Plagiolepis capensis Mayr	Native	0	0	4	0	0	0	2	1	1	0	0
Plagiolepis deweti Forel[a]	Native	3	1	1	1	2	8	0	1	1	0	1
Tapinolepis trimenii Arnold	Native	0	0	0	0	0	0	1	0	1	0	0
Myrmicinae												
Cardiocondyla sp.	Native	0	0	0	4	9	2	5	1	2	2	3
Crematogaster peringueyi Emery[a]	Native	0	0	6	0	0	0	1	10	0	0	1
Meranoplus peringueyi Emery[a]	Native	42	5	35	11	22	0	0	8	0	0	3
*Messor capensis*Mayr	Native	0	0	0	0	1	8	12	46	2	14	8
Monomorium macrops Arnold[a]	Native	27	16	26	31	243	3	0	33	1	11	3
Monomorium sp.1	Native	9	8	4	4	2	1	2	1	2	5	5
Monomorium sp.2	Native	0	0	0	1	0	0	0	2	0	0	1
Nesomyrmex denticulatus Mayr	Native	0	1	0	0	0	0	0	0	2	0	2
Ocymyrmex barbiger Emery[a]	Native	92	49	21	25	50	55	82	16	113	17	106
Pheidole capensis Mayr[a]	Native	0	1	0	0	295	339	612	208	95	149	110
Pheidole sp.	Native	0	0	0	0	16	6	7	40	0	5	4
Strumigenys sp.	Native	0	1	0	0	0	0	0	0	3	0	0
Syllophopsis modesta Santschi	Native	0	3	2	1	0	0	3	3	3	6	1
Tetramorium arnoldi Forel	Native	0	0	0	0	0	0	2	0	0	2	0
Tetramorium sericeiventre Emery[a]	Native	114	46	64	132	87	143	9	4	0	40	16
Tetramorium sp.1[a]	Native	25	14	6	30	8	3	1	10	1	11	1
Tetramorium sp.2	Native	25	24	3	23	15	4	10	7	9	29	51
Tetramorium sp.3	Native	5	3	0	1	8	0	0	8	0	66	10
Tetramorium sp.4	Native	1	0	0	11	0	0	14	6	10	27	4
Tetramorium sp.5	Native	0	0	0	10	0	0	8	2	5	13	11

Table 2 continued

Ant species	Status	Invaded				Non-Invaded						
		A	Ax	Bx	E	B	C	D	Dx	Ex	F	G
Ponerinae												
Hypoponera sp.	Native	1	0	0	0	0	1	0	0	0	0	0
*Leptogenys intermedia*Emery	Native	0	0	0	0	0	0	0	0	0	0	1
Total number of ants		471	311	237	378	828	1077	2474	470	725	818	1377
Species richness		15	17	20	18	21	22	26	23	30	24	27
Simpson's Index		2.09	1.99	1.93	2.15	1.88	1.53	1.39	2.33	1.63	2.09	2.02
Shannon-Weiner Diversity index		0.85	0.80	0.77	0.84	0.77	0.70	0.66	0.86	0.63	0.77	0.81
Pielou's evenness index		0.77	0.70	0.64	0.74	0.62	0.49	0.43	0.74	0.48	0.66	0.61
Fisher's alpha index		2.95	3.66	4.77	4.53	3.92	3.91	4.05	4.40	5.41	5.35	5.53

[a]Identified in both pitfall and baiting traps

The bold was just to highlight the focal species of this study *L. humile*

Fig. 2 Species-based accumulation curves of epigaeic ant species. Samples collected in **a** Spain and **b** South Africa in invaded (red) and non-invaded (black) sites. Lines shown represent the mean [± SD]

Tetramorium sp.) were the main contributors (> 50%) to this difference in recorded native ant abundance between invaded and non-invaded sites (overall dissimilarity = 90%; Supplementary Table S2). While *Plagiolepis pygmaea* was found to co-exist with *L.*

humile, its detected abundance in pitfall traps did not differ significantly between invaded and non-invaded sites (SIMPER: $p = 0.079$; Supplementary Table S2).

Similar patterns were observed in the Jonkershoek Nature Reserve populations: native ant community

Fig. 3 Ant community composition indexes in Spain and South Africa across invaded (red) and non-invaded (grey) sites. First row: mean number of ants collected in pitfall traps (**a**, **b**). Second row: species richness estimated from pitfall traps (**c**, **d**). Subsequent rows: diversity indices estimated from pitfall traps (**e**–**k**). Box plots showing median scores (with 25–75% quartiles, and outliers)
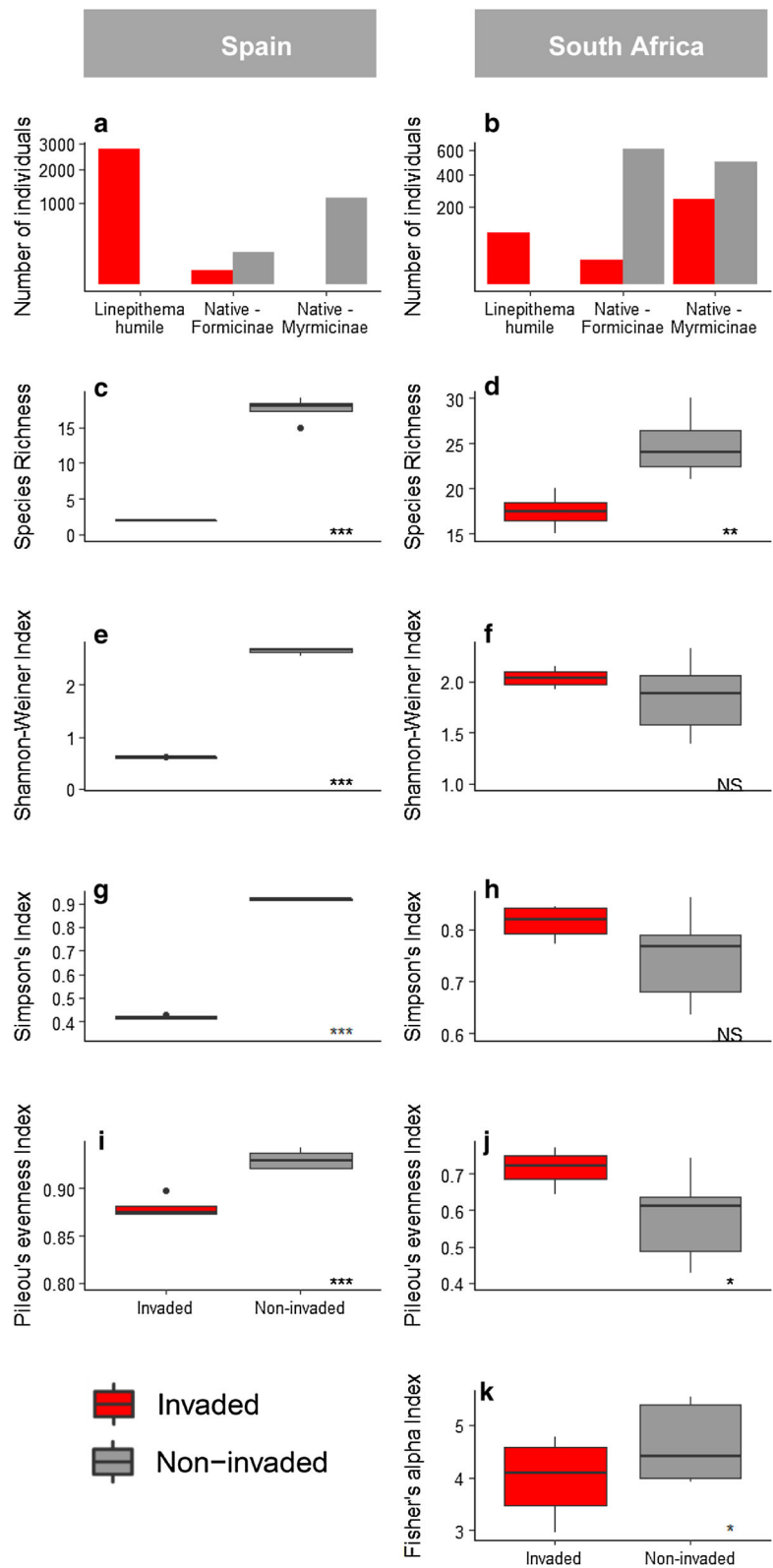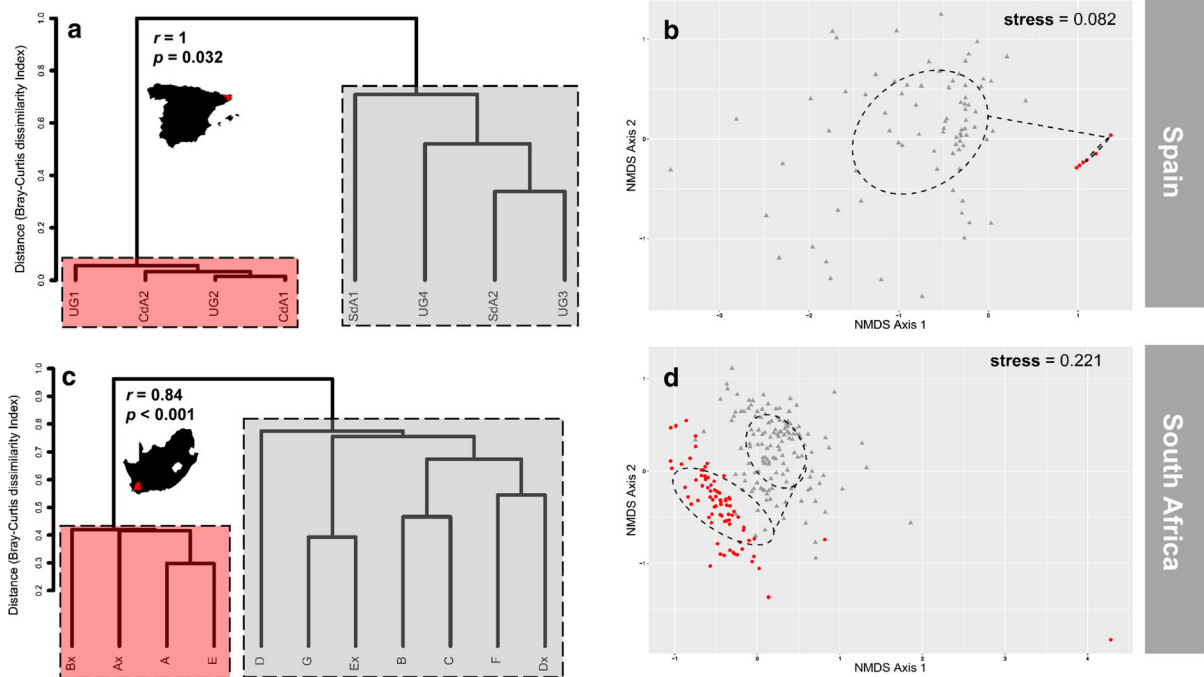
Fig. 4 Comparison of native ant community structure. Between invaded (red circles) and non-invaded (grey triangles) sites in Spain (top row: **a**, **b**) and South Africa (bottom row: **c**, **d**).

Results of the ANOSIM analysis shown on the dendrograms. Sites code key can be found in Supplementary Table S1 and S2

composition (measured in terms of species abundance) differed significantly between invaded and non-invaded sites (ANOSIM: permutations 999, r = 0.84, $p < 0.001$; Fig. 4c). This difference is further reflected in the NMDS analysis, as most of the pitfall traps sampled in invaded sites clustered separately from those in non-invaded sites (Fig. 4d). However, unlike Girona, in Jonkershoek Nature Reserve the spatial arrangement of invaded and non-invaded sites was found to be a significant predictor of native ant community composition (Mantel test: r = 0.57, $p = 0.024$). In addition, SIMPER analysis revealed that nine native ant species (*Anoplolepis custodiens*, *Anoplolepis steingroeveri*, *Lepisiota capensis*, *Lepisiota* sp., *Meranoplus peringueyi*, *Messor capensis*, *Pheidole capensis*, *Pheidole* sp., and *Tetramorium sericeiventre*) were the main contributors (> 50%) to this difference between invaded and non-invaded sites (overall dissimilarity = 55%; Supplementary Table S3).

Differences in the diurnal activities of *L. humile* and native ants

In Girona, ant species presence/absence (at baits) was broadly consistent throughout the four temporal sampling periods (ANOSIM: permutations 999, $r = -0.09$, $p = 0.998$; Fig. 5a), irrespective of measured differences in ground temperatures (ANOVA: $F = 86.2$ DF = 3, $p = 0.002$; $n = 324$).

By contrast, in Jonkershoek Nature Reserve, ant species presence/absence differed significantly across the three temporal sampling periods (ANOSIM: permutations 999, $r = 0.40$, $p < 0.001$; Fig. 5b), in line with rising ground temperatures (ANOVA: $F = 101.6$ DF = 2, $p < 0.001$; $n = 330$). The biggest effect in species composition was found during the midday sampling periods (12–1 pm). This can be seen by the fact that midday samples clustered together, irrespective of invasion status (Fig. 5b). One native thermophilic ant species *Ocymyrmex barbiger* was almost exclusively found at midday baits, and its presence was associated with rising ground temperature (GLM: SE = 0.03, z = 6.07, $p < 0.001$, $n = 330$). Conversely, the detection of *L. humile* decreased with
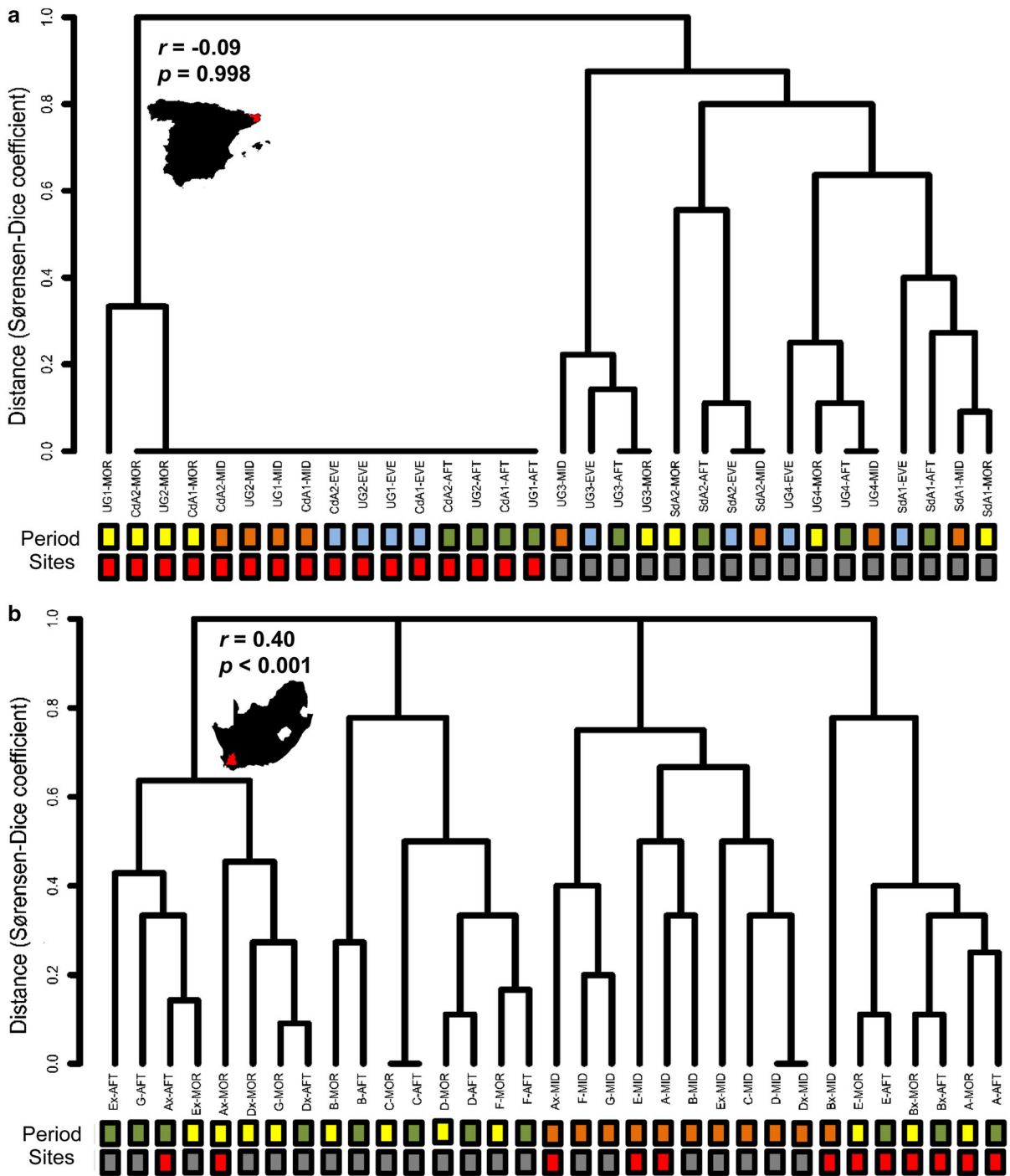
Fig. 5 Diurnal ant activity is not influenced by sampling period. Hierarchical clustering of ant presence at baits sampled within invaded (red) and non-invaded (grey) sites in Spain (**a**) and South Africa (**b**). Baits were sampled across three-time periods: morning (MOR, yellow), midday (MID, orange) and afternoon (AFT, green). In Spain, an additional evening (EVE, blue) sample was performed. Results of the ANOSIM analysis shown on the dendrograms. Sites code key can be found in Tables 1 and 2, respectively

rising ground temperatures in invaded sites (GLM: SE = 0.03, z = − 4.22, $p < 0.001$; $n = 120$).

Discussion

Here we show, by using an identical sampling methodology, how the impact of *L. humile* on native ant community composition can vary across two distinct regions.

Our findings are broadly consistent with other studies that have looked at the impact of *L. humile* within Spain, South Africa, and other Mediterranean-type ecosystems, including the United States and Australia (Ward 1987; De Kock and Giliomee 1989; Suarez et al. 1998; Holway 1998; Christian 2001; Espadaler and Gómez 2003; Gómez and Oliveras 2003; Sanders et al. 2003; Carpintero et al. 2005; Holway and Suarez 2006; Luruli 2007; Rowles and O'Dowd 2009; Mothapo 2013; Naughton et al. 2020). Importantly, our results highlight how variable the native ant community's response to invasion by *L. humile* can be within regions with a Mediterranean climate. Future studies should therefore employ a standardised sampling approach to measure the effect of this invasive species across many regions to better understand local species dynamics and implement appropriate mitigation programmes.

Overall, our data suggest that *L. humile* invasion in Jonkershoek Nature Reserve (South Africa) has been potentially less successful than in Girona (Spain), when viewed in terms of the degree of displacement and the effects on the diversity and abundance of native ant species. This comparative increase in disruption in our Spanish study sites are in line with previous studies conducted in or near our study region (Abril and Gómez 2009; Christian 2001; Gomez and Oliveras 2003; Witt et al. 2004). For example, across invaded sites in Girona, *L. humile* displaced all but one native ant species (*P. pygmaea*), whereas in Jonkershoek Nature Reserve, between 14 and 20 native species were able to co-exist to some degree (e.g., *M. peringueyi, Monomorium* sp. and *O. barbiger*). Although some species in Jonkershoek Nature Reserve showed a reduced abundance in the presence of *L. humile*, at least three native ant species (two *Tetramorium* and one *Meranoplus* species) were more abundant in invaded regions. Attributing this increase in native species abundance directly to the effect of *L.*

humile may be too presumptuous at this stage, especially given the clustered distribution of our invaded plots. However, these results are consistent with the findings of Christian (2001) in the neighbouring Kogelberg Nature Reserve. Determining exactly why these ecosystems show such variable levels of impact is beyond the scope of this study; instead, our findings highlight some of the potential mechanisms underlying this variable invasion success, which we discuss below.

Resilience of the recipient native ant community

Increased resilience to invasion can be explained by the character traits of the recipient native community. For example, many ant genera (including *Crematogaster*, *Meranoplus*, *Myrmica*, *Monomorium* and *Tapinoma*) are known to possess alkaloid repellent chemical compounds which increase their competitive ability in the presence of more aggressive species (Andersen et al. 1991; Holway 1999; Jones et al. 2003; Sorrells et al. 2011). Likewise, several ant genera (including *Cataglyphis, Meranoplus*, *Plagiolepis, Ocymyrmex* and *Tetramorium*) are known to exhibit avoidance mechanisms, such as death-feigning or nest sealing to avoid contact with more aggressive species, such as *L. humile* (Hölldobler 1988; Andersen et al. 1991; Witt and Giliomee 1991; Human and Gordon 1996; Holway 1999; Jones et al. 2003; Rowles and O'Dowd 2009). In some instances, ant genera (including *Aphaenogaster*, *Cataglyphis* and *Ocymyrmex*) may exhibit not only spatial but temporal avoidance mechanisms as well, by foraging during times when competitors (including *L. humile*) are less active. Many of these aforementioned defence and avoidance mechanisms can be found in the list of native ant species present in both our study regions (Tables 1 and 2). There is, therefore, insufficient evidence to suggest that the recipient native ant communities in Jonkershoek Nature Reserve exhibit more of the life history traits that might favour species co-existence and resilience to invasion, when compared to native ant communities in Girona. However, our findings do suggest that the ground surface temperatures appear to actively limit *L. humile* activity more in our South African study sites compared with our Spanish study sites. In Jonkershoek Nature Reserve, *L. humile* was not observed at baits sampled during midday, whereas in Girona, *L. humile* occupied all baits irrespective of

sampling time period (Fig. 5). Consistent with this idea, one resident native ant species in Jonkershoek Nature Reserve (*Ocymyrmex barbiger*) is thermophilic (Bolton and Marsh 1989) and forages during periods when *L. humile* is absent, thereby avoiding direct contact. A similar effect has been observed in other invaded sites in Southern Spain (Carpintero et al. 2007; Angulo et al. 2011), where *L. humile* actively avoids foraging during midday hours, thereby allowing for the co-existence of the native thermophilic ant species *Cataglyphis floricola*.

Availability of resources and microhabitats

Competitive interactions are key indicators influencing invasion outcomes. For example, *L. humile* has been previously shown to displace the aggressive and dominant native ant species through direct exclusion of resources (e.g. food or nesting sites) (Rowles and O'Dowd 2006). This may, in part, explain why *L. humile* is disproportionately affecting the more dominant and aggressive native ant species (e.g. *Anoplolepis* sp., *Lepisiota* and *Pheidole*); with smaller effects on less aggressive native ant species in Jonkershoek Nature Reserve (Löhr 1992; Addison and Samways 2000). However, this alone does not adequately explain why so few subordinate ant species were able to co-exist with *L. humile* in Girona.

Alternatively, these contrasting effects may be caused by differences in both habitat complexity and resource availability between our study sites. Resource availability has been shown to play an important role in modulating the biodiversity-invasion relationship (Davis et al. 2000). In particular, several invasive ant species (including *L. humile*) have shown increased aggression, colony size and activity when they have access to carbohydrates resources (Grover et al. 2007; Wittman et al. 2018). Likewise, habitat complexity strongly affects the structure and dynamics of ecological communities, with increased complexity often leading to greater species diversity and abundance.

South Africa (in particular the Cape Floristic Region) is considerably more species rich (with over twice the number of plant species) than Spain (Cowling et al. 1996; Linder 2003). Greater habitat complexity in our sites in South Africa, which are located in a relatively undisturbed nature reserve, could explain why more native ant species were able to co-exist with *L. humile* in Jonkershoek Nature Reserve, compared with urban/peri-urban sites in Spain. For example, ants in more 'simple' (less species rich) environments are better able to discover, occupy and monopolise resources (Gibb and Parr 2010). *Linepithema humile* is therefore potentially less likely to be able to monopolise resources in Jonkershoek Nature Reserve sites compared with sites sampled in Girona.

Invasion history

The magnitude of *L. humile* impact may be a product of the variable invasion history of our sites (Morrison 2002; Simberloff and Gibbons 2004; Walker 2006). Given that invasions often have an acute and chronic phase (Strayer et al. 2006), it is considered to be more appropriate to sample sites with a long (and well documented) invasion history if one is to achieve a more accurate picture of the longer term impacts of an ant invader on native ant community structure. It is for this reason we chose our sites; however, given the nondescript nature of *L. humile*, it means that the actual first appearance of these invaders in these sites remains unknown. That being said, a recent study of the long-term impacts of *L. humile* on native ant species richness in Northern California found the impact to be unaffected by time; instead, the magnitude of the effect was thought to be driven by site-specific factors (Menke et al. 2018).

Caveats and limitations

There are several limitations to this study that preclude us extrapolating our findings too broadly, particularly the lack of replication across countries/biomes. While the shared sampling methodology is its strength, replicating these approaches across more sites and in different countries is required to ascertain more clearly the specific effects of *L. humile*. Ultimately, two key aims for future work should be to identify if the impact of *L. humile* on native communities depends (1) more on the Argentine ant abundance, or (2) on differences between biogeographic regions. This requires replication of the same sampling regime across several countries with different biomes to identify specific effects common to a biome/geographic region/environment. Such information would be vital in advising management of the invasive species, and in prioritising conservation action. For example, further

confirmation of the results presented here may lead to recommendations to prioritise conservation management in areas where invasion impact is high, as we showed for Girona sites.

Our study uses a snapshot approach that lacks experimental manipulations, which limits our ability to generalize our results; a shortcoming that many studies of this nature suffer from (Porter and Savignano 1990; Suarez et al. 1998; Vanderwoude et al. 2000; Carpintero et al. 2005; Guénard and Dunn 2010), given that some studies have found that native ant diversity is already depleted prior to invasion (King and Tschinkel 2013). It is vital that more prior invasion studies be undertaken, in order to corroborate these findings and support the idea that it is not just spatial patterns driving differences in native ant communities before invasion.

Finally, in conclusion, it is important that future research be undertaken to identify what elements, if any, can be used to better predict and model the extent and scale of *L. humile* impacts. To achieve this, it is vital that we start to focus research and data collection on under-sampled biomes (in addition to the Mediterranean biome) where *L. humile* has been recorded, such as parts of West and Southern Africa, Southern Spain and Southern France, as well as novel regions within currently well studied biomes (i.e. other sites with a Mediterranean climate, such as Northern Africa, California and Japan). More importantly, research should be prioritised in regions or areas where *L. humile* invasion has been relatively unsuccessful. Only then can we truly begin to understand why ecosystems show such variable levels of impact, particularly with regard to what factors make ecosystems more resilient (or vulnerable) to invasion, and how we can use these data to better predict and mitigate the future impact of invaders on novel environments.

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