



Discovered just before extinction? The first endemic ant from the Balearic Islands (*Lasius balearicus* sp. nov.) is endangered by climate change

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ABSTRACT

Aim We analyse the taxonomic status, phylogenetic relationships, distribution and age of a newly discovered ant taxon found in the mountaintops of the island of Mallorca (Spain). We also consider the potential impact of short-term climate change on the survival of this ant and make proposals on its conservation status, risks and management.

Location Balearic Islands (Spain).

Methods We used morphological, molecular and ecological evidence to assess the specific status of the potential new species. We gathered distribution data to conduct climate-based distribution modelling of present and future occupancy under several SRES emission scenarios.

Results The existence of a new non-cryptic species of ant (*Lasius balearicus* Talavera, Espadaler & Vila, sp. nov.) is described from the island of Mallorca. Its distribution was found to be extremely restricted (Serra de Tramuntana) and elevationally constrained to island summits (between 800 and 1400 m a.s.l.). Molecular dating indicated that this species diverged about 1.51 million years ago from its nearest relatives, from which it can be distinguished based on several morphological traits. Ecological niche modelling shows a dramatic reduction of areas with suitable climatic conditions under the different scenarios studied.

Main conclusions *Lasius balearicus* represents the first endemic ant to be described in the Balearic Islands, as well as the first endemic *Lasius* species in the Mediterranean islands. Distribution modelling predictions, the low intra-specific genetic diversity observed, and the geographical and elevational isolation of the populations indicated a low probability for the survival of the species in the short term, thus making it a potential model to study real-time climate-based biodiversity loss. As a consequence, we strongly recommend including *L. balearicus* in the IUCN Red List of Threatened Species under the category 'Endangered'. This case illustrates that a fraction of biodiversity remains unexplored even within Europe, arguably the best-studied region of the planet, and that the available time-window for us to study and protect it may be in some instances notably narrow.

Keywords

Conservation, ecological niche modelling, Formicidae, global warming, island endemism, *Lasius balearicus*, Mallorca, new species, phylogeny, threatened species.

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INTRODUCTION

It is frequently stated that many species will become extinct before being scientifically described (e.g. Crawford *et al.*, 2010; Fontaine *et al.*, 2012), but it is intrinsically difficult to measure the truth of such a claim. Whereas a substantial number of probable species extinctions have been reported in the last century (Turvey, 2009; IUCN, 2012), relatively few have been linked to climatic changes during the Quaternary period (Willis *et al.*, 2004; Botkin *et al.*, 2007). Nevertheless, future scenarios are pessimistic (Thomas *et al.*, 2004; Butchart *et al.*, 2010; Bálint *et al.*, 2011) and some studies suggest that climate change could surpass habitat destruction as the greatest global threat to biodiversity over the next few decades (Leadley *et al.*, 2010; Bellard *et al.*, 2012). Projections for future species extinction rates indicate that they will probably exceed background rates estimated from the Cenozoic fossil record by more than two orders of magnitude (Mace *et al.*, 2005; Pereira *et al.*, 2010).

The described effects of climate change on biodiversity are not expected to be constant across space. For example, it has been argued that organisms on islands, both in a literal and ecological sense, are especially vulnerable (Cronk, 1997; Losos & Ricklefs, 2010). In these cases, except for species with exceptional dispersal abilities, there is practically no possibility of a spatial shift to follow climatic conditions, either latitudinally (in sea or oceanic islands) or elevationally (for example on mountain tops). This effect is expected to be most severe in areas displaying extremely isolated ecological and spatial conditions, as is the case for island mountain-tops. Thus, these types of habitats represent prime locations in which to search for species on the brink of extinction and yet unknown to science.

In this work we document the discovery of the first endemic ant in the Balearic Islands, and show that it appears to inhabit only the summits of the island of Mallorca, displaying an extremely restricted and elevationally constrained distribution. The finding of a new non-cryptic endemic ant species in Europe is of remarkable interest because this is a relatively well-studied area of the world where ant endemism is not common. Climate-based distribution modelling and genetic diversity analyses suggest that the long-term survival of this species is uncertain and, based on the IUCN criteria, we propose that it be classified as 'Endangered'.

MATERIALS AND METHODS

Sampling

Eight of the major peaks (Puig Galatzó, Mola de Planícia, Puig d'es Teix, Serra d'Alfàbia, Puig Major, Puig de Massanella, Puig Caragoler and Pic Tomir) in the Serra de Tramuntana range (northern Mallorca, Balearic Islands, Spain) were surveyed between 2008 and 2012 (for transect details see Fig. S1 in Appendix S1 of the Supporting Information). In order to record ant diversity at different elevations, an

entire day was devoted to prospect each of the peaks (approximately 10 hours of fieldwork) from the base (sometimes near sea level) to the top, covering habitats along most of the elevational gradient. Some of the peaks were explored twice, at different periods of the year and following alternative paths to increase the sampled area and habitat diversity. Surveys were also extended to other potential areas of Mallorca, nearby islands (Menorca, Eivissa) and nearby mainland (Serra d'Aitana, Alacant, eastern Iberian Peninsula) (Fig. S1). We used a standard myrmecological survey, searching on the ground and under stones. Ants were also detected when attending aphids on vegetation. In some cases, specimens were collected from the internal walls of the crevasses within the karst. Most samples were preserved in 100% ethanol for molecular analysis, but a number of specimens were prepared dry for morphological examination. Identification codes and collection localities for the samples used for molecular analysis are listed in Table S1 and the specimens used for ecological niche modelling are listed in Table S2 (see Appendix S1). Voucher specimens were deposited in the R.V. collection at Institut de Biologia Evolutiva (CSIC-UPF) and in the X.E. collection at Universitat Autònoma de Barcelona, both in Barcelona (Spain). Type material was deposited in the Museum of Comparative Zoology (Cambridge, MA, USA), British Natural History Museum (London, UK), Senckenberg Museum für Naturkunde (Görlitz, Germany) and Museu Balear de Ciències Naturals (Sóller, Mallorca).

Biometric analyses

Biometric measures were taken with a Nikon SMZ-U stereomicroscope with variable magnification (from 7.5× to 75×) and two cold light fibre tubes. A white plastic light diffuser was used when measuring pubescence distance on clypeus (PDCL). A total of 51 workers of *Lasius balearicus* sp. nov. corresponding to eight nests from five localities were studied. Twelve biometric characters and derived indexes were measured or calculated (see Table S3 in Appendix S1): head width (HW), head length (HL), cephalic size (CS), scape length (SL), head shape (HL/HW), scape index (SL/HL), relative scape index (SL/CS), pubescence distance on clypeus (PDCL), number of standing hairs on scapus (nHS), number of standing hairs on hind tibia (nHHT), number of standing hairs on head (nBH), and number masticatory dents (MaDe) as defined in Seifert (1992). Nine of these characters were also obtained for queens (HWQ, HLQ, HLQ/HWQ, SLQ, SLQ/HLQ, SLQ/HWQ, MLQ, MHQ, MHQ/MLQ). Mean values for these variables were extracted from the literature (Seifert, 1992; Schlick-Steiner *et al.*, 2003; Herraiz & Espadaler, 2009) for the *Lasius* s. str. taxa *L. niger*, *L. platythorax*, *L. japonicus*, *L. grandis*, *L. cinereus*, *L. emarginatus*, *L. hayashi*, *L. productus*, *L. sakagami*, *L. alienus*, *L. psammophilus*, *L. brunneus*, *L. austriacus*, *L. neglectus*, *L. turcicus* and *L. lasioides*, and from Seifert (1988) for the outgroup *L. mixtus*. Taxa lacking values for some of the variables were measured

based on available specimens from different nests covering the range of distribution (Table S3). A *t*-test (Sokal & Rohlf, 1995) for the measured variables was applied to pairwise comparisons between *L. balearicus* and the most closely related species (*L. grandis*, *L. cinereus*, *L. niger*, *L. japonicus*, *L. platythorax* and *L. emarginatus*). Because multiple comparisons were performed between morphological variables, a caution to control for false discovery rates (FDR) was applied following the procedure in Waite & Campbell (2006) and using $P < 0.001$ (see Table S4 in Appendix S1).

Molecular data for phylogenetic inference

A total of 15 workers from different nests (three nests for each of five populations) of *L. balearicus* covering the whole known distribution range were used to obtain molecular data, as well as workers from different populations of *L. grandis* (5), *L. cinereus* (5), *L. niger* (3), *L. emarginatus* (2), *L. alienus* (2), *L. lasioides* (3), *L. psammophilus* (1), *L. platythorax* (1) and *L. brunneus* (2) (Table S1). Genomic DNA from entire ant bodies was extracted using the DNeasy Tissue Kit (Qiagen Inc., Valencia, CA) and following the manufacturer's protocols. To amplify a fragment by polymerase chain reaction of the mitochondrial gene cytochrome *c* oxidase subunit I (*COI*), we used primers 'Lasius-R' and 'Lasius-L' as described in Maruyama *et al.* (2008). A modified primer named 'Lasius-2L' (5'-TAYCCTCCATTAGCYTCTAA-3') was designed to improve the amplification for *L. balearicus*. The mitochondrial region corresponding to 16S rRNA (*16S*) was also amplified using the primers '16Sar-L' and '16Sar-L2' (Maruyama *et al.*, 2008) and the genomic regions corresponding to the genes long-wavelength rhodopsin (*LR*) and wingless (*Wg*) were amplified using the primers pairs 'LR143F-LR639ER' and 'Wg578F-Wg1032R', respectively, according to the conditions described in Moreau *et al.* (2006). Extra sequences that were matching the same *COI* and *16S* regions from the subgenus *Lasius* s. str. and the out-group *Lasius mixtus* were retrieved from GenBank, corresponding to previous studies by Maruyama *et al.* (2008), Steiner *et al.* (2004) and Cremer *et al.* (2008) (Table S1). PCR products were purified and sequenced by Macrogen Inc. and sequences obtained were deposited in GenBank (accession numbers in Table S1).

Morphological data for phylogenetic inference

A set of morphological characters was used to complement molecular data for phylogenetic inference. A total of 68 characters (see Table S5 in Appendix S1) were defined using various sources: (1) characters that were variable within the genus *Lasius* s. str. in the morphological matrix of Maruyama *et al.* (2008) were selected and adapted, and two new characters (sides of pronotum and thorax coloration for workers) were incorporated; (2) the biometric measurements obtained (Table S3) were converted to discrete characters.

Phylogenetic inference and dating

DNA sequences were edited using GENEIOUS PRO 4.8.3 (Bio-matters Ltd., 2009; <http://www.geneious.com/>) and aligned using MUSCLE (Edgar, 2004). GBLOCKS 091 with relaxed parameters (Castresana, 2000; Talavera & Castresana, 2007) was applied to the *16S* alignment. These analyses resulted in a final alignment of 864 bp for *COI* (73 sequences), 498 bp for *16S* (55 sequences), 554 bp for *LR* (29 sequences) and 400 bp for *Wg* (29 sequences) (Table S1). Two complementary approaches were used for phylogenetic inference. First, BEAST 1.7.2 (Drummond *et al.*, 2012) was used on a combined matrix to construct the phylogeny and estimate node ages based on the molecular characters. Because no reference calibration points were available for this genus, we used a substitution rate of 1.5% uncorrected pairwise distance per million years, inferred from the entire mitochondrial genome of various arthropod taxa (Quek *et al.*, 2004). A constant size coalescent approach and an uncorrelated relaxed clock were used as priors (Drummond *et al.*, 2006). Second, a Bayesian coalescent-based multilocus species tree approach was used to infer phylogenetic relationships among *L. balearicus* and closely related species (*L. cinereus*, *L. grandis*, *L. emarginatus*, *L. niger*, *L. platythorax*, *L. psammophilus* and *L. alienus*) using *BEAST 1.7.2 (Heled & Drummond, 2010). Parameters for both Bayesian inferences were estimated using two independent runs of 50 million generations each and a burn-in of 5 million generations was applied to obtain the final tree. A phylogenetic tree combining molecular and morphological data was also reconstructed using MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001) running two independent chains of 10 million generations each (with a pre-run burn-in of 100,000 generations). Five partitions were set corresponding to each molecular marker and morphological data. For all the analyses, we selected the substitution models with the lowest Akaike information criterion (AIC) score using jMODELTEST 0.1.1 (Posada, 2008): GTR+I+G for both mitochondrial markers, HKY for *LR*, and HKI+I for *Wg*. Six gamma rate categories were assigned when applied and convergence was checked with the program TRACER 1.5 (Rambaut & Drummond, 2007).

Ecological niche modelling

Variables used

Species distribution models were used to estimate distribution limits for *L. balearicus* through time according to environmental climatic data. The layers for 19 climatic variables available in WorldClim (<http://www.worldclim.org/>), described by Hijmans *et al.*, 2005) were used. As WorldClim variables generally show a high collinearity that can lead to statistical bias and model over-prediction, a subselection of variables was employed. Values for all 19 parameters in a Mallorca island raster dataset were extracted from a 30 arc-seconds (approximately 1 km) grid using the DIVA-GIS

software 7.1.7 (Hijmans *et al.*, 2005). Points from the whole raster were used to analyse the level of correlation between pairs of variables in JMP 7.0.2 (SAS Institute, 2008; <http://www.jmp.com/>). When two variables shared a Pearson correlation coefficient of 0.7 or higher, we selected the biologically most meaningful variable for ants, either the most general one, or the one involving the season when ants are active. As a result, five out of 19 variables were selected: BIO1 (annual mean temperature), BIO3 (isothermality), BIO4 (temperature seasonality), BIO7 (temperature annual range) and BIO12 (annual precipitation).

Modelling present distribution

To predict the potential distribution we employed an ensemble forecasting approach including eight species distribution models (SDMs) implemented in the package BIOMOD2 version 3.1-25 (Thuiller *et al.*, 2013): four regression methods [generalized linear model (GLM), generalized additive model (GAM), flexible discriminant analysis (FDA) and multiple adaptive regression splines (MARS)], a recursive partitioning method [classification tree analysis (CTA)], and three machine-learning methods [generalized boosting model (GBM), random forest (RF) and maximum entropy (MAX-ENT)]. The number of replicates was set to 20 and we considered 21 presence records corresponding to 10 cells (Table S2) and a total of 118 true absences for the island (studied cells where no *L. balearicus* nests were observed). Given the condition of being a highly restricted endemic with very few presence points, using standard ways to correct for spatial auto-correlation was not operational in this case. As a solution, first we lumped all presence points that were in close proximity, so that a maximum of one point was used for each climate cell. On the other hand, we conducted several preliminary tests (not shown) removing presence points from contiguous cells that always resulted in very similar predictions, despite the fact that decreasing the number of presence points lowered the resolution of the models. Consensus distributions were obtained by calculating the weighted mean distributions across SDMs. The true skill statistic (TSS) was used as an evaluation metric with a value of 0.7 as a minimum quality threshold. To evaluate the accuracy of the ensemble models, three different parameters were calculated: the area under the curve of a receiver operating characteristic plot (AUC), the TSS and the kappa statistic. To transform the resulting continuous probability values from models to a binary presence-absence form, we established a threshold by maximizing the sum of sensitivity (the percentage of presence correctly predicted) and specificity (the percentage of absence correctly predicted) (Liu *et al.*, 2005).

Estimating future distributions

After calibrating the ensemble models for their current distributions based on present climate, we obtained binary models through projections onto Intergovernmental Panel on

Climate Change (IPCC) (New *et al.*, 1999) future conditions data to predict future potential distributions, using the same climatic variables considered in the present models. We used statistical downscaling (delta method) layers based on the coupled global climate models CGCM2 and CGCM3 created by CCCMA (Canadian Centre for Climate Modelling and Analysis) and under three varied SRES emission scenarios for the years 2050 and 2080: A1b (maximum energy requirements or emissions) (CGCM31), A2a (high energy requirements or emissions) (CGCM2) and B2a (lower energy requirements or emissions) (CGCM2) (see IPCC, 2001, 2007 for scenarios). Thus, we obtained 48 future potential distributions obtained by combining eight modelling algorithms, three SRES scenarios and two different years.

RESULTS

Biometric and morphological analyses

In the majority of numeric characters and derived indexes, *L. balearicus* is statistically different from all closest species (see Tables S3 & S4 and Fig. S2 in Appendix S1). Besides being smaller than the rest of the members of *Lasius* s. str., except for *L. cinereus*, its yellowish brown coloration allows for an immediate separation. Under the microscope its intense hairiness stands out as a remarkable trait. Thus, absolute size and hairiness differentiate *L. grandis* and *L. balearicus*. The most biometrically similar species is *L. cinereus*, from which *L. balearicus* differs by its shorter scape and more developed pilosity in the scape, back of head and extensor profile of the hind tibia (see the section 'Taxonomy' below for description).

Phylogeny and dating

The inferred phylogenies generally agree with previous published hypotheses (Hasegawa, 1998; Janda *et al.*, 2004; Steiner *et al.*, 2004; Cremer *et al.*, 2008; Maruyama *et al.*, 2008), identifying two main deeply diverged clades that segregate hairy and non-hairy taxa. *Lasius balearicus* specimens were recovered as a highly supported clade (posterior probability = 1) within the group formed by *L. cinereus*, *L. grandis*, *L. japonicus*, *L. platythorax*, *L. niger* and *L. emarginatus* in the two trees (Fig. 1). No supported sister species of *L. balearicus* was recovered in the molecular phylogeny and species trees reconstruction (Fig. 1b, and Fig. S3 in Appendix S1). When morphology was also included, a supported sistership of the clade *L. grandis*–*L. cinereus* with *L. balearicus* was recovered (Fig. 1a). The *L. balearicus* clade was well diverged from the rest of species in the group, and the estimated age of this species was 1.51 Ma (95% highest posterior density, HPD: 0.84–2.4 Ma). Remarkably, the intraspecific divergence for *L. balearicus* was very low (99.9% pairwise identity), with no parsimony informative sites in 954 nuclear bases length and only two in the 1351 mitochondrial bases. Four different haplotypes for *L. balearicus* were documented in *COI*, two in

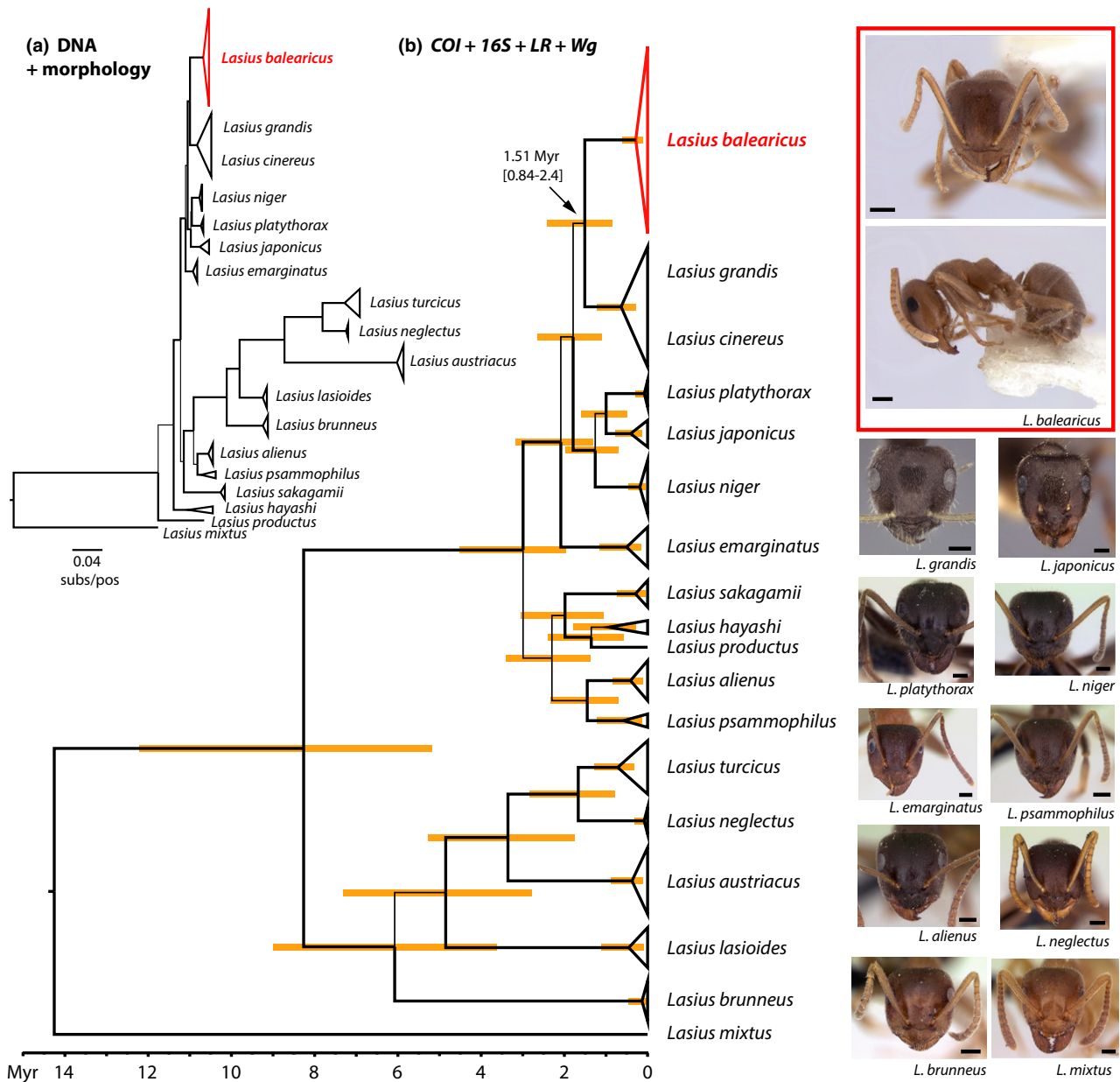


Figure 1 Phylogenetic inference for the subgenus *Lasius* s. str.: (a) combined molecular + morphology phylogram, and (b) Bayesian chronogram based on *COI* + *16S* + *LR* + *Wg*. A relaxed clock rate of 1.5% uncorrected pairwise distance per million years was used as prior for dating nodes. Bars indicate the 95% highest posterior density (HPD) for age estimations according to the axis representing time in millions years before present. Thick lines indicate supported relationships (posterior probabilities ≥ 0.95). Subs/pos: substitutions per position. Scale bars in pictures represent 0.2 mm. Credits for <http://www.antweb.org/> photographs: A. Walker (*L. grandis*), S. Hartman (*L. japonicus*) and A. Nobile (*L. platythorax*, *L. niger*, *L. emarginatus*, *L. psammophilus*, *L. alienus*, *L. neglectus*, *L. brunneus* and *L. mixtus*).

Wg, and the rest of the markers were not variable. Each detected haplotype differed from the rest by a single mutation and no geographical structure was evident.

Ecological niche modelling

According to the AUC, TSS and kappa statistics, all tested modelling techniques displayed excellent performances for *L. balearicus* (AUC > 0.9, TSS and kappa > 0.8), with slightly

lower values for GLM (see Table S6 in Appendix S1). From the five climatic predictors, the annual mean temperature was the stronger contributor to the model (0.75 ± 0.16), followed by temperature seasonality (0.15 ± 0.09), temperature annual range (0.11 ± 0.04), isothermality (0.08 ± 0.03) and annual precipitation (0.09 ± 0.09). The predicted current distribution for *L. balearicus* was limited to the mountainous area of the island, with highest probabilities at the highest elevations of Serra de Tramuntana (Fig. 2). Future projections show a

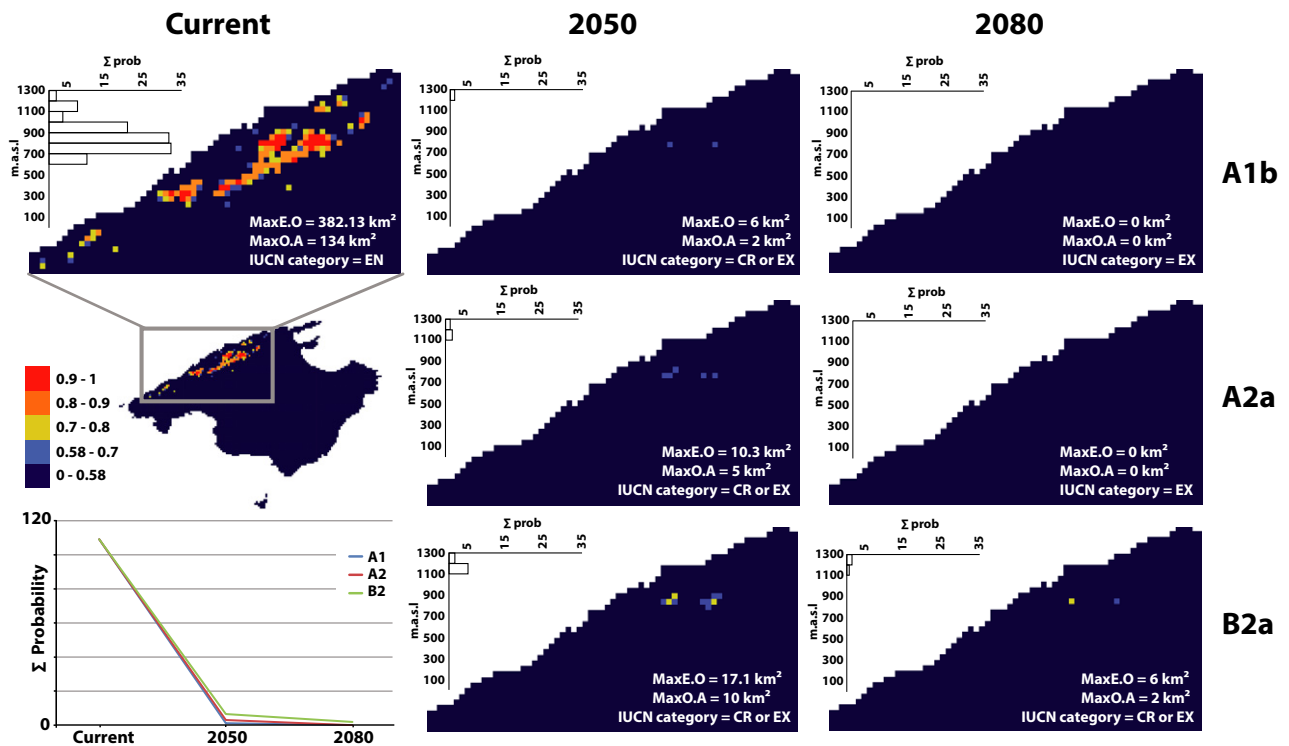


Figure 2 Ecological niche modelling for *Lasius balearicus* sp. nov. Current prediction and future projections for the years 2050 and 2080 are represented for the island of Mallorca. Presence probability output ranges are represented in a colour scale. Bar diagrams show the sum of presence probabilities according to elevation. The graph on the lower left displays the evolution of total presence probabilities through time. Maximum estimates for the extent of occurrence (E.O), area of occupancy (O.A) and the proposed IUCN category are shown (EN, endangered; CR, critically endangered; EX, extinct).

dramatic reduction of areas with suitable climatic conditions under the different scenarios for *L. balearicus*, to the point that it is predicted to become extinct by 2050 or 2080, especially according to the scenarios A1b and A2a.

Habitat and distribution

Specimens attributable to *L. balearicus* were only collected during searches in seven major summits of the Serra de Tramuntana range, between 800 and 1400 m a.s.l. No similar specimens were observed below this elevation on Mallorca or in any other region studied. The observed area of occupancy was 8 km² (Fig. 3). The species was not recorded in forested extensions, as for example in the Mola de Planícia peak (942 m), which is completely covered by trees, even if climatic modelling indicated a rather high presence probability output (83.6%). The area with probability > 0.58 (threshold maximizing the sum of sensitivity and specificity) based on the climatic ensemble modelling prediction is 134 km² (Fig. 3a). To obtain a more accurate estimation, we calculated the area with both suitable land cover and climatic conditions resulting in 105 km² (Fig. 3b) for a maximum occupancy. In summary, because not all peaks could be explored, the real occupancy area probably lies between 8 and 105 km².

Nests seemed to be associated with exposed and rocky calcareous areas, with sparse and shrubby vegetation, frequently composed of the endemic plants *Hypericum balearicum* and *Genista valdes-bermejoi*. Ants were occasionally observed to be attending aphids, as *Lasius* species usually do. Only between one and six nests restricted to summit areas were found per population. A major effort would be necessary to document the exact number and density of nests, but we can conservatively assume that the population size of *L. balearicus* is smaller than 2500 mature individuals (the number of nests is used as equivalent to 'mature individuals' in ants with monogynous colonies), with no peak containing more than 250 nests, which is one of the IUCN criteria for endangered species (IUCN, 2001).

DISCUSSION

Species status of the discovered taxon

The morphology and colour of *L. balearicus* are unique and, in addition to the exclusively high Mediterranean mountain habitat, distinguish this species from all other known *Lasius* s. str. Molecular phylogeny confirms that it is a genetically isolated taxon that split from the sister lineage about 1.51 Ma (95% HPD 0.84–2.4 Ma) (Fig. 1, and Table

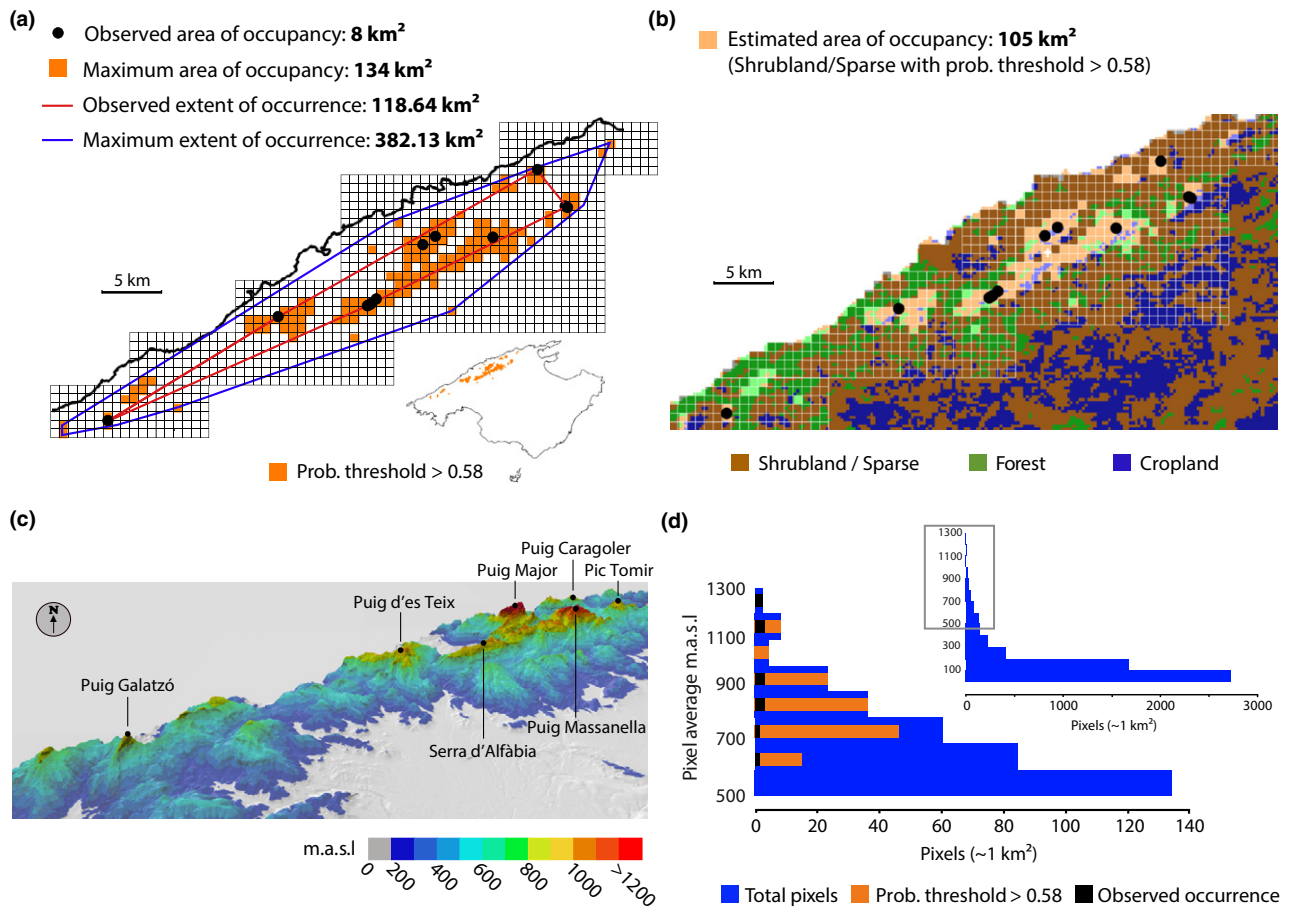


Figure 3 Distribution of *Lasius balearicus* sp. nov. Presence records (black dots) are displayed on maps for Serra de Tramuntana, northern Mallorca, highlighting (a) cells with estimated presence probability > 0.58 (threshold maximizing the sum of sensitivity and specificity) and (b) cells with estimated presence by combining climatic plus land cover data. (c) The peaks with recorded presence are indicated in a 3D view of the mountain range. (d) The elevational distribution of pixels with observed (black) and with estimated presence (orange) is shown on a background distribution of elevations for the entire island (blue). Extent of occurrence and areas of occupancy based on both observed and estimated presence are indicated according to IUCN criteria.

S7 in Appendix S1). The sister lineage comprises several widespread taxa, suggesting that the common ancestor occurred on the mainland. The last land bridge between Mallorca and the mainland existed no more recently than about 5 Ma (Meulenkamp & Sissingh, 2003) and, therefore, the ancestor most likely colonized the island by rafting or dispersal subsequent to the disappearance of the last land bridge. In fact, other *Lasius* species widespread on the mainland are also present in the Balearics (*L. grandis* and *L. lasioides*), proving that dispersal across the Mediterranean is not an uncommon event in this group. Ant endemism in Mediterranean islands is surprisingly low: only four endemic species are known from Corsica (Casevitz-Weulersse, 1996, 2010) and three from Sardinia (Baroni Urbani, 1971; Rigato, 1999), none of them within the genus *Lasius*. Thus, *Lasius balearicus* Talavera, Espadaler & Vila, sp. nov. represents the first endemic ant to be described in the Balearic Islands, as well as the first endemic *Lasius* species in the Mediterranean islands.

Future trends

Fragility of island endemic organisms is well documented, and a high percentage of recorded extinctions have occurred on islands (Turvey, 2009; Fordham & Brook, 2010; Losos & Ricklefs, 2010). The reason seems to be that species with small populations, such as *L. balearicus*, cannot deal with large and rapid ecological changes such as deforestation, natural catastrophes, habitat reduction or climate change. Our data show that the species may collapse in distribution within decades. Certainly, modelling based on future climatic conditions predicts a rapid loss of suitable habitat for this species under all the scenarios studied. The use of three different SRES emission scenarios to assess future climate change allowed us to capture the uncertainty in future climate resulting from human decisions. Indeed, they produce different results in agreement with the levels of global surface warming (IPCC, 2001, 2007) displayed in the three scenarios. The worst cases are shown by the SRES scenarios A1b and

A2a, where the suitable area would be reduced to a minimum by 2050, and apparently to zero in 2080. The A1b scenario is based on converging successful economic development that would minimize richness differences among countries. A2a assumes a differentiated world that consolidates into a series of economic regions, somehow reproducing the present situation and tendencies. Finally, the B2a SRES scenario is based on environmental, social and economical sustainability, and assumes lower energy requirements and greenhouse gas emissions. In the latter case, the model also predicts a fast narrowing of *L. balearicus* potential habitat, although slightly less intense, and by 2080 the species may only survive with very low probability in a single cell at each of the two main peaks of the island (Puig Major and Puig de Massanella).

It is certainly true that several caveats are associated with species distribution models, and these should be considered when such results are translated to conservation policies (Sinclair *et al.*, 2010; Beale & Lennon, 2012; Guisan *et al.*, 2013). These factors traditionally include biases derived from incomplete sampling of niche space, the use of inaccurate climate data, especially for elevational gradients, and the inability to account for time lags or historical accidents that have shaped current distributions. For the last concern, it is often assumed that organisms are in equilibrium with the environmental space that best suits their requirements, but absences in apparently suitable habitats can occur for reasons other than climate, such as dispersal limitations or irregular historical accidents. *Lasius balearicus* seems to be at equilibrium with contemporary climate. The species is present in all apparently suitable mountainous areas, always in a very characteristic habitat, and dispersal is not expected to be a limiting factor for winged adults given the small geographical scale of the island. This is further supported by the low intraspecific genetic divergence observed, which suggests recent gene flow among populations.

Additional factors may play a role in combination with climate change in determining the current restricted distribution of *L. balearicus*. For example, it has been demonstrated that forested areas can shift towards higher elevations as a result of climate change (Walther *et al.*, 2005). Given that *L. balearicus* seems unable to inhabit forested areas, this phenomenon could impose another crucial source of pressure. Besides, goats introduced on the island by humans are having a profound impact on the environment. They are frequent on the highest peaks, and programmes exist to try to control their overpopulation. Potential competition with the phylogenetically closest species on the island, *L. grandis*, may also be considered. *Lasius grandis* is a generalist species and can be found from sea level to high elevations. In a few cases, nests of this species were found a short distance from those of *L. balearicus*, although they are generally found at lower elevations. In addition, fires may have had a negative influence, given their recurrent occurrence in the Mediterranean region during summer. In Mallorca, there have been almost 100 forest fires per year in the last decade

(2001–2011) (data from Servei de Gestió Forestal i Protecció del Sòl, Govern de les Illes Balears, <http://www.caib.es/>). In fact, in the summer of 2013 a fire devastated 2300 hectares in Puig Galatzó, with yet unknown consequences for the southernmost known populations of *L. balearicus*. Moreover, farmers traditionally burned the most abundant plant in the mountain range (*Ampelodesmos mauritanicus*) in order to use the young shoots as food for their animals. Thus, any of these factors in combination with climate change could explain why a species that during the last 1.5 Myr has survived much more extreme climate changes than projected for the near future is facing potential extinction. Overall, the predicted trends are so clear and consistent that, even assuming that climatic models may be imprecise and future range estimations necessarily include a degree of uncertainty, there is no doubt that the species is facing a major threat, irrespective of the exact probabilities of years when it could become extinct.

The potential of *L. balearicus* to cope with climate change by shifting its climatic niche is low. An elevational shift is observed in our projections (Fig. 2), but the species already inhabits the highest peaks and the result is generally the disappearance at the lowest elevations. Because there are no more mountains in the Balearic Islands, a spatial shift would imply a virtually impossible dispersal to suitable habitat on the Iberian mainland or to other mountainous islands such as Corsica or Sardinia. Adaptation to new climatic conditions could be driven through changes in phenology or by intrinsic evolution (Lavergne *et al.*, 2010; Salamin *et al.*, 2010; Bellard *et al.*, 2012), but the population sizes and genetic variability upon which natural selection can act are very low in *L. balearicus*. Moreover, nests of *Lasius* ants may last for several years, indicating long generation times. Thus, all the evidence suggests that it is highly improbable that *L. balearicus* could adapt to new habitats in such a short time.

Conservation status

The extremely low intraspecific genetic diversity, total range, and predictions of future rapid loss of suitable habitat of *L. balearicus*, coupled with the apparent impossibility of dispersal because of its geographical and elevational isolation, suggest the probability of extinction for *L. balearicus* in the short term. As a consequence, we strongly recommend including *Lasius balearicus* Talavera, Espadaler & Vila, sp. nov. in the IUCN Red List of Threatened Species (IUCN, 2001) under the category 'Endangered' [EN B1ab(i,ii,iv); B2ab(i,ii,iv); C2a(i)].

Risks and management

Management for the conservation of this species would require in the first place monitoring of the known populations and assessment of the number of nests with greater precision, as well as exploration of the peaks that have not yet been inspected. This would allow the documentation of

potential future changes in the distribution and densities of populations, which are especially likely on the lowest peaks. Apart from a more in-depth survey, the habitat needs special protection. Indeed, because the future of *L. balearicus* is uncertain as a result of global warming, it is most important to avoid any other sources of pressure that could synergistically affect this species. The Serra de Tramuntana is a UNESCO World Heritage Site and the majority of the range belongs to a local category with medium-level protection (Paratge Natural). The creation of areas where goats are excluded could help in studying their effects on *L. balearicus* populations (as well as on other protected species). Several endemic plants have found refuge on some of the summits or even just on one (Sáez & Rosselló, 2000, 2001; López *et al.*, 2012), which should encourage policymakers to consider directed protection initiatives in these sites. Despite the strongly negative effects of macroclimate on the distribution of *L. balearicus*, microhabitat choice or changes in behaviour may help in maintaining some populations beyond the dates that models suggest. Given that *L. balearicus* does not apparently display intraspecific geographical differentiation based on available genetic data, it should be treated as a single unit from a conservation point of view. As a consequence, we recommend focusing efforts and resources on the two peaks with the highest elevations and extension of suitable habitat (Puig Major and Puig de Massanella), which are those that harbour populations predicted to resist the effects of climate change for longest. In summary, we propose that monitoring of the presumably rapid decline at minor peaks may lead to a better understanding of how the species is actually affected by climate change and additional factors, and eventually this knowledge may be applied to conservation measures on the highest peaks.

TAXONOMY

Lasius (s. str.) *balearicus* Talavera, Espadaler & Vila, sp. nov.

The species belongs in the subgenus *Lasius* s. str. as conceived by Wilson (1955). The maxillary palp segments V and VI are subequal in length to segment IV and eye length is at least $0.20 \times$ the head width. Those two characters in combination define *Lasius* s. str. The small size, high pilosity, and a distinct coloration are the three main diagnostic characteristics typifying *Lasius balearicus* sp. nov. (Fig. 4). Its description follows.

Standard measurements and indices

Absolute measures, indices and description scheme follow Seifert (1992) to allow a direct comparison with Palaearctic members of *Lasius* s. str.

HL. Head length, in millimetres. Measured in full face view, the maximum head capsule length, mandibles excluded. From the anterior clypeal midpoint to the posterior margin

of the occiput. HL/HW (900) and SL/HL (900) are values calculated for a worker with HL = 900 as proposed by Seifert (1992).

HW. Head width, in millimetres. Maximum width of the head.

SL. Scape length, in millimetres. The maximum scape length, excluding the neck close to the articular bulb.

nBH. In full face view, number of standing hairs from occipital profile to hind margin of the eye. The number refers to one half of the head.

PDCL, in micrometres. Average distance of pubescence hairs on the clypeus, obtained as defined by Seifert (1992).

nHS. Number of standing hairs projecting from the dorsal profile of the scape. Hairs on distal apex of the scape are not included.

nHHT. Number of standing hairs projecting from the extensor profile of the hind tibia. Hairs on distal apex of the tibia are not included.

Digital colour images were captured with a Leica DFC420 digital camera mounted on a Leica M80 stereomicroscope. The software FireCam 1.7 and Combine ZP were used.

Type material

Holotype: worker collected in Coll des Prat, Escorca, Mallorca, Spain, 39°48'29.86" N 2°51'4.52" E, 1194 m, 13.x.2008, code 08R384, R. Vila & G. Talavera leg. Deposited at the Natural History Museum (London, UK).

Paratypes. 14 workers from the same nest as the holotype. Coll des Prat, Escorca, Mallorca, Spain, 39°48'29.86" N 2°51'4.52" E, 1194 m, 13.x.2008, code 08R384, R. Vila & G. Talavera leg. 15 workers, Puig des Teix, Mallorca, Spain, 39°43'56.74" N, 2°38'53.03" E, 919 m, 12.x.2008, code 08I725, R. Vila & G. Talavera leg. 15 workers, pic Tomir, Mallorca, Spain, 39°50'13.88" N, 2°55'19.46" E, 1048 m, 14.x.2008, code 08R372, R. Vila & G. Talavera leg. Two workers, Coma de n'Arbona, Mallorca, Spain, 39°48'5"N, 2°47'8.99"E, 1200 m, 2009, code PM053, A. Traveset leg. One worker, Puig des Teix, Mallorca, Spain, x.1982, C.A. Collingwood leg. One worker, ses Clotades, Mallorca, Spain, 39°48'33.99"N, 2°47'49.99" E, 1330 m, 15.vi.2011, code PM1006, C. Tur leg.

Three paratype workers from the same nest as the holotype deposited at each of the following institutions: Museum of Comparative Zoology (Cambridge, MA, USA), Natural History Museum (London, UK) and Senckenberg Museum (Görlitz, Germany). Three paratype workers from Puig des Teix deposited at the Museu Balear de Ciències Naturals (Sóller, Mallorca). Other paratype material in the authors' collections [Institut de Biologia Evolutiva (CSIC-UPF) and Universitat Autònoma de Barcelona, both in Barcelona, Spain].

Description of worker [$n = 51$ for all variables but PDCL ($n = 20$) and mandibular dents ($n = 48$)]. See also Tables S3 and S4 in Appendix S1 for biometric statistical comparisons within Palaearctic *Lasius* s. str.

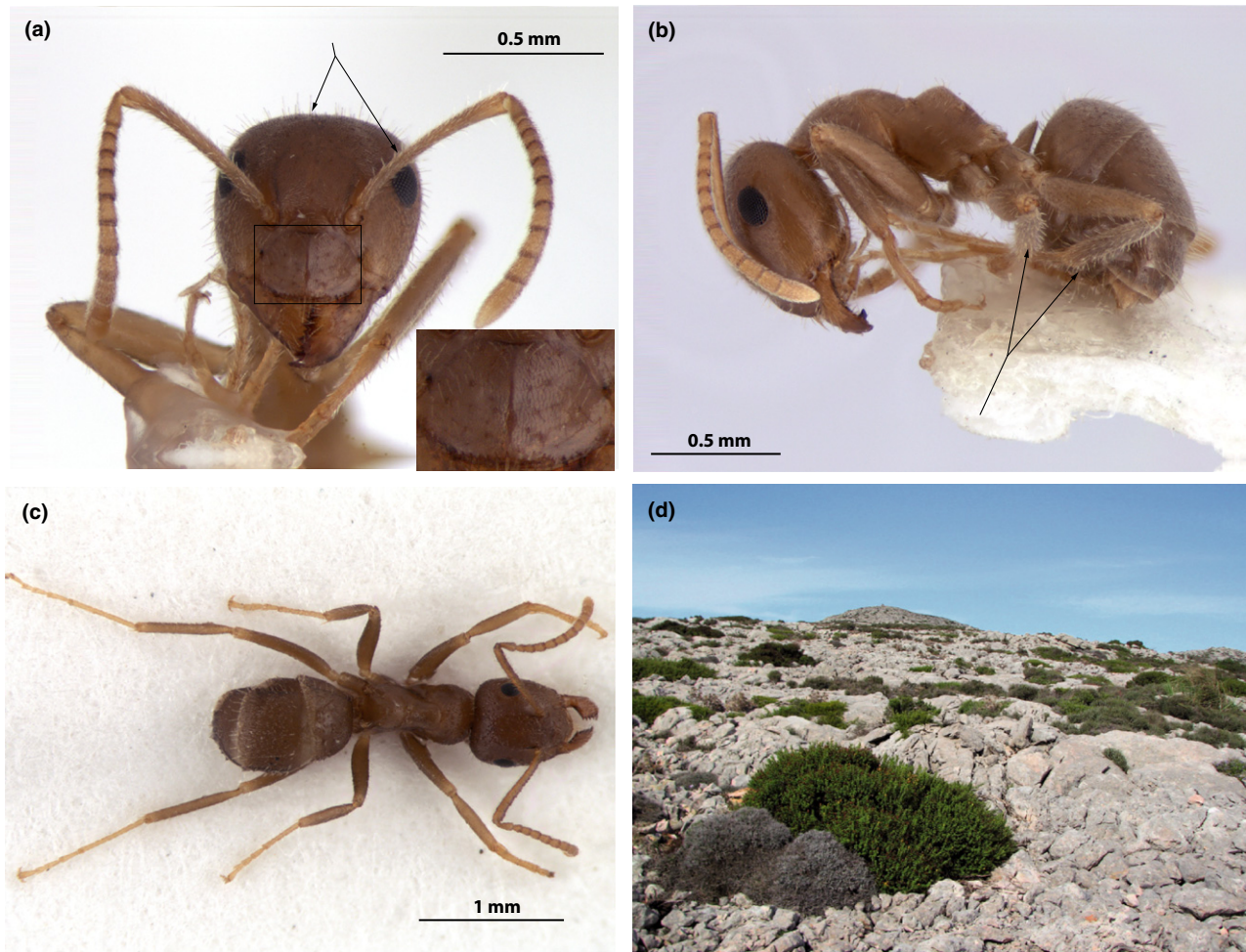


Figure 4 The three main diagnostic characteristics combined (small size, high pilosity, and a distinct coloration) define *Lasius balearicus* sp. nov. (a) Frontal view shows a general hairiness all over the cephalic capsule and scape (arrows). A very diluted clypeal pubescence (inset) is also noteworthy. (b) Lateral view displays marked hairiness in the middle and hind tibiae (arrows). (c) Dorsal view illustrates the small absolute size and characteristic yellowish brown coloration. (d) Characteristic habitat for the species: summital areas with sparse shrubby vegetation on calcareous substrate.

Measurements: mean; SD (range). Head longer than wide; HL 0.88; 0.05 (0.73–0.97), HW 0.80; 0.05 (0.65–0.89), HL/HW 1.09; 0.02 (1.04–1.12). HL/HW (900) 1.101. In frontal view the head profile is entirely hairy, up to the mandible base (Fig. 4a); nBH 22.92; 3.28 (13–30). Clypeal pubescence rather diluted, similar in density to *L. platythorax*; PDCL 26.43; 4.87 (19–42). Clypeal carina variable, even in individuals of the same nest: from being clearly expressed in the anterior two-thirds to totally absent. Scape usually shorter than head length; SL 0.85; 0.05 (0.67–0.93), SL/HL 0.96; 0.02 (0.91–1.03). SL/HL (900) 0.966. Very hairy scape; nHS 35.82; 5.38 (26–52). Very hairy tibiae (Fig. 4b); nHHT 29.78; 4.61 (17–40). Mandibular dents 8.55; 0.57 (8–10). Surface characters: frontal head with very visible punctures. Microreticulum is more developed at the posterior third of the head surface, and most developed in the disk of pronotum. Space between punctures and microreticulum is shining. Colour: the entire body is yellowish brown (Fig. 4c), with antennae and tarsi clearer (Fig. 4b).

Differential diagnosis

Using the dichotomous key in Seifert (1992) this species would key to couplet 28 although its morphology does not fit either of the two species under the dichotomy *L. platythorax* and *L. grandis*. Specifically, by the character HL/HW (900) it would correspond to *L. grandis* and by the character SL/HL (900) it would be *L. platythorax*. Coloration of *L. balearicus* is also clearly distinct from that of those two species. Seifert's (1992) key could be amended as follows in order to include *L. balearicus*:

- 28 HL/HW (900) < 1.070..... *platythorax*
- HL/HW (900) > 1.070..... 28a
- 28a SL/HL (900) > 0.982. Size much bigger (HL 1037 ± 0.06) and less hairy (nHS 22.8 ± 7.3)..... *grandis*
- SL/HL (900) < 0.982. Size smaller (HL 0.88 ± 0.05) and hairier (nHS 35.8 ± 5.3)..... *balearicus*

The combination of morphology and colour of *L. balearicus* is unique. Small body size, AND coloration AND marked hairiness characterize *L. balearicus*. Specifically, the number of standing hairs on dorsal profile of the scape (Fig. 4a) is the highest among known species of Palaearctic *Lasius*. The number of tibial hairs is also very high (Fig. 4b), only surpassed by the Asiatic *L. hirsutus*, from which it differs by the much denser gaster tergite pubescence in *L. balearicus*. Colour is also diagnostic (Fig. 4c). Taken in isolation, workers of *L. balearicus* are reminiscent of recently eclosed *L. grandis* or *L. cinereus*, which are the morphologically and phylogenetically (see Fig. 1) closest species. All examined workers have the same, consistent, coloration. When dry, the gaster is somewhat darker than the head and alitrunk.

Within the Palaearctic *Lasius* s. str. species, the closest species are *L. grandis* Forel and *L. cinereus* Seifert, both species having a Western Mediterranean distribution (Seifert, 1992; Espadaler *et al.*, 2011). *Lasius grandis*, as its name indicates, has a bigger size, with HL (standard deviation) 1.03 (0.06), a less hairy scape and legs, with nHS 22.8 (7.3) and nHHT 25.6 (6.7), and denser clypeal pubescence (PDCL 19.3 (4.9)). *Lasius cinereus*, with its entirely dull mesosoma, is clearly separable from *L. balearicus*, whose pronotum sides are shining. Hairiness is less developed in *L. cinereus*, especially in the scape, with nHS 22.2 (3.5), and nHHT 21.7 (2.4). Clypeal pubescence is denser (20.5 (5.1)) in *L. cinereus*. The molecular phylogeny (Fig. 1, Fig. S3) shows that *L. balearicus* is sister to both *L. grandis* and *L. cinereus*, from which it apparently diverged approximately 1.5 Ma.

Ecology

Lasius balearicus displays a peculiar geographical distribution, as it has been solely reported from the top summits of the island of Mallorca. All localities where the species has been collected lay between 800 and 1400 metres above sea level. A typical habitat composition included rocky calcareous surfaces, with sparse and shrubby vegetation, and frequently composed of the endemic plants *Hypericum balearicum* and *Genista valdes-bermejoi* (Fig. 4d). Specimens were collected from nests under stones and on nearby vegetation, frequently tending aphids.

Etymology

The specific name is derived from the Balearic Islands.

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REFERENCES

- Bálint, M., Domisch, S., Engelhardt, C.H.M., Haase, P., Lehrian, S., Sauer, J., Theissinger, K., Pauls, S.U. & Nowak, C. (2011) Cryptic biodiversity loss linked to global climate change. *Nature Climate Change*, **1**, 313–318.
- Baroni Urbani, C. (1971) Catalogo delle specie di Formicidae d'Italia. *Memorie della Società Entomologica Italiana*, **50**, 1–287.
- Beale, C.M. & Lennon, J.J. (2012) Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 247–258.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.
- Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J. & Stockwell, D.R.B. (2007) Forecasting the effects of global warming on biodiversity. *BioScience*, **57**, 227–236.
- Butchart, S.H., Walpole, M., Collen, B. *et al.* (2010) Global biodiversity: indicators of recent declines. *Science*, **328**, 1164.
- Casevitz-Weulersse, J. (1996) Biogeographical aspects of the ant fauna of Corsica (Hymenoptera: Formicidae). *Pan-Pacific Entomologist*, **72**, 193–201.
- Casevitz-Weulersse, J. (2010) A propos des fourmis de la Corse: *Aphaenogaster corsica* n. sp. (Hymenoptera: Formicidae: Myrmicinae). *Le Bulletin d'Arthropoda*, **43**, 4–8.
- Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, **17**, 540–552.
- Crawford, A.J., Lips, K.R. & Bermingham, E. (2010) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proceedings of the National Academy of Sciences USA*, **107**, 13777–13782.
- Cremer, S., Ugelvig, L.V., Drijhout, F.P., Schlick-Steiner, B.C., Steiner, F.M., Seifert, B., Hughes, D.P., Schulz, A., Petersen, K.S., Konrad, H., Stauffer, C., Kiran, K., Espadaler, X., d'Ettorre, P., Aktaş, N., Eilenberg, J., Jones, G.R., Nash, D.R., Pedersen, J.S. & Boomsma, J.J. (2008) The evolution of invasiveness in garden ants. *PLoS ONE*, **3**, e3838.
- Cronk, Q.C.B. (1997) Islands: stability, diversity, conservation. *Biodiversity and Conservation*, **6**, 477–493.
- Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biology*, **4**, e88.

- Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–1973.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797.
- Espadaler, X., Casevitz-Weulersse, J. & Imbert, E. (2011) *Lasius cinereus* Seifert, une espèce nouvelle pour la France (Hymenoptera, Formicidae), sa distribution en Espagne et en France et remarques sur sa biologie. *Revue Française d'Entomologie*, **32**, 105–112.
- Fontaine, B., Perrard, A. & Bouchet, P. (2012) 21 years of shelf life between discovery and description of new species. *Current Biology*, **22**, R943.
- Fordham, D.A. & Brook, B.W. (2010) Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation*, **19**, 329–342.
- Guisan, A., Tingley, R., Baumgartner, J.B. *et al.* (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424–1435.
- Hasegawa, E. (1998) Phylogeny and host–parasite relationships in social parasitism in *Lasius* ants. *Entomological Science*, **1**, 133–135.
- Heled, J. & Drummond, A. (2010) Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution*, **27**, 570–580.
- Herreraiz, J.A. & Espadaler, X. (2009) Descripción de la reina de *Lasius cinereus* Seifert (Hymenoptera: Formicidae). *Boletín de la Sociedad entomológica Aragonesa*, **44**, 143–146.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.
- IPCC (2001) *Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- IPCC (2007) *Climate change 2007: Working Group I: the physical science basis*. Cambridge University Press, Cambridge, UK. Available at: http://www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html.
- IUCN (2001) *IUCN Red List categories and criteria: version 3.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.
- IUCN (2012) *IUCN Red List of Threatened Species. Version 2012.2*. Available at: <http://www.iucnredlist.org/> (downloaded on 18 October 2012).
- Janda, M., Folkova, D. & Zrzavy, J. (2004) Phylogeny of *Lasius* ants based on mitochondrial DNA and morphology, and the evolution of social parasitism in the Lasiini (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, **33**, 595–614.
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 321–350.
- Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarrés, J.F., Proença, V. & Scharlemann, J.P.W. (2010) *Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services*. Technical Series no. 50. Secretariat of the Convention on Biological Diversity, Montreal.
- Liu, C., Berry, P.M., Dawson, P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.
- López, J.M., Martinell, C., Massó, S., Blanché, C. & Sáez, L. (2012) The ‘paradigm of extremes’: extremely low genetic diversity in a extremely narrow endemic species, *Coristospermum huteri* (Umbelliferae). *Plant Systematics and Evolution*, **299**, 439–446.
- Losos, J.B. & Ricklefs, R.E. (eds) (2010) *The theory of island biogeography revisited*. Princeton University Press, Princeton, NJ.
- Mace, G.M., Masundire, H. & Baillie, J.E.M. (2005) Biodiversity. *Ecosystems and human well-being: current state and trends* (ed. by B. Scholes and R. Hassan), pp. 79–122. Island Press, Washington, DC.
- Maruyama, M., Steiner, F.M., Stauffer, C., Stauffer, C., Aki-no, T., Crozier, R.H. & Schlick-Steiner, B.C. (2008) A DNA and morphology based phylogenetic framework of the ant genus *Lasius* with hypotheses for the evolution of social parasitism and fungiculture. *BMC Evolutionary Biology*, **8**, 237–251.
- Meulenkamp, J.E. & Sissingh, W. (2003) Tertiary palaeogeography and tectonostratigraphic evolution of the Northern and Southern Peri-Tethys platforms and the intermediate domains of the African–Eurasian convergent plate boundary zone. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **196**, 209–228.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, **312**, 101–104.
- New, M., Hulme, M. & Jones, P. (1999) Representing twentieth-century space–time climate variability. Part 1. Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12**, 829–856.
- Pereira, H.M., Leadley, P.W., Proença, V. *et al.* (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.
- Posada, D. (2008) jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, **25**, 1253–1256.
- Quek, S.P., Davies, S.J., Itino, T. & Pierce, N.E. (2004) Codiversification in an ant–plant mutualism: stem texture and the evolution of host use in *Crematogaster* (Formicidae: Myrmicinae) inhabitants of *Macaranga* (Euphorbiaceae). *Evolution*, **58**, 554–570.
- Rambaut, A. & Drummond, A.J. (2007) *Tracer version 1.5*. Available at: <http://beast.bio.ed.ac.uk/Tracer>.

- Rigato, F. (1999) *Myrmecina melonii* n. sp., a new ant from Sardinia, with a review of the West Palaearctic *Myrmecina* (Hymenoptera Formicidae). *Bollettino della Societa Entomologica Italiana*, **131**, 83–92.
- Sáez, L. & Rosselló, J.A. (2000) A new species of *Agrostis* (Gramineae) belonging to the *A. alpina* complex. *Botanical Journal of the Linnean Society*, **133**, 359–370.
- Sáez, L. & Rosselló, J.A. (2001) *Llibre vermell de la flora amenaçada de les Illes Balears*. Govern de les Illes Balears, Palma de Mallorca.
- Salamín, N., Wüest, R.O., Lavergne, S., Thuiller, W. & Pearman, P.B. (2010) Assessing rapid evolution in a changing environment. *Trends in Ecology and Evolution*, **25**, 692–698.
- Schlick-Steiner, B.C., Steiner, F.M., Schödl, S. & Seifert, B. (2003) *Lasius austriacus* sp. n., a Central European ant related to the invasive species *Lasius neglectus*. *Sociobiology*, **41**, 725–736.
- Seifert, B. (1988) A revision of the European species of the ant subgenus *Chthonolasius* (Insecta, Hymenoptera, Formicidae). *Entomologische Abhandlungen Staatlichen Museum für Tierkunde Dresden*, **51**, 143–180.
- Seifert, B. (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). *Abhandlungen Berichte Naturkundemuseums Görlitz*, **66**, 1–67.
- Sinclair, S.J., White, M.D. & Newell, G.R. (2010) How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society*, **15**, 8.
- Sokal, R.R. & Rohlf, J.F. (1995) *Biometry*, 3rd edn. Freeman, New York.
- Steiner, F.M., Schlick-Steiner, B.C., Schödl, S., Espadaler, X., Seifert, B., Christian, E. & Stauffer, C. (2004) Phylogeny and bionomics of *Lasius austriacus* (Hymenoptera, Formicidae). *Insectes Sociaux*, **51**, 24–29.
- Talavera, G. & Castresana, J. (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology*, **56**, 564–577.
- Thomas, C.D., Cameron, A., Green, R.W., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thuiller, W., Georges, D. & Engler, R. (2013) *biomod2: ensemble platform for species distribution modeling*. R package version 3.1-25. Available at: <http://CRAN.R-project.org/package=biomod2>.
- Turvey, S.T. (ed.) (2009) *Holocene extinctions*. Oxford University Press, Oxford, UK.
- Waite, T.A. & Campbell, L.G. (2006) Controlling the false discovery rate and increasing statistical power in ecological studies. *Ecoscience*, **13**, 439–442.
- Walther, G.-R., Beißner, S. & Pott, R. (2005) Climate change and high mountain vegetation shifts. *Mountain ecosystems: studies in treeline ecology* (ed. by G. Broll and B. Keplin), pp. 77–95. Springer, Berlin, Heidelberg.
- Willis, K.J., Bennett, K.D. & Walker, D. (2004) The evolutionary legacy of the ice ages. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 155–303.
- Wilson, E.O. (1955) A monographic revision of the ant genus *Lasius*. *Bulletin of the Museum of Comparative Zoology*, **113**, 1–201.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting tables (Tables S1–S7) and figures (Figs S1–S3).

BIOSKETCHES

Gerard Talavera is a postdoctoral researcher currently at the Museum of Comparative Zoology at Harvard University. His research is currently focused on insect biodiversity, phylogenetics and evolution.

Xavier Espadaler is a professor at Universitat Autònoma de Barcelona. As a myrmecologist, he studies ant diversity, ecology and social behaviour, as well as trophic interactions in arthropod communities.

Roger Vila is a CSIC researcher at Institut de Biologia Evolutiva (CSIC-UPF) in Barcelona. He is interested in the study of insect diversity, evolution and conservation with specific interest in speciation, climate change and biogeography in the European/Mediterranean area.

Author contributions: G.T. and R.V. conceived the study and collected the data; X.E. examined the samples and conducted morphometric measurements; G.T. obtained molecular data and performed phylogenetic and niche modelling analyses. G.T. led the writing. All authors contributed in the form of discussions and suggestions, and approved the final manuscript.

Editor: Richard Ladle

SUPPORTING INFORMATION

Discovered just before extinction? The first endemic ant from the Balearic Islands (*Lasius balearicus* sp. nov.) is endangered by climate change

Gerard Talavera, Xavier Espadaler and Roger Vila

Appendix S1 Supporting tables (Tables S1–S7) and figures (Figs S1–S3).

Table S1 Species of *Lasius* studied, specimen codes, GenBank codes, localities and sources of DNA sequences: [1] = this study; [2] = Maruyama *et al.* (2008); [3] = Steiner *et al.* (2004); [4] = Cremer *et al.* (2008).

Species	Sample code	COI	16S	LR	Wg	Locality	Source
<i>L. balearicus</i>	RVcoll.08J418	KC820339	KC820295	KC820371	KC820393	Valldemossa, Es Teix. Mallorca. Spain (920 m)	[1]
<i>L. balearicus</i>	RVcoll.08J419	KC820336	KC820296			Valldemossa, Es Teix. Mallorca. Spain (920 m)	[1]
<i>L. balearicus</i>	RVcoll.08J420	KC820335	KC820297			Valldemossa, Es Teix. Mallorca. Spain (920 m)	[1]
<i>L. balearicus</i>	RVcoll.08J421	KC820338	KC820298	KC820375	KC820395	Coll des Prat, Escorca. Mallorca. Spain (1194 m)	[1]
<i>L. balearicus</i>	RVcoll.08J422	KC820334	KC820299			Coll des Prat, Escorca. Mallorca. Spain (1194 m)	[1]
<i>L. balearicus</i>	RVcoll.08J423	KC820333	KC820300			Coll des Prat, Escorca. Mallorca. Spain (1194 m)	[1]
<i>L. balearicus</i>	RVcoll.08J424	KC820332	KC820301	KC820372	KC820396	Pic Tomir. Mallorca. Spain (1035 m)	[1]
<i>L. balearicus</i>	RVcoll.08J425	KC820337	KC820302			Pic Tomir. Mallorca. Spain (1041 m)	[1]
<i>L. balearicus</i>	RVcoll.08J426	KC820340	KC820303			Pic Tomir. Mallorca. Spain (1048 m)	[1]
<i>L. balearicus</i>	RVcoll.12L413	KC820351	KC820304	KC820373	KC820394	Serra d'Alfàbia. Mallorca. Spain (1066 m)	[1]
<i>L. balearicus</i>	RVcoll.12L414	KC820346	KC820305			Serra d'Alfàbia. Mallorca. Spain (1056 m)	[1]

<i>L. balearicus</i>	RVcoll.12L419	KC820343	KC820306			Serra d'Alfàbia. Mallorca. Spain (1025 m)	[1]
<i>L. balearicus</i>	RVcoll.12L421	KC820352	KC820307	KC820374	KC820398	Puig Galatzó. Mallorca. Spain (1006 m)	[1]
<i>L. balearicus</i>	RVcoll.12L424	KC820344	KC820308			Puig Galatzó. Mallorca. Spain (1012 m)	[1]
<i>L. balearicus</i>	RVcoll.12L425	KC820345	KC820309			Puig Galatzó. Mallorca. Spain (998 m)	[1]
<i>L. grandis</i>	RVcoll.08J433	KC820327	KC820291	KC820363	KC820400	Riera de Fuirosos. Catalonia. Spain	[1]
<i>L. grandis</i>	RVcoll.08J435	KC820326	KC820292	KC820378	KC820401	Campus UAB. Catalonia. Spain	[1]
<i>L. grandis</i>	RVcoll.08J437	KC820325	KC820293	KC820379	KC820402	Campus UAB. Catalonia. Spain	[1]
<i>L. grandis</i>	RVcoll.08J438	KC820330	KC820294	KC820364	KC820397	Valldemossa, Son Moragues. Mallorca. Spain	[1]
<i>L. grandis</i>	RVcoll.12L453	KC820357	KC820317	KC820365	KC820414	Eivissa. Spain	[1]
<i>L. cinereus</i>	RVcoll.08J427	KC820328		KC820384	KC820415	Riera de Fuirosos. Catalonia. Spain	[1]
<i>L. cinereus</i>	RVcoll.08J428	KC820341	KC820287	KC820370	KC820416	Riera de Fuirosos. Catalonia. Spain	[1]
<i>L. cinereus</i>	RVcoll.08J429	KC820329	KC820288	KC820362	KC820419	Riera de Fuirosos. Catalonia. Spain	[1]
<i>L. cinereus</i>	RVcoll.08J430	KC820331	KC820289	KC820376	KC820403	Pont de Muntanyana. Catalonia. Spain	[1]
<i>L. cinereus</i>	RVcoll.08J431	KC820342	KC820290	KC820377	KC820413	Coll d'Ares. Catalonia. Spain	[1]
<i>L. niger</i>	RVcoll.13S106	KC820354	KC820319	KC820367	KC820406	Ferreras de Abajo. Zamora. Spain	[1]
<i>L. niger</i>	RVcoll.13S107	KC820355	KC820320	KC820368	KC820417	Montesquiu. Catalonia. Spain	[1]
<i>L. niger</i>	RVcoll.13S108	KC820356	KC820321	KC820369	KC820407	Landau. Germany	[1]
<i>L. emarginatus</i>	RVcoll.13S104	KC820359	KC820323	KC820383	KC820391	Montesquiu. Catalonia. Spain	[1]
<i>L. emarginatus</i>	RVcoll.13S105	KC820353	KC820324	KC820366	KC820392	Montesquiu. Catalonia. Spain	[1]
<i>L. alienus</i>	RVcoll.13S100	KC820350	KC820315	KC820380	KC820410	Serra del Cadí. Catalonia. Spain	[1]
<i>L. alienus</i>	RVcoll.13S101	KC820360	KC820316	KC820381	KC820399	Serra del Cadí. Catalonia. Spain	[1]
<i>L. lasioides</i>	RVcoll.12L301	KC820347	KC820310	KC820386	KC820404	Lluçmajor. Mallorca. Spain	[1]
<i>L. lasioides</i>	RVcoll.12L333	KC820348	KC820311	KC820387	KC820418	Artà. Mallorca. Spain	[1]
<i>L. lasioides</i>	RVcoll.12L459	KC820349	KC820312	KC820388	KC820405	Mallorca. Spain	[1]
<i>L. psammophilus</i>	RVcoll.13S111	KC820358	KC820322	KC820382	KC820408	Melby Overdrev. Halsnaes. Denmark	[1]
<i>L. platythorax</i>	RVcoll.13S109	KC820361	KC820318	KC820385	KC820409	Bollemosen. Skodsborg. Denmark	[1]
<i>L. brunneus</i>	RVcoll.13S102		KC820313	KC820389	KC820411	Collsupina. Catalonia. Spain	[1]
<i>L. brunneus</i>	RVcoll.13S103		KC820314	KC820390	KC820412	Aiguamolls de l'Empordà. Catalonia. Spain	[1]
<i>L. japonicus</i>	MMANT19	AB371015	AB371061			Kagawa-ken, Takamatsu-shi. Japan	[2]
<i>L. japonicus</i>	MMANT55	AB371014	AB371060			Chiba-ken, Kimitsu-shi. Japan	[2]
<i>L. japonicus</i>	MMANT76	AB371016	AB371062			Hokkaido, Sapporo-shi. Japan	[2]
<i>L. niger</i>	MMANT26	AB371019	AB371065			Vienna. Austria	[2]
<i>L. niger</i>		AY225866				Vienna. Austria	[3]
<i>L. platythorax</i>	MMANT28	AB371020	AB371066			Moosbrunn. Austria	[2]
<i>L. platythorax</i>		AY225867				Moosbrunn. Austria	[3]
<i>L. emarginatus</i>	MMANT41	AB371011	AB371057			Vienna. Austria	[2]
<i>L. emarginatus</i>		AY225868				Vienna. Austria	[3]

<i>L. hayashi</i>	MMANT46	AB371013	AB371059	Gifu-ken, Kamitakara-mura. Japan	[2]
<i>L. hayashi</i>	MMANT54	AB371012	AB371058	Chiba-ken, Kimitsu-shi. Japan	[2]
<i>L. productus</i>	MMANT18	AB371021	AB371067	Kagawa-ken, Takamatsu-shi. Japan	[2]
<i>L. sakagamii</i>	MMANT29	AB371022	AB371068	Gifu-ken, Gifu-shi. Japan	[2]
<i>L. sakagamii</i>	MMANT56	AB371023	AB371069	Tōkyō-to, Edogawa-ku. Japan	[2]
<i>L. sakagamii</i>		AY225864		Gifu. Japan	[3]
<i>L. alienus</i>	MMANT21	AB371008	AB371054	Braunsberg. Austria	[2]
<i>L. alienus</i>		AY225865		Braunsberg. Austria	[3]
<i>L. psammophilus</i>		AY225863		Gföhl. Austria	[3]
<i>L. brunneus</i>		AY225877		Hof. Austria	[3]
<i>L. brunneus</i>	MMANT25	AB371010	AB371056	Rassing. Austria	[2]
<i>L. austriacus</i>	MMANT27	AB371009	AB371055	Feldberg. Austria	[2]
<i>L. austriacus</i>		AY225870		Feldberg. Austria	[3]
<i>L. austriacus</i>		AY225869		Braunsberg. Austria	[3]
<i>L. austriacus</i>		AY225873		Retz. Austria	[3]
<i>L. austriacus</i>		AY225871		Feldberg. Austria	[3]
<i>L. austriacus</i>		AY225872		Feldberg. Austria	[3]
<i>L. neglectus</i>	MMANT20	AB371018	AB371064	Budapest. Hungary	[2]
<i>L. neglectus</i>		AY225875		Budapest. Hungary	[3]
<i>L. neglectus</i>		AY225876		Debrecen. Hungary	[3]
<i>L. turcicus</i>		DQ975435		Maltepe. Turkey	[4]
<i>L. turcicus</i>		DQ975428		Mueezzinler. Turkey	[4]
<i>L. turcicus</i>		DQ975426		Bilecik. Turkey	[4]
<i>L. turcicus</i>		DQ975417		Kuelcueler. Turkey	[4]
<i>L. turcicus</i>		DQ975401		Pazaryeri. Turkey	[4]
<i>L. lasioides</i>		AY225874		Sant Cugat del Vallès. Catalonia. Spain	[3]
<i>L. mixtus</i>		AB370988	AB371034	Göpfritz. Austria	[3]

Table S2 Geographical coordinates of *Lasius balearicus* presence records used for ecological niche modelling.

Locality	Longitude	Latitude
Valldemossa (Puig des Teix)	39.732428	2.648064
Coll des Prat (Puig Massanella)	39.808294	2.851256
Coll des Prat (Puig Massanella)	39.808347	2.852008
Coll des Prat (Puig Massanella)	39.808483	2.852017
Pic Tomir	39.837189	2.922072
Pic Tomir	39.836853	2.922008
Pic Tomir	39.836767	2.92215
Pic Tomir	39.836967	2.922389
Pic Tomir	39.838011	2.921797
Pic Tomir	39.837967	2.920722
Coma n'Arbona (Puig Major)	39.801389	2.785833
Ses Clotades (Puig Major)	39.809444	2.797222
Serra d'Alfàbia	39.743472	2.732889
Serra d'Alfàbia	39.74425	2.734944
Serra d'Alfàbia	39.744889	2.735806
Serra d'Alfàbia	39.748917	2.741056
Puig Galatzó	39.633917	2.486889
Puig Galatzó	39.633722	2.4865
Puig Galatzó	39.634222	2.486611
Puig Caragoler	39.87199	2.89341
Puig Caragoler	39.87146	2.89360

Table S3 Biometric measures and indexes for the *Lasius* s. str. species included in our study plus *L. mixtus*. Measures obtained by us are highlighted in red. The rest of the values were extracted from literature (Seifert, 1988, 1992; Schlick-Steiner *et al.*, 2003; Herraiz & Espadaler, 2009). The number of specimens measured for each species is shown at the top of the columns or, if different, next to the character values.

	<i>balearicus</i>	<i>niger</i>	<i>platythorax</i>	<i>japonicus</i>	<i>grandis</i>	<i>cinereus</i>	<i>emarginatus</i>	<i>hayashi</i>	<i>productus</i>	<i>sakagami</i>	<i>alienus</i>	<i>psammophilus</i>	<i>brunneus</i>	<i>austriacus</i>	<i>neglectus</i>	<i>turcicus</i>	<i>lasioides</i>	<i>mixtus</i>
	(n=51)	(n=5)	(n=5)	(n=4)	(n=5)	(n=5)	(n=5)		(n=1)					(n=5)	(n=17)			(n=10)
HW	811.30	926.72	952.80	923.21	973.26	831.37	929.41	980.87	1011.52	841.03	781.75	785.57	915.27	666.31	663.55	813.52	793.36	990.10
HL	886.58	981.40	985.20	982.30	1037.50	917.00	1001.90	1010.30	1114.70	914.20	848.20	843.70	947.30	747.60	793.60	896.50	848.10	1056.30
CS	848.94	954.06	969.00	952.76	1005.38	874.18	965.65	995.59	1063.11	877.62	814.98	814.63	931.28	706.96	728.57	855.01	820.73	1023.20
SL	857.56	920.55	937.91	953.81	1021.94	898.66	1003.90	951.70	1207.22	914.20	781.19	796.45	807.10	654.15	743.92	846.03	804.00	913.71
SL/CS	1.01	0.96	0.97	1.00	1.02	1.03	1.04	0.96	1.14	1.04	0.96	0.98	0.87	0.93	1.02	0.99	0.98	0.89
HL/HW	1.09	1.06	1.03	1.06	1.07	1.10	1.08	1.03	1.10	1.09	1.09	1.07	1.04	1.12	1.20	1.10	1.07	1.07
SL/HL	0.97	0.94	0.95	0.97	0.99	0.98	1.00	0.94	1.08	1.00	0.92	0.94	0.85	0.88	0.94	0.94	0.95	0.84
PDCL	26.44 35.82	13.00	25.90	18.70	19.40	20.50	27.30	20.80	18.10	14.60	17.30	22.50	27.60	33.17	31.24	32.15	31.40	14.70
nHS	35.82	16.00	21.00	15.70	22.80	22.20	12.80	21.30	10.60	29.90	0.10	0.60	0.00	0.05	0.32	0.06	0.00	5.60
nHHT	29.78	17.70	23.30	16.90	25.70	21.70	20.60	22.40	9.10	27.80	0.90	2.30	0.20	0.16	0.29	0.53	0.00	7.26
MaDe	8.55	8.22	8.25	8.14	8.48	8.00	8.67	8.00	8.45	8.60	8.11	8.21	7.00	7.33	7.35	7.35	7.02	8.30
nBH	22.92	15.80	14.00	15.50	18.80	14.00	13.40	16.40	12.10	23.60	4.70	8.50	2.30	4.83	10.02	8.55	3.20	14.60
HWQ	1599 (n=2)	1617.30	1568.90	1609.00	1674.80	1508.00	1592.20	1693.00	1825.00	1591.50	1542.00	1612.90	1541.40	1399.00	1340.00	1380.80	1396.30	1495.00
HLQ	1499 (n=2)	1430.10	1388.20	1445.00	1529.80	1400.00	1454.60	1518.00	1671.00	1444.00	1383.20	1417.20	1384.70	1253.00	1200.00	1230.00	1234.90	1365.00
HLQ/HWQ	0.94 (n=2)	0.88	0.88	0.90	0.91	0.94	0.91	0.90	0.92	0.91	0.90	0.88	0.90	0.90	0.89	0.89	0.89	0.91
SLQ	1299 (n=2)	1680.69	1622.11	1696.61	1773.06	1198.00	1632.36	1878.71	1528.00	1682.00	1648.04	1650.59	1754.56	1082.00	1030.00	1428.24	1392.22	1141.00
SLQ/HLQ	0.87 (n=2)	0.85	0.86	0.85	0.86	0.87	0.89	0.81	0.90	0.86	0.84	0.86	0.79	0.86	0.86	0.86	0.89	0.84
SLQ/HWQ	0.81 (n=2)	0.75	0.76	0.76	0.79	0.81	0.81	0.72	0.84	0.78	0.75	0.75	0.71	0.77	0.77	0.77	0.79	0.76
MLQ	2906 (n=1)	3011.00	2781.00	2740.00	3078.00	2763.00	2924.00	2796.00	3233.00	3043.00	2914.00	3041.00	2647.80	2859.00	2473.00	2726.00	2470.90	2213.00
MHQ	1506 (n=1)	1800.58	1479.49	1471.38	1557.47	1362.00	1403.52	1328.10	1600.00	1710.17	1693.03	1766.82	1218.52	1659.00	1273.00	1433.00	1141.56	1279.00
MHQ/MLQ	0.52 (n=1)	0.60	0.53	0.54	0.51	0.49	0.48	0.48	0.49	0.56	0.58	0.58	0.46	0.58	0.51	0.53	0.46	0.58

Measures and indexes for workers and, those ending in 'Q', for queens: HW, head width (in mm); HL, head length (in mm); CS, cephalic size (in mm); SL, scape length (in mm); HL/HW, head shape; SL/HL, scape index; SL/CS, relative scape index; PDCL, pubescence distance on clypeus (in μm); nHS, number of standing hairs on scapus; nHHT, number of standing hairs on hind tibia; nBH, number of standing hairs on head; MaDe, number masticatory dents (MaDe) as defined in Seifert (1992).

Table S4 Student *t*-tests, false discovery rates (FDR) and Bonferroni corrections for morphological character pair comparisons between *Lasius balearicus* and the closest *Lasius* s. str. taxa (*niger*, *platythorax*, *japonicus*, *grandis*, *cinereus* and *emarginatus*). Pair comparisons in red indicate $P > 0.001$ for FDR.

Character	Pair comparison	d.f.	<i>t</i>	<i>P</i>	order	FDR	Bonferroni
HW	bal-nig	51	-15.5958818	0	1	0.000757576	0.000909091
HL	bal-nig	51	-13.45527349	0	2	0.001515152	0.000909091
SL	bal-nig	51	-8.648149874	0	3	0.002272727	0.000909091
HL/HW	bal-nig	51	9.873328064	0	4	0.003030303	0.000909091
SL/HL	bal-nig	51	8.238030783	0	5	0.003787879	0.000909091
PDCL	bal-nig	19	11.68386695	0	6	0.004545455	0.000909091
nHS	bal-nig	51	26.04355663	0	7	0.00530303	0.000909091
nHHT	bal-nig	51	18.51193198	0	8	0.006060606	0.000909091
nBH	bal-nig	51	15.31086278	0	9	0.006818182	0.000909091
HW	bal-pla	51	-19.1199749	0	11	0.008333333	0.000909091
HL	bal-pla	51	-13.9944816	0	12	0.009090909	0.000909091
SL	bal-pla	51	-11.03119456	0	13	0.009848485	0.000909091
HL/HW	bal-pla	51	16.99880377	0	14	0.010606061	0.000909091
nHS	bal-pla	51	19.47470703	0	15	0.011363636	0.000909091
nHHT	bal-pla	51	9.933305053	0	16	0.012121212	0.000909091
nBH	bal-pla	51	19.18073394	0	17	0.012878788	0.000909091
HW	bal-jap	51	-15.12174253	0	19	0.014393939	0.000909091
HL	bal-jap	51	-13.58298067	0	20	0.015151515	0.000909091
SL	bal-jap	51	-13.21457214	0	21	0.015909091	0.000909091
HL/HW	bal-jap	51	8.448232922	0	22	0.016666667	0.000909091
nHS	bal-jap	51	26.4376876	0	23	0.017424242	0.000909091
nHHT	bal-jap	51	19.73745011	0	24	0.018181818	0.000909091
nBH	bal-jap	51	15.95584131	0	25	0.018939394	0.000909091
HW	bal-gra	51	-21.88450487	0	27	0.020454545	0.000909091
HL	bal-gra	51	-21.41568799	0	28	0.021212121	0.000909091
SL	bal-gra	51	-22.56763673	0	29	0.021969697	0.000909091
HL/HW	bal-gra	51	7.878194865	0	30	0.022727273	0.000909091
nHS	bal-gra	51	17.10992118	0	31	0.023484848	0.000909091
nHHT	bal-gra	51	6.256750658	0	32	0.024242424	0.000909091
nBH	bal-gra	51	8.861077525	0	33	0.025	0.000909091
SL	bal-cin	51	-5.642338228	0	35	0.026515152	0.000909091
nHS	bal-cin	51	17.89818313	0	36	0.027272727	0.000909091
nHHT	bal-cin	51	12.38434132	0	37	0.028030303	0.000909091
nBH	bal-cin	51	19.18073394	0	38	0.028787879	0.000909091
DeMa	bal-cin	47	6.508849562	0	40	0.03030303	0.000909091
HW	bal-ema	51	-15.95840511	0	41	0.031060606	0.000909091
HL	bal-ema	51	-16.36415936	0	42	0.031818182	0.000909091
SL	bal-ema	51	-20.09171245	0	43	0.032575758	0.000909091
SL/HL	bal-ema	51	-9.714202537	0	44	0.033333333	0.000909091
nHS	bal-ema	51	30.24762037	0	45	0.034090909	0.000909091
nHHT	bal-ema	51	14.06942875	0	46	0.034848485	0.000909091
nBH	bal-ema	51	20.47069099	0	47	0.035606061	0.000909091
PDCL	bal-jap	19	6.72799567	0.000002	49	0.037121212	0.000909091
PDCL	bal-gra	19	6.119379898	0.000007	50	0.037878788	0.000909091
SL/HL	bal-gra	51	-4.945640561	0.00001	51	0.038636364	0.000909091
DeMa	bal-jap	47	4.861609942	0.00002	52	0.039393939	0.000909091
HL/HW	bal-ema	51	4.457966525	0.00005	53	0.040151515	0.000909091
PDCL	bal-cin	19	5.162983686	0.00006	54	0.040909091	0.000909091
SL/HL	bal-pla	51	4.310979745	0.00008	55	0.041666667	0.000909091

HL	bal-cin	51	-4.317114944	0.00008	56	0.042424242	0.000909091
DeMa	bal-nig	47	3.920330159	0.0003	57	0.043181818	0.000909091
DeMa	bal-pla	47	3.567350241	0.0009	58	0.043939394	0.000909091
SL/HL	bal-cin	51	-3.543122333	0.0009	59	0.04469697	0.000909091
HW	bal-cin	51	-2.711658179	0.0092	60	0.045454545	0.000909091
HL/HW	bal-cin	51	-2.667509183	0.011	61	0.046212121	0.000909091
DeMa	bal-ema	47	-1.374368619	0.18	62	0.046969697	0.000909091
SL/HL	bal-jap	51	-1.018589522	0.32	63	0.047727273	0.000909091
DeMa	bal-gra	47	0.861170865	0.4	64	0.048484848	0.000909091
PDCL	bal-ema	19	-0.749283808	0.47	65	0.049242424	0.000909091
PDCL	bal-pla	19	0.467947735	0.65	66	0.05	0.000909091

Table S5 Morphological set of characters used in phylogenetic inference. Orange: numbers correspond to selected characters from Maruyama *et al.* (2008) (characters 103 and 104 were newly incorporated). Blue: criteria to convert biometric measurements to discrete data. Below, resulting character states for the studied species. Discrete values for biometric measures and labelled morphological characters (*) were used as ordered characters for phylogenetic inference.

Discrete values for biometric measures

HW	<750(0), >750 and <900 (1), >900 (2)
HL	<800(0), >800 and <950 (1), >950(2)
CS	<750(0), >750 and <900 (1), >900 (2)
SL	<700(0), >700 and <800 (1), >800 and < 1100 (2), >1100 (3)
SL/CS	<0.95(0), >0.95 and <1.1 (1), >1.1(2)
HL/HW	<1.05(0), >1.05 and <1.15 (1), >1.15(2)
SL/HL	<0.90(0), >0.90 and <1.05 (1), >1.05(2)
PDCL	<15(0), >15 and <25 (1), >25 and < 30 (2), >30 (3)
nHS	<1 (0), >1 and <20 (1), >20 and <25 (2), >25 (3)
nHHT	<5(0), >5 and <15 (1), >15(2)
MaDe	<7.5(0), >7.5(1)
nBH	<5(0), >5 and <18 (1), >18 (2)
HWQ	<1400(0), >1400 and <1800 (1), >1800(2)
HLQ	<1300(0), >1300 and <1600 (1), >1600(2)
HL/HW	<0.89 (0), >0.89 and <0.90 (1), >0.90 and <0.93 (2), >0.93 (3)
SLQ	<1600 (0), >1600 and <1800 (1), >1800 (2)
SL/HL	<0.8 (0), >0.8 and <0.83 (1), >0.83 and <0.85 (2), >0.85 and <0.88 (3) >0.88 (4)
SL/HW	<0.75 (0), >0.75 and <0.8 (1), >0.8 and <0.83 (2), >0.83 (3)
MLQ	<2400 (0), >2400 and <2600 (1), >2600 and <3200 (2), >3200 (3)
MHQ	<1300(0), >1300 and <1600 (1), >1600(2)
MHQ/MLQ	<0.49 (0), >0.49 and <0.55 (1), >0.55 (2)

- 1* QM, Body colour: black to brown pigmentation (0), without pigmentation, yellow to reddish yellow (1).
- 2* W, Body colour: black to brown pigmentation (0), without pigmentation, yellow to reddish yellow (1).
- 3 WQ, Mouthparts: mandible with last basal tooth not clearly separated from masticatory boarder (0), basal border in right angle with masticatory border (1).
- 4* W, Mouthparts: mandible without offset tooth absent (0), with offset tooth as minute projection (1), with offset tooth (2).
- 7 M, Mouthparts: mandible with preapical cleft (0), without preapical cleft (1).
- 8 M, Mouthparts: mandible with masticatory margin emarginate (0), convex (1).
- 11 W, Mouthparts: maxillary palpus reaches to neck cavity (0), does not reach to neck cavity (1).
- 12 QM, Mouthparts: maxillary palpus long, reaching level of posterior margin of eye (0), reach to level of frontier margin of eye (1).
- 13 WQ, Mouthparts: maxillary palpus with 5th and 6th segments almost as long as 4th (0), 5th and 6th segments conspicuously reduced compared to 4th (1).
- 14 W, Mouthparts: maxillary palpus with 4th segment as long as 3rd (0), 4th conspicuously reduced to 3rd (1).
- 15 W, Mouthparts: maxillary palpus with 6th segment longer to only slightly shorter than 5th (0), conspicuously shorter than 5th (1).
- 18 W, Antenna: scape with pubescence erect, rough surface (0), decumbent to suberect surface, with hairs (1), appressed, smooth surface (2).
- 19* W, Antenna: scape with setae many (2), few (1), absent (0).
- 20* Q, Antenna: setae on scape many (2), few (1), absent (0).
- 21* Q, Antenna: scape long, more than 0.7 as long as head width (1), short, less than 0.7 as long as head width (0).
- 24* W, Genae with setae absent (0), few (1), many (2).
- 25 Q, Genae setae absent (0), present (1).
- 28 W, Head: setae simplified (0), more or less flattened and serrate laterally (1).
- 30 Q, Head: occipital margin almost strait or slightly emarginate (0), conspicuously emarginate (1).
- 32* WQ, Head: mandibular gland not developed, less than 0.3 as long as head length (0), well developed, more than 0.5 as long as head length (1).
- 33 QM, Mesosoma broader than head (0), narrower than head (1).
- 34 W, Mesosoma: setae simplified (0), more or less flattened and serrate laterally (1).
- 35 Q, Mesosoma: setae simplified (0), more or less flattened and serrate (1).
- 36 M, Mesosoma: pronotum in lateral view slightly narrowed anteriorly (0), conspicuously narrowed anteriorly part less than 0.5 as high as highest part (1).
- 38 Q, Mesosoma: mesonotum 0.8-1.2 as high as pronotum in height (0), less than 0.5 as high as pronotum (1).
- 41 Q, Mesosoma: suture between katepisternum and propodeum clear (0), not clear, poorly differentiated (1).
- 49 QM, Mesosoma: max. dimension of metapleural gland opening less wide than max. diameter of outer margin of propodeal spiracle (0), more wide (1).
- 54 M, Mesosoma: metapleural gland with sulcus its anterior (0), without sulcus (1).
- 57 QM, Wings: hyaline uniformly in basal 1/3 (0), brownish in basal part (1).
- 61* W, Petiole: in frontal view sides parallel (0), convex (1), diverging dorsad (2).
- 62* W, Petiole: shape of dorsal crest straight (0), emarginated (1), curved (2).
- 64* Q, Hind tibia: setae absent (0), few (1), many (2).
- 65* W, Hind tibia: setae absent (0), few (1), many (2).
- 66* W, Hind tibia: length of setae less than 30 μ m (0), 30 to 60 μ m (1), over 60 μ m (2).
- 67* Q, Gaster more than 1.5 as broad as mesosoma (0), less than 1.3 as broad as mesosoma (1).
- 75* Q, Overall body size not over 5 mm (0), about 5 mm and more (1).
- 86 Colony founding independent (0), parasitic on *Lasius* s. str. (1)
- 87 Activity of workers epigaeic (0), hypogaeic (1).
- 88 Colony monogynous (0), oligogynous or polygynous (1).
- 90* M, Number of teeth on masticatory border 1-4 (0), over 6 (1), nil (2).
- 91* WQ, Maxillary palp: length of 4th segment less than 0.12 head width (0), more than 0.14 head width (1).
- 92* W, Occipital head margin straight (0), straight to feebly convex (1), strongly convex (2).
- 99* Q, Scape length/head length ratio below 0.65 (0), between 0.66 and 0.81 (1), between 0.82 and 0.91 (2), over 0.91 (3).
- 101* Q, Scape pubescence character: fully appressed, smooth surface (0), moderately pubescent, decumbent (1), subdecumbent, rough surface (2).
- 102 Q, Whole surface of head without setae (0), covered by setae (1).
- 103 W, Side of pronotum smooth, shining (0), dull, mat (1)
- 104 W, Thorax coloration lighter than gaster (1), homogeneous coloration for thorax and gaster (0)

	Maruyama <i>et al.</i> (2008) (adapted)																						
	1	2	3	4	7	8	11	12	13	14	15	18	19	20	21	24	25	28	30	32	33	34	35
<i>L. balearicus</i>	1	1	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	?
<i>L. grandis</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	0
<i>L. cinereus</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	0
<i>L. brunneus</i>	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	1	0
<i>L. neglectus</i>	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	(01)	1	0	0	0	1	0
<i>L. sakagamii</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	0
<i>L. emarginatus</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	(12)	1	2	1	1	0	0	0	1	0
<i>L. platythorax</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	0
<i>L. niger</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	0
<i>L. japonicus</i>	0	0	0	0	1	1	0	0	0	0	0	0	2	2	1	2	1	1	0	0	0	1	0
<i>L. alienus</i>	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0
<i>L. hayashi</i>	0	0	0	0	1	1	0	0	0	0	0	1	2	2	1	1	1	1	0	0	0	1	0
<i>L. productus</i>	0	0	0	0	1	1	0	0	0	0	0	1	2	2	1	1	1	1	0	0	0	1	0
<i>L. austriacus</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	(01)	0	1	0	0	0	1	0
<i>L. mixtus</i>	1	1	1	1	0	0	1	1	1	1	1	1	2	1	1	0	0	0	1	1	1	0	0

	Maruyama <i>et al.</i> (2008) (adapted)																							
	36	38	41	49	54	57	61	62	64	65	66	67	75	86	87	88	90	91	92	99	101	102	103	104
<i>L. balearicus</i>	1	0	0	1	0	0	0	(01)	?	2	2	0	1	0	0	?	2	1	0	?	?	?	0	0
<i>L. grandis</i>	1	0	0	1	0	0	1	1	2	2	2	0	1	0	0	0	2	1	0	2	2	1	0	(01)
<i>L. cinereus</i>	1	0	0	1	0	0	0	1	2	2	2	0	1	0	0	0	2	1	0	2	2	1	1	0
<i>L. brunneus</i>	1	0	0	1	0	0	0	1	1	0	4	0	1	0	0	(01)	2	1	0	1	0	0	0	1
<i>L. neglectus</i>	1	0	0	1	0	0	1	(01)	1	1	2	0	1	0	0	1	2	1	0	2	2	1	0	0
<i>L. sakagamii</i>	1	0	0	1	0	0	0	(01)	2	2	2	0	1	0	0	1	2	1	0	2	2	1	0	1
<i>L. emarginatus</i>	1	0	0	1	0	0	(01)	(012)	2	2	2	0	1	0	0	0	2	1	0	2	2	1	0	1
<i>L. platythorax</i>	1	0	0	1	0	0	1	(01)	2	2	2	0	1	0	0	0	2	1	0	2	2	1	0	0
<i>L. niger</i>	1	0	0	1	0	0	1	1	2	2	2	0	1	0	0	0	2	1	0	2	2	1	0	0
<i>L. japonicus</i>	1	0	0	1	0	0	1	1	2	2	2	0	1	0	0	(01)	2	1	0	2	2	1	0	(01)
<i>L. alienus</i>	1	0	0	1	0	0	1	(01)	1	1	0	0	1	0	0	0	2	1	0	2	1	0	0	0
<i>L. hayashi</i>	1	0	0	1	0	0	1	(02)	2	2	2	0	1	0	0	0	2	1	0	2	2	1	0	1
<i>L. productus</i>	1	0	0	1	0	0	1	(01)	1	1	2	0	1	0	0	0	2	1	0	2	2	1	0	1
<i>L. austriacus</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	(01)	0	1	0	0	0	1	0	0
<i>L. mixtus</i>	0	1	1	0	1	1	1	(01)	2	2	1	1	1	1	1	0	1	0	2	0	1	1	0	0

Discrete values for biometric measures

	HW	HL	CS	SL	SL/CS	HL/HW	SL/HL	PDCL	nHS	nHHT	MaDe	nBH	HWQ	HLQ	HL/HW	SLQ	SL/HL	SL/HW	MLQ	MHQ	MHQ/MLQ	
<i>L. balearicus</i>	1	1	1	1	1	1	1	2	3	2	1	2	1	1	3	0	3	2	2	2	1	1
<i>L. grandis</i>	2	2	2	2	1	1	1	1	2	2	1	2	1	1	2	1	3	1	2	1	1	1
<i>L. cinereus</i>	1	1	1	2	1	1	1	1	2	2	1	1	1	1	3	0	3	2	2	1	1	1
<i>L. brunneus</i>	2	1	2	2	0	0	0	2	0	0	0	0	1	1	1	1	0	0	2	0	0	0
<i>L. neglectus</i>	0	0	0	1	1	2	1	3	0	0	0	1	0	0	1	0	3	1	1	0	1	1
<i>L. sakagamii</i>	1	1	1	2	1	1	1	0	3	2	1	2	1	1	2	1	3	1	2	2	2	2
<i>L. emarginatus</i>	2	2	2	2	1	1	1	2	1	2	1	1	1	1	2	1	4	2	2	1	0	0
<i>L. platythorax</i>	2	2	2	2	1	0	1	2	2	2	1	1	1	1	0	1	3	1	2	1	1	1
<i>L. niger</i>	2	2	2	2	1	1	1	0	1	2	1	1	1	1	0	1	3	1	2	2	2	2
<i>L. japonicus</i>	2	2	2	2	1	1	1	1	1	2	1	1	1	1	1	1	3	1	2	1	1	1
<i>L. alienus</i>	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	2	1	2	2	2	2
<i>L. hayashi</i>	2	2	2	2	1	0	1	1	2	2	1	1	1	1	1	2	1	0	2	1	0	0
<i>L. productus</i>	2	2	2	3	2	1	2	1	1	1	1	1	2	2	2	0	4	3	3	1	1	1
<i>L. austriacus</i>	0	0	0	0	0	1	0	3	0	0	0	0	0	0	1	0	3	1	2	2	2	2
<i>L. psammophilus</i>	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	3	1	2	2	2	2
<i>L. lasioides</i>	1	1	1	2	1	1	1	3	0	0	0	0	0	0	0	0	4	1	1	0	0	0
<i>L. turcicus</i>	1	1	1	2	1	1	1	3	0	0	0	1	0	0	1	0	3	1	2	1	1	1
<i>L. mixtus</i>	2	2	2	2	0	1	0	0	1	1	1	1	1	1	2	0	2	1	0	0	0	2

Table S6 Evaluation metrics for the different models employed. Mean values for area under the curve of the receiver operating characteristic (AUC), the true skill statistic (TSS) and kappa statistic (KAPPA) are detailed. Accuracy classification for AUC: 1 > excellent > 0.9 > good > 0.8 > fair > 0.7 > poor > 0.6 > fail; TSS and KAPPA: 1 > excellent > 0.8 > good > 0.6 > fair > 0.4 > poor > 0.2 fail.

	AUC	TSS	KAPPA
CTA	0.96 ± 0.12	0.94 ± 0.15	0.92 ± 0.13
FDA	0.98 ± 0.06	0.97 ± 0.11	0.95 ± 0.11
GAM	1 ± 0	1 ± 0	1 ± 0
GBM	1 ± 0.01	0.99 ± 0.02	0.94 ± 0.1
GLM	0.89 ± 0.12	0.78 ± 0.25	0.77 ± 0.2
MARS	0.99 ± 0.01	0.99 ± 0.02	0.94 ± 0.11
MAXENT	1 ± 0.01	0.99 ± 0.02	0.97 ± 0.08
RF	1 ± 0.01	0.99 ± 0.02	0.96 ± 0.09

CTA, classification tree analysis; FDA, flexible discriminant analysis; GAM, generalized additive model; GBM, generalized boosting model; GLM, generalized linear model; MARS, multiple adaptive regression splines; MAXENT, maximum entropy; RF, random forest.

Table S7 Intraspecific genetic distances, evolutionary ages and monophyly supports estimated for the *Lasius* species studied.

Taxa	<i>n</i>	Monophyly support	Intraspecific genetic distance	Ma [95% HPD]
<i>L. balearicus</i>	15	100	0.001	1.51 [0.84-2.4]
<i>L. cinereus</i>	3	paraphyletic	0.004	n.a.
<i>L. grandis</i>	4	paraphyletic	0.004	n.a.
<i>L. japonicus</i>	3	100	0.006	1 [0.49-1.59]
<i>L. niger</i>	2	100	0.001	1.26 [0.70-1.96]
<i>L. platythorax</i>	2	100	0.000	1 [0.49-1.59]
<i>L. emarginatus</i>	2	100	0.004	2.1 [1.32-3.17]
<i>L. hayashi</i>	2	71	0.022	1.35 [0.57-2.38]
<i>L. sakagamii</i>	3	100	0.003	1.98 [1.06-3.05]
<i>L. alienus</i>	2	100	0.004	1.45 [0.71-2.33]
<i>L. psammophilus</i>	1	100	0.015	1.45 [0.71-2.33]
<i>L. brunneus</i>	2	100	0.000	6.08 [3.62-8.98]
<i>L. austriacus</i>	6	100	0.003	3.36 [1.76-5.28]
<i>L. neglectus</i>	3	100	0.000	1.67 [0.8-2.84]
<i>L. turcicus</i>	5	100	0.011	1.67 [0.8-2.84]
<i>L. lasioides</i>	1	100	0.003	4.85 [2.78-7.31]
<i>L. productus</i>	1	monotypic	n.a.	1.35 [0.57-2.38]



1- Puig Caragoler - Mola de Planícia



2- Es Teix - Serra d'Alfàbia



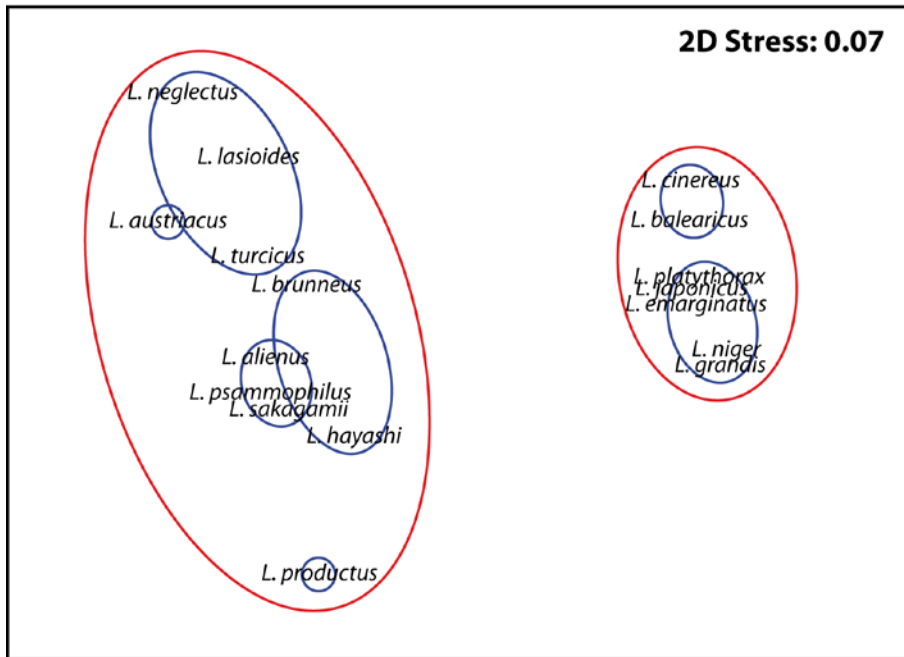
3- Puig Major - Puig Massanella



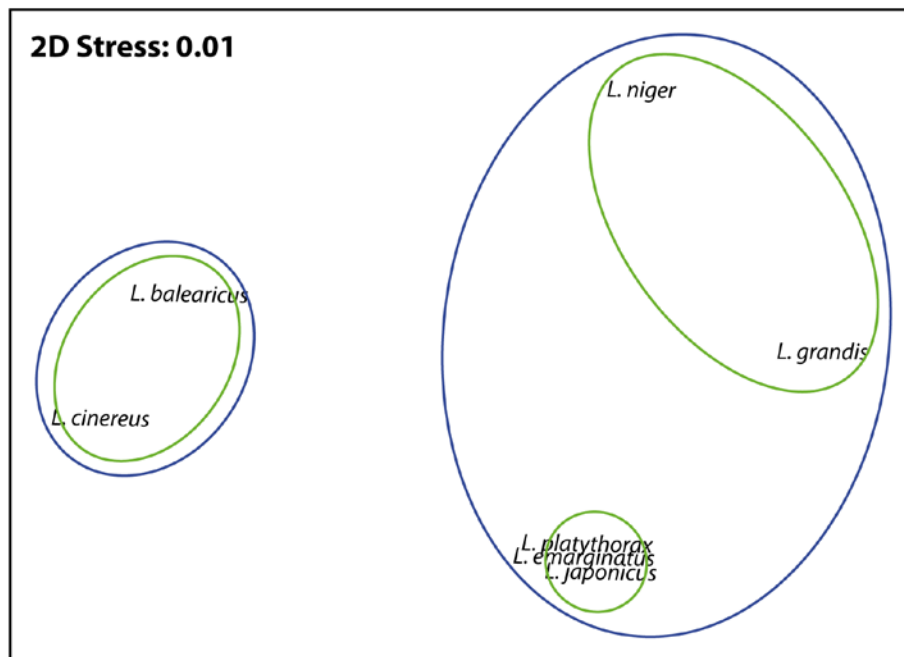
4- Pic Tomir - Puig Caragoler

Figure S1 Sampling localities surveyed (dots) during this study in the Balearic Islands and nearest mainland (Serra d'Aitana, Alicante). Detailed tracks explored in the main peaks of Serra de Tramuntana are also shown. Ant diversity was assessed in each locality and along the tracks, and red dots indicate the presence of *Lasius balearicus*.

a)



b)



Euclidean Distance

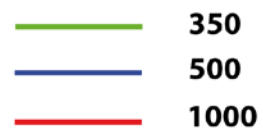


Figure S2 Non-metric multidimensional scaling (NMDS) using biometric data and Euclidean distances for (a) *Lasius* s. str. and (b) the *L. balearicus* group.

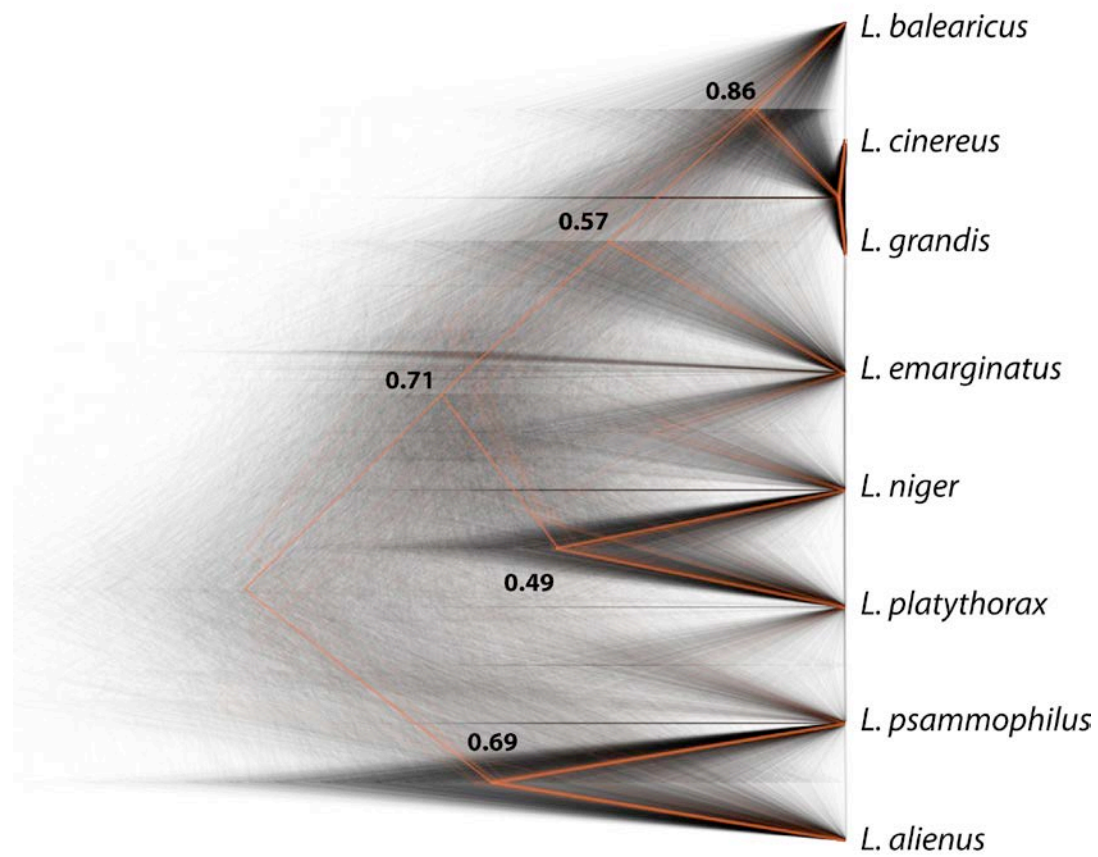


Figure S3 *BEAST species tree for *Lasius balearicus* and the closest *Lasius* s. str. taxa based on four genetic markers. Trees are figured with DENSITREE (Bouckaert, 2010). Higher line densities represent higher levels of certainty. Black lines display a Markov chain Monte Carlo of 10,000 trees. Recovered posterior probabilities for the most popular consensus tree (orange lines) are shown.

References

- Bouckaert, R.R. (2010) DensiTree: making sense of sets of phylogenetic trees. *Bioinformatics*, **26**, 1372–1373.
- Cremer, S., Ugelvig, L.V., Drijfhout, F.P. *et al.* (2008) The evolution of invasiveness in garden ants. *PLoS ONE*, **3**, e3838.
- Herraiz, J.A. & Espadaler, X. (2009) Descripción de la reina de *Lasius cinereus* Seifert (Hymenoptera: Formicidae). *Boletín de la Sociedad entomológica Aragonesa*, **44**, 143–146.
- Maruyama, M., Steiner, F.M., Stauffer, C., Akino, T., Crozier, R.H. & Schlick-Steiner, B.C. (2008) A DNA and morphology based phylogenetic framework of the ant genus *Lasius* with hypotheses for the evolution of social parasitism and fungiculture. *BMC Evolutionary Biology*, **8**, 237–251.
- Schlick-Steiner, B.C., Steiner, F.M., Schödl, S. & Seifer, B. (2003) *Lasius austriacus* sp.n., a Central European ant related to the invasive species *Lasius neglectus*. *Sociobiology*, **41**, 725–736.
- Seifert, B. (1988) A revision of the European species of the ant subgenus *Chthonolasius* (Insecta, Hymenoptera, Formicidae) *Entomologische Abhandlungen Staatlichen Museum für Tierkunde Dresden*, **51**, 143–180.
- Seifert, B. (1992) A taxonomic revision of the Palaearctic members of the ant subgenus *Lasius* s. str. (Hymenoptera: Formicidae). *Abh. Ber. Naturkundemus. Görlitz*, **66**, 1–67.
- Steiner, F.M., Schlick-Steiner, B.C., Schödl, S., Espadaler, X., Seifert, B., Christian, E. & Stauffer, C. (2004) Phylogeny and bionomics of *Lasius austriacus* (Hymenoptera, Formicidae). *Insectes Sociaux*, **51**, 24–29.