COMPETITION, ENVIRONMENTAL FILTERING AND FUNCTIONAL DIVERSITY IN ANT COMMUNITIES

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Setembre 2025

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COMPETITION, ENVIRONMENTAL FILTERING AND FUNCTIONAL DIVERSITY IN ANT COMMUNITIES

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Per optar al grau de Doctora

Amb l'aprovació dels directors:

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Programa de Doctorat en Ecologia Terrestre

CREAF- Universitat Autònoma de Barcelona

Setembre, 2025

Olga Boet Escarcellé, 2025

Competition, environmental filtering and functional diversity in ant communities

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A la Isa i la Vane,

estimades i admirades.

CONTINGUTS

Agraïments

Als meus directors, Javi i Xavi, per acompanyar-me en aquest camí tan llarg, no només com a mestres de la recerca sinó també en la vessant més personal. Ens coneixem de fa molts anys i sabíeu les meves virtuts i mancances, i malgrat això vau afrontar aquest repte. Us ho agraeixo de tot cor.

Malgrat estar a la secció d'agraïments, també vull anomenar un culpable: l'interès per les formigues em va arribar a una certa edat de la mà del Javier Retana. Ell em va transmetre la seva passió per les formigues, i des de llavors aquests petits animalons han estat l'objecte d'una de les meves principals aficions. Tot per la seva culpa!

A la Yolanda Melero, l'Anselm Rodrigo, en Francesc Uribe i en David García Callejas per la bona feina en la comissió de seguiment, el bon ambient de les sessions i les aportacions interessants que sovint m'han fet mirar més enllà del meu treball.

Als socis i sòcies de la AIM, especialment amb els assistents al Taxomara, amb qui comparteixo l'afició mirmecològica i dels qui he aprés moltíssim. Especialment al Xim i l'Elena, que sempre s'han preocupat per mi i m'han acollit a casa.

A la meva família que ha viscut i patit aquest procés al meu costat, espacialment als meus pares, als meus fills i al Lluís. Soc molt afortunada de tenir-vos al meu costat. Probablement soc de les poques mares qui els fills han fet el seguiment del seu procés d'aprenentatge. Per tot el temps que ens ha robat la tesi. Us estimo molt.

Als meus amics i amigues que m'heu animats durant aquest procés i heu suportat estoicament alguna conversa (o monòleg) sobre les meves limitacions, maldecaps i preocupacions durant aquest procés, però també sobre el fascinant comportament i adaptacions de les formigues.

Finalment agraeixo a totes aquelles persones que em fan la vida més fàcil i alegre, especialment les que van amb un somriure dibuixat a la cara.

Resum general

Comprendre els patrons de biodiversitat i l'assemblatge de les comunitats és un objectiu central en ecologia, especialment en l'acceleració del canvi global. L'estructuració de les comunitats s'estableix a partir de processos de filtratge ambiental i biòtic, juntament amb la història evolutiva, les limitacions de dispersió i els processos estocàstics. El filtratge ambiental domina a àmplies escales espacials, seleccionant espècies amb trets funcionals que confereixen tolerància a condicions abiòtiques com la temperatura, la humitat i la salinitat. Ara bé, la coexistència de les espècies en una comunitat també depèn de les interaccions biòtiques que faciliten el seu establiment i manteniment. Malgrat la gran quantitat d'estudis, el paper de la competència en l'estructuració de les comunitats de formigues segueix essent controvertit. Aquesta tesi investiga els mecanismes ecològics que estructuren les comunitats de formigues al llarg del territori europeu, posant l'èmfasi en el paper del filtratge ambiental i de la competència interespecífica. Aquests processos s'examinen a través de diferents gradients ambientals i d'escales espacials, utilitzant l'aproximació funcional de les espècies i incorporant el concepte de la diversitat fosca per revelar patrons ocults en els processos d'estructuració de les comunitats.

Al capítol 1 es van analitzar diferents tipus de trets funcionals per dilucidar les contribucions del filtratge ambiental i de la competència en l'estructuració de les comunitats de formigues d'Europa considerant l'escala d'estudi i el tipus de tret funcional. Concretament es van avaluar els patrons de la divergència funcional i la co-ocurrència d'espècies a través de tres escales espacials (continental, regional i local) i distingint entre els trets de tolerància (vinculats a les condicions ambientals) i els trets de nínxol (associats a l'explotació dels recursos). Les nostres troballes indiquen que el filtratge ambiental predomina a àmplies escales espacials, particularment a nivell continental i de regió biogeogràfica. Tot i això, a nivell de regió, també

es va detectar un paper important de la competència en l'estructuració de les comunitats, principalment en el mediterrani on les condicions climàtiques afavoreixen l'activitat de les formigues. En canvi, en la regió alpina no es va detectar la dominància de cap dels dos mecanismes. Finalment, a escala local, tampoc es va observar una major rellevància per part del filtre ambiental ni de la competència.

Al capítol 2, es va explorar la variació latitudinal de la diversitat fosca de formigues a Europa, incloent la interacció amb l'elevació com a factor modulador. Addicionalment, es va investigar la força de la pressió biòtica per augmentar la diversitat fosca a nivell local. Es va detectar un gradient latitudinal negatiu pronunciat, accentuat a majors elevacions. A més, la diversitat fosca va respondre més fortament a la latitud que la riquesa observada. El conjunt d'aquests patrons assenyalen que hi ha un reservori major d'espècies en cotes elevades de les latituds meridionals. A nivell local, es va detectar que la diversitat fosca augmentava amb l'abundància d'espècies dominants, una dinàmica sovint passada per alt en els estudis clàssics. Malgrat això, s'han de considerar altres factors locals en l'estructuració de les comunitats, com ara la limitació de la dispersió o la qualitat de l'hàbitat.

Al capítol 3, es va examinar la dissimilitud funcional entre les espècies de formigues observades i fosques per inferir el paper de la competència en l'estructuració de les comunitats de formigues en cinc biomes d'Europa. Es van utilitzar cinc trets funcionals relacionats amb l'explotació dels recursos per calcular la dissimilitud funcional entre les espècies observades i les fosques de la mateixa localitat (FDiss), i es van calcular les mitjanes dels trets funcionals (CM) per a les espècies observades i per les fosques de cada localitat. Els valors constantment baixos de FDiss en tots els trets funcionals i tots els biomes assenyalen una forta petjada del filtratge competitiu, mitjançant el qual s'han exclòs espècies ecològicament similars. No obstant això, es van detectar diferències entre biomes: el boreal, el continental i l'atlàntic van mostrar els valors més baixos de FDiss, suggerint una major exclusió competitiva en condicions ambientals dures per a les espècie de formiga. En canvi, els biomes mediterrani i alpí van mostrar una FDiss més alta, probablement causada per factors diferents: una major diversitat de recursos i heterogeneïtat espacial en el mediterrani, mentre que les característiques del bioma alpí suggereixen l’actuació d'una força més forta que estaria reduint considerablement la petjada de la competència, com podria ser el filtratge ambiental. Les anàlisis de MC van revelar que els eixos dels trets funcionals que impulsen l'exclusió varien segons el bioma, amb la mida i el polimorfisme de les obreres com a trets funcionals més rellevants en algunes regions, i els trets funcionals relacionats amb la dieta o amb la partició temporal de l’activitat en altres.

Abstract

Understanding biodiversity patterns and community assemblage is a central goal in ecology, especially in accelerating global change. The structuring of communities is established from processes of environmental and biotic filtering, together with evolutionary history, dispersal limitations and stochastic processes. Environmental filtering dominates at wide spatial scales, selecting species with functional traits that confer tolerance to abiotic conditions such as temperature, humidity and salinity. However, the coexistence of species in a community also depends on the biotic interactions that facilitate their establishment and maintenance. Despite the large number of studies, the role of competition in the structuring of ant communities remains controversial. This thesis investigates the ecological mechanisms that structure ant communities throughout Europe, emphasizing the role of environmental filtering and interspecific competition. These processes are examined through different environmental gradients and spatial scales, using the functional approach of species and incorporating the concept of dark diversity to reveal hidden patterns in community structuring processes.

In chapter 1, different types of functional traits were analyzed to elucidate the contributions of environmental filtering and competition in the structuring of ant communities in Europe, considering the scale of study and the type of functional trait. Specifically, the patterns of functional divergence and co-occurrence of species were evaluated across three spatial scales (continental, regional and local) and distinguishing between tolerance traits (linked to environmental conditions) and niche traits (associated with resource exploitation). Our findings indicate that environmental filtering predominates at wide spatial scales, particularly at the continental level and biogeographic region. However, at the regional level, an important role of competition was also detected in the structuring of communities, mainly in the Mediterranean where climatic conditions favour ant activity. In contrast, in the Alpine region, the dominance

of either mechanism was not detected. Finally, at the local level, there was no greater relevance on the part of the environmental filter or the competition.

In Chapter 2, we explored the latitudinal variation of dark ant diversity in Europe, including interaction with elevation as a modulating factor. Additionally, the strength of biotic pressure to increase dark diversity at the local level was investigated. A pronounced negative latitudinal gradient was detected, accentuated at higher elevations. In addition, dark diversity responded more strongly to latitude than observed richness. Taken together, these patterns indicate that there is a greater reservoir of species at high altitudes in southern latitudes. At the local level, dark diversity was found to increase with the abundance of dominant species, a dynamic often overlooked in classical studies. However, other local factors must be considered in the structuring of communities, such as the limitation of dispersal or the quality of habitat.

In Chapter 3, we examined the functional dissimilarity between observed and dark ant species to infer the role of competition in the structuring of ant communities in five biomes in Europe. Five functional traits related to resource exploitation were used to calculate the functional dissimilarity between observed and dark species of the same locality (FDiss), and the means of functional traits (MC) were calculated for the observed species and for the dark ones of each locality. Consistently low FDiss values across all functional traits and all biomes point to a strong competitive filtering footprint, whereby ecologically similar species have been excluded. However, differences were detected between biomes: the boreal, continental and Atlantic showed the lowest FDiss values, suggesting greater competitive exclusion in harsh environmental conditions for ant species. On the other hand, the Mediterranean and Alpine biomes showed a higher FDiss, probably caused by different factors: a greater diversity of resources and spatial heterogeneity in the Mediterranean, while the characteristics of the Alpine biome suggest the action of a stronger force that would be considerably reducing the footprint of competition, such as environmental filtering. The MC analyses revealed that the axes of the functional traits that drive exclusion vary according to the biome, with the size and polymorphism of the workers as the most relevant functional traits in some regions, and the functional traits related to diet or the temporal partition of activity in others.

INTRODUCCIÓ GENERAL

Introducció general

Els patrons de biodiversitat i els factors que els determinen

La biodiversitat és essencial per garantir la provisió i la resiliència dels serveis ecosistèmics, com el reciclatge de nutrients, la purificació de l'aigua, la regulació del clima i els serveis culturals entre d'altres, els quals inclouen aspectes fonamentals per al benestar humà (Bastian 2013, Lecina-Diaz et al. 2019). No obstant això, els canvis globals d'origen antropogènic estan provocant impactes generalitzats en els ecosistemes, comprometen la seva biodiversitat i, per tant, la seva capacitat per continuar oferint aquests serveis de manera efectiva (Johnson et al. 2017). Davant d'aquest escenari, es fa evident la necessitat urgent d'avaluar amb precisió la biodiversitat i entendre els factors que la configuren, especialment en el context de la pèrdua actual de biodiversitat i de la futura derivada del ràpid canvi climàtic (Lovejoy and Hannah 2019).

La biodiversitat local depèn de la composició de les comunitats ecològiques, és a dir, de les espècies que coexisteixen en un mateix espai i temps. Aquesta coexistència implica interaccions, directes o indirectes, entre les espècies. En conseqüència, el conjunt de les espècies que alberga una comunitat depèn en primera instància que les condicions ambientals siguin les propícies, però també que les interaccions biòtiques els hi permetin establir-se i mantenir-se (Weiher i Keddy 1995, Cadotte i Tucker 2010, Gallien 2016). A més dels factors ambientals i biòtics, hi ha elements no deterministes que poden influir en la composició de les comunitats, com ara la història evolutiva, les limitacions en la dispersió de les espècies i els processos estocàstics (Snyder i Chesson 2004; Mittelbach et al. 2007, Cornell and Harrison 2014, Economo et al. 2018).

En el context de l'ecologia de comunitats, es considera que el *filtratge ambiental* exerceix un paper predominant a escales espacials àmplies, com ara les dels continents o dels biomes. Aquest procés actua afavorint aquelles espècies que presenten característiques compatibles amb les condicions climàtiques i ambientals específiques de cada regió (Lebrija-Trejos et al. 2010, Cornell i Harrison 2014, Kraf et al. 2015, Cadotte i Tucker 2017) que els permeten establir-se, créixer i reproduir-se. Arrel d'aquest filtratge ambiental s'observen patrons consistents de biodiversitat a escala continental o planetària (per exemple Barthlott, W. et al. 1996, Mittelbach et al. 2007, Kinlock et al. 2018). Per a la majoria dels taxons es registra una major diversitat d'espècies en zones properes a l'equador, amb una disminució progressiva cap a les latituds més septentrionals (Gaston et al. 1995, Willig et al. 2003, Dunn et al. 2009, Kass et al. 2022). En canvi, a escales més locals, sembla que les interaccions biòtiques (principalment la competència, la facilitació, o la depredació) són les que acaben definint la composició final de les comunitats (Cavender-Bares et al. 2004, Slingsby and Verboom 2006, Mayfield and Levine, 2012, Cornell i Harrison 2014, Kraft et al. 2015), determinant quines espècies poden coexistir en un mateix hàbitat i quines tendeixen a excloure's mútuament. Malauradament, la immensitat de taxons, de condicions ambientals, d'escales d'estudi i de graus de pertorbacions del medi, fa que els resultats dels diferents estudis no sempre atorguin la mateixa importància als mecanismes que implicats en l'estructuració de les comunitats. Per aprofundir en l'estudi s'han utilitzat diferents enfocaments, entre els que destaquen l'anàlisi de la diversitat taxonòmica, filogenètica i funcional (Narwani et al. 2015).

Els trets funcionals

L'estudi de les característiques de les espècies, la seva funcionalitat i els grups funcionals té una llarga trajectòria en ecologia, com ho exemplifica l'estudi dels becs dels pinsans de les Illes

Galápagos dut a terme per Darwin (1859), que il·lustra com les característiques morfològiques poden reflectir adaptacions funcionals. No obstant això, el concepte formal de tret funcional no es va definir fins molt més tard (McGill et al. 2006; Violle et al. 2007). Tot i que la definició de tret funcional ha estat objecte de debat, existeix consens en considerar que, en el cas dels animals, aquests trets inclouen atributs morfològics, fisiològics, de comportament o relacionats amb el cicle de vida que incideixen directament en l'eficàcia biològica (fitness) de l'individu, afectant-ne el creixement, la reproducció i/o la supervivència. En general, es tracta de trets mesurables a nivell d'individu, tot i que no sempre és així (aquesta tesi n'és un exemple atès les característiques de les espècies d'estudi).

Els trets funcionals s'han utilitzat àmpliament, tant per analitzar les respostes de les comunitats davant de canvis ambientals com per avaluar l'impacte que aquestes exerceixen sobre el funcionament dels ecosistemes (Nock et al. 2016). Aquesta doble perspectiva, la resposta a l'ambient i l'efecte sobre l'ecosistema, ha contribuït significativament a la comprensió dels processos d'estructuració de les comunitats i dels serveis ecosistèmics associats. En aquesta tesi, però, ens centrem principalment en el paper dels trets funcionals per explicar les respostes de les comunitats als canvis ambientals i, en particular, en els processos d'assemblatge de les comunitats. És a dir, en aquells trets que determinen la capacitat d'una espècie per colonitzar un hàbitat, establir-s'hi i persistir-hi davant de les alteracions ambientals (Nock et al. 2016). Pel que fa a les comunitats vegetals, la gran quantitat d'estudis disponibles ha permès assolir un grau elevat de coneixement i consens sobre quins trets funcionals descriuen millor els processos d'establiment comunitari. Entre aquests destaquen característiques de les llavors (com el pes i la forma), de les fulles (com l'àrea foliar i el contingut hídric), de la planta (com l'alçada), així com estratègies regeneratives (Nock et al. 2016). En el cas dels animals, l'explotació de recursos es pot emmarcar en el domini del comportament, l'estratègia d'alimentació, la dieta i el lloc de nidificació (Retana et al. 2015).

L'embranzida de l'enfocament funcional ha permès considerar els trets com a unitats d'anàlisi equivalents a les taxonòmiques, facilitant l'aplicació d'índexs ecològics preexistents. Així, bona part dels treballs inicials es van centrar en la diversitat funcional a nivell α, és a dir, en descriure patrons dins les comunitats i avaluar com es distribueixen els trets funcionals entre les espècies presents (Petchey i Gaston 2006, Podani i Schmera 2006, Villéger et al. 2008). Aquest enfocament ha estat clau per explorar fins a quin punt les comunitats s'estructuren seguint determinades regles d'estructuració, com ara filtres ambientals o mecanismes de partició de recursos. Malgrat aquests avenços, diversos estudis han assenyalat que analitzar només la diversitat funcional de les espècies observades en les comunitats pot resultar insuficient per identificar els processos subjacents, especialment aquells relacionats amb les interaccions biòtiques (de Bello et al. 2012, Kraft et al. 2015, Cadotte i Tucker 2017). Per exemple, una comunitat local amb baixa diversitat funcional en els trets relacionats amb l'explotació de recursos podria no reflectir un filtratge competitiu intens (Hardin 1960, MacArthur i Levins 1967). Posteriorment, el focus s'ha ampliat cap a la β-diversitat funcional, la qual permet quantificar la dissimilitud entre comunitats i ha estat aplicada, per exemple, per entendre patrons d'heterogeneïtat funcional en el paisatge i el paper dels filtres ambientals a escales més àmplies (de Bello et al. 2012, Arnan et al. 2015). En general, els estudis que han tingut en compte el conjunt d'espècies potencials, generalment a nivell de regió (el *pool* regional) (Zobel 1997, Cornell and Harrison 2014, Bruelheide et al. 2020) han estat escassos. Malgrat això, l'ús de la dissimilitud funcional comparant els conjunts d'espècies observades amb els conjunts d'espècies esperades o potencials, que encara no s'ha abordat de manera sistemàtica, representa una via prometedora per aprofundir en la comprensió dels processos d’assemblatge de les comunitats.

La diversitat fosca

L’anàlisi ecològica basada exclusivament en les espècies observades no permet detectar allò que els filtres o altres processos no han inclòs en la comunitat. El concepte emergent de la **diversitat fosca** esdevé particularment rellevant, ja que considera espècies que estan absents d'una comunitat local però que, tanmateix, en podrien formar part atès les seves característiques biològiques i la seva distribució geogràfica (Pärtel et al. 2011). La diversitat fosca inclou aquelles espècies que pertanyen al conjunt regional i que, en teoria, podrien colonitzar un hàbitat determinat, però que no estan presents en la comunitat establerta per factors ecològics (i no pas a deficiències en el mostreig). L’interès en els patrons de la diversitat fosca existeix perquè, entre d’altes aspectes, podrien aportar informació valuosa per aplicar en les estratègies de conservació i restauració (Real et al. 2016, Cantanhêde et al. 2022). Així, un estudi recent sobre aus reproductores a Dinamarca va evidenciar que l’homogeneïtzació de l’hàbitat provocada per l’agricultura intensiva, les pertorbacions antropogèniques i la proximitat a la costa incrementava la diversitat fosca. En aquest cas, les espècies d’aus catalogades com a amenaçades mostraven una major propensió a formar part de la diversitat fosca (Holm et al. 2023), de manera que s’havia de considerar una estratègia per recuperar-les.

Quan la recerca se centra en els processos d’estructuració de les comunitats, l’anàlisi dels trets funcionals associats a la diversitat fosca permet desvetllar respostes que romanen ocultes (Andersen et al. 2023). En comunitats vegetals europees, s’ha demostrat que la diversitat fosca està condicionada per factors abiòtics locals, la configuració del paisatge i els trets funcionals de les espècies, especialment aquells relacionats amb la capacitat de dispersió, la competitivitat i la tolerància a l'estrès (Riibak et al. 2017, Belinchón et al. 2020, Cantanhêde et al. 2022). Tanmateix, altres factors poden contribuir a l'augment de la diversitat fosca a escala local, com ara la baixa qualitat de l'hàbitat (Dalle Fratte et al. 2022) o les limitacions en la dispersió d'espècies que, tot i estar presents a nivell regional, no arriben a colonitzar la localitat estudiada (Riibak et al. 2017, Belinchón et al. 2020). Els estudis que combinen diversitat fosca i trets funcionals en fauna són escassos, probablement per les dificultats associades a l'obtenció de dades tant de presència de les espècies com de característiques funcionals. Un exemple destacat és l'estudi sobre sírfids (Diptera) al sud-est d'Europa, que va identificar el mode d'alimentació larvària com el tret més rellevant per determinar la probabilitat de formar part de la diversitat fosca (Miličić et al. 2020). Malgrat l'interès creixent per integrar la diversitat fosca amb els trets funcionals, persisteix un buit significatiu en els estudis que analitzen conjuntament les espècies presents i absents en les comunitats. Així, si les espècies observades en la comunitat comparteixen trets funcionals amb les espècies fosques de la mateixa localitat, aquest patró podria indicar que la competència ha exclòs espècies ecològicament similars. Omplir aquest buit pot ser fonamental per comprendre els mecanismes ecològics subjacents a l'estructuració de les comunitats i per millorar les prediccions sobre la reorganització de les comunitats en resposta al canvi ambiental (McGill et al. 2006, Kunstler et al. 2016).

Les formigues europees com a cas d'estudi de la tesi

Les formigues (Formicidae) constitueixen un grup d'invertebrats terrestres ecològicament dominant i funcionalment divers, amb aproximadament 14.000 conegudes distribuïdes pràcticament arreu del món (excepte l'Antàrtida, Islàndia, Groenlàndia, Nunavut i algunes illes llunyanes dels continents), de les quals 600 espècies són de distribució predominantment europea (Czechowski et al. 2002). Aquests insectes són especialment sensibles als gradients ambientals, com ara la temperatura, la precipitació, la cobertura vegetal i les pertorbacions, fet que els converteix en valuosos indicadors ecològics (Dunn et al. 2009, Arnan et al. 2014, Vasconcelos et al. 2018). Aquesta sensibilitat els fa especialment útils per a l'anàlisi de patrons ecològics a gran escala (Cushman et al. 1993, Sanders et al. 2003, Perillo et al. 2021, Kass et al. 2022), així com per a l'estudi dels processos d'assemblatge comunitari (per exemple, Savolainen i Vepsäläinen 1989, Lessard et al. 2012, Wiescher et al. 2012, Cerdá et al. 2013).

Figura 1. D'esquerra a dreta i de dalt a baix: obreres de *Formica* grup *rufa* atenent els pugons dels quals obtenen la melassa. Dues obreres de dimensions diferents, una minor i l'altra major, de la mateixa colònia de *Messor barbarus* durant l'activitat de recol·lecció de l'aliment. Niu de *Formica rufa* en bosc de pi negre. Niu de *Camponotus* sp. en la fusta morta.

Les formigues presenten una elevada diversitat de trets funcionals (morfològics, fisiològics, conductuals i cicles de vida) (exemples en la figura 1) que modulen tant les seves respostes als factors ambientals com les interaccions biòtiques que estableixen (Diamond et al. 2008, Retana et al. 2015, Arnan et al. 2017, Parr et al. 2017).

A diferència de la majoria de tàxons animals, les formigues viuen en societats fortament estructurades, on la major part dels individus no es reprodueix i l'eficàcia biològica es mesura a nivell de colònia (és a dir, de la reina i el seu conjunt d'obreres). Aquesta estructura social comporta una estratègia i comportament grupal, on el que es prioritza és el creixement i la supervivència de la colònia (i no pas de l'individu). Les espècies han evolucionat sota aquesta premissa i han sorgit adaptacions que només són òptimes en el cas de les societats. Per exemple, han sorgit les castes, és a dir, tipus d'individus diferents segons la seva funció social. Principalment les formigues presenten tres castes: les reines, els mascles i les obreres. Dins d'aquestes castes podem trobar diferents morfologies, sobretot en les obreres i en menor mesura també en les reines, resultat d'estratègies d'adaptacions a les seves funcions. En el cas de les obreres la diferència morfològica (també anomenat polimorfisme de les obreres) pot arribar a ser molt elevada, donant lloc a individus altament especialitzats en alguna tasca, però poc eficients o fins i tot inútils per altres. Per exemple, en *Colobopsis truncata* trobem obreres amb la part davantera del cap molt modificada, totalment aplanada, de manera que quan l'individu es situa a l'entrada del niu, "tanca" l'accés talment com si fos una porta, evitant l'entrada d'individus aliens a la colònia (Arcos i Fede, 2024) (Figura 2). O bé, en les espècies de *Messor* trobem individus de mides molt diferents, amb el cap desproporcionadament més gros en les obrers més grans; aquest elevat polimorfisme de les obreres permet més eficàcia recol·lectant i transportant les llavors (Heredia i Detrain 2000, Arnan et al. 2011), que són la font de la seva dieta. En aquest sentit, els trets funcionals poden ser mesurats tant a nivell de colònia (per exemple, la mida de la colònia, el grau de polimorfisme de les obreres, el número de reines per colònia o l'estratègia de recol·lecció) o bé a nivell de les obreres (com és el cas de la mida del cos, la morfologia, o la tolerància fisiològica), depenent de l'escala i de la pregunta ecològica plantejada.

El fet de viure en societat fa que les formigues siguin altament dependents del lloc on s'estableix aquesta, és a dir, del niu. El niu constitueix l'estructura permanent que acull tota la colònia, i aquest vincle espacial ha conduït a considerar sovint les formigues com a organismes sèssils (encara que hi ha excepcions, com el cas de les formigues legionàries). Per la gran majoria d'espècies, la ubicació del niu condiciona de manera significativa diversos factors ecològics clau, com ara la disponibilitat i proximitat als recursos alimentaris, la intensitat de la llum incident, així com la densitat i composició específica de les colònies veïnes. Per tot això, no és d'estranyar que hi hagi una certa competència per aquest recurs, és a dir, per la ubicació del niu.

Figura 2. Secció del tronc d'un roure on s'aprecia el polimorfisme de dues obreres de *Colobopsis truncata*, una d'elles situada a l'entrada del niu evitant l'accés d'intrusos gràcies a la morfologia de la part frontal del cap. Il·lustració de Isa Loureiro.

La competència entre espècies de formigues ha estat àmpliament documentada, i tot i que se'n distingeixen dos mecanismes principals, l'explotació del recurs i la interferència (Lach et al. 2010), a escala de comunitat sovint s'analitzen de manera conjunta. L'explotació de recursos, com ara l'aliment o els llocs de nidificació, es produeix en absència de l'espècie competidora, minvant o esgotant el recurs en qüestió. En canvi, la interferència té lloc quan individus de diferents espècies entren en contacte, i una d'elles s'interposa directament en l'activitat de l'altra, afectant l'eficiència en la recol·lecció de l'aliment, la integritat física dels individus o, fins i tot, la capacitat reproductiva o la supervivència de la colònia. Aquest tipus d'interacció competitiva sovint es manifesta en forma d'enfrontaments agressius, els quals han permès establir jerarquies de dominància entre espècies segons el seu comportament (Hölldobler i Wilson 1990, Andersen 1997, Stuble et al. 2017). En la part superior d'aquesta jerarquia es troben les espècies que defensen activament els seus territoris (Savolainen i Vepsäläinen 1988, Hölldobler i Wilson 1990) i/o monopolitzen els recursos alimentaris (Cerdá et al. 2013). En nivells intermedis s'ubiquen les espècies subordinades, que protegeixen activament les fonts d'aliment i el niu, mentre que en el nivell més baix es troben les espècies submises o discretes, que generalment no participen en conflictes per recursos i es limiten a defensar la colònia. A més de tota aquesta riquesa d'elements en la competència interespecífica en formigues, s'han identificat diversos mecanismes compensatoris que poden modular els resultats esperats de la competència interespecífica i afavorir la coexistència. Entre aquests mecanismes destaquen la tolerància tèrmica en contraposició a la dominància conductual, la capacitat de descobriment de recursos versus la dominància conductual, i l'impacte de parasitoides (Feener 2000, Cerdá et al. 2013, Stuble et al. 2013). Atès tota aquesta complexitat, el paper de la competència en l'establiment de les comunitats de formigues encara és objecte de debat actiu entre els (mirm)ecòlegs (Cerdá et al.1998, 2013). A dia d'avui, no hi ha estudis que integrin els trets funcionals, les espècies observades i les espècies fosques amb la intenció de fer aflorar els principals mecanismes que estructuren les comunitats de formigues segons diferents condicions ambientals.

Objectius de la tesi

Amb aquesta tesi pretenem dilucidar els principals mecanismes ecològics que configuren les comunitats de formigues d'Europa posant especialment atenció al paper de la competència interespecífica, al llarg de diferents condicions ambientals i de diferents escales espacials. Hem utilitzat diferents aproximacions per analitzar els mecanismes d'estructuració de les comunitats, analitzant principalment els trets funcionals i tenint en compte la diversitat fosca.

Capítol 1

En aquest primer estudi hem analitzat la importància relativa de la competència i el filtratge ambiental en l'estructuració de les comunitats de formigues mitjançant l'anàlisi de la diversitat funcional observada i els patrons de co-ocurrència entre parelles d'espècies de formigues, segons tres escales de treball: local, regional i global. Concretament hem caracteritzat les espècies segons una sèrie de trets funcionals relacionats amb la tolerància ecològica i el nínxol ecològic. Els nostres objectius específics són: 1) analitzar el paper relatiu del filtratge ambiental i la competència en l'estructura de les comunitats de formigues europees a escala local, biogeogràfica i continental; i 2) analitzar si el tipus de tret funcional juga un paper rellevant en la determinació de la importància relativa del filtratge ambiental i la competència. La nostra hipòtesi és que el paper relatiu del filtratge ambiental i la competència depèn de: a) l'escala espacial, és a dir, el filtratge ambiental supera la competència a escales espacials més grans (és a dir, Europa i regions biogeogràfiques), mentre que la competència supera el filtratge ambiental a escales espacials locals; i b) tipus de tret funcional, de manera que els 'trets de tolerància ecològica' es relacionaran amb processos de filtratge ambiental, mentre que els 'trets de nínxol ecològic' estaran més relacionats amb processos de competència.

Capítol 2

Els patrons latitudinals i altitudinals de la riquesa d'espècies de formigues a Europa estan ben establerts, però no passa el mateix amb els patrons de la diversitat fosca. Atenent la rellevància d'aquest enfocament per dilucidar als mecanismes que constitueixen les comunitats, aquest estudi pretén ser el primer en definir el patró de la diversitat fosca de les formigues a Europa segons els gradients ambientals determinats per la latitud i l'elevació, i segons la pressió biòtica exercida per l'abundància de les espècies dominants dins de la comunitat. Partim de dues hipòtesis: 1) La diversitat fosca serà més gran en comunitats de latituds més meridionals que en les de latituds més septentrionals a causa de condicions ambientals més favorables, tot i que l'elevació afectarà aquesta relació; 2) La diversitat fosca augmentarà amb l'abundància d'espècies dominants dins la comunitat a causa de l'augment de la pressió biòtica que suposa.

Capítol 3

En aquest estudi, investiguem com les espècies de formigues observades i les que constitueixen la diversitat fosca contribueixen a les funcions clau d'explotació de recursos a través d'amplis gradients ambientals. Analitzant els patrons de dissemblança funcional i identificant els mecanismes que els donen forma, pretenem descobrir els processos ecològics que impulsen l'estructuració de les comunitats de formigues en els cinc biomes més representatius d'Europa: Alpí, Atlàntic, Boreal, Continental i Mediterrani. La nostra hipòtesi és que en biomes on la competència interespecífica és una força estructurant dominant, les espècies de la diversitat fosca exhibiran trets funcionals similars als de les espècies observades, cosa que suggereix l'exclusió competitiva.

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CAPÍTOL 1

THE ROLE OF ENVIRONMENTAL VS. BIOTIC FILTERING IN THE STRUCTURE OF EUROPEAN ANT COMMUNITIES: A MATTER OF TRAIT TYPE AND SPATIAL SCALE

Boet O., Arnan X. and Retana J. (2020). PLOS ONE 15(2): e0228625.

https://doi.org/10.1371/journal.pone.0228625

Capítol 1. The role of environmental vs. biotic filtering in the structure of European ant communities: a matter of trait type and spatial scale

Abstract

Functional trait-based approaches are increasingly used for studying the processes underlying community assembly. The relative influence of different assembly rules might depend on the spatial scale of analysis, the environmental context and the type of functional traits considered. By using a functional trait-based approach, we aim to disentangle the relative role of environmental filtering and interspecific competition on the structure of European ant communities according to the spatial scale and the type of trait considered. We used a large database on ant species composition that encompasses 361 ant communities distributed across the five biogeographic regions of Europe; these communities were composed of 155 ant species, which were characterized by 6 functional traits. We then analysed the relationship between functional divergence and co-occurrence between species pairs across different spatial scales (European, biogeographic region and local) and considering different types of traits (ecological tolerance and niche traits). Three different patterns emerged: negative, positive and non-significant regression coefficients suggest that environmental filtering, competition and neutrality are at work, respectively. We found that environmental filtering is important for structuring European ant communities at large spatial scales, particularly at the scale of Europe and most biogeographic regions. Competition could play a certain role at intermediate spatial scales where temperatures are more favourable for ant productivity (i.e. the Mediterranean region), while neutrality might be especially relevant in spatially discontinuous regions (i.e. the Alpine region). We found that no ecological mechanism (environmental filtering or competition) prevails at the local scale. The type of trait is especially important when looking

for different assembly rules, and multi-trait grouping works well for traits associated with environmental responses (tolerance traits), but not for traits related to resource exploitation (niche traits). The spatial scale of analysis, the environmental context and the chosen traits merit special attention in trait-based analyses of community assembly mechanisms.

Introduction

A central goal in ecology is to understand the processes underlying community assembly (Kraft et al. 2008, Mouchet et al. 2013, Asefa et al. 2017, Jetschke 2001). A plethora of processes (e.g. evolutionary history, environmental constraints, biotic interactions) operating at different spatial and temporal scales contribute to community assembly patterns (Kneitel and Chase 2004). Environmental filtering is the first filter that selects a subset of species from the regional species pool (Lebrija-Trejos et al. 2010, Cadotte and Tucker 2017). It is primarily determined by evolutionary and historical factors, as well as dispersal barriers (Cornell and Harrison 2014). In turn, species interactions (i.e. biotic filtering) can exert a strong influence on the final number of species that co-occur in a community, mainly through competitive exclusion (Hardin 1960). On those taxa where interspecific competition might be an important process structuring local assemblages, it is particularly useful to understand the relative contribution of environmental filtering vs. competition (Mouchet et al. 2013, Silvertown et al. 2006). A relevant point is not which mechanism is in operation, but which mechanism has the strongest influence on communities under particular conditions. The relative influence of different assembly rules might depend on the spatial and temporal scales of analysis (Silvertown et al. 2006) and the environmental context (Kraft et al. 2015, Xu et al. 2017). While environmental filtering is assumed to be strongest at the regional scale (Levine 2016, Díaz et al. 1999, Cornwell et al. 2006), species interactions (i.e. competition) predominate at local spatial scales (Cavender-

Bares et al. 2004, Slingsby and Verboom 2006). Meanwhile, environmental filtering is expected to dominate during early succession (Bhaskar et al. 2014) and high elevations (Zobel 1997, Pottier et al. 2013, Xu et al. 2017) where environmental conditions are harshest, with biotic filtering becoming increasingly important in the later stages of succession (Kunstler et al. 2016).

Functional traits provide important insights into mechanisms of community assembly (McGill et al. 2006, Mouchet et al. 2010, Spasojevic and Suding 2012, Kunstler et al. 2016, Levine 2016). A given environmental condition selects for individuals with similar traits, meaning particular traits are necessary or better adapted to that condition. Thus, environmental filtering is predicted to result in local communities comprised of species with similar functional traits that allow species to persist ('functional clustering') (Asefa et al. 2017). On the other hand, if functionally similar groups of individuals compete more intensively with one another than functionally dissimilar species ('competitive exclusion principle', Hardin 1960), this allows functional dissimilar individuals to coexist ('limiting similarity principle', MacArthur and Levins 1967). Consequently, biotic filtering is predicted to result in a local community with different functional traits ('functional over-dispersion'). Moreover, neutral theory assumes that species coexist and persist in a system independently of their traits (Jetschke 2001). These three mechanisms (environmental filtering, biotic filtering and neutral theory) might even co-occur simultaneously and blur the patterns, or they might occur sequentially along environmental gradients (McGill et al. 2006).

An important issue to consider when testing for assembly processes using functional traits is that, depending on the type of functional traits we use, different patterns might emerge (Mayfield and Levine 2010, Spasojevic and Suding 2012, Kraft et al. 2015). Some functional traits clearly relate to environmental responses ('ecological tolerance traits') (Arnan et al. 2014), and they might only respond to environmental filtering rather than to competition processes. In these cases, assembled species might show functional clustering. Other traits relate to the way species exploit resources (‘ecological niche traits’) and so they lead to species exclusion or niche segregation as a result of competition processes (Kraft et al. 2015). These traits might not respond to environmental filtering, so species could show functional over-dispersion. Finally, traits directly related to the species’ competitive abilities to exploit one or a few limited resources (‘competitive abilities traits’) might be selected by competition processes (and not by any environmental filter). This is because they provide better fitness and then, similarly to when environmental filtering is at work, functional clustering instead of functional over-dispersion might be found (Mayfield and Levine 2010, Kraft et al. 2015). When multiple trait dimensions are considered, the ecological differentiation between species may be elucidated, because these sets of traits are likely to be relevant to the ecological tolerance, ecological niche and competitive ability of a species (Cadotte et al. 2011). This can be even more complex when there are positive or negative correlations among traits linked to tolerance and competitive outcomes (Kraft et al. 2015).

Ants are a suitable model system when it comes to analysing community assembly processes. Ants are among the most diverse, abundant and ecologically relevant organisms on earth (Hölldobler and Wilson 1990). They are highly sensitive to environmental change along climatic (Gibb et al. 2015), habitat (Retana and Cerdá 2000), productivity (Kaspari et al. 2000) or disturbance gradients (Arnan et al. 2013). Ants, like plants and other sessile organisms, have the ability to monopolize space and other resources, and therefore influence other species in the areas they occupy (Andersen 1992). Thus, competitive interactions have been widely reported among ant species, which have usually been organized into behavioural dominance hierarchies (Andersen 1995, Arnan et al. 2013). Even though competition is one of the most addressed topics in myrmecological research, there is still a contentious debate about the role of competition in structuring ant communities (Andersen 2008, Cerdá et al. 2013, Stuble et al. 2017, Arnan et al. 2018). Meanwhile, research in ant functional ecology has made important progress in recent years. Nowadays, we have different ant trait databases covering a wide range of traits (e.g. morphological, behavioural, physiological and life-history traits) for thousands of ant species (Diamond et al. 2008, Arnan et al. 2014, 2017, Parr et al. 2017, Ant Web). Interestingly, many studies have demonstrated that several functional traits act as the link between ant species distribution and the environment (Arnan et al. 2012, 2013, 2014, Arnan and Blüthgen 2015, Parr et al. 2017), i.e. they are 'ecological tolerance traits' that might be influenced by environmental filtering processes. Meanwhile, other functional traits relate to resource exploitation (Retana et al. 2015), i.e. they are 'ecological niche traits' or 'competitive ability traits' that might be more sensitive to competition rather than to environmental filtering.

Through the analysis of functional divergence and co-occurrence patterns between pairs of ant species, we investigate the contexts that make some assembly rules more influential than others in structuring ant communities. Specifically, we investigate how these rules vary according to the scale of analysis (local, regional and global) and the type of functional trait considered. To address this topic, our trait-based approach takes advantage of a large database on ant species composition that encompasses 361 ant communities distributed across the five most representative biomes of Europe, which clearly differ in climatic, physical and historical conditions (Arnan et al. 2017). These communities were composed of a total of 155 species, characterized by functional traits that were grouped according to their functional role. Aware of the importance of the choice of functional traits when seeking to meet the objectives of the study (Kraft et al. 2015, Kunstler et al. 2016, Cadotte and Tucker 2017), we have only characterized species according to ecological tolerance and ecological niche traits, and not to competitive ability traits. Thus, similar patterns are obtained (functional clustering) despite the fact that they have been generated by different processes (i.e. environmental or biotic filtering) when using ecological tolerance and competitive ability traits (Cadotte and Tucker 2017). Our specific objectives are: 1) to analyse the relative role of environmental filtering and competition on the structure of European ant communities at local, biogeographic and continental scales; and 2) to analyse whether the type of functional trait plays a relevant role in determining the relative importance of environmental filtering and competition. We hypothesize that the relative role of environmental filtering and competition depends on: a) the spatial scale, that is to say, environmental filtering surpasses competition at larger spatial scales (i.e. Europe and biogeographic regions), while competition exceeds environmental filtering at local spatial scales; and b) ant functional trait type, that is to say, the analyses with 'ecological tolerance traits' will relate to environmental filtering processes, while the analyses with 'ecological niche traits' will be more related to competition processes.

Materials and methods

Ant community data

To measure co-occurrence patterns between pairs of ant species, first we assembled species composition data of local ant communities in Western Europe, which allowed us to perform analyses at different spatial scales: continental (hereafter, European scale), biogeographic and local scales. We considered the five most representative biogeographic regions of Europe (Mediterranean, Continental, Atlantic, Boreal and Alpine), which clearly differ in their climatic and historical conditions (Arnan et al. 2017). These ant communities comprised a total of 155 ant species, belonging to 29 genera and 5 subfamilies. Beforehand, we removed two ant species (*Solenopsis* sp., *Lasius neglectus*) from the original database (containing 157 ant species), since we did not obtain functional data for most traits analysed. At the European and biogeographic scales, we used the 361 local ant communities which were distributed across five biogeographic regions: Mediterranean (211 communities, 127 species), Continental (71, 51), Atlantic (27, 44), Boreal (29, 31) and Alpine (23, 27) (Fig 1). This database includes primary data collected during the author's own field work in the past and data derived from an exhaustive search of the scientific literature (see Arnan et al. 2014, 2017, Retana et al. 2015, for more details on this database). We focused our analyses on presence-absence data. Therefore, this database was composed of six species x site matrices with occurrence data (one for Europe, and one for each of the five biogeographic regions). At the local scale (i.e., the scale of each local community), we looked for communities in which the occurrences of species were not at the whole plot level, but where there was data at the level of different baits within the plot. Overall, we used 24 local ant communities (also included in the general database) from the Mediterranean region, which encompassed 37 ant species. These communities were compiled from our own field work (Retana and Cerdá 2000, Arnan and Blüthgen 2015). In each site, four-five series of five-six baits each were laid randomly over the entire study area (with 5-m spacing between two adjacent baits and also between series) for a total of four-six sampling days of 24 hr each. Baits were plastic discs, each of them with a different large food reward attractive to ants that tried to cover a wide range of potential types of food for ants. Each hour of every 24-hr sampling period, the identity of each ant species feeding at each bait was noted. This database contained 24 species x trap matrices with occurrence data at different baits (between 10 and 60) within a plot. We tried to obtain other databases from the other biogeographic regions in order to perform local scale analysis. However, we managed no more than a few localities in each region, and so we were unable to extend the analysis locally to regions other than the Mediterranean.

Figure 1. Map of the study area showing ant community distribution across the five biogeographic regions of Europe. EEA is original source of the biogeographical regions map Copyright holder: Council of Europe (CoE), Directorate-General for Environment (DG ENV). (https://www.eea.europa.eu/legal/copyright).
https://doi.org/10.1371/journal.pone.0228625.g001

Trait data

The 155 ant species were characterized according to six functional traits that clearly relate to species responses to environmental change ('ecological tolerance traits') or to competition ('ecological niche traits') (Table 1). Information about traits was obtained from the literature (see Arnan et al. 2013, 2014, 2017, Retana et al. 2015). It is worth noting that since ants are social, functional traits have been quantified at both the level of individual worker and that of the colony. The following traits were used: (i) ecological tolerance traits: number of queens, colony size (log-transformed) and brood cycle; and (ii) ecological niche traits: diet, diurnality and worker size. Trait characterization and functional significance is provided in Table 1. In order to check for highly correlated traits, we first carried out pairwise Pearson correlations among all traits. Most correlations were significant ($p < 0.05$), but with Pearson r coefficients < 0.7 (Supp. Mat. C1. 1). We then assumed that our chosen traits were not highly correlated and all of them were included in further analyses.

Table 1. Ant functional traits used in this study assembled in two main groups as regards they are 'ecological tolerance' or 'ecological niche' traits. A trait description, data type, empirical evidences to categorize traits as response or ecological niche traits are shown.

Group of traits / Functional trait	**Description**	**Data type**	**Empirical evidences**
(A) Ecological tolerance			Ants have achieved great ecological success due to their social structure. As other social organisms, the response of ant species to the environment is mainly conditioned by the morphological specialization and flexibility of castes within colonies.
• Number of queens	Monogynous (one queen), polygynous (more than one queen), or both	Qualitative	Polygyny tends to be correlated with abundant resources that permit rapid growth, enabling species to benefit from productive resource environments in ways unavailable to monogynous species.
• Colony size	The mean number of workers per colony	Quantitative	Colony size has a clear impact on resource exploitation because large colonies are competitively superior to small colonies by sending out more workers to collect food resources or battle neighbors.
• Brood cycle	Species with larvae within the nests from March to September, or species with larvae within the nests during the whole year	Qualitative	The annual cycles of ants, characterized by the presence or not of hibernating brood, are well adapted to the climate environments where they live.

(B) Ecological niche			Resource exploitation in ants aligns along two main trait dimensions of competitive interactions: one related to behavioral dominance, associated with large colony size, presence of multiple nests per colony and a collective foraging strategy, and another related to resource partitioning along dietary and microhabitat lines.
• Diet	Proportion of seeds, insect corpses, and liquid foods in diet	Qualitative (Fuzzy-coded)	The type of resources and the size of these resources are considered important in mediating competition for resources among ant species.
• Diurnality	Strictly diurnal or non-strictly diurnal species	Qualitative	In ant communities, subordinate species are subject to interspecific competition, although they can avoid dominants by being less temperature-limited and foraging at different temperatures.
• Worker size	Distance from the tip of mandibles to the tip of the gaster (mm)	Quantitative	Worker size may constrain where and when ants are able to forage, as it is a prominent characteristic that affects all aspects of insect physiology.

See Supp. Mat. C1. 2 for the bibliographic sources.

Data analyses

Different trait-based approaches have been used to distinguish the stochastic and deterministic (environmental vs. biotic filtering) processes that structure biotic communities. The approach we use can disentangle the role of environmental filtering and competitive exclusion by analysing the relationship between species pair co-occurrence and functional dissimilarity (Mouchet et al. 2013). From this analysis, three different patterns might emerge. First, if species with similar functional traits co-occur more often than expected by chance, the relationship between co-occurrence and functional dissimilarity of pairs of species will be significant and negative (i.e. environmental filtering process). Contrary to this, if species with divergent traits co-occur more often than expected at random, the relationship will be significant and positive (i.e. competitive exclusion process). Finally, non-significant relationships between co-occurrence and functional dissimilarity of species pairs are also possible (i.e. neutral theory processes). This would be the case where species co-occur independently of their functional similarity, or alternatively, if environmental filtering and competition exclusion are simultaneously at work with similar contributions. Here, we assume that two species co-occur when they occur spatially in the same community, although they might not share the same foraging time.

The co-occurrence index for each species pair was calculated within each species x site (European and regional scales) and species x bait (local scale) matrix. Data for the co-occurrence analyses consist in binary presence-absence matrices, where each row was a species, each column a site (or a bait), and the entries were presence (1) or absence (0) of a species in a site or a bait. Pairwise co-occurrence was calculated using the Jaccard index of similarity (JIab) for each pair of species in each matrix (Real and Vargas 1996):

$$JIab = AB \div (A + B + AB)$$

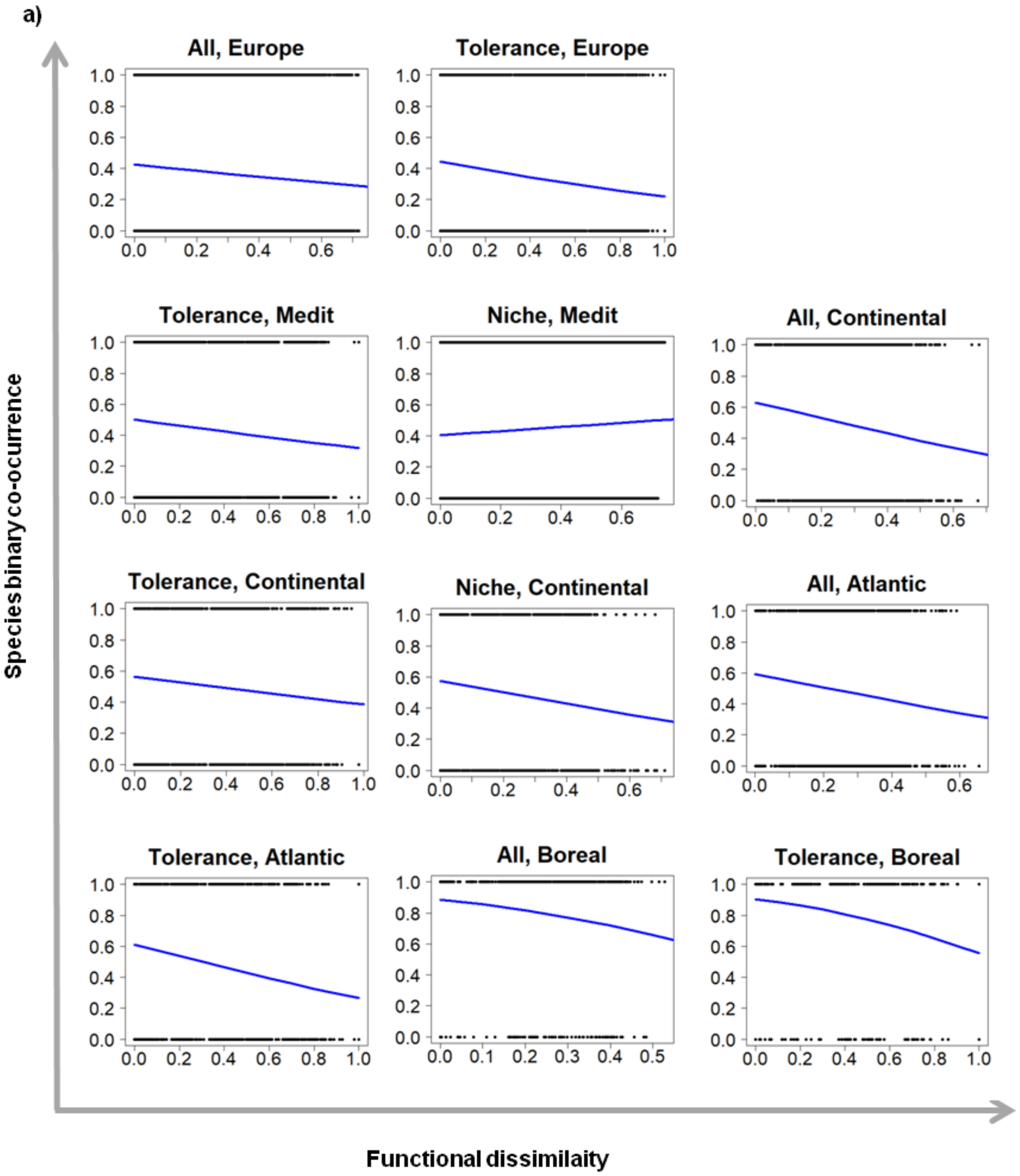
where A and B are the number of sites where only species a and species b occur, respectively, and AB the number of sites where species a and b co-occur. The Jaccard similarity index takes values between 0 and 1, where 0 means that the two species are never found in the same site, and in our case, that co-occurrence is null; while 1 indicates that the two species are always together, and in our case, that the co-occurrence is total.

In order to measure functional dissimilarity between species pairs, we computed Gower's dissimilarity between two species based on each functional trait separately, pooling traits according to whether they are 'ecological tolerance' or 'ecological niche' traits, and pooling all traits together. We used Gower's dissimilarity, so that we would be able to deal with quantitative and qualitative traits (Gower and Legendre 1986). To compute it, we used a functional matrix where rows were species, columns were traits, and cell values were the trait values. Since Gower's dissimilarity depends on the number of species in the matrix, it was only calculated for each pair of species with data from the largest scale (Europe) where the number of species is highest. For each pair of species, nine functional dissimilarities were calculated: one with all functional traits together; one with only the ecological niche traits; one with the ecological tolerance traits; and one for each of the six traits separately. For these computations we used the 'vegan' (Oksanen et al. 2018) and 'cluster' (Maechler et al. 2016) packages in R software v. 3.2.2 (R Core Team 2016).

The relationship between the functional dissimilarity and the co-occurrence index between species pairs was tested by using linear models. Given the large number of zeros in the co-occurrence index and failure to meet the normal assumptions, we carried out the analyses in two steps. First, we transformed the co-occurrence index into a binary variable indicating whether or not there was occurrence of the pair of species in each matrix. We used a generalized linear model with a binomial distribution and a logit link function to perform the analysis (hereafter, binary co-occurrence analysis). In a second step, we applied a general linear model to make the model with the co-occurrence index where the pair of species occur at least once in the matrix (hereafter, co-occurrence strength analysis). In this case, the co-occurrence index was log-transformed to satisfy normality assumptions. We performed 18 analyses at the European scale (nine analyses for binary occurrence matrices and nine for co-occurrence strength matrices, these last nine comprising one analysis with all traits together, two analyses corresponding to each group of traits, and six analyses corresponding to each trait separately), 90 analyses at the biogeographic scale (forty-five for binary occurrence matrices and forty-five for occurrence strength matrices, of which nine analyses corresponded to each of the five biogeographic regions), and 333 analyses at the local scale (117 for binary occurrence matrices and 216 for co-occurrence strength matrices, comprising 37 analyses with all traits together, 37 for each group of traits and 222 for each singular trait). It is worth noting that binary co-occurrence analyses were only performed in locations where more than five pairs of species showed values of co-occurrence=0. Generalized and general linear models were conducted using the ‘stats’ package in R.

Results

Our analyses revealed different patterns in the relationship between co-occurrence and functional dissimilarity among pairs of species according to the scale of analysis and the type of trait used (Table 2). At the European scale, results are consistent between binary co-occurrence and co-occurrence strength analyses. Both analyses showed significant and negative model coefficients when functional dissimilarity was computed with all traits together and with ecological tolerance traits, but non-significant model coefficients when functional dissimilarity was computed with ecological niche traits (Table 2, Figs 2a and 1b).



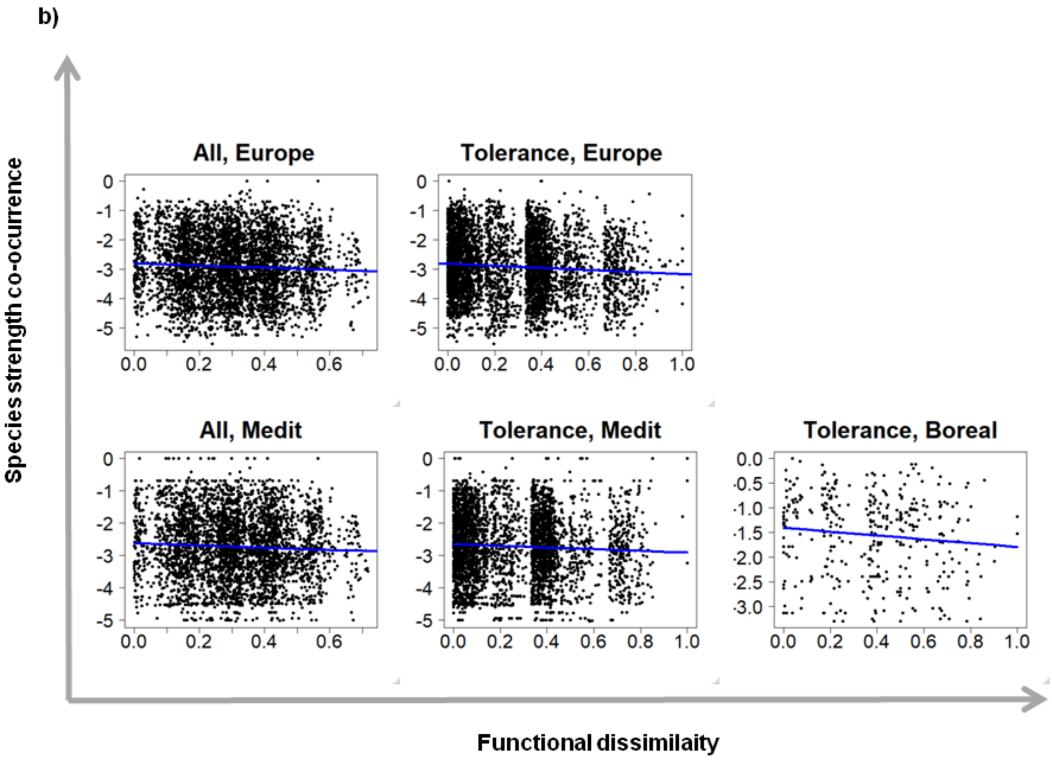


Figure 2. Relationships between species co-occurrence and functional dissimilarity. We show the significant relationships between binary co-occurrence (a) or co-occurrence strength (b) and functional dissimilarity for all traits together, ecological tolerance traits, ecological niche traits between pairs of species at the European and biogeographic region scales. Abbreviations: All, all traits together; Tolerance, ecological tolerance traits; Niche, ecological niche traits; Medit, Mediterranean.

Table 2. Statistical outputs from the binary co-occurrence and co-occurrence strength analyses analyzing the relationship between species co-occurrence and functional dissimilarity between species pairs at the Europe and biogeographic region scales. Different analyses were conducted for functional dissimilarity computed with all traits together, ecological niche traits and ecological tolerance traits.

	Binary co-occurrence analysis				**Co-occurrence strength analysis**			
	Value	**Std. Error**	**z value**	**Pr(>|z|)**	**Value**	**Std. Error**	**t value**	**Pr(>|t|)**
All traits together								
Europe	**-0.8536**	**0.1298**	**-6.5750**	**<0.0001**	**-0.3521**	**0.1082**	**-3.252**	**0.0011**
Mediterranean	-0.1713	0.1510	-1.1340	0.2566	**-0.3545**	**0.1162**	**-3.051**	**0.0023**
Continental	**-2.0021**	**0.3938**	**-5.0840**	**<0.0001**	-0.0632	0.2064	-0.306	0.7590
Atlantic	**-1.7249**	**0.5082**	**-3.3940**	**0.0007**	0.2528	0.4132	0.612	0.5410
Boreal	**-2.8099**	**0.9675**	**-2.9040**	**0.0037**	-0.3840	0.3475	-1.105	0.2700
Alpine	-0.7934	0.8098	-0.9800	0.3270	-0.0595	0.3916	-0.152	0.8790
Ecological tolerance								
Europe	**-1.0475**	**0.0818**	**-12.8010**	**< 0.0001**	**-0.4323**	**0.0703**	**-6.146**	**<0.0001**
Mediterranean	**-0.7722**	**0.1001**	**-7.7180**	**<0.0001**	**-0.2542**	**0.0790**	**-3.215**	**0.0013**
Continental	**-0.7253**	**0.2246**	**-3.2290**	**0.0012**	-0.0948	0.1200	-0.791	0.4290
Atlantic	**-1.4734**	**0.2869**	**-5.1360**	**<0.0001**	-0.1783	0.2360	-0.756	0.4500
Boreal	**-2.0166**	0.4985	-4.0450	0.0001	**-0.3851**	**0.1805**	**-2.134**	**0.0335**
Alpine	-0.5906	0.5046	-1.1700	0.2420	-0.0781	0.2384	-0.328	0.7430

	Binary co-occurrence analysis				**Co-occurrence strength analysis**			
	Value	**Std. Error**	**z value**	**Pr(>|z|)**	**Value**	**Std. Error**	**t value**	**Pr(>|t|)**
Ecological niche								
Europe	0.1500	0.1034	1.4500	0.1470	0.0344	0.0851	0.404	0.6860
Mediterranean	**0.5349**	**0.1224**	**4.3700**	**0.0000**	-0.1434	0.0932	-1.538	0.1240
Continental	**-1.4792**	**0.3542**	**-4.1760**	**0.0000**	0.0996	0.2031	0.49	0.6240
Atlantic	-0.0368	0.4746	-0.0770	0.9380	0.5858	0.3736	1.568	0.1180
Boreal	-0.6189	1.0260	-0.6030	0.5460	0.2701	0.3820	0.707	0.4800
Alpine	-0.2786	0.7469	-0.3730	0.7090	0.0020	0.3799	0.005	0.9960

Significant coefficients ($p<0.05$) are shown in bold.

At the regional scale, binary co-occurrence and co-occurrence strength analyses revealed consistent and complementary results. When analyses were based on all traits together, binary co-occurrence analyses showed significant and negative estimates for the Boreal, Continental and Atlantic regions (from the steepest to the lowest slopes) (Fig 2a); complementarily, co-occurrence strength analysis showed a significant and negative estimate for the Mediterranean region (Table 2, Fig 2b). When using ecological tolerance traits, both binary co-occurrence and co-occurrence strength analyses revealed significant and negative model estimates for the Mediterranean and Boreal regions (Figs 2a and 2b); additionally, the binary co-occurrence

analyses showed significant and negative estimates for the Continental and Atlantic regions (Table 2, Fig 2a). With regard to analyses based on ecological niche traits using the binary co-occurrence approach, significant model estimates were only found for the Mediterranean (positive estimate) and Continental (negative estimate) regions (Table 2). In short, for those biogeographic regions where the relationship between co-occurrence and functional dissimilarity was significant regardless of the analysis employed, all relationships were negative when using all traits together or ecological tolerance traits to compute functional dissimilarity, while relationships did not have a consistent pattern when ecological niche traits were used.

At the local scale, of the one hundred and eleven model coefficients, only eleven were significant (Table 3). Specifically, binary co-occurrence analyses only revealed a significant and positive model coefficient in one site, and this when computing functional dissimilarity with ecological tolerance traits. Meanwhile, co-occurrence strength analyses revealed several significant model coefficients. When functional dissimilarity was computed with all traits together, only four sites depicted significant relationships (three negative and one positive); when computed with ecological tolerance traits, only two sites depicted significant relationships

Table 3. Estimated coefficients from the analyses between functional dissimilarity computed with all traits together, ecological niche traits and ecological tolerance traits, and binary co-occurrence as well as co-occurrence strength between pairs of species at the local scale.

			Binary co-occurrence analysis			**Co-occurrence strength analysis**		
Locality	**n**	**n0**	**All together**	**Ecological tolerance**	**Ecological niche**	**All together**	**Ecological tolerance**	**Ecological niche**
loc.01	45	11	1.5660	0.9093	0.8339	1.6440	**1.7331**	0.4290
loc.02	120	40	1.3924	1.6622	-0.0853	**1.2182**	0.5188	0.7802
loc.03	10	0	-	-	-	**-6.7295**	-3.6431	-3.7509
loc.04	66	29	-0.8883	1.5651	-1.9334	**-1.9270**	**-1.2384**	**-1.4091**
loc.05	6	0	-	-	-	**-9.2907**	-1.5765	-2.5890
loc.06	21	12	8.3800	-0.7843	7.9885	-5.3871	-1.3070	-2.1909
loc.07	21	0	-	-	-	-0.9864	-1.6160	0.2878
loc.08	21	6	-2.6100	-3.7100	-0.5150	0.1842	-0.5069	0.2548
loc.09	120	40	2.9945	0.6239	2.2770	-0.1972	0.3136	-0.4402
loc.10	28	7	5.9686	-3.4477	5.6574	0.1872	0.7015	-0.1607
loc.11	66	20	-0.7810	**6.2998**	-2.7330	0.4620	-0.0859	0.5016
loc.12	55	3	-	-	-	0.4804	0.6585	0.0097
loc.13	21	3	-	-	-	-1.8155	1.2629	**-2.3216**
loc.14	28	4	-	-	**-**	-0.7276	1.1398	**-1.1046**
loc.15	21	6	4.3511	4.2968	1.3112	-0.8123	0.8628	**-1.8472**
loc.16	21	0	-	-	-	-0.3357	0.0022	-0.4171
loc.17	28	1	-	-	-	1.4501	1.2610	0.6379
loc.18	36	2	-	-	-	0.4246	1.2738	-0.4789
loc.19	15	6	-3.7120	-5.9210	-1.3378	-0.8853	-0.1946	-0.9405
loc.20	55	35	1.0030	1.6240	-0.5537	-0.0839	0.5128	-0.7753
loc.21	36	20	1.1635	2.2606	-0.8901	-1.1148	-0.5762	-0.9014

			Binary co-occurrence analysis			**Co-occurrence strength analysis**		
Locality	**n**	**n0**	**All together**	**Ecological tolerance**	**Ecological niche**	**All together**	**Ecological tolerance**	**Ecological niche**
loc.22	28	4	-	-	-	-0.0444	-0.2654	0.1023
loc.23	66	3	-	-	-	0.2591	0.6642	-0.1928
loc.24	45	13	2.1939	-0.7670	2.8689	0.5320	-0.0018	0.5528

Significant coefficients ($p<0.05$) are shown in bold. Abbreviations: n, number of species pairs in each locality (loc.); n0, number of species pairs with co-occurrence=0 in each locality. Note that binary co-occurrence analyses were only performed when at least six pairs of species depicted values of co-occurrence=0.

(one positive and one negative); and when computed with ecological niche traits, only four sites depicted significant relationships (all negative).

When analyses were performed for each single trait at the European and biogeographic region scales, we also found different patterns according to the scale of analysis and type of trait. (Table 4). At the largest scale (Europe), binary co-occurrence analyses revealed significant and negative coefficients for the three ecological tolerance traits (i.e. number of queens, colony size and brood cycle), but no significant coefficients for any of the ecological niche traits (i.e. diet, diurnality and worker size). Complementarily, co-occurrence strength analyses showed significant and negative estimates for number of queens and colony size (ecological tolerance traits), and significant and positive model coefficients for diurnality and worker size (ecological niche traits) (Table 4). At the intermediate spatial scale (biogeographic region scale) and regardless of the analytical approach, significant estimate models were always negative for the three ecological tolerance traits, but negative or positive for ecological niche traits depending on the trait and biogeographic region (Table 4). Thus, when functional dissimilarity was based on the number of queens, binary co-occurrence analyses revealed significant estimates for the Mediterranean, Continental and Atlantic regions; meanwhile, co-occurrence strength analysis revealed significant estimates for the Mediterranean, Atlantic and Boreal regions. With respect to colony size, significant relationships were found for the Boreal region from both binary co-occurrence and co-occurrence strength analyses, and for the Mediterranean region from the binary co-occurrence analysis alone. When using brood cycle, binary co-occurrence analyses revealed significant estimates for all regions except the Alpine, while co-occurrence strength analyses showed no significant estimate. Moving to the ecological niche traits, when functional dissimilarity was based on diet, binary co-occurrence analyses revealed positive estimates for the Mediterranean and Alpine regions, and negative estimates for the Continental region;

meanwhile, co-occurrence strength analyses showed a significant negative effect for the Mediterranean region. When using diurnality, positive and negative estimates were found for the Mediterranean and Alpine regions, respectively, from binary co-occurrence analyses, while co-occurrence strength analyses did not find any significant relationship in any region. Finally, when analyses were based on worker size, binary co-occurrence analyses showed a significant positive estimate for the Mediterranean region, but significant negative estimates for the Continental and Atlantic regions; meanwhile, co-occurrence strength analyses only showed a positive estimate, particularly for the Atlantic region (Table 4).

When analyses were performed for each single trait at the local scale, we only found a few significant coefficients. Of the two hundred and twenty-two estimated coefficients, only eighteen were significant, these breaking down into five positive (all for tolerance traits) and thirteen negative (four for ecological tolerance traits and nine for ecological niche traits) (Supp. Mat. C1. 3).

Table 4. Estimated coefficients from the analyses between co-occurrence (binary co-occurrence and co-occurrence strength) and functional dissimilarity between species pair based on single traits at the European and biogeographic region scales.

	Europe	**Mediterranean**	**Continental**	**Atlantic**	**Boreal**	**Alpine**
Binary co-occurrence						
Ecological tolerance traits						
Number of queens	**-0.3644**	**-0.3019**	**-0.2148**	**-0.4001**	-0.4355	-0.2395
Colony size	**-1.1945**	**-0.9277**	-0.2475	-0.7237	**-2.4034**	-0.8136
Brood cycle	**-0.3034**	**-0.1986**	**-0.2649**	**-0.5512**	**-0.5571**	-0.1761
Ecological niche traits						
Diet	-0.0327	**0.1731**	**-1.1904**	0.2276	-1.2760	**1.4605**
Diurnality	0.1243	**0.2137**	-0.1336	-0.0061	-0.0687	**-0.5479**
Worker size	0.0959	**0.3546**	**-0.8617**	**-1.0333**	0.7673	0.1225
Co-occurrence strength						
Ecological tolerance traits						
Number of queens	**-0.2701**	**-0.1805**	-0.0041	**-0.2344**	**-0.3313**	-0.2478
Colony size	**-0.3730**	-0.2393	-0.0160	-0.1242	**-0.7977**	0.6684
Brood cycle	-0.0324	0.0034	-0.0587	0.0686	0.0228	0.0556
Ecological niche traits						
Diet	-0.0967	**-0.2379**	0.2596	0.1721	-0.4340	-0.0237
Diurnality	**0.0655**	0.0465	-0.0370	0.1065	0.1534	0.0066
Worker size	**0.1917**	0.1465	-0.2232	**0.9352**	0.1889	0.1269

Significant coefficients ($p<0.05$) are shown in bold.

Discussion

Our first objective was to analyse the relative role of environmental filtering and competition on the structure of European ant communities at different spatial scales. We partially corroborated our first hypothesis, because our results suggest that environmental filtering is the main mechanism influencing ant community structure at the largest spatial scale (European). Meanwhile, different patterns emerge at the intermediate spatial scale depending on the biogeographic region (although environmental filtering is the main mechanism at play), but no ecological mechanism (environmental filtering or competition) is more important than the other at the local scale in the Mediterranean region. Overall, as the scale of analysis increases, environmental filtering becomes more important as a structuring mechanism for European ant communities.

When we analyse assembly rules at the continental scale, we encounter more widely contrasting environmental conditions than at smaller spatial scales, such as different habitat types and even biogeographic regions. Thus, the larger the scale, the more likely it is that more widely contrasting environmental conditions will be found. Species inhabiting environments with severe environmental conditions must adapt morphologically, behaviourally and/or ecologically to the harsh conditions. Therefore, species co-occurring in similar harsh habitats have more functional similarities in terms of their traits that will allow them to persist in those conditions when compared with species living in different environmental conditions (Zobel 1997, Asefa et al. 2017).

When we go down to smaller spatial scales, high spatial heterogeneity with very widely contrasting conditions is less likely to be found. At the smallest spatial scale we analysed, local scale, and contrary to our predictions (we expected competition effects to exceed environmental filtering effects), our results indicate that no one ecological mechanism predominates over the other in determining community structure, at least in the Mediterranean region. The explanation here might be twofold. First, although behaviourally dominant ant species exclude other species from near their nests (Savolainen et al. 1989) and from high-value food resources that are spatially and temporally concentrated (Andersen 1992), the role of dominant ants influencing other species at the community level has recently been questioned (Andersen 2008, Cerdá et al. 2013, Stuble et al. 2017, Arnan et al. 2018). In ant communities there are several compensatory mechanisms (e.g. thermal tolerance-behavioural dominance trade-off, dominance-discovery trade-off and its modulation by parasitoids) that may act on ant community organization by modifying the expected competitive outcome and thereby allowing coexistence (Cerdá et al. 2013, Stuble et al. 2013). In our study, all local communities come from the Mediterranean region, which is highly diverse in microhabitats with varying conditions, especially with respect to temperature (Retana and Cerdá 2000). In Mediterranean ant communities, dominant species usually have low thermal tolerance, whereas subordinate species have high thermal tolerance; therefore, subordinate species can forage at different times of the day or in different seasons compared with dominant species, leading to species coexistence and high diversity (Retana and Cerdá 2000). If so, we might only be able to detect what is no longer the result of past competition if we use a set of ecological traits that are hard to measure for a high number of species, such as physiological thermal tolerance, food resource discovery time and vulnerability to parasitoid attack. Whatever the case, our results support recent works that throw into doubt the role of competition as an important ecological mechanism structuring ant communities at the local scale (Cerdá et al. 2013, Stuble et al. 2017). We of course do not seek to generalize our conclusions at the local scale from the Mediterranean region to other regions. Indeed, assembly rules can clearly differ among biogeographic regions, as they probably provide contrasting evolutionary histories of ant faunas (Economo et al. 2018, Vasconcelos et al. 2018). Thus, in much colder regions than the Mediterranean (i.e., boreal and alpine), where habitat heterogeneity is low and the abundance of behavioral ant dominant species is high, the biotic filter might play a more relevant role and thus competition might be the predominant force structuring local ant communities (Savolainen and Vepsäläinen 1989, Czechowski and Markó 2005, Alinvi et al. 2008, Gibb and Parr 2010). Still, the role of competitive exclusion in the ant low-diversity systems typical from boreal and alpine forests remains unclear (Arnan et al. 2018). And secondly, an alternative explanation might be that both environmental filtering and competition are similarly important at the local scale, and then their effect on community structure is compensated. This might only be possible if there is high spatial heterogeneity in microhabitats with contrasting environmental conditions. The fact that most of the few significant coefficients at the local scale were negative might suggest some role of environmental filtering in local Mediterranean communities. At any rate, conducting tests in local communities from other biogeographic regions might help to disentangle the relative role of environmental filtering and competition at small spatial scales.

Meanwhile, at intermediate spatial scales, i.e. at the biogeographic region scale, we found that environmental filtering is also the prominent mechanism structuring ant communities. In the Mediterranean, Continental, Atlantic and Boreal regions in particular, ant communities are predominantly structured by environmental filtering, with different effect magnitudes (i.e. different slopes of the relationship between species dissimilarity and species co-occurrence among biogeographic regions). Otherwise, in the Alpine biogeographic region, our results indicate a neutral model where no mechanism is more relevant than the other in the structuring of ant communities, or communities are randomly structured. This result suggests that differences in abiotic, biotic and historical conditions among biogeographic regions could be important in explaining differences in the dominant assembly rules in ant communities. On the one hand, the main biogeographic regions of Western Europe present varying climatic conditions (Arnan et al. 2017) and are distributed across a clear latitudinal gradient (35 – 70ºN). The relevance of environmental filtering might increase from low to high latitudes following a gradient of increased climatic variation (e.g. variation between the minimum and maximum temperatures) (Stevens 1989). Accordingly, we found the role of environmental filtering increases following a clear latitudinal pattern (from the Mediterranean to the Boreal region).

On the other hand, and in contrast to the other regions, the Alpine region is distributed discontinuously across the study area, which might explain the highest beta functional community diversity in this region in relation to the other biogeographic regions of Europe (Arnan et al. 2017). The strong dispersal limitations of European ant species (Arnan et al. 2015, Helms 2018) might account for high functional turnover, probably due to divergent evolution. If account is taken of all these factors, the structure of Alpine ant communities might be determined by stochastic mechanisms, assuming that population dynamics do not depend on environmental characteristics and are primarily driven by ecological drift and dispersal (Jetschke 2001).

With regard to our second aim to analyse whether the type of functional trait plays a relevant role in determining the relative importance of environmental filtering and competition, we corroborated our hypothesis. Our results indisputably indicate that trait type matters. However, we failed to predict the mechanism at work suggested by each trait type. This is because, as predicted, the analyses of the relationship between species pair co-occurrence and functional divergence with grouping of ‘ecological tolerance traits’, when significant, always revealed negative coefficients (environmental filtering effects). However, when the analyses were performed with grouping of ‘ecological niche traits’, significant relationships were associated with positive (competition effects) and negative (environmental filtering effects) coefficients. This does not support our hypothesis that ‘ecological niche traits’ are more related to competition processes. This is even clearer when looking at the patterns when analyses were performed with single traits, because the significant coefficients of single ecological tolerance traits were always negative; meanwhile, ecological niche traits displayed significant positive and negative coefficients. Whatever the case, classifying traits in ‘ecological tolerance traits’ seems to be appropriate in order to detect environmental filtering effects. In contrast, the balance for each single ecological niche trait can be either positive or negative, and this classification appears to be somewhat problematic. On the other hand, our results also demonstrate that, in general, performing assembly rules analyses with multi-trait grouping is good enough, since responses are the balance of different and contrasted responses. However, when conducted with a set of traits that clearly refer to only one ecological process, multi-trait analyses might be much more informative than pooling together traits of such diverse origin. Thus, the separate analyses of ‘ecological tolerance traits’ and ‘ecological niche traits’ provide more significant patterns than when pooling all of them together, given that opposite patterns can cancel each other out.

The analyses performed separating groups of traits fostered a more in-depth understanding of the assembly rules at work among the different biogeographic regions. We found no effect from any group of traits in the Alpine region. This might confirm that the lack of a significant relationship between species pair co-occurrence and functional dissimilarity is not due to compensation between the two mechanisms, but to randomly structured communities, probably as a result of historical factors and dispersal limitations, as previously suggested. Moreover, we found significant relationships for the Continental, Atlantic and Boreal regions for ‘ecological tolerance traits’ alone, and for the Mediterranean region for both ‘ecological tolerance’ and ‘ecological niche’ traits. These results suggest that the Continental, Atlantic and Boreal regions are mainly structured by environmental filtering, while competition can also be similarly relevant in the Mediterranean region. Ant activity and productivity are strongly related to temperature (Hölldobler and Wilson 1990, Andersen 1995), and the effects of competition typically increase with increasing productivity (Andersen 1995, Rees 2013). Mean temperatures in the Continental, Atlantic and Boreal regions are much lower than in the Mediterranean region (Fig 2 in Arnan et al. 2017).

In short, environmental filtering is important for structuring European ant communities at large spatial scales, particularly at the continental scale and in most biogeographic regions. Competition could also play a role at intermediate spatial scales in those regions where environmental conditions are more favourable for ant productivity (i.e. the Mediterranean region). Meanwhile, stochasticity might be especially relevant in spatially discontinuous regions (i.e. the Alpine region). Different abiotic and biotic factors might therefore play an important role in determining which mechanism is more relevant in the structuring of ant communities at intermediate spatial scales. However, we failed to demonstrate the prevalence of any mechanism at the local scale in the Mediterranean region. We also conclude that the type of trait is important when seeking different assembly rules, and multi-trait grouping works well for traits that directly relate to environmental responses (i.e. ecological tolerance traits that respond to environmental filtering), but not for traits that are related to the way species exploit resources (i.e. ecological niche traits that respond to competition). Moreover, ecological niche traits might not be associated with competition, but also with other ecological processes such as equalizing fitness and facilitation (Spasojevic 2012). We need more studies that address what directly links morphological and life-history traits with ecological processes, especially in animals, in order that we may disentangle the ecological processes that structure diversity at different spatial scales. Clearly, spatial scale of analysis, environmental context and chosen traits merit special attention in trait-based analyses of community assembly mechanisms.

Acknowledgements

We are very grateful to Daniel Sol for their comments on an earlier draft of this manuscript and to Xim Cerdá for providing data.

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CAPÍTOL 2

THE LATITUDINAL GRADIENT IN EUROPEAN ANT DARK DIVERSITY: PATTERNS AND POTENTIAL MECHANISMS

Boet, O., Arnan, X. and Retana, J. (2025). Oikos e10656.

https://doi.org/10.1002/oik.10656

Capítol 2. The latitudinal gradient in European ant dark diversity: patterns and potential mechanisms

Abstract

Observed richness has long been the basis for studies of species distribution patterns and community ecology, but dark diversity (i.e., the group of species in the regional pool that can live under the specific local environmental conditions but which are not part of the local species richness) has recently gained prominence for providing complementary ecological information. In this study we aim to determine the role of latitude on shaping ant dark diversity in Europe, with special attention to the effects of elevation and biotic pressure. We computed dark diversity from observed and expected richness in 415 ant communities distributed through Europe. We found that ant dark diversity in Europe shows a negative latitudinal pattern (with greater values where there are more favorable environmental conditions), and this trend is more pronounced at higher elevations. Moreover, dark diversity increases more strongly with decreasing latitude than observed richness, suggesting the existence of a larger species reservoir at southern latitudes. Our results also show that dark diversity tends to increase with biotic pressure (i.e., abundance of dominant species). This suggests an effect of behaviourally dominant ants in structuring ant communities, an effect that is hardly detected in classical studies of ant community structure. Despite the fact that different mechanisms might shape the latitudinal pattern of dark diversity, our results suggest that in southern latitudes the important role of interspecific competition is prominent, while in northern latitudes the environmental filter is

more important. At the local level, biotic pressure tends to increase dark diversity, although small-scale species dispersal limitation and habitat quality may also play important roles. The analysis of dark diversity patterns in ants allowed us to better understand the mechanisms that shape ant diversity, which might not be detectable only by analyzing observed richness.

Introduction

Understanding species distributions and richness across the globe is a hot topic in ecology. Species richness determines the complexity of ecological networks (Ives et al. 2000), the provision of ecosystem services (Lecina-Diaz et al. 2019), and/or the strategies to successfully promote biodiversity conservation (Titley et al. 2021). However, recent studies have emphasized the importance of the dark diversity (Pärtel et al. 2011), that is, the subset of species in the regional pool that can live under the specific local environmental conditions but which are not part of the local species richness (Pärtel et al. 2011). In other words, dark diversity is the set of species that are present in the region (also called "regional pool", "specific species pool" or "expected richness") (Zobel 1997, Cornell and Harrison 2014, Bruelheide et al. 2020), have the potential to colonize and establish in a given local site but are currently locally absent. It can also be understood as a species reservoir in the face of possible species loss in a local community (e.g., through local extinctions), even more accurate than the regional species pool (Cornell and Harrison 2014, Pärtel et al. 2013). A concept closely related to dark diversity is community completeness, which is a relative value of dark diversity (i.e., the ratio between observed species richness and dark diversity) that allows comparisons between widely disparate taxa and habitats (Pärtel et al. 2011). Community completeness expresses how much of the specific species pool is noticed within a local community. Approaching the study of species richness from the perspective of dark diversity can contribute to the application of better biodiversity conservation management strategies (Lewis et al. 2017), to the detection of processes of species expansion or invasion (for example, by detecting species first in dark diversity than in the community) and improve the understanding of the processes underlying community assembly (Fløjgaard et al. 2020, Belinchón et al. 2020). For instance, it is hard to detect interspecific competition effects on ant community structure without the use of exclusion experiments, which are time consuming and very costly (Gibb and Hichuli 2004), but dark diversity can inform us on this (see below). Dark diversity is a recent ecological concept and has only been analyzed mainly with plants, with only scarce animal studies that do not allow generalizations.

Latitudinal patterns of species richness have been widely studied around the world for a large array of plants and animals (Field 2002, Mittelbach et al. 2007). In general, species richness increases as we approach the tropics; however, we can also find the opposite pattern or no clear pattern (Willig et al. 2003). Generally, high species richness across large spatial scales has been linked to high productivity and more favorable climatic conditions for the studied taxon (Hawkins et al. 2003, Moura et al. 2016). Latitudinal patterns in dark diversity have been much less studied, as only two studies with plants (Pärtel et al. 2011, Ronk et al. 2015) and one with fungi (Pärtel et al. 2017) have addressed this topic. These studies conclude that, in Europe, plant dark diversity increases at lower latitudes, whereas fungi dark diversity decreases. In these cases, dark diversity has always been positively correlated with species richness along the latitudinal gradient.

Aside from the influence of latitude at large spatial scales, elevation is also an important factor influencing species richness at intermediate scales, as abiotic conditions change over short distances (Field 2002). Increasing elevation is usually associated with decreasing species richness due to harsher environmental conditions and reduced land area (McCain and Grytnes

2010, Körner 2004), although this cannot be the case for all elevation ranges and taxa (McCain and Grytnes 2010, Rahbek 1995). Latitude and elevation can interact to shape species richness, and similar elevational ranges in different latitudes can exhibit different underlying gradients. For instance, tropical mountains usually have lower temperature at a given elevation than mountains in temperate regions at a similar altitude (Rahbek et al. 2020). Widely, the observed richness shows a unimodal elevation pattern at lower mid-altitude, with peaks decreasing in elevation with increasing latitude (Guo et al. 2013). As far as we know, only one study analyzes elevational effects on dark diversity (Trindade et al. 2021), and reveals that both species richness and dark diversity of lichens in spruce forests simultaneously increase with elevation.

Biotic pressure varies along the latitudinal and elevation gradients (Schemske et al. 2009), thus being a key factor determining species richness along these gradients (Hulshof et al. 2013). While biotic pressure can remove species from local communities by competitive exclusion (Staniczenko et al. 2018) (diminishing species richness), it would simultaneously increase dark diversity. Unfortunately, there are still few studies that demonstrate the role of biotic pressure in dark diversity. Some recent studies with vascular plants in Europe have found that high dark diversity is driven by the exclusion of the competitively weakest species from communities as a result of increased biotic pressure (Fløjgaard et al. 2020, Riibak et al. 2015, Belinchón et al. 2020). Despite this, there may be other factors that increase dark diversity locally, such as the low quality of the habitat (Dalle Fratte et al. 2022) and the dispersal limitation within the distribution range of species (Riibak et al. 2017, Belinchón et al. 2020).

Ants offer an excellent opportunity to analyze diversity patterns across environmental and biotic gradients. Ants are abundant and widely distributed across all continents (except Antarctica), occupying most terrestrial habitats where they provide basic ecological services (Hölldobler and Wilson 1990, Elizalde et al. 2020). There is also an excellent knowledge on the environmental variables that determine ant species distributions, mainly related to temperature, precipitation and land cover (Dunn et al. 2009, Arnan et al. 2014, Vasconcelos et al. 2018), which can determine their latitudinal and elevational patterns. Specifically, a negative relationship has been found between latitude and ant species richness, at least in the northern hemisphere (Cushman et al. 1993, Kumschick et al. 2009, Dunn et al. 2009, Economo et al. 2018), and three elevational patterns of ant species richness have been described: low-elevation plateaus (Brühl et al. 1999), mid-elevational peaks (Sanders et al. 2003) and decreasing trends (Sanders et al. 2003, Dunn et al. 2009, Perillo et al. 2021). Moreover, there is also wide research on the mechanisms and/or processes that affect the assembly of ant communities at different scales (Arnan et al. 2015, Boet et al. 2020), such as the role of competition on shaping ant community structure and composition (Andersen and Patel 1994, Blüthgen and Fiedler 2004, Cerdá et al. 2013). Ants usually have a dominance behavioral hierarchy, in which there are dominant (including subdominant) and non-dominant species (Cerdá et al. 2013, Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990). Behaviourally dominant species are usually aggressive ants that exclude other species from food sources, and/or actively defend their territories (Cerdá et al. 2013). Thus, communities with a high abundance of dominant species, and in the absence of other compensatory mechanisms (Feener et al. 2008, Cerdá et al. 2013), may usually have lower ant species richness (Parr et al. 2005, Arnan et al. 2018). Consequently, we might expect that communities with greater abundance of dominant ant species, and regardless of climatic conditions, will have greater dark diversity.

This study aims to determine the role of latitude, elevation, and biotic pressure on shaping ant dark diversity in Europe. We have the following hypotheses: 1) Dark diversity will be greater in communities from lower than from higher latitudes due to more favorable environmental conditions, although elevation will shape this relationship; 2) Dark diversity will increase with the abundance of dominant species due to increased biotic pressure within the community. To achieve these goals, we have estimated species richness, dark diversity, and the abundance of dominant ants in 415 ant communities distributed across Europe. To estimate dark diversity (as the subtraction between the expected and observed richness), we have computed the expected richness by using binary stacked species distribution models from the 278 main ant species from Europe.

Material and methods

Study area

The study area was Europe, considering the geographic limits of 34º 30' N, 71º 17' N, 10º 30' W and 32º 48' E (geographical coordinates, datum WGS84).

Observed species richness

For species richness, we collected data from 415 local ant communities in Europe (Fig. 1). We obtained data on ant communities from published literature and our own past studies (Supp. Mat. C2. 1). These communities cover a latitudinal range larger than 25º, from 36.75º N to 62.0º N, and elevation ranges from 0 m to 2,252 m.a.s.l.

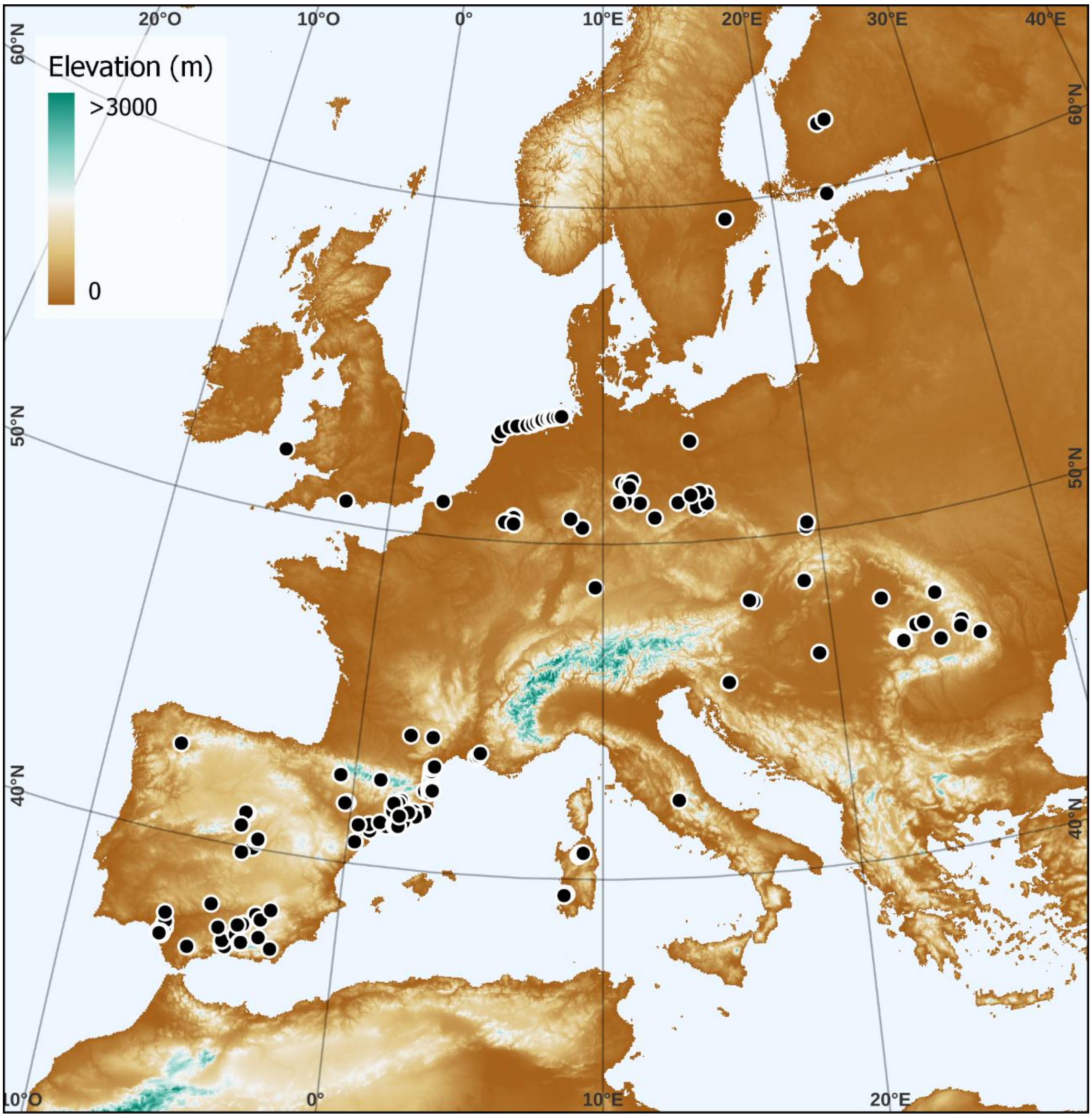

Fig. 1: Map of Europe showing the study area and the 415 ant communities (black dots) on the relief of elevations. Background map: WorldClim version 2.1 climate data for 1970-2000.

Estimated dark diversity

Dark diversity cannot be directly measured since it cannot be observed, so it must be estimated. There are two main approaches for estimating it. On the one hand, there is the species co-occurrence approach (SCO), based on the idea that if two species are found in the same community, they share environmental conditions and therefore belong to the same species pool. Several studies with plants (we are not aware of similar studies with animals) have evaluated the co-occurrence method using the Beals index or hypergeometric method and concluded that it yields good results (Lewis et al., 2016, Ronk et al. 2016, Carmona et al. 2020, Paganeli et al. 2024). On the other hand, the other approach starts from the environmental requirements of each species to estimate expected richness (from which the dark diversity is calculated), often based on stacking the species' potential distribution models (SDMs) (Elith et al. 2006, Benito et al. 2013). There are many examples of using this method to estimate the potential distribution of species, for both plants and animals (D'Amen et al. 2015, Guisan and Zimmermann 2000, Ronk et al. 2016). The comparison of the two methodologies, SCO and SDM, to study patterns of dark diversity in plants concludes that both provide similar results, especially at large scales (Ronk et al. 2016, de Bello et al. 2016). Considering these results and the characteristics of our data, such as the non-systematic collection of occurrence data (see below "Data collection"), we calculated the dark diversity with the environmental requirements approach (restricted to species dispersal limitations, see below) following the scheme in Fig. 2. In the following subsections, we explain how we estimate the expected species richness from the environmental requirements approach, and based on this, we calculated the dark diversity.

Expected richness

We built a map of the expected species richness (specific species pool or filtered species pool) of ants in Europe relied on the stacking of binary species habitat suitability models (S-SDMs hereafter) (Benito et al. 2013). The 415 ant communities were located well within the area considered by the S-SDMs, to avoid the prediction margin effect (Ronk et al. 2016). Three steps were followed to make the S-SDMs (Fig. 2).

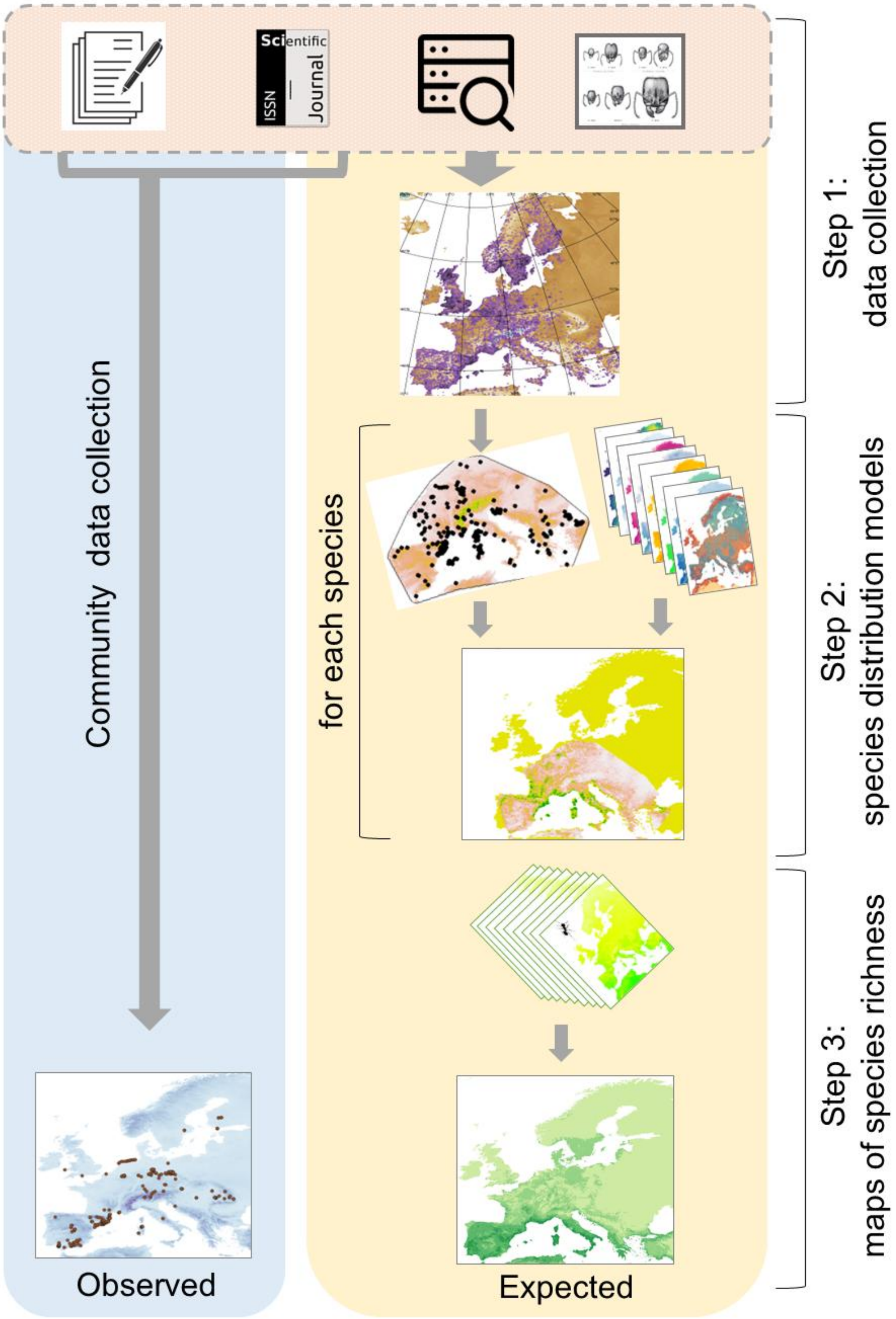

Fig. 2: Graphical outline of the process to obtain the maps used to estimate dark diversity from observed and expected species richness for each community.

Data collection

The first step was to compile a comprehensive database of European native ant species records from Europe, gathering data from online data portals, queries from museum collections and extensive research in the scientific literature (Supp. Mat. C2. 2) and our past field data. To ensure the robustness of the database, we carried out a rigorous process of data cleaning and harmonization (for details see Supp. Mat. C2. 3), including the consistency of species names according to the Bolton's catalogue (Bolton et al. 2006) and the removal of: (i) pre-1950 citations; (ii) parasitic species, as they are difficult to detect and are often not considered in the species richness in community studies; (iii) exotic species observed only in urban environments, as they are not part of the study communities; and (iv) typically Asian or African species that only appear in Europe at the edges of their distribution range. At the end of the first step, we obtained an extensive database of ant records from Europe with 63,111 data records comprising 278 species (Supp. Mat. C2. 4 and Supp. Mat. C2. 5). For each species, we compared the record maps with the known distributions from the AntMap maps (https://antmaps.org) and verified that they were a good representation of their distribution. Since there are about 600 native species in Europe (Czechowski et al. 2002), parasites and those of marginal distribution included, we consider that our study has a very good representation of ant diversity in the study area.

Species distribution models

The second step was to perform species distribution models (SDMs hereafter) to generate habitat suitability (as a proxy of occurrence probability) maps for each species. To do this, we needed environmental variables related to ant occurrence, such as climatic, topographical and vegetation cover variables. We initially considered raster maps of 23 environmental variables (Supp. Mat. C2. 6). Then, we conducted correlations between all pairs of variables, and when two variables were highly correlated (Pearson $r > 0.7$), we removed one and the most relevant variable for ant ecology was selected (Williams et al. 2012). All the variables removed had a Pearson $r > 0.75$ with at least one of the variables selected (Supp. Mat. C2. 7). Finally, seven variables were left, with which we performed SDMs: mean annual temperature, mean temperature of the wettest quarter, annual precipitation, precipitation seasonality (coefficient of variation), elevation, land cover, and continentality.

We performed SDMs with MaxEnt, which makes predictions only with presence data (Elith et al. 2011). Despite some limitations to the use of Maxent (Fitzpatrick et al. 2013), which have subsequently been refuted (Merow and Silande 2014), this algorithm has been succesfully used for predicting the potential distribution of ants (Procter et al. 2015, Depa et al. 2017, Silva et al. 2022). We used the Dismo package (Hijmans et al. 2017) in R (R Core Team, 2020). To avoid pseudoreplication, we balanced the distribution of the occurrence points of each species by eliminating any point less than 10 km away, but maintaining those points that had extreme values in the environmental variables using the ‘thinning’ function (Benito 2021). We then took into account species dispersal limitations to prevent species distributions from extending into environmentally suitable but geographically unrealistic areas far from their current presences. For this reason, we restricted the working area of MaxEnt by considering the current distribution of each species plus an estimated dispersal distance of ants over a period of 70 years (corresponding to the time period of the occurrence records considered in this study, from 1950 to 2020) (for details see Supp. Mat. C2. 8). Subsequently, we obtained a specific area of occurrence for each species (henceforth envelope) for the MaxEnt model, i.e., each species had a different envelope in the model and therefore the background points were also restricted in this area) (see Supp. Mat. C2. 9).

Map of expected species richness

In the third step, we transformed the SDMs into binary maps of Europe, applying the method of maximization of the sum of sensitivity-specificity. This method is widely used to select the optimal threshold value in classification tasks, where predictions of presence or absence are evaluated for each species (Jiménez-Valverde and Lobo 2007) (Supp. Mat. S2.5). Sensitivity is the fraction of true positives (the model predicts presence where there are occurrences) and specificity is the fraction of true negatives (the model predicts absence of the species in places where there are no occurrences). Sensitivity and specificity are complementary and as one increases the other decreases. By maximizing their sum, the threshold reaches an equilibrium where presences and absences are well predicted. We calculated threshold values using the Dismo package in R. Finally, the sum of all binary maps (i.e., S-SDMs) was the expected species richness map of Europe, from which we obtained the values of the expected richness for each community (Supp. Mat. C2. 10).

Dark diversity and completeness

To analyze ant dark diversity along the latitudinal and elevational gradients, we estimated two metrics for each of the 415 ant communities:

- The dark diversity, (i.e. the portion of the specific species pool not observed locally (Pärtel et al. 2011)) was estimated as the difference between expected and observed species richness. Dark diversity cannot have negative values (Pärtel et al. 2011), so any negative results from the subtraction were converted to zero, that is, all expected species were into communities. This transformation does not affect the interpretation of our results, as the analyses conducted with and without the transformation yield similar outcomes.

- The relative value, the Community Completeness Index (CCI), was estimated as the ratio of observed species richness to dark diversity using the following formula (Pärtel et al. 2013):

$$CCI = \ln (S / Kdiv)$$

where S is species richness. Positive CCI values indicate that there are more species inside than outside a community, while negative values indicate the opposite. To calculate this index we have not taken into account the communities where the dark diversity was zero (note that, according to the formula, including zeros in the denominator would result in infinite values) and for this reason CCI was only computed for 360 communities, those that had positive values of dark diversity.

Abundance of dominant ant species

The relative abundance of behaviourally dominant species within a community is a good proxy for ant biotic pressure (Arnan et al. 2018). We considered the relative abundance of behaviourally dominant ant species in each community (i.e., the sum of the abundance of dominant ants with respect to the total abundance of ants in the community; 0-1 range value) as a measure of biotic pressure. Previously we classified all ant species present in the communities as dominant/non-dominant species based on the literature and our combined expert knowledge. We considered as behaviourally dominant any aggressive species that exclude other species at local food resources (Savolainen and Vepsäläinen 1988, Cerdá et al. 2013, Arnan et al. 2018). Accordingly, we considered 44 behaviourally dominant ant species (see list and references in Supp. Mat. C2. 11).

Statistical analyses

We used generalized least squares (GLS) models, using the geographic coordinates as a random factor to control for possible spatial autocorrelation (Dormann et al. 2007), to analyze the relationship between dark diversity and CCI with the explanatory variables. We previously used an AIC-based model comparisons approach to determine the optimal spatial correlation structure, which was the exponential model. Then, we looked at the semivariograms (Cressie 1993) and found that the spatial effects were almost completely eliminated when the spatial exponential models were run. For both the dark diversity and CCI models, the explanatory variables were latitude, elevation, their interaction and the relative abundance of dominant ant species. We previously confirmed the low collinearity between relative abundance of dominant ant species and both latitude (Pearson r = -0.17, p < 0.0001) and elevation (Pearson r = 0.01, p =0.039), despite being significantly correlated.

We further carried out model selection procedures to identify the best combination of explanatory variables to explain dark diversity and CCI, using the 'dredge' function in the R-package 'MuMin' (Bartón 2022). We then selected suitable models from the global model, which included all the explanatory variables. We considered ΔAICc < 2 to select the best fitted models (Anderson and Burnham 2004). To be conservative, explanatory variables were only considered important if their confidence intervals did not overlap with zero. All analyses were performed with the arcsine square root transformed relative abundance of dominants ant species in order to satisfy normality assumptions. All statistical analyses were done in R.

Results

Ant species richness in Europe ranged from 2 to 38 species (mean ± SE: 12.04 ± 0.31). Overall, dark diversity ranging from 0 to 95 (39.04±1.32), and the CCI ranged from -3.17 to 3.04 (-

1.20±0.05). The model selection approach showed that only one model was selected for both the dark diversity and CCI, where the confidence intervals of all included variables did not overlap zero (Supp. Mat. C2. 12). The best selected model for the dark diversity was the global model with all the explanatory variables included (Table 1). Overall, dark diversity increased with decreasing latitude (Fig. 3a), with increasing elevation (Fig. 3b), and with the increase in the relative abundance of behaviourally dominants ant species (Fig. 3c). The interaction between latitude and elevation was also added in the best selected model (Table 1), indicating that dark diversity decreased as latitude increased; this effect was much stronger at higher elevations (Fig. 4). The variables included in the best selected model for dark diversity accounted for 60 % of the variability in dark diversity (Table 1).

Regarding the CCI (i.e., the ratio between species richness and dark diversity), the best selected model only included latitude (Table 1): CCI showed a latitudinal pattern opposite to that of dark diversity (Fig. 3d), so that in southern latitudes communities displayed more negative CCI values (dark diversity was much greater than species richness) than in northern latitudes, where the communities had less negative or even positive values of CCI. This pattern indicated that dark diversity varied more strongly along the latitudinal gradient than along the observed richness. The only variable included in the best selected model for CCI (i.e., latitude) accounted for 10 % of the variability in CCI across Europe (Table 1).

Table 1. Summary of the best supported model analyzing the relationship between dark diversity and CCI with latitude, elevation, their interaction, and the relative abundance of behaviourally dominant ants across Europe. The estimates for the intercept and explanatory variables of the best models are shown.

Variable	Intercept	Dominant	Latitude	Elevation	Lat x Elev	R^2	Weight	N
Dark diversity	116.0	7.808	-1.669	0.206	-5.17×10^{-3}	0.62	1	415
Community Completeness Index	-3.3	--	0.047	--	--	0.10	0.742	360

Abbreviations: “Dominant”, the relative abundance of behaviourally dominant ants transformed by arcsine square root; “Lat x Elev”, the interaction between latitude and elevation; “N”, number of communities included in the model; “-”, variable not included in the best model. In all cases, only one model was the best supported (Delta <2).

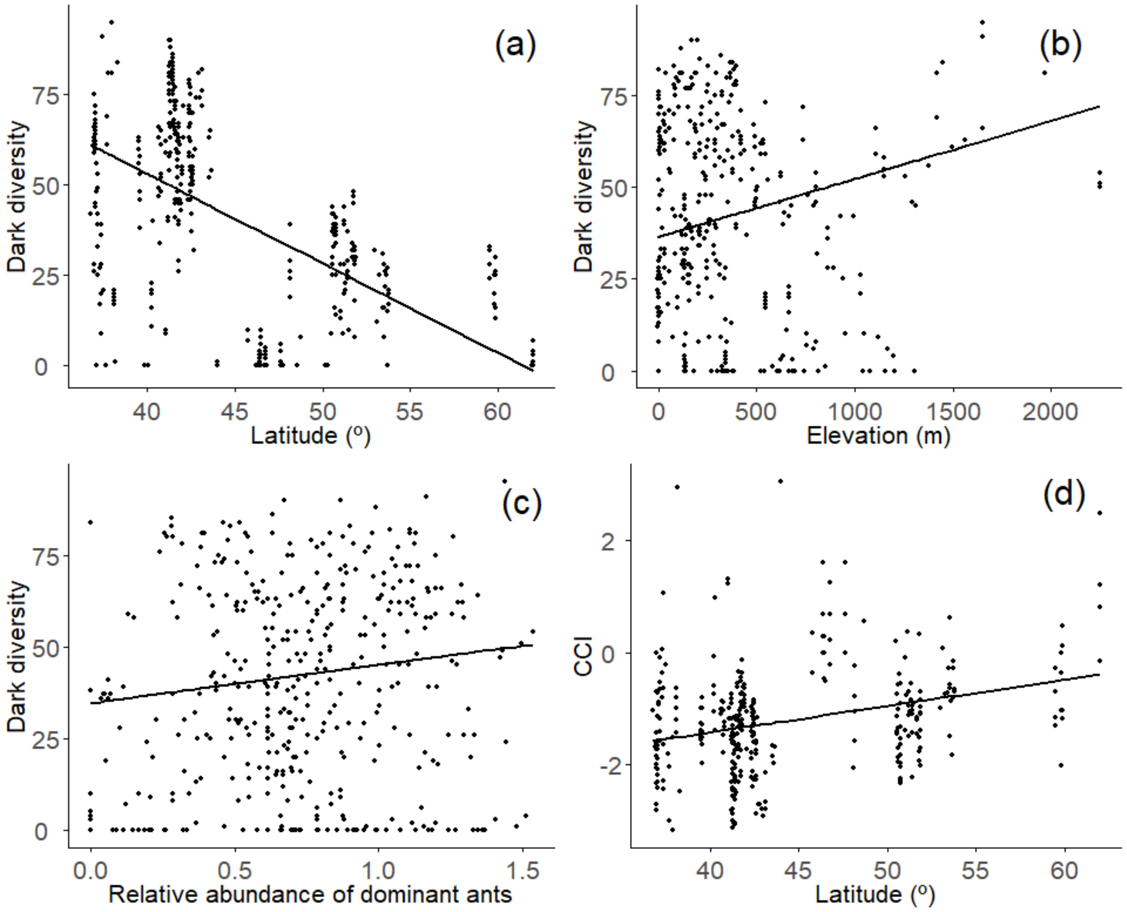

Fig. 3: Scatter plots showing the relationship between dark diversity and: a) latitude; b) elevation; and c) the relative abundance of behaviourally dominant ants (arc-sin sqrt transformed; note that these transformed values cover the entire gradient of original relative abundances, from 0 to 1); and d) between CCI and latitude. Line slopes were estimated from the GLS models.

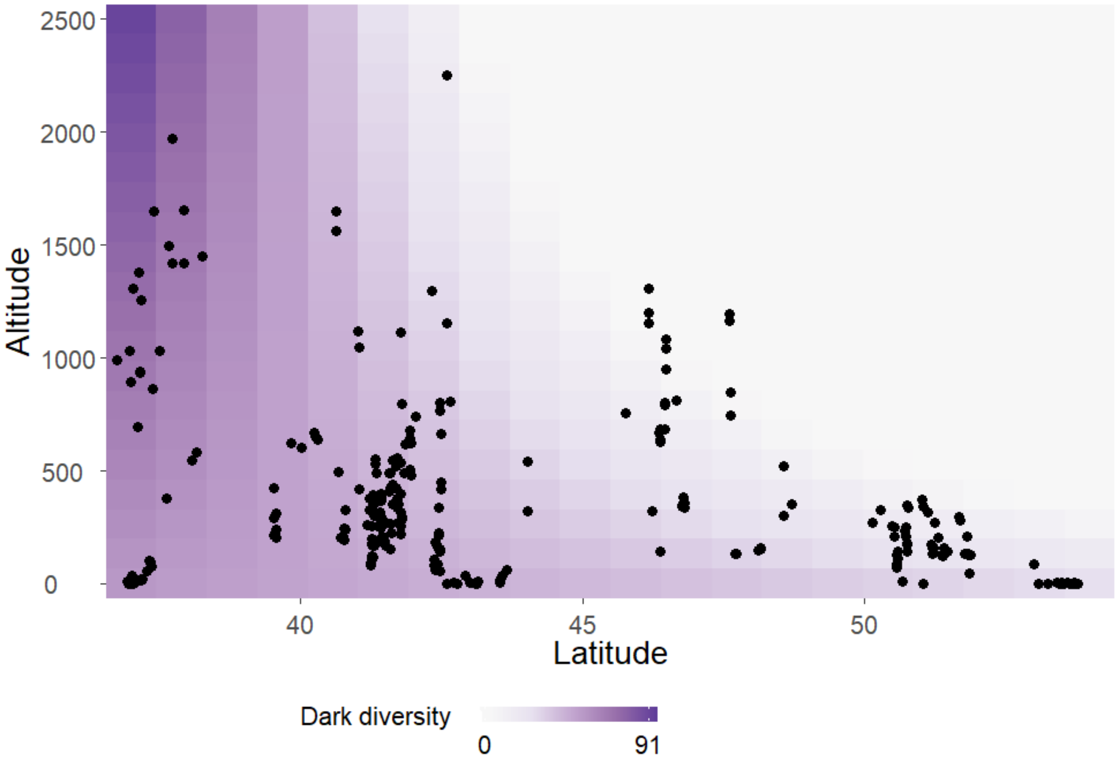

Fig. 4: Heatmaps showing the interaction effects between latitude and elevation on dark diversity. Darker purple color indicates higher values of dark diversity. Black points correspond to the ant communities of this study, some of which may overlap. The plotted latitudinal range is from 37º to 54º.

Discussion

Our results demonstrate the existence of a negative latitudinal pattern of ant dark diversity at the European scale, and a positive effect of biotic pressure on dark diversity at the local scale. As we expected with our first hypothesis, we found higher values of dark diversity in communities that were at lower latitudes than those that were at northern latitudes, indicating that environmental conditions strongly affect dark diversity at large spatial scales. The greatest values of the dark diversity were where the environmental conditions are the most favorable for ant activity, an analogous pattern to that of ant observed diversity (Cushman et al. 1993, Kumschick, et al. 2009, Dunn et al. 2009, Wang et al. 2023). Both latitudinal patterns in dark diversity and species richness are also similar in plants (Pärtel et al. 2011, Ronk et al. 2015).

This similarity in patterns between ants and plants could indicate the importance of interactions between ants and plants in species distribution (Corro et al. 2019), or it could be the result of parallel evolutionary histories in both taxa: the Southern Europe region became a refuge for many species of different taxa in the coldest periods, such as the last glaciations (for ants see Economo et al. 2018; for plants see Normand et al. 2011), and enabled the origin of new species. Thus, past and current environmental conditions may be fostering the existence of a large number of plant and ant species capable of occupying southern communities. However, at this latitude, dark diversity is very high (indicating a high species reservoir). The main causes could be limited dispersal at a small scale, poor habitat quality, or competition. A detailed analysis of the composition of dark diversity in a particular community could determine the primary mechanism, which could be very useful for specifying conservation actions. Otherwise, in northern latitudes we found low values of observed richness and even lower values of dark diversity, probably due to high environmental filtering (Riibak et al. 2017, Cornwell et al. 2006, Arnan et al. 2015) and lower diversification time (Economo et al. 2018). Thus, in the taiga or tundra, where the climatic conditions are harsher for ant activity, ant species must have specific adaptations that allow them to survive in those periods of the year with most extreme cold conditions (Heinze and Hölldobler 1994, Berman et al. 2012). In these cases, once a small community has been established from the small specific pool as a result of environmental filtering (Cornwell et al. 2006, Arnan et al. 2015), very few species remain excluded from the community for other reasons. Then, these low values of dark diversity indicate that species reservoir is the lowest at this point of the gradient, so that species that gets locally extinct can hardly be replaced by another species.

This latitudinal pattern of dark diversity is affected by the interaction with elevation. The effects of this interaction could be driven by the greater anthropogenic disturbance at lower elevations

(McCain and Grytnes 2010, Guo et al. 2013), which affects habitat quality, and by temperature, which affects ant species distributions (Machac et al. 2011). Typically, in the Northern Hemisphere the temperature decreases systematically with elevation and does so more pronounced at high latitudes (Barry 2008), coinciding with the pattern found for dark diversity in our study. However, in southern latitudes, the best environmental conditions for ant activity might be at intermediate elevations, where there is a more favorable temperature range, more water availability and even lower human pressure than in the lowlands (Sanders et al. 2003, Szewczyk and McCain 2016, Schifani et al. 2024). Then, in these intermediate elevations of the southern latitudes we found a much greater number of species capable of living there than the richness observed. The species that remain outside the community have either been excluded by biotic pressure or have not arrived at the site due to species dispersal limitations on a small scale (local or regional), two ecological processes that seem to have more importance in the low or middle latitudes of Europe (Normand et al. 2011, Riibak et al. 2017). Otherwise, this does not avoid the question of whether southern communities could harbor more species if they were better preserved (see Lewis et al. 2017). Overall, the pattern of dark diversity that we have shown reaffirms the important role of environmental filtering in structuring ant communities in northern latitudes, while competition might play a greater role in southern latitudes (Arnan et al. 2017, Boet et al. 2020) and at moderate elevations (Machac et al. 2011).

In relation to this, and according to our second hypothesis, our study interestingly shows that dark diversity increases with the relative abundance of behaviourally dominant species in European ant communities. The negative effect of dominant ants on observed species richness has been widely demonstrated in different regions of the world (Parr 2008, Baccaro et al. 2012). However, in other regions this effect is not so clear because there are compensatory mechanisms (e.g., dominance-discovery trade-off, thermal tolerance-behavioral dominance trade-off) that ensure that their observed richness is not affected, such as in the European Mediterranean region (Retana and Cerdá 2000), in eastern North America (Stuble et al. 2013) or in South America (Berstelmeyer 2000). The existence of these compensatory mechanisms has led researchers to conclude that competition might not be a so much important filter structuring ant communities (Cerdá et al. 2013). However, from the perspective of dark diversity, we here demonstrate that dominant ants do usually have an effect on the structure of ant communities, because several species that could be there are not. This effect is impossible to detect from classic studies with observed richness. Another point to highlight is the great variability found in the relationship between dark diversity and the relative abundance of behaviourally dominant ant species, which agrees with other works analyzing the relationship of dominant ants with the observed richness (Parr et al 2005, Arnan et al 2018). These works point out that communities with similar species richness can show disparity in dominant species abundance, and vice versa. In other words, the intensity of the biotic pressure exerted by dominant species depends not only on their relative abundance but also on other factors, such as the potential of the habitat to host a certain number of species or the climatic conditions of the site (Kumschick et al. 2009, Seifert 2017). Then, contrary to what we would expect, we can find very low dark diversity despite high abundance of behaviourally dominant ants, and vice versa. For instance, communities dominated by behaviourally dominant ants with high population densities, such as those from the *Formica rufa* group in northern latitudes and higher elevations in Europe, often have low values of dark diversity, probably because climatic constraints are much stronger than biotic pressure (see above).

In a nutshell, this study shows a negative pattern of dark diversity in ant communities along the latitudinal gradient in Europe, which is more pronounced at higher elevations, while dark diversity is locally enhanced by increased biotic pressure (i.e., abundance of dominants). Our results show that dark diversity is highest where environmental conditions are favorable for ants and allow a greater number of species to occur, while dark diversity is lowest where the environmental filter constrains the number of species that can occur. This latitudinal pattern is similar to the pattern of observed richness, but dark diversity varies more strongly than observed richness. Although there might be different mechanisms shaping the latitudinal dark diversity pattern, it stands out important roles of interspecific competition in meridional latitudes and of environmental filtering in septentrional latitudes, leading to different species reservoir sizes. At a local scale, biotic pressure increases dark diversity, although small-scale dispersal limitation and/or habitat quality may also play an important role. We highlight that the study under the perspective of dark diversity can contribute to improving community assembly knowledge and deepen on the effect of interspecific competition. Furthermore, knowing the composition of dark diversity and its main drivers, it can be very useful to determine the best conservation actions or to foresee trends of change in biodiversity.

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CAPÍTOL 3

LOW FUNCTIONAL DISSIMILARITY BETWEEN OBSERVED AND DARK SPECIES HIGHLIGHTS THE ROLE OF COMPETITION IN EUROPEAN ANT COMMUNITY ASSEMBLY

Capítol 3. Low functional dissimilarity between observed and dark species highlights the role of competition in European ant community assembly

Abstract

Understanding the mechanisms underlying community assembly is central in ecology and essential for conserving biodiversity. Among these mechanisms, competition has long been recognized as a powerful but elusive force, because its imprint is difficult to detect when focusing only on observed assemblages. Dark diversity—the set of species absent from local communities despite suitable conditions—provides a unique opportunity to uncover hidden assembly processes. In this study, we analyze functional dissimilarity between observed and dark ant species across Europe, as a way to assess whether competitive filtering plays a decisive role in community assembly. To this end, we compiled data on five functional traits related to resource exploitation (worker size, worker polymorphism, diet, diurnality, nesting site) for 213 native species recorded across 360 localities spanning the five main European biomes (Alpine, Atlantic, Boreal, Continental, Mediterranean). We quantified pairwise functional dissimilarity (FDiss) and compared community means (CM) between observed and dark species to evaluate both overall similarity and the specific trait axes involved. We found consistently low FDiss values across traits and biomes, supporting the idea of the "ghost of competition past": species with similar ecological strategies have already been excluded through competitive filtering. Nevertheless, significant variation among biomes was detected. Boreal, Continental, and Atlantic biomes, characterized by colder climates, shorter growing seasons, and lower habitat

heterogeneity, showed the lowest FDiss values, suggesting particularly intense competitive exclusion even under adverse environmental conditions for ants. In contrast, the Mediterranean and Alpine biomes displayed comparatively higher FDiss, pointing to weaker competitive filtering. This may be explained by the greater resource diversity and species richness of Mediterranean habitats, which reduce direct competition by promoting trophic and niche diversification, and by the strong environmental filtering in Alpine regions, which substantially diminishes the role of competition. CM analyses further clarified these results, revealing that the functional axes along which exclusion occurs differ from one biome to another. In some contexts, worker size or polymorphism were most relevant, while in others dietary strategies or temporal activity patterns were more decisive. This emphasizes the importance of trait-specific and context-dependent assessments: no single trait universally explains competitive filtering across Europe. Overall, our study demonstrates the potential of combining functional traits and dark diversity to reveal the imprint of past competition. By integrating both perspectives, we provide a novel framework to detect the long-term role of competitive exclusion in community assembly and to anticipate how ant communities—and the ecosystem functions they sustain—may reorganize under ongoing global change.

Introduction

Explaining patterns of biodiversity and community structure is a fundamental goal in ecology, especially in the context of rapid global change (Lovejoy and Hannah 2019). Community assembly is driven by the interplay between environmental and biotic filters (Weiher and Keddy 1995, Cadotte and Tucker 2011, Gallien 2016), as well as by evolutionary history, dispersal limitation, and stochastic processes (Snyder and Chesson 2004, Economo et al. 2018). Environmental filtering tends to predominate at broad spatial scales —such as biomes, which are defined by dominant vegetation and climatic conditions—by selecting species with functional traits that confer tolerance to abiotic factors like temperature, moisture, or salinity (Weiher and Keddy 1995, Cadotte and Tucker 2011, Lebrija-Trejos et al. 2010). These broad-scale environmental filters act as a first sieve, while biotic interactions further shape community composition at finer scales, favoring or excluding species based on functional traits associated with interspecific interactions, particularly those related to resource exploitation (McGill et al. 2006). Consequently, functional traits—defined as morphological, physiological, behavioral or life-history features that influence fitness (Violle et al. 2007, Nock et al. 2016)—represent a powerful biotic lens through which to understand community assembly.

In this context, the recent concept of dark diversity becomes particularly relevant, as it considers species that are absent from a local community but could potentially exist there under suitable conditions (Pärtel et al. 2011). The dark diversity approach reveals patterns that remain hidden when focusing solely on observed species richness, offering insights into the processes that structure communities and limit species occurrence (Boet et al. 2020, Andersen et al. 2023). For instance, research—particularly in European plant communities— has shown that dark diversity is shaped by local abiotic conditions, landscape configuration, and species' functional traits, especially those related to dispersal ability, competitive ability, and tolerance to environmental stress (Riibak et al. 2017, Belinchón et al. 2020, Cantanhêde et al. 2022, Trindade et al. 2023). Although interest in dark diversity and functional traits has grown, there remains a striking gap in studies that integrate functional trait data to jointly examine species both present and absent in communities. Bridging this gap is essential to uncover the ecological mechanisms behind community assembly and to better predict how communities may reorganize under environmental change (McGill et al, 2006, Kunstler et al. 2016, Cadotte and Tucker, 2017). Thus, comparing the functional traits of observed species with those of the species from dark diversity (hereafter, dark species) can offer key insights into the processes structuring communities, insights that are often missed when focusing solely on the observed assemblage. A local community with low functional diversity in traits related to resource exploitation might not suggest strong competitive filtering (Hardin 1960, MacArthur and Levins 1967, Chesson 2000, Grime 2006, Mayfield and Levine 2010). However, if the set of dark species is functionally like those present, this pattern may indicate that competition has excluded ecologically similar species (De Bello et al. 2012). In such cases, trait convergence between both sets of species reflects past biotic filtering rather than an absence of it, highlighting the importance of integrating dark diversity to fully understand the imprint of ecological processes on community assembly. This is particularly important under ongoing global change, where species losses and arrivals may rapidly alter community composition.

Ants (Formicidae) are one of the most ecologically dominant and functionally diverse groups of terrestrial invertebrates, making them an excellent model for investigating community assembly processes, particularly those related to resource partitioning and competitive dynamics (Wiescher et al. 2012, Cerdá et al. 2013, Boet et al. 2020). They are globally distributed, extremely abundant, and inhabit a wide array of ecosystems (Schultheiss et al. 2022). Moreover, ants are highly responsive to environmental gradients—such as temperature, precipitation, vegetation cover, and anthropogenic disturbance—, making them sensitive indicators of ecological change (Dunn et al. 2009, Arnan et al. 2014, Vasconcelos et al. 2018). Ants exhibit a wide array of functional traits that mediate their responses to environmental conditions and shape their biotic interactions (Wiescher et al. 2012, Arnan et al. 2014, Diamond et al. 2008, Retana et al. 2015, Arnan et al. 2017, Parr et al. 2017, Boet et al. 2020). For instance, dietary strategies range from granivory and herbivory to carnivory and omnivory (Hölldobler and Wilson 1990). Variation in dietary specificity promotes resource partitioning and facilitates coexistence. Morphological traits such as worker size and polymorphism are key determinants of foraging efficiency and resource access (Geraghty et al. 2007, Oster and Wilson 1976): worker size influences the ability to exploit specific microhabitats and resource types—smaller workers navigate confined spaces, while larger workers handle bulkier or more energetically demanding items, while worker polymorphism within colonies enhances division of labor and task partitioning. Beyond morphology, behavioral traits like temporal foraging strategies are critical in mediating interspecific interactions. Many behaviorally subordinate species reduce encounters with dominant competitors by foraging during thermally extreme periods of the day, when behaviorally dominant ants are inactive (Bestelmeyer 1997, Retana and Cerdá 2000). This temporal segregation minimizes aggressive interactions and supports coexistence through niche partitioning in time. Collectively, these traits and strategies highlight the complex ways ants adapt to both environmental constraints and competitive dynamics within communities.

Previous studies aiming to identify the key mechanisms underlying ant community structure have yielded inconclusive results. While some studies highlight the predominant role of competition in structuring ant communities (Savolainen and Vepsäläinen 1988, 1989; Hölldobler and Wilson 1990; Parr and Gibb 2009), others emphasize the influence of environmental conditions (Dunn et al. 2009, Wiescher et al. 2012, Reymond et al. 2013), and some suggest that the dominant community assembly mechanism depends on the spatial scale of analysis. This is exemplified by the study of Boet et al. (2020) on European ant communities, based on functional trait analysis. Their findings indicate that, at the regional scale, environmental filtering is the prevailing mechanism, with increasing strength at higher latitudes—except in the Alpine region, which exhibited no clear pattern. At the local scale, specifically in the Mediterranean region, no clear dominance of either competition or environmental filtering was detected. This was attributed to the presence of compensatory mechanisms, as well as the high productivity and habitat heterogeneity characteristic of Mediterranean ecosystems.

In this study, we analyze the functional dissimilarity between observed and dark ant species across European biomes. This comparison provides a basis to evaluate whether competition, through processes of competitive exclusion, has played a central role in shaping ant community assembly. To this aim, we have selected five of the most representative biomes in Europe—Alpine, Atlantic, Boreal, Continental, and Mediterranean—each defined by distinct environmental conditions and habitat structures. Across 360 localities within these biomes, we have compiled data of five functional traits related to resource exploitation for 213 species, including both observed and dark species. We hypothesize that in biomes where interspecific competition is a dominant structuring force, dark species will exhibit functional traits similar to those of observed species, suggesting exclusion due to competitive displacement. In these contexts, we would expect differences in functional dissimilarity depending on the competition pressure for resource exploitation in each locality across the different biomes. Accordingly, we expect competitive pressure to be lower in biomes characterized by abundant resources, such as the Mediterranean.

Material and methods

Study area and data sets

This study was carried out in 360 localities distributed in western Europe (geographic limits of 34º 30' N, 71º 17' N, 10º 30' W and 32º 48' E, datum WGS84) across the five main biomes of Europe: Alpine, Atlantic, Boreal, Continental and Mediterranean. In each locality, ant occurrence data were obtained from two sets of species (i) the observed species and (ii) the dark species. To ensure taxonomic consistency (following Bolton et al. 2006) and dataset reliability, all species underwent rigorous validation and data cleaning protocols (see below). We excluded the following types of species from the study: (i) socially parasitic inquiline ant species, given their difficult detection in community studies; (ii) exotic urban species not part of local ant assemblages; (iii) Asian or African species occurring at the periphery of their distribution range.

Data of observed species

We compiled observed species data from local ant communities in Europe from an exhaustive search of the literature and our previous research (Supp. Mat. C3. 1). We only included studies that had the following information: i) the name of all observed species; ii) data of the specific community location. We obtained data from 360 communities distributed in the following biogeographic regions: Alpine (11), Atlantic (25), Boreal (20), Continental (72) and Mediterranean (232). The range of species observed into one community was 3 to 36, covering 151 species.

Estimation of dark species

We estimated the set of dark species in each locality as the difference between the expected and the observed species pools (Pärtel et al. 2011). Expected species were estimated using Species Distribution Models (SDMs) (Elith et al. 2006, Benito et al. 2013), which rely on a dataset distinct from that of the observed communities. This approach enables the inclusion of species with typically European distributions, even if they were not present in the observed species set, and ensures statistical independence (Cornell and Harrison 2014). This way of estimating dark species is increasingly used across taxa (Guisan and Zimmermann 2000, D'Amen et al. 2015, Ronk et al. 2016), and its accuracy has improved substantially with the development of ensemble modelling techniques (Matus-Olivares et al. 2021). Thus, we estimated, for each locality, the set of ant species that could potentially occur there based on habitat suitability, regardless of whether they were actually observed in the ant community, ensuring that we do not underestimate the set of dark species. For this approach we followed the methodology outlined in Boet et al. 2025 (summarized in Supp. Mat. C3. 2). Finally, to determine the set of dark species for each of the 360 localities, we removed the observed species (i.e., the species in the community) from the list of species expected at each locality. This allowed us to establish both the composition and the number of dark species per locality. The number of dark species per site ranged from 4 to 90, encompassing a total of 210 ant species.

Ant functional traits

We compiled data of all observed and dark species (Supp. Mat. C3. 3) on five functional traits, each of which determines distinct strategies for resource exploitation (Retana et al. 2015; Boet et al. 2020). These traits were: worker size, worker polymorphism, diet, activity periods outside the nest (hereafter referred to as diurnality), and nesting site (Table 1). These functional traits are considered essential for resource exploitation, a primary ecological mechanism through which species may be excluded from a community (and therefore, contributing to dark diversity) if competition for resources plays a structuring role. Functional trait data were obtained through a comprehensive and systematic review of existing scientific literature (see Supp. Mat. C3. 4).

Table 1: Ant functional traits related to resource exploitation used in this study. For each functional trait, a definition, variable type, and evidence of its role in resource exploitation are shown.

Functional trait	**Definition**	**Type of variable**	**Role in resource exploitation**
Worker size	Mean worker body size, measured from the tip of mandibles to tip of the gaster (in mm).	Quantitative variable	Body size is strongly correlated with a wide range of physiological, ecological, and life-history traits, including patterns of resource utilization (Kaspari & Weiser, 1999). For example, larger ant workers exhibit greater strength, allowing them to carry or break larger seeds, whereas smaller workers are more efficient in brood care tasks (Wilson, 1953). Furthermore, larger ants tend to move over the surface of structurally complex microhabitats, while smaller ants navigate through the interstices within these environments (Yanoviak and Kaspari 2000, Farji-Brener et al. 2004; Gibb and Parr 2010).
Worker polymorphism	Rang of woker size divided by mean worker size, calculated as (maximum worker size-minimum worker size)/mean worker size (in mm)	Quantitative variable	Worker size variation is closely linked to division of labor, leading to individual specialization. Therefore, having workers with distinct specializations within the same colony enhances efficiency across a broader range of tasks, including foraging, territorial exploration, and nest defense (Wilson 1953, Mertl and Traniello 2009).
Diet	It is measured as the proportion of seeds, liquid food and insects in the diet.	Fuzzy coding: proportion for each of the three food categories (seeds, liquid food and insects) according to proportion classes: 0 0.25 0.50 0.75 and 1. The sum of the three categories must be 1.	Refers to the type and proportion of food resources a species exploits. Dietary preferences influence competitive interactions with other ant species, facilitating the coexistence of species with different diets, while the intensity of competition for the same resource may vary according to its availability within the habitat (Hölldobler & Wilson, 1990).

Functional trait	Definition	Type of variable	Role in resource exploitation
Diurnality	Indicates when individuals are actively foraging: species active only in daytime, or during the day and nighttime.	Binary categorical trait: Non strictly diurnal (0); Strictly diurnal (1).	Interspecific interactions primarily occur during foraging activities. Ant species display distinct daily activity patterns that influence both resource acquisition and the likelihood of competitive encounters. Therefore, species with differing activity schedules may coexist under reduced competitive pressure (Fellers, 1989; Cerdá et al. 1997).
Nesting site	Indicates where the species nest, either on the ground or in the vegetation.	Binary categorical trait: ground (0); vegetation (1).	Unlike most animals, ants permanently occupy nests that protect them from climatic adversity and predators. Furthermore, the nest's location within the habitat influences access to favorable abiotic conditions and proximity to food resources, while also shaping the colony's territorial range. Since certain sites within a habitat are more suitable for nesting and not all species are equally capable of nest construction, the nesting site can be considered a resource over which ants may compete (Hölldobler, 1976, 1979; Levings & Traniello, 1981).

Data analysis

To test our hypothesis and analyze whether the dark species set exhibited functional traits closely aligned with those of the observed species in the same locality, we first estimated functional dissimilarity via pairwise comparisons of sets of species (i.e. between observed and dark species) (hereafter referred to as FDiss pairwise); first considering all traits jointly, and second, by evaluating the dissimilarity of each functional trait individually. To quantify the functional dissimilarity between species pairs, we used Gower distances from the "FD" package (Laliberté and Legendre 2010, Laliberté et al. 2014), in R version 4.3.1 (2023-06-16 ucrt) (R Core Team 2024). Then, to estimate FDiss pairwise we applied the additive partitioning approach to compute beta functional dissimilarity (βRao) for each pairwise species set, employing the R function "rao" provided in de Bello et al. (2010). Afterwards, to better understand the patterns of FDiss pairwise, we explored the distribution of functional traits in the observed and dark species separately across biomes. Specifically, we computed community means (CM) for each trait or category (i.e., the three components of diet, and two categories of diurnality and nesting site). For these categorical traits, CM represents the proportion of species in each category within the community. We calculated CM for both species sets (observed and dark) per locality within each biome using the dbFD function from the FD package (Laliberté and Legendre 2010, Laliberté et al. 2014).

For statistical analyses, we employed Generalized Least Squares (GLS) models to account for potential spatial autocorrelation, incorporating geographic coordinates as a random effect (Dormann et al. 2007). First, to assess the influence of biome on FDiss pairwise, we fitted six GLS models with βRao as the response variable (one model with all traits together and five for each trait separately) and biome as a predictor variable. To control for Rao's potential correlation with gamma diversity (Botta-Dukát, 2005) despite its lower sensitivity to species richness (Mouchet et al. 2010), we incorporated total species count per locality (including observed and dark species) as a covariate. Afterwards, to examine how CM values varied across species sets and biomes, we fitted seven GLS models with CM as the response variable and biome, species set, and their interaction as fixed effects. Although we analyzed diet components separately, for the binary traits diurnality and nesting site we included only one category each, as the two categories are complementary. We were particularly interested in the effect of the interaction between biome and species set. For both response variables, FDiss pairwise and CM, we applied analysis of variance (ANOVA) to the GLS model outputs using the Anova function from the car package in R (Fox and Weisberg 2019). For the FDiss pairwise models, which did not include interaction terms, we used Type II sums of squares, whereas for the CM models, which tested the biome × species set interaction, we used Type III sums of squares. This allowed us to test whether mean FDiss pairwise values differed significantly among biomes, and whether the interaction between biome and species set significantly affected CM. When the ANOVA indicated significance, we conducted post hoc pairwise comparisons using Tukey's HSD adjustment, based on estimated marginal means (EMMs) from the "emmeans" package (Lenth, 2025). These tests were used to determine which biomes differed from each other (for FDiss pairwise comparisons) and which combinations of the biome × species set interaction were significantly different (for CM analyses). All GLS models were implemented using the "nlme" package (Pinheiro et al., 2025), and all analyses were performed in R (for more details on data analysis, see Supp. Mat. C3. 5).

Results

In the studied localities, the maximum number of expected species (observed plus dark) ranged from 36 in the Boreal to 94 in the Mediterranean (Supp. Mat. C3. 6), with the number of observed species lower than the dark ones in 92.5% of the localities. A relevant result is that all the values of the FDiss pairwise were very low when we analyzed all the localities together, both when considering all functional traits together (mean ± SD: 0.0257 ± 0.0169) and when analyzing each trait individually: worker size (0.0099 ± 0.0093), worker polymorphism (0.0170 ± 0.0140), diet (0.0567 ± 0.0611), diurnality (0.0362± 0.0559), and nesting site (0.0303 ± 0.0454). These low values of the FDiss pairwise were maintained across biomes, with all functional traits together and separately (Figure 1 and Supp. Mat. C3. 7).

Table2. Results of the type II ANOVA from generalized least squares models analyzing the effects of biome and total number of species (N) on the pairwise functional dissimilarity (FDiss pairwise) between observed and dark species, calculated both with all traits combined and with each trait separately as factors. Significance: *** $p<0.001$, ** $p< 0.01$, $p<0.05$.

	df	χ^2	P	
All traits combined				
Biome	4	71.9	< 0.001	***
N	1	12.5	< 0.001	***
Worker size				
Biome	4	9.6	0.048	*
N	1	0.0	0.085	
Worker polymorphism				
Biome	4	36.8	< 0.001	***
N	1	0.1	0.783	
Diet				
Biome	4	92.3	< 0.001	***
N	1	13.8	< 0.001	***
Diurnality				
Biome	4	23.2	< 0.001	***
N	1	7.9	0.005	**
Nesting site				
Biome	4	9.7	0.045	*
N	1	1.7	0.301	

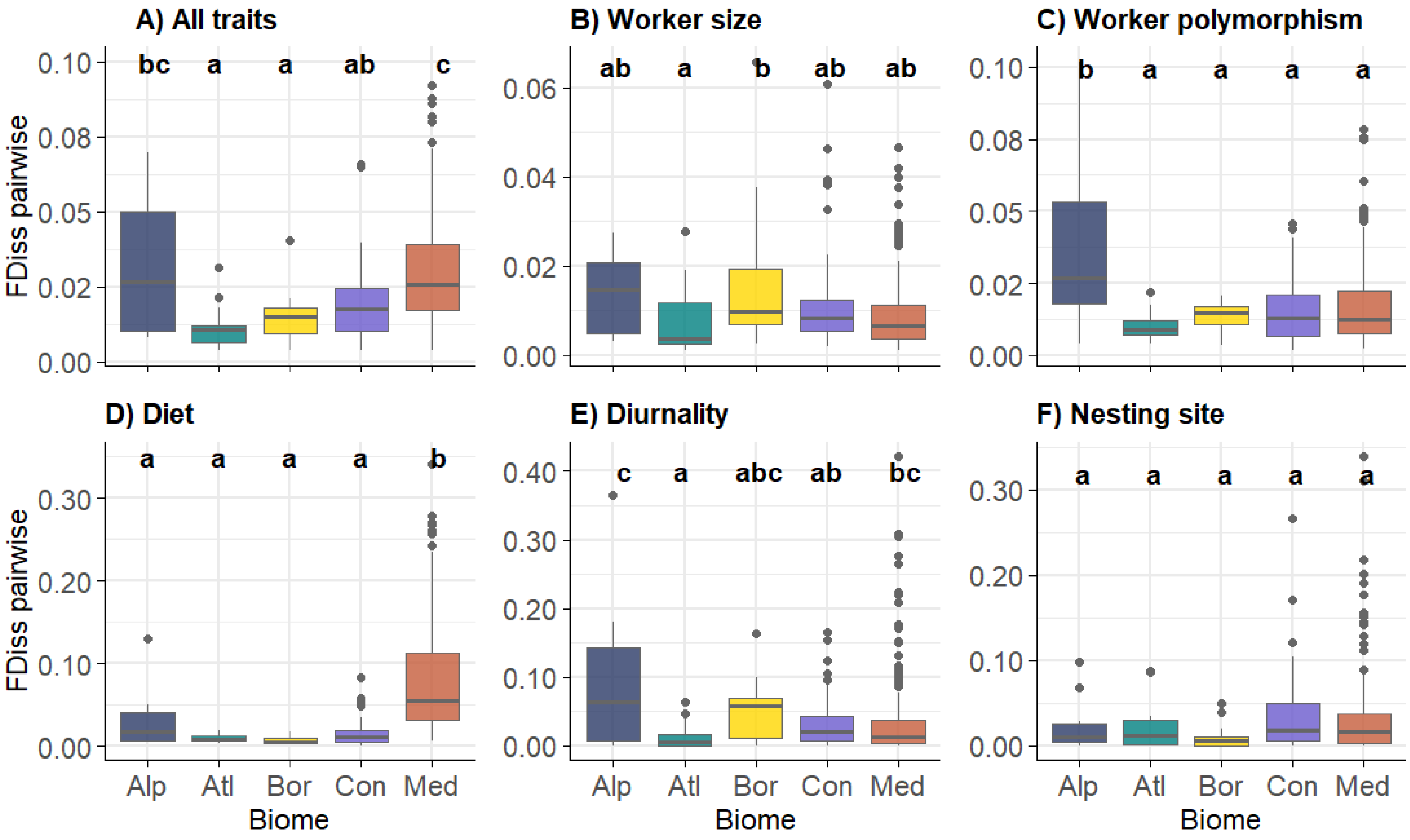

Figure 1. Boxplot of pairwise functional dissimilarity (FDiss pairwise) between observed and dark species across biomes for: A) All functional traits combined, B) Worker size, C) Worker polymorphism, D) Diet, E) Diurnality, and F) Nesting site. All models showed statistically significant differences among biomes, except the Nesting Site model. Small capital letters above the boxes denote significant differences between biomes according Tukey's post-hoc test using Estimated Marginal Means ($p < 0.05$). Biome abbreviations: Alp, Alpine; Atl, Atlantic; Bor, Boreal; Con, Continental; Med, Mediterranean.

The results of the GLS models analyzing the effect of biome on FDiss pairwise revealed significant differences among biomes (Table 2). This was true both in the model that considered all traits together and in the models that considered each trait individually. Specifically, for all traits together (Figure 1A), the Mediterranean and, to a lesser extent, the Alpine biomes displayed the highest FDiss pairwise. For worker size, the lowest FDiss pairwise values were found in the Atlantic biome, while the highest were in the Boreal biome (Figure 1B). The FDiss pairwise values for worker polymorphism showed that the Alpine biome had higher values than the other biomes (Figure 1C). The diet trait also differentiated a single biome from the rest, in this case the Mediterranean, which showed the highest values (Figure 1D). In the case of diurnality, the biome with the highest FDiss pairwise was the Alpine, followed by the Boreal and the Mediterranean (Figure 1E). Finally, in the case of nesting site, although the effect of biome was significant in the model (Table 2), the post hoc test did not detect differences between any specific biome. Regarding the total number of species in each locality, included in the GLS model as a covariate, it had a significant effect in the analysis of all functional traits together and for two of the individual traits, diet and diurnality (Table 2), so that when the number of species increased, the FDiss pairwise decreased.

The generalized least squares (GLS) models used to analyze CM values for each functional trait revealed significant interaction effects between biome and species set (observed vs. dark) across all analyses (Table 3). These results indicate that differences in the means of functional traits between the two species sets were biome-dependent. Post hoc analyses uncovered diverse patterns in both the number and type of functional traits that differed between observed and dark species (Figure 2; Supp. Mat. C3. 8). Regarding worker size (Figure 2a), all biomes except the Boreal exhibited significant differences in mean values. In the Alpine and Mediterranean biomes, observed species had larger average worker sizes than dark species, indicating that species present within communities tend to have larger workers than those absent. For worker polymorphism (Figure 2b), no significant differences were found in the Atlantic and Boreal biomes, while both the Alpine and Mediterranean biomes showed higher polymorphism ratios among observed species compared to dark species, with the Mediterranean exhibiting a particularly pronounced difference. This indicates that species within Mediterranean communities are substantially more polymorphic than those outside, a pattern also present in Alpine communities, albeit to a lesser extent. Diet-related traits revealed especially notable results (Figure 2e–g). The Mediterranean biome stood out for its markedly higher proportion of seeds in the diet for both observed and dark species (Figure 2e). Moreover, it exhibited the greatest divergence between species sets across all three food categories; seeds, insects, and liquid food. Dark species consumed fewer seeds and liquid food and more insects than observed species. In terms of diurnality (Figure 2c), significant differences were detected in the Boreal and Continental biomes, with opposite patterns: whereas the non-strictly diurnal species were in greater proportion in the dark species of the Boreal biome, in the Continental biome, the reverse was true. Finally, the proportion of species nesting in different microhabitats (Figure 2d) differed between observed and dark species in all biomes except the Boreal. In these biomes, most species nested on the ground, and this proportion was consistently higher in the observed set than in the dark set.

Table 3. Summary of the Type III ANOVA outputs from the generalized least squares models analyzing the effects of biome, species set, and their interaction on the community mean of each trait separately. *Seed proportion*, *Insect proportion* and *Liquid proportion* are the proportions of seeds, insects and liquid food in the diet, respectively. *Diurnality and Nesting site* also indicate the proportions of each of the two categories. Significance: *** p<0.001, ** p<0.01, * p<0.05.

	df	χ^2	P			df	χ^2	P	
Worker size					**Diurnality - Non strictly diurnal**				
(Intercept)	1	9287.2	< 0.001	***	(Intercept)	1	459.0	< 0.001	***
Biome	4	379.2	< 0.001	***	Biome	4	89.1	< 0.001	***
Type	1	88.8	0.003	**	Type	1	3.6	0.058	
Biome:Type	4	464.2	< 0.001	***	Biome:Type	4	27.4	< 0.001	***
Worker polymorphism					**Diurnality - Strictly diurnal**				
(Intercept)	1	439.5	< 0.001	***	(Intercept)	1	1126.0	< 0.001	***
Biome	4	38.5	< 0.001	***	Biome	4	89.1	< 0.001	***
Type	1	19.5	0.009	***	Type	1	3.6	0.058	
Biome:Type	4	126.4	< 0.001	***	Biome:Type	4	27.4	< 0.001	***
Seed proportion					**Nesting site - Ground**				
(Intercept)	1	0.5	0.492		(Intercept)	1	683.3	< 0.001	***
Biome	4	218.1	< 0.001	***	Biome	4	44.5	< 0.001	***
Type	1	0.0	0.859		Type	1	9.0	0.003	**
Biome:Type	4	18.8	< 0.001	***	Biome:Type	4	28.5	< 0.001	***
Insect proportion					**Nesting site - Vegetation**				
(Intercept)	1	895.1	< 0.001	***	(Intercept)	1	18.0	< 0.001	***
Biome	4	55.8	< 0.001	***	Biome	4	44.5	< 0.001	***
Type	1	9.2	0.002	**	Type	1	9.0	0.003	**
Biome:Type	4	90.6	< 0.001	***	Biome:Type	4	28.5	< 0.001	***
Liquid proportion									
(Intercept)	1	496.8	< 0.001	***					
Biome	4	96.6	< 0.001	***					
Type	1	6.1	0.014	*					
Biome:Type	4	18.1	0.001	**					

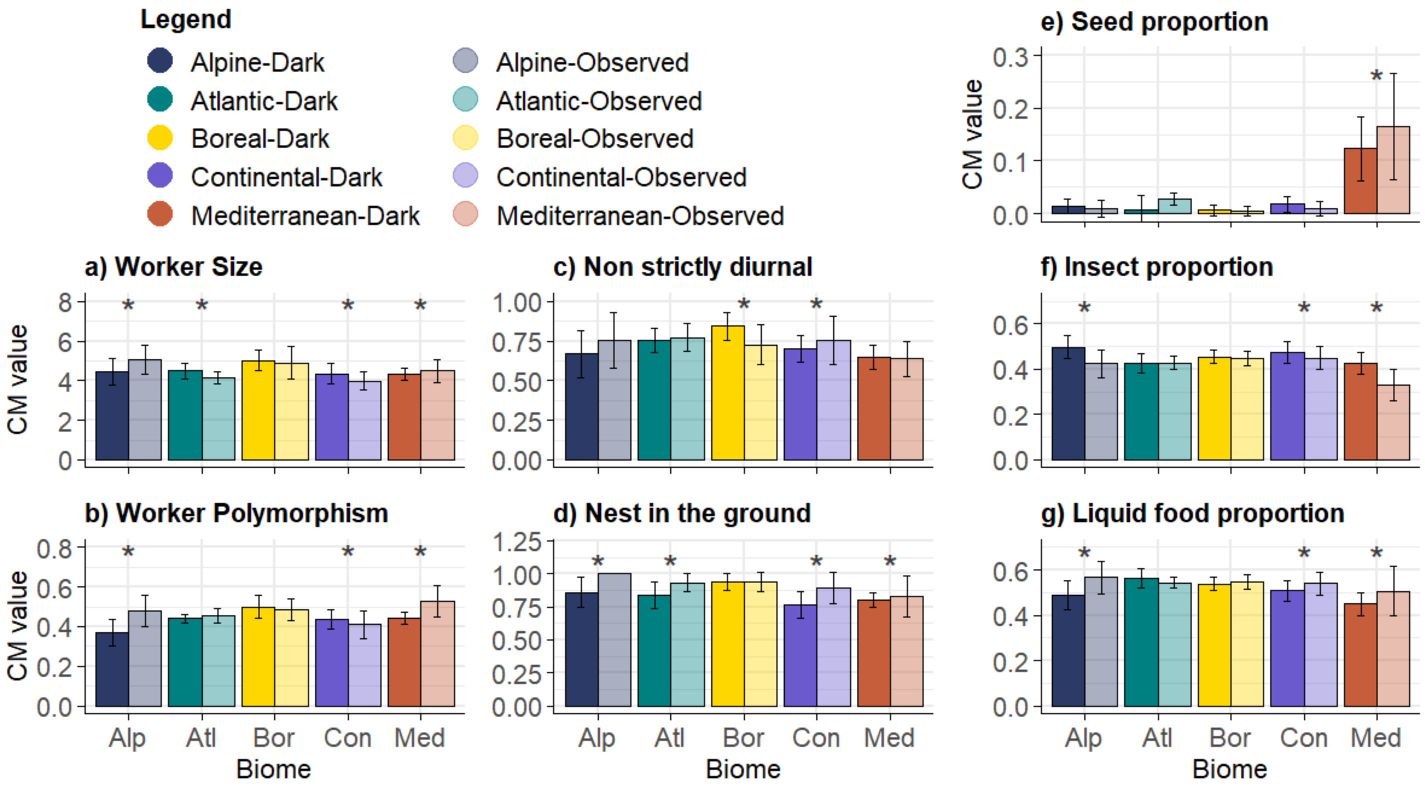

Figure 2. Bar graph comparing community mean (CM) values between observed and dark species across five biomes. Standard deviations are shown and calculated using Bessel's correction. Biome abbreviations are as follows: Alp, Alpine; Atl, Atlantic; Bor, Boreal; Con, Continental; and Med, Mediterranean. The Y-axis represents CM values: worker size is expressed in centimeters (cm), while all other traits are ratios or proportions without units. For diet components (plots e, f, and g), the three values sum to 1 for each biome and species type. For diurnality (plot c) and nesting site (plot d), each value represents one category, and the complementary category (not shown) completes the total to 1. Asterisks denote statistically significant differences between species sets within each biome, based on post-hoc Tukey comparisons using Estimated Marginal Means.

Discussion

This study provides the first large-scale assessment of functional dissimilarity between observed and dark ant species across European biomes, offering an innovative perspective on the role of competition in community assembly. The most striking and consistent pattern is the very low functional dissimilarity between species present within communities and those absent but potentially able to occur. Such low values suggest that competition —especially in the form of competitive exclusion (Hardin 1960)—, has left a strong imprint on the structure of ant assemblages, regardless of biome. This result contrasts with the historical view that competition, though important, is difficult to detect and often overshadowed by abiotic filters (Cerdá et al. 2013; Stuble et al. 2017, Boet et al. 2020). By integrating dark diversity, our approach allows us to detect what Connell (1980) described as the 'ghost of competition past': the low functional dissimilarity between observed and dark species suggests that species with similar ecological strategies of resource exploitation have already been excluded during community assembly, leaving the present assemblages as the outcome of past competitive filtering. In this sense, the similarity we observe between observed and dark species does not reflect a lack of competitive structuring, but rather the long-term outcome of strong biotic filtering that continues to shape local diversity patterns.

Although functional dissimilarity was generally low, we also detected significant variability among biomes. Interestingly, these differences aligned to some extent with our initial expectations. We anticipated that competition would leave the strongest signal in biomes characterized by low availability of resource, and a similar pattern indeed emerged: in the Boreal, Continental, and Atlantic biomes—characterized by lower primary producers, short growing seasons, or relatively low habitat heterogeneity, all of which represent fewer available resources for ants (Cushman et al. 1993, Savolainen et al. 1989, Kaspari 2000, Arnan et al. 2014, Seifert 2018) and often the abundance of behavioral ant dominant species is higher (Savolainen and Vepsäläinen 1989)—observed and dark species were highly similar functionally, suggesting strong competitive exclusion. By contrast, the Mediterranean and Alpine biomes showed comparatively higher functional dissimilarity, implying that competition may play a weaker role in structuring communities there. In the case of Mediterranean communities, this is consistent with the results of Boet et al. (2020), probably due to the pronounced structural complexity and habitat heterogeneity characteristic of these regions (Blondel and Aronson 1999, Allen 2014), the greater diversity of resources (Cowling et al. 1996) and the higher species richness typical of the Mediterranean (Blondel and Aronson 1999, Médail and Quezél 1999). In the case of Alpine communities, the most plausible explanation for the reduced role of competition is the presence of a stronger structuring force, such as environmental filtering, which substantially diminishes the importance of competition. It should be noted that the Alpine region is strongly characterized by a steep altitudinal gradient that causes constant species turnover along the gradient according to adaptations to abiotic conditions (Körner 2004, Arnan et al. 2015, Körner et al. et al. 2017). This counterintuitive result underscores the complexity of disentangling the relative contributions of abiotic and biotic filters (Silvertown et al. 2006, Mouchet et al. 2013, Boet et al. 2020). It suggests that competition can be pervasive even under conditions of environmental stress, as such central and septentrional biomes, and that its imprint does not always follow simple gradients of productivity or resource availability.

Analyzing all traits jointly confirmed the general pattern but evaluating traits separately highlighted important nuances. In the Mediterranean, diet was the main driver of dissimilarity. We found a high number of granivorous species only in the Mediterranean, such as *Messor* and

Gonioma, since these ants are more common in temperate or tropical regions (Hölldobler and Wilson 1990) and are rare in central or northern Europe (see antmaps.org in Janicki et al. 2016, Seifert 2018). This result suggests that the diversification of food resources in the Mediterranean—seeds, insects, and liquid food—reduces the intensity of direct competition and allows a broader set of species to coexist. Such patterns are consistent with the high structural complexity and heterogeneity characteristic of Mediterranean ecosystems (Blondel and Aronson 1999, Allen 2014), which provide multiple ecological opportunities for ants. In the Alpine biome, worker polymorphism exhibited greater dissimilarity, and to a lesser extent worker size and diurnality, suggesting a selective force favoring these traits in mountain communities. In contrast, nesting site preferences showed uniformly low dissimilarity across all biomes, suggesting that competition for nesting microhabitats is intense and ubiquitous throughout Europe, regardless of biome.

The analysis of community means (CM) further clarified these results. Comparing CM values between observed and dark species revealed the trait axes along which exclusion or selection is most pronounced in each biome. In the Mediterranean, observed species had larger workers and higher degrees of polymorphism, which may give them competitive advantages in exploiting a wide variety of resources (Cushman et al. 1993, Heredia i Detrain 2000, Arnan et al. 2011). Their greater reliance on seeds further underscores the role of granivory as a successful strategy in this biome (Seifert 2018). In the Alpine, observed species were characterized by larger workers, greater worker polymorphism, higher proportion of liquid food in the diet and the highest proportion of species nesting on the ground, reinforcing the idea that these traits are essential for competitive success and survival in high mountain habitats. In the Boreal biome, observed species were disproportionately strictly diurnal, indicating that temporal partitioning of activity may be a relevant axis of exclusion under colder climates with short growing seasons.

Conversely, in the Continental biome, dark species were more frequently strictly diurnal, suggesting that observed communities there may be structured by other trait dimensions, with temporal niche use playing a weaker role. Together, these results demonstrate how combining FDiss pairwise values with CM analyses provides a powerful framework: FDiss quantifies the overall degree of overlap between observed and dark species, while CM highlights which traits are driving these differences in specific biomes.

Despite the robustness of our dataset and the novelty of the approach, some limitations must be acknowledged. First, our analysis was limited to a subset of functional traits directly related to resource exploitation. Other important dimensions, such as thermal tolerance or behavioral dominance, were not included, and these may also mediate competitive outcomes (Arnan et al. 2012, Cerdá et al. 2013, Retana et al. 2015). Second, some traits, such as diurnality, were necessarily simplified into broad categories (strictly vs. non-strictly diurnal), which may mask finer temporal dynamics that are known to be ecologically relevant (Retana and Cerdá 2000). Third, estimates of dark diversity rely on species distribution models, which cannot fully account for microhabitat features such as vegetation structure, soil type, or successional stage (Arnan et al. 2009, Azcárate and Peco 2012). Finally, as in other functional dissimilarity studies, there is no absolute benchmark for interpreting the magnitude of values, and conclusions must be drawn in relative terms.

Even with these limitations, our results have important implications for ecology and biodiversity conservation. First, they provide strong evidence that competition is not only present but decisive in structuring ant communities across Europe, leaving a detectable functional imprint even in cases where it is not obvious from observed species alone. Second, the variability among biomes emphasizes the importance of trait-specific and context-dependent analyses: the axes of competition differ from one biome to another, and no single trait can be assumed to drive exclusion universally. Third, our study illustrates the value of integrating dark diversity into functional analyses. By revealing the “ghost of competition past,” this approach makes it possible to detect the signature of competition in community assembly even when excluded species are no longer present. Finally, these insights have direct conservation relevance. If competitive exclusion has already shaped communities to such a degree, then environmental changes that alter competitive hierarchies (Johansson and Gibb 2016)—such as climate warming or biological invasions—may rapidly reorganize communities in unpredictable ways. Ants, given their key ecological roles in seed dispersal, soil turnover, and trophic interactions (Del Toro et al. 2012, Elizalde et al. 2020), could thus transmit these changes to entire ecosystems.

In conclusion, our findings demonstrate that European ant communities bear the clear imprint of competition, revealed through the consistently low functional dissimilarity between observed and dark species. This pattern provides evidence for the “ghost of competition past,” showing that biotic filtering has already excluded functionally similar species from local assemblages. At the same time, the variability in patterns among biomes highlights that the axes and intensity of competition are context-dependent, with traits such as diet, diurnality, worker size, and polymorphism playing contrasting roles across regions. By integrating dark diversity into functional analyses, this study offers a promising framework to better understand community assembly processes and anticipate how ant communities—and the ecosystem functions they sustain—may reorganize under ongoing global change.

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CONCLUSIONS GENERALS

Conclusions generals

Capítol 1

- A escala continental, hem constatat que el filtratge ambiental constitueix el mecanisme principal en l'estructura de les comunitats de formigues d’Europa. Les espècies que coocorren amb més freqüència presenten una major similitud funcional, tant si es consideren conjuntament tots els trets funcionals com si s’analitzen exclusivament els trets de tolerància ecològica.
- A escala de regió biogeogràfica, les comunitats de formigues també es troben estructurades predominantment pel filtratge ambiental, tot i que la intensitat d’aquest mecanisme varia segons la regió. Les regions mediterrània, continental, atlàntica i boreal mostren pendents negatives diferenciades en la relació entre la dissimilitud funcional i la concurrència de les espècies. Aquestes diferències en els pendents indiquen que el filtratge ambiental adquireix una rellevància creixent amb l’augment de la latitud, seguint la distribució latitudinal de les regions, des de la mediterrània fins a la boreal.
- La competència podria tenir un paper complementari a escala de regió biogeogràfica en aquelles zones on les condicions ambientals són més favorables per a les formigues, com és el cas de la regió mediterrània. En canvi, a la regió biogeogràfica alpina no s’han detectat evidències que cap dels dos mecanismes analitzats —ni el filtratge ambiental

ni la competència— tingui un paper predominant en l'estructuració de les comunitats de formigues, probablement a causa de factors històrics i de limitacions en la dispersió.

- A escala local, i concretament en la regió mediterrània, tampoc s'ha observat un predomini clar d'un dels dos mecanismes ecològics en l'estructuració de les comunitats de formigues. Els resultats obtinguts reforcen estudis recents que qüestionen el paper de la competència en aquest context local.
- En conjunt, els resultats indiquen que el filtratge ambiental esdevé progressivament més rellevant com a mecanisme estructurador de les comunitats de formigues a mesura que augmenta l'escala d'anàlisi, actuant amb més intensitat a escala continental, amb menor força a escala de regió biogeogràfica i de manera feble a escala local.
- D'altra banda, els resultats obtinguts indiquen que el tipus de tret funcional és determinant per identificar els mecanismes ecològics que estructuren les comunitats. L'anàlisi mitjançant conjunts de trets funcionals, en lloc de considerar-los de manera individual, es mostra com l'enfocament més adequat, especialment quan s'agrupen aquells trets que estan principalment associats a un únic procés ecològic.
- Els resultats confirmen que l'agrupació de trets funcionals és eficaç quan inclou trets vinculats directament amb les respostes ambientals, com és el cas dels trets de tolerància ecològica, que responen al filtratge ambiental. En canvi, els trets associats al nínxol ecològic, és a dir, aquells que descriuen com les espècies exploten els recursos disponibles, no han resultat ser bons indicadors per detectar la competència com a mecanisme estructurador de les comunitats de formigues.

Capítol 2

- S'ha detectat un patró negatiu de diversitat fosca de formigues al llarg del gradient latitudinal europeu, amb valors més elevats de diversitat fosca en comunitats situades a latituds meridionals en comparació amb les latituds septentrionals. Aquest patró indica que les condicions ambientals exerceixen una influència significativa sobre la diversitat fosca a gran escala espacial.
- Els resultats obtinguts mostren que la diversitat fosca és més alta en zones on les condicions ambientals són favorables per a les formigues i permeten la presència d'un nombre elevat d'espècies. En canvi, la diversitat fosca disminueix en aquelles àrees on el filtratge ambiental limita el nombre d'espècies potencials.
- El patró latitudinal negatiu de la diversitat fosca d'espècies de formigues a Europa és coincident amb el patró de riquesa observada, tot i que la diversitat fosca presenta una variació més marcada amb la latitud. A les latituds meridionals s'observen valors alts de riquesa observada i valors encara més elevats de diversitat fosca, mentre que a les latituds més septentrionals la riquesa observada mostra valor més baixos respecte els meridionals, encara que la diversitat fosca mostra valors per sota de l'observada.
- Ates que la diversitat fosca es pot considerar com el reservori d'espècies d'una comunitat, aquest patró latitudinal de la diversitat fosca assenyala diferències en la mida dels reservoris d'espècies que són substancialment més grans a les latituds meridionals. En canvi, a les latituds septentrionals, el reservori d'espècies és molt reduït, fet que implica que les espècies que s'extingeixen localment tenen poques probabilitats de ser reemplaçades.
- A més, hem constatat que el patró latitudinal de la diversitat fosca es veu intensificat per la interacció amb l'elevació, mostrant-se més pronunciat en zones de major altitud.

- La pressió biòtica, mesurada com l’abundància de les espècies dominants, augmenta la diversitat fosca a escala local. Malgrat això, hi ha altres factors que condicionen fortament la diversitat fosca a aquesta escala, com podria ser la limitació de la dispersió de les espècies i/o la qualitat de l'hàbitat.
- Destaquem que els estudis sota la perspectiva de la diversitat fosca pot contribuir a millorar el coneixement de les assemblees comunitàries i aprofundir en l'efecte de la competència interespecífica.

Capítol 3

- Aquest estudi constitueix la primera avaluació de la dissimilitud funcional entre les espècies de formigues observades i fosques dins d’una mateixa comunitat en els biomes europeus, aportant una perspectiva innovadora sobre el paper de la competència en l’estructuració de les comunitats.
- Hem demostrat que les comunitats de formigues europees presenten una empremta clara de la competència, evidenciada pels valors sistemàticament baixos de dissimilitud funcional entre les espècies observades i fosques de cada comunitat. Aquest patró és indicatiu de processos d’exclusió competitiva.
- Hem identificat diferències en la dissimilitud funcional entre biomes, amb el boreal, el continental i l’atlàntic mostrant una empremta més marcada de la competència. En canvi, els biomes mediterrani i alpí presenten els valors més elevats de dissimilitud funcional, la qual cosa suggereix un paper més feble de la competència en l’estructuració de les comunitats en aquests entorns.
- En el bioma boreal, hem trobat una proporció més elevada d’espècies estrictament diürnes dins de la comunitat, mentre que en el bioma continental s’observa la situació

inversa. Aquest contrast assenyala que la partició temporal de l'activitat pot constituir un eix d'exclusió rellevant en climes més freds.

- En el cas del Mediterrani, els nostres resultats són coherents amb els presentats en el primer capítol d'aquesta tesi, i aporten noves evidències que permeten matisar el paper que històricament s'ha atribuït a la competència com a mecanisme estructurador de les comunitats de formigues. A la Mediterrània, la dieta ha estat el principal motor de la major dissimilitud funcional entre les espècies observades i les fosques, degut principalment a la diversificació alimentària, amb una proporció més elevada de llavors en comparació amb la resta de biomes.
- Pel que fa a les comunitats alpines, l'explicació més plausible del paper reduït de la competència és la presència d'una força estructuradora dominant que minimitza la pressió biòtica, com podria ser el filtratge ambiental o la història evolutiva. En aquestes comunitats, hem observat una predominança d'espècies amb un grau elevat de polimorfisme en les obreres, obreres de major mida, espècies no estrictament diürnes, una dieta amb més proporció d'aliments líquids i una major proporció d'espècies que nidifiquen a terra. Aquests trets reforcen la hipòtesi d'una força selectiva que afavoreix determinades estratègies ecològiques en entorns de muntanya.
- Hem posat de manifest que els eixos i la intensitat de la competència varien segons el context. En concret, la dieta, la diürnalitat, la mida de les obreres i el polimorfisme assenyalen contrastos significatius entre regions. En canvi, l'exclusió competitiva pel lloc de nidificació es manté uniformement alta en tots els biomes, la qual cosa indica que la competència pels microhàbitats de nidificació és intensa i omnipresent arreu d'Europa, independentment del bioma.

- En integrar la diversitat fosca en les anàlisis funcionals, aquest estudi proporciona un marc prometedor per aprofundir en la comprensió dels processos d’estructuració comunitària i anticipar com les comunitats de formigues, així com les funcions ecosistèmiques que sustenten, poden reorganitzar-se en resposta al canvi global actual.

MATERIAL COMPLEMENTARI

Material complementari del capítol 1

Supp. Mat. C1. 1 Table. Pearson correlation coefficients *r* among all traits.

Significant coefficients are shown in bold (p<0.05). Abbreviations correspond to the following traits: Nqueen, number of queens; lnCS, colony size; BrCy, brood cycle; pSeed (proportion of seeds in diet), pInsects (proportion of insects in diet), pLiquid (proportion of liquid foods in diet); Diurn, diurnality; Ws, worker size.

	Nqueen	**lnCS**	**BrCy**	**pSeed**	**pInsects**	**pLiquid**	**Diurn**
lnCS	**0.310**						
BrCy	**-0.139**	**-0.168**					
pSeed	**-0.188**	0.036	**0.231**				
pInsects	0.112	**-0.189**	**-0.450**	**-0.405**			
pLiquid	0.070	**0.139**	**0.198**	**-0.552**	**-0.539**		
Diurn	**-0.230**	**-0.065**	**-0.458**	**-0.005**	**0.161**	**-0.142**	
Ws	0.003	**0.335**	**-0.317**	**0.170**	-0.117	-0.049	**0.304**

Supp. Mat. C1. 2. References. Bibliographic sources from Table 1 to categorize traits as response or ecological niche traits.

(A) Ecological tolerance

Arnan, X. et al. 2014. Ant functional responses along environmental gradients. - J. Anim. Ecol. 83: 1398–1408.

Hölldobler, B. and Wilson, E. O. 1990. The ants. - Harvard University Press.

Parr, C. L. et al. 2017. GlobalAnts : a new database on the geography of ant traits (Hymenoptera: Formicidae). - Insect Conserv. Divers. 10: 5–20.

Number of queens

Hölldobler, B. and Wilson, E. O. 1977. The number of queens: An important trait in ant evolution. - Naturwissenschaften 64: 8–15.

Colony size

Beckers, R. et al. 1989. Size, communication and ant foraging strategy. - A J. Entomol. 96: 239–256.

Linksvayer, T. A. and Janssen, M. A. 2008. Traits underlying the capacity os ant colonies to adapt to disturbance and stress regimes. - Syst. Res. Behav. Sci. 26: 315–329.

McGlynn, T. P. and Kirksey, E. S. 2000. The effects of food presentation and microhabitat upon resource monopoly in a ground-foraging ant (Hymenoptera : Formicidae) community. - Rev. Biol. Trop. 48: 629–642.

Retana, J. et al. 2015. A multidimensional functional trait analysis of resource exploitation in European ants. - Ecology 96: 2781–2793.

Brood cycle

Kipyatkov, V. E. 1993. Annual cycles of development in ants: diversity, evolution, regulation. - Proc. Colloq. Soc. insects in press.

(B) Ecological niche

Retana, J. et al. 2015. A multidimensional functional trait analysis of resource exploitation in European ants. - Ecology 96: 2781–2793.

Diet

Cerda, X. I. M. et al. 1997. Thermal of transitive hierarchies in disruption ant communities Mediterranean. - J. Anim. Ecol. 66: 363–374.

Cerdá, X. et al. 1998. Prey size reverses the outcome of interference interactions of scavenger ants. - Oikos 82: 99–110.

Retana, J. and Cerdá, X. 1994. Worker size polymorphism conditioning size matching in two sympatric seed-harvesting ants. - Oikos: 261–266.

Diurnality

Cerda, X. I. M. et al. 1997. Thermal of transitive hierarchies in disruption ant communities Mediterranean. - J. Anim. Ecol. 66: 363–374.

Cros, S. et al. 1997. Spatial and temporal variations in the activity patterns of Mediterranean ant communities. - Ecoscience 4: 269–278.

Savolainen, R. and Vepsäläinen, K. 1989. Niche Differentiation of Ant Species within Territories of the Wood Ant Formica polyctena. - Oikos 56: 3–16.

Worker size

Gibb, H. and Parr, C. L. 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents. - Oecologia 164: 1061–1073.

Retana, J. and Cerdá, X. 1994. Worker size polymorphism conditioning size matching in two sympatric seed-harvesting ants. - Oikos: 261–266.

Retana, J. et al. 2015. A multidimensional functional trait analysis of resource exploitation in European ants. - Ecology 96: 2781–2793.

Supp. Mat. C1. 3 Table. Estimated coefficients from the analyses between co-occurrence and functional dissimilarity between species pair based on single traits at the local scale.

Abbreviations: n, number of species pairs in each locality; n0, number of species pairs with co-occurrence=0 in each locality; Nqueen, number of queens; lnCS, colony size; BrCy, brood cycle; Diet, diet; Diurn, diurnality; Ws, worker size; NA, not available coefficient. Note that binary co-occurrence analyses were only performed when at least six pairs of species depicted values of co-occurrence=0. Significant coefficients ($p<0.05$) are shown in bold.

			Binary co-occurrence analysis						**Co-occurrence strength analysis**					
Locality	**n**	**n0**	**Nqueen**	**lnCS**	**BrCy**	**Diet**	**Diurn**	**Ws**	**Nqueen**	**lnCS**	**BrCy**	**Diet**	**Diurn**	**Ws**
loc.01	45	11	0.6291	-4.5823	0.1542	0.7445	-0.0645	2.0917	0.4604	-1.5548	0.4674	0.3929	-0.0825	2.1075
loc.02	120	40	**1.1526**	**-5.2759**	0.0703	0.2728	0.2022	**-2.3185**	0.1709	-0.0946	0.1332	0.4510	0.1447	0.1064
loc.03	10	0	-	-	-	-	-	-	-1.2039	2.2763	NA	-1.9384	NA	**-9.2679**
loc.04	66	29	**3.8874**	-2.6141	-0.9395	2.0346	**-1.3416**	**-3.2931**	**-0.9656**	1.5737	-0.0811	-0.6045	-0.3302	**-1.5363**
loc.05	6	0	-	-	-	-	-	-	-0.7517	2.7007	NA	-1.6098	NA	8.5905
loc.06	21	12	2.7726	-6.2594	-0.5596	4.5746	NA	7.7535	1.0767	-5.6266	-0.6960	-1.2369	NA	-1.5616
loc.07	21	0	-	-	-	-	-	-	-0.0841	2.1958	-0.6307	1.2660	-0.2909	-0.9021
loc.08	21	6	-0.7951	-4.9216	NA	2.3043	-1.3863	-4.5769	-0.0848	-1.4478	NA	-0.6292	0.6860	-3.2183
loc.09	120	40	0.0992	-0.0654	0.3610	1.3722	0.1728	1.4018	0.1192	0.8348	0.0055	-0.5901	0.1627	0.0382
loc.10	28	7	-0.6404	-10.132	NA	3.4739	< 0.0001	1.6498	0.2795	-.4263	NA	-0.7721	0.4557	0.2599
loc.11	66	20	**2.2943**	-4.8572	1.6635	-1.8917	-0.6678	-0.6074	-0.1620	**-3.6630**	0.2830	0.3884	0.1127	-0.1451
loc.12	55	3	-	-	-	-	-	-	0.0159	1.0777	0.3709	0.5200	-0.4191	0.3951
loc.13	21	3	-	-	-	-	-	-	0.3774	1.7086	NA	**-1.3137**	NA	**-1.2834**
loc.14	28	4	-	-	-	-	-	-	0.4014	0.4431	NA	-0.4730	-0.0782	**-1.0763**
loc.15	21	6	0.8267	10.492	0.9163	0.2898	0.9163	-0.6026	0.4040	1.0752	-0.0384	-1.1362	-0.0384	-1.2078

			Binary co-occurrence analysis						**Co-occurrence strength analysis**					
Locality	**n**	**n0**	**Nqueen**	**lnCS**	**BrCy**	**Diet**	**Diurn**	**Ws**	**Nqueen**	**lnCS**	**BrCy**	**Diet**	**Diurn**	**Ws**
loc.16	21	0	-	-	-	-	-	-	**-1.1898**	1.3156	0.5563	-0.4524	0.2458	-1.7270
loc.17	28	1	-	-	-	-	-	-	0.2565	0.7692	0.4772	0.8046	0.1183	-2.0016
loc.18	36	2	-	-	-	-	-	-	0.5846	0.9184	0.2584	-0.6406	0.2312	-0.2906
loc.19	15	6	-1.8330	-1.5853	-1.2528	< 0.0001	-0.9163	-4.982	-0.4595	1.5735	0.5200	-0.6382	-0.2771	-0.2498
loc.20	55	35	0.9067	-3.2073	0.1611	0.1355	-0.3725	0.3064	-0.1749	-1.4090	**0.6064**	**-1.2584**	0.3893	0.4620
loc.21	36	20	-0.5242	-2.6601	2.6931	0.4352	-0.4520	-0.6929	-0.0411	-0.8413	-0.3906	0.2434	-0.5100	-0.6572
loc.22	28	4	-	-	-	-	-	-	-0.4452	-0.6430	0.2977	-0.0113	0.1289	-0.3155
loc.23	66	3	-	-	-	-	-	-	0.0725	-0.5449	**0.5303**	-0.2888	0.1749	-0.7027
loc.24	45	13	0.8265	-4.1010	-0.8755	2.8445	-0.4055	1.9540	0.1400	-0.3063	-0.1454	0.1772	0.0770	0.8219

Material complementari del capítol 2

Supp. Mat. C2. 1. Bibliography of the ant communities

We compiled data on terrestrial ant communities from an exhaustive exploration of the published literature and our research team own work. We tried to obtain data from most regions in Europe. We compiled species composition data from local terrestrial ant communities in Europe from as many sites as possible. We only considered studies that specified the name of the species in each plot and provided abundance or presence-absence data. We did not consider data from urban communities or highly disturbed sites. Since the two community sampling methodologies (pit-falls and baits) were applied covering the entire latitudinal gradient, we assume that the sampling error (not detecting species that are present in the community) is equivalent between communities along the gradient.

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Supp. Mat. C2. 2. Sources of ant species occurrence data

Consultation of digital datasets of museum collections:

Museu de Ciències Naturals de Barcelona, Arthropods collection. Barcelona. Spain.

Naturkundemuseum im Ottoneum Kassel, Germany.

Finnish Museum of Natural History LUOMUS: Finnish Biodiversity Information Facility/FinBIF. http://tun.fi/HBF.34433 (accessed 2019-03-05), only ant records.

Biodiversity data portals:

The Global Biodiversity Information Facility (GBIF). https://www.gbif.org/; July 2019 – September 2019.

NBN Atlas (National Biodiversity Network). https://nbnatlas.org; accessed on 24 April 2019.

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Finnish Biodiversity Information Facility (FinBIF). https://laji.fi/en; accessed on 12 July 2019.

Unpublished personal data

Gema Trigos Peral (occurrence data in Poland) and Olga Boet (occurrence data in Spain).

Supp. Mat. C2. 3. Criteria and steps considered to build, clean and harmonize the European ant record database

Criteria for considering ant records:

- Observed occurrences prior to 1950 were not taken into account to represent the current distribution of ant species, so occurrence data are from 1950 to 2020.

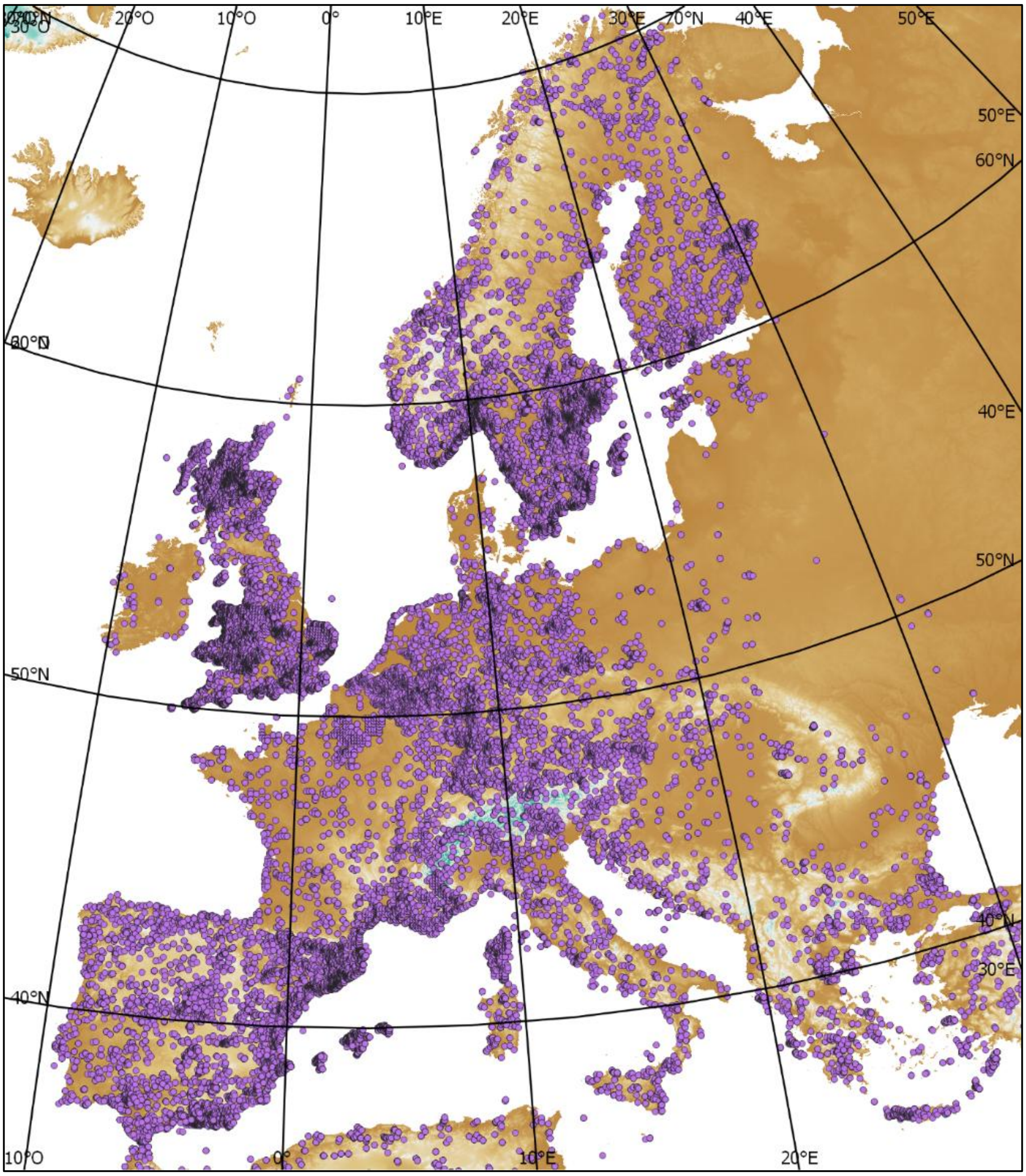
- Species with a typically European distribution were selected: species whose known range is largely outside this geographical range, i.e., only one extreme of their distribution occupies this territory, were not taken into account. The reference distribution areas were consulted in AntMap, from October 2019 to February 2020; https://antmaps.org.
- As far as the geographical range is concerned, observations were considered from the west coast of Portugal, Spain and the United Kingdom, inland up to the longitude of 32º 48' E, while the latitudinal range was from 34º 30' N to 71º 17' N (geographical coordinates, datum WGS84).
- Occurrence data of individuals that might be dispersing and therefore not found in their habitat were eliminated, and therefore quotations of winged males/females were not considered.
- Records with taxonomic identification higher than species (genus, family...) or fossil species were not included.
- Obligate parasitic species (e.g. *Myrmica hirsuta*, *Camponotus universitatis*) were not included as they rarely form part of the observed richness (they are very difficult to detect), whereas temporarily parasitic species (e.g., *Lasius umbratus, Lasius carniolicus, Formica lugubris, Formica exsecta*) were included.
- Exotic species that colonize mainly indoors ("Introduced indoors", according to AntMap and AntWiki) such as *Tapinoma melanocephalum, Monomorium pharaonis, Nylanderia vividula, Tetramorium bicarinatum, Pheidole megacephala*, and *Tetraponera allaborans* were not included. The latter is exotic and not widespread in Europe. However, it was present in one of the communities, from which it was removed to maintain concordance between the species list in the European occurrence database and the species list in the communities.
- Exotic species occupying open environments were considered (as they are part of the communities and affect observed species richness) (e.g., *Lasius neglectus, Linepithema humile, Nylanderia jaegerskioeldi, Pheidole indica, ...*).
- The species names were standardized using Bolton World Catalog (Bolton 2003); https://www.antweb.org/taxonomicPage.do?rank=species&project=worldants
- Occurrence data with inconsistencies between the toponym of the collection and the coordinates were eliminated. Similarly, occurrence data whose coordinates referred to

the toponym of the country were disregarded, as the coordinate was considered inaccurate. Duplicate observations were also eliminated.

Once the data had been filtered according to the above criteria, the following steps were taken:

1. Species for which we had a minimum of 30 occurrences and which showed good representation throughout their known distribution were selected. To make this assessment, the occurrences of each species were projected onto a map of Europe and validated, one by one, by comparing them with the AntMaps distribution, consulting other sources such as Antweb.org, and also based on our research team experience. Isolated observation points that were too far from the known distribution range or sets of occurrences were eliminated, except for those cases where correct identification could be verified. Unfortunately, we have noticed a lack of data on species records and local communities mainly in the east and north-east of Europe, corresponding to Poland, Bulgaria, Hungary, Romania, or Russia.
2. We confirmed that all species present in the communities were included in the European record database. Three species occurring in communities did not have sufficient data to map their potential distribution, and were accordingly eliminated from the study (*Messor celiae, Lasius balcanicus* and *Temnothorax caesari*).

Supp. Mat. C2. 4. Map of ant occurrences in Europe.



Map of Europe showing the study area. It contains 63,111 occurrence data (purple dots) for 278 species. Background map: WorldClim version 2.1 climate data for 1970-2000.

Supp. Mat. C2. 5. Table of species distribution model descriptors for each species.

Abbreviations: “N” was the number of occurrences after balancing the distribution of occurrence points (10 km thinning); “S-S” was the maximization of the sum of sensitivity-specificity as a threshold value for making binary map; and “Boyce” was the Boyce Index.

Species	N	S-S	Boyce
Anochetus ghilianii	6	0.841	0.604
Aphaenogaster balcanica	15	0.551	0.833
Aphaenogaster campana	7	0.663	0.627
Aphaenogaster cardenai	29	0.275	0.498
Aphaenogaster cecconii	12	0.664	0.638
Aphaenogaster dulciniae	109	0.481	0.912
Aphaenogaster epirotes	36	0.477	0.776
Aphaenogaster gibbosa	517	0.541	0.993
Aphaenogaster iberica	381	0.522	0.994
Aphaenogaster muelleriana	16	0.461	0.799
Aphaenogaster picena	30	0.401	0.876
Aphaenogaster semipolita	25	0.456	0.566
Aphaenogaster senilis	350	0.377	0.984
Aphaenogaster simonellii	20	0.726	0.906
Aphaenogaster spinosa	53	0.620	0.839
Aphaenogaster striativentris	16	0.556	0.909
Aphaenogaster subterranea	412	0.330	0.981
Aphaenogaster subterraneoides	21	0.097	0.596
Bothriomyrmex communista	31	0.529	0.697
Bothriomyrmex corsicus	50	0.505	0.893
Bothriomyrmex meridionalis	16	0.308	0.818
Camponotus aegaeus	37	0.557	0.845
Camponotus aethiops	719	0.366	0.987
Camponotus baldaccii	21	0.681	0.626
Camponotus barbaricus	30	0.399	0.860
Camponotus boghossiani	25	0.589	0.873
Camponotus candiotes	34	0.344	0.874
Camponotus cruentatus	891	0.644	0.999
Camponotus dalmaticus	26	0.386	0.890
Camponotus fallax	234	0.525	0.976
Camponotus foreli	328	0.650	0.983
Camponotus gestroi	117	0.300	0.913
Camponotus herculeanus	854	0.347	0.994
Camponotus ionius	20	0.510	0.841
Camponotus jaliensis	15	0.188	0.931
Camponotus kiesenwetteri	28	0.581	0.766
Camponotus lateralis	807	0.318	0.997
Camponotus ligniperda	669	0.374	0.989
Camponotus micans	206	0.506	0.974
Camponotus oertzeni	29	0.456	0.802
Camponotus piceus	997	0.390	0.983
Camponotus pilicornis	404	0.430	0.989
Camponotus ruber	41	0.058	0.929
Camponotus samius	48	0.630	0.962
Camponotus sanctus	22	0.350	0.682
Camponotus sicheli	53	0.680	0.902
Camponotus sylvaticus	381	0.341	0.992
Camponotus vagus	434	0.238	0.982
Cardiocondyla batesii	110	0.409	0.965
Cardiocondyla bulgarica	19	0.392	0.194
Cardiocondyla elegans	67	0.454	0.799
Cardiocondyla mauritanica	106	0.138	0.885
Cataglyphis aenescens	52	0.530	0.871
Cataglyphis cursor	77	0.554	0.845
Cataglyphis floricola	18	0.672	0.964
Cataglyphis hispanica	169	0.507	0.946
Cataglyphis humeya	20	0.499	0.912
Cataglyphis iberica	247	0.505	0.970
Cataglyphis nodus	75	0.547	0.901
Cataglyphis piliscapa	114	0.221	0.938
Cataglyphis rosenhaueri	98	0.470	0.847

Species	N	S-S	Boyce
Cataglyphis velox	127	0.302	0.986
Colobopsis truncata	368	0.403	0.979
Crematogaster auberti	552	0.575	0.984
Crematogaster ionia	45	0.431	0.867
Crematogaster laestrygon	28	0.480	0.917
Crematogaster schmidti	68	0.523	0.908
Crematogaster scutellaris	1167	0.308	0.994
Crematogaster sordidula	444	0.462	0.996
Cryptopone ochracea	27	0.561	0.837
Dolichoderus quadripunctatus	292	0.452	0.980
Formica aquilonia	580	0.481	0.993
Formica bruni	15	0.519	0.829
Formica cinerea	262	0.581	0.978
Formica clara	131	0.301	0.874
Formica cunicularia	835	0.641	0.991
Formica decipiens	95	0.509	0.958
Formica dusmeti	18	0.704	0.909
Formica exsecta	477	0.447	0.994
Formica foreli	27	0.165	0.926
Formica forsslundi	53	0.479	0.723
Formica frontalis	30	0.377	0.703
Formica fusca	1874	0.554	0.995
Formica fuscocinerea	82	0.400	0.890
Formica gagates	224	0.372	0.976
Formica gagatoides	117	0.350	0.975
Formica gerardi	173	0.540	0.917
Formica lemani	960	0.406	0.989
Formica lugubris	502	0.500	0.984
Formica picea	166	0.488	0.890
Formica polyctena	506	0.373	0.996
Formica pratensis	830	0.565	0.980
Formica pressilabris	119	0.598	0.910
Formica rufa	2283	0.409	0.996
Formica rufibarbis	782	0.485	0.995
Formica sanguinea	815	0.439	0.988
Formica selysi	175	0.681	0.975
Formica suecica	41	0.417	0.921
Formica truncorum	251	0.468	0.994
Formica uralensis	96	0.654	0.872
Goniomma baeticum	23	0.222	0.509
Goniomma blanci	64	0.402	0.886
Goniomma collingwoodi	13	0.329	0.804
Goniomma hispanicum	122	0.551	0.974
Goniomma kugleri	40	0.583	0.677
Hypoponera eduardi	209	0.286	0.980
Hypoponera punctatissima	130	0.269	0.949
Hypoponera ragusai	20	0.429	0.396
Iberoformica subrufa	402	0.520	0.994
Lasius alienus	871	0.419	0.993
Lasius balcanicus	11	0.592	0.631
Lasius bicornis	32	0.729	0.790
Lasius brunneus	715	0.428	0.993
Lasius carniolicus	26	0.418	0.620
Lasius cinereus	45	0.133	0.843
Lasius citrinus	32	0.336	0.781
Lasius distinguendus	32	0.344	0.855
Lasius emarginatus	615	0.380	0.993
Lasius flavus	1703	0.501	0.997
Lasius fuliginosus	1147	0.391	0.995
Lasius grandis	203	0.458	0.978
Lasius jensi	32	0.522	0.797
Lasius lasioides	51	0.551	0.808
Lasius meridionalis	53	0.465	0.831
Lasius mixtus	126	0.589	0.953
Lasius myops	207	0.361	0.978
Lasius neglectus	49	0.626	0.830
Lasius niger	3057	0.438	0.999
Lasius paralienus	115	0.422	0.972
Lasius piliferus	18	0.230	0.764
Lasius platythorax	719	0.448	0.992
Lasius psammophilus	258	0.427	0.963
Lasius sabularum	36	0.479	0.371
Lasius turcicus	56	0.643	0.917
Lasius umbratus	256	0.407	0.984
Lepisiota frauenfeldi	47	0.478	0.969

Species	N	S-S	Boyce
Lepisiota melas	17	0.542	0.777
Lepisiota nigra	17	0.075	0.838
Leptanilla revelierii	61	0.256	0.938
Leptothorax acervorum	888	0.486	0.999
Leptothorax gredleri	69	0.382	0.928
Leptothorax muscorum	156	0.427	0.859
Linepithema humile	290	0.138	0.960
Liometopum microcephalum	88	0.502	0.938
Manica rubida	134	0.283	0.916
Messor barbarus	756	0.320	0.996
Messor bouvieri	414	0.377	0.970
Messor capitatus	448	0.574	0.997
Messor hellenius	28	0.811	0.926
Messor hispanicus	28	0.611	0.900
Messor ibericus	28	0.573	0.944
Messor lusitanicus	43	0.364	0.788
Messor marocanus	22	0.325	0.723
Messor minor	29	0.306	0.793
Messor oertzeni	19	0.461	0.843
Messor ponticus	17	0.751	0.910
Messor structor	464	0.348	0.995
Messor wasmanni	57	0.459	0.932
Monomorium algiricum	29	0.323	0.849
Monomorium creticum	16	0.636	0.854
Monomorium monomorium	29	0.329	0.797
Monomorium salomonis	157	0.275	0.944
Monomorium subopacum	31	0.188	0.735
Myrmecina graminicola	469	0.406	0.986
Myrmica aloba	177	0.414	0.976
Myrmica constricta	41	0.402	0.917
Myrmica gallienii	29	0.480	0.829
Myrmica hellenica	39	0.444	0.729
Myrmica lobicornis	332	0.501	0.992
Myrmica lobulicornis	75	0.103	0.815
Myrmica lonae	133	0.473	0.984
Myrmica rubra	1461	0.504	0.998
Myrmica ruginodis	1979	0.305	0.999
Myrmica rugulosa	289	0.391	0.934
Myrmica sabuleti	1216	0.453	0.987
Myrmica scabrinodis	1136	0.424	0.999
Myrmica schencki	320	0.356	0.988
Myrmica specioides	155	0.438	0.906
Myrmica spinosior	61	0.130	0.916
Myrmica sulcinodis	286	0.395	0.980
Myrmica vandeli	56	0.484	0.919
Myrmica wesmaeli	69	0.331	0.914
Nylanderia jaegerskioeldi	13	0.848	0.840
Oxyopomyrmex saulcyi	93	0.610	0.963
Pheidole pallidula	906	0.391	0.997
Plagiolepis pallescens	90	0.534	0.951
Plagiolepis pygmaea	569	0.361	0.994
Plagiolepis schmitzii	228	0.447	0.971
Polyergus rufescens	83	0.563	0.973
Ponera coarctata	309	0.588	0.982
Ponera testacea	126	0.587	0.945
Prenolepis nitens	85	0.305	0.887
Proceratium melinum	51	0.634	0.849
Proformica ferreri	43	0.584	0.903
Proformica longipilosa	28	0.398	0.810
Proformica longiseta	12	0.387	0.692
Proformica nasuta	66	0.707	0.659
Solenopsis fairchildi	33	0.429	0.657
Solenopsis fugax	295	0.455	0.991
Solenopsis latro	37	0.616	0.908
Solenopsis lusitanica	14	0.644	0.806
Solenopsis orbula	19	0.659	0.757
Stenamma debile	194	0.594	0.960
Stenamma petiolatum	22	0.731	0.808
Stenamma striatulum	52	0.399	0.955
Stenamma westwoodii	145	0.476	0.968
Stigmatomma denticulatum	30	0.500	0.874
Strumigenys argiola	30	0.387	0.808
Strumigenys membranifera	17	0.407	0.870
Tapinoma darioi	13	0.346	0.887
Tapinoma erraticum	466	0.503	0.986
Tapinoma ibericum	14	0.742	0.654

Species	N	S-S	Boyce
Tapinoma madeirense	80	0.640	0.927
Tapinoma magnum	54	0.354	0.920
Tapinoma nigerrimum	451	0.498	0.997
Tapinoma simrothi	133	0.417	0.882
Tapinoma subboreale	46	0.565	0.817
Technomyrmex albipes	21	0.284	0.808
Technomyrmex difficilis	10	0.055	0.642
Temnothorax affinis	130	0.521	0.979
Temnothorax albipennis	55	0.343	0.777
Temnothorax algiricus	55	0.458	0.886
Temnothorax angustulus	57	0.636	0.968
Temnothorax aveli	72	0.547	0.900
Temnothorax bulgaricus	42	0.508	0.917
Temnothorax cagnianti	17	0.636	0.765
Temnothorax clypeatus	35	0.666	0.800
Temnothorax corticalis	49	0.203	0.749
Temnothorax crasecundus	63	0.439	0.916
Temnothorax crassispinus	194	0.461	0.976
Temnothorax exilis	120	0.536	0.943
Temnothorax flavicornis	19	0.490	0.891
Temnothorax formosus	49	0.505	0.896
Temnothorax fuentei	32	0.713	0.672
Temnothorax gredosi	39	0.280	0.834
Temnothorax grouvellei	43	0.369	0.952
Temnothorax helenae	23	0.322	0.913
Temnothorax interruptus	129	0.446	0.896
Temnothorax kraussei	64	0.627	0.897
Temnothorax leviceps	15	0.638	0.881
Temnothorax lichtensteini	111	0.344	0.950
Temnothorax luteus	78	0.533	0.826
Temnothorax mediterraneus	58	0.351	0.944
Temnothorax muellerianus	56	0.551	0.931
Temnothorax nadigi	30	0.298	0.574
Temnothorax niger	73	0.353	0.921
Temnothorax nigriceps	78	0.323	0.817
Temnothorax nylanderi	337	0.274	0.977
Temnothorax pardoi	36	0.417	0.888
Temnothorax parvulus	116	0.573	0.976
Temnothorax racovitzai	112	0.615	0.954
Temnothorax ravouxi	30	0.585	0.846
Temnothorax recedens	246	0.314	0.987
Temnothorax rogeri	18	0.310	0.654
Temnothorax schaufussi	13	0.370	0.899
Temnothorax semiruber	45	0.436	0.909
Temnothorax sordidulus	30	0.323	-0.090
Temnothorax tergestinus	30	0.332	0.765
Temnothorax tuberum	281	0.324	0.977
Temnothorax tyndalei	36	0.546	0.662
Temnothorax unifasciatus	257	0.499	0.983
Tetramorium alpestre	68	0.227	0.816
Tetramorium biskrense	29	0.421	0.854
Tetramorium brevicorne	11	0.614	0.960
Tetramorium caespitum	1843	0.521	0.999
Tetramorium chefketi	78	0.520	0.901
Tetramorium diomedeum	46	0.128	0.743
Tetramorium ferox	46	0.544	0.884
Tetramorium forte	209	0.516	0.983
Tetramorium hungaricum	87	0.429	0.867
Tetramorium immigrans	191	0.401	0.987
Tetramorium impurum	409	0.350	0.944
Tetramorium lucidulum	17	0.701	0.944
Tetramorium meridionale	65	0.058	0.806
Tetramorium moravicum	68	0.390	0.848
Tetramorium punicum	23	0.475	0.237
Tetramorium semilaeve	389	0.359	0.985
Trichomyrmex perplexus	17	0.527	0.635

Supp. Mat. C2. 6. Further methodological details.

Selection of environmental variables for building species distribution models

We initially considered 23 environmental variables: the aridity index obtained from the Wetness of Global Climate Aridity (Trabucco and Zomer, 2018), land cover map from the Copernicus Land Monitoring Service (Buchhorn et al 2019), the degree of continentality from the ENVIronmental Rasters for Ecological Modeling (Title and Bemmels, 2018), 19 climate variables and the elevation of the territory from the WorldClim-Global Climate Data (Fick and Hijmans 2017). Variable maps had a spatial resolution of 30 arc-seconds (approximately ~ 1 sq km). All of them were continuous variables and were standardized (multiplying each value by the mean and dividing it by the standard deviation, using SAGA's Raster standardization tool in Qgis), except for the categorical land cover variable. To evaluate correlations among environmental variables, we created a network of 9,296 points evenly distributed over the study area and separated by 0.4 degrees, covering the entire area with non-zero values of the environmental variables to have a good representation of the values of the variables in the whole study area. Correlation coefficients were calculated from the values obtained in the point network using the Pearson test (see Supp. Mat. C2. 7).

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Supp. Mat. C2. 7. The latitudinal gradient in European ant dark diversity: pattern and potential mechanisms.

Pearson's product-moment correlation

	r.continent	**r.elev**	**r.aridityI**	**r.Combinats**	**r.bio07**	**r.bio16**	**r.bio19**	**r.bio18**	**r.bio01**	**r.bio17**	**r.bio14**	**r.bio15**
continent	1.0000000											
elev	-0.1456051	1.0000000										
aridityI	-0.0215108	-0.0387283	1.0000000									
Combinats	0.1730104	-0.1090857	0.2011102	1.0000000								
bio07	0.7372222	-0.0091985	-0.5230616	-0.0367152	1.0000000							
bio16	-0.1155940	0.0222334	0.8584984	0.2208208	-0.5976556	1.0000000						
bio19	-0.3483146	0.0939843	0.7408122	0.1098158	-0.6697527	0.9163612	1.0000000					
bio18	0.2070597	-0.1450862	0.8507865	0.2824818	-0.3843820	0.7814019	0.5202145	1.0000000				
bio01	-0.3723200	0.0645143	-0.7432862	-0.2868476	0.2537763	-0.6489720	-0.4093659	-0.8323548	1.0000000			
bio17	-0.1059810	-0.0540728	0.8740793	0.2017575	-0.6010047	0.8354786	0.7304185	0.8818255	-0.6686568	1.0000000		
bio14	-0.0861543	-0.0774673	0.8695499	0.1981612	-0.5841080	0.8121120	0.6989650	0.8882362	-0.6718340	0.9932145	1.0000000	
bio15	-0.1456990	0.1034306	-0.4523322	-0.1389885	0.2098350	-0.2984460	-0.1879459	-0.5804594	0.4877370	-0.6322001	-0.6349380	1.0000000
bio13	-0.0994355	0.0257248	0.8478045	0.2258802	-0.5820962	0.9968917	0.9097593	0.7765629	-0.6538615	0.8248326	0.8003738	-0.2853449
bio03	-0.6630449	0.2196013	-0.5723967	-0.2964920	-0.0480195	-0.4767763	-0.2054600	-0.7433813	0.8585237	-0.5094726	-0.5174656	0.4792881
bio10	-0.1502230	0.0360652	-0.7954789	-0.2644956	0.4638440	-0.7221039	-0.5201776	-0.8432605	0.9709104	-0.7421971	-0.7423283	0.4830092
bio12	-0.1380712	0.0166699	0.9005319	0.2158421	-0.6324710	0.9758317	0.8973667	0.8306265	-0.6690616	0.9266285	0.9055516	-0.4392276
bio09	-0.4525936	0.2424117	-0.6476574	-0.2824074	0.1461672	-0.5294097	-0.2288596	-0.8468388	0.9128938	-0.6081306	-0.6254991	0.5304859
bio11	-0.5618314	0.0944747	-0.6506146	-0.2925991	0.0395309	-0.5402032	-0.2705638	-0.7866523	0.9741895	-0.5637053	-0.5720661	0.4689430
bio06	-0.6531037	0.0790308	-0.5667114	-0.2829672	-0.1065774	-0.4482779	-0.1712908	-0.7225532	0.9325285	-0.4707718	-0.4811501	0.4277580
bio08	0.2820143	-0.3083786	-0.4721824	-0.0627025	0.4835539	-0.4963702	-0.5937744	-0.2315064	0.4083161	-0.4087769	-0.3874933	0.1021501
bio04	0.9665066	-0.1325158	-0.0729892	0.1391163	0.8006009	-0.1776107	-0.3914781	0.1382889	-0.3145523	-0.1645841	-0.1464437	-0.1221133
bio05	-0.1276633	0.0631705	-0.8042991	-0.2677223	0.5038557	-0.7459027	-0.5482760	-0.8569699	0.9614841	-0.7674416	-0.7663796	0.4967634
bio02	-0.1444902	0.2041172	-0.7739537	-0.2755492	0.5292846	-0.7492534	-0.5609365	-0.8464058	0.8819645	-0.7689968	-0.7663014	0.5096178

(continuació de la taula, columnes de la dreta a partir de la fila 13)

	r.bio13	**r.bio03**	**r.bio10**	**r.bio12**	**r.bio09**	**r.bio11**	**r.bio06**	**r.bio08**	**r.bio04**	**r.bio05**	**r.bio02**
bio13	1.0000000										
bio03	-0.4839762	1.0000000									
bio10	-0.7228248	0.7445636	1.0000000								
bio12	0.9682451	-0.4890111	-0.7486534	1.0000000							
bio09	-0.5335653	0.8567639	0.8666679	-0.5543921	1.0000000						
bio11	-0.5485808	0.9178323	0.8951497	-0.5531528	0.9203336	1.0000000					
bio06	-0.4586855	0.8991728	0.8279591	-0.4566949	0.8914927	0.9866392	1.0000000				
bio08	-0.4919068	0.1148135	0.4957553	-0.5052095	0.1054498	0.2916367	0.2322623	1.0000000			
bio04	-0.1600805	-0.6234497	-0.0825206	-0.2000141	-0.3922637	-0.5176922	-0.6163897	0.2940144	1.0000000		
bio05	-0.7456639	0.7525027	0.9959344	-0.7739803	0.8616521	0.8807067	0.8051684	0.4901871	-0.0579667	1.0000000	
bio02	-0.7469819	0.8147079	0.9054981	-0.7749657	0.8181464	0.8104065	0.7121184	0.3727204	-0.0744337	0.9343310	1.0000000

	p.value. continent	p.value. elev	p.value. aridityI	p.value. Combinats	p.value. bio07	p.value bio16	p.value. bio19	p.value. bio18	p.value. bio01	p.value. bio17	p.value. bio14
continent	0										
elev	3.20E-45	0									
aridityI	0.03808	0.000188	0								
Combinats	2.22E-63	5.21E-26	1.96E-85	0							
bio07	0	0.37519	0	0.00040	0						
bio16	5.05E-29	0.03206	0	4.82E-103	0	0					
bio19	2.24E-263	1.08E-19	0	2.44E-26	0	0	0				
bio18	1.46E-90	6.58E-45	0	4.32E-170	0	0	0	0			
bio01	1.55E-303	4.79E-10	0	1.48E-175	1.46E-136	0	0	0	0		
bio17	1.24E-24	1.82E-07	0	5.51E-86	0	0	0	0	0	0	
bio14	8.72E-17	7.47E-14	0	5.92E-83	0	0	0	0	0	0	0
bio15	2.81E-45	1.56E-23	0	2.54E-41	5.22E-93	1.48E-190	1.16E-74	0	0	0	0
bio13	7.28E-22	0.01312	0	7.46E-108	0	0	0	0	0	0	0
bio03	0	6.68E-102	0	5.57E-188	3.62E-06	0	3.62E-89	0	0	0	0
bio10	4.72E-48	0.00050	0	1.34E-148	0	0	0	0	0	0	0
bio12	8.52E-41	0.10802	0	2.00E-98	0	0	0	0	0	0	0
bio09	0	2.05E-124	0	5.35E-170	1.46E-45	0	9.63E-111	0	0	0	0
bio11	0	6.97E-20	0	6.60E-183	0.00014	0	1.14E-155	0	0	0	0
bio06	0	2.33E-14	0	1.08E-170	6.78E-25	0	3.82E-62	0	0	0	0
bio08	1.64E-169	5.72E-204	0	1.44E-09	0	0	0	2.41E-113	0	0	0
bio04	0	1.09E-37	1.84E-12	2.14E-41	0	9.48E-67	0	6.39E-41	1.42E-212	1.90E-57	9.96E-46
bio05	4.43E-35	1.09E-09	0	2.46E-152	0	0	0	0	0	0	0
bio02	1.50E-44	5.25E-88	0	1.30E-161	0	0	0	0	0	0	0

	p.value.bio15	**p.value.bio13**	**p.value.bio03**	**p.value.bio10**	**p.value.bio12**	**p.value.bio09**	**p.value.bio11**	**p.value.bio06**	**p.value.bio08**	**p.value.bio04**	**p.value.bio05**	**p.value.bio02**
bio15	0											
bio13	1.16E-173	0										
bio03	0	0	0									
bio10	0	0	0	0								
bio12	0	0	0	0	0							
bio09	0	0	0	0	0	0						
bio11	0	0	0	0	0	0	0					
bio06	0	0	0	0	0	0	0	0				
bio08	5.43E-23	0	1.19E-28	0	0	2.11E-24	1.15E-181	4.29E-114	0			
bio04	3.22E-32	2.09E-54	0	1.60E-15	1.65E-84	0	0	0	9.65E-185	0		
bio05	0	0	0	0	0	0	0	0	0	2.23E-08	0	
bio02	0	0	0	0	0	0	0	0	3.11E-304	6.69E-13	0	0

Supp. Mat. C2. 8. Further methodological details.

Species range estimation for developing species distribution models by MaxEnt

To develop SDMs, we restricted the working area of MaxEnt by taking into account the current distribution of each species and dispersal distance of ants over a period of 70 years (corresponding to the time range of occurrence data, from 1950 to 2020). To do this, we delimited the current distribution of each species by creating an area that included all species records so that we obtained a spatial convex hull for each species (i.e., a hull with all internal angles less than 180°) (Meyer et al. 2017) which was subsequently expanded with a buffer of 100 km in order to obtain a range of potential distribution of the species large enough to ensure the inclusion of the entire current distribution area, but small enough to avoid over-distribution. We calculated the dispersal buffer width as the sum of the following two distances: a) the uncertainty of the observed distribution; since species observation data are not the actual limits of their distribution and the species is probably around the convex hull, we agreed to extend the area by a strip of 50 km; and b) the maximum dispersal distance of the species over a period of 70 years. Since ant species present different strategies and dispersal distances (Hakala et al 2019), we considered the flight distance of winged females as the maximum distance of creation of new nests (i.e., colonization), that is, as a measure of the increase in spatial distribution. Because there is a significant gap in flight distances for each species, we estimated a single maximum distance for all species in Europe based on the female flight distance values reported by Helms (2018). From the species studied by Helms, we chose 3 genera present in Europe: *Crematogaster, Pheidole* and *Solenopsis*. We obtained an average flight distance of 3,000 m per year and added a time of 5 years in each dispersal cycle (average time estimated by the authors to establish a new colony and be able to produce new winged individuals). For a period of 70 years, we computed a value of 42 km of maximum dispersal distance and rounded it to

50 km. We used the *gConvexHull* function to create the occurrence distribution area and the Rgeos R package (Bivand and Rundel 2022) for the dispersal buffer.

References

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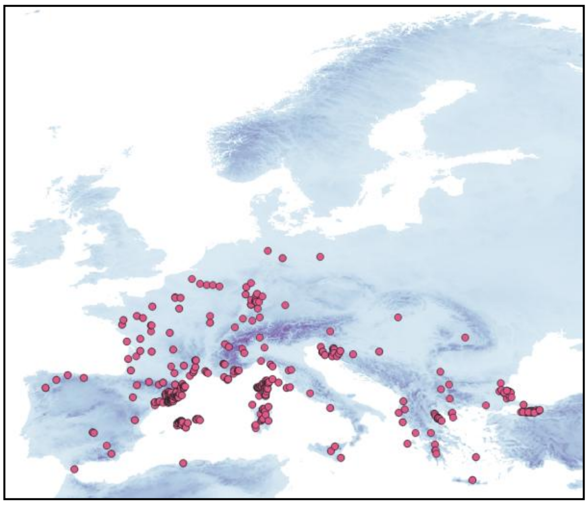
Supp. Mat. C2. 9. Further methodological details.

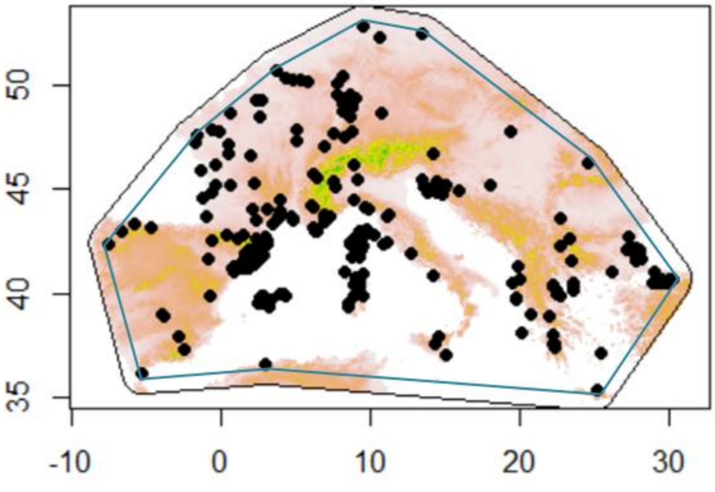
Process of elaboration and validation of the species distribution models developed by MaxEnt. As an example, images for *Aphaenogaster subterranea* are shown

The next steps were followed:

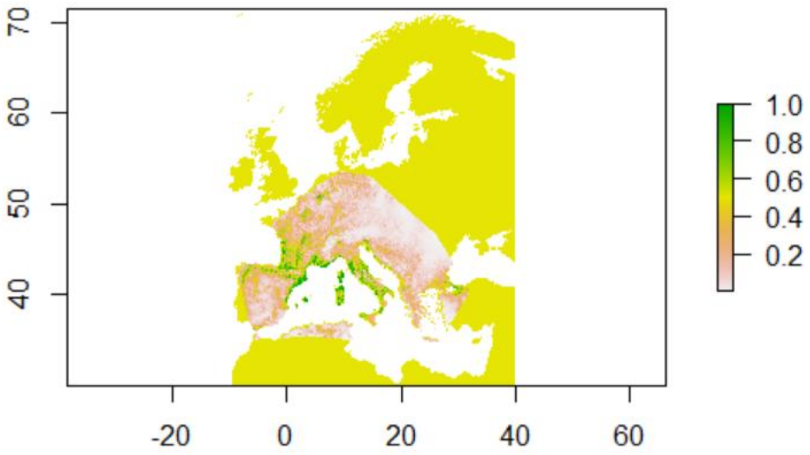
A) To obtain all occurrence data from 1950 onwards and check that we have a good representation of their known distribution (by consulting AntMaps and our expert judgement).



B) To delimit the envelope (convexHull) for each species starting from the occurrence points (blue line) and adding the 100 km buffer around it (black line). The background points were also restricted in this area (Elith et al. 2011, Merow et al. 2013). To balance the number of background points according to the surface of the envelope, the areas of the envelopes of all species were considered: to the smallest 10,000 background points were assigned, and to the largest 1,000,000 were assigned; the rest was scaled in function of each surface of the envelope.



C) Species distribution model for *Aphaenogaster subterranea* by MaxEnt. The legend represents the habitat suitability value for the species. Outside the envelope, the habitat suitability value is zero, although potentially suitable habitats exist for this species.



D) To make the models and as commonly practiced, 80 % of the data was used for calibration and 20 % for evaluation, which were ran on different random selections. To validate the models mathematically, the Boyce index was used (Boyce and McDonald 1999, Boyce et al., 2002, Hirzel et al. 2006). This index assesses how well the predicted suitability values from a model align with observed occurrences of a particular species. The Boyce Index ranges from −1 to +1, where values close to 1 correspond to the model's predictions align well with observed occurrences; values negative correspon to the model's predictions are misleading (as areas with high predicted suitability have low occurrence density); and vaules close to zero mean the model is no better than predicted randomly. See Boyce's values in Table S1.

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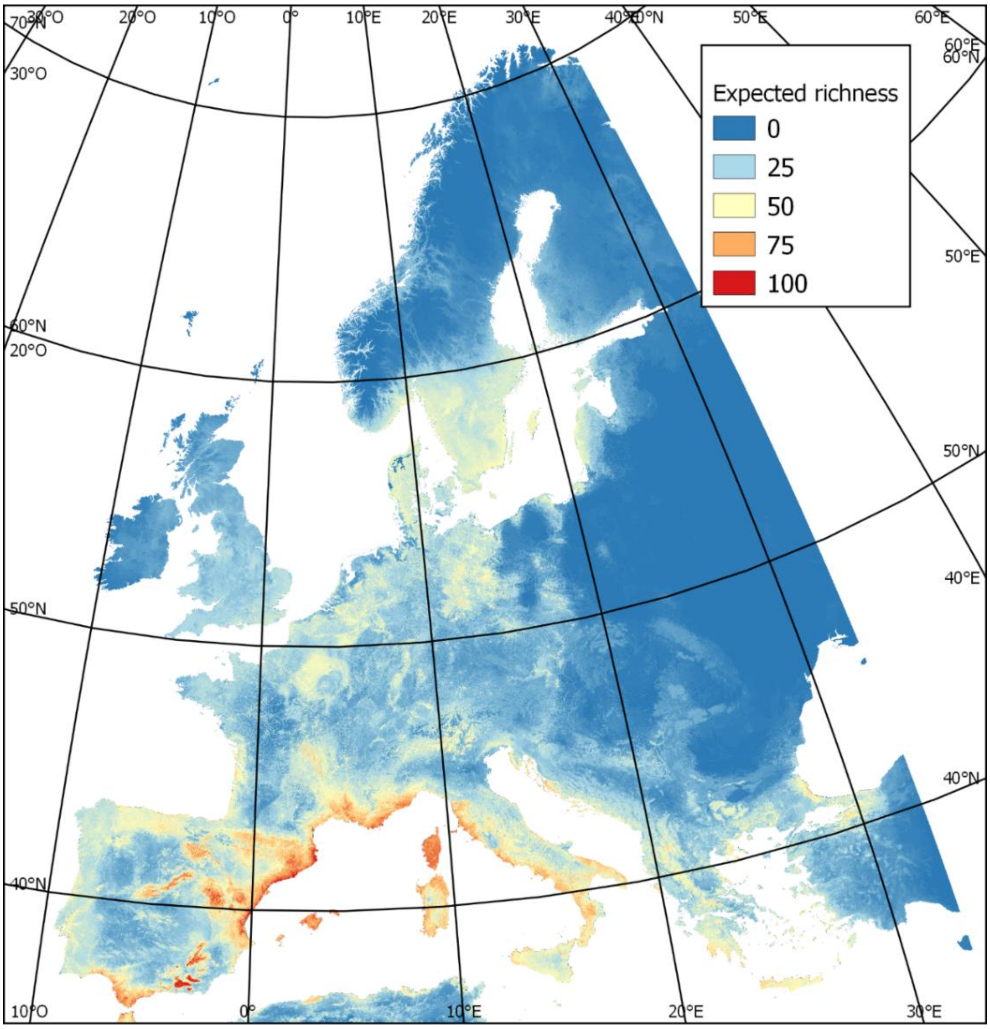
Supp. Mat. C2. 10. Expected ant species richness map in Europe.



The legend shows a color scale indicating the expected number of species suitable to live there, taking into account the environmental variables used in the species distribution models and the estimated dispersal limitation of the species.

Supp. Mat. C2. 11. Categorization of behaviorally dominant ants.

Of the 278 ants species considered in this study, 155 were present in the communities and were categorized in behaviourally dominant or not behaviorally dominant ant species based on the literature (see below for the bibliographic reference list) and our combined expert knowledge. According to this, we considered the following dominant species: *Camponotus aethiops, Camponotus cruentatus, Camponotus herculeanus, Camponotus ligniperda, Camponotus pilicornis, Camponotus sylvaticus, Camponotus vagus, Formica aquilonia, Formica cinerea, Formica clara, Formica lugubris, Formica polyctena, Formica pratensis, Formica rufa, Formica sanguinea, Formica truncorum, Lasius alienus, Lasius cinereus, Lasius emarginatus, Lasius fuliginosus, Lasius grandis, Lasius lasioides, Lasius niger, Lasius paralienus, Linepithema humile, Liometopum microcephalum, Tapinoma erraticum, Tapinoma nigerrimum, Tapinoma simrothi, Crematogaster scutellaris, Messor barbarus, Messor celiae, Messor capitatus, Messor hispanicus, Messor structor, Monomorium salomonis, Pheidole pallidula, Tetramorium caespitum, Tetramorium impurum, Tetramorium forte, Tetramorium hispanicum, Tetramorium ruginode, Tetramorium semilaeve,* and *Tetramorium punicum*.

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Supp. Mat. C2. 12. Statistical outputs

Statistical outputs from the model selection applied to test for the effects of latitude (Lat), elevation (Elev) and the relative abundance of dominant ant species (arcsine square root transformed) (Dominant) on dark diversity (A) and community completeness index (CCI) (B).

A. Response variable: Dark diversity.

Model selection table

	Intercept	Elevation	Dominant	Latitude	Lat x Elev	R^2	df	AICc	Delta	Weight
16	**116.0**	**2.06E-01**	**7.808**	**-1.669**	**-5.17E-03**	**0.621**	**7**	**3542.7**	**0.00**	**1**
7	140.6		9.487	-2.363		0.570	5	3567.5	24.82	0
14	118.9	2.32E-01		-1.625	-5.73E-03	0.594	6	3571.7	29.00	0
8	147.8	-6.70E-03	10.300	-2.486		0.574	6	3576	33.34	0
5	152.0			-2.473		0.531	4	3604.8	62.13	0
6	158.6	-5.63E-03		-2.579		0.533	5	3614.5	71.82	0
3	34.6		10.450			0.453	4	3664.2	121.45	0
4	32.5	9.35E-03	9.020			0.460	5	3670.2	127.51	0
2	36.4	1.59E-02				0.405	4	3710.6	167.94	0
1	41.7					0.386	3	3712.6	169.89	0

In bold, the selected model (Delta<2).

Confidence interval

	2.5%	97.5%
Intercept	95.129	136.840
Elevation	0.149	0.264
Dominant	5.057	10.560
Latitude	-2.133	-1.204
Lat x Elev	-0.007	-0.004

B. Response variable: CCI.

Model selection table

	Intercept	Elevation	Dominant	Latitude	Lat x Elev	R^2	df	AIC	Delta	Weight
5	**-3.31**			**$4.72\text{x}10^{-02}$**		**0.099**	**4**	**982.2**	**0**	**0.771**
7	-3.58		$1.95\text{x}10^{-01}$	$4.87\text{x}10^{-02}$		0.104	5	984.7	2.49	0.222
6	-3.81	$3.89\text{x}10^{-04}$		$5.53\text{x}10^{-02}$		0.122	5	991.8	9.60	0.006
8	-3.93	$3.72\text{x}10^{-04}$	$1.32\text{x}10^{-01}$	$5.60\text{x}10^{-02}$		0.125	6	995.1	12.91	0.001
Null	-1.21					0.014	3	1003.5	21.35	0
14	-3.35	$-2.87\text{x}10^{-03}$		$4.41\text{x}10^{-02}$	$7.93\ \text{x}10^{-05}$	0.136	6	1007.0	24.84	0
3	-1.22		$1.15\text{x}10^{-02}$			0.011	4	1007.4	25.25	0
16	-3.49	$-3.10\text{x}10^{-03}$	$1.95\text{x}10^{-01}$	$4.42\text{x}10^{-02}$	$8.44\text{x}10^{-05}$	0.140	7	1009.6	27.45	0
2	-1.25	$1.13\text{x}10^{-04}$				0.013	4	1020.9	38.68	0
4	-1.24	$1.17\text{x}10^{-04}$	$-2.19\text{x}10^{-02}$			0.013	5	1024.7	42.54	0

In bold, the selected model (Delta<2).

Confidence interval

	2.5%	97.5%
Intercept	-4.130	-2.588
Lat	0.031	0.064
Dominants	-0.105	0.496
Elevation	0.000	0.001
Lat x Elev	0.000	0.000

Material complementari del capítol 3

Supp. Mat. C3. 1. Bibliographic sources of ant community data in Europe

We assembled data on terrestrial ant communities through an extensive review of the published literature, complemented by original data collected by our research team. Our aim was to gather information from a broad range of European regions. Specifically, we compiled species composition data from as many local terrestrial ant communities as possible across the five main biomes of Europe. Only studies that clearly provided a list of species at the plot level were included. We excluded data from urban environments and highly disturbed habitats. The references used to compile the ant community composition data are listed below.

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Supp. Mat. C3. 2. Summary of the methodology for estimating the expected ant species

The methodology used to estimate expected ant species via Species Distribution Models (SDM) is detailed in Boet et al. (2025). For clarity and ease of reference, a summary is provided below.

Occurrence data for estimating expected species

To develop the SDMs, we first compiled a comprehensive database of native European ant species occurrences by integrating occurrence data from online platforms, museum collections, scientific literature and our previous field surveys. We then applied data cleansing protocols (see Boet et al. 2025 Supp. Mat.1.3), resulting in a final dataset comprising 62,716 occurrence records across 213 species, including 62 species not detected in the community data (that is, the observed species). Considering that Europe hosts approximately 600 native ant species (Czechowski et al., 2002), including marginal and parasitic taxa, our dataset offers extensive coverage of regional ant diversity. The distributions of each species occurrence points were cross-validated using AntMap (https://antmaps.org) and confirmed through expert judgment by the authors.

Modelling expected ant species

The SDM method estimates the expected distribution of species across the study area by first modelling the predicted habitat suitability for each species individually from an occurrence dataset, then converting these models into binary presence–absence maps and stacking these maps. Below we detail these two stages.

1. Habitat suitability models

SDMs were used to predict habitat suitability for each species in the area bounded by the geographical coordinates 36º N to 62º N latitude and 10º 30' W to 24.7º E longitude, based on the WGS84 datum. We confirmed that all 360 communities were located well within this modelled area, thereby minimizing edge effects and prediction uncertainties (Ronk et al. 2016). To make the SDMs, we used the sevent most relevant environmental variables as relevant predictors for ant ecology (Williams et al. 2012): Mean annual temperature, Mean temperature of the wettest quarter, Annual precipitation, Precipitation seasonality (coefficient of variation), Elevation, Continentality and Land cover. SDMs were implemented using MaxEnt, a presence-only modelling technique (Elith et al. 2011) that has previously been successfully applied to predicting ant distributions (Procter et al. 2015, Depa et al. 2017, Silva et al. 2022). To avoid overestimating the spatial extent of species distributions based solely on environmental suitability, we constrained the MaxEnt projection area to the distribution of occurrence points extended with a buffer of 100 km. This resulted in distinct occurrence envelopes for each species, refining the spatial resolution of background sampling. SDMs were constructed using the Dismo package (Hijmans et al. 2017) in R (R Core Team, 2020).

2. Expected ant species

Next, the SDMs were converted into binary presence–absence maps using, for each species, the threshold derived from the sum of sensitivity and specificity maximization method, a commonly applied approach in classification tasks (Jiménez-Valverde & Lobo, 2007). Sensitivity quantifies the proportion of correctly predicted presences, while specificity measures the proportion of correctly predicted absences. Maximizing their sum provides a threshold that optimally balances model performance. Finally, we stacked all binary maps and picked up the list of expected species for each locality where observed species data were available.

Supp. Mat. C3. 3. Ant species included in the study

List of ant species included in the study, showing the number of localities where each species was recorded within the community (Loc.Obs) and outside the community (Loc.Dark). The species list includes the 213 native ant species of Europe that were present in the observed and/or dark sets. Of these, three species were detected exclusively within communities, whereas 62 species occurred only outside them.

Species	**Loc. Obs**	**Loc. Dark**
Aphaenogaster cardenai	1	19
Aphaenogaster dulcineae	22	61
Aphaenogaster gibbosa	89	115
Aphaenogaster iberica	22	40
Aphaenogaster senilis	69	87
Aphaenogaster spinosa	12	0
Aphaenogaster striativentris	0	7
Aphaenogaster subterranea	91	94
Camponotus aethiops	86	122
Camponotus amaurus	1	1
Camponotus barbaricus	0	42
Camponotus cruentatus	77	93
Camponotus fallax	21	234
Camponotus foreli	29	101
Camponotus gestroi	7	60
Camponotus herculeanus	13	41
Camponotus lateralis	88	132
Camponotus ligniperdus	24	97
Camponotus micans	8	48
Camponotus piceus	72	100
Camponotus pilicornis	92	107
Camponotus sylvaticus	79	132
Camponotus vagus	4	195
Cardiocondyla batesii	7	51
Cardiocondyla elegans	0	73
Cardiocondyla mauritanica	2	39
Cataglyphis cursor	13	113
Cataglyphis floricola	12	9
Cataglyphis hispanica	5	6
Cataglyphis humeya	0	2
Cataglyphis iberica	19	123
Cataglyphis piliscapa	0	76
Cataglyphis rosenhaueri	17	33
Cataglyphis velox	12	34
Colobopsis truncata	23	218
Crematogaster auberti	60	113
Crematogaster laestrygon	0	20
Crematogaster scutellaris	111	111
Crematogaster sordidula	53	156
Cryptopone ochracea	0	109
Dolichoderus quadripunctatus	13	153
Formica aquilonia	7	8
Formica bruni	0	8
Formica cinerea	7	131
Formica clara	7	189
Formica cunicularia	52	158
Formica decipiens	1	21
Formica dusmeti	0	12
Formica exsecta	0	51
Formica foreli	1	17
Formica frontalis	0	62
Formica fusca	121	40
Formica fuscocinerea	0	9
Formica gagates	52	100
Formica gerardi	19	119
Formica lemani	19	33
Formica lugubris	12	16
Formica picea	0	5
Formica polyctena	17	73
Formica pratensis	13	76
Formica pressilabris	0	19
Formica rufa	24	92
Formica rufibarbis	39	227
Formica sanguinea	20	108
Formica selysi	0	3
Formica truncorum	6	30
Formica uralensis	1	4
Goniomma baeticum	2	28

Species	**Loc. Obs**	**Loc. Dark**
Goniomma blanci	5	118
Goniomma collingwoodi	1	0
Goniomma hispanicum	26	53
Goniomma kugleri	1	33
Hypoponera eduardi	6	189
Hypoponera punctatissima	1	150
Hypoponera ragusai	0	24
Iberoformica subrufa	68	107
Lasius alienus	52	252
Lasius balcanicus	0	6
Lasius bicornis	0	34
Lasius brunneus	34	104
Lasius carniolicus	0	26
Lasius cinereus	3	126
Lasius distinguendus	0	83
Lasius emarginatus	38	155
Lasius flavus	61	61
Lasius fuliginosus	21	97
Lasius grandis	12	119
Lasius jensi	0	44
Lasius lasioides	3	144
Lasius meridionalis	0	40
Lasius mixtus	0	29
Lasius myops	45	117
Lasius niger	186	130
Lasius paralienus	5	108
Lasius platythorax	9	50
Lasius psammophilus	4	75
Lasius sabularum	0	40
Lasius umbratus	1	193
Lepisiota frauenfeldi	0	17
Leptanilla revelierii	2	29
Leptothorax acervorum	37	19
Leptothorax gredleri	2	4
Leptothorax muscorum	24	35
Linepithema humile	5	158
Liometopum microcephalum	0	4
Manica rubida	3	86
Messor barbarus	57	150
Messor bouvieri	30	157
Messor capitatus	46	142
Messor celiae	2	0
Messor hispanicus	9	44
Messor ibericus	0	126
Messor lusitanicus	10	24
Messor marocanus	23	22
Messor minor	11	7
Messor structor	34	173
Messor wasmanni	9	10
Monomorium algiricum	0	7
Monomorium monomorium	0	74
Monomorium salomonis	1	101
Monomorium subopacum	0	33
Myrmecina graminicola	38	208
Myrmica aloba	15	55
Myrmica constricta	0	37
Myrmica gallienii	0	32
Myrmica hellenica	0	9
Myrmica lobicornis	0	50
Myrmica lobulicornis	24	27
Myrmica lonae	3	20
Myrmica rubra	63	50
Myrmica ruginodis	84	39
Myrmica rugulosa	1	46
Myrmica sabuleti	71	121
Myrmica scabrinodis	78	35
Myrmica schencki	48	61
Myrmica specioides	17	215

Species	Loc. Obs	Loc. Dark
Myrmica spinosior	4	94
Myrmica sulcinodis	4	47
Myrmica vandeli	0	16
Myrmica wesmaeli	3	21
Oxyopomyrmex saulcyi	17	45
Pheidole pallidula	153	72
Plagiolepis pallescens	2	89
Plagiolepis pygmaea	170	61
Plagiolepis schmitzii	38	70
Ponera coarctata	19	191
Ponera testacea	0	117
Proceratium melinum	0	37
Proformica ferreri	15	8
Proformica longiseta	0	5
Proformica nasuta	1	17
Stenamma debile	3	191
Stenamma orousetti	1	1
Stenamma petiolatum	1	17
Stenamma striatulum	4	121
Stenamma westwoodi	21	155
Strumigenys argiola	1	148
Strumigenys membranifera	0	52
Tapinoma darioi	0	12
Tapinoma erraticum	50	186
Tapinoma ibericum	0	2
Tapinoma madeirense	0	112
Tapinoma magnum	0	150
Tapinoma nigerrimum	122	103
Tapinoma simrothi	19	28
Tapinoma subboreale	1	38
Temnothorax affinis	0	68
Temnothorax albipennis	0	34
Temnothorax algiricus	0	25
Temnothorax angustulus	2	48
Temnothorax caesari	2	2
Temnothorax cagnianti	0	9
Temnothorax corticalis	0	61
Temnothorax crassispinus	8	35
Temnothorax exilis	22	118
Temnothorax formosus	0	53
Temnothorax fuentei	15	24
Temnothorax gredosi	1	26
Temnothorax grouvellei	1	26
Temnothorax interruptus	10	50
Temnothorax kraussei	14	148
Temnothorax leviceps	0	33
Temnothorax lichtensteini	49	98
Temnothorax luteus	8	106
Temnothorax mediterraneus	2	142
Temnothorax muellerianus	0	80
Temnothorax nadigi	0	68
Temnothorax niger	25	105
Temnothorax nigriceps	5	43
Temnothorax nylanderi	67	169
Temnothorax pardoi	2	41
Temnothorax parvulus	13	149
Temnothorax racovitzai	74	72
Temnothorax ravouxi	0	123
Temnothorax recedens	40	166
Temnothorax schaufussi	0	13
Temnothorax sordidulus	0	9
Temnothorax tergestinus	0	31
Temnothorax tuberum	11	101
Temnothorax tyndalei	17	16
Temnothorax unifasciatus	27	201
Tetramorium alpestre	0	8
Tetramorium biskrense	0	34
Tetramorium caespitum	143	135

Species	Loc. Obs	Loc. Dark
Tetramorium ferox	0	4
Tetramorium forte	40	61
Tetramorium hungaricum	0	5
Tetramorium immigrans	0	126
Tetramorium impurum	9	66
Tetramorium meridionale	7	82
Tetramorium moravicum	0	8
Tetramorium punicum	2	43
Tetramorium semilaeve	82	139

Supp. Mat. C3. 4. Bibliographic sources of functional trait information for the different ant species included in this study

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Supp. Mat. C3. 5. Additional data analysis details

To compute functional dissimilarities between species pairs using Gower distances, we constructed a single trait matrix including all species in the study. This ensured that distance values remained consistent across biomes. We calculated Gower distances using the gawdis function from the “gawdis” package (de Bello et al. 2021) when combining multiple traits, and the gowdis function from the "FD" package (Laliberté and Legendre 2010, Laliberté et al. 2014) for single functional traits, in R version 4.3.1 (2023-06-16 ucrt) (R Core Team 2024). In the distance matrix, the diet trait was treated as a dummy variable, with fuzzy coding, for FDiss pairwise calculations. Then, to estimate FDiss pairwise we applied the additive partitioning approach to compute beta functional dissimilarity (βRao) for each pairwise species set, calculated as the difference between gamma functional diversity and the mean alpha functional diversity. To this end, we employed the ‘rao’ function provided in de Bello et al. (2010) that uses the Rao*'s quadratic entropy (Q)* index (Rao, 1982) as a metric of functional diversity.

For statistical analyses, we employed Generalized Least Squares (GLS) models to account for potential spatial autocorrelation, incorporating geographic coordinates as a random effect (Dormann et al. 2007). To identify optimal models, we used Akaike’s information criterion to determine the optimal spatial correlation structure. First, to evaluate the influence of biome on FDiss pairwise, we fitted a GLS model with βRao pairwise (i.e. FDiss pairwise) as the response variable and biome as a predictor variable. To account for the potential correlation between Rao’s quadratic entropy and gamma diversity (Botta-Dukát, 2005), while acknowledging its reduced sensitivity to species richness (Mouchet et al., 2010), we included total species richness per locality—encompassing both observed and dark species—as a covariate in the model. We then applied an analysis of variance (ANOVA) to the statistical outputs of the GLS model, using the Anova function from the “car” package in R (Fox and Weisberg 2019), to test whether mean values of functional dissimilarity (FDiss pairwise) differed significantly among biomes. When a significant biome effect was detected, we conducted post-hoc pairwise comparisons between biomes using Tukey's HSD adjustment, based on estimated marginal means (EMMs) calculated with the “emmeans” package (Lenth, 2025).

Afterwards, to better understand the patterns of FDiss pairwise, we explored the distribution of functional traits in the observed and dark species separately. Specifically, we calculated community mean (CM) as the mean of the trait values in the community for each trait individually, and for both species sets (observed and dark) per locality within each biome using the dbFD function from the FD package (Laliberté and Legendre 2010, Laliberté et al. 2014). For quantitative traits, CM represents the average trait value; for categorical traits, it reflects the proportion of each category in the community (de Bello et al. 2010). For the calculation of CM, the three components of diet (proportions of seed, insect, and liquid food consumption) were treated as separate variables to better capture their variation across biomes. For the trait ‘diurnality’, which violated the Euclidean assumptions required by dbFD, we applied the Cailliez correction (de Bello et al. 2021). We used the same statistical approach as for the FDiss pairwise analyses. To characterize how CM varied across species sets and biomes, we fitted nine GLS models, with CM as the response variable and biome, species set, and their interaction as fixed effects. We were particularly interested in the effect of the interaction between biome and species set. When the interaction term was significant, pairwise differences between levels of the species set factor within each biome were examined using the post-hoc tests. All GLS models were implemented using the ‘nlme’ package (Pinheiro et al., 2025), and all analyses were performed in R.

Supp. Mat. C3. 6. Descriptive statistics

Descriptive statistics (range, mean, and standard deviation) of the main variables used in the study, provided for each biome: number of observed species per locality, number of dark species per locality, total species richness per locality, and pairwise functional dissimilarity (FDiss pairwise) values calculated with all functional traits combined.

		Alpine	Atlantic	Boreal	Continental	Mediterranean
Observed species	range	4 - 10	4 - 21	4 - 21	3 - 16	4 - 36
	mean	6.2	11.0	11.0	8.4	13.7
	SD	2.0	3.5	4.5	3.1	6.8
Dark species	range	6 - 51	10 - 46	4 - 30	7 - 43	5 - 90
	mean	19.3	23.5	17.2	28.0	53.4
	SD	19.0	10.4	8.7	9.7	17.4
Total species	range	10 - 57	21 - 54	14 - 36	11 - 56	23 - 94
	mean	25.5	34.5	28.2	36.4	67.1
	SD	20.4	9.6	8.3	10.1	15.3
FDiss pairwaise	range	0.008 - 0.069	0.004 - 0.031	0.004 - 0.040	0.004 - 0.066	0.003 – 0.092
	mean	0.032	0.011	0.014	0.019	0.030
	SD	0.023	0.006	0.008	0.012	0.017

Supp. Mat. C3. 7. Descriptive statistics of pairwise functional dissimilarity

Descriptive statistics (mean, standard deviation, minimum, and maximum) of FDiss pairwise values (functional beta diversity between observed and dark species sets), calculated for each biome using both all traits combined and each trait independently.

		Alpine	**Atlantic**	**Boreal**	**Continental**	**Mediterranean**
All traits	mean	0.0321	0.0108	0.0142	0.0190	0.0301
	sd	0.0227	0.0059	0.0082	0.0116	0.0174
	min	0.0082	0.0039	0.0038	0.0039	0.0035
	max	0.0696	0.0315	0.0402	0.0660	0.0919
Worker size	mean	0.0136	0.0070	0.0149	0.0115	0.0091
	sd	0.0089	0.0067	0.0145	0.0109	0.0083
	min	0.0029	0.0012	0.0025	0.0018	0.0009
	max	0.0273	0.0277	0.0658	0.0608	0.0466
Worker polymorphism	mean	0.0385	0.0100	0.0136	0.0160	0.0174
	sd	0.0301	0.0045	0.0056	0.0114	0.0139
	min	0.0041	0.0038	0.0034	0.0015	0.0020
	max	0.1020	0.0218	0.0207	0.0455	0.0784
Diet	mean	0.0321	0.0098	0.0075	0.0151	0.0800
	sd	0.0366	0.0047	0.0060	0.0142	0.0642
	min	0.0049	0.0035	0.0017	0.0006	0.0070
	max	0.1300	0.0200	0.0182	0.0825	0.3420
Diurnality	mean	0.0976	0.0120	0.0518	0.0329	0.0356
	sd	0.1110	0.0166	0.0424	0.0371	0.0588
	min	0	0	0.0002	0	0
	max	0.3650	0.0647	0.1640	0.1660	0.4210
Nesting site	mean	0.0243	0.0187	0.0089	0.0382	0.0312
	sd	0.0315	0.0238	0.0133	0.0512	0.0469
	min	0	<0.0001	0	<0.0001	0
	max	0.0989	0.0874	0.0492	0.2670	0.3390

Supp. Mat. C3. 8. Results of post-hoc Tukey tests (based on estimated marginal means) comparing dark and observed species within each biome for the community mean (CM) of each trait or category.

The *estimate* represents the average difference in CM between dark and observed species within a given biome, and the *t ratio* is calculated as estimate/SE. Positive estimates (or t ratios) indicate that the CM of dark species exceeds that of observed species, whereas negative values indicate the opposite. '*Non-strictly diurnal'* and '*Nesting in the ground'* refer to one of the two categories within the Diurnality and Nesting site traits, respectively; the omitted category yields identical estimates with opposite signs. Statistically significant differences are indicated in bold.

	estimate	**SE**	**Lower CL**	**Upper CL**	**t ratio**	**p**
Worker size						
Alpine	-0.613	0.206	-1.018	-0.207	-2.968	**0.003**
Atlantic	0.345	0.137	0.076	0.614	2.518	**0.012**
Boreal	0.109	0.153	-0.192	0.410	0.711	0.477
Continental	0.340	0.081	0.182	0.498	4.213	**<0.001**
Mediterranean	-0.166	0.045	-0.254	-0.078	-3.689	**<0.001**
Worker polymorphism						
Alpine	-0.110	0.025	-0.159	-0.061	-4.420	**<0.001**
Atlantic	-0.016	0.017	-0.049	0.016	-0.982	0.327
Boreal	0.016	0.018	-0.020	0.052	0.860	0.390
Continental	0.025	0.010	0.005	0.044	2.517	**0.012**
Mediterranean	-0.087	0.005	-0.097	-0.076	-16.022	**<0.001**
Seed proportion						
Alpine	0.005	0.027	-0.047	0.058	0.200	0.848
Atlantic	-0.020	0.017	-0.053	0.012	-1.200	0.223
Boreal	0.002	0.018	-0.034	0.038	0.100	0.904
Continental	0.014	0.000	0.014	0.014	1735076.5	**<0.001**
Mediterranean	-0.042	0.006	-0.053	-0.030	-7.200	**<0.001**
Insect proportion						
Alpine	0.071	0.024	0.025	0.117	3.042	**0.002**
Atlantic	-0.001	0.016	-0.032	0.030	-0.067	0.947
Boreal	0.006	0.017	-0.029	0.040	0.326	0.744
Continental	0.025	0.009	0.007	0.043	2.672	**0.008**
Mediterranean	0.099	0.005	0.089	0.109	19.314	**<0.001**

Liquid food proportion						
Alpine	-0.076	0.031	-0.137	-0.015	-2.462	**0.014**
Atlantic	0.021	0.021	-0.019	0.062	1.041	0.298
Boreal	-0.007	0.023	-0.052	0.038	-0.290	0.772
Continental	-0.033	0.012	-0.057	-0.009	-2.735	**0.006**
Mediterranean	-0.057	0.007	-0.070	-0.043	-8.370	**<0.001**
Non strictly diurnal						
Alpine	-0.084	0.044	-0.170	0.003	-1.897	0.058
Atlantic	-0.020	0.029	-0.077	0.038	-0.681	0.496
Boreal	0.117	0.033	0.053	0.181	3.569	**<0.001**
Continental	-0.053	0.017	-0.087	-0.019	-3.065	**0.002**
Mediterranean	0.011	0.010	-0.008	0.030	1.124	0.261
Nesting in the ground						
Alpine	-0.140	0.047	-0.231	-0.048	-3.004	**0.003**
Atlantic	-0.096	0.031	-0.157	-0.036	-3.122	**0.002**
Boreal	0.003	0.035	-0.065	0.070	0.077	0.939
Continental	-0.123	0.018	-0.159	-0.087	-6.758	**<0.001**
Mediterranean	-0.029	0.010	-0.049	-0.009	-2.850	**0.004**