EFECTOS DEL FUEGO SOBRE HORMIGAS Y OTROS ARTRÓPODOS:

Un estudio a diferentes escalas.

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Efectos del fuego sobre hormigas y otros artrópodos:

un estudio a diferentes escalas

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Escuela de Doctorado de Ciencias, Tecnologías e Ingenierías
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Efectos del fuego sobre hormigas y otros artrópodos:

un estudio a diferentes escalas

Memoria presentada por el Licenciado en Biología José Manuel Vidal Cordero para optar al título de Doctor por la Universidad de Granada

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Que José Manuel Vidal Cordero, Licenciado en Biología por la Universidad de Granada y Máster en Conservación, Gestión y Restauración de la Biodiversidad por dicha Universidad, ha realizado bajo su dirección la presente Memoria de Tesis Doctoral, titulada "Efectos del fuego sobre hormigas y otros artrópodos: un estudio a diferentes escalas" y que a su juicio reúne los méritos suficientes para optar al grado de Doctor por la Universidad de Granada.

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A la Dama que me acompañó durante todo el viaje

Índice

Resumen

Efectos del fuego sobre hormigas y otros artrópodos: un estudio a diferentes escalas

Los incendios forestales son una de las perturbaciones más frecuentes en los ambientes mediterráneos. Alteran enormemente los ecosistemas forestales, al modificar la estructura y la composición de las comunidades vegetales, y como consecuencia, la estructura y composición de las comunidades animales que los habitan.

El objetivo general de esta Tesis Doctoral es investigar las respuestas al fuego a corto, medio y largo plazo, en sistemas de coníferas de ambientes mediterráneos de la Península Ibérica sobre tres grupos de artrópodos. Se ha estudiado, desde un punto de vista taxonómico y funcional, la estructura y composición de las comunidades de hormigas, abejas y arañas afectadas por el fuego, así como los efectos del fuego sobre la jerarquía de dominancia en las comunidades hormigas. Para ello, se realizaron muestreos de campo mediante trampas de caída, trampas Moericke y cebos en pinares de la Península Ibérica afectados por incendios forestales de diferente antigüedad.

El fuego tuvo un efecto más acusado sobre las comunidades de hormigas que sobre las de abejas y arañas. La respuesta taxonómica de las hormigas (abundancia, riqueza y diversidad) fue muy variable, disminuyendo estas variables a corto plazo en un caso, recuperándose a corto plazo en otro caso, o incluso incrementándose independiente del tiempo transcurrido tras el incendio. A nivel funcional, las comunidades de hormigas de zonas quemadas se componen de especies más termófilas y subordinadas, así como de especies dominantes de hábitats más abiertos, mientras que las zonas no quemadas presentan especies menos termófilas y asociadas a una vegetación más desarrollada, especialmente al estrato arbóreo y al matorral alto. Por lo tanto, el fuego puede actuar como un mecanismo de filtrado de nichos, con un efecto a largo plazo para algunos rasgos funcionales y a corto plazo para otros rasgos.

En concusión, el fuego altera las comunidades de artrópodos a nivel taxonómico y funcional, especialmente en hormigas. Las alteraciones taxonómicas son variables y dependen más de la escala local (de la recuperación de la vegetación y de la comunidad de hormigas antes del fuego), mientras que las alteraciones funcionales son a más largo plazo, y más predecibles.

Abstract

The effects of fire on ants and other arthropods: a study at different depths

Forest fires are one of the most frequent disturbances in Mediterranean environments. They greatly alter forest ecosystems, modifying the structure and composition of plant communities which consequently affects the structure and composition of the animal communities that inhabit them.

The general objective of this Doctoral Thesis is to investigate the short-, medium- and long-term response three groups of arthropods have to fire in coniferous systems in Mediterranean environments of the Iberian Peninsula. We studied the structure and composition of the communities of ants, bees and spiders affected by fire from a taxonomic and functional point of view. We also measured how fire affects the hierarchy of dominance in ant communities. For this purpose, field sampling was carried out using pitfall traps, Moericke traps and baits in pine forests of the Iberian Peninsula affected by forest fires that occurred varying periods of time.

Fire had a more pronounced effect on the communities of ants than in did on those of bees and spiders. The taxonomic response of ants (abundance, richness and diversity) varied highly. These variables decreased in the short-term in one case, recovered in the short-term in another case, and they even increased, independently of the time elapsed after the fire. At the functional level, the ant communities in burned areas are predominantly composed of thermophilic and subordinate species, and also of dominant species in more open habitats. In unburned areas, however, the species tend to be less thermophilic and are associated with more developed vegetation, especially the tree layer and tall shrubs. Therefore, fire may act as a niche filtering mechanism, with a long-term effect on some functional traits and a short-term effect on other ones.

In conclusion, fire alters arthropod communities at the taxonomic and functional level, especially in ants. Taxonomic alterations are variable and depend more on the local scale (the recovery of the vegetation and the types of ant community present before the fire), while functional alterations are longer-term and more predictable.

Introducción general

Las perturbaciones naturales como los huracanes, los terremotos, las inundaciones, las sequías o los incendios forestales, llevan moldeando ecosistemas y organismos desde hace milenios, y su influencia en la estructura y el funcionamiento de los ecosistemas ha sido ampliamente reconocida en el campo de la ecología (Coyle et al., 2017; Mart-Jan et al., 2003). De los eventos citados, los incendios forestales son el objetivo más frecuente en investigación (Viljur et al., 2022) y suponen un reto global para los esfuerzos de conservación, por lo que resulta esencial comprender cómo afectan a la biodiversidad (Kelly et al., 2020).

Los incendios forestales son un factor ecológico dominante en muchos ecosistemas terrestres, especialmente en bosques boreales y mediterráneos (Bengtsson et al., 2000; Bowman et al., 2009). Su origen acompaña a la aparición de las primeras plantas terrestres y de los primeros ecosistemas forestales (Bond & Scott, 2010; Falcon-Lang, 2000; Keeley & Pausas, 2022), causando grandes alteraciones en la estructura del hábitat, el flujo de energía y la composición de las comunidades bióticas (Bengtsson et al., 2000; Pausas & Keeley, 2009; Pausas & Vallejo, 1999). En los ecosistemas mediterráneos, el fuego es el agente de perturbación natural más importante y desempeña un papel clave en la dinámica y la estructura de las comunidades animales y vegetales (Moreno & Oechel, 1994; Pausas et al., 2008a, 2008b; Pausas & Parr, 2018).

El fuego actúa simultáneamente como una fuerza perturbadora destructiva, pero al mismo tiempo, proporciona una gran variedad de servicios ecosistémicos (McLauchlan et al., 2020; Pausas & Keeley, 2019). En condiciones naturales, moldea los ecosistemas forestales siendo incluso necesario para el inicio del proceso de regeneración y la sucesión ecológica (Bond & Keeley, 2005; Keeley et al., 2011; Pausas et al., 2017). Sin embargo, el régimen natural de los incendios forestales ha cambiado en las últimas décadas, alterados por la acción humana, a un régimen caracterizado fundamentalmente por un aumento en la frecuencia, la intensidad y los patrones espaciales fundamentalmente (Keeley et al., 2012; Pausas, 2004; Pausas & Fernández-Muñoz, 2012) (Figura 1 a y b), además de añadir nuevos tipos de perturbaciones al ecosistema (por ejemplo, pérdida y fragmentación del hábitat, pesticidas, labrado, pastoreo), haciendo que estén fuera del rango de sostenibilidad (Bengtsson, 2002). En los ecosistemas mediterráneos, este cambio a un régimen antrópico, es debido fundamentalmente a la elevada densidad de la población, a la despoblación rural y a los cambios en el manejo de los ecosistemas forestales, que han llevado a un aumento en la disponibilidad de recursos combustibles, incrementando las igniciones y la frecuencia de incendios (Keeley et al., 2012).

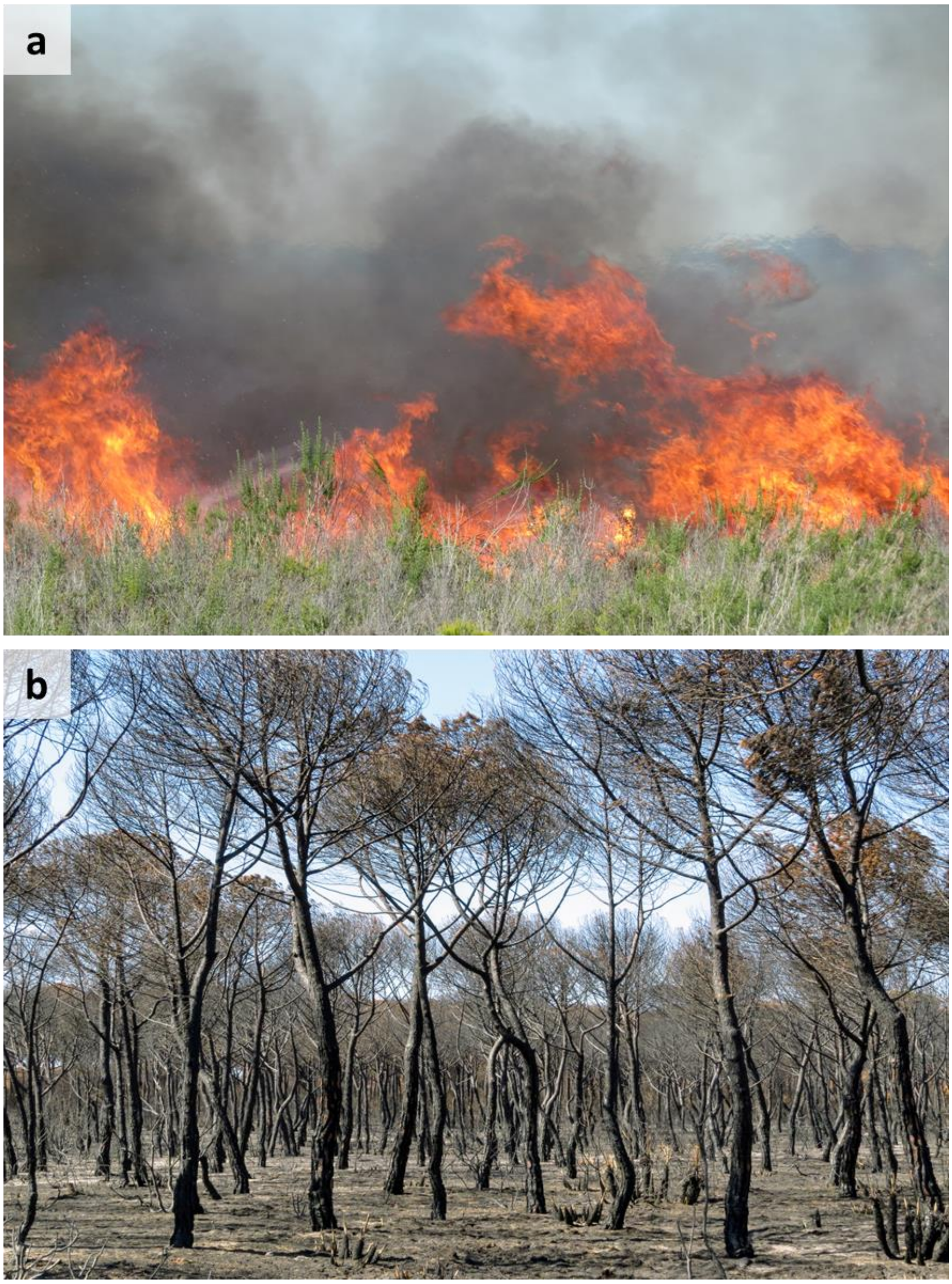

Figura 1. (a) Fuego generado sobre monte mixto en una quema prescrita llevada a cabo en la Reserva Biológica de Doñana (Andalucía, España) en 2020; (b) pinar de pino piñonero (*Pinus pinea*) afectado por un incendio de origen antrópico en el Parque Natural de Doñana (Andalucía, España) en 2017 (Fotos J- Manuel Vidal-Cordero).

Asimismo, el cambio climático está provocando un aumento de la frecuencia y de la duración de los periodos de sequía, propiciando incendios de mayor extensión (Pausas, 2004; Pausas & Fernández-Muñoz, 2012; Piñol et al., 1998). Los modelos predictivos sugieren un aumento continuo en la frecuencia e intensidad del fuego, así como un desplazamiento a áreas con un historial de incendios pasado o nulo (Hantson et al., 2017; Pausas & Fernández-Muñoz, 2012). El cambio en el régimen de los incendios forestales puede tener consecuencias importantes para la estabilidad de los ecosistemas, por lo tanto, comprender las respuestas de las comunidades de los organismos al fuego es de primordial importancia para predecir sus consecuencias en los ecosistemas forestales mediterráneos y establecer las estrategias de gestión y conservación adecuadas.

Comparado con otras perturbaciones naturales, los incendios forestales son el proceso natural de mayor impacto sobre las plantas. Aunque el principal efecto directo de los incendios forestales es la destrucción masiva de los tejidos aéreos en poco tiempo, sus efectos indirectos son diversos y complejos de estudiar. Una amplia literatura indica que, en ambientes propensos a incendios, como ocurre en gran parte de la Península Ibérica y otras áreas de la región Mediterránea, las plantas han adquirido, a lo largo de la evolución, rasgos que les permiten sobrevivir y reproducirse en ambientes con incendios frecuentes (Keeley et al., 2011). Gran variedad de especies vegetales autóctonas presenta adaptaciones a los incendios. Los principales rasgos son los relacionados con el reclutamiento post-fuego (serotinia, la germinación estimulada por el calor o por el humo, o la floración post-fuego), con la supervivencia de los individuos (el rebrote o la presencia de cortezas muy gruesas) y con la inflamabilidad (Bradshaw et al., 2011; Keeley et al., 2011; Pausas et al., 2017) (Figura 2 a y b). Por tanto, la recuperación post-fuego de la comunidad vegetal va a presentar gran variabilidad dependiendo del tipo de cubierta forestal afectada (Rodrigo et al., 2004), aunque también del cambio en la frecuencia en el régimen de los incendios (Keeley, 2012; Pausas, 1999).

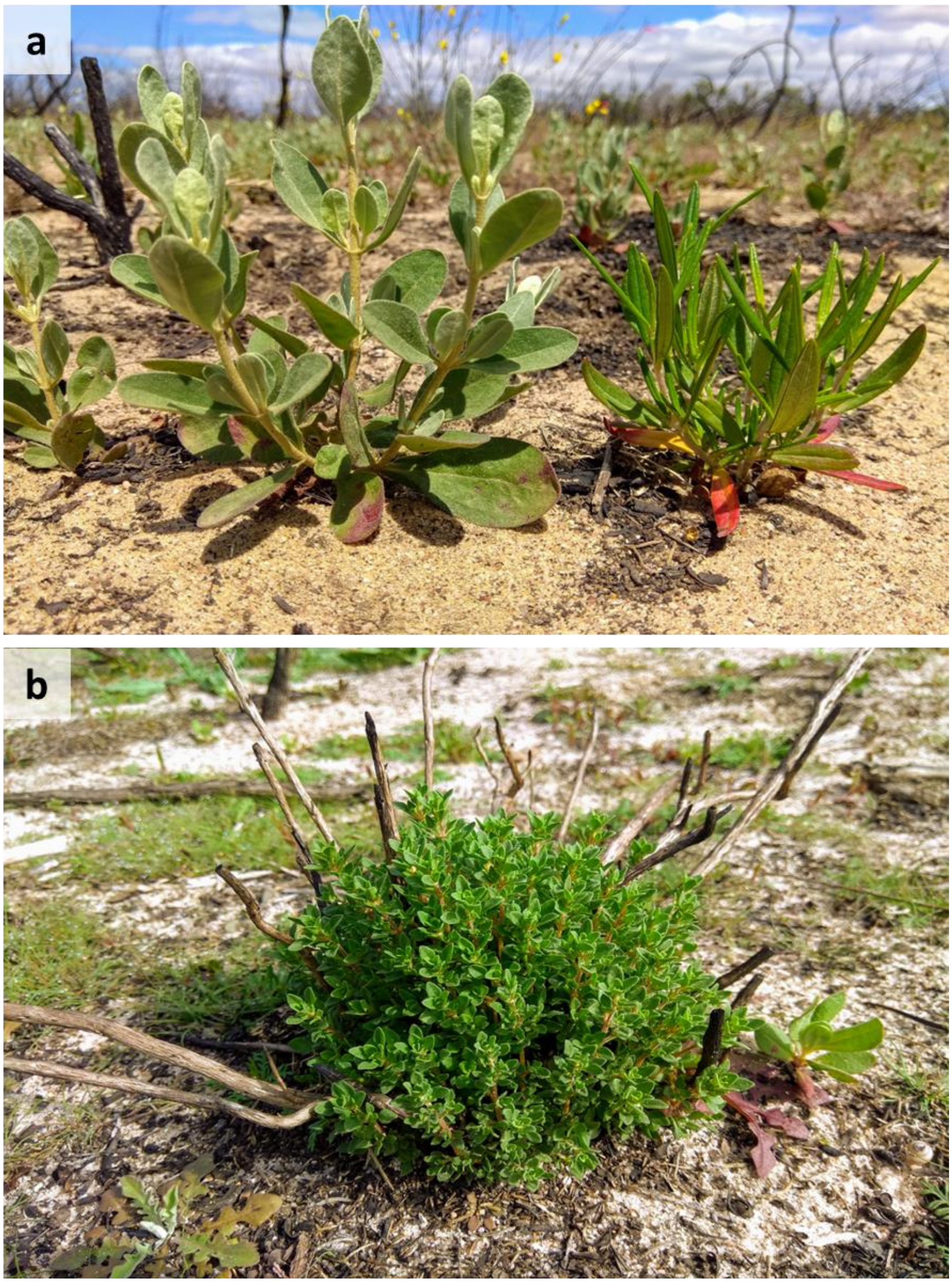

Figura 2. (a) Reclutamiento post-fuego de jaguarzo blanco (*Halimium halimifolium*), a la izquierda y falso romero (*Cistus libanotis*), a la derecha, tal un año después de haber sido afectado por fuego en 2020, (b) rebrote de tomillo (*Thymus mastichina*) un año después de haber sido afectado por fuego en 2020. Reserva Biológica de Doñana (Parque Nacional de Doñana) (Fotos J. Manuel Vidal-Cordero).

La mayoría de trabajos que han estudiado el efecto del fuego en las comunidades biológicas se han centrado tradicionalmente en las plantas (Keeley, 2012; Keeley et al., 2011). La comprensión de cómo la fauna responde al fuego es más limitada y durante mucho tiempo, el papel evolutivo que tiene el fuego en los animales se ha pasado por alto (Parr & Chown, 2003; Pausas & Parr, 2018). No obstante, investigaciones más recientes han explorado el impacto del fuego en los animales, tanto en vertebrados (Geary et al., 2020; Pocknee et al., 2023), como en invertebrados (Carbone et al., 2019; New, 2014; Samways et al., 2018), sugiriendo que, los diferentes comportamientos animales proveen de una fuente rica de adaptaciones al fuego (Pausas & Parr, 2018). Esto es debido a que, en contraste con las plantas, la mayoría de los animales son organismos unitarios, móviles, que tienen una reducida capacidad de supervivencia son afectados por el fuego y pueden moverse lejos de este (Pausas & Parr, 2018). Además, recientemente se ha propuesto una clasificación de las estrategias generales de respuesta al fuego de plantas y animales que incluyen: Resistencia, refugios, evitación, latencia, recolonización, cripsis e intolerancia (Pausas, 2018). Esta agrupación de respuestas proporciona un marco que facilita la búsqueda de vacíos de conocimiento y la dirección de futuras investigaciones para obtener una mejor comprensión del papel del fuego en la biodiversidad.

Los artrópodos son capaces de responder más rápidamente a los cambios ambientales generados por las perturbaciones (como el fuego) que las plantas y los vertebrados (Kremen et al., 1993; Rosenberg et al., 1986) debido a que en general presentan tiempos de generación cortos, tasas de reproducción altas y muestran menos efectos competitivos que las especies de vertebrados de vida larga con tasas de reproducción bajas, permitiéndoles experimentar una presión de selección inmediata frente a cambios ambientales instantáneos (Samways, 1993). La rápida respuesta a las perturbaciones ofrece a muchas especies de artrópodos la posibilidad de actuar como indicadores tempranos del cambio y contribuir de manera útil a los planes de gestión y conservación del ecosistema afectado (Azevedo-Ramos et al., 2006; Basset et al., 1998; Kremen et al., 1993; Lawes et al., 2005). Sin embargo, los artrópodos son un grupo taxonómico muy diverso donde las numerosas especies presentes en él pueden responder de manera muy diferente al fuego (New, 2014). De hecho, esta es una de las limitaciones más importantes de los trabajos que estudian la respuesta al fuego por parte de diferentes comunidades de artrópodos, ya pueden dar lugar a resultados sesgados debido a la falta de conocimiento de la riqueza de especies dentro de cada grupo taxonómico focal, limitando gravemente la información que puede acumularse al estudiarlos (Coleman & Rieske, 2006). Por este motivo, la mayoría de trabajos que estudian las respuestas de las comunidades de artrópodos al fuego se centran en uno (o dos grupos taxonómicos como mucho), generalmente. Algunos ejemplos de ello, son los estudios realizados con hormigas (Arnan et al., 2006; Rodrigo & Retana, 2006; Underwood & Quinn, 2010), abejas (Bogusch et al., 2015; Burkle et al., 2019; Lazarina et al., 2016; Love & Cane, 2016), escarabajos (Moretti et al., 2010; Pausas et al., 2018; Rodrigo et al., 2008) o arañas (De Omena et al., 2018; Foster et al., 2015; Langlands et al., 2011, 2006; Moretti et al., 2002) entre otros. No obstante, no hay que olvidar que evaluar cómo el fuego afecta a diferentes taxones de manera conjunta puede aportar una valiosa información sobre la conservación de la biodiversidad de manera integrada y la gestión del paisaje en tiempos de pérdida de biodiversidad.

El papel que representa la riqueza de especies y, por extensión, su abundancia se ha utilizado a lo largo de la historia para comprender el funcionamiento de las comunidades de artrópodos (Wong et al., 2019) y han sido las medidas más utilizadas para explorar los efectos del fuego en la biodiversidad (Hevia et al., 2016; Lamarre et al., 2016). Sin embargo, para comprender adecuadamente los mecanismos que subyacen a estas respuestas taxonómicas, es importante examinar también los cambios en los rasgos funcionales representados dentro de las comunidades de artrópodos (Braga et al., 2013; Mouillot et al., 2013). La importancia ecológica de la diversidad funcional radica en su influencia en la dinámica del ecosistema, la estabilidad, la productividad, el balance de nutrientes y otros aspectos del funcionamiento del ecosistema (Laureto et al., 2015). En consecuencia, este enfoque puede aclarar cómo responden los organismos a los incendios forestales y revelar las adaptaciones específicas que promueven la supervivencia o la recuperación (Pausas & Parr, 2018). Por lo tanto, en el estudio de las respuestas de los organismos a los incendios forestales, es necesario armonizar la dimensión taxonómica (medidas tradicionales de la biodiversidad como la abundancia, la riqueza y la diversidad) con la dimensión funcional (medida con diferentes índices, como la riqueza funcional, divergencia funcional, etc.) calculada a partir de los datos de composición de especies y los rasgos funcionales de las mismas (Májeková et al., 2016). A menudo, se asume una relación positiva y lineal entre estas dos dimensiones de la diversidad (Bihn et al., 2010; Rocha-Ortega et al., 2018), por lo que una mayor riqueza de especies conduce a una mayor riqueza funcional ('hipótesis de nicho de complementariedad'; Tilman et al. 1997). Sin embargo, y pese a la gran importancia de utilizar conjuntamente un enfoque taxonómico y funcional para contar con conocimientos orientativos que se puedan aplicar en la conservación de especies y la gestión de ecosistemas (Lambeets et al., 2009), los estudios que analizan simultáneamente estas dos dimensiones de la diversidad son escasos (Morelli et al., 2018).

Hormigas (Hymemoptera: Formicidae), abejas (Hymenoptera: Apidae) y arañas (Araneae) son grupos de artrópodos altamente diversos, numéricamente dominantes en la mayoría de los ecosistemas terrestres, que brindan importantes servicios ecosistémicos (Del Toro et al., 2012; Michalko et al., 2019; Underwood & Quinn, 2010) y son altamente sensibles a los cambios ambientales (Buchholz, 2010; Churchill, 1997; Potts et al., 2010; Tiede et al., 2017). Todas estas características citadas, convierte a hormigas, arañas y abejas en excelentes taxones indicadores para monitorear las respuestas de la biodiversidad de artrópodos frente a cambios ambientales (Andersen et al., 2004; Gollan et al., 2011; Pearce & Venier, 2006; Williams et al., 2010). Además, hormigas y abejas tienen un papel clave en la regeneración de los ecosistemas, y más aún en la Península Ibérica, donde mantienen relaciones mutualistas (por ejemplo, dispersión de semillas, polinización) y antagonistas (granivoría) con numerosas plantas (Bosch et al., 2009; Gómez et al., 1996; Ordóñez & Retana, 2004). El género de la hormiga *Messor*, por ejemplo, es el depredador de semillas más importante en muchos hábitats (Cerdá & Retana, 1994). Existen estudios que muestran que las hormigas contribuyen significativamente a la dispersión de frutos y semillas de numerosas plantas herbáceas y arbustivas en la península ibérica (Barroso et al., 2013; Boulay et al., 2007; Retana et al., 2004) y, además, pueden ser claves en la recuperación de la vegetación después del incendio (Arnan et al., 2010, 2009). Por otro lado, el papel de las abejas como eficientes polinizadores de los ecosistemas es bien conocido, proporcionando un servicio ecosistémico esencial para el mantenimiento de la diversidad de las plantas silvestres (Aguilar et al., 2006; Potts et al., 2016, 2010) (Figura 3 a y b). Por último, entre los artrópodos existentes, las arañas son los depredadores por excelencia (Turnbull, 1973) y cambios en su diversidad taxonómica y funcional pueden alterar la composición, la diversidad y la dinámica de la población de los niveles tróficos inferiores (Bruno & Cardinale, 2008; Prieto-Benítez and Méndez, 2011). Dada la importancia de los servicios prestados por las hormigas, abejas y arañas a los ecosistemas forestales, es esencial ampliar nuestro conocimiento de sus respuestas a los incendios.

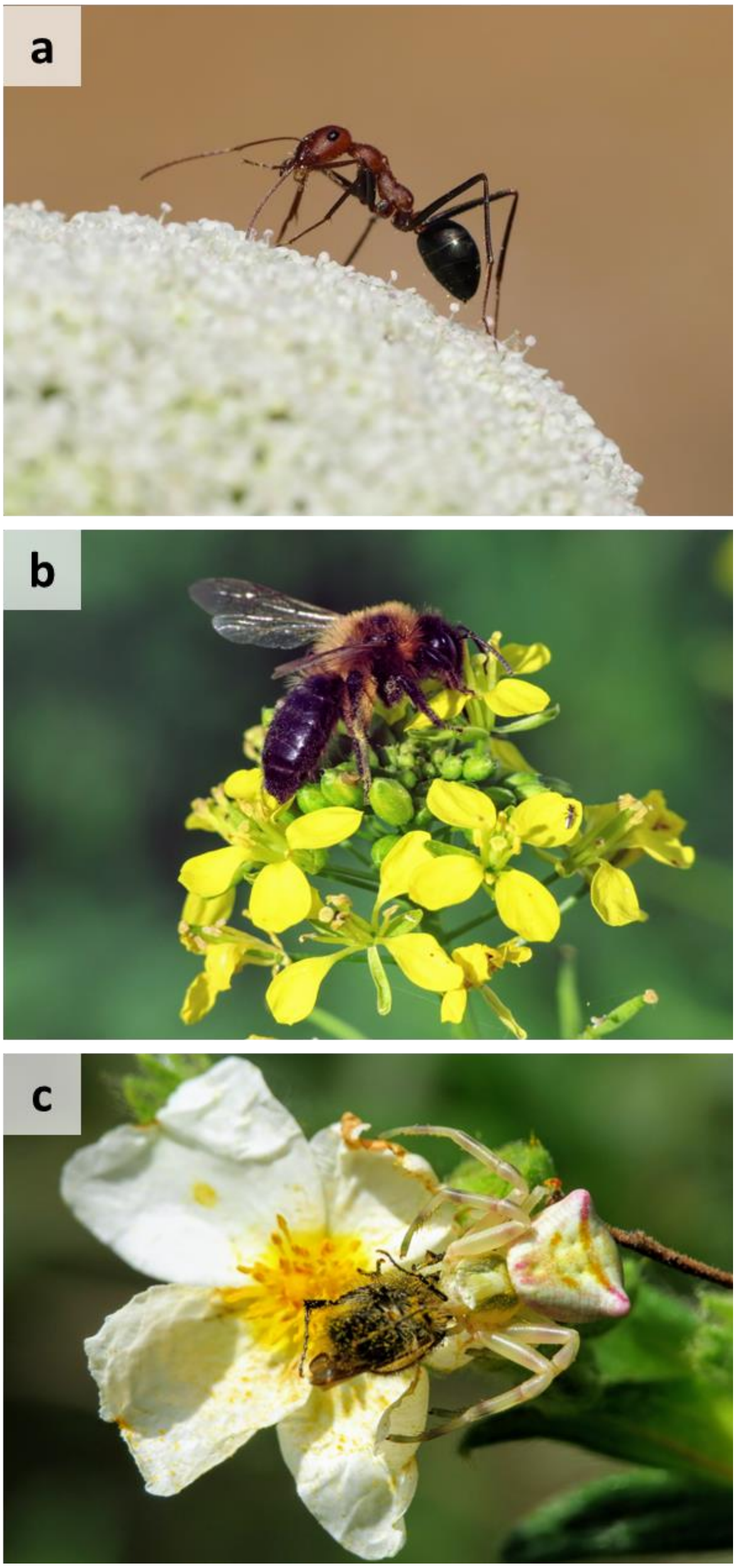

Figura 3. (a) Obrera de *Cataglyphis velox* sobre las flores de una umbelífera, (b) abeja silvestre *Andrena thoracica* libando de las flores de una crucífera y 3) araña cangrejo (*Thomisus onustus*) alimentándose sobre la flor de un jaguarzo negro (*Cistus monspeliensis*). (Fotos J. Manuel Vidal-Cordero).

En líneas generales, podríamos decir que la estructura y composición de las comunidades de hormigas, abejas y arañas después de un incendio depende de dos características de los organismos, como son la capacidad de resiliencia y la de resistencia (Moretti et al., 2006; Oliver et al., 2015). Moretti et al. 2006, define la resiliencia como la rápida recuperación de la composición de especies a las condiciones anteriores al incendio, mientras que la capacidad de resistencia hace referencia al grado de similaridad de la composición de especies inmediatamente (< 1 año) después del fuego.

A su vez, la respuesta de las comunidades de los diferentes grupos taxonómicos al fuego, va a diferir entre biomas, y su composición será el resultado de una combinación de mortalidad directa por el fuego e indirecta debida a cambios en el hábitat en condiciones post-fuego, y a la colonización y recolonización de las áreas quemadas desde áreas periféricas no quemadas (Pausas, 2018; Pausas & Parr, 2018; Wong et al., 2019). En primer lugar, pocos son los trabajos que han estudiado el impacto del calentamiento del suelo en insectos de vida subterránea. Debido a sus propiedades aislantes, la tierra otorga una cierta capacidad de supervivencia contra temperaturas extremas actuando como refugio para aquellas especies de hormigas, abejas y arañas que tienen nidos subterráneos (Cane & Neff, 2011; Parr et al., 2004). Si bien, existen especies que anidan a poca profundidad y otras especies ligadas a la vegetación que construyen sus nidos en plantas que son directamente destruidas por la acción del fuego. Las zonas no quemadas o los recursos que resisten al fuego o que no han sido afectados por este de las zonas quemadas también pueden actuar como refugios para la fauna (New, 2014; Parr & Andersen, 2006).

Segundo, el tipo de vegetación anterior al fuego, así como la identidad y diversidad de las plantas que crecen en el área quemada y que ofrecen recursos directos y / o indirectos a las hormigas y abejas, son factores que determinan la capacidad de persistencia de las comunidades de ambos taxones (Arnan et al., 2019, 2009, 2007, 2006). En las hormigas, se ha demostrado una baja mortalidad de colonias de la especie *Aphaenogaster gibbossa* contra los efectos indirectos del fuego, probablemente debido a una mayor exposición solar, como consecuencia de una reducción en la cobertura vegetal o una modificación de la disponibilidad de alimentos después del fuego (Caut et al., 2014). Por otro lado, las abejas incluyen una amplia gama de especialización polínica, y cambios post-fuego en la composición florística pueden ocasionar cambios en la dieta de las especies supervivientes, afectando su éxito reproductor de manera positiva o negativa (Potts et al., 2003).

Y tercero, la colonización por nuevas especies, o recolonización por las especies que estuvieron presentes antes del incendio desde las zonas no quemadas, está condicionada por la capacidad de dispersión de éstas (Pausas & Parr, 2018). En las hormigas, la distancia de dispersión está relacionada con el modo de fundación de las nuevas colonias, que puede realizarse de forma independiente por una reina voladora (larga distancia) o de manera dependiente por un grupo de hormigas no voladoras (corta distancia; Amor et al. 2011). Sin embargo, en las abejas la dispersión solo está relacionada con la capacidad de vuelo, que es proporcional al tamaño corporal de las especies (Guédot et al., 2009). Por otro lado, la mayoría de especies de arañas en sus estadios juveniles se ven favorecidas por el uso de ‘ballooning’, mediante el cual se dejan arrastrar por hilos de seda por corrientes aéreas recorriendo grandes distancias de forma pasiva (Bell et al., 2005). Y esto unido a la alta movilidad a través de la superficie del suelo por parte de los adultos de vida epigea, las hacen buenas colonizadoras de zonas quemadas como ya se ha puesto de manifiesto anteriormente (Moretti et al., 2002). En resumen, en un escenario post-fuego, podemos encontrar una combinación de especies locales que han sobrevivido al incendio y persisten en las nuevas condiciones, y otras especies que, atraídas por los recursos disponibles, colonizan o recolonizan el área quemada procedentes de áreas no quemadas.

Diversos estudios realizados en diferentes zonas de Europa, han revelado efectos muy diversos de los incendios sobre la abundancia, riqueza y diversidad de hormigas, abejas y arañas (Arnan et al., 2006; Bogusch et al., 2015; Larrivée et al., 2008; Moretti et al., 2002). La abundante literatura centrada en la respuesta de las comunidades de hormigas a los incendios forestales muestra una respuesta muy variable, dependiendo del tiempo transcurrido tras el incendio, la vegetación o la dimensión estudiada (taxonómica, funcional o filogenética). A corto plazo (0-4 años) la mayoría de los estudios reportan un efecto negativo o nulo del fuego sobre las comunidades de hormigas, con valores más bajos de abundancia, riqueza, diversidad, riqueza funcional y dispersión funcional en áreas quemadas en comparación con áreas no quemadas (Rodrigo & Retana 2006; Underwood & Quinn 2010; Matsuda et al., 2011; Pryke &

Samways 2012b, a; Beaumont et al., 2013; Caut et al., 2014; Santos et al., 2014; Yekwayo et al., 2018; Vidal-Cordero et al., 2022; Khayati et al., 2023). Sin embargo, también se ha descrito una mayor abundancia de hormigas en zonas quemadas de pinar y robledal, un año después del incendio (Bishop et al., 2021). Asimismo, estudios realizados durante un periodo de tiempo más largo (hasta 41 años después del incendio) informan de un efecto positivo del fuego sobre las comunidades de hormigas, con valores más altos de abundancia, riqueza y diversidad taxonómica, funcional y filogenética en áreas quemadas en comparación con áreas no quemadas (Arnan et al., 2006, 2020; Izhaki et al., 2009; Gosper et al., 2015; Kaynaş et al., 2018; Vidal-Cordero et al., 2023; Khayati et al., 2023).

En el caso de las abejas, la mayoría de los estudios que tratan sus respuestas taxonómicas de estas a los incendios coinciden en la confirmación de un aumento en la abundancia, riqueza y diversidad de especies debido al aumento en los recursos florales que generalmente se originan en los primeros años después de un incendio (Campbell et al., 2007; Grundel et al., 2010; Moretti et al., 2009; Potts et al., 2003).

Por último, en las arañas también podemos encontrar diferentes respuestas de carácter taxonómico frente al fuego. Moretti et al. (2002) demuestra como el fuego afecta la composición de la comunidad de arañas de los Alpes suizos encontrando un aumento de la riqueza y diversidad durante los dos primeros años tras el fuego y poniendo de manifiesto la gran capacidad de recuperación de las comunidades de arañas. Sin embargo, Underwood & Quinn (2010) observan que la abundancia total de arañas en bosques de quercíneas de California no se ve afectada inmediatamente después del incendio, sino con el transcurso del tiempo durante el primer año debido posiblemente a una disminución de los niveles de presas, el movimiento de estas fuera de las zonas quemadas o en profundidad en el suelo, o la mortalidad frente condiciones ambientales post-fuego.

Sin embargo, no abundan los trabajos que han podido analizar simultáneamente la diversidad taxonómica y funcional en respuesta al fuego (Morelli et al., 2018), destacando los llevados a cabo con hormigas en España (Arnan et al., 2020, 2019, 2013), abejas y escarabajos en Israel y Suiza, respectivamente (Moretti et al., 2010, 2009) y saltamontes en Brasil (Ferrando et al., 2016). El estudio realizado en Israel, por ejemplo, sugiere que las condiciones posteriores al incendio inducen un aumento en la abundancia y una disminución en la diversidad taxonómica de abejas, manteniendo la diversidad funcional (Moretti et al., 2009). No obstante, aún existe mucho desconocimiento acerca de cómo la capacidad de una especie para sobrevivir, persistir o colonizar las áreas quemadas puede verse afectada por características funcionales como el tamaño de las colonias, el tipo de dieta (especialista o generalista), el tamaño corporal, etc.

Toda esta falta de conocimiento y la gran variabilidad en las respuestas de las hormigas, abejas y arañas al fuego es, en parte, debida a las dificultades existentes en el estudio del impacto de los incendios en los insectos. New et al. (2010), enumera una serie de limitaciones de este tipo de estudios para los invertebrados australianos que podrían aplicarse a una alta proporción de estudios llevados a cabo en diferentes zonas del mundo. De entre ellas caben destacar, (1) un enfoque mayoritario en los taxones activos en el suelo, utilizando principalmente trampas de caída como único método de muestreo; (2) duración de muestreos relativamente corta, generalmente de 3 años o menos; (3) un carácter oportunista, muchos de ellos simplemente recopilan datos después de un incendio en lugar de examinar hipótesis con muestreos anteriores y posteriores al incendio y/o sitios de control válidos; (4) la falta de datos previos y posteriores al incendio en las zonas de estudio, incluidos los datos de las zonas no quemadas; (5) una determinación de los insectos muestreados solo a altos niveles taxonómicos, como familias u órdenes, en lugar de determinaciones a niveles de especies/morfoespecies o géneros; (6) con antecedentes muy incompletos sobre suelos, vegetación, topografía, datos de carácter bioclimático; (7) falta de información sobre la intensidad del incendio y otras componentes del régimen, como la extensión y la gravedad; y (8) muestreos de áreas con un historial de incendios incompleto (o desconocido).

Objetivos

El objetivo general de la presente Tesis Doctoral es investigar las respuestas al fuego de las comunidades de tres grupos taxonómicos de artrópodos, hormigas, abejas y arañas, utilizados frecuentemente como indicadores de la salud de los ecosistemas. Los diferentes estudios se llevaron a cabo en sistemas mediterráneos de coníferas con objeto de homogeneizar el tipo de hábitat y así reducir la variación en las respuestas. Se estudiaron diferentes tipos de respuesta, a diferentes escalas relacionadas entre sí, con los siguientes objetivos y predicciones específicas:

A.- Respecto a las variables de respuesta al fuego, se diferencian tres tipos de respuestas:

> A.1.- Se analiza tanto la estructura (mediante el uso de índices de diversidad), como la composición taxonómica de las comunidades de artrópodos seleccionadas. Varias hipótesis son posibles en este escenario. En la mayoría de los casos, se espera una disminución en la diversidad taxonómica en las zonas afectadas por el fuego por la pérdida de aquellas especies ligadas a la vegetación. Alternativamente, puede ocurrir un aumento en la diversidad taxonómica por la incorporación de nuevas especies ante la apertura de nuevos hábitats abiertos en lo que antes eran pinares. Asimismo, se esperan diferencias en la composición taxonómica de las comunidades entre zonas quemadas y no quemadas.
>
> A.2.- También se analiza la estructura y composición funcional de las comunidades de artrópodos. En la misma línea que el objetivo anterior, se espera una disminución de la diversidad funcional en las zonas afectadas por el fuego por la pérdida de funciones asociadas con el estrato arbóreo, o bien, una ganancia de nuevas funciones debido a la mayor disponibilidad de zonas abiertas sin vegetación, con un efecto de filtrado del fuego en los rasgos de historia de vida de las especies más asociadas a zonas abiertas.
>
> A.3.- En las comunidades de hormigas, se analiza las respuestas al fuego en relación a la jerarquía de dominancia. Se esperan cambios en las interacciones

entre especies, a nivel de las relaciones entre dominantes y subordinadas, debido a las diferencias de temperatura en el suelo tras el incendio, como consecuencia de una modificación en la cobertura vegetal.

B.- En relación a las escalas analizadas, se diferencian dos tipos de escalas: la taxonómica, con los tres grupos de artrópodos citados; y la temporal, con zonas afectadas por incendios que se analizan en diferentes tiempos desde la aparición del fuego. Asimismo, se discute la escala espacial, la cual no se ha abordado directamente.

B.1.- Respecto a la escala taxonómica, se comparan las comunidades de tres grupos taxonómicos de artrópodos, de forma pareada (hormigas-arañas y hormigas-abejas), siendo las hormigas el grupo de referencia. Se esperan diferencias en la resistencia y resiliencia de cada grupo al fuego, que variarán atendiendo a las características de la historia de vida y rasgos funcionales de las especies que componen las comunidades de cada grupo. Por ello, se esperan diferencias entre los grupos taxonómicos, tanto en las respuestas de carácter taxonómico, como funcional al fuego.

B.2.- En consideración a la escala temporal, se compara tanto el efecto del fuego a corto plazo (de 0-4 años), como en una escala temporal más amplia (de 0-41 años desde el evento del fuego). Se espera un cambio en las variables de respuesta al fuego a corto plazo, que se recuperarán a medio y/o largo plazo, conforme los cambios en la vegetación vayan alcanzando las condiciones previas al incendio. Alternativamente, el fuego podría tener efectos que no se recuperen en los plazos de tiempo estudiados.

B.3.- En cuanto a la escala espacial, se estudian zonas afectadas por incendios ocurridos en pinares de zonas concretas de la Península Ibérica: 35 incendios en Andalucía, un incendio en Cataluña y un incendio en Portugal. En todos ellos, se comparan zonas quemadas y zonas no quemadas, o control, utilizando una aproximación de substitución del espacio por el tiempo. Esto permite reducir los componentes de variación espacial que pueden venir dados por el tipo de hábitat, la geografía, el tipo de suelo o el clima, entre otros. El estudio del efecto de esos otros componentes espaciales a la recuperación de los incendios en pinares mediterráneos está fuera de los objetivos de la presente tesis, aunque se tienen en cuenta (como covariables en los modelos) cuando se comparan incendios ocurridos en una escala espacial amplia (como los de Andalucía).

Sistema de estudio

Todo el trabajo de campo ha sido llevado a cabo en pinares afectados por incendios forestales y sus respectivos controles en Portugal y España. El trabajo de campo del objetivo específico 1 se desarrolló en el pueblo de Belver, Gavião (distrito de Portalegre), en el centro de Portugal (N 39°32, O 7°59, 221 m sobre el nivel del mar); el objetivo específico 2 se desarrolló en la localidad de Salo (Cataluña), al noreste de España (N 41°52, E1°38′, 540-620 m sobre el nivel del mar); para trabajo de campo del objetivo específico 3 se utilizaron 35 zonas de estudio distribuidas por la comunidad autónoma de Andalucía, al sur de España (Figura 4); y por último, el objetivo específico 3 se desarrolló en tres de las zonas de estudio del capítulo 2, localizadas en la provincia de Huelva, al suroeste de España (N 37°40'N, O7°00) (Figura 5).

El clima en todas las zonas de estudio es típicamente Mediterráneo con inviernos suaves y veranos calurosos. El suelo de las zonas de estudio se encuentra representado por una gama de paisajes litorales de suelos arenosos a paisajes rocosos de suelos pizarrosos, graníticos, con gravas, etc., dependiendo de la altitud la que se encuentren, oscilando desde los 10 m a los 1507 m por encima del nivel del mar. Las zonas de estudio se componen de bosques de coníferas (*Pinus pinea*, *Pinus pinaster*, *Pinus nigra* y *Pinus halepensis*) con un sotobosque compuesto de arbustos mediterráneos típicos, incluyendo *Salvia rosmarinus*, *Thymus vulgaris* y *Lavandula* spp principalmente, que puede incluir otras especies arbustivas, como por ejemplo, *Rhamnus alaternus*, *Pistacea lentiscus*, *Juniperus oxycedrus*, *Erica australis*, *Chamaerops humilis* y diferentes especies de los géneros *Cistus* y *Ulex* y una amplia variedad de plantas herbáceas (principalmente de la familia *Apiaceae*, *Asteraceae* y *Poaceae*) dependiendo de la ubicación de la zona de estudio.

Los motivos por los cuales se han elegido los bosques de coníferas como sistemas de estudio son: (1) Los pinos constituyen un grupo de especies muy diverso que presentan una gran variedad de adaptaciones a los incendios ya que muchos de ellos viven en zonas propensas a estos (Keeley, 2012; Schwilk & Ackerly, 2001); (2) la representativa abundancia que tienen los sistemas de coníferas del género *Pinus* en la Península Ibérica, especialmente en Andalucía, desde la implantación de monocultivos como consecuencia de las plantaciones masivas propias del SXX con objeto de evitar la erosión del suelo, obtener recursos de ellos o crear un ambiente forestal agradable entre otros (Bravo et al., 2011); y (3) estas plantaciones masivas de *Pinus* se caracterizan por presentar una baja biodiversidad al no compartir el hábitat con muchas especies vegetales, lo cual hace que las diferentes zonas de estudio sean más homogéneas y fácilmente comparables (Andrés & Ojeda, 2002; Barbaro et al., 2016).

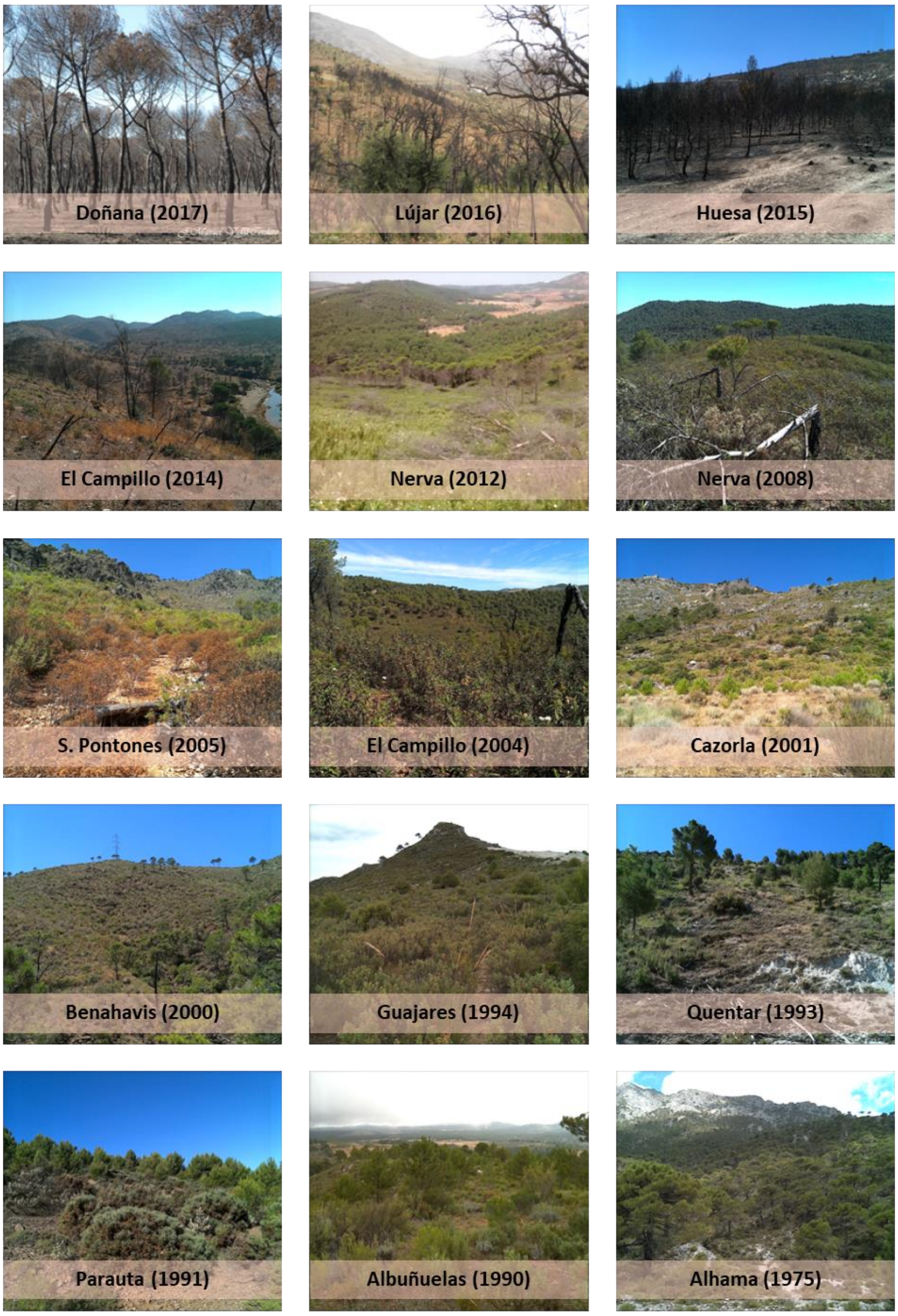

Figura 4. Algunas de las zonas de estudio ordenadas por el año en el que tuvo lugar el incendio (del más reciente al más antiguo).

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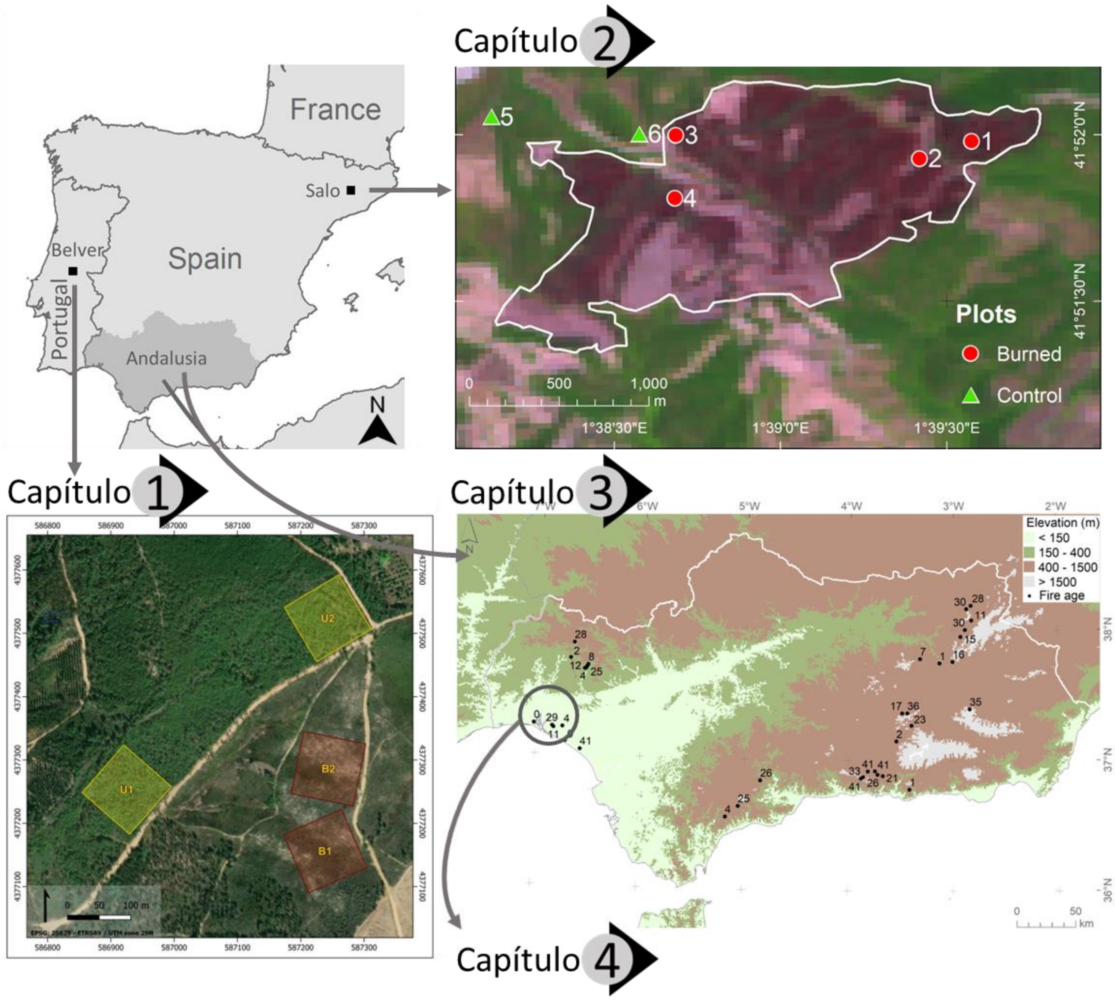


Figura 5. Descripción de las áreas de estudio ordenadas por el tiempo transcurrido desde el incendio. Localidad, provincia, elevación (Elev) y coordenadas geográficas asociadas al área de estudio. *Pinus* sp. indica la principal especie de conífera en el bosque.

Estructura de la Tesis Doctoral

Además de la introducción general, los objetivos, el sistema de estudio, una discusión general y unas conclusiones generales, la presente Tesis Doctoral consta de cuatro capítulos. Los Capítulos 2 y 3 han sido recientemente publicados en revistas de alto prestigio científico, el Capítulos 1 se encuentra enviado a otra revista internacional indexada, y el Capítulo 4 se encuentra en preparación. A continuación, se detalla el contenido y finalidad de cada uno de los capítulos (Figura 6).

En el **Capítulo 1** (*When you lose in hake, but gain in herring: Portfolio effects in ant communities recovering after fire in a pine dominated Portuguese landscape*) se examina el efecto del fuego sobre la estructura y la composición taxonómica de las comunidades de hormigas de una zona afectada por el incendio de Belver (Portalegre, Portugal) de 2017, cuatro años después de que ocurriera dicho incendio, en los meses de mayo, julio y octubre.

En el **Capítulo 2** (*Four-year study of arthropod taxonomic and functional responses to a forest wildfire: ants and epigeic spiders are affected differently*) se estudia el efecto del fuego sobre la diversidad taxonómica y funcional de las comunidades de hormigas y arañas epigeas de una zona afectada por el incendio ocurrido en la localidad de Salo (Cataluña, España) durante cuatro años consecutivos tras el incendio en los meses de mayo, julio y septiembre.

En el **Capítulo 3** (*Long-term recovery of Mediterranean ant and bee communities after fire in southern Spain*) se evalúa el efecto del fuego sobre la diversidad taxonómica y funcional de las comunidades de hormigas y abejas de 35 zonas afectadas por incendios localizados en las provincias de Huelva, Málaga, Jaén y Granada (Andalucía, España) a lo largo de una cronosecuencia (14 días - 41 años de antigüedad).

Finalmente, en el **Capítulo 4** (*Behavioural-dominance relationships after wildfires in southern Spain ant communities*) se describen las relaciones de dominancia ecológica y comportamental existentes en las comunidades de hormigas de tres áreas quemadas de diferente antigüedad (1, 3 y 5 años) en Huelva (Andalucía, España) y sus respectivos controles.

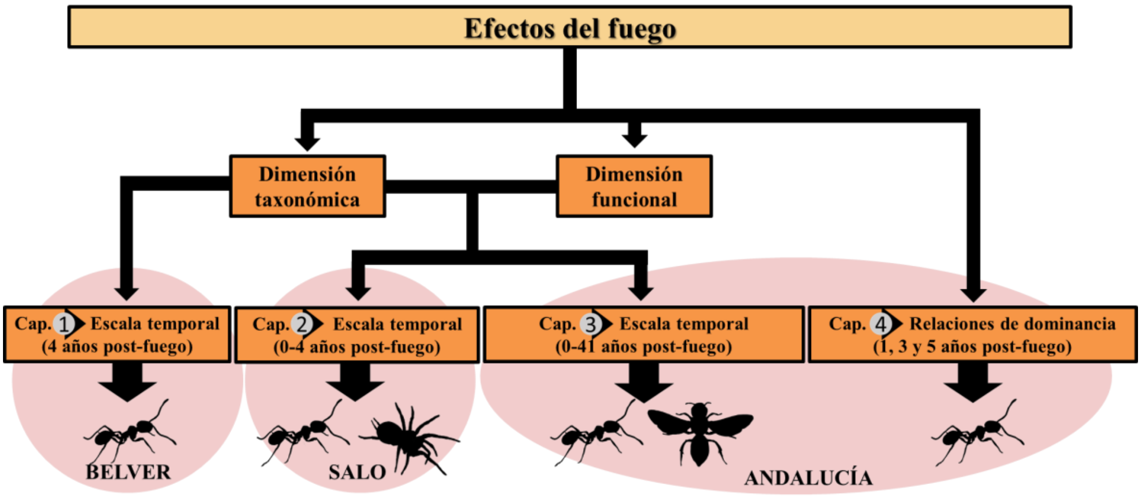
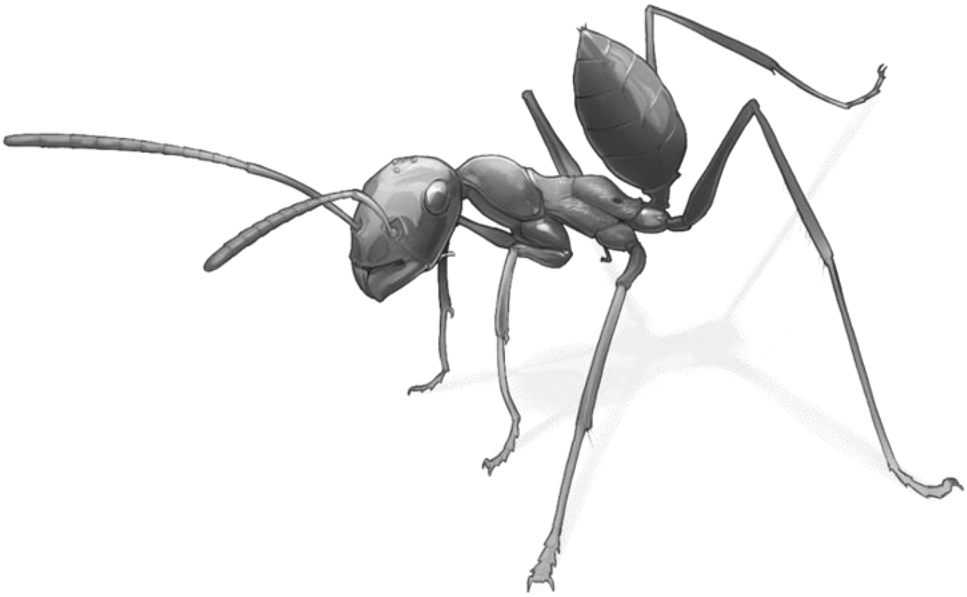


Figura 6. Esquema ilustrativo en el que se resumen los objetivos de la presente Tesis Doctoral y se señalan las distintas escalas utilizadas para el estudio de los efectos del fuego.

Capítulo 1

When you lose in hake, but gain in herring: Portfolio effects in ant communities recovering after fire in a pine dominated Portuguese landscape



Oliveira, D., Vidal-Cordero, J.M., Angulo, E., Gracia, L., Caro de la Barrera, C., Broggi, J. and Cerdá, X., (submitted) When you lose in hake, but gain in herring: Portfolio effects in ant communities recovering from fire in a pine dominated Portuguese landscape. Journal of Insect Conservation.

Resumen

Las hormigas están presentes en prácticamente todos los ecosistemas terrestres y pueden utilizarse como bioindicadores fiables. Ejemplo de ello, es en el caso de la evaluación de la recuperación de las comunidades bióticas tras una perturbación importante. Aquí evaluamos la respuesta de las comunidades de hormigas a un incendio de copa en un bosque mediterráneo de coníferas, cuatro años después de la perturbación. Nuestros resultados mostraron que, aunque la mayoría de los índices de diversidad taxonómica explorados (ocurrencia, riqueza y diversidad) no experimentaron diferencias significativas entre las áreas quemadas y no quemadas, la composición taxonómica de las comunidades de hormigas fue diferente cuatro años después del incendio. Los resultados muestran que los incendios forestales promovieron la sustitución de especies arbóreas de hormigas por otras mejor adaptadas a hábitats abiertos. Los índices taxonómicos, como la riqueza o la diversidad, pueden ser malos indicadores de la recuperación a medio plazo de las comunidades de hormigas tras un incendio forestal. Sugerimos que el uso de las comunidades de hormigas como bioindicador de la recuperación tras un incendio debería incluir un seguimiento continuo y a largo plazo de las comunidades de hormigas y de la cubierta vegetal, desde el año de la perturbación, además del uso de índices de diversidad distintos a los meramente taxonómicos.

Abstract

Ants are prevalent in practically all land ecosystems and can be used as reliable bioindicators. Such is the case for the assessment of biotic communities' recovery after a major disturbance. Here we evaluated the response of ant communities in a Mediterranean coniferous forest to crown wildfire, in a snapshot on the fourth year after disturbance. Our results showed that although most of the taxonomic diversity indices explored (occurrence, richness, and diversity) did not experience significant differences between burned and unburned areas, the taxonomic composition of the ant communities was different four years after fire. The results show that wildfire promoted the replacement of ant arboreal species with those better adapted to open habitats. Taxonomic indexes, such as richness or diversity may be poor indicators of medium-term recovery of the ant communities after wildfire. We suggest that using ant communities as bioindicator of recovery after fire should include a continuous, long-term monitoring of ant communities and vegetation cover, since the year of disturbance, and the use of diversity indices other than merely taxonomic.

Introduction

Natural disturbances, such as storms, floods, drought, and wildfires, can greatly impact the structure and function of ecosystems (Thom and Seidl, 2016). In Mediterranean forests, wildfires are particularly prevalent and, because they change the overall structure of the habitat, they can alter not only the animal communities that live there but also ecosystem processes, such as energy or nutrient flow (Pausas and Fernández-Muñoz, 2012). However, Mediterranean forests are prone to wildfires (Keeley et al., 2011), and when the forest is burned the remaining habitat provides favorable conditions for fire specialist species to develop, and with time leading to ecological succession to a final full recovery (Barros et al., 2018; Hutto, 2008; Hutto et al., 2016). However, over the last decades human activity has led to disturbed fire regimes, particularly in areas where agricultural land and forests were abandoned, leading to an increase in fire frequency and extension that alters ecological succession and promotes land erosion with unpredictable outcomes (Pausas and Fernández-Muñoz, 2012; Puerta-Piñero et al., 2012).

Continental Portugal is a region naturally prone to fire due mostly to its dry and hot summer climate (Pereira et al., 2006, p. 20). Additionally, socio-economic changes in its recent history led to the abandonment of agricultural fields, subsequently encroached on by shrublands or replaced by, mostly, conifer or eucalyptus forests/plantations (Moreira et al., 2009, 2001). In fact, from 1995 to 2015, the area occupied by forests of various eucalyptus species and stone pine (*Pinus pinea* L.) has increased from 717 200 ha to 845 000 ha and from 120 200 ha to 193 600 ha, respectively, while shrubland has increased from 2539 600 ha to 2766200 ha (ICNF, 2015). As in other Mediterranean regions, these extensive coniferous forests are systems with high stand and tree cover density, therefore presenting sparse shrub and herbaceous strata, which increases the risk for wildfires (Chergui et al., 2019, 2018). Furthermore, these newly forested landscapes present little or poor management, leading to the accumulation of combustible material (Fernandes et al., 2011; Meira Castro et al., 2020), which, coupled with increasing of global temperatures and reduced precipitation, exacerbates the potential for frequent and rapidly spreading wildfires (Ferreira-Leite et al., 2013) as in other Mediterranean regions (Pausas, 2004; Pausas and Fernández-Muñoz, 2012; Piñol et al., 1998).

Ants (Hymenoptera: Formicidae) are particularly suitable taxa to use as bioindicators due to their abundance and diversity in terrestrial ecosystems (Moretti et al., 2002; Pearce and Venier, 2006; Stephens and Wagner, 2006; Zhang, 2015). In a recent meta-analysis wildfires have been shown to have a negative impact on ant diversity, but not on their abundance. In addition, the effect of fire depended on the study ecosystem, with tropical ecosystems being the most affected compared to other ecosystems, such as savannahs or deserts. Likewise, wildfire impact on ant diversity was most severe the rarer the phenomenon (Vasconcelos et al., 2017).

In Mediterranean ecosystems, forest fires are a dominant ecological factor (Bowman et al., 2009). The abundant literature focusing on the response of ant communities to wildfire in the Mediterranean region shows a highly variable response, depending on the time elapsed after the fire, the vegetation, or the dimension studied (taxonomic, functional or phylogenetic) (Table 1). In the short term (0-4 years) most studies report a negative effect of fire on ant communities with lower values of abundance, richness, diversity, functional richness and functional dispersion in burned areas compared to unburned areas (Beaumont et al., 2013; Caut et al., 2014; Khayati et al., 2023; Matsuda et al., 2011; Pryke and Samways, 2012a, 2012b; Rodrigo and Retana, 2006; Santos et al., 2014; Underwood and Quinn, 2010; Vidal-Cordero et al., 2022; Yekwayo et al., 2018). However, a higher abundance of ants has also been reported in burned areas of pine and oak forest, one year after fire (Bishop et al., 2021). Likewise, studies conducted over a longer period of time (up to 41 years after the fire) report a positive effect of fire on ant communities with higher values of abundance, richness and taxonomic, functional and phylogenetic diversity in burned areas compared to unburned areas (Arnan et al., 2020, 2006; Gosper et al., 2015; Izhaki et al., 2009; Kaynaş et al., 2018; Khayati et al., 2023; Vidal-Cordero et al., 2023, 2022), but see Arnan et al. (2006). Generally, species associated with tree vegetation are more likely to be negatively affected by wildfires. As a result, burned and unburned areas have different types of species, more typical of open areas after fire and species more associated with vegetation cover and trees in unburned areas (Arnan et al., 2013; Vidal-Cordero et al., 2023).

The lack of clear trends in the impact of wildfire on ant communities’ challenges conservation action, a situation that needs urgently to be reverted. Here we evaluated the effect of fire on the structure and taxonomic composition of the ant community in a

Mediterranean forest in southwestern Portugal, four years after the fire occurred. We compared the ant community of a burned area with a nearby unburned area in spring, summer and autumn. We hypothesize that: 1) four years are not enough time for the structure of the ant communities to recover (specifically, occurrence values, species richness and taxonomic diversity will be lower in burned areas than in unburned areas), and 2) the taxonomic composition of ant communities will be affected by fire, with open-area’ species being more abundant in burned areas, and species more closely linked to vegetation in unburned areas.

Table 1. Literature on the impact of fire on ant communities in Mediterranean areas, separating the taxonomic and the functional effects. The “Variable” is the parameter of the ant community examined, and it corresponds to: “Ab” abundance, “S” richness, “H” diversity, “J” eveness, “CC” community composition, “FRic” functional richness, “FEve” functional eveness, “FDis” functional dispersion, and “FDiv” functional divergence. The response to fire is quoted as “Increase”, “Decrease” and “ns”, when the variable increased or decreased after time, or when there was no significant relationship detected with fire, respectively; “increase at the long term”, means that there is no effect of time; “*” means there is an interaction between “Fire” or “Type of fire” and “Time”; “Fire” means the fire changes the variable; “Different patterns” indicates that fire caused different effects in the ant traits examined. Time since fire indicates when the study was performed in relation with the fire occurrence: when there was a yearly continuous monitoring or time since fire was a continues variable in year it is noted as (T_i-T_f)y, where T_i is the first year of study since fire occurred and T_f is the last year of monitoring. If the study was a snapchot in an specified time since fire, then Ty is noted, where Ty is the number of years since fire when the study was carried out. Location indicates the place or region in which the fires occurred and the country. “Days” indicates the number of days the pitfall traps were open. “Sampling frequency” details how many times the sampling was carried out (“once” or a number of years), when, and describes the intra-year measures when necessary.

Reference	Var	Response to fire	Time since fire	Location	Days	Sampling frequency
Taxonomic effects						
Adams et al. 2018	S	Fire*Time	pre- 1y	California, USA	14d	2 years, [before and after prescribed fire]
Underwood and Quinn, 2010	Ab	Increase	0-1y	California, USA	32d	Once, 13 intra-annual measures
Bishop et al. 2021	Ab Occ S J CC	Increase Increase Increase ns Fire	1y	northwestern Peloponnese, Greece	7d	Once, in June
Caut et al. 2014	Ab	Different individual spp. response	1y	Catalonia, Spain	3d	Once, in June
Matsuda et al. 2011	H CC	Decrease Fire (only 1 habitat)	2-3y	California, USA	10d	2 years, 2 intra-annual measures
Pryke & Samways 2012b	Ab S CC	Increase ns Fire	3m, 1y, 3y	Cape Peninsula, South Africa	7d	3 years

Pryke & Samways 2012a	Ab	ns	1y, 3y	Cape Peninsula, South Africa	7d	2 years
	S	ns				
El Khayati et al. 2023	Ab	ns	3y	Ceuta, northern Africa	6d	Once, 2 intra-annual measures
	CC	Fire				
Vidal-Cordero et al. 2022	Occ	ns	0-4y	Catalonia, Spain	7d	4y*3 intra-annual measures
	S	Decrease				
	H	Decrease				
	J	ns				
	CC	Fire				
Present study	Occ	ns	4y	Belver, Portugal	1d	Once, 3 intra-annual measures
	S	ns				
	H	ns				
	J	Fire*Time				
	CC	Fire				
Santos et al. 2014	S	ns	4y	Catalonia, Spain	15d	Once, 2 intra-annual measures
	J	ns				
	CC	Fire				
Beaumont et al. 2013	Ab Occ	Increase of seed dispersing species	3y, 4y, 5y	Mount Lofty Ranges, south Australia	4d	Once, in summer [prescribed fires]
	dist	Similar seed relocation distances				
Yekwayo et al. 2018	Ab	Increase (1y)	3m, 1y, 7y	Western Cape, South Africa	7d	Once, 2 intra-annual measures
	S	ns				
	H	ns				
	CC	Fire*Time				
Arnan et al. 2006	Ab	Increase	8y	Catalonia, Spain	7d	Once, 2 intra-annual measures
	S	ns				
	H	Decrease				
Arnan et al. 2020	β-diversity	Increase	8y	Catalonia, Spain	7d	Once, 2 intra-annual measures
Khayati et al. 2023	Ab	Increase	5-9y	northern Morocco	6d	Once, 2 intra-annual measures
Izhaki et al. 2009	S	Increase	1y, 14y	Mount Carmel, Israel	3d	2 years, 2 intra-annual measures
Rodrigo and Retana 2006	Ab	Increase at the time	1y, 5y, 13y, 19y	Catalonia, Spain	9-11d	Once, 2 intra-annual measures
	S	Increase at the time				
	H	ns				
Vidal-Cordero et al. 2023	Ab	Increase at the long-term	0-41y	Andalusia, Spain	2d	Once, in summer
	S	Increase at the long-term				
	H	Increase at the long-term				
	J	ns				
	CC	Fire*Time				
Kaynas et al. 2018	Ab	Increase in 9y and 26y	3y, 6y, 9y, 16y, 26y, >50y	Marmaris, Turkey	15-30d	Once, 8 intra-annual measures (March-October)
	S	Increase at the long-term				
	H	Increase at the long-term				
Gosper et al. 2015	Ab	ns	0-300y	southwestern Australia	2d	Once, in spring
	S	ns				
	J	Time since fire				
	CC	ns				
Functional effects						
Bishop et al. 2021	Ab	Increase	1y	northwestern Peloponnese, Greece	7d	Once, in June
	Occ	Increase				
	Traits	Different patterns				
	CC	Fire				
Vidal-Cordero et al. 2022	FRic	Decrease	0-4y	Catalonia, Spain	7d	4years * 3 intra-annual period
	FEve	ns				

	FDis CC	Decrease, Fire*Time Fire*Time				
Arnan et al. 2013	FD 12 traits	Increase Different patterns	8y	Catalonia, Spain	7d	Once, 2 intra-annual measures
Arnan et al. 2020	β-diversity	Increase	8y	Catalonia, Spain	7d	Once, 2 intra-annual measures
Vidal-Cordero et al. 2023	FRic FEve FDis FDiv CC 13 traits	ns ns ns Decrease ns Different patterns	0-41y	Andalusia, Spain	2d	Once, in spring-summer
Gosper et al. 2015	Functional groups	Different patterns	0-300y	southwestern Australia	2d	Once, in spring

Materials and methods

Study site

This work was conducted near the village of Belver, Gavião (Portalegre district), in central Portugal (N 39°32, O 7°59, 221 m above sea level; Fig.1A). This area has a typical Mediterranean climate - Csa on the updated Köppen-Geiger climatic classification (Beck et al., 2018) -, with mean annual temperature and rainfall of 17.14 °C and 693.61 mm, respectively. The study site comprised a mosaic of agricultural areas, transitional woodland-shrubland areas and coniferous forests, that had a relatively dense understory and a broad variety of herbaceous plants. The maritime pine (*Pinus pinaster* Aiton) is the locally dominant pine species in the area, showing high resistance to fires and adaptations for post-fire recovery (Fernandes et al., 2008, 2005; He et al., 2012; Ribeiro et al., 2022).

In July 2017, a crown wildfire burned through the area, ravaging 1203 ha of land (composition: 24% forest, 43% transitional woodland-shrubland, and 33% agricultural areas). We performed our study in two areas separated by ~500m.The burned area was treeless, and had been colonized by dense shrubland composed by diverse species (*Cistus* spp.; *Genista* spp; *Ulex* spp.) and some young cork-oak *Quercus suber* L. trees (hereafter Burned area). The control area was composed by a dense maritime pine forest (hereafter Unburned area, Fig.1B). There was no post-fire treatment in the affected area, such as tree felling or wood extraction, so abundant decaying wood from fallen trunks and branches of burned was spread all over the burned area, with few burned pine trees still standing.

To characterize the structure of the vegetation in the study areas, we established two 50 m-transects at each of the burned and unburned areas; within an area, the two transects were separated by at least 200 m and were parallel (1 m) to the pitfall trap transects (see below). The transects were 75 m long and 2 m wide. In May 2021, we recorded the presence or absence of four strata every five meters: herbaceous plants (0.5 m of height), small shrubs (0.5-1.5 m), large shrubs (1.5-2.5 m), and trees, noting species identity. Later, we calculated the value of a vegetation cover index for each transect using the presence/absence data. This value ranged between 0 and 100%, where 100% meant the four strata were present at all fifteen sampling points, while 0 meant the four strata were absent at all fifteen sampling points.

Ant sampling

Sampling of ants was conducted in May, July and October of 2021. To capture epigeic ants, we resorted to pitfall traps, one of the most commonly used and straightforward methods (Agosti et al., 2000; Jiménez-Carmona et al., 2020; Ward et al., 2001). These traps were 220-cm^3 plastic cups (70 mm in diameter, 95 mm deep) that were 2/3 filled with soapy water. We sampled 4 plots (2 burned plots and 2 unburned plots separated at least 200 m in each area). Each plot was 100m^2 in where 20 pitfall traps were placed along two transects separated by least 50 m. (20 traps x 4 plots). Each transect contained 10 pitfall traps at 5 m intervals (Fig.1C).

Pitfall traps were run for 24h. Any biological material captured was stored in 70% alcohol until identification could occur. Ants were sorted out from the rest of the invertebrates and identified to species level using Gómez and Espadaler's keys for the ants of the Iberian Peninsula (2007) and Fauna Ibérica: Formicidae (Tinaut & Martínez, unpublished).

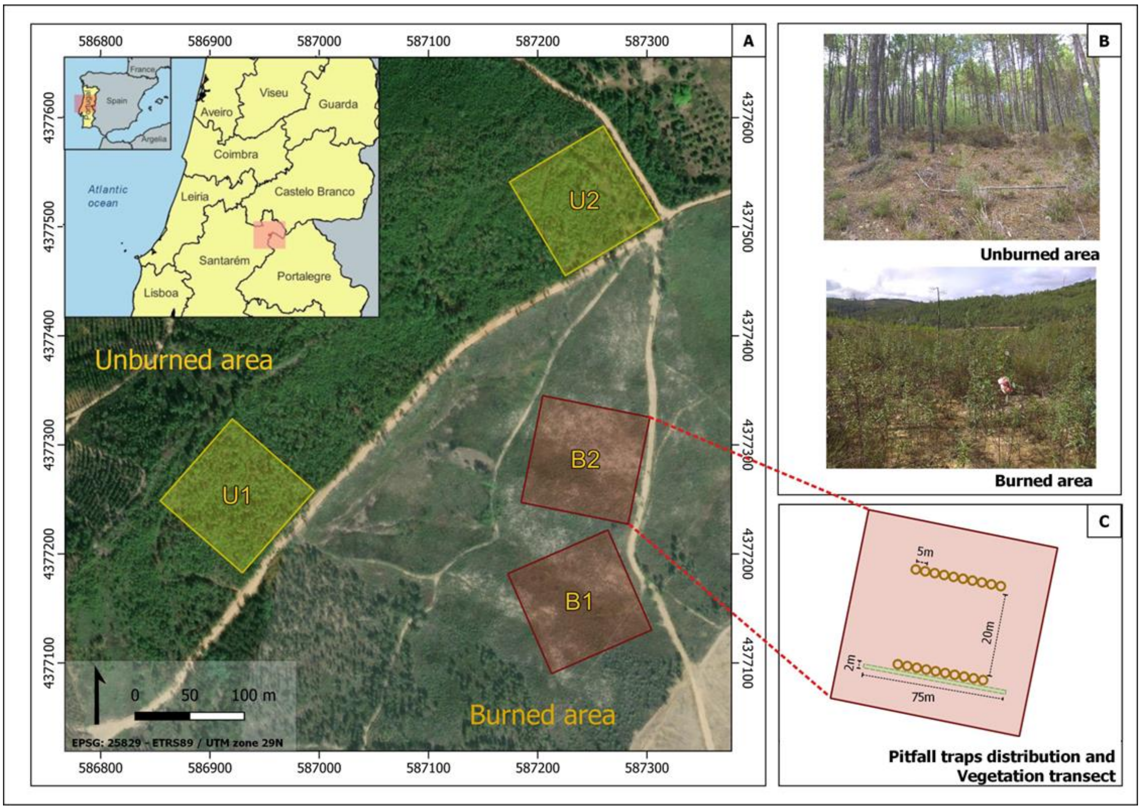


Figure 1. Visualization of the study area: A – aerial view of the study area and the four plots (U1, U2: unburned plots; B1, B2: burned plots); B – photographs of unburned and burned plots at the time of sampling (i.e., 3 years after fire); C – schematic representation of pitfall trap placement within a plot.

Data and statistical analysis

All the analyses were performed using R (v. 4.1.3; R Core Team 2022). First, we explored vegetation differences between the burned and unburned areas. We carried out five linear mixed-effect models using the *lme* function in the *nlme* package (Pinheiro, 2023). The dependent variables of these models were the four plant cover estimates for each stratum (herbs, small shrubs, large shrubs and trees), and the vegetation cover. Mean presence of each stratum across the ten sampled points of each transect was used. The independent variable was the fire, with two categories: burned and unburned. Plot identity was included as a random factor that accounted for the covariance of the two plots sampled on each area. The results of the models were then analyzed using the ANOVA method after the sequential BH/FDR correction (*anova* function and *p.adjust* function with the *fdr* method , respectively, in the *stats* package; Benjamini and Hochberg, 1995).

Second, we compared ant richness between the burned and the unburned plots by calculating abundance-based rarefaction curves for the three sampling months using *specaccum* function in the the *vegan* package (Oksanen et al., 2018).

To analyze the taxonomic structure and composition of ant communities, we calculated species occurrence, defined as the number of traps in which a species occurred per plot and sampling period. The use of occurrence instead of abundance was chosen to avoid any potential bias that could result from the pitfall traps being close to ant trails/ant nests. Then, we calculated taxonomic richness (S) - the number of ant species observed-, the Shannon diversity index (H) and the Pielou's taxonomic evenness index (J). Richness (S) is the number of different species counted. Shannon diversity index (H') is based in species richness and the relative abundance of each species. Pielou index (J) concerns the evenness measures of diversity, it is independent of the number of species and only depends on the distribution of individuals among species. S and H were calculated using the estimate function (*vegan* package, (Oksanen et al., 2018), and J was calculated by dividing the Shannon diversity index by the natural logarithm of the observed taxon richness.

To analyze differences in the taxonomic structure of the ant communities between burned and unburned areas we used linear mixed-effects models, in which the dependent variables were ant occurrence, S, H, J, and the independent variables were the sampling month (May, July and October), the fire (burned vs. unburned), and their interaction. Plot identity was included as a random factor. The models were carried out using the *lme* function in the *nlme* package (Pinheiro, 2023). To meet statistical assumptions regarding normality and homogeneity, we transformed the dependent variables as needed (see results).

To analyze the effects of the fire, sampling month, and their interaction on the taxonomic composition of the ant community, we used permutational analysis of variance (PERMANOVA done with the *adonis* function in the *vegan* package, Oksanen et al. 2018), based on Bray-Curtis dissimilarities with 999 permutations. Homogeneity of the data was verified by utilizing the *betadisper* function of the R package vegan (Anderson, 2006; Anderson et al., 2006) and analyzing the results of this function with the ANOVA method (*anova* function in the stats package). Nonmetric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities was then performed, using the *metaMDS* function of the *vegan* package to visualize the effects of fire and sampling months.

Results

Vegetation recovery in the burned areas four years since fire

Vegetation analysis revealed significant differences between burned and unburned areas for the tree stratum (Table 2). Unburned plots had a higher abundance of trees than the burned plots (Fig. 2). Vegetation cover values, which accounts for the total vegetation cover of all the strata, were lower in burned plots than in unburned plots, but these differences were not significant (Fig. 2).

Table 2. Effects of fire on plant cover strata and vegetation cover. In bold, the tree strata that is significantly different in burned and unburned areas.

Vegetation cover	DF	F-value	p-value
Herbs	1, 6	28.25	0.0685
Small shrubs	1, 6	1.00	0.4449
Large shrubs	1, 6	0.26	0.6278
Trees	**1, 6**	**30.40**	**0.0075**
Vegetation cover	1, 6	1.92	0.3587

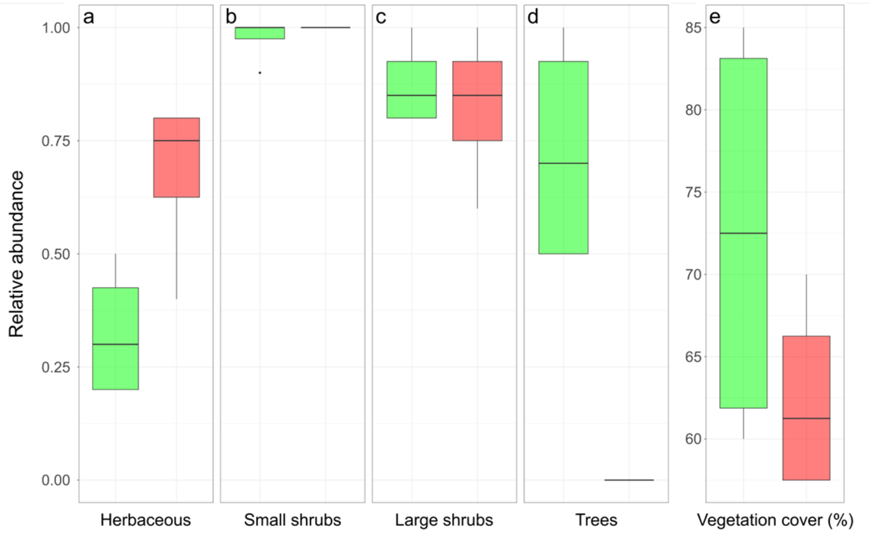


Figure 2. Relative abundance of plant cover strata at burned areas (red) and unburned areas (green) ordered by strata vegetation: (a) herbaceous plants, (b) small shrubs, (c) large shrubs, (d) trees and e) vegetation cover. In the boxplot, the squares represent the distance between the first and third quartiles (Q3-Q1), horizontally divided at the median, while the vertical lines on the top and bottom represent the fourth and first quartiles (Q4 and Q1), respectively. Individual dots represent outliers.

Effects of fire on taxonomic community structure

In total, 3479 ant workers were captured, representing 28 species, belonging to 16 genera and 3 subfamilies (Table 3). The rarefaction analysis using the total number of samples showed that the species accumulation curves for the two types of plots (burned and unburned) almost reached the horizontal asymptote. Moreover, the curves also showed that fewer species were captured in the burned plots than in the unburned plots (Fig. 3).

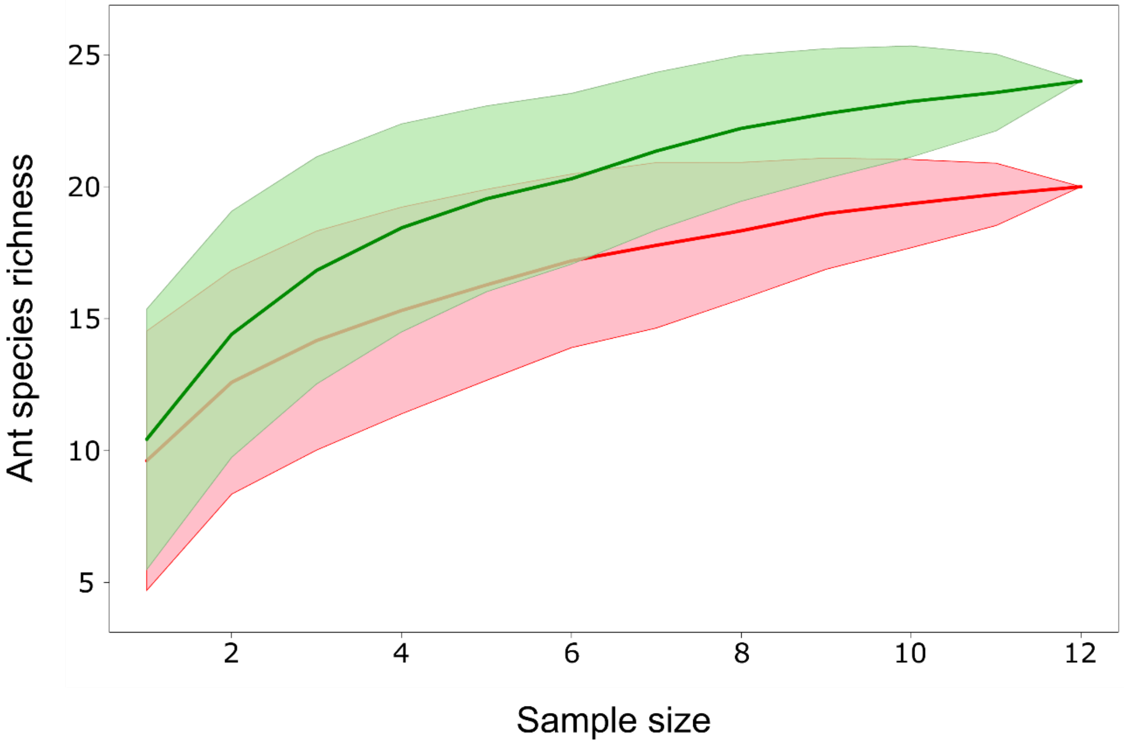


Figure 3. Rarefaction curves for ant species collected by pitfall traps in burned (red color) and unburned (green color) forest patches for three sampling months. The thick lines show the observed species richness and the shading represents the standard error.

Ant occurrence, S and H only differed significantly between time (sampling months: May, July, October) but not between fire treatments (burned and unburned) or the interaction between fire and time. However, fire treatments and the interaction with time was significant for J (Table 4; Fig. 4). In general, occurrence, S and H values decreased over the three months, with the highest values in May and the lowest values in October. The J values in the burned area, contrary to the unburned area, showed the inverse trend during the three months, with the highest values in October and minimum in May, explaining the significant interaction between the fire and time (Fig. 4; Fig. S1).

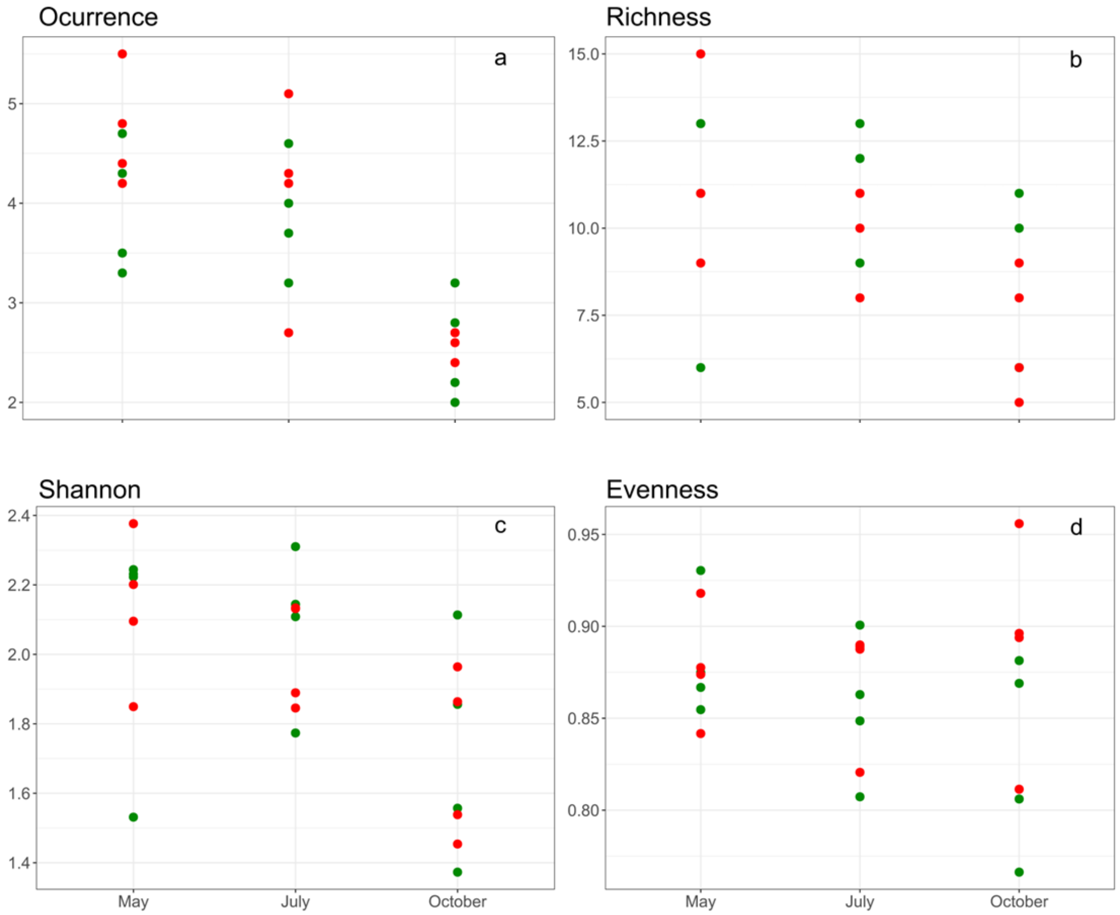


Figure 4. Relationship between sampling months and occurrence (a), richness (b), diversity (c) and evenness (d). Red dots refer to the data from burned plots, while green dots refer to control plots.

Effects of fire on taxonomic community composition

Regarding the PERMANOVA results, the assumption of homogeneity was met (p= 0.924). The analysis revealed significant differences in the taxonomic composition of the communities between fire treatments ($F_{1,23}$ = 9.009, p = 0.001, R^2 = 0.241, Fig. 5a) and time ($F_{2,23}$ = 3.523, p=0.002, R^2 = 0.188, Fig. 5b), but not in the interaction ($F_{2,23}$ = 1.683, p = 0.100, Fig 5c). In the unburned plots, we observed ant species that are associated with vegetated habitats (e.g., *Formica gerardi*, *Polyergus rufescens*, and several *Temnothorax* species). In contrast, in the burned plots, we observed ant species typically found in open areas (e.g., *Cataglyphis hispanica*, C. *iberica*, *Messor bouvieri*, or *Goniomma kugleri*, Fig. 5a). Notably, some species were only present in one fire treatment (Table 3): *Tapinoma* spp., *Camponotus foreli* and *Messor bouvieri* were detected exclusively on the burned plots; while *Polyergus rufescens*, *Crematogaster sordidula*, *Plagiolepis schmitzii* and the three species of *Temnothorax* were only found on unburned plots (although single individuals of *Messor barbarus* and *Myrmecina graminicola* appeared on unburned plots there low abundance indicates that there are not representative species of the habitat).

The differences in the taxonomic composition of the ant communities in the three months (May, July and October) were the result of the strong seasonality of some species. For example, the more cryptic species such as *M. graminicola* or species of the genus *Temnothorax* were more associated with the spring (May), the most thermophilic species *C. hispanicum* and *C. iberica* occurred in summer (July) and the seed-harvester ants *M. bouvieri* and *G. kugleri* in autumn (October, Fig. 5b). Note that these thermophilic species occurred mostly in burned areas in summer, and the latter species (*M. bouvieri* and *G. kugleri*) that are prone to open areas occurred in autumn also mostly in burned areas (Fig 5c).

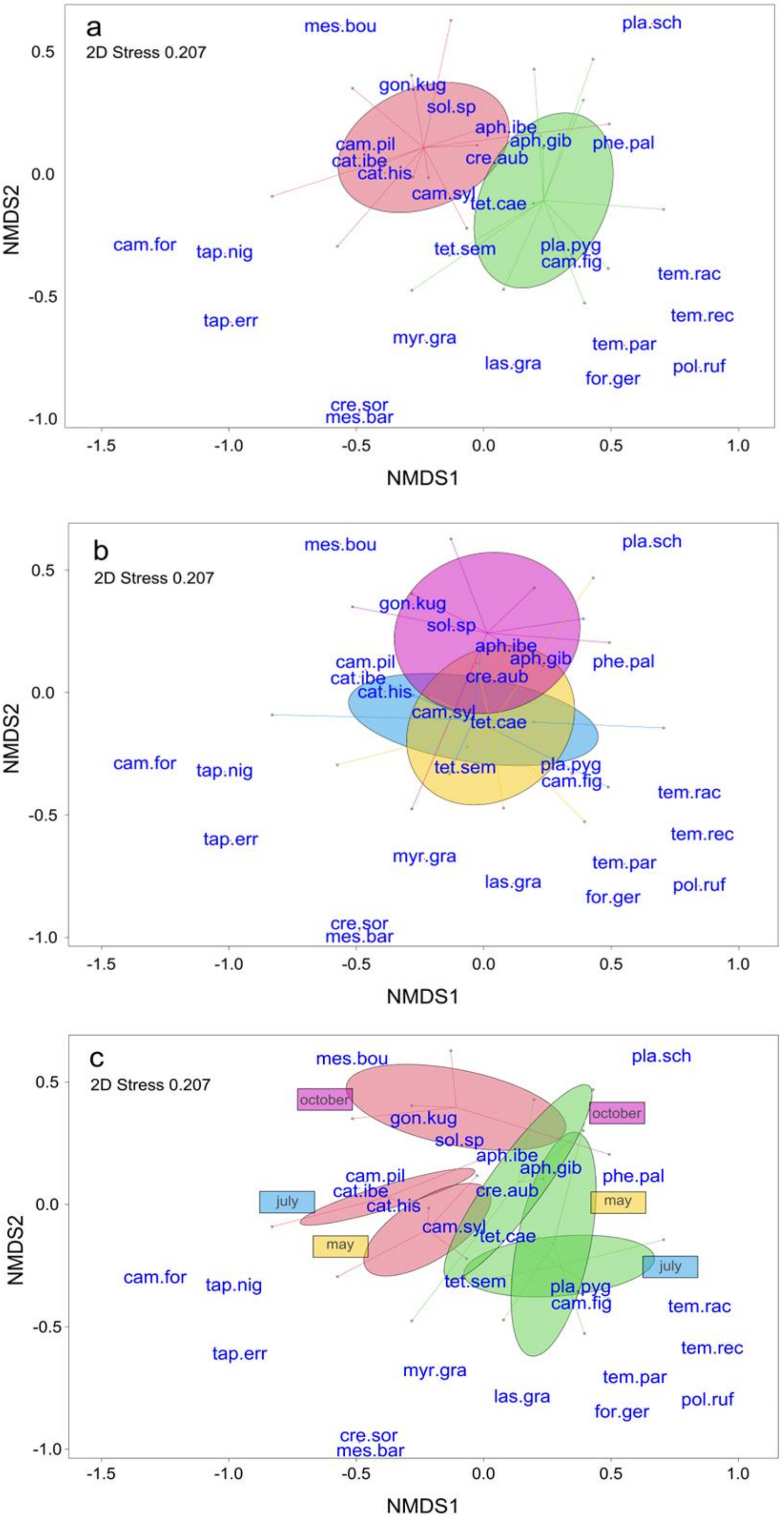


Figure 5. NMDS graph of ant community taxonomic composition for (a) fire treatments (red = burned; green = unburned), (b) time (sampling months; yellow = May; blue = July; pink = October) and (c) for fire treatments separated by sampling months. The ovals represent the different fire treatments or sampling months. The 2D stress coefficients are indicated.

Discussion

Taxonomic indices of community structure (occurrence, species richness and diversity) were similar in the burned area than in the unburned area, indicating a likely recovery of the ant communities four years after time. However, the four years after fire, ant' species composition was significantly different between burned and unburned areas.

The number of species identified in our study (28) is very close to that of other studies in Mediterranean landscapes dominated by conifers in the Iberian Peninsula, even if previous studies had a greater number of traps left for more than 24h, and a greater number of ants collected (Rodrigo and Retana, 2006; Arnan et al. 2020; Vidal-Cordero et al. 2022). For example, Rodrigo & Retana (2006) and Vidal-Cordero et al (2022) identified a total of 34 and 37 species of ants, respectively, from > 30,000 individuals collected in traps open for 7- 11 days.

Our results revealed that four years after the fire, burned areas were not negatively different in relation to the taxonomic structure of ant communities, against our predictions from the first hypothesis. More specifically, we found that there were no significant differences in most of the taxonomic indices analyzed (occurrence, S, and H) between burned and unburned areas. The only exception was the J index, as the burned plots presented a greater uniformity of species than the unburned ones, showing the highest values in October. This result is in line with a study carried out by Arnan et al (2020) in Mediterranean ecosystems in Catalonia, Spain, in where fire affected the degree of homogenisation of the ant community.

In Mediterranean forests shortly after a fire, we expected ant taxonomic diversity to decrease as vegetation-dependent species cannot survive the fire and their habitat is destroyed (Beaumont et al., 2013; Khayati et al., 2023; Matsuda et al., 2011; Rodrigo and Retana, 2006; Underwood and Quinn, 2010; Vidal-Cordero et al., 2022; Yekwayo et al., 2018). However, other works that have studied the effects of fire in Mediterranean forests over a longer period of time have reported positive effects for the taxonomic structure of the ant community (Arnan et al., 2020, 2006; Gosper et al., 2015; Izhaki et al., 2009; Kaynaş et al., 2018; Khayati et al., 2023; Vidal-Cordero et al., 2023, 2022), but see Arnan et al. (2006). This variability in ant community responses to fire may be due to a combination of several factors, such as fire intensity (Gibb and Hjältén, 2007), shelter availability (Underwood and Quinn 2010), nesting behaviour (Andersen, 2019;

Arnan et al., 2013) or local vegetation type (Arnan et al. 2020) which affects survival and recovery of ant communities, and the taxonomic composition itself, as different species respond in different manners to disturbance (Caut et al., 2014). After the initial post-fire period, the vegetation cover, the availability of resources (Arnan et al. 2007; Arnan et al. 2020) and the temperature (Retana and Cerdá 2000) are determining factors in the recovery of ant communities. For example, in our study the recovery of vegetation cover was fast compared to Vidal-Cordero et al. (2023), which could have affected the different trend in taxonomic diversity and richness after fire between both works (see Table 1).

It is important to highlight that most studies suggest that the effects of fire vary greatly when species are analyzed individually (Arnan et al. 2020; Rodrigo and Retana 2006, Underwood and Quinn 2010). Indeed, interspecific variability in how species responded to fire and post-fire conditions is the likely explanation for our results. Species most dependent on existing vegetation or with vulnerable nests disappeared, while the most resistant species, which could have survived the fire by sheltering inside underground nests, increased their abundance which caused an increase in the uniformity of the community (J index). On the other hand, the more resilient species are attracted by the new conditions colonizing the open habitat from the surrounding unburned area. These new species can mitigate the loss of non-resistant species and recover the richness and diversity of ants a few years after the fire.

In line with this, our second hypothesis predicted that the taxonomic composition of ant communities will be different after fire, with species typical of open areas being found in burned areas, and species more closely linked to vegetation in areas not affected by fire. This prediction was supported by our results, as species such as Lasius grandis, Plagiolepis pygmaea and Temnothorax spp. with closer associations to vegetation were found more frequently in the unburned areas. These species are dependent on trees for the construction of nests or foraging (Gómez et al., 2018; Paris and Espadaler, 2009; Seifert, 2020); hence, we can assume that they either died in the fire or were displaced by the bad conditions it created, due to the reduction of their natural arboreal habitat. This is further supported by the fact that, in our study area, the number of trees in burned plots was significantly lower to that in unburned plots. On the other hand, ground-dwelling species, such as the two thermophilic species of Catagylphis (C. hispanica and C. iberica), Crematogaster auberti or Messor bouvieri, adapted to more open habitat, were more prevalent in the burned areas. These species are less dependent on vegetation, as they mostly use the ground for nesting, foraging and taking shelter (Boulay et al., 2017; Lebas et al., 2016; Wehner, 2020). Other studies found similar results in conifer-dominated Mediterranean landscapes (Rodrigo and Retana, 2006; Vidal-Cordero et al., 2022).

Our results suggest that, at least in our study area, the likely loss in taxonomic richness and diversity of ant communities occurring just after fire was compensated within a short period of time (four years) by the colonization of new species and/or the expansion of species that were more resilient. This can be considered a natural example of portfolio theory (Figge, 2004), a vast suite of phenomena analogous to the common practices of bankers and investors that diversify their portfolio so that a loss in one asset is dampened or compensated by the others. In ecological systems, populations, species and phenotypes can be seen as assets, wherein the more assets are available, the better the system can react to disturbances (Bolnick et al., 2011). This effect has been detected in other animal populations (O'Connor et al., 2023; Schindler et al., 2010) and can be used by conservation agents to promote stability and resilience in ecosystems (DuFour et al., 2015; Hoekstra, 2012). Despite the portfolio effect detected in our study, this replacement of species represents changes in the taxonomic composition of the community lasting for four years since fire. It is likely that, the significant decrease in the abundance of trees in our study area, is not yet favorable for ant species more dependent on arboreal vegetation for nesting and feeding. In fact, the vegetation recovery of a forest last for a long time after the fire disturbance (Rodrigo et al., 2004; Seidl and Turner, 2022). In our case, even considering the adaptations of maritime pine to fire disturbance and its subsequent natural regeneration, its growth was very slow (less than 1 m four years after the fire), without having reached pre-fire conditions (Calvo et al., 2008).

In conclusion, we have evaluated the taxonomic structure and composition of ant communities in a conifer forest four years after fire. Our results reveal significant differences in the taxonomic composition of ant communities between burned and unburned areas; nevertheless, their similar ant structure (occurrence, richness and diversity) suggest that the loss of species after fire may be compensated by the gain of other species less dependent on vegetation and more adapted to open and arid habitats. It is important to note, however, that this compensating effect has not always been observed in previous work in Mediterranean environments (Arnan et al. 2006; Vidal-Cordero et al. 2022) and that, in spite of this, fire and other disturbances may still lead to the loss of less common species, especially arboreal ones, and to the increase of more resilient and dominant species (Andersen, 2019; Arnan et al., 2009). Our snapshot of ant communities four years after fire shows that fire shaped their taxonomic composition, leading to a recovery of the occurrence, richness and diversity of ant species. The use of ant communities as indicators of the habitat' post-fire recovery, requires the evaluation of several diversity indices. The sole use of taxonomic structure indices could give misleading results of a false recovery. The analysis of the taxonomic composition is then needed to have a complete picture of the impact of fire; together with continuous monitoring of the effect of fire immediately after the disturbance and in the long-term, or for example functional diversity indices to understand the evolution of ant communities over time.

Acknowledgments

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Appendix

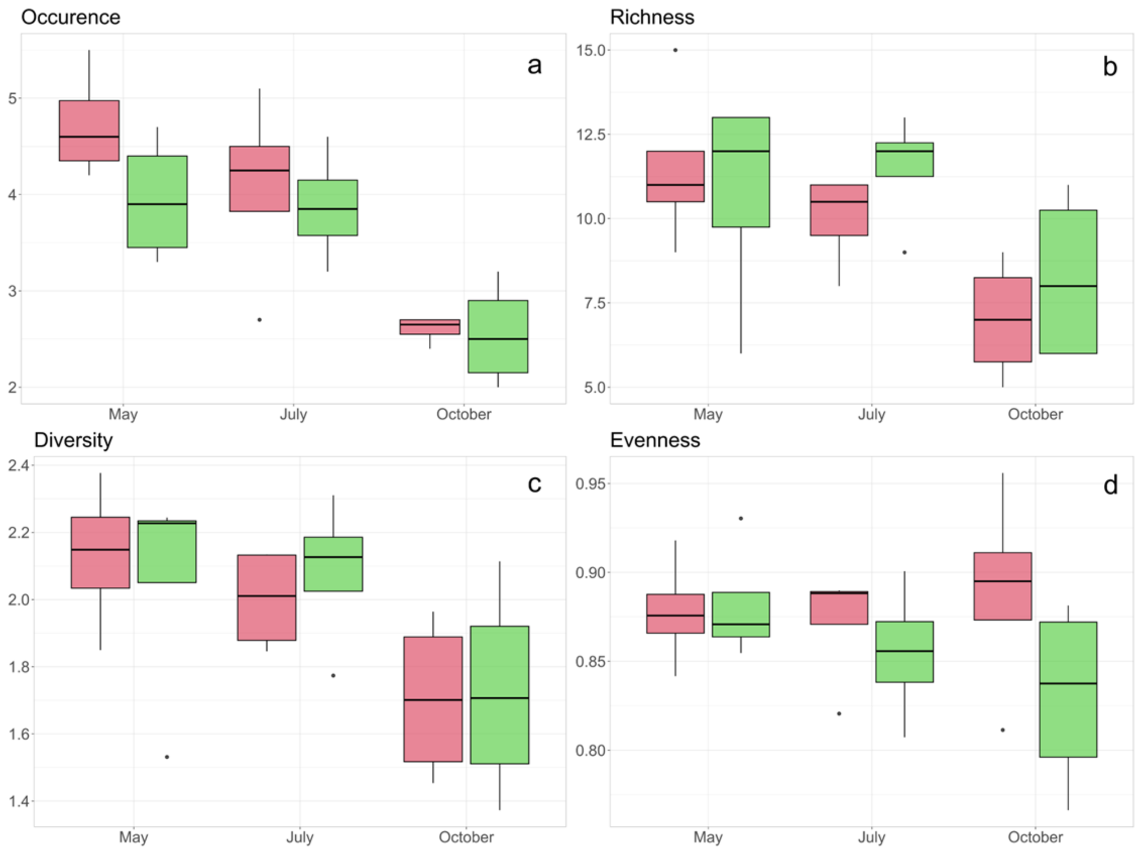
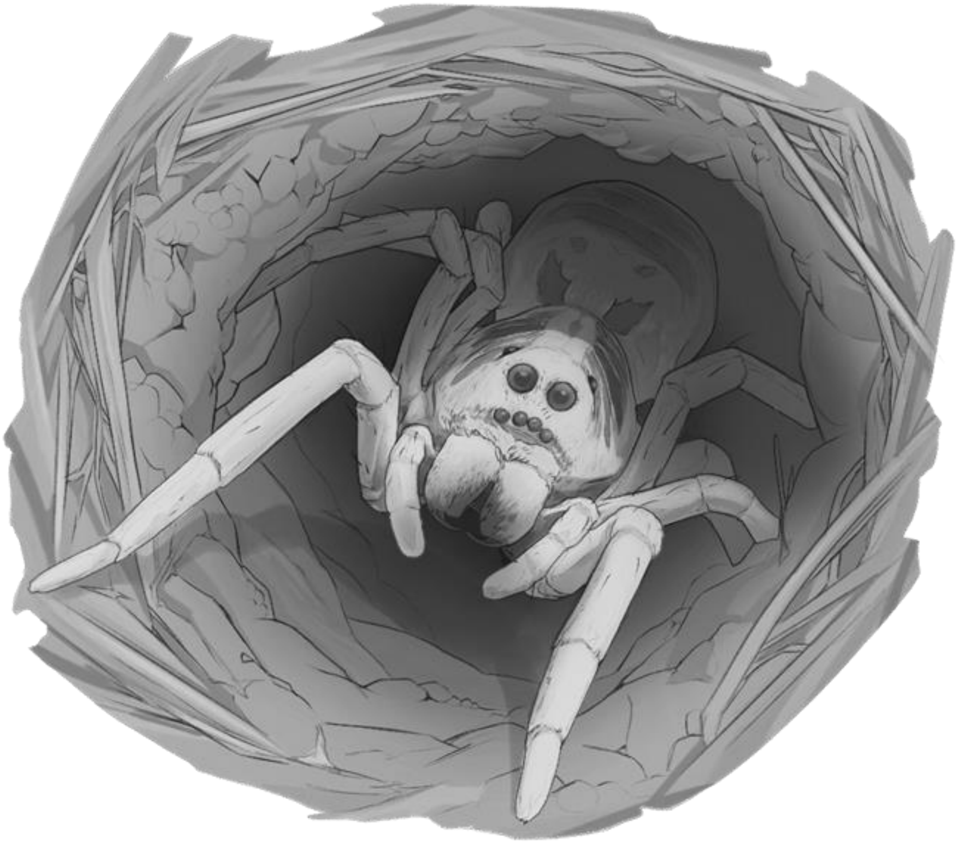


Figure S1. Mean values of occurrence (a), richness (b), diversity (c) and evenness (d) for each sampling month and fire treatment (burned in red, control in green). The squares represent the distance between the first and third quartiles (Q3-Q1), horizontally divided at the median, while the vertical lines on the top and bottom represent the fourth and first quartiles (Q4 and Q1), respectively. Individual dots represent outliers.

Capítulo 2

Four-year study of arthropod taxonomic and functional responses to a forest wildfire: ants and epigeic spiders are affected differently



Vidal-Cordero, J. M., Arnan, X., Rodrigo, A., Cerdá, X. and R. Boulay (2022). Four-year study of arthropod taxonomic and functional responses to a forest wildfire: Epigeic ants and spiders are affected differently. Forest Ecology and Management, Volume 520, 120379.

Resumen

Al estudiar perturbaciones forestales, es esencial examinar la biodiversidad desde distintas perspectivas, lo que incluye considerar la faceta taxonómica y funcional. De hecho, distintos taxones pueden responder de forma diferente en función de sus rasgos funcionales. Analizamos los efectos a corto plazo de un incendio forestal sobre las comunidades de hormigas y arañas epigeas en un bosque mediterráneo. Específicamente planteamos la hipótesis de que (1) el fuego disminuiría inicialmente la diversidad taxonómica y funcional de ambas comunidades taxonómicas y tendría un efecto más pronunciado sobre las arañas que sobre las hormigas porque los nidos de arañas son menos profundos que los de hormigas y, en consecuencia, más susceptibles a los efectos del fuego; (2) el tiempo de recuperación sería mayor para las arañas que para las hormigas; y (3) las respuestas de la diversidad taxonómica y funcional dependerían de las identidades y rasgos funcionales de las especies encontradas en ambos taxones. Nuestros resultados muestran que los incendios forestales afectaron a la estructura y composición de ambas comunidades, pero influyeron más en las hormigas. Estos efectos fueron en su mayoría constantes a lo largo de los cuatro años del estudio. Encontramos que las diferentes facetas de la diversidad mostraron respuestas paralelas al fuego, aunque hubo diferencias específicas de cada taxón. Tanto en arañas como en hormigas, observamos que las parcelas quemadas albergaban especies típicas de hábitats abiertos, mientras que las parcelas no quemadas albergaban especies típicas de hábitats con vegetación. Resaltamos la importancia de 1) realizar un seguimiento a largo plazo tras el incendio para obtener una estimación precisa de la recuperación del ecosistema respecto a las condiciones previas al incendio; y 2) estudiar las respuestas taxonómicas y funcionales al fuego en diferentes taxones para aumentar la potencia de las predicciones de respuesta del ecosistema y utilizarlas en la toma de decisiones de gestión del hábitat.

Abstract

When studying forest disturbances, it is essential to examine biodiversity from different perspectives, which includes considering its taxonomic and functional facets. Indeed, different taxa may respond differently based on their functional traits. We analyzed the short-term effects of a wildfire on epigeic ant and spider communities in a Mediterranean forest. We specifically hypothesized that (1) fire would initially decrease the taxonomic and functional diversity of both taxonomic communities and have a more pronounced effect on spiders than ants because spider nests are shallower than ant nests and are consequently more vulnerable to fire; (2) recovery time would be longer for spiders than ants; and (3) the responses of taxonomic and functional diversity would be dependent on the identities and functional traits of the species found in both taxa. Our results show that wildfire affected the structure and composition of both communities but had a greater influence on ants. Over the four years of the study, these effects were largely constant for ants, whereas spiders displayed recovery. The two facets of diversity showed parallel responses to fire in the structure and composition of ant communities and in the composition of spider communities. However, the taxonomic and functional structure of spider communities reacted differently. In both spiders and ants, we observed that burned plots hosted species typical of open habitats, while unburned plots hosted species typical of vegetated habitats. We highlight the importance of (1) conducting long-term post-fire monitoring to get an accurate estimate of ecosystem recovery relative to pre-fire conditions and (2) studying taxonomic and functional responses to fire in different taxa to increase the power of the ecosystem response predictions used in habitat management decisions.

Introduction

Natural disturbances (e.g., wind, floods, drought, and wildfires) can affect ecosystem structure and function (Mart-Jan et al., 2003; Seidl et al., 2016; Thom and Seidl 2016). Wildfire is a major disturbance, especially in boreal and Mediterranean forests (Bengtsson et al., 2000), and it can profoundly modify ecological succession, habitat structure, energy flow, and biotic community composition (Bengtsson et al., 2000; He et al., 2019; Paillet et al., 2010; Pausas et al., 2008; Pausas and Fernández-Muñoz, 2012). Furthermore, over recent decades, humans have fundamentally altered natural fire disturbance regimes, mainly via land use changes (land abandonment and forest plantations) that are exacerbated by the drier conditions resulting from climate change (Pausas and Fernández-Muñoz, 2012). Thus, understanding how plant and animal communities respond to forest fires is crucial if we want to predict how fire could affect biodiversity in forest ecosystems and establish preliminary groundwork for management and conservation strategies.

To date, most studies exploring the effects of wildfire on forest biodiversity have focused on taxonomic diversity, as expressed via species richness and/or composition (Basset et al., 2008; Hamer and Hill, 2000). However, researchers are increasingly examining other forms of diversity, including functional diversity (Arnan et al., 2020, 2015; Hidasi-Neto et al., 2012). Changes in functional diversity can greatly influence ecosystem dynamics, stability, productivity, nutrient balance, and other functional factors (Laureto et al., 2015). Such work has generated major insights into community responses to disturbance and habitat change while concurrently clarifying the underlying mechanisms at play (Mouillot et al., 2013). It is often assumed that there is an asymptotic relationship between taxonomic and functional diversity, such that greater functional richness leads to greater species richness (Poos et al., 2009). However, it is important that such assumptions be verified by simultaneously applying taxonomic and functional approaches when gathering information that will ultimately inform species conservation and ecosystem management (Birkhofer et al., 2015; Lambeets et al., 2009).

Arthropods are key members of ecosystems and carry out a wide array of important functions, including nutrient cycling, decomposition, seed dispersal, plant pollination, predation, and scavenging. Although there are studies that have examined the effect of fire on arthropod diversity from a multi-taxa approach (Dawes-Gromadzki, 2007; Valkó et al., 2016), most of the research has focused on a single taxon or functional group (e.g., Langlands et al., 2011; Arnan et al., 2013; Lazarina et al., 2016). However, it is important to assess how fire affects different taxa if we wish to improve biodiversity conservation and landscape management efforts in an era of biodiversity loss. In this study, we examined two groups with contrasting ecologies: ants and spiders. With very few exceptions, Mediterranean ant species are ground-dwellers. Spiders, however, may live on the ground or in the vegetation, as is the case of orb weavers (Cardoso et al., 2011). Ant species are dietary generalists that exploit a variety of food resources, including dead insects, seeds, nectar, and honeydew (Arnan et al., 2019). Spiders, on the other hand, are predators that hunt mostly arthropod prey (Michalko and Pekár, 2016; Wise, 1995). Both ants and spiders display high levels of species diversity, are numerically dominant in most terrestrial habitats and ecosystems, provide important ecosystem services (Del Toro et al., 2012; Hogg and Daane, 2011; Michalko et al., 2019; Underwood and Quinn, 2010), and are highly sensitive to environmental change (Hsieh et al., 2003; Matevski and Schuldt, in press; Gosper et al., 2015; Tiede et al., 2017). As a result, ants and spiders have been used as indicators of ecosystem health capable of revealing the impacts of ecological disturbances (Oliver et al., 2000; Pearce and Venier, 2006; Underwood and Fisher, 2006; Céréghino et al., 2019; Tiede et al., 2017; Buchholz, 2010).

Generally, fire initially decreases the taxonomic diversity (Arnan et al., 2006; Vickers and Culin, 2014) and functional diversity (Arnan et al., 2013; Langlands et al., 2011) of both ants and spiders. However, taxonomic and functional diversity might be able to return to pre-fire levels over the course of secondary succession, according to some models (Kadmon and Benjamini, 2006). That said, there are dramatic differences in how arthropod communities respond to fire that are mediated by habitat type, fire regime, functional composition, and focal taxa (Andersen, 2019; Kral et al., 2017; New, 2014). For example, responses to fire may differ among taxa given that certain traits boost the likelihood of surviving a fire, the ability to cope with the subsequent environmental conditions, and the prospect of colonizing burned areas (Arnan et al., 2013; Bengtsson, 2002; Langlands et al., 2011). Such species traits can predict the level of community resistance (i.e., the degree of similarity in species composition immediately after a disturbance) and resilience (i.e., the time needed to recover predisturbance community structure and composition) in relation to fire (Moretti et al., 2006).

A fire will kill ants foraging outside their nests as well as spiders in their webs or outside their underground retreats. Consequently, in both taxa, survival is dependent on the characteristics of nesting sites, which can provide shelter during a fire event. Many ground-dwelling arthropods are able to survive canopy or low-intensity surface fires because they build their nests underground, and heat from a fire does not penetrate more than 30 cm below the ground surface (Cane and Neff, 2011; Matsuda et al., 2011). Indeed, most Mediterranean ant species nest in the soil. However, the majority of epigeic spider species are at greater risk of exposure because their nests tend to occur under rocks, near the soil surface, or at shallow depths below the surface (Moretti et al., 2002; Underwood and Quinn, 2010). Of the species initially killed by fire, some will be able to recolonize the newly created habitat via dispersal. Between the two taxa, spiders have much better dispersal abilities (in terms of time and distance) than do ants (Arnan et al., 2013; Bonte et al., 2003; Bonte and Saastamoinen, 2012). In addition, burned areas can be colonized by species that were not present before the fire (Arnan et al., 2006; Bonte et al., 2003). Differences in dispersal traits will determine the success of ants and spiders in colonizing or recolonizing habitats after fire.

We conducted a four-year study of the effects of a lightning-caused wildfire on the taxonomic and functional diversity of epigeic ant and spider communities. Our study area was a Mediterranean pine forest in northeastern Spain. We tested three hypotheses. First, we expected fire to initially decrease both the taxonomic and functional diversity of ant and spider communities, with spiders showing a steeper decline than ants (i.e., ants should be more resistant than spiders). Second, we expected both the taxonomic and functional diversity of ant and spider communities to increase over time during the post-fire period, with spiders showing faster recovery than ants because spiders are among the first to arrive after fire due to their better dispersal abilities (i.e., spiders should be more resilient than ants). Lastly, we expected taxonomic and functional composition to vary between burned and unburned areas: burned areas should contain species with traits better suited to open areas (e.g., species build nests and search for food on the ground/in the soil and disperse over longer distances), while unburned areas should contain species with traits better suited to more vegetated habitats (e.g., species build nests and search for food in the vegetation and disperse over shorter distances).

Materials and methods

Study site

This research was conducted near the village of Salo, in northeastern Spain (N 41°52, E1°38′, 540–620 m above sea level; Appendix A Fig. A.1). This area has a typical Mediterranean climate, where mean annual temperature and rainfall are 12.4 ºC and 626.4 mm, respectively (Lázaro-González et al., 2013). The study site was in a rocky landscape comprising a mosaic of agricultural fields and pine forests (Pinus nigra and, to a lesser extent, Pinus halepensis). The forests had a relatively dense understory composed of common Mediterranean shrubs, including Rosmarinus officinalis, Thymus vulgaris, Rhamnus alaternus, and Lavandula latifolia. In June 2009, a crown wildfire burned through an area of 194 ha, composed by 74% of pine forests, 24% cropland, and 2% scrubland. We performed our study in a zone where almost all the pine trees had been burned away and canopy cover was limited within the burned areas and was essentially composed of the occasional surviving pine tree and resprouting holm oaks. Over all four years of the study, the density of trees and large shrubs was significantly lower in the burned area than in the unburned area. In contrast, the density of herbaceous vegetation increased significantly between 2010 and 2012 in both types of areas (Appendix B, Fig. B.1, Table B.1).

Ant and spider sampling

We established six 1,000 m^2 (50 m x 20 m) rectangular plots: four plots in the burned area (hereafter, the burned plots) and two plots in the unburned area (hereafter, the unburned plots). There were 550 m between the unburned plots; 270–1,300 m between the burned plots; and 200–2,000 m between the unburned plots and the burned plots (Appendix A Fig. A.1). Furthermore, each of the plots was located at least 100 m from the edge of the burned area. This distance is sufficient to avoid capturing epigeic ants and spiders coming from outside the area being sampled (Rodrigo and Retana, 2006).

We used open pitfall traps without roofs to catch epigeic ants and spiders. These traps were 20-cl plastic vials (65 mm in diameter, 95 mm deep) that were half filled with soapy water and salt. This method of capture yields reliable assessments of both arthropod groups and has frequently been used to study ant (Parr et al., 2004; Arnan et al., 2006, 2007) and spider communities (Cardoso et al., 2008; Carvalho et al., 2012). Researchers seeking to exhaustively characterize spider communities use more than one sampling method (Cardoso et al. 2008, 2011), but we had a different aim in this study. We needed a relatively rapid assessment approach that would allow us to compare epigeic ant and spider communities between the burned and the unburned plots across time. It is for this reason that we employed pitfall trapping, a method inherently biased toward capturing epigeic, highly active species (Montgomery et al., 2021).

In each plot, 20 pitfall traps were placed along two 50-m transects; the transects were separated from each other by 15 m. Within the transects, the pitfall traps were separated by 5 m. We carried out the first round of sampling in July 2009, three weeks after the wildfire, and the second round of sampling in September 2009. Then, in 2010, 2011, and 2012, we sampled three times per year—in May, July, and September—to maximize the diversity of ants and spiders collected. Each of the 6 plots were thus sampled 11 times, and there were 66 sampling events in total: 44 in the burned plots and 22 in the unburned plots. We observed low levels of trap disturbance (54 traps disturbed/1267 traps set). We dealt with the missing data by extrapolating ant and spider occurrence and abundance data based on the total number of functional traps per plot.

During each sampling period, pitfall traps were run for a week. The biological contents of the traps were stored in 70% ethanol until identification could occur. Ants and spiders were separated out from the other invertebrates found in the traps. Ants were identified to species level. In most cases, it was only possible to identify the spiders to genus level. Juvenile spiders could not be identified with certainty beyond family level and were thus excluded from consideration in this study. The family Lyniphiidae was treated as a single taxon due to the difficulty of identifying its members to genus. In the Mediterranean, spider genus richness is considered a good proxy for species richness (Cardoso et al., 2004). To identify the ants, we used Gómez and Espadaler (2007); to resolve any doubts, we contacted Xavier Espadaler (Universitat Autònoma de Barcelona) and Joaquín Reyes (Universidad de Córdoba). To identify the spiders, we used the keys published by GIA (Barrientos, 2006); when needed, Iñigo Sánchez (ZooBotánico Jérez) helped resolve any uncertainty. In our analyses, we thus used species- and genus-level data for ants and spiders, respectively.

Life-history traits

We characterized 15 and 12 functional traits for the ant species and the spider genera, respectively. These traits represented three functional trait groups of recognized importance in ant and spider autecology and/or ecosystem functioning because they contribute to survival, persistence, and colonization. Such characteristics are highly useful for explaining how both ants (Arnan et al., 2013) and spiders (Langlands et al., 2011) respond to fire. While some spider species in the same genus have different functional traits, it is more common for congeners to share most traits. The ability to physically survive fire is associated with nesting site in ants and microhabitat use in spiders. The ability to persist after fire is associated with behavioral dominance, colony size, body size, and diet. The ability to colonize burned areas is associated with colony founding type in ants and ballooning capacity in spiders. The full description of the functional traits used in this study is provided in Appendix C (Tables C.1 and C.2). The information on ant traits came from past research (Arnan et al., 2013; Retana et al., 2015). For the spider traits, we conducted a literature search (Bell et al., 2005; Cardoso et al., 2011; Langlands et al., 2011; Pedley and Dolman, 2014; Schirmel et al., 2012). In both cases, we gathered additional trait data from unpublished sources provided by experts: Xavier Espadaler and Alberto Tinaut for ants and Jesús Miñano for spiders.

Data and statistical analyses

All the analyses were performed using R (v. 4.1.3; R Core Team 2022). To analyze the taxonomic structure and composition of ant and spider communities, we calculated species occurrence for ants and genus abundance for spiders (hereafter, ant occurrence and spider abundance). For the ants, we defined species occurrence per plot and sampling period as the number of traps in which a species occurred divided by the total number of traps in operation (i.e., relative frequency of traps in which the species occurred). We chose this definition to avoid any potential bias that could result from the pitfall traps being close to ant trails/ant nests. For the spiders, we defined genus abundance per plot and sampling period as the pooled number of individuals per trap across all the traps in operation (i.e., regardless of whether a given genus occurred in a given trap). Then, we calculated the following community indices per plot and sampling period for both groups:

(1) taxonomic richness (S)—the number of ant species or spider genera observed; (2) the Shannon diversity index (H); and (3) the taxonomic evenness index (Pielou's J).

To characterize the functional composition of ant and spider communities per plot and sampling period, we used two approaches that have been widely employed in ecological research. First, we determined the “trait average” (CWM), which conveys which traits are the most common in a community after accounting for differences in taxon presence (i.e., here, ant occurrence and spider abundance) (Laliberté and Legendre, 2010). The method for determining CWM differs depending on whether the traits are continuous or categorical. For continuous traits, CWM corresponds to the abundance-weighted mean and was calculated as follows:

$$\bar{x} = \sum_{i=1}^{s} p_i x_i$$

where p_i is ant occurrence or spider abundance i and x_i is the trait value for species (or genus) i. For categorical traits, CWM corresponds to the ant occurrence or spider abundance associated with each trait category.

Second, we examined “trait dissimilarity” or functional diversity (FD), which indicates the degree to which species within a community differ in their traits (Arnan et al., 2013; Ricotta and Moretti, 2011). We broke FD down into three different facets that were expressed via the following indices: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) (Villéger et al., 2008). Functional diversity indices can be used to help decipher the processes that structure biological communities (Mouchet et al., 2010). FRic conveys the amount of functional space filled by the community, but it does not incorporate information on relative abundances. We thus need other indices like FEve, which describes how evenly trait abundances are distributed within this functional space (Mason et al., 2005). However, FEve does not reveal patterns of species dispersion within functional trait space. Instead, this information is reflected by FDis, which estimates the mean distance in multidimensional trait space between individual species and the centroid of all species (Laliberté and Legendre 2010). These three facets thus provide a meaningful framework for quantifying this form of diversity and examining the mechanisms that underlie the links between diversity and ecosystem functions.

We employed the *functcomp* and *dbFD* functions in the *FD* package (v. 1.0-12; Laliberté et al., 2010) to calculate the CWM values and the FRic, FEve, and FDis values, respectively.

To analyze differences in the taxonomic and functional structure of the ant and spider communities (dependent variables: ant occurrence, spider abundance, S, H, J, FRic, FEve, and FDis), we used linear and quadratic mixed-effects models (LMMs). Quadratic models were also used because we preliminarily observed quadratic relationships between some response variables over time. To compare linear and quadratic models, we used the Akaike information criterion (AIC). We chose the model with the lowest AIC. For differences of less than two units, we retained the linear model following the principle of simplicity. The explanatory variables were year of sampling (continuous variable), plot type (categorical variable: burned treatment vs. unburned treatment), and their interaction. Plot identity was a random effect that accounted for the same plots being repeatedly sampled over time. To meet the statistical assumptions regarding normality and homogeneity, we transformed 2 of the 14 variables used (log transformation of ant FRic and square root transformation of spider abundance). The models were carried out using the *lme* function in the *nlme* package (Pinheiro et al., 2020). We compared taxonomic richness, Shannon diversity, and Pielou's evenness between the burned and unburned plots for the ants and spiders using sample-based rarefaction curves that included data for the entire four years of the study. We built one curve per plot using EstimateS 9.1.0 (Colwell, 2009).

We employed permutational analysis of variance (PERMANOVA; the *Adonis* function) based on Bray-Curtis dissimilarities (with 999 permutations) to analyze the effects of plot type, sampling year, and their interaction on the taxonomic and functional composition of ant and spider communities. First, we created matrices that combined information on plot taxonomic and functional composition (for each sampling period). In the case of the taxonomic analysis, the matrix cell values reflected ant occurrence and spider abundance; in the case of the functional analysis, they were the abundance-weighted trait values. Second, we ran models in which sampling year (continuous variable), plot type (categorical variable), and their interaction were included as explanatory variables, and plot identity was a random factor. Third, we used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities to explore differences in the taxonomic and functional composition of communities among plots and years. The assumption that the data displayed homogeneity of dispersion was tested using the *betadisper* function in the *vegan* package (Oksanen et al., 2018). We also tested for correlations among traits using the Spearman method (*cor* function in the *stats* package). We considered that two traits were highly correlated when rho ≥ 0.9.

Results

Taxonomic diversity and composition

We captured a total of 31,833 ant workers representing 37 species (Appendix D, Table D.1), 15 genera, and 3 subfamilies as well as 3,391 individual spiders representing 63 genera (Appendix D, Table D.2) and 25 families. The rarefaction curves were more asymptotic for the ants than for the spiders (Appendix E, Fig. E.1a,d).

Ant occurrence was significantly related to year (but not to plot type); the relationship was U shaped (Table 1), with ant occurrence decreasing from 2009 to 2011 and then increasing from 2011 to 2012 (Fig. 1a). Meanwhile, ant richness (S) and diversity (H) differed significantly between plot types but not among years (Table 1); lower values were seen in the burned versus unburned plots (Fig. 1b-c). For spiders, diversity was significantly and linearly related to year (Table 1) and increased from 2009 to 2012 (Fig. 1f). The interaction between plot type and year was significant for spider abundance and richness (Table 1). In the unburned plots, both variables had constant intermediate values across years; in the burned plots, values were low in 2009 but reached high levels in 2012 (Fig. 1d,e). There were no differences in taxonomic evenness over time between plot types, nor was there a year-by-plot-type interaction for either ants or spiders (Tables 1 and 2). These results were echoed in the rarefaction curves, where, for ants, taxonomic richness and Shannon diversity values were higher in the unburned versus burned plots. In contrast, there was overlap in the curves for ant and spider taxonomic evenness and for spider taxonomic richness and Shannon diversity, meaning these variables did not differ between the burned and unburned plots (Appendix D, Fig.D.1).

Table 1: Statistical output of the linear and quadratic mixed-effects models analyzing the effects of fire (plot type: burned vs. unburned), sampling year (year and year^2), and their interaction on occurrence, taxonomic richness (S), Shannon diversity (H), Pielou's evenness (J), log-transformed functional richness (log[FRic]), functional evenness (FEve), and functional dispersion (FDis) for the ant communities. -, indicates that the quadratic year term was not used in the linear models. The blank spaces correspond to the quadratic models that had a poor fit for a particular explanatory variable. In bold are the significant values for a given explanatory variable in a given model.

Ants								
	Linear model				***Quadratic model***			
Occurrence	DF	F-value	p-value	AIC	DF	F-value	p-value	AIC
Fire	1,4	2.94	0.161	77.122	1,4	2.95	0.161	**75.125**
Year	1,16	2.08	0.168		1,14	3.11	0.099	
Year^2	-	-	-		1,14	**7.15**	**0.018**	
Fire x Year	1,16	1.19	0.293		1,14	1.77	0.205	
Fire x Year^2	-	-	-		1,14	2.72	0.121	
Taxonomic richness (S)								
Fire	1,4	31.00	0.005	124.965	1,4	**34.68**	**0.004**	**121.514**
Year	1,16	0.70	0.415		1,14	0.78	0.39	
Year^2	-	-	-		1,14	1.68	0.216	
Fire x Year	1,16	2.28	0.151		1,14	2.55	0.133	
Fire x Year^2	-	-	-		1,14	2.69	0.123	
Shannon diversity (H)								
Fire	1,4	**19.63**	**0.011**		-	-	-	
Year	1,16	3.35	0.086		-	-	-	
Year^2	-	-	-		-	-	-	
Fire x Year	1,16	2.39	0.141		-	-	-	
Fire x Year^2	-	-	-		-	-	-	
Pielou's evenness (J)								
Fire	1,4	1.54	0.281	**-52.068**	1,4	1.55	0.281	-36.344
Year	1,16	2.54	0.131		1,14	2.7	0.122	
Year^2	-	-	-		1,14	1.8	0.200	
Fire x Year	1,16	0.24	0.629		1,14	0.26	0.619	
Fire x Year^2	-	-	-		1,14	1.24	0.284	
Functional richness (log[FRic])								
Fire	1,4	12.4	0.024	134.164	1,4	**12.27**	**0.025**	**131.999**
Year	1,16	0.18	0.676		1,14	0.18	0.678	
Year^2	-	-	-		1,14	1.12	0.307	
Fire x Year	1,16	0.07	0.791		1,14	0.07	0.792	
Fire x Year^2	-	-	-		1,14	0.67	0.426	
Functional evenness (FEve)								
Fire	1,4	0.80	0.423		-	-	-	
Year	1,16	0.34	0.567		-	-	-	

Year^2	-	-	-		-	-	-	
Fire x Year	1,16	0.02	0.896		-	-	-	
Fire x Year^2	-	-	-		-	-	-	
Functional dispersion (FDis)								
Fire	1,4	1.77	0.254	**-89.396**	1,4	1.77	0.255	-67.133
Year	1,16	**12.97**	**0.002**		1,14	11.77	0.004	
Year^2	-	-	-		1,14	0.49	0.495	
Fire x Year	1,16	**7.56**	**0.014**		1,14	6.87	0.020	
Fire x Year^2	-	-	-		1,14	0.04	0.849	

For ants, there was a significant effect of plot type and sampling year on community species composition (PERMANOVA: plot type—F = 10.3, p = 0.001, R^2 = 0.30; sampling year—F = 2.6, p = 0.001, R^2 = 0.08; Fig. 2a), but the interaction between plot type and sampling year was not significant (F = 0.98, p = 0.083, Fig. 2a). The taxonomic composition of spider communities was significantly influenced by plot type (F = 6.9, p = 0.001, R^2 = 0.21), sampling year (F = 5.1, p = 0.001, R^2 = 0.15), and their interaction (F = 1.5, p = 0.040, R^2 = 0.05). The assumption of homogeneity of dispersion was met for both the ants (p = 0.124) and the spiders (p = 0.329). Community composition differed between burned and unburned plots and among sampling years for both taxa (Fig. 2a,b). In the unburned plots, we observed ant species that are associated with vegetated habitats (e.g., *Crematogaster scutellaris, Camponotus lateralis*, and several *Temnothorax* species) and spider genera or species that live in vegetation or under stones (e.g., *Saites barbipes, Cercidia prominens*, *Hahnia* sp., *Trabea* sp., *Zora* sp., *Parachtes* sp., *Dysdera* sp., and members of the Linyphiidae family). In contrast, in the burned plots, we observed ant species typically found in open areas (e.g., *Cataglyphis iberica*, *Iberoformica subrufa*, *Pheidole pallidula*, *Plagiolepis pygmaea*, and *Tetramorium semilaeve*) and spider genera or species typically found in dry, stony grasslands and along the edges of coniferous forests (e.g., *Synema globosum*, *Atypus affinis*, *Alopecosa* sp., *Pardosa* sp., *Euophrys* sp., *Zodarion* sp., *Eresus* sp., and *Nemesia* sp.) (Fig. 2a,b). Ant and spider communities differed between 2009 (immediately after the fire) and the other three years of the study. In 2009, we observed ant species such as *Iberoformica subrufa*, *Camponotus piceus*, *Plagiolepys pygmaea*, and *Tapinoma nigerrimum* and mainly spiders from the genus *Nemesia*.

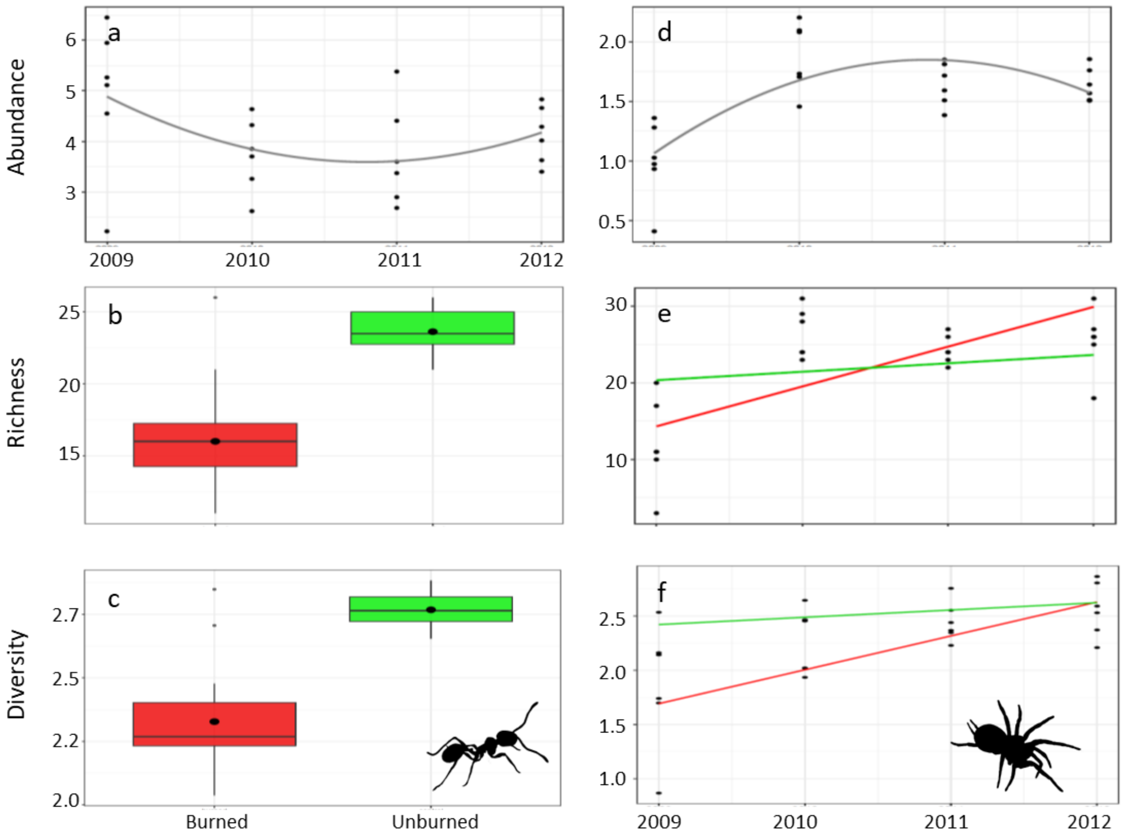


Figure 1. Relationship between sampling year and ant occurrence (a) and mean (± SE) ant richness (b) and Shannon diversity (c) in burned versus unburned plots. Relationship between sampling year and plot type for spider square-root-transformed abundance (d) and richness (e) and the relationship between sampling year and spider diversity (f). The gray line indicates the linear or quadratic fit of the model, and the colors indicate the linear fit of the models for each plot type (red = burned; green = unburned).

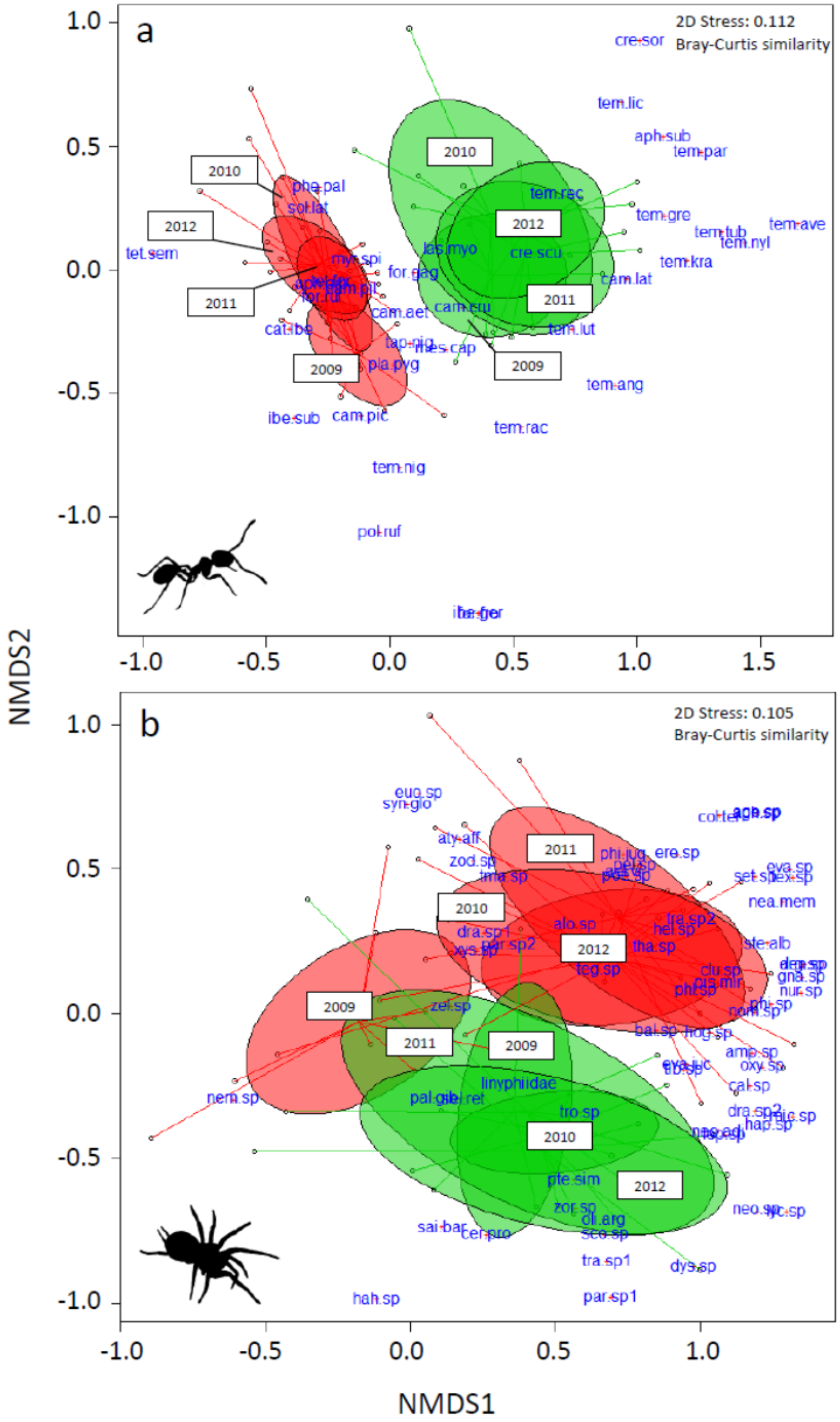


Figure 2. Results of the NMDS analysis of community taxonomic composition for ants (a) and spiders (b). The ovals depict the standard deviation of the point scores and represent the different sampling years. The colors indicate plot type (red = burned; green = unburned).

Functional diversity and composition

None of the functional diversity indices for either the ants or spiders differed significantly between the burned and unburned plots, apart from functional richness (FRic) and functional dispersion (FDis) for ants (Table 1). Ant FRic was higher in the unburned plots than in the burned plots (Fig. 3a). Ant functional dispersion (FDis) was affected by the interaction between plot type and sampling year (Table 1): while it was high and constant across all years in the unburned plots, it climbed from low values in 2009 to high values (equivalent to those in unburned plots) in 2012 in the burned plots. (Fig. 3b). For the spiders, FRic showed a significant linear increase only across years and FDis showed a significant interaction between plot types and the year in the quadratic model (Table 2, Fig. 3c-d). Thus, FDis in burned plots decreased the first year after fire, but increased to the unburned values the fourth year after fire (Fig 3d). There were no differences in spider functional evenness (FEve), spider functional dispersion (FDis), or ant functional evenness among years and between plot types. These variables were also unaffected by the year-by-plot-type interaction (Tables 1 and 2).

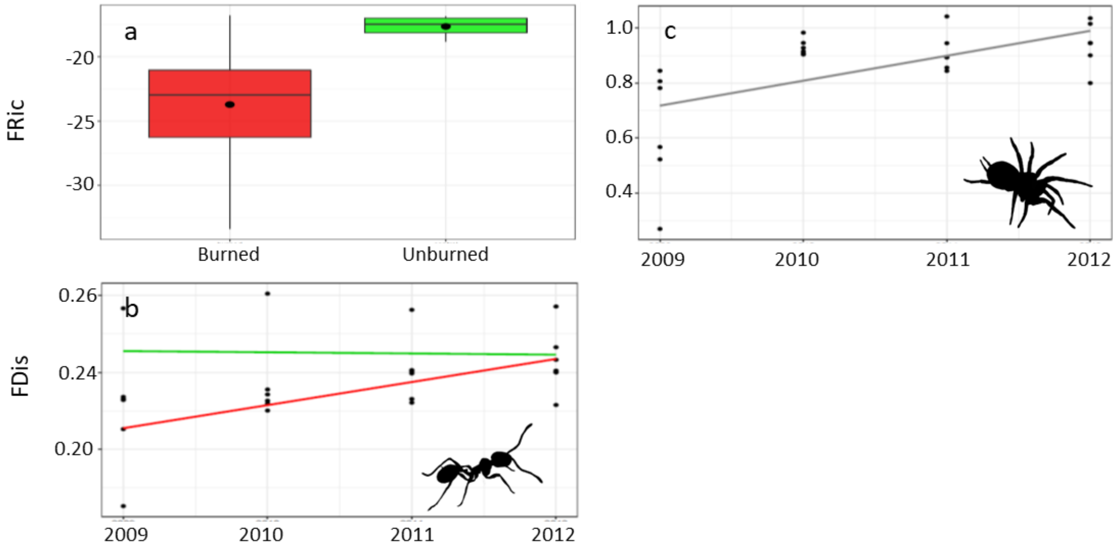


Figure 3. Mean (± SE) log-transformed ant functional richness in burned versus unburned plots (a); the relationship between sampling year and ant functional dispersion; (b) the relationship between sampling year and spider functional richness (c) and the relationship between sampling year and spider functional dispersion (d). The gray line indicates the linear fit of the model, and the colors indicate the linear fit of the models for each plot type (red = burned; green = unburned).

Table 2: Statistical output of the linear mixed-effects and quadratic models analyzing the effects of fire (plot type: burned vs. unburned), sampling year (year and year^2), and their interaction on square-root-transformed abundance, taxonomic richness (S), Shannon diversity (H), Pielou's evenness (J), functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) for the spider communities. -, indicates that the quadratic year term was not used in the linear models. The blank spaces correspond to quadratic models that had a poor fit for a particular explanatory variable. In bold are the significant values for a given explanatory variable in a given model.

Spiders								
	Linear model				***Qadratic model***			
Abundance$^{1/2}$	DF	F-value	p-value	AIC	DF	F-value	p-value	AIC
Fire	1,4	0.97	0.381	116.28	1,4	1.56	0.279	**107.06**
Year	1,16	18.04	<0.001		1,14	**29.18**	**<0.001**	
Year^2	-	-	-		1,14	**12.82**	**0.003**	
Fire x Year	1,16	6.95	0.018		1,14	**11.24**	**0.005**	
Fire x Year^2	-	-	-		1,14	1.53	0.237	
Taxonomic richness (S)								
Fire	1,4	0.00	0.961	147.29	1,4	0.00	0.955	**132.596**
Year	1,16	14.43	0.002		1,14	**29.52**	**0.000**	
Year^2	-	-	-		1,14	**17.85**	**0.001**	
Fire x Year	1,16	3.67	0.074		1,14	**7.50**	**0.016**	
Fire x Year^2	-	-	-		1,14	2.70	0.123	
Shannon diversity (H)								
Fire	1,4	6.19	0.068		-	-	**-**	
Year	1,16	**21.96**	**0.000**		-	-	-	
Year^2	-	-	-		-	-	-	
Fire x Year	1,16	**5.52**	**0.032**		-	-	-	
Fire x Year^2	-	-	-		-	-	-	
Pielou's evenness (J)								
Fire	1,4	6.06	0.070		-	-	-	
Year	1,16	0.30	0.594		-	-	-	
Year^2	-	-	-		-	-	-	
Fire x Year	1,16	0.00	0.987		-	-	-	
Fire x Year^2	-	-	-		-	-	-	
Functional richness (FRic)								
Fire	1,4	2.63	0.180	**-0.971**	1,4	3.41	0.139	5.545
Year	1,16	**13.39**	**0.002**		1,14	17.33	0.001	
Year^2	-	-	-		1,14	7.69	0.015	
Fire x Year	1,16	2.41	0.140		1,14	3.12	0.099	
Fire x Year^2	-	-	-		1,14	0.21	0.656	
Functional evenness (FEve)								
Fire	1,4	6.06	0.070		-	-	**-**	
Year	1,16	0.30	0.594		-	-	-	

Year^2	-	-	-		-	-	-	
Fire x Year	1,16	0.00	0.987		-	-	-	
Fire x Year^2	-	-	-		-	-	-	
Functional dispersion (FDis)								
Fire	1,4	1.05	0.364	**-42.497**	1,4	1.05	0.364	-39.794
Year	1,16	0.02	0.887		1,14	0.05	0.825	
Year^2	-	-	-		1,14	17.66	0.001	
Fire x Year	1,16	0.50	0.490		1,14	1.23	0.286	
Fire x Year^2	-	-	-		**1,14**	**7.88**	**0.014**	

The functional composition of ant communities was affected by plot type, sampling year, and their interaction (PERMANOVA: plot type—F = 1.6, p = 0.003, R^2 = 0.06; sampling year—F = 3.1, p = 0.003, R^2 = 0.12; interaction—F = 1.4, p = 0.020, R^2 = 0.05, Fig. 4a). The functional composition of spider communities was also affected by plot type (F = 5.7, p = 0.004, R^2 = 0.16), sampling year (F = 7.4, p = 0.004, R^2 = 0.20), and their interaction (F = 3.0, p = 0.014, R^2 = 0.08) (Fig. 4b). The assumption of homogeneity of dispersion was met for both ants (p = 0.08) and spiders (p = 0.302). Similarly, the functional composition of ant and spider communities differed between plot types and among sampling years (Fig. 4a,b). In the unburned plots, we observed ant species that build their nests in the vegetation; that forage individually; and that consume a sugar-based diet. In the burned plots, we observed ant species that are predominantly diurnal; that consume insect- and seed-based diets; that forage collectively; and that display dependent colony foundation, polydomy, and polygyny (Fig. 4a). In the unburned plots, we found spiders that are predominantly nocturnal and that hunt using webs. In the burned plots, we found spiders that are predominantly diurnal; that hunt using an ambush strategy; that excavate burrows; and that have specialized diets. We did not see a clear effect on body size distribution for either taxa. The functional composition of the spider communities in the burned plots differed between 2009 and the other three years of the study; in 2009, the burned plots were more similar to the unburned plots. Traits like ambush hunting and burrowing were more common in the burned plots in 2009 (Fig. 4).

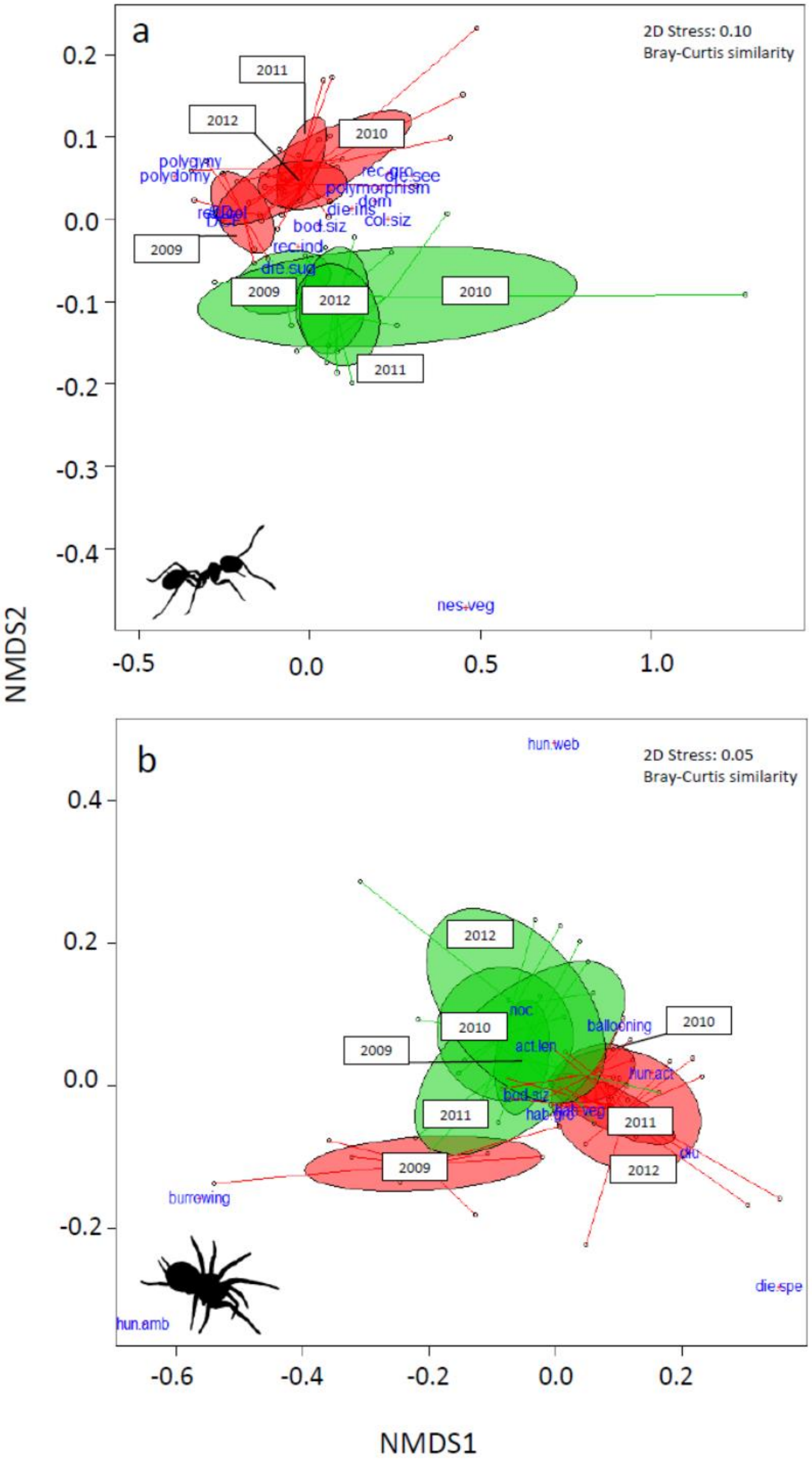


Figure 4. Results of the NMDS analysis of community trait composition for ants (a) and spiders (b). The ovals depict the standard deviation of the point scores and represent the different sampling years. The colors indicate plot type (red = burned; green = unburned).

We observed some strong correlations (rho ≥ 0.9) between the focal traits for both taxa (Appendix C: Tables C.3 and C.4). For the ants, it was interesting to note that dependent colony foundation (DCF) was negatively correlated with having an insect-based diet. Competitive dominance was positively correlated with collective foraging, worker polymorphism, and colony size. Moreover, colony size was correlated with collective foraging. Having a sugar-based diet was positively correlated with nesting in vegetation (Table C.3). In spiders, ballooning was positively correlated with active hunting and was negatively correlated with ambush hunting and burrowing. The length of time that females remained active was negatively correlated with being strictly diurnal and having a specialized diet. Active hunting was negatively correlated with burrowing. Ambush hunting was positively correlated with body size and burrowing. Both active and ambush hunting were negatively correlated with foraging for food on the ground. Finally, burrowing was positively correlated with body size.

Discussion

In this study, we examined the taxonomic and functional responses of both ant and spider communities to a wildfire that completely changed forest habitat conditions. We sampled immediately after the fire and over the subsequent four years. This longitudinal approach allowed us to clarify the patterns and mechanisms associated with the short-term survival, persistence, and colonization dynamics of two distinct taxa. This work is an important step in establishing a theoretical framework for understanding invertebrate responses to forest wildfires and for developing appropriate biodiversity monitoring strategies. We observed that although taxonomic and functional diversity displayed parallel responses to fire, such responses were also taxon specific. This result highlights the importance of approaching diversity from several perspectives and using different taxonomic groups, especially if the ultimate objective is to inform conservation efforts.

Our first hypothesis predicted that the taxonomic and functional diversity of both ant and spider communities would decrease immediately after the fire and that the effect would be more dramatic for spiders than ants. This prediction was not supported by our results. Notably, several diversity indices did not differ between plot types for either group immediately after the fire. In fact, contrary to our expectations, the effects of fire were always more marked in ants than in spiders. More specifically, we found that ant FDis was lower after the fire but increased over the years. We also observed that fire negatively affected ant richness, diversity, and FRic but did not spider taxonomic and functional diversity in any form. Past research has revealed that arthropod taxonomic diversity can respond in a wide variety of ways to fire (review in Kral & al. 2017). Our results are similar to those seen in earlier studies, which found that fire had a weak effect on spider taxonomic diversity (Underwood and Quinn, 2010) and that the immediate taxonomic responses of spiders to fire were generally positive or neutral (Podgaiski et al., 2013). In contrast, in ants, the immediate taxonomic responses to fire can be neutral (Underwood and Quinn, 2010), positive (Andersen et al., 2014; Maravalhas and Vasconcelos, 2014), or negative (Punttila and Haila, 1996; Verble-Pearson and Yanoviak, 2014). This greater variability of responses might be due to differences in habitat type and plant species composition (Andersen, 2019) as well as in fire intensity, frequency, and/or severity. In our case, the sampling area was dominated by the sub-Mediterranean pine species Pinus nigra, a species that does not recover from crown wildfires (Rodrigo et al., 2004). As a result, the ants were negatively affected by the major environmental modifications that took place. Interestingly, the effects on taxonomic diversity translated into effects on functional diversity in ants. This result furnishes further evidence that strong linear relationships exist between taxonomic and functional diversity along successional gradients in forests, as previously observed in trees (Lohbeck et al., 2012) and in ants (Rocha-Ortega et al., 2018). It also provides support for the predictions of the niche complementarity hypothesis: the presence of more species should lead to the more exhaustive use of resources, resulting in higher rates of ecosystem functioning (Tilman et al., 1997). Whatever the case, we have demonstrated that ant communities are not necessarily more resistant than spider communities to fire.

Our second hypothesis predicted that the taxonomic and functional diversity of both the ant and spider communities would increase over time, with the spiders recovering more quickly than the ants. We found support for this hypothesis. While spider abundance and richness initially declined after the fire, both recovered within two years, a result that has been seen in other studies (Polchaninova et al., 2016; Vasconcelos et al., 2009). In ants, several taxonomic and functional variables were affected by fire (richness, diversity, Fric, and FDis) and did not recover over the four years of the study, with the exception of FDis. Past work suggests that dramatic variability exists in how well ant communities recover following a fire. Some studies have found that the taxonomic structure of ant communities can completely recover quite quickly (in 1–8 months; Parr et al., 2004; Verble-Pearson and Yanoviak, 2014) and that ants may even be among the first wave of colonizers following forest fires (Antunes et al., 2009). However, other studies have shown that ant community structure may not have recovered fully even 8 years later (Arnan et al., 2006). This variability may be shaped by forest type, which influences forest recovery dynamics (Arnan et al., 2006) and/or the ability of ants to persist under post-fire conditions (Parr et al., 2004). Following a fire, ant taxonomic and functional diversity may decrease because of changes in vegetation structure (Arnan et al., 2007), temperature (Arnan et al., 2014; Raymons et al., 2013), aridity (Arnan et al., 2018), resource availability (Lázaro-González et al., 2013), and the functional properties of soils (Antunes et al., 2009). Indeed, certain species in our study area—namely species that have strong associations with the vegetation (e.g., *Crematogaster scutellaris*, *Lasius myops*, and *Camponotus lateralis*) and/or that have cryptic lifestyles (e.g., *Temnothorax* species)—cannot cope with the new environmental conditions. More specifically, temperature and aridity climb as a result of post-fire conditions, as the cover previously provided by the tree canopy has disappeared. This situation can intensify the fire's negative effects and reduce the diversity of food acquisition strategies represented within the community (Arnan et al., 2018), thus impeding recovery. It is important to note that the practical constraints of sampling hinder replication. Indeed, it is often challenging to successfully implement a fully segregated sampling regime in fire ecology research (Parr and Chown, 2003). While this limitation might have reduced the statistical power of our models, our rarefaction curves suggest otherwise. They showed that ant taxonomic richness and Shannon diversity were higher for the two unburned plots than for the four burned plots, which indicates that our sampling efforts were sufficient to detect consistent differences between plot types.

Our third hypothesis predicted that the burned and unburned plots would contain different types of species displaying certain sets of traits. In the burned plots, we expected to see species more typically found in open areas, notably those that build their nests and search for food in/on the ground and that disperse longer distances. In the unburned plots, we expected to see species more typically associated with vegetated habitats, such as those that disperse shorter distances. Our results support this hypothesis: we found significant differences in the taxonomic and functional composition of ant and spider communities between the burned and unburned plots. Examining the species' traits more closely revealed more detailed patterns.

First, the likelihood of surviving the fire was enhanced by certain traits. Ants or spiders that nest in the ground or that excavate burrows (e.g., ants: *Pheidole pallidula*, *Tetramorium semilaeve*; spiders: *Atypus affinis*, *Eresus* sp.) (Antunes et al., 2009) had higher survival rates than species that live in close association with the vegetation (Matsuda et al., 2011). Indeed, in the burned plots, we less frequently observed ants that nest in the vegetation (e.g., *Crematogaster scutellaris* and several *Temnothorax* spp.) and spiders that use the vegetation when building webs or hunting (e.g., *Saites barbipes*, *Cercidia prominens*, *Hahnia* sp., and Linyphiidae spp.). Because they rely more heavily on the vegetation, tree-dwelling ants and spiders were more negatively affected by the fire (Moretti et al., 2002; Underwood and Quinn, 2010).

Second, persistence following the fire was enhanced by other traits. The survivors had to cope with warmer, drier, and structurally simplified habitats. Past work has shown that the surface upon which ants and spiders forage (e.g., the vegetation or the ground) and the type of food resources they exploit can also influence species persistence (Arnan et al., 2007; Rodrigo and Retana, 2006). Consequently, we expected that species foraging on the vegetation would be more negatively affected by post-fire conditions. What we found was that species in the burned plots displayed certain dietary traits (insect- and seed-based diets in ants, specialized diets in spiders) and foraging/hunting strategies (collective foraging in ants and ambush hunting in spiders). The availability of different food resources can shift dramatically following fire (Arnan et al., 2007) because burned areas are more open, resulting in a greater abundance of dead insects (due to greater sun exposure) and seeds (from successional, herbaceous plants). It thus made sense that persistence levels were higher for ant species (e.g., *Iberoformica subrufa*, *Pheidole pallidula*, and *Tetramorium semilaeve*) that collectively forage upon these resources (Arnan et al., 2015; Retana et al., 1992). The two most abundant epigeic spider genera in the burned plots were generalist insectivores and strict myrmecophages (*Pardosa* sp. and Zodarion sp., respectively), which is likely linked to the presence of ants in the plots. Post-fire conditions also favored the persistence of spiders that ambush their prey rather than using webs (e.g., *Synema globosum* and *Nemesia* sp.) since little to no vegetation was available for web building. In addition, the burned plots contained ants and spiders that are predominantly diurnal, probably because the thermophilic species in the two taxa are predominantly diurnal and prefer open habitats. In contrast, in the unburned plots, ants tended to be group foragers, and spiders tended to use web-based hunting. This pattern likely resulted because the unburned plots contained a large number of *Temnothorax* species, which all forage collectively. As for the spiders, they generally belonged to genera (or species) that build webs on the vegetation. In fact, some species in the ant genus *Temnothorax* and in the spider family Linyphiidae are commonly found in intact forests and serve as bioindicators of forest health (Moretti et al., 2002) because they are very sensitive to disturbance.

However, one facet of our third hypothesis was not supported because the burned plots did not contain ants and spiders capable of dispersing longer distances. The ant species observed in the burned plots use dependent colony foundation (DCF), a system in which a portion of a mature colony slowly disperses a short distance to found a new colony. This finding contrasts with that of Punttila and Haila (1996), who found that ants in burned areas utilized independent colony foundation (ICF). It is important to note, though, that their study was experimental, and they quantified the presence of founding queens in artificial nest sites and stumps. In contrast, in our study, we indirectly identified colonizers based on worker presence in pitfall traps. This difference in methodologies could explain the difference in results because, in the first few years following nest foundation, ICF colonies have smaller numbers of foragers, while DCF colonies have larger numbers of foragers (between 1/3 to 1/4 of the number in the mother colony; Amor et al., 2011; Chéron et al., 2011). As a consequence, it would be harder to detect the presence of ICF species versus DCF species using pitfall trapping. Another factor to consider is the distance between the burned and unburned plots. In our study, this distance was not always very large, and the burned plots could thus have acted as reservoirs (Antunes et al., 2009). However, it is important to note that DCF was strongly and negatively correlated with having an insect-based diet, so we cannot know whether one or both traits were directly operated on by fire. It is possible that we did not find more ICF species in the burned plots simply because certain resources (e.g., liquid resources) were absent. In our study area, many of the ant species displaying ICF (62%) also have a sugar-based diet, which is largely composed of flower nectar and honeydew. Honeydew production is higher in forests than in open areas because the aphids responsible for its production display higher yields when feeding on woody versus herbaceous plants (Dixon 1975). We also predicted that the burned plots would contain more species of spiders that use ballooning, a behavior whereby juveniles move through the air using silk threads (Bell et al., 2005). This dispersal strategy allows spiders to move longer distances. However, ballooning species were found in both the burned and the unburned plots, probably because this trait is displayed by the majority (63%) of the spider genera that we observed in our study area (Bell et al., 2005). It is also possible that the strong and negative correlation we found between ballooning and ambush hunting could have biased the ballooning results.

It is worthwhile to consider whether these responses to disturbance could influence ecosystem functioning. First, ecosystems can display functional resistance if a disturbance eliminates certain species, but remaining species and/or new species can serve the same functions as those that have disappeared. We observed that, in ants, both taxonomic and functional diversity were affected by fire; in spiders, in contrast, neither diversity type was dramatically affected. Second, ecosystems can display functional resilience if changes in community composition result in a new community that is functionally similar. Such was not the outcome in our study system: there were pronounced differences in the functional traits represented in the burned versus unburned plots (e.g., nesting site, foraging and hunting strategies, and diurnality). Overall, we discovered that there were major changes in the taxonomic composition of ant and spider communities that then translated into functional changes. Past research has highlighted that functional diversity has a greater influence than taxonomic diversity on ecosystem processes (Gagic et al., 2015). As a result, the functional changes we observed might have important consequences for ecosystem functioning.

Conclusions

We found that forest fire can affect both ant and spider communities and that the effect is greater on the former than the latter. The fire changed both community structure (taxonomic and functional diversity) and composition in ants. In contrast, it had little effect on the structure of spider communities, although it did impact their taxonomic and functional composition. In their responses to fire, ants were not more resistant than spiders, but spiders were more resilient than ants. However, the effects of fire were certainly taxon dependent. By conducting an analysis of taxonomic and functional diversity across taxa, we were able to clarify the biotic responses of major arthropod groups to disturbance and explore the mechanisms in operation over time (i.e., survival, persistence, and colonization). Furthermore, we identified traits that allow species to better survive, persist, and colonize. We can use this information to analyze the functional composition of communities and then predict their responses to fire. We call for more long-term studies that will further enhance our knowledge in this area. Such research will greatly improve our ability to predict ecosystem responses, manage biodiversity, and implement conservation programs in the face of global changes.

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Appendix A

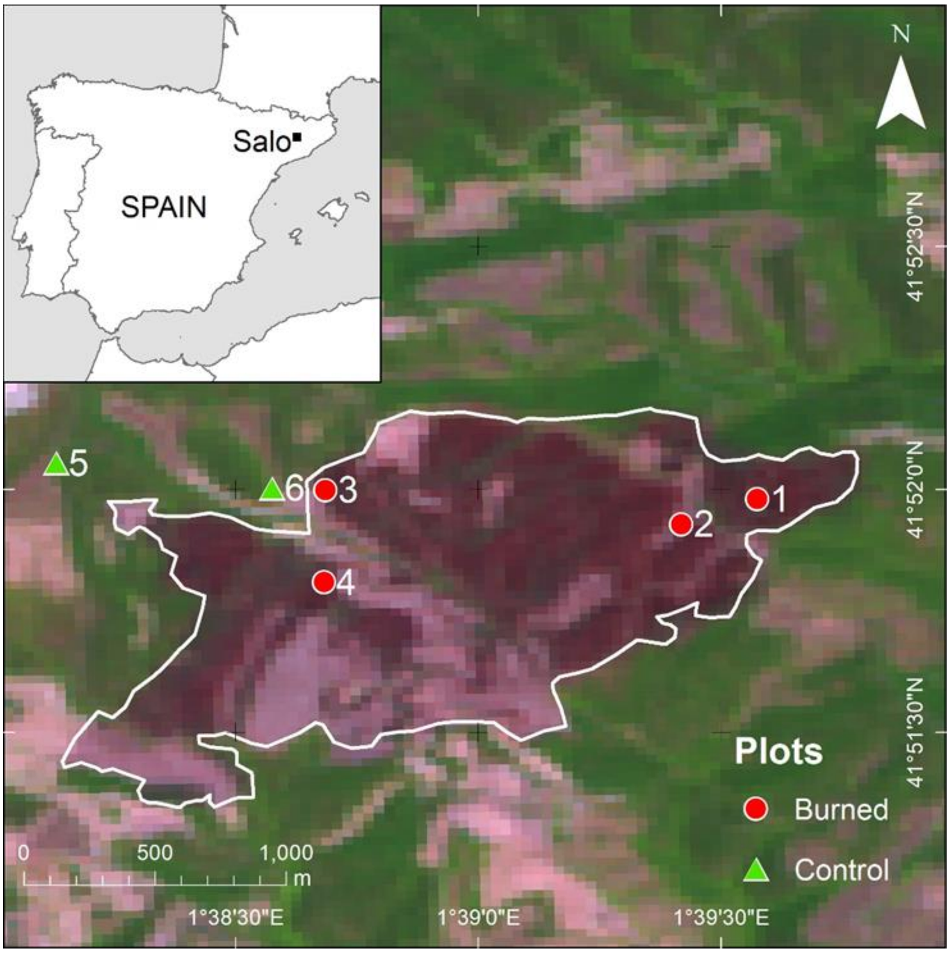


Figure A.1: Location of burned (red circles) and unburned (green triangles) sampling plots in the study area (Salo, Catalonia, north-eastern Spain). Background image is a false color composition (SWIR, NIR, Red) from 1 July 2009 Landsat 5 tematic mapper (TM) after the fire (short wave infrared, near infrared, red) (SWIR, NIR, Red).

Appendix B

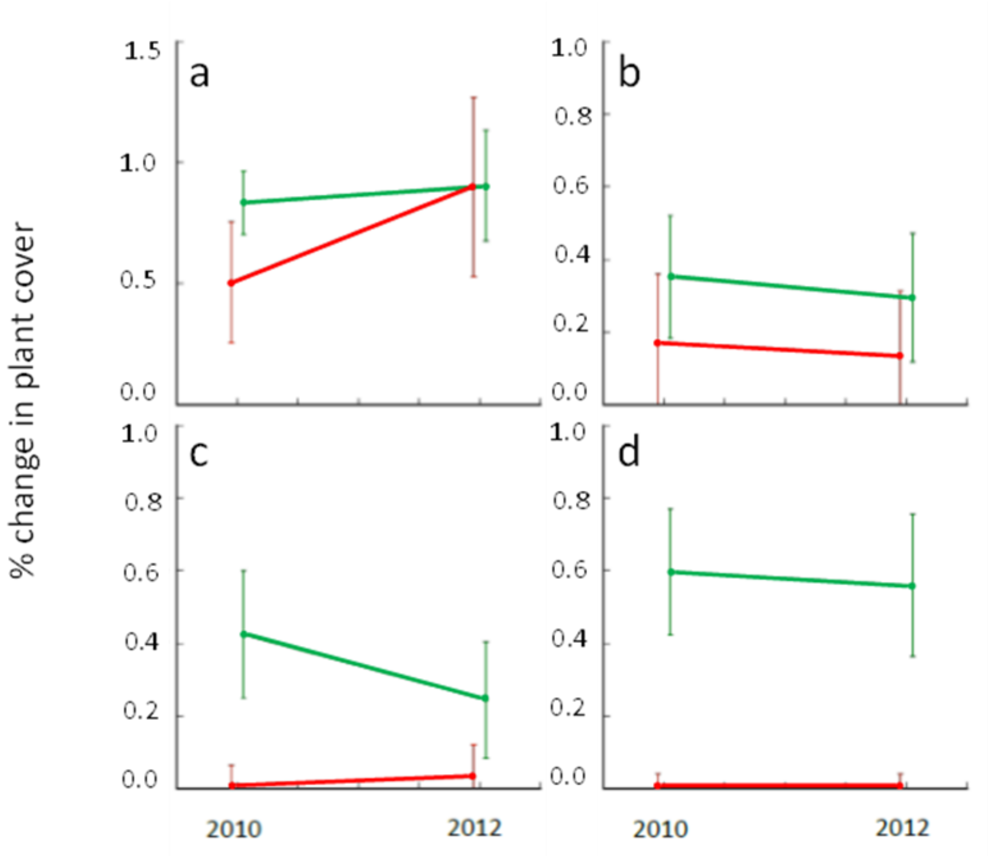


Figure B.1: Changes of vegetation cover between 2010 and 2012: a) herbs; b) low shrubs; c) high shrubs; d) trees. Vegetation cover was assessed in the 6 sampling plots (4 burned plots, red lines, and 2 control unburned plots, green lines) in July 2010 and July 2012. Values are mean±SD. See more details about methods in Table B.1.

Table B.1: Statistical outputs of the linear mixed effect models analysing of effects of fire, year and its interaction on each category of vegetation cover. In bold, significant p values after the sequential Benjamini & Hochberg (1995) correction [1]. Vegetation cover was assessed in the 6 sampling plots (4 burned plots, red lines, and 2 control unburned plots, green lines) in July 2010 and July 2012. For that purpose, four vegetal strata (herbaceous = 0.5 m, low shrub = 0.5-1.5 m, high shrub = 1.5-2.5 m and arboreal) were recorded every half meter in July 2010 and every meter in July 2012 along two 50 m transects per plot. Vegetation transects were parallel (1 m) to the pitfall trap transects.

Vegetation cover	Effect	DF	F	Adjusted p
Herbs	Fire	1, 4	2.93	0.278
	Year	1, 10	**20.13**	**0.002**
	Fire x Year	1, 10	5.73	0.076
Small shrubs	Fire	1, 4	10.44	0.076
	Year	1, 10	1.048	0.453
	Fire x Year	1, 10	0.056	0.817
Large shrubs	Fire	1, 4	**40.18**	**0.013**
	Year	1, 10	0.96	0.453
	Fire x Year	1, 10	4.15	0.117
Trees	Fire	1, 4	**698.43**	**0.001**
	Year	1, 10	0.37	0.600
	Fire x Year	1, 10	0.75	0.481

[1] Benjamini Y, Hochberg Y (1995) Controlling the False Discovery Rate: a Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society. Series B 57: 289–300.

Appendix C

Table C.1: Description of the ant functional traits used in this study. Traits were obtained from [2].

Trait group	**Functional traits**	**Data type**	**States**	**Abbrev.**
Survival	Nesting site	Binary	Ground	
			Vegetation	veg.nes
Persistence	Behavioral dominance	Binary	Subordinate	
			Dominant	dom
	Body size	Quantitative	Worker size mean (1.6-10.0)	bod.siz
	Colony size	Quantitative	Colony size mean (50-20000)	col.siz
	Number of nests	Binary	Monodomy	
			Polydomy	pol.dom
	Number of queens	Binary	Monogyny	
			Polygyny	pol.gyn
	Diurnality	Binary	Non- predominantly diurnal (NSD)	
			Predominantly diurnal (SD)	SD
	Foraging strategy	Nominal	1, Individual	rec.ind
			2, Group	rec.gro
			3, Collective	rec.col
			4, Various	
	Diet - Insects	Binary	(0) No	
			(1) Yes	ins.die
	Diet - Seeds	Binary	(0) No	
			(1) Yes	see.die
	Diet - Sugar	Binary	(0) No	
			(1) Yes	sug.die
	Worker polymorphism	Binary	Low polymorphism	
			High polymorphism	poly
Colonization	Colony foundation type	Binary	Dependent Colony Foundation (DCF)	DCF
			Independent Colony Foundation (ICF)	

[2] Arnan X, Cerdá X , Rodrigo A, Retana J (2013) Response of ant functional composition to fire. Ecography 36:1182–1192. // Retana J, Arnan X, Cerdá X (2015) A multidimensional functional trait analysis of resource exploitation. Ecology 96: 2781–2793.

Table C.2: Description of the spider functional traits used in this study. Superscript letters indicate references where traits were obtained.

Trait group	Functional traits	Data type	States	Abbrev.
Survival	Burrowing[c,d]	Binary	No	
			Yes	bur
	Microhabitat[c]	Nominal	Ground	hab.gro
			Vegetation	hab.veg
			Both	
Persistence	Activity length (female)[a]	Ordinal	(1) Short (3-5 months)	
			(2) Medium (6-7 months)	
			(3) Long (>7 months)	act.len
	Activity[c]	Binary	Non-strictly diurnal (NSD)	
			Strictly diurnal (SD)	act.diu
	Body size (female)[a,b,d,e]	Ordinal	(1) Very small (<3.1mm)	
			(2) Small (3.1-4.5mm)	
			(3) Medium (4.6-8.5mm)	
			(4) Large (>8.5mm)	bod.siz
	Diet specialization[c,d]	Binary	No	
			Yes	die.spe
	Hunting strategy[a,b,c,d]	Nominal	Active	hun.act
			Ambush	hun.amb
			Active and ambush	hun.bot
			Web	hun.web
Colonization	Ballooning[a,b,d,e]	Binary	No	
			Yes	bal

[a] Pedley SM, Dolman PM (2014) Multi-taxa trait and functional responses to physical disturbance. J Anim Ecol: 1542–1552.

[b] Schirmel J, Blindow I, Buchholz S (2012) Life-history trait and functional diversity patterns of ground beetles and spiders along a coastal heathland successional gradient. Basic and Applied Ecology 13: 606–614.

[c] Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. – PLoS One 6: e21710.

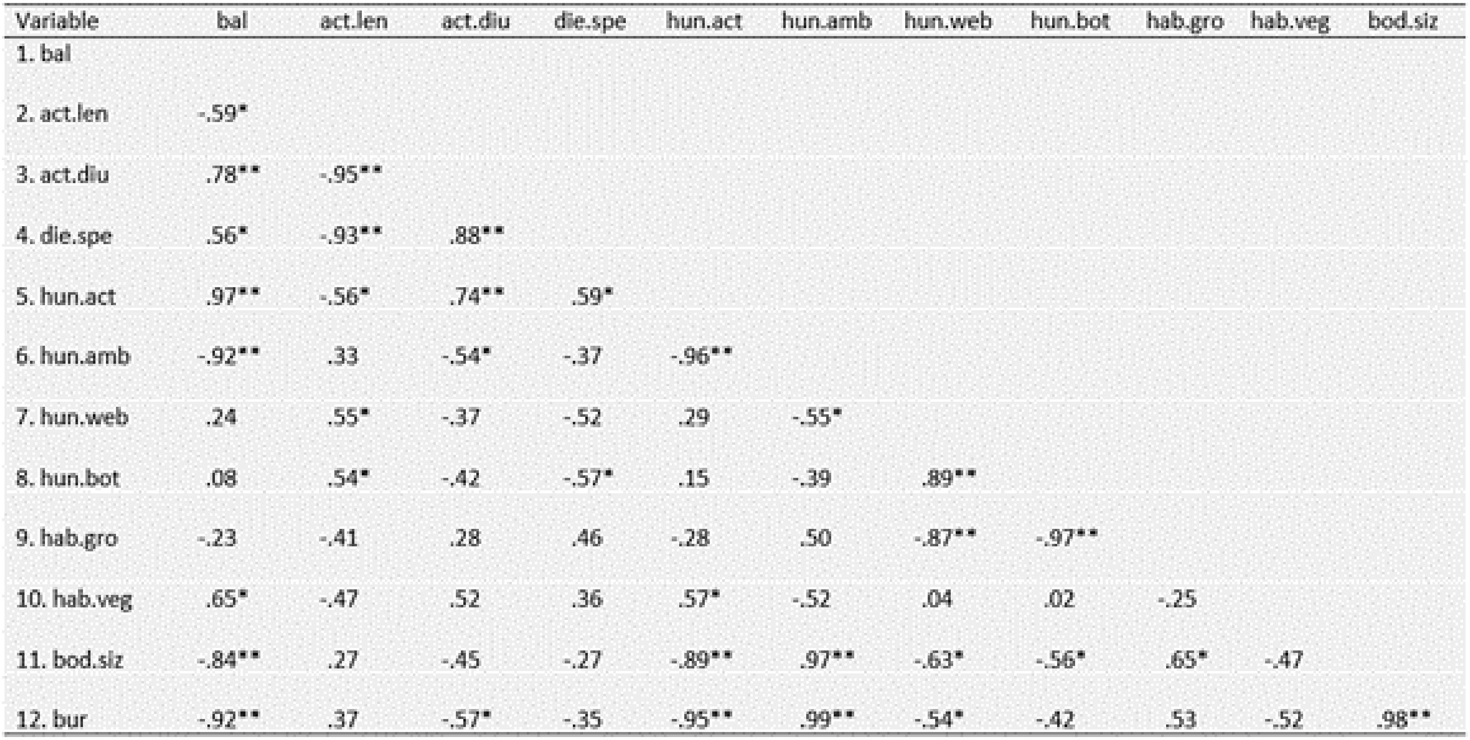
[d] Langlands PR, Brennan KEC, Framenau VW, Main BY (2011) Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. J Anim Ecol 80: 558–568.

[e] Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bull. Entom. Res. 95: 69–114.

Table C.3: Correlations of the studied ant traits. Spearman's rho statistic is used to estimate a rank-based measure of association. * indicates p < .05. ** indicates p < .01. Trait abbreviations listed in Table C.1

Variable	DCF	pol.dom	pol.gyn	dom	SD	rec.col	rec.gro	rec.ind	ins.die	see.die	sug.die	veg.nes	bod.siz	poly
1. DCF														
2. pol.dom	.68**													
3. pol.gyn	.77**	.67**												
4. dom	.44	.21	.81**											
5. SD	-.75**	-.19	-.45	-.46										
6. rec.col	.26	.26	.74**	.94**	-.27									
7. rec.gro	-.62*	-.46	-.56*	-.55*	.81**	-.55*								
8. rec.ind	.47	.37	-.08	-.35	-.57*	-.39	-.54*							
9. ins.die	-.94**	-.41	-.63*	-.42	.86**	-.16	.57*	-.46						
10. see.die	-.45	-.16	.19	.48	.52*	.64*	.22	-.88**	.55*					
11. sug.die	.53*	.07	-.07	-.26	-.72**	-.46	.84**	-.38	-.68**	-.96**				
12. veg.nes	.60*	.17	.11	-.02	-.86**	-.16	.87**	-.68*	-.71**	-.83**	.93**			
13. bod.siz	-.36	-.19	-.16	-.19	.70**	-.25	.88**	-.69**	.35	.38	-.50	-.76**		
14. poly	.13	-.05	.61*	.91**	-.15	.85**	-.17	-.69**	-.15	.71**	-.51	-.36	.17	
15. col.siz	.53*	.34	.88**	.98**	-.48	.94**	-.61*	-.27	-.46	.43	-.23	.02	-.25	.85**

Table C.4: Correlations of the studied spider traits. Spearman's rho statistic is used to estimate a rank-based measure of association. * indicates p < .05. ** indicates p < .01. Trait abbreviations listed in Table C.2.



Variable	bal	act.len	act.diu	die.spe	hun.act	hun.amb	hun.web	hun.bot	hab.gro	hab.veg	bod.siz
1. bal											
2. act.len	-.59*										
3. act.diu	.78**	-.95**									
4. die.spe	.56*	-.93**	.88**								
5. hun.act	.97**	-.56*	.74**	.59*							
6. hun.amb	-.92**	.33	-.54*	-.37	-.96**						
7. hun.web	.24	.55*	-.37	-.52	.29	-.55*					
8. hun.bot	.08	.54*	-.42	-.57*	.15	-.39	.89**				
9. hab.gro	-.23	-.41	.28	.46	-.28	.50	-.87**	-.97**			
10. hab.veg	.65*	-.47	.52	.36	.57*	-.52	.04	.02	-.25		
11. bod.siz	-.84**	.27	-.45	-.27	-.89**	.97**	-.63*	-.56*	.65*	-.47	
12. bur	-.92**	.37	-.57*	-.35	-.95**	.99**	-.54*	-.42	.53	-.52	.98**

Appendix D

Table D.1: List of ant species grouped into subfamilies and ordered in alphabetical order with the total occurrence of each species in each treatment (unburned and burned sites) and in brackets, the number of samplings in which the species has been found of the 22 total samplings in unburned plots and 44 samplings in burned plots.

Species	Unburned	Burned
Dolichoderinae		
Tapinoma nigerrimum	72 (14)	72 (31)
Formicinae		
Camponotus aethiops	124 (22)	212 (38)
Camponotus cruentatus	77 (19)	77 (18)
Camponotus lateralis	69 (16)	11 (5)
Camponotus piceus	20 (10)	67 (21)
Camponotus pilicornis	117 (20)	224 (43)
Cataglyphis iberica	20 (10)	149 (16)
Formica frontalis	0 (0)	1 (1)
Formica gagates	209 (20)	288 (26)
Formica gerardi	91 (19)	403 (44)
Formica rufibarbis	0 (0)	2 (1)
Iberoformica subrufa	3 (3)	60 (19)
Lasius myops	12 (8)	10 (6)
Plagiolepis pygmaea	124 (19)	186 (35)
Polyergus rufescens	1 (1)	10 (5)
Myrmicinae		
Aphaenogaster gibbosa	129 (21)	492 (44)
Aphaenogaster subterranea	75 (11)	2 (2)
Crematogaster scutellaris	66 (19)	10 (8)
Crematogaster sordidula	34 (10)	0 (0)
Messor capitatus	18 (6)	9 (9)
Myrmica spinosior	89 (22)	232 (43)
Pheidole pallidula	276 (22)	577 (44)
Solenopsis latro	8 (5)	21 (15)
Temnothorax angustulus	2 (2)	0 (0)
Temnothorax aveli	2 (1)	0 (0)
Temnothorax gredosi	19 (10)	0 (0)
Temnothorax kraussei	11 (8)	0 (0)
Temnothorax lichtensteini	76 (15)	1 (1)
Temnothorax luteus	33 (12)	3 (3)
Temnothorax niger	2 (2)	10 (5)
Temnothorax nylanderi	11 (5)	0 (0)
Temnothorax parvulus	49 (10)	1 (1)
Temnothorax racovitzai	16 (2)	10 (3)
Temnothorax recedens	91 (21)	3 (3)
Temnothorax tuberum	3 (3)	0 (0)
Tetramorium forte	3 (3)	31 (18)
Tetramorium semilaeve	0 (0)	1 (1)

Table D.2: List of spider genus grouped into families and ordered in alphabetical order with the total abundance of each species in each treatment (unburned and burned sites) and in brackets, the number of samplings in which the genus has been found of the 22 total samplings in unburned plots and 44 samplings in burned plots.

Genera	**Unburned**	**Burned**
Agelenidae		
Agelena spp.	0 (0)	1 (1)
Lycosoides spp.	1 (1)	0 (0)
Tegenaria spp.	49 (10)	46 (21)
Textrix spp.	0 (0)	1 (1)
Amaurobidae		
Coleotes terrestris	0 (0)	1 (1)
Araneidae		
Cercidia prominens	4 (3)	0 (0)
Neoscona adianta	1 (1)	0 (0)
Atypidae		
Atypus affinis	0 (0)	1 (1)
Clubionidae		
Clubiona spp.	1 (1)	2 (2)
Dictynidae		
Argenna spp.	0 (0)	1 (1)
Dysderidae		
Dysdera spp.	4 (3)	0 (0)
Parachtes spp.	5 (5)	0 (0)
Eresidae		
Eresus spp.	0 (0)	2 (2)
Gnaphosidae		
Aphantaulax spp.	0 (0)	1 (1)
Callilepis spp.	83 (8)	103 (20)
Drassodes spp.	8 (6)	20 (14)
Drassyllus spp.	2 (1)	2 (2)
Gnaphosa spp.	0 (0)	5 (3)
Haplodrassus spp.	1 (1)	2 (2)
Micaria spp.	24 (9)	111 (13)
Nomisia spp.	12 (5)	69 (23)
Poecilochroa spp.	2 (2)	3 (2)
Pterotricha simoni	1 (1)	0 (0)
Setaphis spp.	0 (0)	11 (6)
Trachyzelotes spp.	2 (1)	1 (1)
Zelotes spp.	40 (13)	49 (22)
Hahniidae		
Hahnia spp.	0 (0)	1 (1)
Linyphiidae	87 (15)	86 (20)
Liocranidae		
Scotina spp.	22 (9)	1 (1)
Lycosidae		
Alopecosa spp.	73 (11)	141 (21)

Hogna spp.	2 (1)	23 (10)
Pardosa spp.	71 (19)	826 (40)
Trabea spp.	168 (16)	6 (4)
Trochosa spp.	27 (11)	9 (8)
Nemesiidae		
Nemesia spp.	43 (11)	64 (17)
Oxyopidae		
Oxyopes spp.	2 (2)	12 (10)
Palpimanidae		
Palpimanus gibbulus	1 (1)	3 (3)
Philodromidae		
Philodromus spp.	1 (1)	3 (2)
Thanatus spp.	4 (2)	17 (9)
Tibellus spp.	1 (1)	1 (1)
Pisauridae		
Pisaura mirabilis	8 (4)	20 (11)
Salticidae		
Aelurillus v.insignitus	0 (0)	57 (18)
Ballus spp.	1 (1)	2 (2)
Dendryphantes spp.	0 (0)	3 (3)
Euophrys spp.	1 (1)	5 (5)
Evarcha spp.	14 (10)	19 (13)
Heliophanus spp.	2 (2)	21 (12)
Leptorchestes spp.	1 (1)	2 (2)
Neaetha membrosa	0 (0)	24 (13)
Pellenes spp.	3 (2)	99 (19)
Philaeus jugatus	0 (0)	1 (1)
Phlegra spp.	13 (6)	40 (19)
Saitis barbipes	60 (10)	5 (4)
Sparassidae		
Olios argelasius	2 (2)	0 (0)
Theridiidae		
Neottiura spp.	19 (6)	5 (5)
Steatoda albomaculata	0 (2)	17 (7)
Thomisidae		
Synema globosum	2 (2)	14 (11)
Tmarus spp.	1 (1)	0 (0)
Xysticus spp.	4 (3)	71 (20)
Titanoecidae		
Nurscia spp.	0 (0)	38 (8)
Zodariidae		
Amphiledorus spp.	17 (3)	11 (7)
Selamia reticulata	19 (9)	10 (8)
Zodarion spp.	24 (9)	332 (40)
Zoridae		
Zora spp.	30 (14)	7 (4)

Appendix E

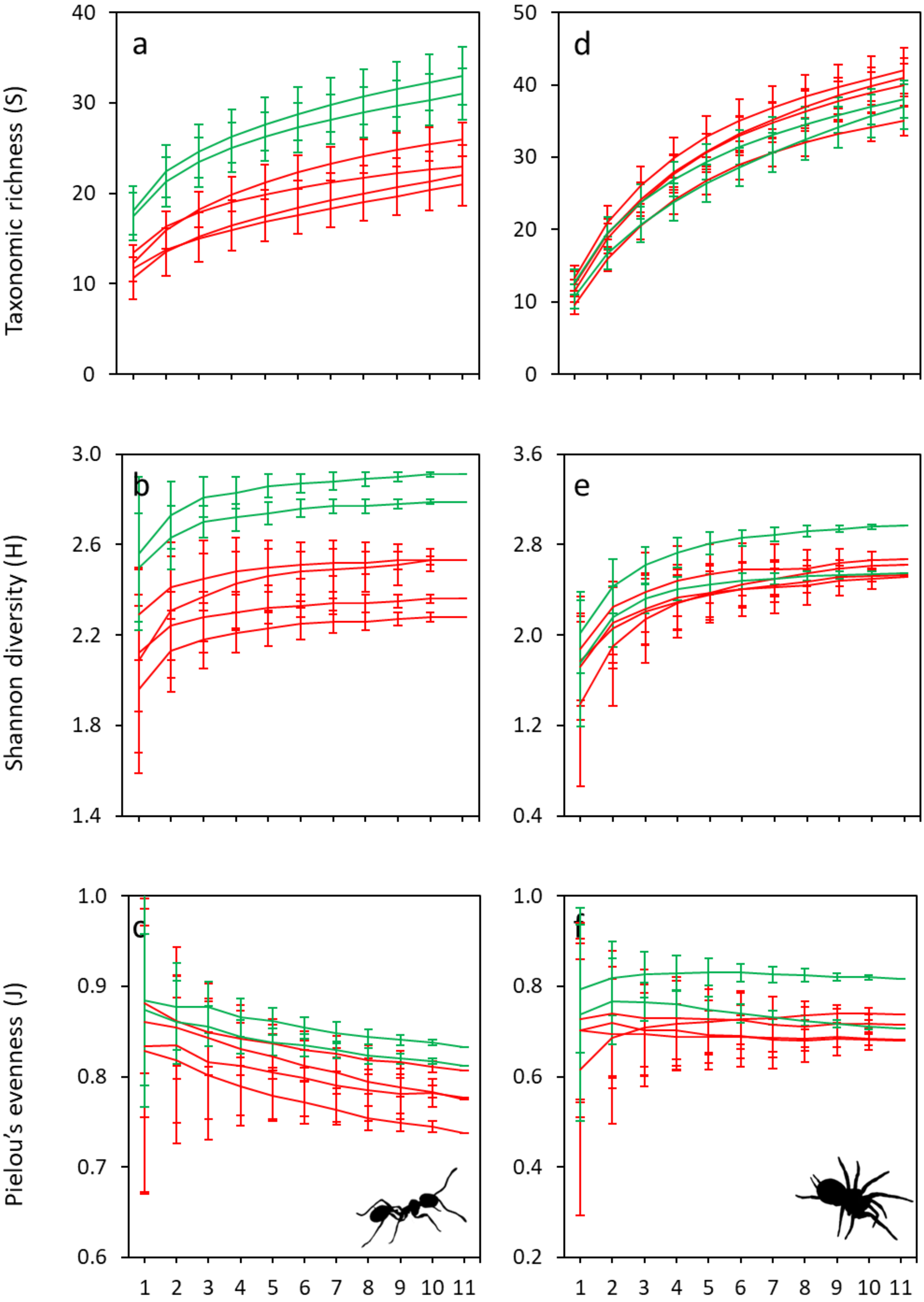
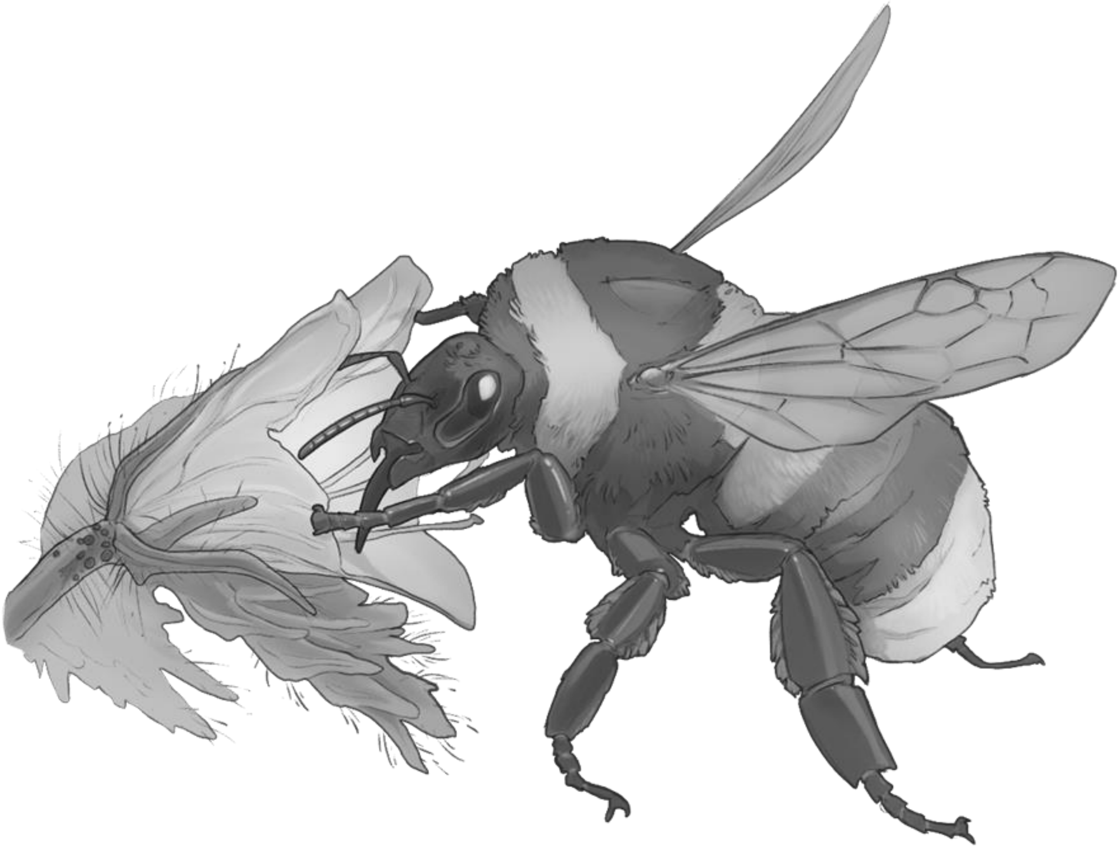


Figure E.1: Rarefaction curves for ant species (a-c) and spider genera (d-f) collected by pitfall traps in burned (red color) and unburned (green color) sampling plots for four consecutive years. The thick lines show rarefaction curves of temporal samplings of each plot (4 burned plots and 2 unburned plots) for taxonomic richness (a,d), Shannon diversity (b,e) and Pielou's evenness (c,f) and the bars represents the standard deviation.

Capítulo 3

Long-term recovery of Mediterranean ant and bee communities after fire in southern Spain



Vidal-Cordero, J. M., Angulo, E., Molina, F. P., Boulay, R. & X. Cerdá (2023). Long-term recovery of Mediterranean ant and bee communities after fire in southern Spain. Science of The Total Environment, 887: 164132.

Resumen

Los incendios forestales desempeñan un papel determinante en la estructura y composición de las comunidades animales, especialmente en el caso de grupos estrechamente asociados a la vegetación y el suelo, como las hormigas o las abejas. Los efectos del fuego en las comunidades animales dependen de los rasgos funcionales de cada grupo. Aquí evaluamos los impactos del fuego y el tiempo transcurrido desde el incendio sobre las respuestas taxonómicas y funcionales de las comunidades de hormigas y abejas. Tomamos muestras de 35 pinares de Andalucía (sur de España) que habían sufrido incendios en el pasado (de 0 a 41 años atrás). En concreto, exploramos si a) el fuego aumentaba la diversidad taxonómica y funcional y cambiaba la composición de las comunidades a corto plazo y b) si la influencia del fuego (aumento o disminución) en las comunidades de hormigas dependería del tiempo transcurrido desde el incendio. Encontramos que la riqueza taxonómica de hormigas y abejas aumentó independientemente del tiempo transcurrido desde el incendio. Diferentes aproximaciones dieron el mismo resultado, como los índices de diversidad taxonómica, los cambios en la riqueza de especies en las comunidades de hormigas y abejas, así como el mayor número de especies de hormigas y abejas propensas al hábitat quemado que al no quemado, usando el Índice $I_{habitat}$. Además de las variables ambientales (como los efectos de las diferentes especies de *Pinus* o la elevación), el tiempo transcurrido desde el incendio modificó la composición taxonómica de las comunidades de hormigas y la composición funcional de las comunidades de abejas. Además, seis de los 13 rasgos funcionales de las hormigas estudiados diferían entre las zonas quemadas y las no quemadas, y el grado de diferencia disminuía a medida que aumentaba el tiempo transcurrido desde el incendio. Por ejemplo, las zonas quemadas contenían comunidades de hormigas con más especies que anidaban en el suelo y especies estrictamente diurnas, rasgos funcionales característicos de las zonas abiertas. Por el contrario, otros rasgos persistieron en las zonas quemadas a largo plazo, en particular un mayor grado de polimorfismo en las obreras y de monoginia de las especies. Nuestro estudio muestra hasta qué punto difieren los efectos a corto y largo plazo del fuego sobre las comunidades de hormigas y abejas; mientras que la riqueza aumenta a largo plazo, algunos rasgos funcionales también se filtran a corto plazo. Sugerimos que el fuego en los ecosistemas mediterráneos de coníferas podría tener un efecto positivo sobre estos grupos y no debería pasarse por alto.

Abstract

Wildfires play a determinant role in the composition and structure of animal communities, especially for groups closely associated with the vegetation and soil, such as bees or ants. The effects of fire on animal communities depend on the functional traits of each group. Here, we assessed the impacts of fire and time since fire on the taxonomic and functional responses of ant and bee communities. We sampled 35 pine forests in Andalusia (southern Spain) that had experienced fire in the past (0 to 41 years ago). Specifically, we explored whether a) fire increased taxonomic and functional diversity and changed community composition in communities in the short term and b) fire influence (increase or decrease) on ant communities would be dependent on time since fire. We found that ant and bee taxonomic richness increased regardless of time since fire. Different approaches gave the same result, such as taxonomic diversity indexes (ant abundance, ant richness and ant Shannon diversity index), the changes in species richness in ant and bee communities, as well as the higher number of ant and bee species prone to the burned habitat than to the unburned habitat, using the $I_{habitat}$ Index. Besides environmental variables (such as the effects of different *Pinus* species or elevation), time since fire changed the taxonomic composition of ant communities and the functional composition of bee communities. Moreover, six of the 13 ant functional traits explored differed between burned and unburned areas, with the degree of difference declining as time since fire increased. For example, burned areas contained ant communities with more ground-nesting species and strictly diurnal species, functional traits that are characteristic of open areas. In contrast, other traits persisted in burned areas over the long term, notably a higher degree of worker polymorphism and species monogyny. Our study shows how much short- and long-term effects of fire on ant and bee communities differ; while richness increases in the long-term, some functional traits are also filtered in the short-term. We suggest that fire in Mediterranean coniferous ecosystems could have a positive effect on these groups and should not be overlooked.

Introduction

Fire is a crucial ecological process that simultaneously acts as a destructive disturbance force and provides a variety of ecosystem services (McLauchlan et al., 2020; Pausas and Keeley, 2019). Wildfires are the most frequent target of research on disturbance events (Viljur et al., 2022). They greatly alter forest ecosystems by reshaping the landscape and modifying the dynamics and structure of communities (Pausas and Keeley, 2009). They may also pose a global challenge to conservation efforts, making it essential to understand how biodiversity is affected by fire regimes (Kelly et al., 2020). While studies have traditionally focused on plants (Keeley et al., 2012, 2011), more recent research has explored fire's impact on animals, including arthropods (New, 2014; Yekwayo et al., 2018; Carbone et al., 2019).

Arthropods play critical roles in forest ecosystems and must be considered in any forestry management plan that seeks to maintain biodiversity (Kremen et al., 1993). This group's responses to fire have mostly been studied from a taxonomic perspective. Essentially, species abundance and richness have been found to increase rapidly after fire; they then either remain fairly constant until the next fire occurs, or their levels may begin to decline 7 to 15 years after fire occurrence (New, 2014). However, to properly understand the mechanisms behind these taxonomic responses, it is important to also examine shifts in the functional traits represented within arthropod communities (Braga et al., 2013; Mouillot et al., 2013). This approach can clarify how organisms respond to wildfire and reveal the specific adaptations that promote survival or recovery (Pausas and Parr, 2018). To this end, researchers can utilize both, data on the taxonomy of species and functional traits found within communities (Májeková et al., 2016).

Ants and bees are known to provide important ecosystem services (Del Toro et al., 2012; Kremen et al., 1993). In Mediterranean ecosystems, where wildfires are frequent (Keeley et al., 2012) both groups play a key role in ecosystem regeneration. Bees provide pollination services and thus influence the diversity of flowering plants (Galbraith et al., 2019; Koh et al., 2016). Ants have mutualistic relationships with plants, which include dispersing seeds and fruits (Barroso et al., 2013; Boulay et al., 2007; Ordóñez and Retana, 2004; Retana et al., 2004) and pollination (De Vega et al., 2014; Gómez et al., 1996). They also have antagonistic relationships; for example, they are seed predators (Arnan et al., 2010; Azcárate et al., 2005).

In general, fire changes the composition and state of Mediterranean ant and bee communities by inducing both direct and indirect mortality attributable to habitat modifications and by setting the stage for colonization and recolonization from neighboring unburned areas (Ne'eman et al., 2000; Pausas, 2019; Pausas and Parr, 2018; Wong et al., 2019). First, many ant and bee species nest in the ground, which increases their likelihood of surviving fire's extreme above-ground temperatures (Cane and Neff, 2011). However, those that nest at shallow depths or on vegetation face the direct effects of fire (fire can burn ant nests and thus kill the ants inside). Besides, survival ants face the indirect effects of fire (fire can diminish the overall resource availability by changing vegetation structure, e.g., Rosa et al. 2021). Second, community resilience is shaped by the identity and diversity of plants present before and after the fire, which provide direct and indirect resources to ants and bees (Arnan et al., 2019, 2009, 2007, 2006; Caut et al., 2014; Fagundes et al., 2015; Mola et al., 2020; Potts et al., 2003). Third, colonization dynamics are conditioned by species dispersal capacity (Pausas and Parr, 2018). In ants, dispersal distance is linked to colony foundation mode, which may be independent (i.e., a winged queen able to fly long distances) or dependent (i.e., a group of ants that travel short distances on foot) (Amor et al., 2011; Cronin et al., 2013). In contrast, in bees, dispersal distance is determined exclusively by flight capacity, which is greater for larger species (Guédot et al., 2009; Ne'eman et al., 2000). Therefore, burned habitats host a combination of species: those that survived the fire and can persist under the new environmental conditions and those that arrive from unburned areas, attracted by the available resources.

Most research looking at the taxonomic responses of bee communities to fire has found an increase in species abundance or diversity: either because there is an increase in floral resources and boring insect exit holes used by cavity-nesting bees (Galbraith et al., 2019); because bee abundance is negatively related to canopy cover (Grundel et al., 2010); or because floral abundance persisted for longer time in burned sites (Mola and Williams, 2018; Moretti et al., 2009; Potts et al., 2003); in all these cases, the pattern that usually emerges is a rapid recovery with a peak in diversity of both flowers and bees in the first years after a fire. For ants, however, taxonomic responses have been quite variable across the world (New, 2014): in the Brazilian rupestrian complex, the ant fauna of burned areas maintained a constant species diversity along time but greatly changed species assemblage due to the occurrence of several species not found in the unburned area (Anjos et al., 2015); in the Australian pindan savanna woodland, the ant fauna was highly resilient to fire and most of the 84 ant species (except 2) did not show any positive change in abundance over time since fire (Andersen et al., 2014); but after experimental fires in a similar savanna woodland Parr and Andersen (2008) observed a dramatic decline in dominance of the patchily distributed forest-associated species *Oecophylla smaragdina* and *Papyrius* sp., although fire had no effect on overall dominance by open savanna species of *Iridomyrmex*. Yet, relatively little is known about how ants and bees respond functionally to fire over the intermediate and long term. Functional redundancy has been observed in bees: after a fire, bee abundance climbs, and while taxonomic diversity may decrease, functional diversity is maintained (Moretti et al., 2009). In Mediterranean ant communities, fire results in greater functional diversity, mainly due to the presence of rare species that are functionally unique (Arnan et al., 2019). In both cases, such changes could have major consequences for ecosystem processes and services.

Thus, to properly understand how fire impacts bee and ant communities over time, it is important to approach the topic from both a taxonomic perspective (i.e., traditional measures of biodiversity such as species abundance, species richness, and diversity measured with different indexes) and a functional perspective (i.e., indices such as functional richness and functional divergence), utilizing data on the composition and functional traits of communities (Májeková et al., 2016). A large number of studies have recently examined both functional and taxonomic diversity in animal assemblages (e.g., snakes: Adams et al., 2022; bats: López-Baucells et al., 2022; fishes: Villéger et al. 2010; birds: Morelli et al. 2018; mammals, beetles, and snakes: Guiden et al. 2021; spiders and carabids: Ridel et al., 2021; forest arthropods: Wermelinger et al., 2017; ants: Arnan et al., 2017, 2018; and bees: Villalta et al., 2022). However, research focusing specifically on fire is scarce (e.g., beetles: Moretti et al., 2010, Barber et al., 2017; ants: Arnan et al. 2013, 2020; and bees: Lazarina et al., 2016, Moretti et al., 2009).

The objective of our study was to assess the effects of fire and time since fire on two taxonomic groups—ants and bees. We conducted our research along a regional gradient in southern Spain in 35 pine forests that had experienced a wildfire at some point in the past (between 0 and 41 years ago). We characterized the forests' geographical and climatic conditions, and we assessed vegetation cover and the diversity and composition of ant and bee communities. Within each study area, we compared a burned area with a nearby unburned area. We tested the following hypotheses: (1) since fire reduces canopy and vegetation cover, and thus reduces vegetation structural complexity and the amount of feeding resources, we expected that, in the short term, fire could decrease taxonomic and functional diversity at burned versus unburned areas; alternatively, the appearance of new ecological niches (open areas in the forest) could boost taxonomic and functional diversity at burned versus unburned areas; (2) since recently burned areas tend to harbor species typical of open habitats but less recently burned areas harbor species with greater ties to vegetation, we expected that taxonomic and functional diversity would decline over time at the burned areas until they reached the values found at the unburned areas; (3) the null hypothesis for hypotheses 1 and 2 was that taxonomic and functional diversity would be related to environmental variables (i.e. latitude, longitude, elevation, climate, lithology or the pine species present previous to fire) rather than time since fire; and (4) in accordance with the above-noted changes in vegetation, we expected the taxonomic and functional composition of ant and bee communities to be largely characterized by species typical of open habitats at recently burned areas and by species more associated with vegetation at less recently burned areas.

Methods

Study areas and fire effect variables

To select our study areas, we used databases provided by the Environmental Information Network of Andalusia (Junta de Andalucía REDIAM, 2022). Specifically, we employed two databases that contain records of fires in the region: one contains information for the period between 1975 and 2008 and the other for the period between 2008 and 2013. Both were merged with a database with information on land use since 1956. Between 1975 and 2013, a total of 56,289 fires were recorded in Andalusia. Using geographic information systems (QGIS), we preliminarily selected areas in which older conifer forests had burned (n = 3,614). To obtain as much homogeneity as possible among study areas, we further filtered the results based on the following criteria: 1) the burned area had to exceed 4,000 ha; 2) the wood had not to be removed; 3) the distance from the center of the burned area to the edge had to exceed 200 meters; 4) suitable unburned (control) areas must exist nearby; 5) the burned area had to have experienced a single fire. We thus obtained a list of 95 burned areas that we visited during the spring and summer of 2015 to assess ease of sampling (e.g., access) and comparability of the burned areas with their unburned counterparts (e.g., similar slope, orientation). Access was the criteria that finally discarded most of the 95 areas, as many times burned areas had no available roads or paths to get there or there were unavailable sampling places due to steep slopes or fallen trees. Thus, we finally obtained a total of 35 study areas that had experienced fire at different years in the past (Fig. 1; Table S.1).

To study the effect of fire, we used different variables. The "fire effect" distinguished between burned and unburned areas. We used a paired design with a space-for-time substitution approach, in which each burned area (the treatment) had a paired unburned area (the control), which represents the native community of the burned area before the fire. The control areas were between 275 and 2900m from their paired burned areas (mean of 691m). To take into account when the area experienced fire, we used the "time since fire" variable that represents how long ago the fire occurred (0 to 41 years) and could be used as a continuous variable or a categorical one (see next section).

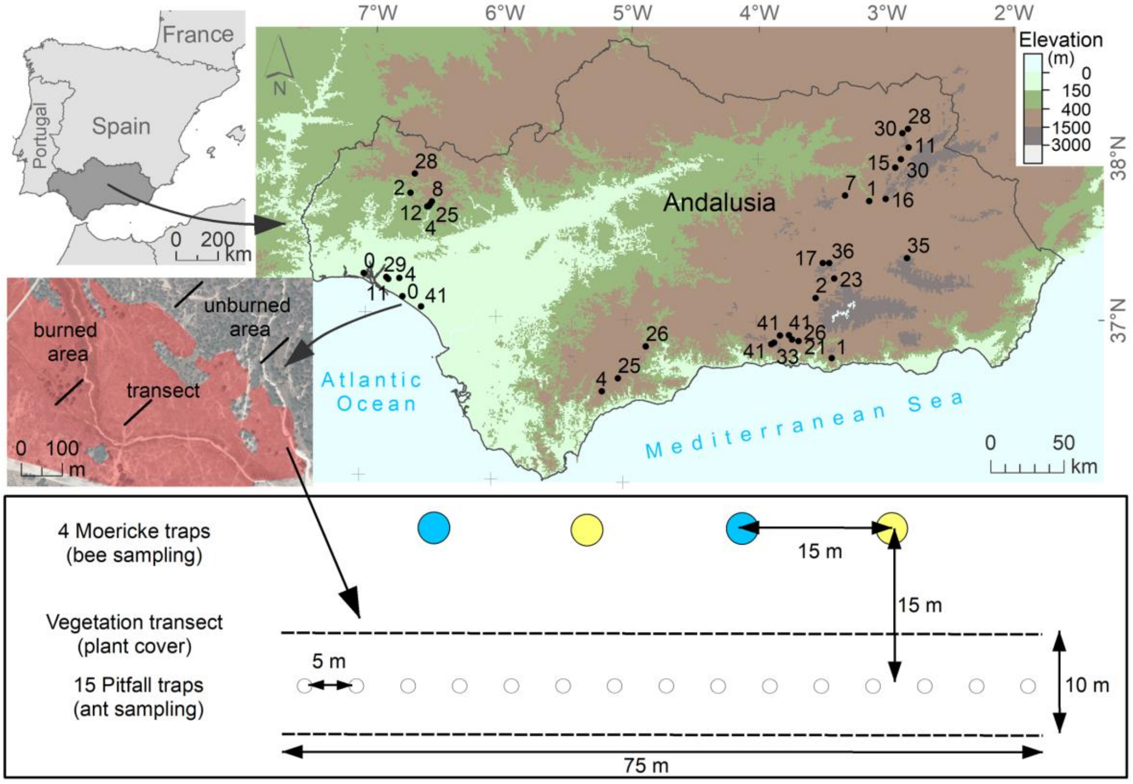


Figure 1. (a) Map of the study areas and (b) diagram of the sampling protocol. The black dots on the map are the sampling areas, and the numbers indicate the time since the fire (years).

Vegetation cover

The 35 study areas were all found in pine forests (*Pinus halepensis*, *P. pinaster*, *P. nigra*, and *P. pinea*; see Table S1) that had a relatively dense understory composed of typical Mediterranean shrubs, including *Salvia rosmarinus*, *Pistacea lentiscus*, *Juniperus oxycedrus*, *Chamaerops humilis*, *Halimium* spp., *Lavandula* spp., *Cistus* spp., *Ulex* spp., *Erica* spp., and a broad variety of herbaceous plants (mainly members of Apiaceae, Asteraceae, and Poaceae). To characterize the structure of the vegetation in the study areas, we established two transects at each of the burned and unburned areas; within an area, the two transects were separated by 200 m minimum. The transects were 75 m long and 10 m wide. Every five meters, we recorded the presence or absence of four strata: herbaceous plants, small shrubs, large shrubs, and trees, noting species identity (Fig. 1).

We calculated the value of a plant cover index (Veg) for each transect using the presence/absence data (Dataset S1, spreadsheet data.veg). This value ranged between 0 and 100%, where 100% meant the four strata were present at all fifteen sampling points, while 0 meant the four strata were absent at all fifteen sampling points.

We performed a preliminary analysis to clarify two issues: did vegetation cover vary across the burned areas in association with time since fire? Was vegetation cover similar across all the unburned areas? To answer these questions, we carried out linear models using the lme function (nlme4 package; Bates et al. 2015). One model was performed in which the dependent variable was the Veg index and the independent variables were fire (burned vs. unburned), time since fire (continuous: 0 to 41 years), and their interaction. Four additional models had the same independent variables, but the dependent variable was the mean presence of each stratum across the 15 points sampled. As we expected, at burned areas, vegetation cover differed significantly with time since fire, except for the herbaceous strata (Table S2a). In contrast, there were no differences associated with time since fire among any of the strata at unburned areas (Table S2b). The interaction between fire and time since fire was significant for all the strata with the exception of the herbaceous plants, which indicates that this stratum does not provide information about the area’s recovery from fire (Table S2c, Fig. S1).

Given the importance of plant community recovery in ant and bee community recovery, we explored whether vegetation cover formed natural groups based on time since fire. To this end, we performed a cluster analysis using the *hclust* function (cluster package; Maechler et al., 2022). The dependent variable was the vegetation cover at the burned areas for the three strata found to be significant above. The results revealed the presence of three categories (Fig. S2): category 1—fire occurred 0 to 4 years ago; category 2—fire occurred 7 to 12 years ago; and category 3—fire occurred 15 to 41 years ago. These categories are similar to those used by Peralta et al. (2017) when studying fire's effects on plant-bee networks.

Ant and bee sampling

Sampling of ants and bees was conducted in 2016, from May through August. The goal was not to comprehensively sample ant and bee diversity, but rather to rapidly assess group presence at burned and unburned areas for the sake of comparison. We therefore used the most common and straightforward sampling method for each group: pitfall traps for ants (Retana and Cerdá, 2000; Ward et al., 2001) and Moericke pan traps for bees (Bogusch et al., 2015; Grundel et al., 2010). For the ants, the open pitfall traps were 220-cm3 plastic cups that were 2/3 filled with soapy water. For the bees, the Moericke pan traps were 1000-cm3 yellow and blue plastic dishes that were filled with soapy water. Bee species trapped in Moericke pan traps are normally biased to larger bees or those that fly higher in the vegetation (Prendergast et al. 2020). In each study area, we placed 60 pitfall traps (i.e., 60 traps x 35 study areas) and 16 Moericke traps (i.e., 16 traps x 30 study areas) along 4 transects (2 at the burned area and 2 at the unburned area). Each transect contained 15 pitfall traps separated by 5 m; along a parallel line were 4 Moericke traps (2 yellow and 2 blue in an alternating sequence) separated by 15 m (Fig. 1).

The pitfall traps and Moericke traps were run for 48 h. Any biological material captured was stored in 70% alcohol until identification could occur. Ants and bees were sorted out from the rest of the invertebrates. Ants were identified to species level; bees were identified to genus level, or to species level whenever possible (Dataset S2). Taxonomic identification was carried out by the two taxonomist authors (JM Vidal-Cordero and FP Molina) using their own knowledge and the guides (see Appendix S1). Taxonomic doubts were sent to experts (ants: Joaquín L. Reyes-López; bees: Luis Óscar Aguado Martín) to confirm the identification. In the following analyses, we used species-level information for ants. For bees, we used either genus- or species-level information, depending on how much taxonomic resolution was possible.

Life-history traits

We characterized 13 and 6 functional traits for ants and bees, respectively. These traits are associated with three important processes (survival, persistence, and colonization) that play a crucial role in autecology and ecosystem functioning and that offer up a potential mechanistic explanation for how fire affects both ants (Arnan et al., 2013) and bees (Grundel et al., 2010; Love and Cane, 2016).

First, we looked traits related to surviving fire, notably nesting site (ants and bees nesting in the ground rather than in the vegetation, wood, snail shells, or hives) (Tables S3, S4). Next, we examined traits related to persistence after fire. For ants, according with Arnan et al. (2020) and Vidal-Cordero et al. (2022), the traits allowing to persist after fire are: behavioral dominance (dominants, following Arnan et al. 2012; Cerdá et al. 2013 have a higher probability of persistence), body size (larger ants), colony size (larger colony size), nest number (polydomous ,with more than one nest per colony), queen number (polygynous, more than one queen per colony), diurnality (strictly diurnal), foraging strategy (collective), diet type (insects or seeds, highly available after fire), and degree of worker polymorphism (more pronounced worker polymorphism) (Table S3). For bees, these traits were body size (four categories) and intertegular distance (wildfires may select for larger bees, Burkle et al., 2019), degree of floral specialization (polylectic or oligolectic; e.g. oligoleges are more abundant in open areas, Grundel et al., 2010), and tongue length (short-tongued bees are more frequent in recently burned areas, Moretti et al. 2009) (Table S4). Finally, we explored traits related to the colonization of burned areas, which were colony foundation type (dependent, independent, or both) for ants and lifestyle (solitary, social, or parasitic) for bees (Tables S3, S4).

Information about functional traits was mostly obtained from the literature (Appendix S1). Data on ant traits came from Arnan et al. (2013) and Retana et al. (2015) (Table S3, Dataset S1, spreadsheet ant.traits). Data on bee traits were gathered via an extensive search of public databases and the scientific literature (Table S4, Dataset S1, spreadsheet bee.traits). We also measured the intertegular distance of the bees we captured using a micrometer and stereomicroscope. For some species of both groups, we additionally drew on unpublished data provided by experts (ants: Joaquín L. Reyes-López; bees: Luis Óscar Aguado Martín).

Taxonomic diversity

All the analyses were performed using R (v. 4.1.3; R Core Team 2022). First, we characterized the taxonomic structure and composition of the ant and bee communities. We defined ant abundance (A_{ants}) as the mean number of ants per transect (N = 15) using the total number of ants in each trap in the calculation. We defined bee abundance (A_{bees}) as the total number of bees captured per transect. When traps were missing, we extrapolated ant and bee abundance data to the total number of traps for each transect (for ants, 103 traps across 46 transects went missing; for bees, 11 traps across 8 transects went missing; total transects = 140, Dataset S2). For each transect, we calculated the following taxonomic diversity indices (Dataset S1, spreadsheets data.ants and data.bees): (1) observed taxon richness (S_{ants} and S_{bees}), which was the total number of species/genera observed per transect; (2) the Shannon diversity index (H_{ants} and H_{bees}), which accounts for both the number of species/genera and their relative abundance; and (3) Pielou's evenness (J_{ants} and J_{bees}), which is the Shannon diversity index divided by the natural logarithm of the observed taxon richness. S and H were calculated using the estimate function (*vegan* package, Oksanen et al. 2018).

Functional diversity

To characterize the functional composition of ant and bee communities, we used two widely recognized approaches in ecological research: 1) the community weighted mean (CWM) of traits, which indicates a community’s most common traits after accounting for differences in taxon abundance (Laliberté and Legendre, 2010) and 2) the functional diversity (FD) in traits, which indicates how much species within a community vary in their traits (Arnan et al., 2013; Ricotta and Moretti, 2011). CWM and FD values were calculated for each transect.

The method for calculating CWM differs depending on whether traits are continuous or categorical. For continuous traits, CWM corresponds to the abundance-weighted mean and was determined as follows:

$$\bar{x} = \sum_{i=1}^{s} p_i x_i$$

where p_i is the relative abundance of species (or genus) i and x_i is the trait value for species (or genus) i. For categorical traits, CWM corresponds to the relative abundance of a species (or genera) associated with each trait category.

Different aspects of functional diversity have the potential to reveal the processes structuring biological communities (Mouchet et al., 2010). FD was thus broken down into four subindices that can help clarify the mechanistic effects of functional diversity on ecosystems: functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), and functional divergence (FDiv). FRic expresses the amount of functional space filled by the community, but it does not account for relative abundances. Consequently, we can use FEve, which describes the evenness of abundance distribution in a functional trait space (Mason et al., 2005). However, FEve does not reveal the dispersion of species in trait space. The next step is therefore to calculate FDis (Laliberté and Legendre, 2010), which is the mean distance of individual species to the centroid of all species in multidimensional trait space. Finally, FDiv measures how abundances tend to be on the outer margins of the functional space while controlling for functional richness. These four metrics are independent of each other and of species number, evenness, and taxonomic diversity. We calculated CWM with the *functcomp* function and the four FD subindices with the *dbFD* function (FD *package*, Laliberté and Legendre 2010) (Dataset S1, spreadsheets data.ants and data.bees).

Environmental variables

Given the regional scale of our study, we gathered information on the environmental characteristics of each study area. The resulting set of variables was used as covariables in the analyses (Dataset S1, spreadsheets data.ants and data.bees). This list comprised latitude, longitude, and elevation (Lat, Long, and Elev) as determined from GPS coordinates; lithological types (igneous, sedimentary, and metamorphic rock) (CSIC-IARA, 1988), as different type of soil affect ant richness and bee nesting for ground-dwelling bees (Angulo et al. 2016; Lybrand et al. 2020; Antoine et al. 2021); pine species (*Pine halepensis, P. nigra, P. pinaster*, and *P. pinea*) because pines can differ in their responses to fire (He et al., 2012); and eight bioclimatic variables (WorldClim database v. 2.0— www.worldclim.org; Hijmans et al., 2005). The latter covered the period from 1970 to 2000, and the values had a spatial resolution of about 1 km^2. Using principal components analysis (PCA), we reduced them to two uncorrelated components that accounted for 92.3% of the original variation (Clim. 1 and Clim. 2; Table S5).

Exploring the effects of fire

Rarefaction curves in burned and unburned areas

To determine whether we had sampled most of the species/genera in the study areas, we calculated abundance-based rarefaction curves for the ants and bees. We utilized the total number of observations of each taxon (species/genus) for each group (ants and bees) at the burned and unburned areas. The curves were obtained via the *specaccum* function (*vegan* package, Oksanen et al. 2018).

Effects of fire on taxon richness

We wanted to compare taxon richness (species/genus) at burned vs unburned areas. First, we calculated the difference in ant and bee occurrence between burned and unburned areas using a habitat use index, modified from Suggitt et al. (2012): $I_{habitat}$ = [(2 * unburned occurrence values)/(unburned occurrence values + burned occurrence values)]–1. The value of the index ranges from −1 to 1, where negative values indicate more frequent association with burned habitats, and positive values denote taxa more associated with unburned habitats.

We also conducted this comparison by determining the absolute difference in taxon richness (species/genus) between the burned and unburned transects for each area study. The difference in richness was the mean richness value of the burned transects minus the mean richness value of unburned transects. We explored whether the resulting value was correlated with time since fire, accounting for environmental variables. We used one linear model (*lm* function, *stats* package; Pinheiro and Bates, 2022, 2000) for the ants and one for the bees. The difference in richness was the dependent variable, time since fire (continuous: 0 to 41) was a fixed effect, and the environmental variables were included as covariables.

We obtained a map of the differences in richness across the study areas to gain insight into the relevance of the spatial variables that could be affecting (such as latitude, longitude or altitude). We used the interpolation tool in ArcGIS 10.7, which employs the inverse distance weighted (IDW), with a neighbor search algorithm implemented with smooth circulars. This method is one of the most flexible interpolation methods. It assigns predicted values to unknown points by using surrounding observed values from a set of known points obtained from our sampling. Each measured point (the calculated difference in richness) has a local influence that diminishes with distance (ArcGis Pro 3.0). In our case, IDW interpolation assumes that the influence of the values of observed richness differences on the predicted values diminish as a function of geographic distance, with closer values having a greater influence on the predicted values than those farther away.

Finally, we examined the patterns of occurrence for each ant species across the three time-since-fire clusters for the burned and unburned areas. We calculated the average time since fire (and standard error) for the burned and unburned areas.

Effects of fire on taxonomic and functional community structure

We examined the effects of fire and time since fire on the taxonomic and functional community structure indexes (indices: A, S, H, J, FRic, FEve, FDis and FDiv). The ant and bee data were analyzed separately using linear mixed-effects models (*lme* function, *nlme* package; Pinheiro and Bates, 2022, 2000). In the models, the dependent variable was one of the indices; fire (burned and unburned), time since fire (continuous: 0 to 41), and their interaction were fixed effects. The environmental variables were covariates, and study area was a random factor to account for the fact that different transects were sampled within the same study area. To meet statistical assumptions regarding normality, homogeneity and heteroscedasticity, we transformed the dependent variables using the transformation that better suit normality assumptions in each case (see Results, Table 1).

Effects of fire on taxonomic and functional community composition

We examined the effects of fire and time since fire on the taxonomic and functional community composition of ants and bees. To this end, we created matrices that combined information on taxonomic and functional composition for each transect. For the taxonomic analysis, the matrix cell values were ant occurrence (the number of traps in which each species occurred per transect) and bee abundance (the number of individuals of each species/genus per transect). For the functional analysis, we used the abundance-weighted trait values. We ran PERMANOVA tests using the *adonis* function (*vegan* package, Oksanen et al. 2018). Fire (burned and unburned), time since fire (continuous: 0 to 41 years), and their interaction were fixed effects. Study area was added as a random factor to account for the fact that different transects were sampled within the same study area. We used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities to visually explore how the taxonomic and functional composition metrics were associated with fire (burned and unburned) or time since fire (three clusters).

Effects of fire on functional traits

While the community-level analysis allowed us to evaluate different facets of the functional space occupied by entire communities, comprising multiple traits, we were also interested in determining whether individual traits were associated with fire or time since fire. Thus, we tested the influence of fire (burned and unburned), time since fire (continuous: 0 to 41), and their interaction on each of the functional traits of ants and bees. We used linear mixed-effects models that included study area as a random factor. We transformed the dependent variables to achieve normality whenever required.

Results

Effects of fire on community richness

We captured a total of 71,050 ant workers belonging to 61 species, 23 genera, and 5 subfamilies (Table S6). There were 322 individual bees from 37 species, 24 genera, and 6 families (Table S7).

For the ants, the species accumulation curves were nearly asymptotic in both burned and unburned areas (Fig. 2a), suggesting that we had sampled most of the species present in the study areas. However, for the bees, the curves did not approach an asymptote, indicating that we had not comprehensively characterized this group (Fig. 2b). Interestingly, for both ants and bees, the curve for the unburned area lay below the curve for the burned area, indicating that richness was greater in burned areas.

We found further support for this pattern when we analyzed ant and bee occurrence: out of the 61 ant species, 56% had negative $I_{habitat}$ values, and 34% had positive values, indicating that ants were more likely to be found at burned areas (Fig. 2c). Similarly, out of the 37 bee species, 62% had negative $I_{habitat}$ values, and 27% had positive values, indicating that bees were more likely to occur at burned areas (Fig. 2d). It is important to note that burned areas were more open habitat.

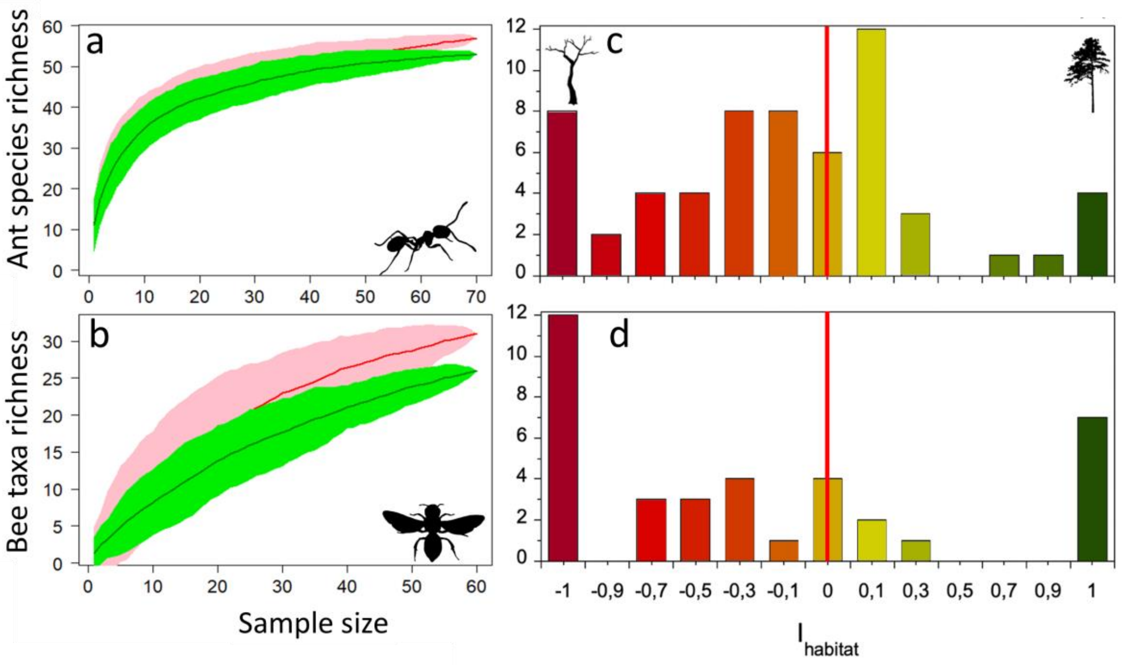


Figure 2. Rarefaction curves for (a) ants and (b) bees and distribution of $I_{habitat}$ values for (c) ants and (d) bees at burned and unburned areas. Ants were sampled using pitfall traps, and bees were sampled using Moericke traps. Occurrence data were used for ants, while abundance data were used for bees. The thick lines in (a) and (b) show the observed taxa richness for ants and bees; the red curves indicate the burned areas, and the green curves indicate the unburned areas; the shaded area is the standard error.

Additionally, when differences in species richness were mapped across the study areas (Fig. 3), the same result was seen. The richness of ant and bee communities was greater at burned than unburned areas (more red vs. blue), a pattern that was seemingly more pronounced in ants. However, time since fire did not significantly affect the differences in species richness ($F_{1,22}$ = 0.00, p =0.948 for ants; $F_{1,22}$ = 1.56, p =0.228 for bees). Out of all the environmental variables, only latitude was correlated with differences in community richness and only in the case of ants ($F_{1,22}$ = 5.26, p = 0.03) (Table S8).

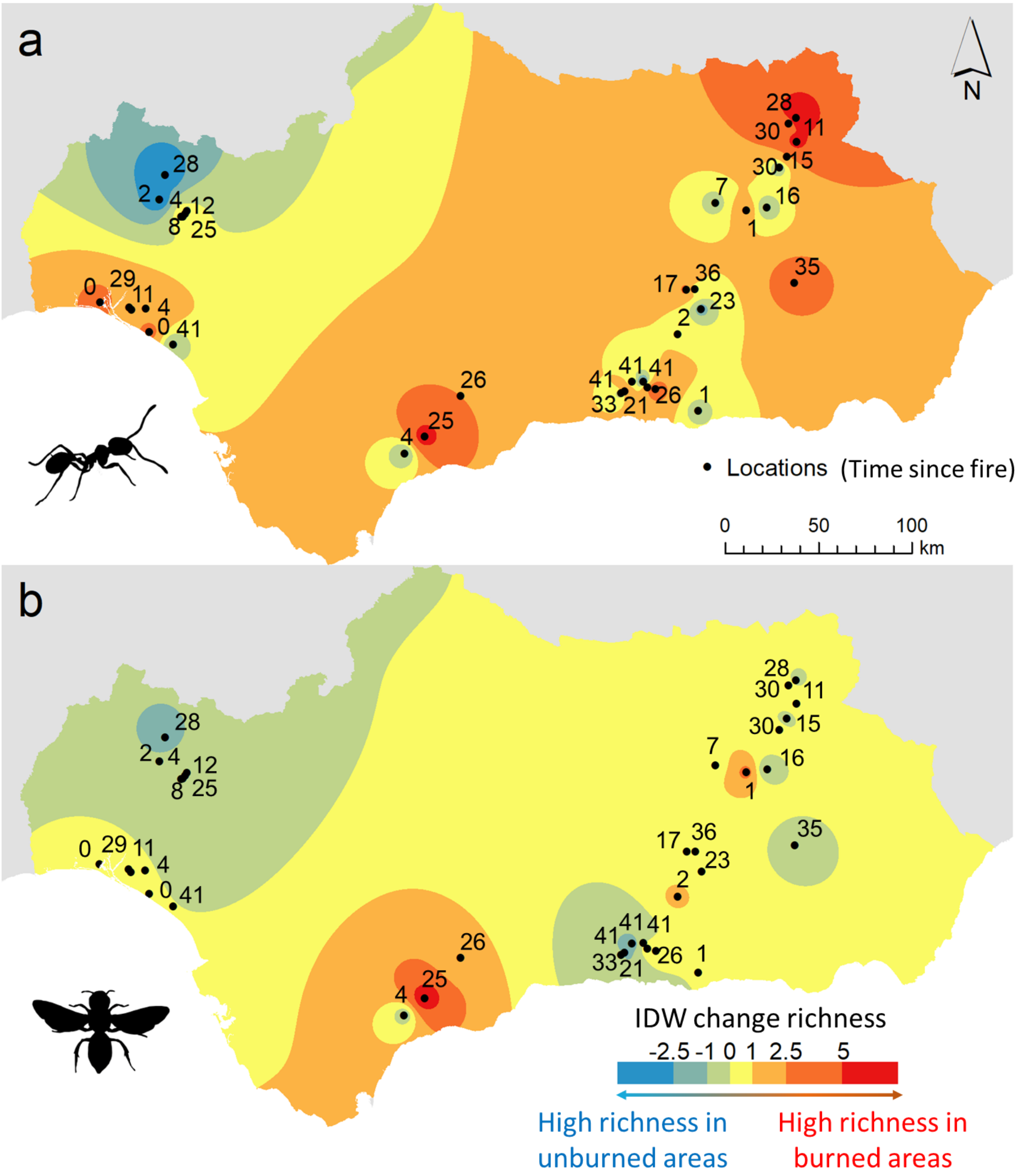


Figure 3. Differences in richness of (a) ant species and (b) bee taxa between burned and unburned areas. For each study group and area, the difference in richness was the difference between the mean richness value of the burned transects and the mean richness value of unburned transects (i.e., positive number = greater richness in the burned transects). The black dots on the map are the study areas, and the numbers indicate the time since the fire (years).

Finally, when we examined the relationship between ant species occurrence and time since fire, we observed differential responses among species (Fig. 4). The most frequently occurring ant species (on the top of Fig 4) were found at burned areas that had experienced fire more than 15 years ago. Some frequently occurring species (occurrence > 10, on the center of Fig 4) were found at areas that had burned less recently (15 to 41 years ago) as well as moderately recently (4 to 12 years ago): *Aphaenogaster senilis*, *Messor bouvieri*, *Cataglyphis tartessica*, *Messor barbarus*, *Cataglyphis rosenhaueri*, *Goniomma kugleri*, *Oxyopomyrmex saulcyi*, and *Messor marocanus*. Three species, Cat*aglyphis hispanica*, *Tetramorium forte*, and *Messor lusitanicus* tended to occur at areas of moderately recent burns (4 to 12 years ago), while *Temnothorax gredosi* was most common at recently burned areas (0 to 4 years ago). The other ant species associated with recent burns occurred at extremely low levels (occurrences < 3, on the bottom of Fig. 4).

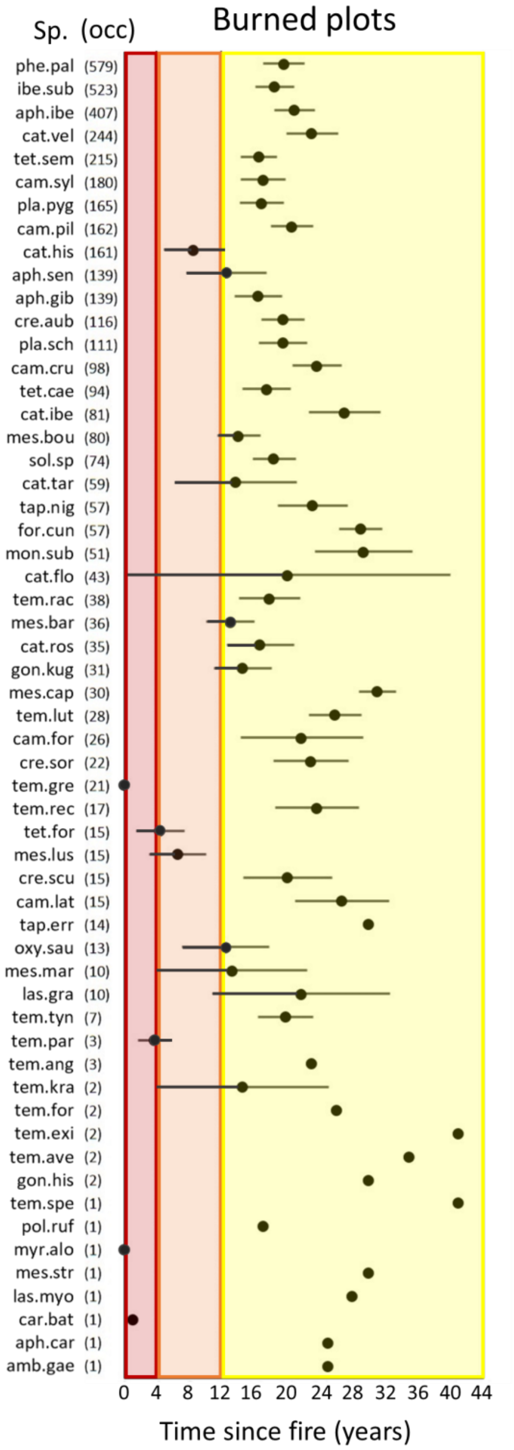


Figure 4. Ant species occurrence and time since fire in burned plots. The species are sorted by decreasing order of occurrence (mean ± SE). On the left axis is the total number of occurrences for each species. In red are the most recently burned areas (category 1: fire occurred 0 to 4 years ago). In orange are the moderately recently burned areas (category 2: fire occurred 7 to 12 years ago). In yellow are the least recently burned areas (category 3: fire occurred 15 to 41 years ago). Occurrence is the number of pitfall traps containing a given species. The abbreviations are listed in Table S6.

Effects of fire on taxonomic community structure

Ant abundance, ant richness, and ant diversity were significantly greater at burned versus unburned areas (A_{ants}, S_{ants}, H_{ants}; Table 1a, Fig. 5a,b,c). For bees, there was the same trend in all three metrics (A_{bees}, S_{bees}, H_{bees} and J_{bees}), but it was not statistically significant (Table 1b), except bee abundance, which was significantly higher at areas that had burned more recently (Fig. S3a).

That said, the interaction between fire and time since fire was not significant for any of the taxonomic indices for either ants or bees (Table 1a,b). Some of the taxonomic indices were associated with certain environmental variables (Table S9). S_{ants}, H_{ants}, and J_{ants} were significantly lower at higher latitudes but significantly higher at higher elevations. A_{ants} was negatively correlated with vegetation cover. Finally, A_{ants} and J_{ants} were impacted differently by the presence of pines: A_{ants} was highest in association with *P. pinaster* and *P. halepensis*, while J_{ants} was highest in association with *P. nigra* (Table S9, Fig S3b,c).

Table 1. Effects of fire and time since fire on the taxonomic community structure of ants (a) and bees (b); and on the functional community structure of ants (c) and bees (d). Metrics are A = abundance, S = richness, H = Shannon diversity index, and J = Pielou's evenness; FRic: functional richness; FEve: functional evenness; FDis: functional dispersion; and FDiv: functional divergence. The abbreviations Log, ^{2}, and ½ indicate the use of a logarithmic, squared, or square-root transformation, respectively. Fire: fire treatment (burned and unburned); Time: how long ago the fire occurred (0 to 41 years); FxT: the interaction between the former two variables. Statistically significant results are in bold. The complete models are in Table S9, S10.

a) Ants		***Log(A)***		***S***		***H^2***		***J^2***	
	DF	F	P	F	P	F	P	F	P
Fire	1, 101	**9.36**	**0.003**	**9.54**	**0.003**	**6.62**	**0.011**	0.37	0.547
Time	1, 23	0.06	0.815	0.44	0.515	0.64	0.431	0.16	0.693
F x T	1, 101	1.81	0.182	0.08	0.772	0.35	0.557	2.01	0.159

b) Bees		***Log(A)***		***S***		***H^2***		***J^2***	
	DF	F	P	F	P	F	P	F	P
Fire	1, 51	2.83	0.099	2.19	0.145	0.58	0.451	2.45	0.130
Time	1, 17	**6.16**	**0.024**	0.21	0.651	0.43	0.522	2.53	0.143
F x T	1, 51	0.20	0.653	0.10	0.753	0.80	0.375	2.61	0.119

c) Ants		***FRic***		***FEve***		***$FDis^2$***		***FDiv***	
	DF	F	P	F	P	F	P	F	P
Fire	1, 101	2.97	0.088	0.36	0.551	0.07	0.788	**9.63**	**0.002**
Time	1, 23	2.44	0.132	0.00	0.952	4.01	0.057	3.26	0.084
F x T	1, 101	0.05	0.832	0.04	0.838	0.31	0.581	0.01	0.934

d) Bees		***Log(FRic)***		***FEve***		***$FDis^{1/2}$***		***FDiv***	
	DF	F	P	F	P	F	P	F	P
Fire	1, 51	0.03	0.882	3.86	0.188	1.27	0.265	0.41	0.586
Time	1, 17	0.00	0.992	0.07	0.813	2.33	0.145	0.06	0.828
F x T	1, 51	1.09	0.406	3.21	0.215	0.69	0.411	5.57	0.142

Effects of fire on functional community structure

In ants, there were a few key results with regards to functional community structure. $FDiv_{ants}$ was higher at unburned versus burned areas (Table 1c, Fig 5d), and $FDis_{ants}$ was lower for more recent fires (Table 1c, Fig S4a). That said, the interaction between fire and time since fire was not significant for any of the functional indices examined in ants. Some of the functional indices were influenced by environmental variables (Table S10): *P. pinaster and P. halepensis* were associated with the highest $FDis_{ants}$ values (Fig S4b), while $FRic_{ants}$ and $FDis_{ants}$ increased with elevation (Table S10, Fig S4c,d). In bees, there were no significant results with regards to functional community structure and fire (Table 1d). We only observed a negative relationship between $FDis_{bees}$ and the Clim. 1 component (Table S10, Fig S4e).

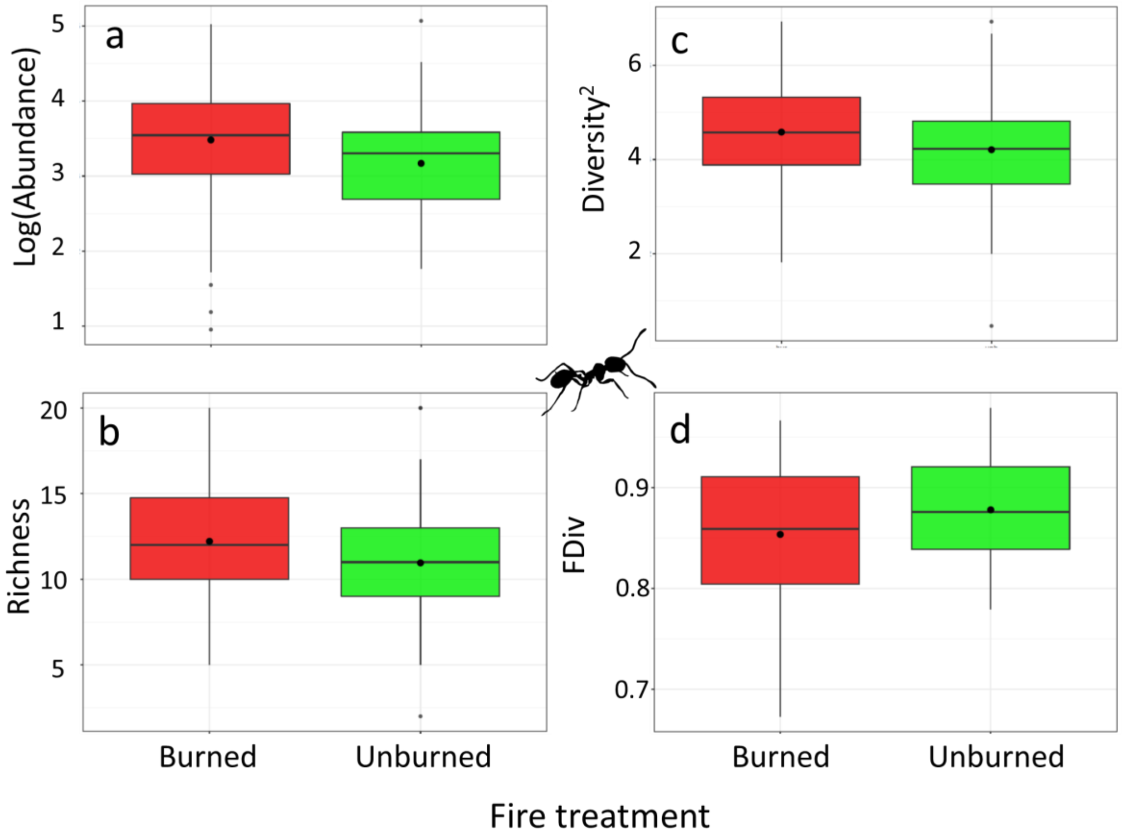


Figure 5. Effects of fire on the taxonomic and functional community structure of ants. (a) Mean (± SE) log-transformed ant abundance for burned versus unburned areas as well as (b) ant species richness, (c) square-transformed Shannon diversity, and (d) mean (± SE) ant functional divergence for burned versus unburned areas. In red are the burned areas, and in green are the unburned areas. Only statistically significant results are presented (i.e. only some of the explored indices for ants, see Table 1 and Tables S8-S10).

Effects of fire on taxonomic and functional community composition

The taxonomic community composition of ants was significantly influenced by fire, time since fire, and their interaction (fire: $F = 2.38$, $p = 0.001$, $R^2 = 0.02$; time: $F = 3.98$, $p = 0.001$, $R^2 = 0.05$; and interaction: $F = 1.09$, $p = 0.002$, $R^2 = 0.01$; Fig. 6a-c). Ant communities at burned areas occupied a smaller and more distinct area in NMDS space than did ant communities at unburned areas, especially when the fire was moderately to less recent (7–12 years ago and 15–41 years ago; Fig. 6b,c). This pattern was not seen for the most recent fires (0–4 years ago), which could explain the interaction (Fig. 6a). This can be seen by a reduction of the overlapping of the two ellipses (burned and unburned ant communities) from Fig. 6a to Fig. 6c. Within the burned areas, there was more community similarity in the case of moderately to less recent fires than for recent fires and less recent fires (Fig. S5a,b).

However, for bees, only the fire treatment significantly affected community composition ($F = 1.55$, $p = 0.02$, $R^2 = 0.02$, Fig. S5c); there was no effect of time since fire ($F = 3.60$, $p = 0.07$) or the interaction ($F = 0.72$, $p = 0.34$). Bee communities in burned areas although highly overlapping in NMDS space with the communities in unburned areas, occupied a smaller area (as in ant communities).

There were no significant effects of fire on the functional composition of ant communities (fire: $F = 0.24$, $p = 0.58$; time: $F = 2.88$, $p = 0.16$; and interaction: $F = 1.53$, $p = 0.09$). The same was mostly true for bees (fire: $F = 0.94$, $p = 0.42$ and time: $F = 3.66$, $p = 0.20$; and interaction: $F = 1.18$, $p = 0.08$, $R^2 = 0.03$) (Fig. 6d-f). We observed that the functional communities of bees at burned areas occupied a larger and more distinct area in NMDS space than did functional communities of bees at unburned areas (Fig. 6d-f).

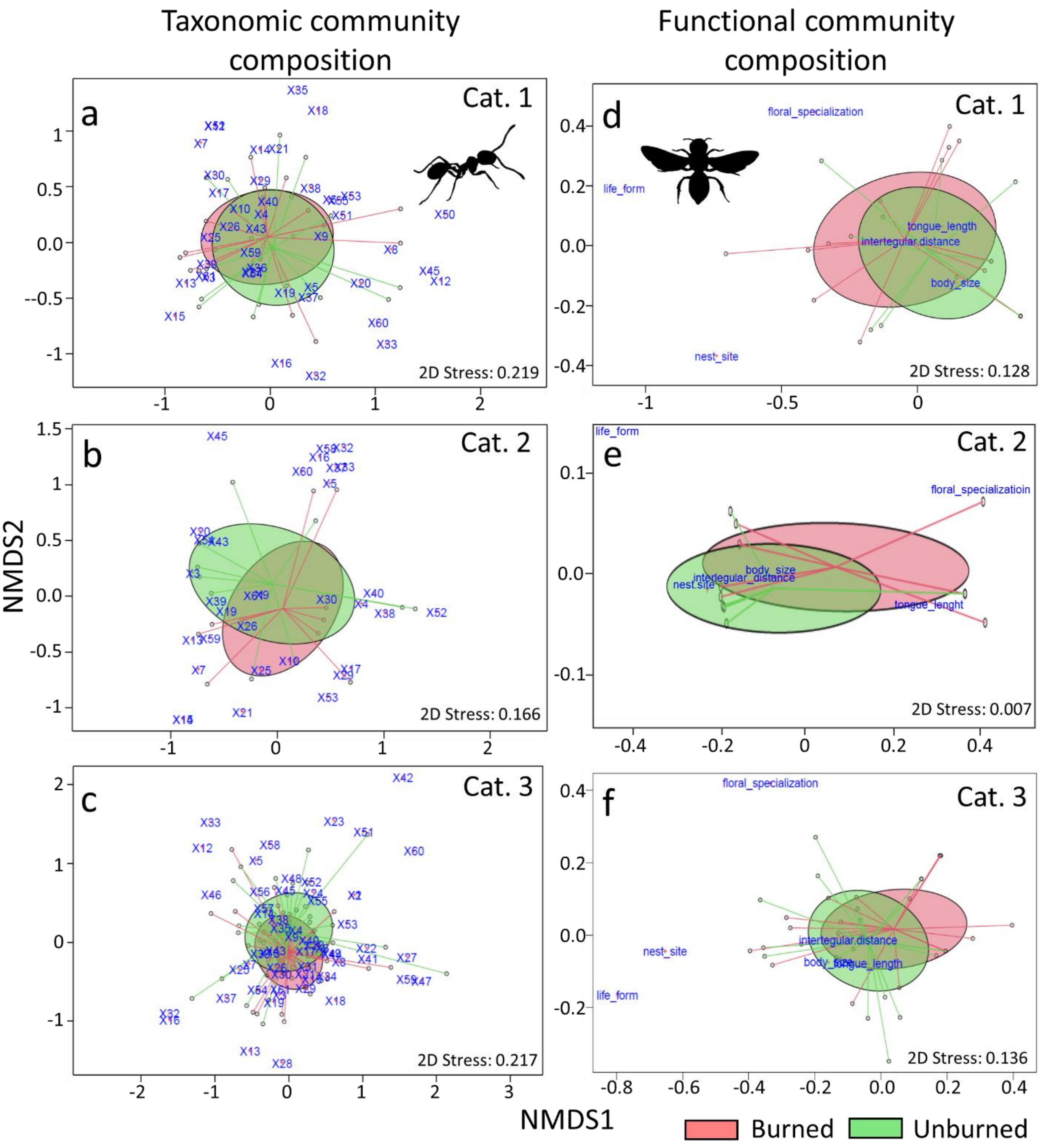


Figure 6. Non-metric multidimensional scaling analysis of the taxonomic community similarity of ants and the functional community similarity of bees with time since fire. Ant taxonomic similarity at areas that burned (a) recently, (b) moderately recently, and (c) less recently. Bee functional similarity in areas that burned (d) recently, (e) moderately recently, and (f) less recently. In red are the burned areas, and in green are the unburned areas. The 2D stress coefficients are indicated. See species codes in Tables S6, S7.

Effects of fire on functional traits

For ants, six of the 13 functional traits analyzed were affected by the interaction between fire and time since fire (Table S11): differences between burned and unburned areas were more pronounced for more recent fires (Fig. 7). At recently burned areas, there were more ground-nesting species (Fig. 7a), more strictly diurnal species (Fig. 7b), species with greater worker polymorphism (Fig. 7c), more monogynous species (Fig. 7d), more species with dependent colony foundation (Fig. 7e), and species that consumed seeds (Fig. 7f). These differences became less dramatic as the time since the fire increased. Other ant traits were affected only by fire (independently of time since fire): burned areas hosted more monodomous species (Fig S6a), more species that use individual foraging (Fig S6b), larger species (Fig S6c), and species that consumed no insects (Fig S6d).

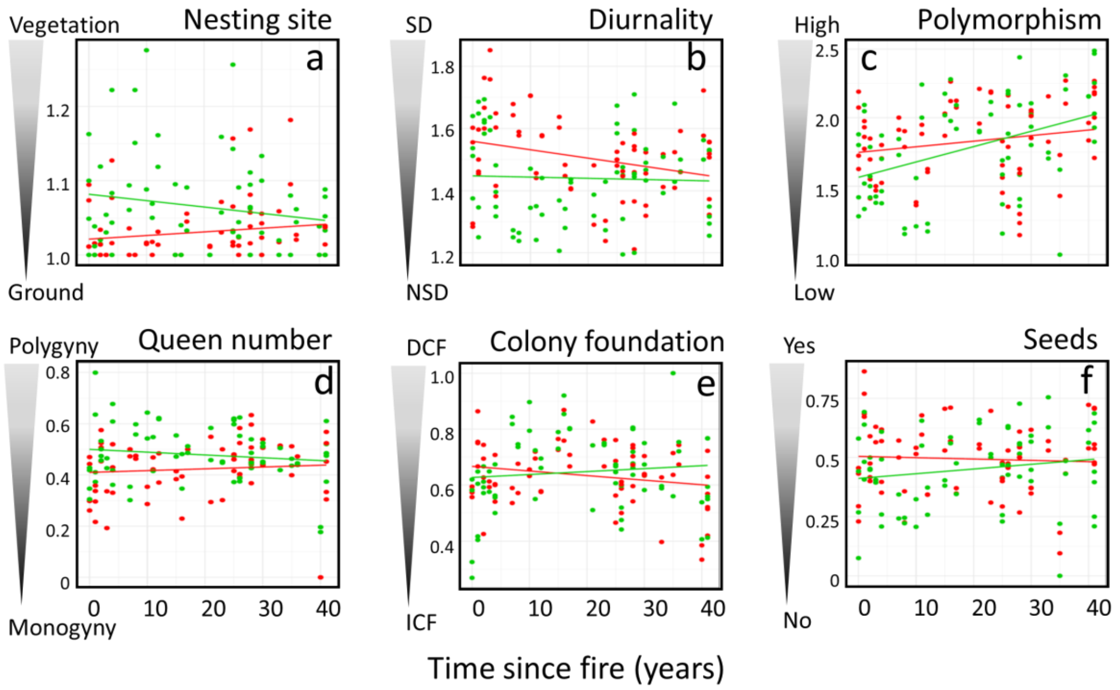


Figure 7. Effects of fire and time since fire on ant traits: (a) nesting site (ground or vegetation); (b) diurnality (non-strictly diurnal species [NDS] or strictly diurnal species [DS]); (c) degree of worker polymorphism (low, medium, or high); (d) queen number (monogyny, polygyny, or both); (e) seed-based diet (no or yes); (f) colony foundation type (independent colony foundation [ICF], dependent colony foundation [DCF], or both). The burned areas are in red, and the unburned areas are in green. For a detailed description of the traits, see Table S3.

In contrast, for bees, only two of the six traits (nesting site and floral specialization) were affected by the interaction between fire and time since fire (Table S11), and they displayed more opaque patterns.

Discussion

In this study, we explored the taxonomic and functional responses of ant and bee communities to wildfires in Andalusian pine forests that had burned at various moments in the past. Our main finding was that values of most of the taxonomic indices (species richness, abundance, and taxonomic diversity) were higher at burned areas, while Fdiv was lower in burned areas (Fig. 5d), at least for ants. Fire also shaped the taxonomic community composition. An effect of fire treatment was seen in both ants and bees. There was also an impact of time since fire in ants. Although neither the functional indices (except for functional divergence) nor functional composition responded in a clear way to fire, we did observe pronounced differences in six ants' functional traits. These differences were largest at the most recently burned areas and then became less dramatic with greater time since fire. Our results confirm that fire alters ant communities more than bee communities; firstly taxonomically, increasing ant richness, abundance and diversity at the long term; and secondly functionally, with some ant traits altered in the short term or persisting over the long term. All these short- and long-term changes seem to suggest that fire in Mediterranean coniferous ecosystems is not as negative as one might expect and even could have a positive effect specially on some facets of ant communities.

Do taxonomic and functional diversity increase immediately after fire?

Our first hypothesis was that the taxonomic and functional diversity of ants and bees would be higher at burned areas, where fire creates new niches, or lower because fire simplify the complexity of the ecosystem. We found that richness of both ants and bees was higher at burned areas, and ant abundance and ant diversity were significantly higher at burned areas, independently of the time since fire. The fire clears out existing vegetation and favors the appearance of ant species that generally occur in open areas (Arnan et al., 2006; Rodrigo and Retana, 2006). It is thanks to these new arrivals, consisting on species living in open areas, plus the resident species that survived the fire, that ant species richness and diversity are greater at burned areas.

For bees, it has been extensively shown that communities increase in species richness and abundance in the first years after a fire (Galbraith et al., 2019; Grundel et al., 2010; Mason et al., 2021; Mola and Williams, 2018; Moretti et al., 2009; Petanidou and Ellis, 1996; Potts et al., 2003; Simmons and Bossart, 2020). Fire's removal of the vegetation promotes the appearance of a herbaceous understory that includes flowering plants, thus boosting food availability (Burkle et al., 2019). The greater resource offered by extrafloral nectaries of plants after fire could also benefit interacting ant species, as has been showed by da Silva et al. (2020). The bee community can also be recomposed in burned areas due to the movement of species in the metacommunity (Perillo et al., 2020). Although we did not observe significant differences between burned and unburned areas for bees, it is possible that this new resource pool could augment bee visits and abundance.

Do taxonomic and functional diversity decrease progressively with time since fire?

Our second hypothesis was that the taxonomic and functional structure of the ant and bee communities at the burned and unburned areas would become more similar the longer the time since fire. After 10 to 15 years have passed since fire, bee richness and abundance decline dramatically (Carbone et al., 2019; Potts et al., 2003). Here, we observed a significant decrease in bee abundance with time since fire, but this pattern did not extend to the other taxonomic or functional metrics of bee communities.

Ants display much more heterogenous responses to fire than bees, as illustrated by research conducted across the globe (New, 2014). We show that fire had a constant significant effect on different taxonomic and functional diversity indexes, regardless of how much time had passed. In contrast, other systems seem to spring back quite quickly, not only because the habitat are different, but also because the ecological effects result from experimental or prescribed fires. For example, in certain US oak forests, ant communities rapidly recovered their taxonomic structure after a prescribed fire, just one month later (Verble-Pearson and Yanoviak, 2014). Similarly, in tropical Australia, savanna ant communities recovered within four months (Parr and Andersen, 2008), and African savanna communities recovered within eight months (Parr et al., 2004). Dynamics took yet another course in different Brazilian ecosystems: in the rupestrian ecosystem, the level of diversity was constant at burned sites even if the ant species assemblage changed dramatically (Anjos et al., 2015); in the Pantanal, only ten days after fire, species composition substantially changed and increased species richness, but these effects decreased at one year and disappeared after four years (Arruda et al., 2022). The Brazilian Cerrado, which has a highly diverse and specialized fauna of arboreal ants, is very susceptible to the direct effects of fire: burned trees showed a strong decline in species richness and marked changes in species composition and no sign of community recovery after two years of the last fire event (Rosa et al. 2021). But fire was not strong enough to modify the whole structure of the ant-plant networks between ants and plants with extrafloral nectaries (Fagundes et al. 2018). However, in campo rupestre (Brazilian savanna), fire impacts on ant-plant interactions were evident only one month post-fire, when burned plots had lower interactions diversity and frequency than unburned plots; these differences between burned and unburned plots were no longer observed four months post-fire (Costa et al. 2018). In Mediterranean P. nigra forests, the taxonomic composition of ant communities had not returned to pre-fire conditions even after 19 years, which was also the case for the vegetation (Rodrigo and Retana, 2006). Finally, it is also possible that disturbance events in natural ecosystems can trigger a decrease in the functional structure of ant and bee communities (Arnan et al., 2018; Bihn et al., 2010; Rader et al., 2014). Here, we found no effect of time since fire on the functional diversity of either ants or bees.

Do environmental variables or time since fire better explain taxonomic and functional diversity?

Our third hypothesis postulated that differences in taxonomic and functional diversity between burned and unburned areas could be explained by environmental variables if they were not explained by the fire. Elevation, altitude or the pine species modified some taxonomic indices (richness, diversity and eveness) and functional diversity in ants, while climate modified functional diversity in ants. This is in agreement with previous works that show that in ants taxonomic diversity increased with elevation (Bishop et al., 2014; Karaman, 2011; Sanders, 2002) although temperature can inverse this relationship (Fontanilla et al., 2019; Siqueira de Castro et al., 2020); even functional traits such as body size (Shik et al., 2019) may be related to elevation.

The plant species occurring in the area that burned provide resources and microhabitat for a variety of ants. Consequently, the forest's composition before the fire also has an influence on how well ant communities recover over the intermediate term

(Arnan et al., 2006). Not all pine forests have the same type of fire adaptations (He et al., 2012; Keeley, 2012). In zones with *P. pinaster* and *P. halepensis*, pine forests can eventually re-emerge after fire. These pines produce serotinous cones, which need to be exposed to fire to open and release their seeds (Elvira et al., 2021; González-De Vega et al., 2016; Madrigal et al., 2021; Ne'eman et al., 2004). In contrast, in zones that originally hosted forests of *P. nigra* or *P. pinea*, fire created rather open areas with a more or less developed understory. These species do not have serotinous cones. While *P. pinea* can withstand low-intensity fires, thanks to its thick bark, it is unable to resprout after fire-induced mortality (Madrigal et al., 2019). This fact could also explain why, in our study, the ant communities associated with P. nigra were significantly more uniform (i.e., had higher values of Pielou's evenness) than the communities associated with *P. pinaster, P. halepensis,* and *P. pinea*.

Do taxonomic and functional composition differ with time since fire?

Our results revealed that the fire, the time since fire, and their interaction had an effect on the taxonomic composition of ant communities. We discovered that ant species with an arboreal lifestyle or an association with forests (e.g., *Camponotus lateralis, Crematogaster scutellaris, Formica cunicularia*, and various *Temnothorax* species) were more likely to occur at areas that had burned at least 15 years ago. In these areas, enough time had passed to allow the vegetation to become re-established. Other ant species (e.g., *Messor marocanus, M. lusitanicus, Aphaenogaster senilis, Cataglyphis floricola, C. tartessica, C. hispanica, Oxyopomyrmex saulcy*, and *Goniomma kugleri*) were more strongly associated with recent and moderately recent fires, which means the burned area would have less developed vegetation. Such environmental conditions are especially favorable for behaviorally subordinate ant species that live in open areas and that forage at high temperatures when behaviorally dominant ants are absent (Cerdá et al., 1998, 1997). Similar patterns have been seen elsewhere: the bare ground revealed by fire is a boon for thermophilic ant species such as *Forelius pruinosus* in Florida (Izhaki et al., 2003) and *Doryrmyrmex* species in Argentina (Sackmann and Farji-Brener, 2006). Our finding that the functional composition was similar could suggest the presence of functional redundancy, where different species can fulfill similar ecosystem functions following a change in environmental conditions, as has been showed in recent works (Arnan et al., 2019; Houadria et al., 2016; Houadria and Menzel, 2017).

Which functional traits are filtered by fire?

Several studies have shown that fire broadly shapes terrestrial arthropod communities by causing the local extinction of existing populations and facilitating the arrival of species with a strong dispersal capacity, a tolerance for open areas with little shade, and an ability to exploit the diverse resources available in the post-fire habitat (see a review in Wong et al., 2019). We observed that fire (or the environmental conditions it creates) may act as a trait filter. First, the ant traits most common at recently burned areas promoted survival (ground nesting), persistence (diurnality, monogyny, seed-based diet), and colonization (dependent colony foundation). Second, there were other ant traits related to persistence that were common at the burned areas but that showed no relationship with time since fire (monodomy, individual foraging behaviour, larger body size, and an insect-free diet). These functional traits seem to be advantageous to ants in landscapes resulting from fire disturbance (Arnan et al., 2020; Vidal-Cordero et al., 2022). The fact that some trait differences diminished with time since fire may stem from the fact that vegetation cover develops over time, causing open areas to disappear.

In the case of bees, taxonomic community composition was only affected by the fire, while functional composition of bee communities was affected by the interaction between fire and time since fire. The bees at unburned areas (which had more developed vegetation) were cavity nesters. They create nests in pre-existing holes in trees, tree trunks, and reeds (e.g., *Lithurgus cornutus* and *Chelostoma* species) or vertical galleries in the thick stems of larger plant species (various *Ceratina* species) (Aguado Martín, 2015; Michener, 2000). At the burned areas, we observed bees that nest on the ground in open and sunny places (e.g., *Amegilla quadrifasciata*, *Halictus smaragdulus*, and *Thyreus* sp., a parasitic species of *Amegilla*) or on tree stumps, such as those that remain after fires (*Xylocopa cantabrita*) (Aguado Martín, 2015; Michener, 2000). Similar results have been seen for specific functional traits, such as body size, in other forest bee communities (Burkle et al., 2019). Moreover, recently burned areas hosted polylectic bees, which mainly nest on the ground and in woody materials. Such is unsurprising given the greater availability of herbaceous flowering plants, open sandy areas, and dead wood immediately after fire. Areas that had burned less recently hosted oligolectic species, which makes sense since certain plant species have become dominant and the floral community is not as rich. In addition, the greater amount of vegetation cover increases moisture levels, supporting snail populations and the presence of trees in which hive nesters can establish themselves.

Limitations and uncertainties

Sampling protocols are sufficiently accurate to provide good quality data about ant and bee community structure and composition after wildfires. However, our study has some limitations. First, we used a paired design to select burned and unburned areas with a space-for-time substitution approach in which unburned areas represented native communities before the fire (Blois et al., 2013; Kelly et al., 2011; Moretti and Legg, 2009). There were large areas (> 4,000 ha) of burned Pinus forests without fire recurrence (only one fire event) and where the wood was not removed. Moreover, paired control areas had similar slope and orientation characteristics to burned areas. Some components of the fire regime could not be taken into account and could influence the results. For example, fire season, because most of the selected fires were burned along the summer season, when the majority of fires occur; and fire intensity, because this information was not available for all the fires studied. A second issue could be the *Pinus* species. As we have discussed in the section 4.2, pine species have different fire adaptation strategies (He et al., 2012; Keeley, 2012), and our sites include forests of four different Pinus species: *P. pinaster, P. halepensis, P. pinea* and *P. nigra*, that mainly affect the speed of vegetation recovery. Although, pine species was added as a factor in the analysis performed, it is possible that some bias around the time since fire could remain.

Third, an issue could arise from insect phenology. We sampled during a relatively short time-window (from May through August), and did 48-h of sampling per site, only once in each plot. Although this seemed to be sufficient for ant results (abundances and responses consistent with previous works), it was not the case for bees (low abundances and responses were hard to understand). Bee abundance was much lower overall than that observed in previous studies (Bogusch et al., 2015; Burkle et al., 2019). Such could reflect the relatively limited understory communities and soil acidification found in conifer forests (Augusto et al., 1998; De Schrijver et al., 2006). Another reason could be that bee communities were only sampled with pan traps, and sometimes too late in the season (end July- August may be too hot for bees, Bosch et al. 1997). This could have biased not only bee richness but also their traits (Wong et al.

2019); although we did not include any trait related to phenology of the bee species. Bee sampling mainly in spring and with a combination of transect walks and pan traps could lead to a more comprehensive characterization of this group (Nielsen et al., 2011; Westphal et al., 2008).

Implications for management

Assessments of the response of arthropods to disturbances can be used as early indicators of change and inform management and conservation plans for the affected ecosystem (Kremen et al. 1993, Lawes et al. 2005). These may be especially important in global change scenarios where it is crucial to take advantage of synergies between forestry and biodiversity conservation planning, which operate on the same physical space, and even on the same elements.

Our study reveals increased taxonomic richness and diversity for ants regardless of time since fire, suggesting that fire can have a positive effect on ant communities. Therefore, rejuvenation of coniferous systems within forest planning should be considered as a promoter of richness and diversity, not only in ants but also in bees (Gelles et al., 2022). It would be beneficial to develop a long-term effective monitoring system using standardized protocols of arthropods for the detection of ecosystem changes and recovery assessments after wildfires.

Conclusions

Our study of how ant and bee communities respond to wildfires over the longer term has allowed us to explore differing patterns in taxonomic diversity, functional diversity, community structure, and community composition. Although we did not clearly identify the factors that influence community recovery, from either a taxonomic or functional perspective, we show that fire acted as a niche-filtering mechanism, with a long-term effect for some traits (such as ant body size) and a short-term for other traits (such as ant- and bee-nesting type or colony foundation). Knowledge about these functional traits can help generate predictions about how species will respond following fire. Future studies should investigate further additional fire characteristics that could impact community recovery, which were not considered in this study, such as fire recurrence, intensity or severity, or other management options of burned areas after fire.

Acknowledgments

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Appendix

Table S1. Description of study areas ordered by time since fire. Locality, province, elevation (Elev), and geographical coordinates associated with the study area. *Pinus* sp. indicates the main conifer species in the forest.

ID #	Locality	Province	Elev (m)	Time since fire (years)	Coordinates (long, lat)	*Pinus* sp.*
1	Las Peñuelas	Huelva	59	0	37.1021279732, -6.71786675371	*P. pinea*
2	Gibraleón	Huelva	10	0	37.2346229131, -7.02097134551	*P. pinea*
3	Lújar	Granada	625	1	36.7784306, -3.4181896	*P. halepensis*
4	Huesa	Jaén	541	1	37.7467052174, -3.13251288455	*P. halepensis*
5	Cenes de la Vega	Granada	830	2	37.1475300811, -3.54414835462	*P. halepensis*
6	El Campillo	Huelva	512	2	37.7400074429, -6.68761710874	*P. pinea*
7	Moguer	Huelva	55	4	37.2137135628, -6.74655456073	*P. pinea*
8	Nerva	Huelva	247	4	37.6627064065, -6.54098329016	*P. pinea*
9	Pujerra	Málaga	1009	4	36.5545262091, -5.17028376791	*P. pinaster*
10	Jódar	Jaén	717	7	37.7802082271, -3.32042191294	*P. halepensis*
11	Nerva	Huelva	283	8	37.691371, -6.518774	*P. pinea*
12	Moguer	Huelva	39	11	37.2048691411, -6.83177227193	*P. pinea*
13	Santiago Pontones	Jaén	799	11	38.0767906409, -2.82666680151	*P. pinaster*
14	El Campillo	Huelva	247	12	37.6609797063, -6.55207848406	*P. pinea*
15	Cazorla	Jaén	917	15	37.9512501422, -2.93141918295	*P. pinaster*
16	Quesada	Jaén	957	16	37.759592063, -3.00630998518	*P. halepensis*
17	Iznalloz	Granada	1093	17	37.3628693625, -3.49099607847	*P. halepensis*
18	Los Guajares	Granada	1146	21	36.8812851687, -3.67340859179	*P. pinaster*
19	Quéntar	Granada	1507	23	37.2687324571, -3.40102898392	*P. halepensis*
20	Nerva	Huelva	334	25	37.6768553039, -6.52914116562	*P. pinea*
21	Parauta	Málaga	1307	25	36.6379878117, -5.05027295554	*P. pinaster*
22	Albuñuelas	Granada	1320	26	36.8912408777, -3.72341763628	*P. pinaster*
23	Carratraca	Málaga	787	26	36.8371212821, -4.84259163558	*P. halepensis*
24	Alájar	Huelva	451	28	37.8581533761, -6.65782078761	*P. pinaster*
25	Sorihuela del Guadalimar	Jaén	927	28	38.1897564727, -2.83064690602	*P. pinaster*
26	Moguer	Huelva	40	29	37.2162661287, -6.84579723043	*P. pinea*
27	SantoTomé	Jaén	751	30	38.0036741233, -2.88666749444	*P. pinaster*
28	Villanueva del Arzobispo	Jaén	1215	30	38.1630413957, -2.87434652533	*P. pinaster*
29	Alhama de Granada	Granada	1130	33	36.8715791711, -3.85920216114	*P. pinaster*
30	Baza	Granada	1648	35	37.3954835425, -2.84093551698	*P. nigra*
31	Iznalloz	Granada	1066	36	37.3637592343, -3.43997381569	*P. halepensis*
32	Almonte	Huelva	37	40	37.0439545809, -6.57172286314	*P. pinea*
33	Albuñuelas	Granada	1253	41	36.9185306732, -3.74733242061	*P. pinaster*
34	Alhama de Granada	Granada	1223	41	36.8608108054, -3.88037561051	*P. pinaster*
35	Jayena	Granada	1041	41	36.9161962738, -3.81613776349	*P. halepensis*

*As per He et al. (He T., Pausas J.G., Belcher C.M., Schwilk D.W., Lamont B.B. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. New Phytologist 751–759. doi: 10.1111/j.1469-8137.2012.04079.x), the traits of the *Pinus* species are as follows:

- *P. pinea*: no serotiny, no resprouting, no associated with any fire regime
- *P. halepensis*: serotiny, no resprouting, association with crown fire
- *P. pinaster:* serotiny, no resprouting, association with crown/surface fires
- *P. nigra*: no serotiny, no resprouting, association with surface fire

Table S2. Effects of fire, time since fire, and their interaction on plant cover strata (herbaceous plants, small shrubs, large shrubs, and trees) and vegetation cover (Veg). Statistics F, p-values (P) and DF (degrees of freedom) are the results of the linear mixed-effect models. In bold are the significant F and p values, following sequential Benjamini & Hochberg (1995) correction*.

		Herb. plants		**Small shrubs**		**Large shrubs**		**Trees**		**Veg**	
	DF	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
a) Burned sites											
Time	1, 33	3.18	0.0836	**11.32**	**0.0025**	**24.32**	**<0.0001**	**43.34**	**<0.0001**	**27.52**	**<0.0001**
b) Unburned sites											
Time	1, 33	1.23	0.2764	1.65	0.2079	3.57	0.0677	0.20	0.6207	0.78	0.3838
c) Both site types											
Fire	1, 103	**10.32**	**0.0027**	**5.37**	**0.0269**	**14.86**	**<0.0001**	**122.33**	**<0.0001**	**27.86**	**<0.0001**
Time	1, 33	3.02	0.1000	**7.40**	**0.0140**	**19.37**	**<0.0001**	**43.34**	**<0.0001**	**19.63**	**0.0007**
Fire x Time	1, 103	1.55	0.2155	**12.10**	**0.0012**	**21.13**	**<0.0001**	**124.08**	**<0.0001**	**52.24**	**<0.0001**

*Benjamini Y, Hochberg Y (1995) Controlling the False Discovery Rate: a Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society. Series B 57: 289–300.

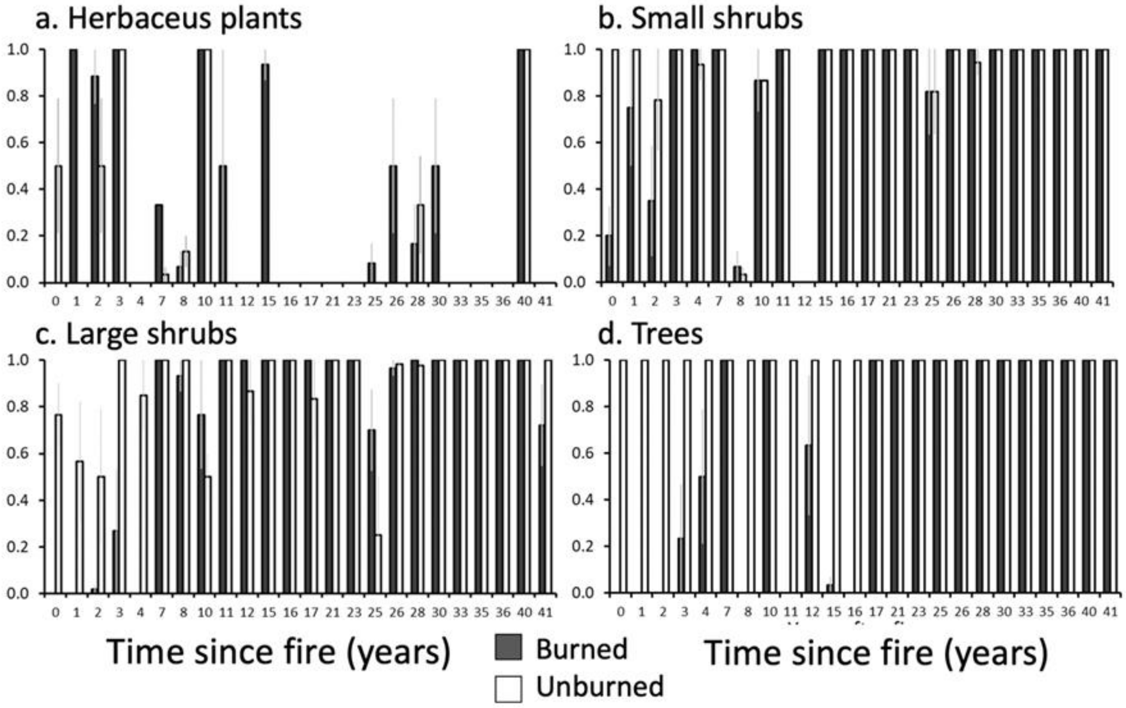


Figure S1. Relative abundance of plant cover strata at burned areas (gray) and unburned areas (white) ordered by time since fire. (a) herbaceous plants, (b) small shrubs, (c) large shrubs, and (d) trees. When the time since fire is 0, it means that the study area was sampled the same year that the fire occurred. For each study area, the data for the two burned transects and the two unburned transects were averaged.

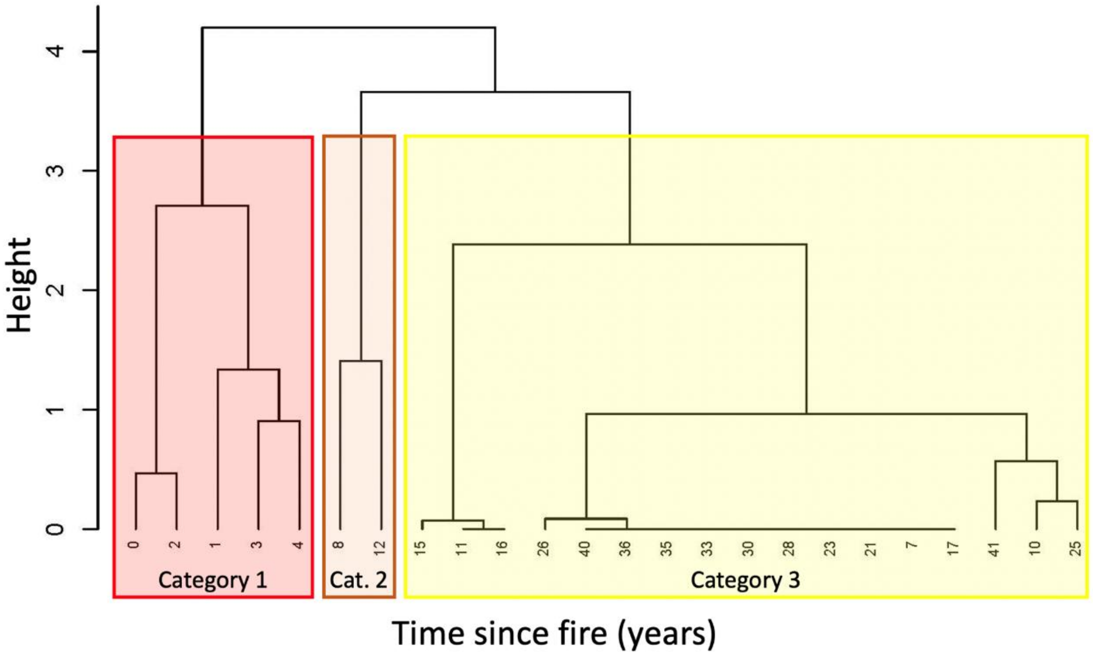


Figure S2. Cluster dendrogram of plant cover strata at burned areas (small shrubs, large shrubs, and trees). The results revealed that the vegetation clustered into three time-based categories: red = fire occurred 0–4 years ago, orange = fire occurred 7–12 years ago, and yellow = fire occurred 15–41 years ago. The absolute time since fire is indicated below the branches. When the time since fire is 0, it means that the study area was sampled the same year that the fire occurred.

Table S3. Description of the ant functional traits used in this study. Traits can be grouped based on their relationship to fire: survival—likelihood of surviving the fire itself; persistence—ability to persist in burned habitats; and colonization—ability to colonize burned areas. Traits were obtained from Arnan et al. 2012, 2014 (*).

Trait group	Functional trait	Data type	Trait states	Abbrev.
Survival	Nesting site	Categorical (Binary)	(1) Ground (2) Vegetation	nes.sit
Persistence	Behavioral dominance	Categorical (Binary)	(1) Subordinate (2) Dominant	dom
	Body size	Quantitative	Mean worker size (1.6–10.0)	bod.siz
	Colony size	Quantitative	Mean colony size (50–20,000)	col.siz
	Number of nests	Categorical	(0) Monodomy (0.5) Both monodomy and polydomy (1) Polydomy	num.nes
	Number of queens	Categorical	(0) Monogyny (0.5) Both monogyny and polygyny (1) Polygyny	num.que
	Diurnality	Categorical (Binary)	(1) Non-strictly diurnal (NSD) (2) Strictly diurnal (SD)	SD
	Foraging strategy	Categorical	(1) Individual (2) Group (3) Collective	for.str
	Insects	Categorical (Binary)	(0) No (1) Yes	ins.die
	Seeds	Categorical (Binary)	(0) No (1) Yes	see.die
	Sugary liquids	Categorical (Binary)	(0) No (1) Yes	liq.die
	Degree of worker polymorphism	Categorical	(1) Low (2) Medium (3) High	poly
Colonization	Colony foundation type	Categorical	(0) Dependent colony foundation (DCF) (0.5) Both dependent and independent CF (1) Independent colony foundation (ICF)	col.fou

* Arnan X, Cerdá X, Retana (2012) Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ant species. Oecologia 170: 489–500. Electronic Appendix: Table S1, https://doi.org/10.1007/s00442-012-2315-y

Arnan X, Cerdá X, Retana (2014) Ant functional responses along environmental gradients. Journal of Animal Ecology 83: 1398–1408 . Data set available in the 'digital CSIC' repository: http://hdl.handle.net/10261/94809

Table S4. Description of the bee functional traits used in this study. Traits can be grouped based on their relationship to fire: survival—likelihood of surviving the fire itself; persistence—ability to persist in burned habitats; and colonization—ability to colonize burned habitats. The superscript letters indicate the references for the traits.

Trait group	Functional trait	Data type	Trait states	Abbrev.
Survival	Nesting site[a]	Categorical	(0) Ground (1) Wood (2) Snail shells (3) Hives	nes.sit
Persistence	Body size[b]	Categorical	(0) Very small (1) Small (2) Medium (3) Large	bod.siz
	Intertegular distance[c]	Quantitative	Mean intertegular distance (mm)	int.dis
	Floral specialization[a,d]	Categorical (Binary)	(1) Polylectic (2) Oligolectic	flo.spe
	Tongue length[a,e]	Categorical (Binary)	(1) Short (2) Long	ton.len
Colonization	Lifestyle[a,d]	Categorical	(0) Solitary (0.5) Parasitic (1) Social	lif.for

[a] Michener Ch. D. (2000) The bees of the world. Johns Hopkins University Press.
[b] Molina, C. and I. Bartomeus (2019) Guía de campo de las abejas de España. Tundra Ediciones.
[c] Kendall L. K. et al (2018) Pollinator size and its consequences: predictive allometry for pollinating insects. Ecology and Evolution, 9(4), 1702– 1714
[d] Aguado Martín L. O. (2015) Guía de campo de los polinizadores de España. Ediciones Mundi-Prensa.
[e] Cariveau D. P. et al (2016) The allometry of bee proboscis length and its uses in ecology. PLOS ONE 11(3): e0151482.

Table S5. Principal components analysis—factor coordinates and cumulative eigenvalues for each climate variable obtained from WorldClim. The variables grouped into two principal components—Clim. 1 and Clim. 2.

Climate variable	Clim. 1	Clim. 2
Annual mean temperature (°C)	**-0.75**	-0.64
Maximum temperature of the warmest month (°C)	-0.09	**-0.90**
Minimum temperature of the coldest month (°C)	**-0.93**	-0.30
Temperature seasonality	**0.95**	-0.03
Annual precipitation (mm)	-0.33	**0.91**
Precipitation in the wettest month (mm)	**-0.69**	0.66
Precipitation in the driest month (mm)	**0.93**	0.13
Precipitation seasonality (CV = SD/mean*100)	**-0.98**	0.18
Cumulative eigenvalue %	59.5%	32.8%

Table S6. List of ant species grouped into subfamilies and placed in alphabetical order. Indicated is the total occurrence of each species at unburned and burned sites. In parentheses is the number of transects at which the species was found out of the 70 total transects in the unburned and burned areas. A numeric code for each species is used in Fig. 6 and S5.

Species	Abbreviation	Code	Unburned	Burned
Amblyoponinae				
Amblyopone gaetulica	amb.gae	X1	0 (0)	1 (1)
Dolichoderinae				
Tapinoma erraticum	tap.err	X44	4 (2)	14 (2)
Tapinoma nigerrimum	tap.nig	X45	57 (14)	57 (15)
Formicinae				
Camponotus cruentatus	cam.cru	X6	64 (13)	98 (18)
Camponotus foreli	cam.for	X7	31 (6)	26 (6)
Camponotus lateralis	cam.lat	X8	15 (12)	15 (7)
Camponotus pilicornis	cam.pil	X9	146 (51)	162 (49)
Camponotus sylvaticus	cam.syl	X10	186 (43)	180 (38)
Cataglyphis floricola	cat.flo	X12	46 (4)	43 (4)
Cataglyphis hispanica	cat.his	X13	82 (13)	161 (12)
Cataglyphis iberica	cat.ibe	X14	58 (11)	81 (16)
Cataglyphis rosenhaueri	cat.ros	X15	2 (2)	35 (7)
Cataglyphis tartessica	cat.tar	X16	38 (6)	59 (5)
Cataglyphis velox	cat.vel	X17	160 (21)	244 (27)
Colobopsis truncata	col.tru	X18	2 (2)	0 (0)
Formica cunicularia	for.cun	X22	59 (17)	57 (12)
Formica fusca	for.fus	X23	34 (5)	0 (0)
Iberoformica subrufa	ibe.sub	X26	303 (43)	523 (56)
Lasius grandis	las.gra	X27	3 (1)	10 (4)
Lasius myops	las.myo	X28	0 (0)	1 (1)
Plagiolepis pygmaea	pla.pyg	X39	181 (38)	165 (45)
Plagiolepis schmitzii	pla.schm	X40	129 (42)	111 (42)
Polyergus rufescens	pol.ruf	X41	1(1)	1 (1)
Myrmicinae				
Aphaenogaster cardenai	aph.car	X2	0 (0)	1 (1)
Aphaenogaster gibbosa	aph.gib	X3	183 (32)	139 (30)
Aphaenogaster iberica	aph.ibe	X4	309 (40)	407 (54)
Aphaenogaster senilis	aph.sen	X5	118 (16)	139 (15)
Cardiocondyla batesii	car.bat	X11	1(1)	1 (1)
Crematogaster auberti	cre.aub	X19	94 (32)	116 (34)
Crematogaster scutellaris	cre.scu	X20	25 (17)	15 (9)
Crematogaster sordidula	cre.sor	X21	6 (5)	22 (10)
Goniomma hispanicum	gon.his	X24	2 (2)	2 (2)
Goniomma kugleri	gon.kug	X25	6 (6)	31 (21)
Messor barbarus	mes.bar	X29	6 (5)	36 (18)
Messor bouvieri	mes.bou	X30	12 (6)	80 (22)
Messor capitatus	mes.cap	X31	13 (6)	30 (11)
Messor lusitanicus	mes.lus	X32	2 (2)	15 (4)

Messor marocanus	mes.mar	X33	7 (4)	10 (5)
Messor structor	mes.str	X34	1 (1)	1 (1)
Monomorium subopacum	mon.sub	X35	69 (8)	51 (6)
Myrmica aloba	myr.alo	X36	0 (0)	1 (1)
Oxyopomyrmex saulcyi	oxy.sau	X37	7 (5)	13 (10)
Pheidole pallidula	phe.pal	X38	539 (54)	579 (55)
Solenopsis sp.	sol.sp	X43	166 (51)	74 (37)
Temnothorax angustulus	tem.ang	X46	0 (0)	3 (1)
Temnothorax aveli	tem.ave	X47	0 (0)	2 (2)
Temnothorax exilis	tem.exi	X48	3 (2)	2 (1)
Temnothorax formosus	tem.for	X49	3 (2)	2 (1)
Temnothorax gredosi	tem.gre	X50	0 (0)	21 (2)
Temnothorax kraussei	te.kra	X51	5 (3)	2 (2)
Temnothorax luteus	tem.lut	X52	31 (11)	28 (15)
Temnothorax pardoi	tem.par	X53	23 (8)	3 (3)
Temnothorax racovitzai	tem.rac	X54	102 (27)	38 (21)
Temnothorax recedens	tem.rec	X55	27 (11)	17 (7)
Temnothorax specularis	tem.spe	X56	0 (0)	1 (1)
Temnothorax tyndalei	tem.tyn	X57	2 (2)	7 (5)
Temnothorax unifasciatus	tem.uni	X58	1 (1)	0 (0)
Tetramorium caespitum	tet.cae	X59	47 (17)	94 (26)
Tetramorium forte	tet.for	X60	13 (6)	15 (6)
Tetramorium semilaeve	tet.sem	X61	105 (36)	215 (47)
Ponerinae				
Ponera testacea	pon.tes	X42	1 (1)	0 (0)

Table S7. List of bee species and genera grouped into subfamilies and placed in alphabetical order. Indicated is the total abundance of each species/genus at unburned and burned transects. In parentheses is the number of transects at which the species/genus was found out of the 70 total transects in the unburned and burned areas. A numeric code for each species is used in Fig. 6 and S5.

Species	Code	Unburned	Burned
Andrenidae			
Andrena hispania	X2	0 (0)	2 (2)
Andrena sp.	X3	48 (13)	64 (8)
Flavipanurgus venustus	X18	1 (1)	2 (2)
Panurgus sp.	X33	9 (6)	5 (3)
Apidae			
Amegilla quadrifasciata	X1	0 (0)	4 (3)
Anthophora bimaculata	X4	1 (1)	0 (0)
Anthophora sp.	X6	0 (0)	1 (1)
Apis mellifera	X7	3 (2)	13(5)
Bombus hortorum	X8	1 (1)	0 (0)
Bombus terrestris	X9	5 (3)	0 (0)
Ceratina cucurbitina	X10	6 (5)	0 (0)
Ceratina mocsaryi	X11	2 (2)	3 (3)
Ceratina sp.	X12	0 (0)	5 (4)
Eucera sp.	X17	1 (1)	1 (1)
Nomada sp.	X31	2 (2)	1 (1)
Thyreus sp.	X35	0 (0)	1 (1)
Xylocopa cantabrita	X36	0 (0)	1 (1)
Colletidae			
Hylaeus sp.	X25	0 (0)	2 (2)
Hylaeus variegatus	X26	0 (0)	1 (1)
Halictidae			
Halictus gemmeus	X19	0 (0)	1 (1)
Halictus smaragdulus	X20	3 (3)	10 (9)
Halictus sp.	X21	7 (4)	4 (3)
Halictus subauratus	X22	2 (2)	2 (2)
Lasioglossum sp.	X27	32 (20)	32 (19)
Melittidae			
Dasypoda cingulata	X15	1 (1)	4 (2)
Dasypoda sp.	X16	0 (0)	6 (2)
Megachilidae			
Anthidium cingulatum	X5	0 (0)	1 (1)
Chelostoma florisomne	X13	1 (1)	0 (0)
Chelostoma sp.	X14	2 (2)	0 (0)
Heriades sp.	X23	1 (1)	1 (1)
Hoplitis sp.	X24	1 (1)	3 (3)
Lithurgus cornutus	X28	2 (2)	0 (0)
Megachile leachella	X29	1 (1)	4 (3)
Megachile sp.	X30	1 (1)	2 (2)

Osmia sp.	X32	1 (1)	2 (2)
Rhodanthidium stictucum	X34	2 (1)	7 (3)

Table S8. Effects of time since fire and environmental variables on differences in richness for ant and bee communities. Richness difference is the increase in burned areas with respect to unburned areas. Time: how long ago the fire occurred (0 to 41 years); Pine: predominant pine species; Veg: vegetation cover index; Litho: lithological type; Lon, Lat, and Elev: longitude, latitude, and elevation, respectively; Clim. 1 and Clim. 2: components 1 and 2 from the PCA; and d: direction of the relationship: for Fire + indicates higher values in unburned areas and – lower values in unburned areas; for Time + indicates positive relationship.

Richness difference	***Ants***				***Bees***			
	DF	F	P	d	DF	F	P	d
Time	1, 22	0.00	0.9477	-	1, 17	1.56	0.2283	-
Pine	3, 22	0.95	0.4357		3, 17	1.00	0.4131	
Veg	1, 22	0.50	0.4888	+	1, 17	2.71	0.1179	-
Litho	2, 22	0.32	0.7265		2, 17	1.94	0.1740	
Lon	1, 22	0.21	0.6511	-	1, 17	0.25	0.6240	-
Lat	1, 22	**5.26**	**0.0317**	+	1, 17	0.45	0.5114	+
Elev	1, 22	0.01	0.9032	+	1, 17	0.44	0.5175	+
Clim. 1	1, 22	0.08	0.7768	+	1, 17	1.02	0.3266	-
Clim. 2	1, 22	1.75	0.2000	+	1, 17	0.08	0.7867	+

Table S9. Effects of fire and time since fire on the taxonomic community structure of (a) ants and (b) bees. Any effects of environmental variables are also indicated. Taxonomic metrics are A = abundance, S = richness, H = Shannon diversity index, and J = Pielou's evenness. The abbreviations Log, 2, and ½ indicate the use of a logarithmic, squared, or square-root transformation, respectively. Fire: fire treatment (burned and unburned); Time: how long ago the fire occurred (0 to 41 years); Fire x Time: the interaction between the former two variables; Veg: vegetation cover index; Pine: predominant pine species; and Litho: lithological type; Lon, Lat, and Elev: longitude, latitude, and elevation, respectively; Clim. 1 and Clim. 2: components 1 and 2 from the PCA; and d: direction of the relationship: for Fire + indicates higher values in unburned areas and – lower values in unburned areas; for Time + indicates positive relationship.

a) Ants		*Log(A)*			*S*			H^2			J^2		
	DF	F	P	d	F	P	d	F	P	d	F	P	d
Fire	1, 101	**9.36**	**0.0028**	-	**9.54**	**0.0026**	-	**6.62**	**0.0115**	-	0.37	0.5468	+
Time	1, 23	0.06	0.8154	-	0.44	0.5150	-	0.64	0.4306	-	0.16	0.6932	-
Fire x Time	1, 101	1.81	0.1816	+	0.08	0.7725	+	0.35	0.5570	-	2.01	0.1590	-
Veg	1, 101	**10.82**	**0.0014**	-	0.53	0.4685	+	2.04	0.1562	+	1.50	0.2242	+
Pine	3, 23	**11.53**	**0.0001**		1.73	0.1896		1.31	0.2942		**3.86**	**0.0226**	
Litho	2, 23	0.30	0.7407		0.90	0.4211		1.45	0.2550		**3.86**	**0.0358**	
Lon	1, 23	2.44	0.1319	-	0.73	0.4033	+	0.37	0.5507	+	0.37	0.5473	+
Lat	1, 23	0.12	0.7344	-	**6.14**	**0.0210**	-	**6.74**	**0.0161**	-	**4.33**	**0.0489**	-
Elev	1, 23	2.78	0.1090	+	**3.67**	**0.0677**	+	**4.67**	**0.0413**	+	**4.39**	**0.0473**	+
Clim. 1	1, 23	0.14	0.7106	+	0.05	0.8191	+	0.11	0.7480	-	2.64	0.1823	-
Clim. 2	1, 23	0.15	0.7021	+	1.41	0.2470	+	0.38	0.5418	+	1.89	0.1590	-

b) Bees		*A*			*Log(S)*			$H^{1/2}$			J^2		
	DF	F	P	d	F	P	d	F	P	d	F	P	d
Fire	1, 51	2.83	0.0986	-	2.19	0.1447	-	0.58	0.4506	-	2.45	0.1303	-
Time	1, 17	**6.16**	**0.0239**	-	0.21	0.6506	+	0.43	0.5224	+	2.53	0.1428	-
Fire x Time	1, 51	0.20	0.6531	+	0.10	0.7534	+	0.80	0.3746	+	2.61	0.1191	+
Veg	1, 51	1.68	0.2010	+	0.61	0.4391	+	0.32	0.5736	+	2.56	0.1226	+
Pine	3, 17	2.42	0.1012		0.08	0.9722		0.24	0.8653		3.35	0.0638	
Litho	2, 17	2.96	0.0791		3.26	0.0635		1.34	0.2885		0.67	0.5348	
Lon	1, 17	0.19	0.6696	+	0.21	0.6527	+	0.01	0.9178	-	0.28	0.6059	-
Lat	1, 17	0.05	0.8260	+	0.00	0.9917	+	0.00	0.9401	+	0.00	0.9782	+
Elev	1, 17	0.40	0.5343	-	1.12	0.3039	-	1.49	0.2381	-	0.25	0.6293	-
Clim. 1	1, 17	1.56	0.2286	-	1.94	0.1814	-	2.15	0.1607	-	0.00	0.9546	+
Clim. 2	1, 17	0.12	0.7287	-	0.07	0.7942	+	0.83	0.3748	+	0.40	0.5432	+

Table S10. Effects of fire and time since fire on the functional community structure of (a) ants and (b) bees. Effects of environmental variables are also indicated. Functional metrics are FRic: functional richness; FEve: functional evenness; FDis: functional dispersion; and FDiv: functional divergence. The abbreviations Log, 2, and ½ indicate the use of a logarithmic, squared, or square-root transformation, respectively. Fire: fire treatment (burned and unburned); Time: how long ago the fire occurred (0 to 41 years); Fire x Time: the interaction between the former two variables; Veg: vegetation cover index; Pine: predominant pine species; and Litho: lithological type; Lon, Lat, and Elev: longitude, latitude, and elevation, respectively; Clim. 1 and Clim. 2: components 1 and 2 from the PCA; and d: direction of the relationship for Fire + indicates higher values in unburned areas and – lower values in unburned areas; for Time + indicates positive relationship.

a) Ants		*FRic*			*FEve*			*FDis*^{2}			*FDiv*		
	DF	F	P	d	F	P	d	F	P	d	F	P	d
Fire	1, 101	2.97	0.0877	-	0.36	0.5514	-	0.07	0.7877	+	**9.63**	**0.0025**	+
Time	1, 23	2.44	0.1320	-	0.00	0.9519	+	**4.01**	**0.0572**	+	3.26	0.0843	-
Fire x Time	1, 101	0.05	0.8317	-	0.04	0.8385	-	0.31	0.5807	-	0.01	0.9345	+
Veg	1, 101	0.72	0.3991	+	0.04	0.8363	-	2.03	0.1577	-	3.07	0.0827	+
Pine	3, 23	2.36	0.0978		0.07	0.9755		**7.450**	**0.0012**		0.55	0.6519	
Litho	2, 23	0.96	0.3981		1.95	0.1658		1.01	0.3811		0.46	0.6358	
Lon	1, 23	**5.11**	**0.0335**	-	0.95	0.3390	+	0.08	0.7765	-	3.06	0.0936	-
Lat	1, 23	0.80	0.3811	-	0.00	0.9743	-	0.22	0.6409	-	0.03	0.8651	-
Elev	1, 23	**5.85**	**0.0239**	+	0.65	0.4289	+	**7.37**	**0.0124**	+	0.36	0.5571	+
Clim. 1	1, 23	0.23	0.6354	+	0.47	0.4983	+	0.00	0.9953	-	0.77	0.3901	+
Clim. 2	1, 23	0.95	0.3389	+	1.54	0.2277	-	1.69	0.2060	-	0.23	0.6357	+

b) Bees		*Log(FRic)*			*FEve*			*FDis*$^{1/2}$			*FDiv*		
	DF	F	P	d	F	P	d	F	P	d	F	P	d
Fire	1, 51	0.03	0.8823	+	3.86	0.1883	-	1.27	0.2650	-	0.4133	0.5862	-
Time	1, 17	0.00	0.9922	+	0.07	0.8126	-	2.33	0.1450	-	0.0608	0.8282	-
Fire x Time	1, 51	1.09	0.4058	+	3.21	0.2151	+	0.69	0.4112	+	5.5704	0.1422	-
Veg	1, 51	2.98	0.2263	-	0.07	0.8207	+	0.37	0.5470	+	0.9437	0.4338	+
Pine	3, 17	0.63	0.6623		4.45	0.1891		0.93	0.4479		1.1892	0.4871	
Litho	2, 17	0.47	0.6814		8.96	0.1004		1.06	0.3677		0.1614	0.8610	
Lon	1, 17	0.65	0.5053	+	0.25	0.6686	+	0.16	0.6917	-	0.8625	0.4511	-
Lat	1, 17	0.11	0.7671	-	0.03	0.8702	-	0.01	0.9119	+	2.3476	0.2652	+
Elev	1, 17	0.00	0.9604	-	1.07	0.4100	+	0.60	0.4504	-	1.2001	0.3876	+
Clim. 1	1, 17	0.00	0.9807	-	0.00	0.9855	-	**5.21**	**0.0356**	-	0.5363	0.5402	+
Clim. 2	1, 17	1.86	0.3055	-	0.28	0.6472	-	1.37	0.2583	+	0.7416	0.4799	+

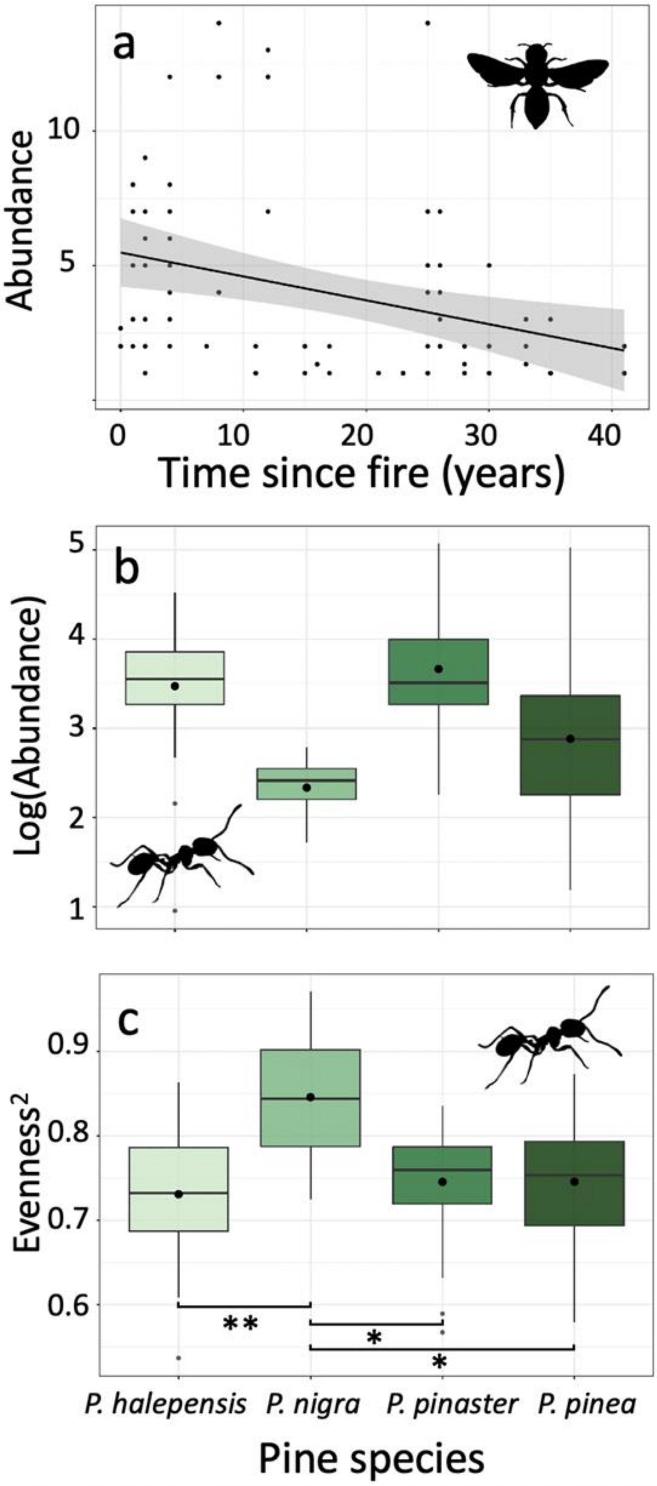


Figure S3. Effects of time since fire and pine species on the taxonomic community structure of ants and bees. (a) Relationship between bee abundance and time since fire. The line indicates the linear fit of the model, and the shaded area indicates the standard error. (b) Mean (± SE) ant abundance in forests dominated by different pine species. The abundance data were log transformed. (c) Pielou's evenness for ant communities in forests dominated by different pine species. The index was square transformed.

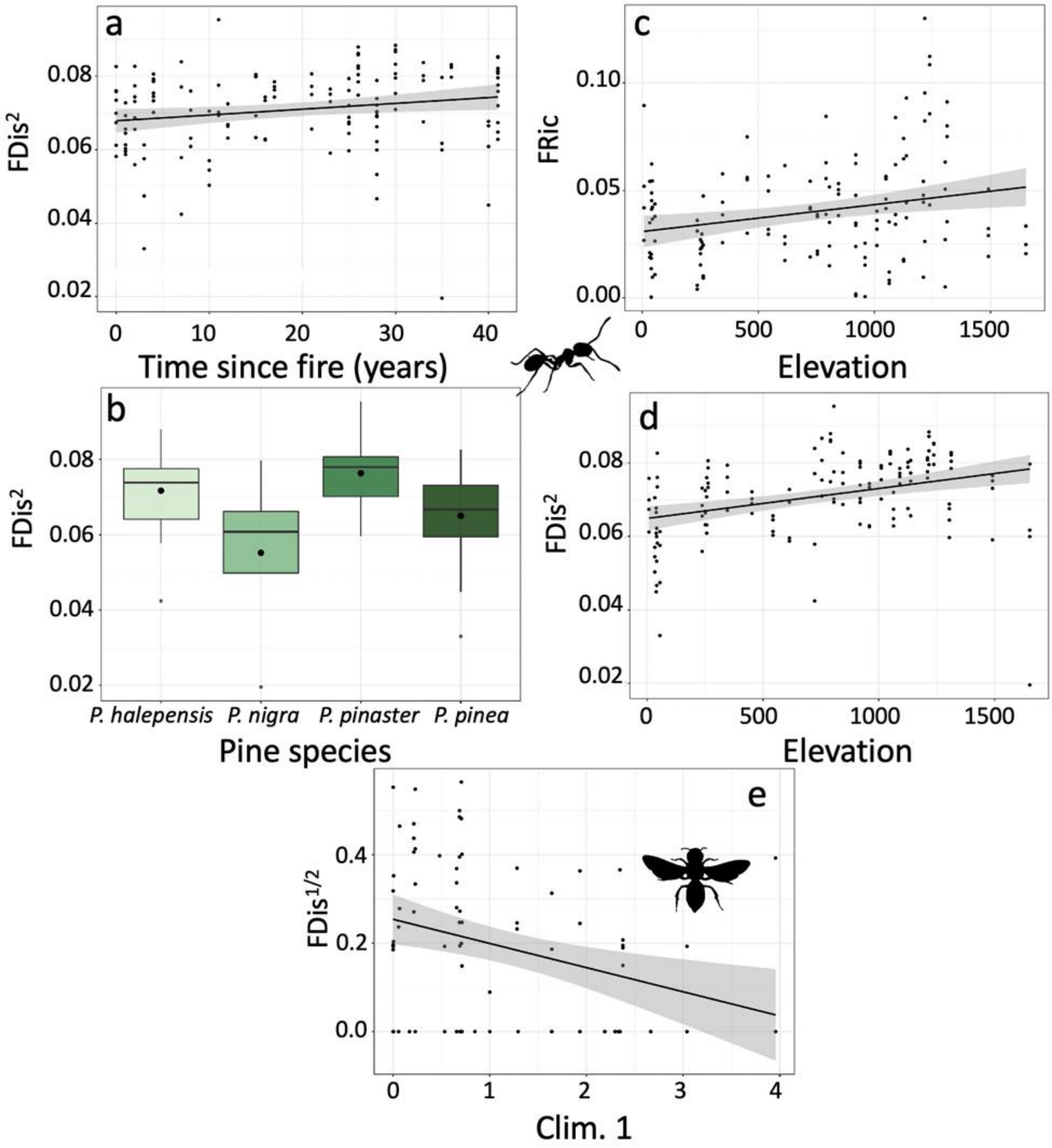


Figure S4. Effects of time since fire and environmental variables on the functional community structure of ants and bees. (a) Relationship of ant functional dispersion with time since fire. (b) Mean (± SE) ant functional dispersion in forests dominated by different pine species. Relationship of elevation with (c) ant functional richness and (d) ant functional dispersion. (e) Relationship of bee functional dispersion with principal component Clim. 1. Except in (b), the lines indicate the linear fit of the models, and the shaded areas indicate the standard error. Ant functional dispersion was square transformed, and bee functional dispersion was square-root transformed.

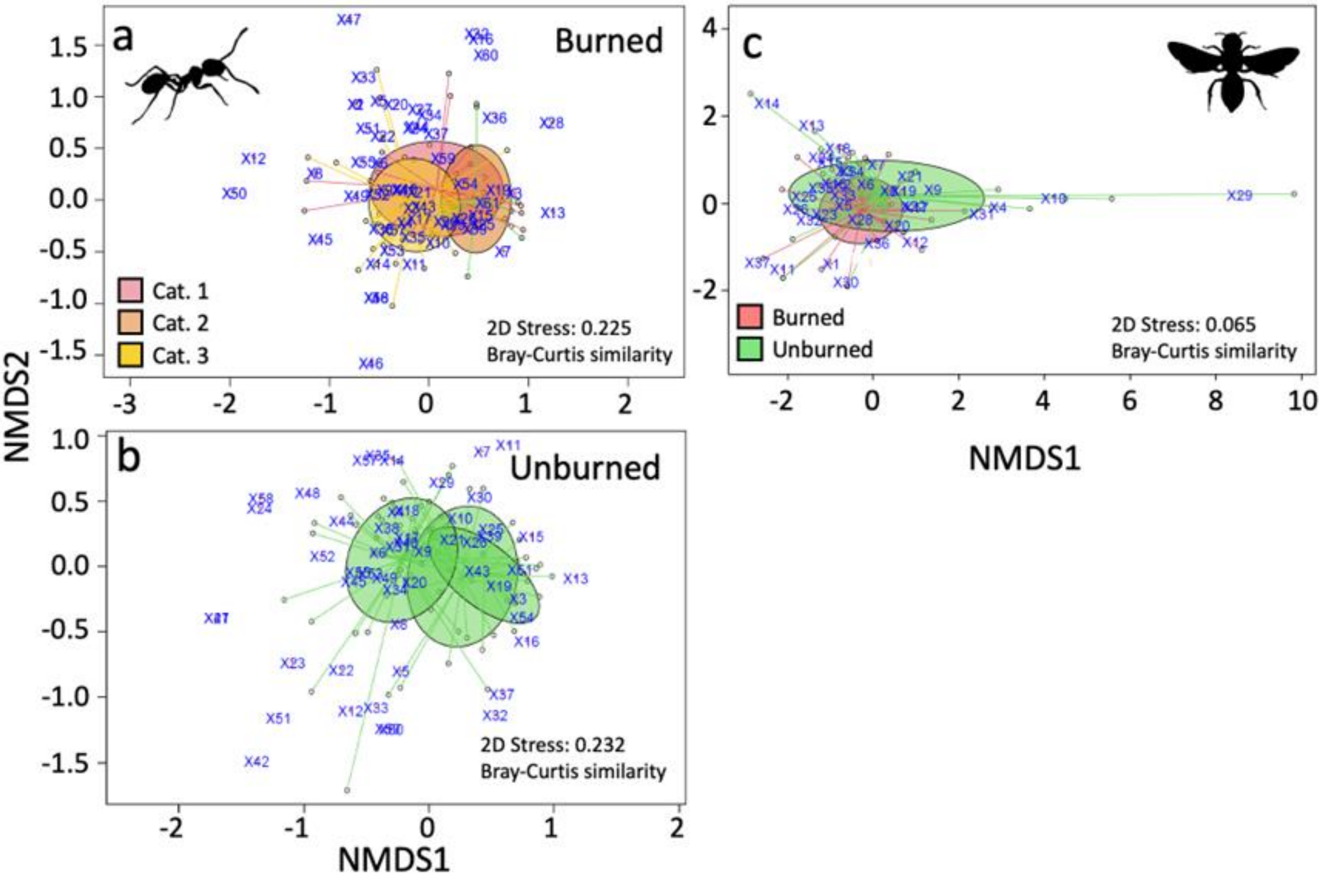


Figure S5. Results of the non-metric multidimensional scaling analysis of taxonomic community similarity of ants found at (a) burned areas and (b) unburned areas. Indicated for the burned areas is the categorical time since fire: 0–4 years ago (red), 7–12 years ago (orange), and 15–41 years ago (yellow). For the unburned sites in (b), the categories are all in green. (c) Results for bee communities at burned sites (red) and unburned sites (green). See species codes in Tables S6, S7.

Table S11. Effects of fire and time since fire on the functional traits of (a) ants and (b) bees. The description of the trait abbreviations is available in Tables S3 and S4. Fire is fire treatment (burned vs. unburned), time is time since fire (0 to 41 years ago), and fire x time is their interaction. d indicates the direction of the relationship. Shown for each trait is the transformation that was required to meet the assumption of normality: Log (trait): natural logarithm; trait1/2: square root.

	a	**Ant traits**					**b**	**Bee traits**	
	nes.sit			***dom***			***nes.sit***		
	F	P	d	F	P	d	F	P	d
Fire	**21.07**	**<.0001**	+	0.49	0.4865	+	0.23	0.6300	-
Time	0.16	0.6917	+	**4.15**	**0.0498**	+	2.95	0.0975	-
Fire x Time	**5.84**	**0.0174**	-	0.05	0.8276	-	**6.84**	**0.0116**	+
	bod.siz			*Log*(***col.siz***)			***bod.siz***		
	F	P	d	F	P	d	F	P	d
Fire	**24.39**	**<.0001**	-	0.27	0.6077	-	0.69	0.4086	+
Time	0.02	0.8805	-	0.72	0.4033	+	0.98	0.3310	+
Fire x Time	1.70	0.1954	+	0.26	0.6105	+	1.85	0.1792	-
	num.nes$^{1/2}$			***num.que***$^{1/2}$			*Log*(***int.dis***)		
	F	P	d	F	P	d	F	P	d
Fire	**9.77**	**0.0023**	+	**18.67**	**<.0001**	+	0.27	0.6060	-
Time	1.75	0.1945	+	0.03	0.8674	+	0.00	0.9733	+
Fire x Time	2.84	0.0950	-	**3.57**	**0.0616**	-	0.05	0.8256	-
	SD			***for.str***			***flo.spe***$^{1/2}$		
	F	P	d	F	P	d	F	P	d
Fire	**14.45**	**0.0002**	-	**13.21**	**0.0004**	+	0.16	0.6865	-
Time	1.58	0.2175	-	1.22	0.2776	+	1.00	0.3269	-
Fire x Time	**3.17**	**0.0778**	+	0.30	0.5853	-	**7.09**	**0.0103**	+
	ins.die			***see.die.***			*Log*(***ton.len***)		
	F	P	d	F	P	d	F	P	d
Fire	**8.47**	**0.0044**	+	**8.15**	**0.0052**	-	0.00	0.9504	-
Time	2.66	0.1125	+	0.18	0.6736	-	0.15	0.7049	-
Fire x Time	0.38	0.5389	+	**4.93**	**0.0286**	+	0.71	0.4034	+
	liq.die$^{1/2}$			***pol***			***lif.form***		
	F	P	d	F	P	d	F	P	d
Fire	0.14	0.7108	+	2.44	0.1214	-	0.16	0.6905	-
Time	0.93	0.3430	-	**4.88**	**0.0342**	+	2.52	0.1242	-
Fire x Time	0.51	0.4786	-	**10.81**	**0.0014**	+	2.34	0.1325	+
	col.fou								
	F	P	d	**Ant traits**	DF		**Bee traits**	DF	
Fire	0.59	0.4432	-	F	1,103		F	1,52	
Time	0.06	0.8073	-	T	1,33		T	1,27	
Fire x Time	**5.53**	**0.0206**	+	F x T	1,103		F x T	1,52	

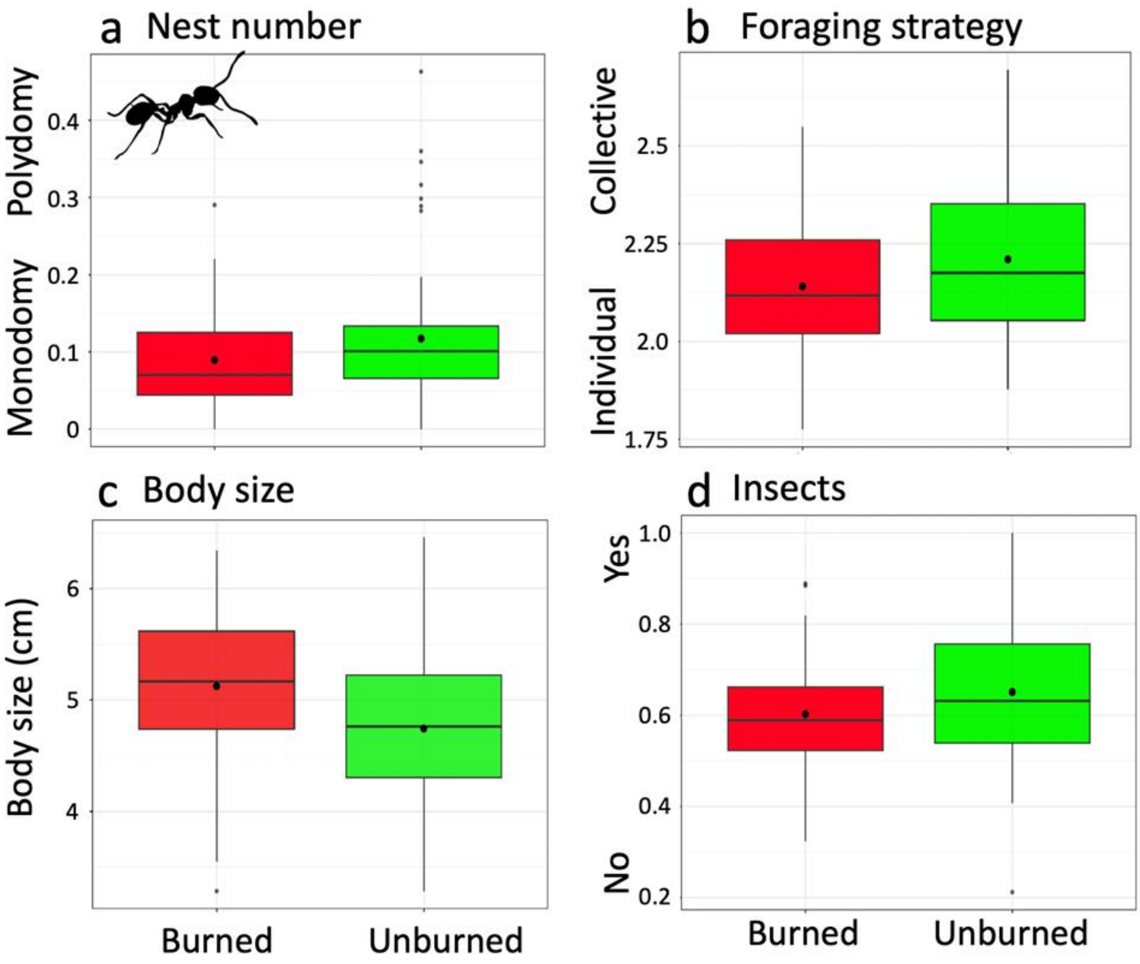
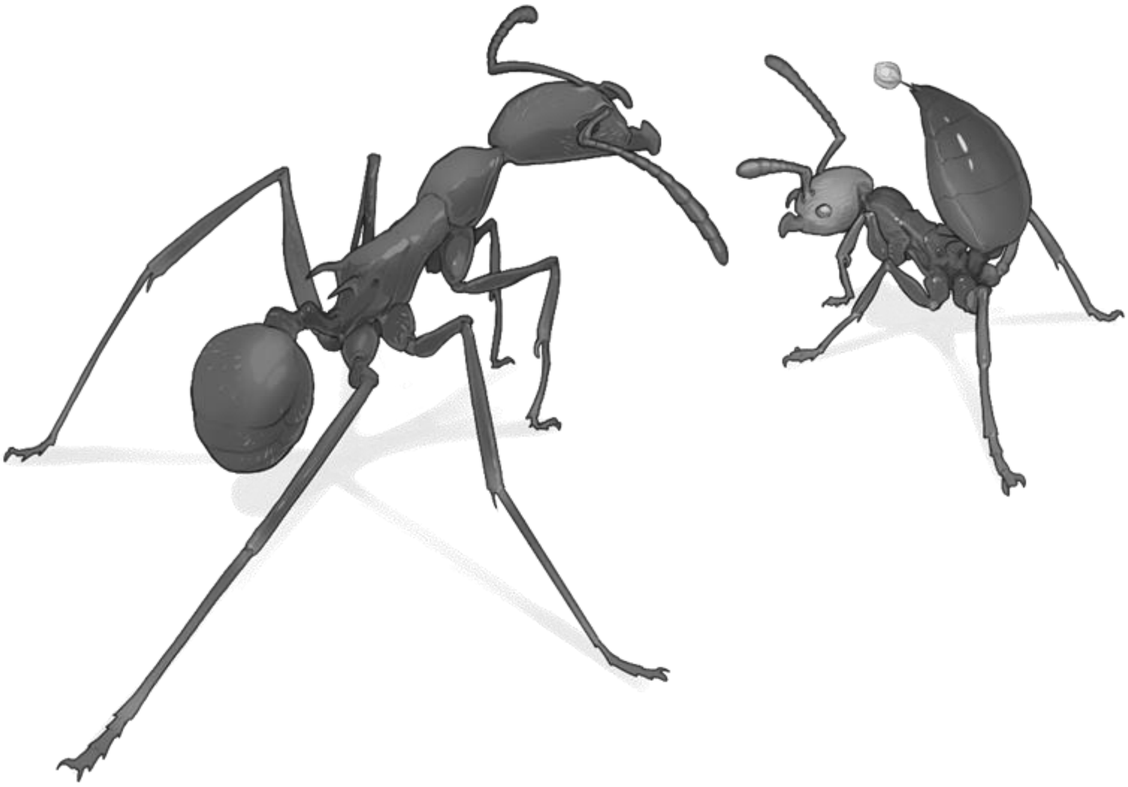


Figure S6. Effects of fire on the relative occurrence of ant functional traits. (a) Nest number (monodomy, both monodomy and polydomy, or polydomy) at burned and unburned areas. (b) Foraging strategy (individual, group, or collective) at burned and unburned areas. (c) Body size at burned and unburned areas. (d) Presence of insects in diet (no or yes) at burned and unburned areas. For a description of the traits, see Table S3.

Capítulo 4

Behavioural-dominance relationships after wildfires in southern Spain ant communities



Vidal-Cordero, J.M., Angulo, E., Boulay, R. and Cerdá, X. Behavioural-dominance relationships after wildfires in southern Spain ant communities. In preparation.

Resumen

El fuego puede afectar a diferentes parámetros de la estructura y composición de las comunidades de hormigas. Estos cambios en la comunidad de hormigas están causados principalmente por cambios indirectos en la estructura del hábitat, el microclima, la disponibilidad de recursos y las interacciones competitivas. Sin embargo, nunca se han comprobado las diferencias de comportamiento entre comunidades de hormigas tras un incendio. Analizamos el efecto del fuego y el tiempo transcurrido desde el incendio en las relaciones de dominancia de la comunidad de hormigas, utilizando interacciones de hormigas en cebos en tres áreas del suroeste de España que difieren en el tiempo transcurrido desde el incendio (uno, tres y cinco años desde el incendio) y comparando parcelas quemadas con parcelas cercanas no quemadas. Encontramos que el número de interacciones era bajo y no variaba consistentemente con el tiempo transcurrido desde el incendio. El aumento de la temperatura en las zonas quemadas, debido al impacto del fuego sobre la cubierta vegetal, favoreció el éxito de las interacciones tanto de las especies subordinadas como de las dominantes; aunque las especies subordinadas tuvieron éxito a temperaturas más altas. La jerarquía de comportamiento cambió en mayor medida justo después del incendio, y los cambios disminuyeron a medida que aumentaba el tiempo transcurrido desde el incendio. Asimismo, el tiempo de descubrimiento de los cebos fue significativamente menor en las zonas quemadas y diferente según el tiempo transcurrido desde el incendio. Además, las especies más descubridoras en las zonas quemadas fueron siempre especies termófilas subordinadas, mientras que en las zonas no quemadas fueron especies dominantes. Nuestros resultados rechazan la hipótesis del trade-off descubrimiento-dominancia: las especies que primero descubrieron el cebo fueron generalmente las mismas que lo dominaron, y este resultado fue consistente independientemente del fuego y del tiempo transcurrido desde el incendio.

Abstract

Fire can affect different parameters of the structure and composition of ant communities. These changes in the ant community are mainly caused by indirect changes in habitat structure, microclimate, resource availability, and competitive interactions. However, behavioral differences between ant communities after a fire have never been tested. We analyzed the effect of fire and time since fire on the dominance relationships of the ant community, using ant interactions in baits in three areas in southwestern Spain differing in the time since fire (one, three, and five years since fire) and comparing burned plots with unburned plots nearby. We found that the number of interactions was low and did not vary consistently with time since fire. The increase in temperature in the burned areas, due to the fire impact on vegetation cover, favored the success of the interactions of both, subordinate and dominant species; although subordinate species were successful at higher temperatures. The behavioral hierarchy changed the most just after fire, and the changes decreased as time since fire increased. Also, discovery time of the baits was significantly lower in the burned areas and different according to time since fire. In addition, the top-discoverer species in burned areas were always subordinate thermophilic species, while in unburned areas they were dominant species. Our results reject the discovery-dominance trade-off hypothesis: the species first discovering the bait were generally the same that dominated the bait, and this result was consistent independently of the fire and time since fire.

Introduction

Natural disturbances such as hurricanes, earthquakes, floods, droughts or forest fires have been shaping ecosystems and organisms for millennia, and their influence on the structure and functioning of ecosystems has been widely recognized in the field of ecological science (Mart-Jan et al., 2003; Coyle et al., 2017). Of these events cited, forest fires are the most frequent (if not the first) disturbance agent (Sommerfeld et al., 2018) and the most frequent research target (Viljur et al., 2022). They pose a global challenge to conservation efforts, making it essential to understand how they affect biodiversity (Mart-Jan et al., 2003; Coyle et al., 2017; Kelly et al., 2020; Viljur et al., 2022).

Wildifres show a high variability in drivers and initial system properties what also means a very variable ecological effect (Peters et al., 2023). The main immediate and direct effect of wildfire is the destruction of vegetation, fauna and soil microbioma by direct heating (Scott et al., 2014; Köster et al., 2021). But there are other indirect effects that are mediated through changes in other ecosystem components and affect plant composition and recovery (Tyler 1995; Laughlin and Fulé 2008), such as microbial mortality through changes of soil physiochemical conditions (Köster et al., 2021), or the increase of soil carbon losses and rapid soil carbon decomposition (Mekonnen et al., 2022). Wildifre disrupts most ecosystem components through changes of resource availability or the physical environment, creates heterogeneity on the landscape, promotes diversity and entails ecosystem renewal or reorganization (Seidl et al., 2017; Seidl and Turner 2022).

Studies on fire's impacts have traditionally focused on plants (Keeley et al., 2011, 2012) but during the last decade there is increasing research exploring fire's impact on animals (Engstrom 2010; Beale et al., 2018; Nimmo et al., 2018, 2021; Pausas and Parr 2018; Pausas 2019; Jolly et al., 2022) and especially on insects (New 2014). Regarding ants, most studies of fire effects analysed taxonomic richness and abundance (Farji-Brener et al., 2002; Parr et al., 2004; Moretti et al., 2004; Arnan et al., 2006; Sackmann and Farji-Brener 2006; Kwon 2015; Anjos et al., 2015, 2017; Vasconcelos et al., 2017; Adams et al., 2018; Rosa et al., 2021; Bonoan and McCarthy 2022; Staff et al., 2023), sometimes combined with functional diversity (Arnan et al., 2013, 2020; Bishop et al., 2021; Vidal-Cordero et al., 2022, 2023), or focusing on some after-fire specific ecological responses such as ant-seed dispersal (Arnan et al., 2009;

Beaumont et al., 2013, 2018), female production (Caut et al., 2014), diet shifts (Lázaro-González et al., 2013), or cavity use by arboreal ants (Arruda et al., 2020). Finally, recent behavioural studies show how fire can have an effect on ant behaviour, specifically relationships of dominance between species (Sensenig et al., 2017; Tavella and Cagnolo, 2018).

Ant community changes due to fire are mainly caused by the indirect changes in habitat structure, microclimate, resource availability and competitive interactions (Andersen et al., 2019). Fire changes can affect ant richness, abundance or composition (Arnan et al., 2006; Anjos et al., 2017; Vidal-Cordero et al., 2022, 2023) but also other community parameters such as species co-occurrence patters (Tavella and Cagnolo, 2018). After fire, Tavella and Cagnolo (2018) observed changes in species roles and species interactions (while species richness and aggregated network properties remained stable), which translated into changes in the spatial distribution of ant species. Other example of the effects of fire at the ant community level is that of Sensenig et al. (2017): in areas dominated by acacias in Kenya, fire can disrupt the mutualistic associations of dominant ant species with acacia trees, by colony mortality and/or decreasing colony size. This favors other subordinate species, which are more fire resilient, maintaining diversity despite the established dominance hierarchy (Sensening et al., 2017). Therefore, the study of the effect of fire on functional aspects, such as dominance relationships, is necessary for a better understanding of the effect of fire on ant communities.

Dominance is a frequently misused term and it is important to consider that its definition arises from a competition framework and it is relative to ants occupying the same guild (Cerdá et al., 2013). According to Cerdá and Retana (1997), two types of species dominance can be contemplated in ant communities: 1) behavioural dominance, which refers to access to the food resource as a result of their competitive abilities when interactions occur at resources and 2) ecological dominance by which species can be dominant due to their proportion in food resources at different periods of the day. More recently, Stuble et al. (2017) considered that dominance hierarchies are created to understand ant communities, and they are nothing more than the ranks of species based on either their numerical or behavioural dominance. Being numerical (or ecological) dominance based on the relative abundance of a species, while behavioural dominance is based on the outcome of interspecific encounters (Stuble et al., 2017).

In Mediterranean areas, the effects of fire have focused on some species ecological responses (Lázaro-González et al., 2013; Caut et al., 2014) or on ant taxonomic and functional diversity (e.g.., Arnan et al., 2013, 2020; Vidal-Cordero et al., 2022, 2023), however nothing is known about how fire affects the competitive dominance relationships of the ant communities. In this study, we aim to analyse the effect of fire on the ant dominance relationships of three burned areas in southwestern Spain differing in their time since fire. We expect sequential changes in the role and identity of the ant species along the three post-fire scenarios that will be associated with changes in the behavioural dominance. We will test the next four hypothesis: 1) The number of interactions at resources will be greater in more recent than in older burned areas, because species richness increases due to the appearance of subordinate and opportunistic species after the fire disturbance (Vidal-Cordero et al., 2023). 2) In the most recent burned areas, the absence of vegetation will allow higher ground temperatures and during more hours along the day, and this will favour the success of subordinate species in aggressive interactions; by the contrary, older burned areas will have as dominant species those that are more associated with a more developed vegetation, and the shade provided by the vegetation will favour that dominant species will have a higher success during aggressive interactions at baits. 3) In the recent burned areas, the reduction of habitat complexity will facilitate the foraging activity of different species, accelerating the discovery of food resources with respect to older burned areas. Furthermore, in most recent areas, subordinates and more thermophilic species will be the first discoverer of food resources and will spend more time on them. 4) In case there is a trade-off between discovery and dominance in food resources, it will be more evident in older burned areas, where a higher presence of dominant species is expected.

Material and methods

Study area and vegetation cover

The field study was conducted in Huelva province, Andalusia (southwestern Spain Fig. 1a). A total of three study areas were established in three localities: Moguer (37°12'N, 6°44'W, 55 m above sea level), El Campillo (37°44'N, 6°41'W, 241 m above sea level) and Gibraleón (37°14'N, 7° 1'W, 10 m above sea level) respectively (Fig. 1a). The ecosystem in the three sites is a pine forest dominated by *Pinus pinea* with a main understory of *Cistus ladanifer*, *Ulex* sp., *Pistacia lentiscus*, *Halimium halimifolium*, *Cistus monspeliensis* and *Chamaerops humilis*. Each study area was affected by a crown fire that wiped out all the vegetation; the three areas differed in the year since fire, with one recent fire (Gibraleón in 2016), a three years old fire (El Campillo in 2014) and a five years old fire (Moguer in 2012).

In each study area we established two sampling plots in the control (unburned) areas and two plots in the burned area separated by a distance of 100-300 meters each other (Fig. 1). In order to know the structure of the vegetation in burned and unburned areas, in each sampling plot we established a vegetation transect of 75 meters long and 10 meters wide. Every five meters, we recorded the presence or absence of herbaceous, low shrub, high shrub and arboreal stratum and the plant species present in each transect.

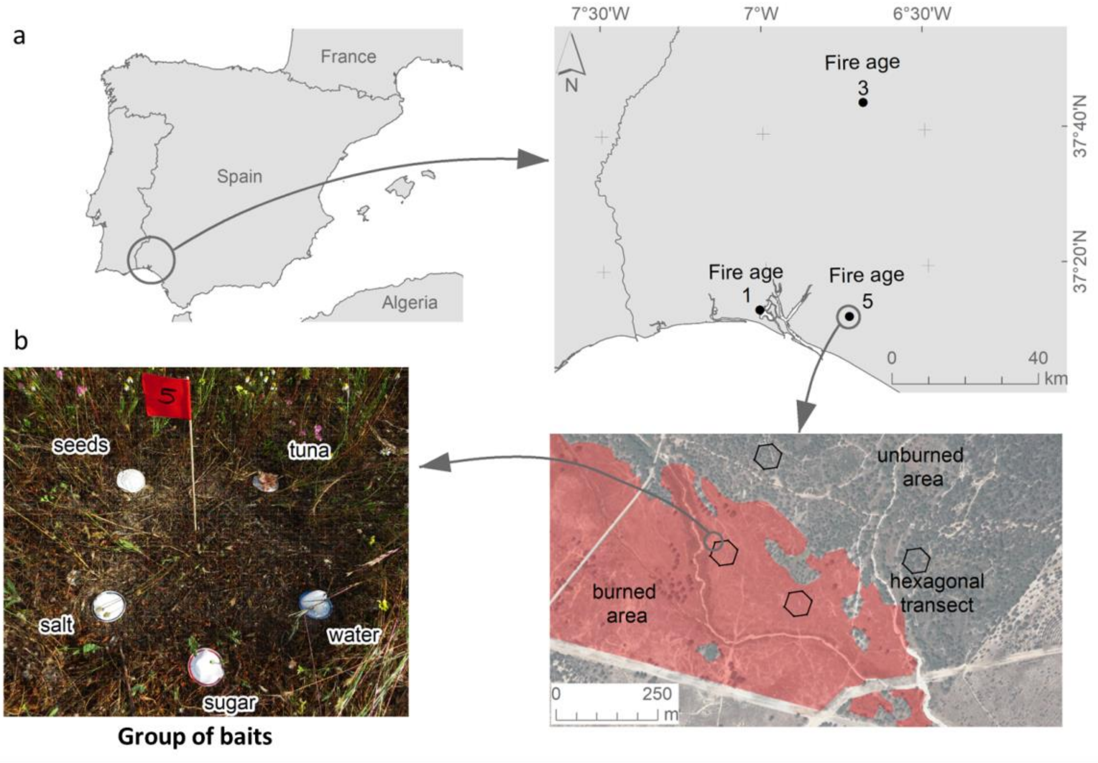


Figure 1. (a) Map of the study areas and (b) plot baits dispositions. The black dots on the map are the sampling areas, and the numbers indicate the time since the fire (in years). Each vertex of the hexagonal transects corresponds to a group of 5 baits.

Ant sampling at baits

The sampling was made in 2017 in two seasons, in spring (May) and in summer (July). It was done in the four sampling plots of each area (two burned and two unburned plots (Fig. 1), and during three times of the day in each plot: in the morning (9:00-12:00 a.m.), at midday (13:00-16:00 p.m.) and in the afternoon (18:00-21:00 p.m.). In each sampling plot we placed six groups of baits in a hexagonal transect, separated 10 meters from each other (Figure 1b). Each group of baits was composed of five different types of food (sugar, salt, water, tuna and seeds) offered on cut plastic cups (diameter 50 mm) and distributed forming a pentagon (Figure 1b). Tuna and seeds were placed directly on the bottom of the cut plastic cup, while the sugar (water diluted at 20%), the salt (water diluted at 1%) and the water (control) were provided in soaked cottons of the different solutions.

Each group of baits was placed five minutes apart one from the next and was visited at 5, 15, 30, 60, 90 and 120 minutes of being placed for each period of the day (morning, midday and afternoon). At each visit we recorded the time of day, the surface ground temperature in the centre of the group of baits with an infrared thermometer (PCE instruments PCE-777N) located one meter high, and the abundance of each ant species of ants in each bait. Individuals that could not be determined at the species level in the field, were kept in ethanol for its determination in the laboratory.

Competitive interactions and behavioural dominance

Competitive hierarchies were based on the outcomes of the observed aggressive interactions between ant species at baits: one species was successful when it drove the opposite ant away and it was unsuccessful in the interaction when it was forced to abandon the bait. For each species, we calculated its behavioural dominance index (DI) obtained from its percentage of success when confronted at baits with the other species: DI = % success = [(N cases with success) / (N cases with success + N cases with failures)] * 100, where N cases is the number of observations of the focal species sharing the bait with other species. A DI is obtained for each species in each study plot (in burned and unburned) of each study site. Competitive hierarchies can be built from these DI values.

Statistical analysis of behavioural interactions and dominance

First, we tested whether the number of interactions was different between fire treatments (burned vs unburned areas) and time since fire (one, three and five years old) by using generalized linear models (GLMMs: *glmer* function from the lme4 package, Bates et al., 2015). The dependent variable was the number of interactions in each plot (sum of interactions in the five baits of each plot) for each sampling time (5, 15, 30, 60, 90, 120 min) and it was modeled with a generalized lineal model performed with the *glmer* function from the lme4 package (Bates et al., 2015) using the Poisson family. Fire treatment, time since fire and their interaction were included as fixed effects. The identity of the groups of baits (1 to 24) was added as random factor in order to account for repeated measures over time of the same plot. Besides, we also included in this model as independent variables the period of the day (morning, midday and afternoon) and the season (spring or summer sampling along the study period). We performed a backward stepwise regression of this complete model, in order to obtain a final model containing the fixed and random factors and only the independent variables that were significant.

Second, we tested whether the success in the interactions was different between fire treatments (burned vs unburned areas) and time since fire (one, three and five years old). All interactions were grouped by the category of the species participating in the interaction according with Arnan et al., (2014) to consider them as dominant or subordinate. We carried out one analysis for the interactions of ants of each category, in order to know whether the same factors affect the success in the interactions for dominant and subordinate ants. We used a generalized lineal model (GLMs: *glm* function from the *stats* package, R Core Team, 2019), in which the dependent variable was the success or the failure in the interaction, which was modeled using the binomial family. Fire treatments (unburned and burned), time since fire (one, three and five years old), their interaction and the temperature were included as fixed effects. Besides, as in the previous analysis, we also included as independent variables the time of the day (morning, midday and afternoon) and the season (spring, or summer, sampling). We performed a backward stepwise regression of the complete model, in order to obtain a final model containing the fixed effects and only the independent variables that were significant.

Third, we established a behavioural dominance hierarchy among the ant species of each ant community; we created matrices raking the species for each fire treatment (burned vs unburned areas) and time since fire (one, three and five years old), with the success rate of each species against the rest of community (DI). The highest values of the dominance index (DI) corresponded to the first positions in the ranking of behavioural dominance.

Bait discovery, bait dominance and dominance-discovery trade-off

First, we calculated the percentage of baits occupied by each species for each fire treatment (burned vs unburned areas), each time since fire (one, three and five years old) and for each period of the day (morning, midday and afternoon) (Figure S1).

Second, we tested whether discovery time was different between fire treatments (burned vs unburned areas), time since fire (one, three and five years old) and their interaction. In each plot there were 6 groups of baits with 5 different food resources; we considered time of discovery when we observed the first ant reaching any of the five baits of a given group in a given time of the day (morning, midday or afternoon). When any of the baits of a group were discovered along a given time of the day, we assigned the maximum observation time, that is 120 min. Differences in the discovery time of baits were analyzed by using linear mixed models (LMMs: *lmer* function from the *lme4* package, Bates et al., 2015) in which the dependent variable was the discovery time. Fire treatment (burned vs unburned areas), time since fire (one, three and five years old), their interaction and the temperature were included as fixed effects. The identity of the group of baits (1 to 24) was included as random factor. As in previous analyses, we also included as independent variables the period of the day and the season (spring or summer). We performed a backward stepwise regression of this complete model, in order to obtain a final model containing the fixed and random effects and only the independent variables that were significant. Because period of time was a significant variable, we performed the same models for each period (morning, midday and afternoon), in order to know what were the factors affecting discovery time in each period of time.

Third, we calculated the mean discovery time of the baits and the number of baits occupied at time 5min for each ant species. We have used the number of baits at time 5 as a proxy of discovery to rank the species of each community. The first position in the discovery ranking is the species with the highest number of occupied baits at time 5min.

Finally, to test the existence of a trade-off between bait dominance and bait discovery (the inverse relationship observed between dominance at baits and the relative speed with which baits were found, described by Fellers 1987) we have used the number of baits at time 120min as a proxy of a dominance ranking. We consider that the species which remain in the bait after 120 min is because they are dominating the bait. Hence, we compare dominance rank (species ranked according with number of baits occupied at time 120) with discovery rank (species ranked according with number of baits occupied at time 5) with a simple linear regression.

Results

In total, 66832 ant workers were observed on baits, representing 26 species, belonging to 13 genera and 3 subfamilies (Table S1). The three study sites represented well a gradient of time since fire, regarding the vegetation cover. First, burned and unburned plots differed in the tree and large shrub strata, that was reduced or completely absent in the burned plots. Differences in the time since fire affect also other strata: In the burned plots of the one year since fire area the vegetation cover was absent for all the strata except the small shrubs. In the burned plots of the three years since fire area, the herbaceous and small strata was partially recovered, and in the burned plots of the five years since fire area these strata were completely recovered, and the large shrub and tree strata were recovering at 50% in one of the plots (Fig. S1).

Behavioural interactions

The number of interactions per plot did not differ between fire treatments (X^2 = 2.55, p = 0.110, N = 432), but it differed between time since fire and its interaction with fire treatment (X^2 = 12.15, p = 0.002, X^2 = 41.21, p < 0.001, respectively; N = 432). Thus, there are no differences in the number of interactions between burned and unburned plots; however, the interactions shows that there in two areas (1 and 5 years since fire) the number of interactions was higher in burned than in unburned areas while in the other area (3 years since fire) the pattern was the opposite (Fig. 2). Season and period of day were also significant variables affecting the number of interactions (X^2 = 17.64, p < 0.001; X^2 = 45.85, p < 0.001, respectively, N = 432).

The factors affecting the success of the interactions of dominant species were temperature, time since fire, fire treatment and the interaction between fire treatment and time since fire (X^2 = 6.43, p = 0.011; X^2 = 6.93, p = 0.031; X^2 = 17.38, p < 0.001; X^2 = 11.05, p = 0.004 respectively; N = 415). The time of the day (morning, midday and afternoon) and the season (spring or summer) were removed along the backward stepwise regression process. By the contrary, only temperature affected the success of the interactions of subordinate species (X^2 = 10.01, p = 0.002, N = 567), while time since fire, fire treatment and the interaction between fire treatment and time since fire were non-significant in the final model (X^2 = 2.47, p = 0.291; X^2 = 0.01, p = 0.941; X^2 = 4.93, p = 0.085; N = 567). In the unburned and burned areas of the three areas burned at different time since fire, the majority of interactions (successes and failures) of dominant and subordinate species occurred with temperatures on the ground surface between 25-38ºC (Fig. 3). However, most of the interactions of subordinate species in the burned areas occurred in a temperature range around 30-49ºC.

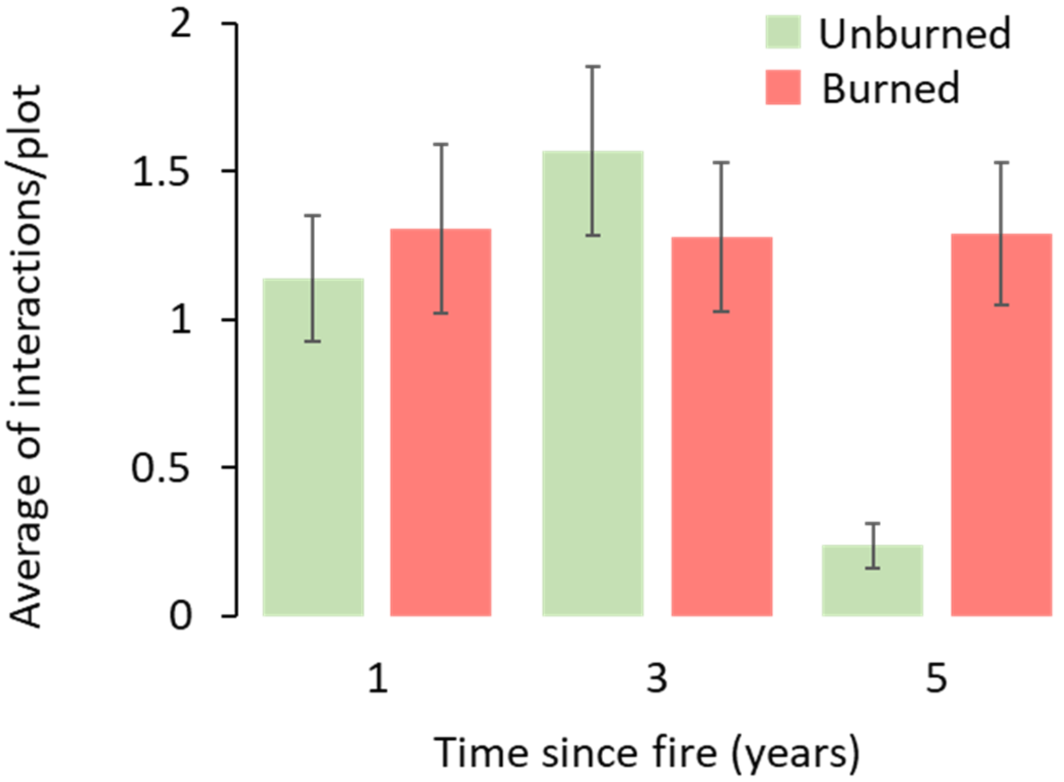


Figure 2. Number of interactions (mean ± SE) in burned and unburned plots for the three areas differing in the time since fire (1, 3 and 5 years after fire).

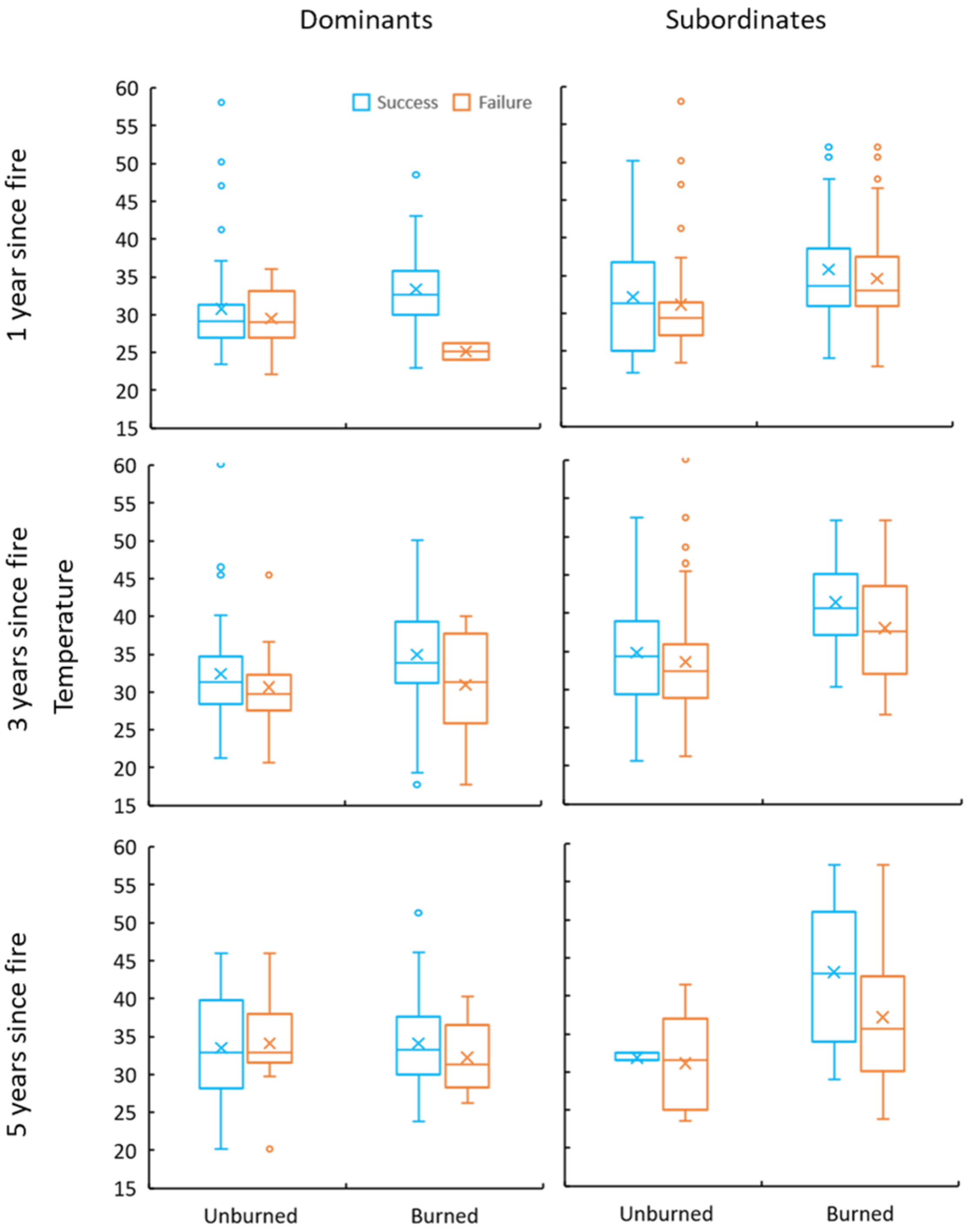


Figure 3. Temperature effects in the success of the interactions, when a dominant or a subordinate ant is interacting in the bait, for the three areas differing in the time since fire (1, 3 and 5 years after fire).

The behavioural dominance index allows us to compare the ant communities of areas burned at different time (Fig. 4). The most recent fire had more changes between burned and unburned areas than for less recent fires (3 and 5 years since fire): more species appearing and disappearing, as well as species moving down or up in the behavioural hierarchy. These movements are lower (zero, one or two positions) in the less recent fires than in the most recent fire (up to five positions). Unburned areas presented dominant ants of the genus *Crematogaster* spp. but also subordinate *Plagiolepis* spp. in the first four positions in the ranking (DI values above 1.5), as well as other species such as *Pheidole. pallidula* (1 year since fire), *I. subrufa* (3 years since fire), ants of genus *Tetramorium* spp. (3 and 5 years since fire) and ants of genus *Aphaenogaster* (5 years since fire) (Fig. 4). Burned areas always presented the dominant *C. auberti* in the top of the ranking and *Tetramorium* spp. in the second or third position (with values in the dominance index above 2) for the three time since fire areas. Furthermore, other ant species occupied the first positions of the rank as well, such as *Tapinoma nigerrimum* (second in 1 year since fire), *Iberoformica subrufa* (second in 3 years since fire) and *P. pallidula* and *Tetramorium forte* (second in 5 years since fire) (Fig. 4).

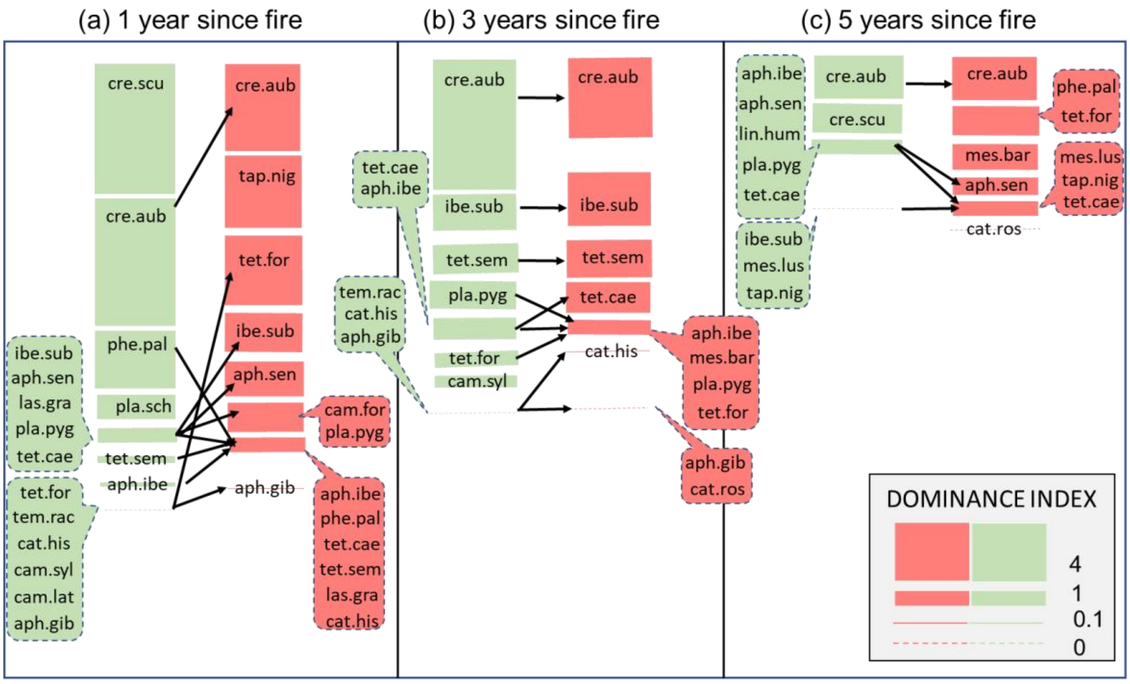


Figure 4. Changes in the hierarchy of behavioural dominance of the ant community of unburned site (green) and burned site (red) in the three areas differing in the time since fire (1, 3 and 5 years after fire). Dominance has been calculated from interspecific interactions during bait observations. Bar thickness is relative to values of interspecific dominance (DI). Species abbreviations are indicated in the Table S2.

Discovery time

Discovery time differed between fire treatment, time since fire and their interaction, period and temperature (F = 15.77, p = 0.0005; F = 6.90, p = 0.0005; F = 7.39, p = 0.0007; F = 19.73, p < 0.0001; and F = 28.78, p < 0.0001, respectively; N = 432 in all cases, Fig. 5a); season was not significantly affecting the discovery time (F= 3.39, p = 0.0066, N = 432). In the same way, when focusing in the morning, discovery time differed between fire treatments, time since fire, their interaction and temperature (F = 15.65, p = 0.0013; F = 3.24, p = 0.0426; F = 6.69, p = 0.0023; F = 12.13, p = 0.0013, respectively; N = 432 in all cases, Fig. 5b), but at midday, discovery time differed between fire treatments, time since fire and temperature (F = 10.83, p = 0.0028; F = 12.43, p < 0.0001; F = 29.91, p < 0.0001, respectively; N = 432 in all cases), but the interaction was not significant (F = 0.80, p = 0.4524, N = 432). In the afternoon, mean discovery time differed only as a function of temperature (F = 5.39, p = 0.0218) but not by fire treatment, time since fire or their interaction (F = 0.56, p = 0.6542; F = 2.45, p = 0.1801; F = 0.93, p = 0.4562, respectively; N = 432 in all cases) (Fig. 5c-d).

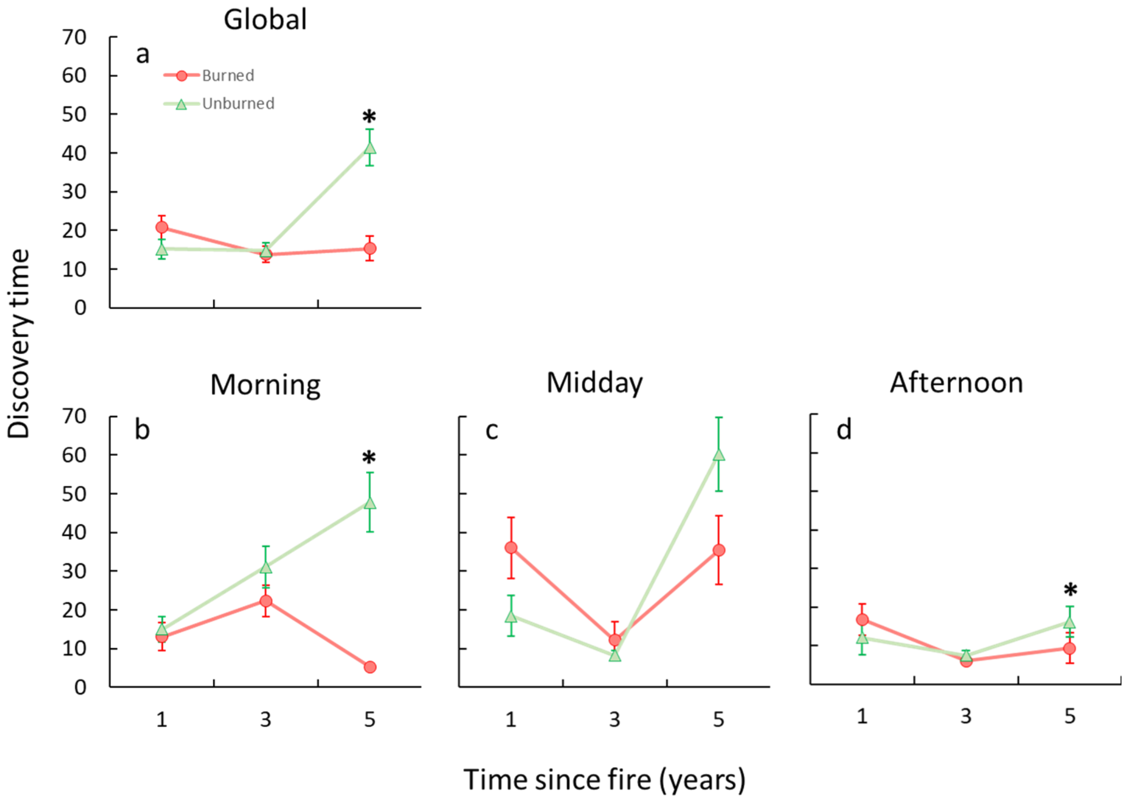


Figure 5. Variation of discovery time with time since fire: (a) global discovery time; (b) discovery time in the morning, (c) at midday, and (d) in the afternoon.

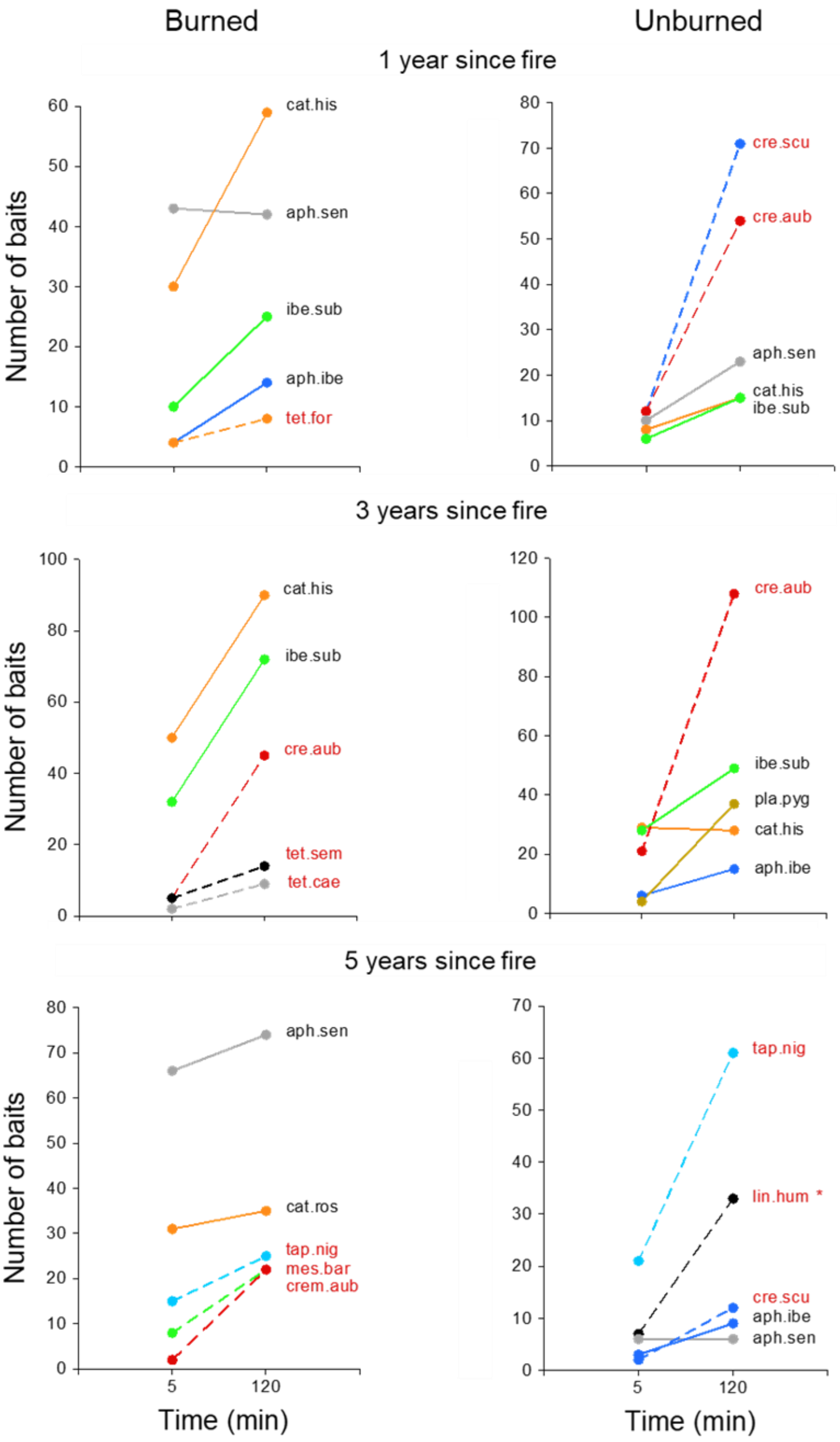


Figure 6. Changes in the occupation of baits between the discovery (time 5 min) and the final occupation (time 120 min) by the five top-discoverer species in each plot, in the three areas differing in the time since fire (1, 3 and 5 years after fire) and in burned and unburned plots. Species abbreviations are indicated in the Table S2 (ecologically dominant species have red abbreviations and with dashed lines). * *Linepithema humile* is an exotic introduced species.

If we focus in the species that first discovered the baits, taking into account the number of occupied baits during the first 5min, we see that unburned areas of the three areas with different time since fire have different top-discoverer species (Fig. 6): the ecological dominant species *Crematogaster scutellaris* (1 year since fire), the ecological subordinate species *Cataglyphis hispanica*. (3 years since fire), and the dominant *Tapinoma nigerrimum* (5 years since fire). However, burned areas presented different species in the first positions of the ranking, having *Aphaenogaster senilis* in the burned area 1 and 5 years since fire; and with the exception 3 years since fire, where the top discoverer species was *C. hispanica*, in the burned area as well as in the unburned area.

Bait occupation

Otherwise, if we focus on the percentage of bait occupancy, unburned areas presented in the first place of the ranking dominant ants such as *C. scutellaris* (1 year since time), *C. auberti* (3 years since time) and *T. nigerrimum* (5 years since time), while the top-ranking positions in the burned areas were occupied by species of subordinate ants such as ants of the genus *Cataglyphis* spp., A. senilis and *I. subrufa* in the three time since fire areas (Fig. 7). Considering the three periods of the day, dominant ant species of the unburned areas whose occupation percentage was higher in the baits maintained the supremacy for each of the periods of the day (with the exception of *T. nigerrimum*, which disappeared at midday), while in burned areas there are important changes in the percentages of occupation of the baits by the subordinate species during the three periods of the day. Being the midday the period in which the ants of the *Cataglyphis* spp. genus presented the highest percentage of occupation of the baits, while during the morning and afternoon other species of subordinate character (e.g., *A. senilis*, *I. subrufa*) presented the highest percentages of occupation of the baits (Fig. S2 and S3).

Bait dominance and dominance-discovery trade-off

From our bait observations, we did not find the inverse relationship between dominance at baits and the relative speed with which baits were found (Figure 8): in most cases, the first discoverer species were the same that remained dominating the baits along the observation period (120 min) (Figure 6). This pattern was similar in both burned and unburned plots. The most striking result is the presence of subordinate species top-ranked in the Bait Dominance rank (after 120min), not only in the burned sites, but also in one unburned site (*C. hispanica*, 3 years since fire).

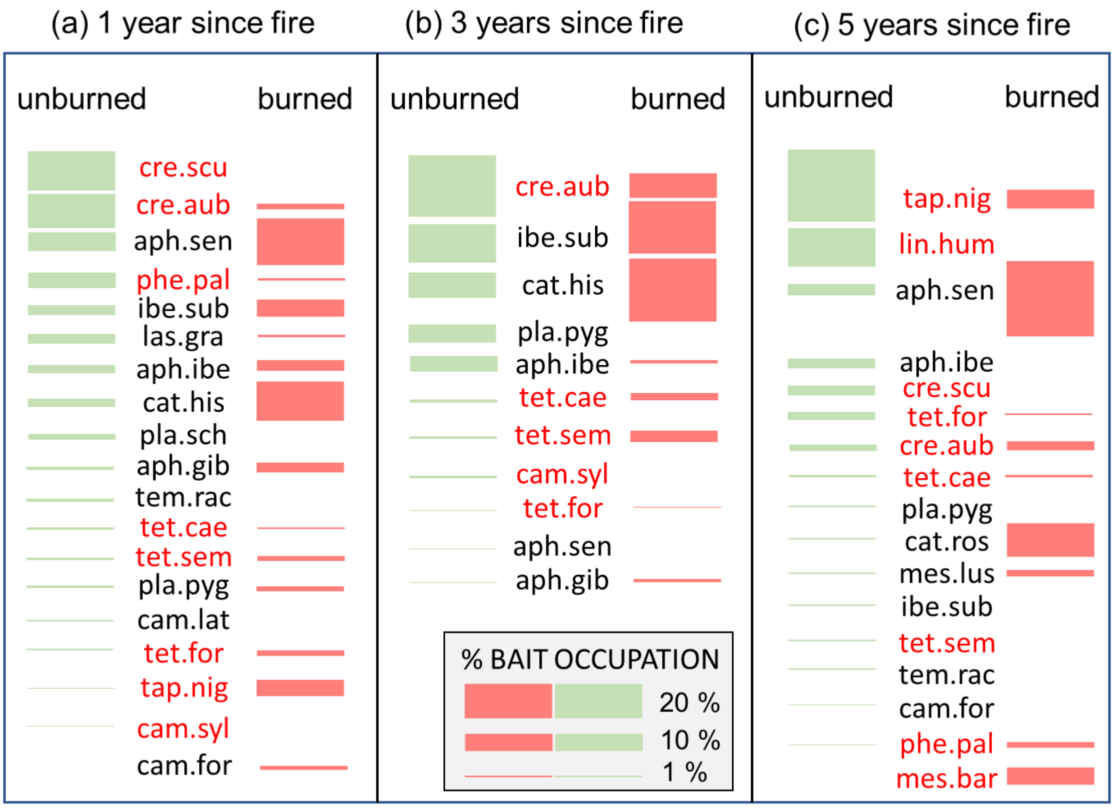


Figure 7. Relative abundance (%) of ant species in occupied baits in unburned and burned plots in the three areas differing in the time since fire: a) one year since fire (N=1113 observations in unburned baits, 1101 in burned baits); b) three years since fire (N=1182 unburned baits, 1130 burned baits); c) five years since fire (N=643 unburned baits, 1051 burned baits). Bar thickness is relative to values of bait occupation. Species abbreviations are indicated in the Table S2, species' names in red are behaviourally dominant.

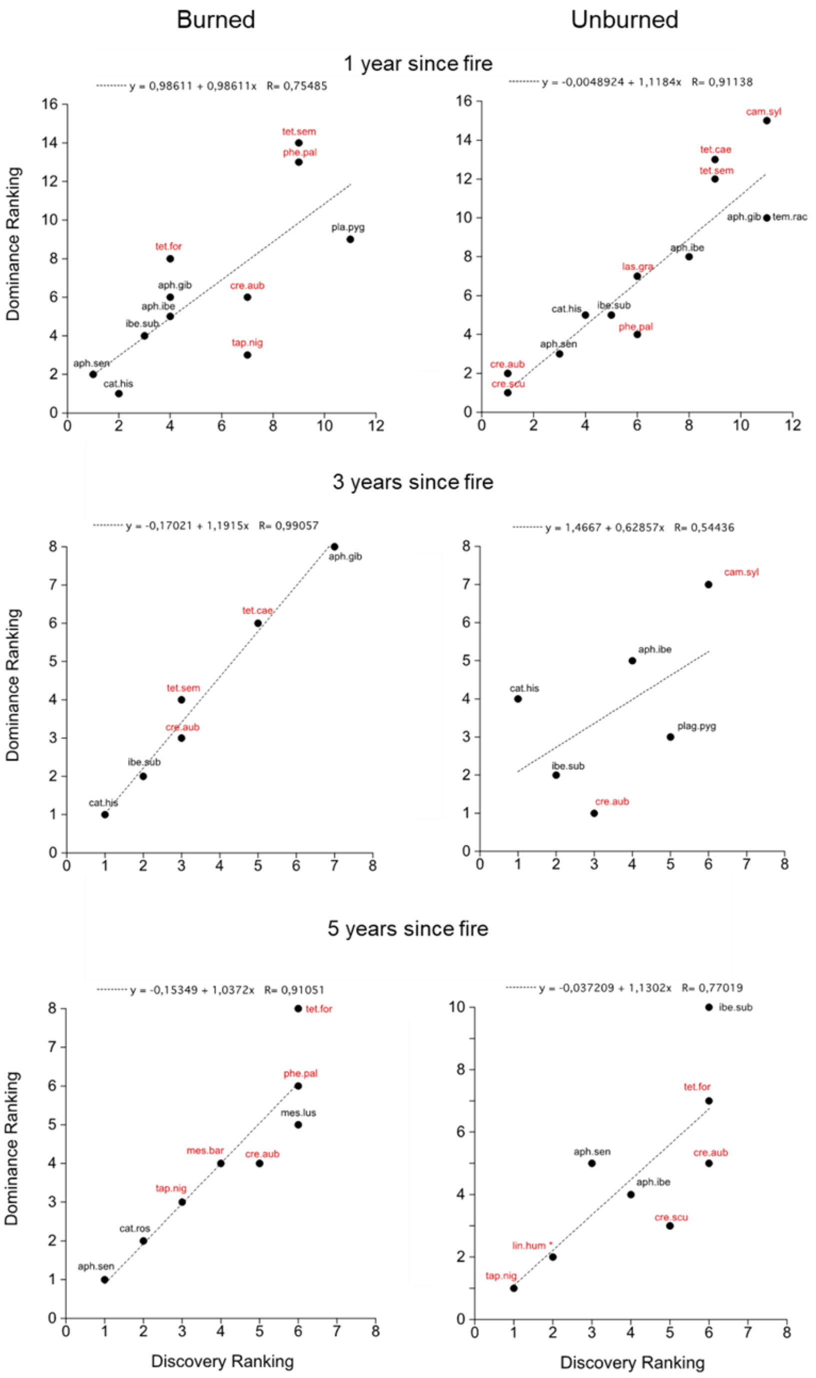


Figure 8. Dominance-discovery relationships in ant assemblages of the three study sites differing in the time since fire (1, 3 and 5 years after fire) in burned and unburned plots. Species were ranked according to their ability to dominate the baits (at time 120 min) from highest (1, top-dominant) to lowest (8 or 16) and to their ability to discover baits (at time 5 min) from highest discoverer (1) to lowest discoverers (8 or 12). Species abbreviations are indicated in the Table S2 (ecologically dominant species are in red). * *Linepithema humile* is an exotic introduced species.

Discussion

Behavioural differences among ant communities after fire disturbance have never been tested, and one possible reason could be the difficulty to detect behavioural changes. Our first hypothesis predicted that the number of interactions at baits should be greater in more recent than in older burned areas, because the occurrence after the recent fire disturbance of subordinate and opportunistic species that are expected to interact more frequently. Changes in the composition of species interaction and role of the species with a maintenance of the species richness and the properties of the interactions after fire has been previously described by Tavella and Cagnolo (2018). Our results show a similar number of interactions in burned areas in spite of the time since fire. However, the number of interactions per transect were extremely low (lower than 2). In order to compare these results with other Mediterranean ant communities, Cerdá et al. (1997) observed between ~20 and close to 100 interspecific interactions at baits, and similar interaction values were also obtained in the relatively poor ant communities of Doñana National Park (Sánchez-García et al. 2022). One possible explanation to be tested in the future could be that both type of habitats (unburned pine forest and open burned areas) have a very low abundance of ants, doing interspecific encounters rare events. Another explanation to the no-significant effect of fire on number of interactions should be that the ant species which disappear after fire are replaced for other opportunistic and recently arrived species, maintaining a similar frequency of interactions. In this case it could be applied the concept of functional redundancy (Houadria et al. 2016), where the influence of species richness depends on the relative functional contribution of the most efficient species.

Our second hypothesis proposed that the absence of vegetation in the more recent burned areas will entail higher ground temperatures, which favor the success of subordinate heat-tolerant species in aggressive interactions (Cerdá et al. 1997); by the contrary, older burned areas will have a more developed vegetation, with dominant heat-intolerant species associated with shade and lower thermal environments, and they will have a higher success during aggressive interactions at baits. Our results show that the majority of interactions (successes and failures) of both dominant and subordinate species occurred with temperatures between 25-38ºC, which are in the temperature range in which the ants carry out their daily activity (Cros et al. 1997). However, as we expected, the increase in temperature in the burned areas, favoured the success of the interactions of the subordinate species, which presented most of their interactions (but not necessarily successful, both successes and failures) in a wider temperature range (29-49ºC in the ground surface) than the dominant species. In addition, in the burned areas this temperature range became greater the more years since the area burned because the presence of herbaceous and low shrub strata, as a consequence of the recovery of the vegetation, causes a mosaic of temperatures due to the presence of shaded and sunny areas.

On the other hand, our results showed that temperature affected the success of the interactions of both dominant and subordinate species, so that at higher temperatures there were more success in the interactions of both groups. However, fire treatment and time since fire only had an effect on the success of the interactions of the dominant species, but not on success of the interactions of subordinate species. It is the opposed result to bait observations described in Cerdá et al. (1997), where an increase of temperature gave the opportunity to subordinate heat-tolerant species to have success in the interactions even against dominant species. But probably it is due to the species composition of our burned and unburned sites, where some of the subordinate species are opportunist and heat-tolerant (e.g., *Cataglyphis* spp., *I. subrufa*, *Aphaenogaster* spp.), and they can forage at high temperatures (Cerdá et al., 1998; Cerdá et al. 2009), while dominant species of unburned areas (e.g., *C. scutellaris* or L. grandis) are heat-intolerant and have a narrower thermal niche (Cerdá et al., 1998a, 1998b).

The absence (or the no-significance) of a thermal advantage for subordinates during interactions, give as a result that the top-ranked species according with the Dominance Index are always dominant species (*C. auberti* or *C. scutellaris*) independently of the fire treatment or time since fire, and it is the same for the second-ranked species in the DI ranking (with the exception of *I. subrufa*, which is the second in both burned and unburned plots of the 3 years since fire areas). Probably the presence of *I. subrufa* as second is due to its success against other subordinate species such as those of *Aphaenogaster* and *Cataglyphis* genera. The absence of these species in the top positions ranking in the plots of 5 years since fire areas is probably due to the environmental changes during forest recovery and increasing of vegetal cover, what makes the habitat less favorable to this species. Dominant species of *Crematogaster* genus (*C. scutellaris* and *C. auberti*) are the top dominant ants of DI ranking for the three areas, but *C. scutellaris* is only present in unburned sites, because it nests in the trees or shrub vegetation (Vidal-Cordero et al. 2022), while *C. auberti* is a soil-dwelling ant that can nests anywhere, with or without a tree cover.

The third hypothesis proposed that the reduction of habitat complexity in the recent burned areas, with respect to older burned areas, will facilitate the foraging activity of different species, accelerating the discovery of food resources. As predicted, discovery time of baits was significantly lower in burned areas, and significantly different according with time since fire. But the trend following time since fire was not expected: the lowest discovery time was in the 3 years since fire area (not in the 1 year since fire area). Besides, the period of the day also significantly affected discovery time. During the morning and midday, discovery time was significantly lower in burned than in unburned sites, that is, the foraging time of thermophilic efficient species (Cerdá et al., 1998) that prefer open habitats such as burned sites. In the afternoon, when temperatures are colder, the thermal differences between burned and unburned sites decrease and there are not thermophilic species active.

Following with this hypothesis, we predicted that in most recent burned areas, subordinates and more thermophilic species will be the first in finding the food resources and will spend more time on them. This prediction comes true: the first discoverer species in burned areas were always subordinate thermophilic species, while in unburned areas they were dominant species.

Finally, the occupation of baits at time 5 (discoverers) and time 120 (dominants) allowed us to analyse the possible existence of the discovery-dominance trade-off described by Fellers (1987). Our results show that there is not trade-off in our case: we did not find the inverse relationship between dominance at baits and the speed of discovery with which baits were found, but a positive relationship. In most cases, the first discoverer species was the same that remained dominating the bait along the full observation period. This pattern was similar in both burned and unburned plots. This absence of trade-off is found in other Mediterranean and temperate ecosystems (Santini et al. 2007, Lessard et al. 2009). However, because we have not data about abundance (prevalence) of each species, our results could be wrong. According with Edward G. LeBrun (personal communication in Cerdá et al. 2013): "If foraging success is driven entirely by chance processes, highly prevalent species will both discover and dominate a large fraction of the resource base, and low prevalence species will do the reverse. Therefore, the null expectation for a "trade-off" curve between dominance and discovery ability (when the traits are measured in a manner that does not factor out prevalence) is a positive relationship". This possibility cannot be ignored, but if we consider the species abundance (sampled in a previous year, see Table S2), the top-ranked discoverers and top-ranked dominant were not the most abundant species.

Camarota et al. (2018) described a common discovery-defense strategy among arboreal ants (and reject the discovery-dominance trade-off hypothesis). In their study, most species are able to be the first discoverer of newly available food resources within the complex canopy, and the discovery is coupled with the ability to defend the food resource. In our case, probably the absence of true dominant species could allow this discovery-defense strategy. A behaviourally dominant species exerts a strong influence on other species, initiating attacks or only by its presence eliciting avoidance behaviour during interspecific encounters (Cerdá et. al. 2013). The aggressive, dominant species use interference to behaviourally exclude other ants from resources (Savolainen & Vepsäläinen 1988, Pisarski & Vepsäläinen 1989). But the dominant species (according with Arnan et al. 2012) of our Mediterranean study sites are subdominant that win most competitive interactions with other species and might be considered dominant, but they are not "extirpators" such as Formica red wood ants, Atta leaf-cutter ants or *Oecophylla* weaver ants. They are relatively peaceful (in the sense of Tanner and Adler, 2009) Mediterranean subdominants which give the possibility to subordinate species to exploit food resources. As van Oudenhove et al. (2018) stated: there appears to be enough niche space for both dominant and subordinate strategies and the individual-foraging niche of subordinate is far from being “suboptimal”.

Acknowledgment

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Appendix

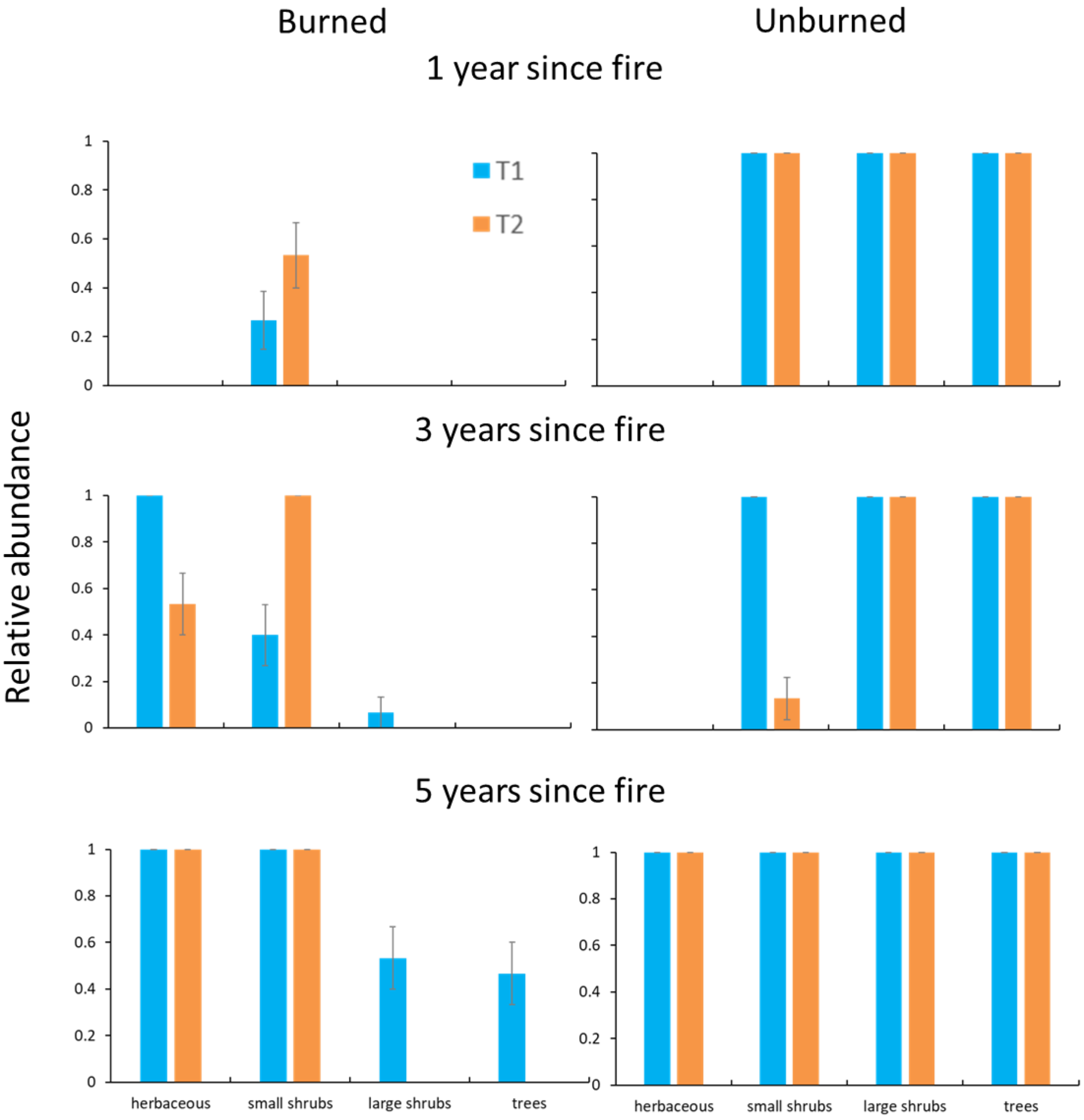

Figure S1. Differences of the vegetation cover in burned and unburned plots in the three study sites differing in the time since fire (1, 3 and 5 years after fire). The vegetation cover is measured as the mean presence of each stratum along the 15 sampling points in the two transects (T1, T2) sampled in burned and unburned areas. Burned and unburned plots differ in the tree and large shrub strata, that is reduced or completely absent in the burned plots. Differences in the time since fire affect also other strata: In the burned plots of the one year since fire area the vegetation cover is absent for all the strata except the small shrubs. In the burned plots of the three years since fire area, the herbaceous and small strata is partially recovered, and in the burned plots of the five years since fire area these strata are completely recovered, and the large shrub and tree strata are recovering at 50% in one of the plots.

Table S1. List of ant species of the study area (alphabetical order). Indicated is the total abundance of each species on baits at unburned and burned sites for each study area. Abbreviation for each species is used in Fig. 4, 6, 7, 8 and S2.

		Gibraleón (1 year since fire)		**El Campillo (3 years since fire)**		**Moguer (5 years since fire)**	
Species	**Abbr**	**Unburned**	**Burned**	**Unburned**	**Burned**	**Unburned**	**Burned**
Aphaenogaster gibbosa	aph.gib	64	424	5	74	0	0
Aphaenogaster iberica	aph.ibe	360	161	565	18	203	0
Aphaenogaster senilis	aph.sen	511	1493	14	0	291	1295
Camponotus foreli	cam.for	0	89	0	0	2	0
Camponotus lateralis	cam.lat	16	0	0	0	0	0
Camponotus pilicornis	cam.pil	0	0	0	0	0	0
Camponotus sylvaticus	cam.syl	10	0	21	0	0	0
Cataglyphis hispanica	cat.his	59	436	207	713	0	0
Cataglyphis rosenhaueri	cat.ros	0	0	0	2	7	265
Cataglyphis tartessica	cat.tar	0	0	0	0	0	0
Crematogaster auberti	cre.aub	5835	922	8024	3550	543	1011
Crematogaster scutellaris	cre.scu	5756	0	0	0	890	0
Iberoformica subrufa	ibe.sub	131	457	736	1086	7	0
Lasius grandis	las.gra	569	212	0	0	0	0
Linepithema humile	lin.hum	0	0	0	0	4238	0
Messor barbarus	mes.bar	0	0	0	18	0	1791
Messor bouvieri	mes.bou	0	20	0	0	0	0
Messor lusitanicus	mes.lus	0	0	0	0	12	546
Pheidole pallidula	phe.pal	826	106	0	92	1	606
Plagiolepis pygmaea	pla.pyg	139	285	937	229	107	0
Plagiolepis schmitzii	pla.sch	409	0	0	0	0	0
Tapinoma nigerrimum	tap.nig	64	3569	0	0	7655	2658
Temnothorax racovitzai	tem.rac	30	0	4	0	5	0
Tetramorium caespitum	tem.cae	143	143	554	466	179	259
Tetramorium forte	tet.for	171	1147	115	118	499	152
Tetramorium semilaeve	tet.sem	316	79	231	829	50	0

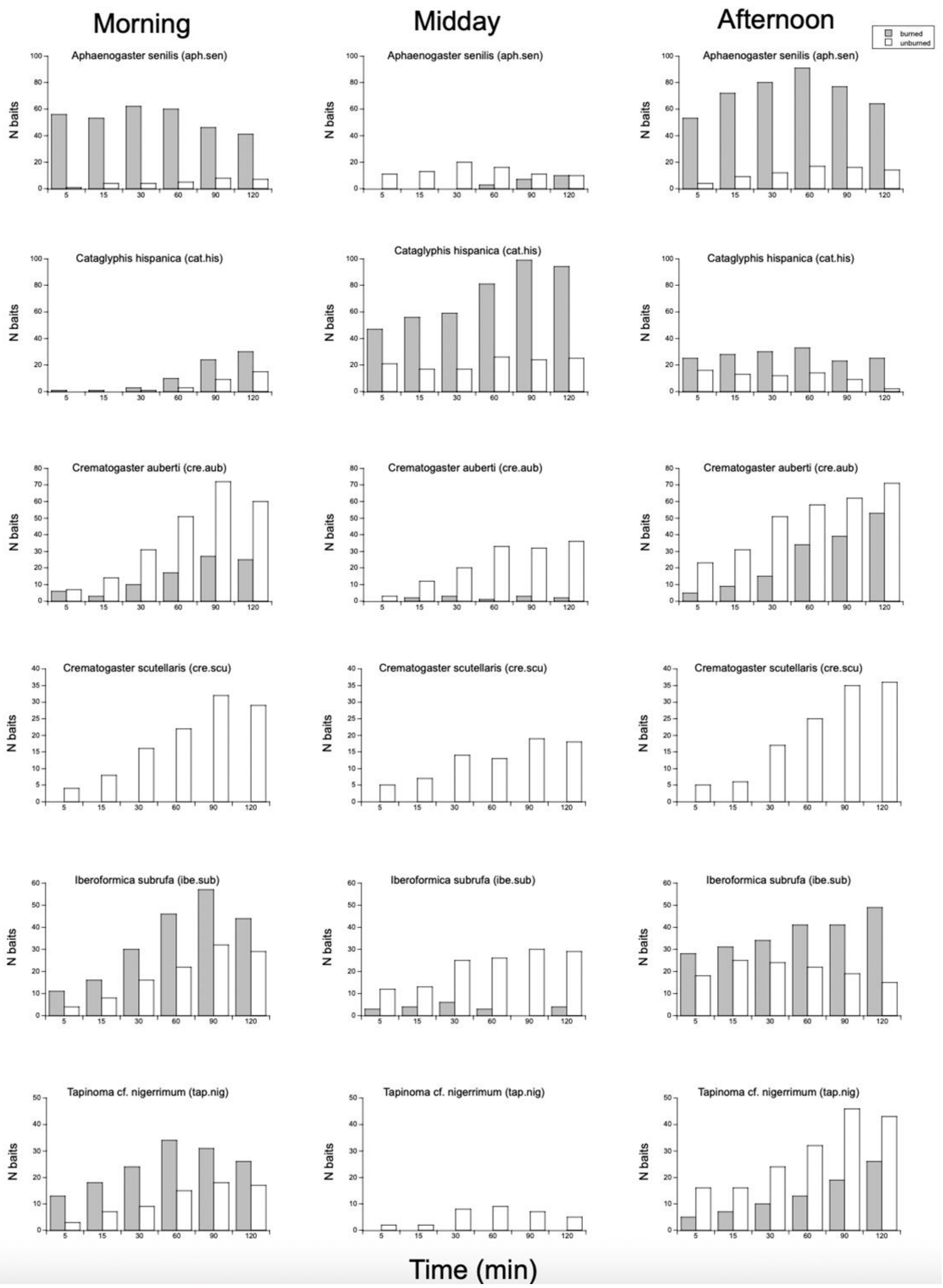

Figure S2. Total number of occupied baits in burned (grey bars) and unburned (white bars) plots along time (from 5 to 120 minutes) by the most frequent ant species during the three periods of the day: morning (8-10h), midday (13-15h), and afternoon (18-20h).

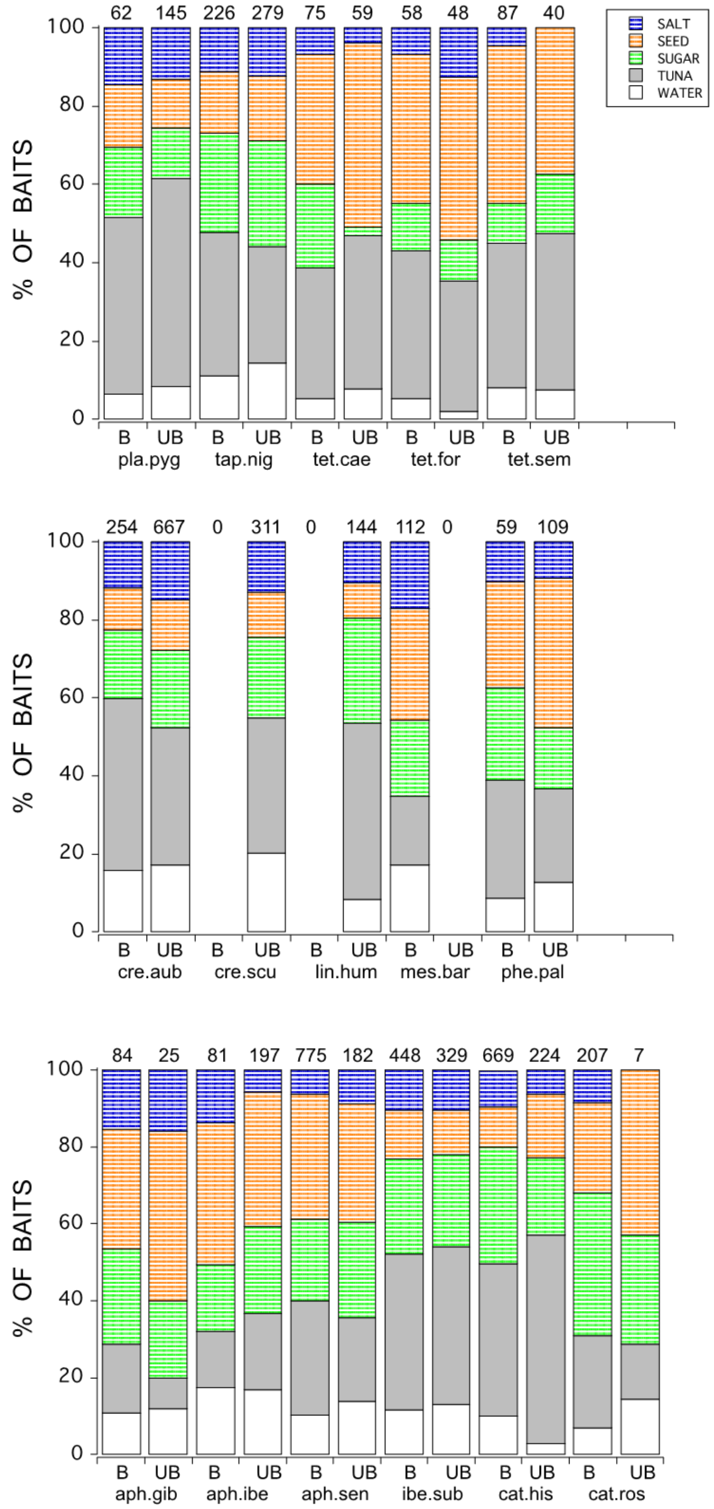

Figure S3. Percentage of occupation of the different type of baits (salt, seeds, sugar, tuna, water) by the most frequent ant species in burned (B) and unburned plots (UB). Values on the top of bars indicate the total number of baits in each case. Species abbreviations are indicated in the Table S2. Panels of the first two rows are ecologically dominant species (in the Arnan et al., 2012 sense) with the exception of Plagiolepis pygmaea (pla.pyg). The species of the third row are subordinate species.

Discusión general

En la presente tesis se subraya el importante papel que ejerce el fuego como agente de perturbación, tanto natural como antrópico, en los ecosistemas forestales mediterráneos desempeñando un papel clave en la estructura y dinámica de las comunidades animales y vegetales (Keeley et al., 2012; Moreno & Oechel, 1994; Pausas et al., 2008a; Pausas & Parr, 2018). Por tanto, se respalda la importancia de estudiar los efectos que tiene el régimen actual de incendios forestales sobre la biodiversidad, a fin de conocer las respuestas de los organismos al fuego y poder usar la información de forma integrada en los nuevos escenarios de cambio global, en los que es crucial aprovechar las sinergias entre la planificación forestal y la conservación de la biodiversidad, que operan sobre el mismo espacio físico, e incluso sobre los mismos elementos.

El objetivo general de la presente Tesis Doctoral ha sido el de investigar las respuestas taxonómicas, funcionales y comportamentales al fuego de tres grupos diferentes de artrópodos (hormigas, abejas y arañas), utilizados frecuentemente como indicadores de la salud de los ecosistemas (Buchholz, 2010; Churchill, 1997; Potts et al., 2010; Tiede et al., 2017). El trabajo se ha llevado a cabo en sistemas de coníferas de la Península Ibérica y a dos tipos de escalas diferentes: la taxonómica, con 3 grupos de artrópodos (hormigas, abejas y arañas); y la temporal, con zonas afectadas por incendios que se analizan en diferentes tiempos desde la aparición del fuego (a corto plazo, 0-4 años; y a largo plazo 0-41 años). Para abordar los objetivos planteados en la presente tesis se llevaron a cabo muestreos intensivos tanto pasivos, mediante trampas de caída (para hormigas y arañas epigeas) y trampas Moericke (para abejas), como activos, mediante el uso de cebos con distintos recursos alimentarios para estudiar in situ las relaciones de dominancia de las distintas especies de hormigas de las zonas de estudio.

Tradicionalmente, la mayoría de estudios enfocados en conocer las respuestas de los organismos al fuego han sido enfocados principalmente en flora (Keeley et al., 2012, 2011), mientras que el estudio los efectos de los incendios forestales sobre la fauna es mucho más limitado (Parr & Chown, 2003; Pausas, 2018). Sin embargo, en los últimos años, son cada vez más los trabajos que exploran la respuesta de los animales al fuego, entre los que se encuentran los artrópodos (New, 2014). En este sentido, esta Tesis avanza, especialmente, en el conocimiento sobre las respuestas de los artrópodos a los incendios propios del régimen actual, utilizando aproximaciones variadas y complementarias y abordando aspectos con el fin poder usar algunos grupos taxonómicos como indicadores tempranos del cambio e informar a los planes de gestión y conservación del ecosistema afectado.

La necesidad de estudiar de forma combinada las respuestas al fuego por parte de más de un taxón

Existe una amplia literatura en la que se han estudiado las respuestas de los artrópodos al fuego en gran variedad de taxones, y de forma simultánea (Anjos et al., 2016; Collett, 2003; Goud, 2017; Manwaring et al., 2015; Uehara-Prado et al., 2010; Warren et al., 1987). No obstante, hay pocas generalizaciones para artrópodos, existiendo grandes variaciones en la forma en la que las comunidades de éstos responden al fuego. En una revisión de las respuestas de los artrópodos al fuego, de Kral et al. (2017) encuentran tendencias en las respuestas al fuego de algunos órdenes (negativas para Araneae y Lepidoptera; y positivas para Coleoptera y Orthoptera); sin embargo, las respuestas fueron aún variables y posiblemente dependientes de otros factores como el tipo de hábitat, el régimen de fuego o los grupos taxonómicos objeto de estudio (Andersen, 2019; New, 2014; Rodrigo & Retana, 2006; Warren et al., 1987). Cuando se trabaja con grupos taxonómicos muy diversos, numerosos estudios tienden a reducir los costes de los análisis de la clasificación de los artrópodos colectados en los muestreos, categorizando a éstos en niveles por encima de especie o género, lo cual, puede llevar a la recogida de grandes variaciones en las respuestas (Panzer, 2002) y a la creación de falsas inferencias (New et al., 2010). Si bien este tipo de estudios pueden ayudar a indicar la capacidad de recuperación de funciones ecológicas clave, los altos niveles taxonómicos contienen diversas especies con muy variadas respuestas a una perturbación ambiental dada y la asignación de estos grupos puede enmascarar gran variedad de respuestas y especializaciones (New, 2014). Como resultado de estas limitaciones, siguen existiendo lagunas de conocimiento sobre las respuestas de las especies y géneros individuales y los mecanismos específicos que permiten que los individuos persistan después de un incendio (Kral et al., 2017).

El estudio comparativo de las respuestas al fuego de dos grupos taxonómicos diferentes de artrópodos ofrece ciertas ventajas frente a los estudios multitaxón, y que hace más práctica la determinación de los organismos a nivel de especie o género, sin perder la visión integrada de recoger diferentes estrategias de respuesta por parte de ambos grupos. De esta forma, nos permite definir mecanismos generales y resaltar grupos taxonómicos con respuestas particulares. Algunos ejemplos de ello son los llevados a cabo con arañas y escarabajos (Polchaninova et al., 2016; Schirmel & Buchholz, 2013), hormigas y arañas (Melliger et al., 2018; Underwood & Quinn, 2010), o mariposas y saltamontes (Kati et al., 2012). En este camino, en la presente tesis doctoral quisimos trabajar en las respuestas al fuego de hormigas y arañas (**capítulo 2**) y hormigas y abejas (**capítulo 3**) de manera conjunta. Las respuestas fueron diferentes para los distintos grupos taxonómicos estudiados. En ambos capítulos las comunidades de hormigas fueron afectadas por el fuego de forma más marcada que las comunidades de arañas y las abejas. Esto pone de manifiesto una vez más la importancia de estudiar las respuestas de los artrópodos al fuego de forma conjunta para comprender los mecanismos a través de los cuales esta perturbación impacta, y permite el desarrollo de predicciones más precisas en la restauración de la biodiversidad y de las funciones ecosistémicas (Figura 1).

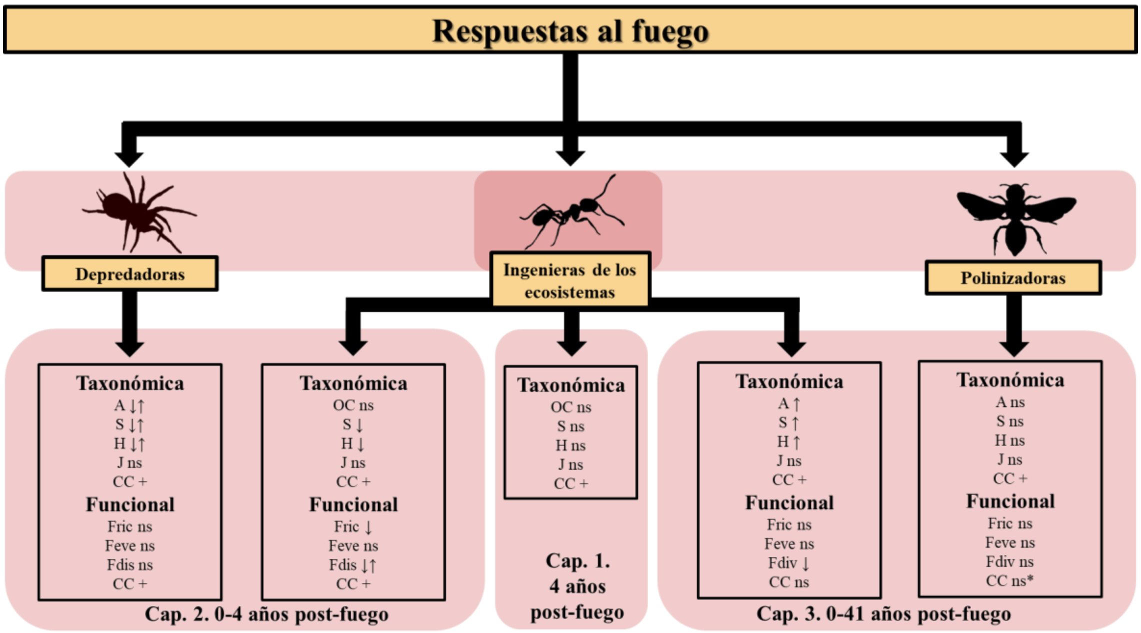

Figura 1. Esquema del efecto del fuego en la estructura y composición taxonómica y funcional de las comunidades de hormigas, abejas y arañas en los diferentes capítulos de la tesis. Abundancia (A), Riqueza de especies (S), Diversidad taxonómica (H), Índice de equidad de Pielou (J), Riqueza funcional (Fric), Equidad funcional (Feve), Dispersión funcional (Fdis), Divergencia funcional (Fdiv), Composición de las comunidades (CC). Las flechas indican: (↓) un efecto negativo, (↑) un efecto positivo, (↓↑) un efecto negativo, que con el tiempo se recupera, (+) hay efecto del fuego, (ns) no hay diferencias significativas, (ns*) diferencias marginalmente significativas.

La necesidad de estudiar conjuntamente las respuestas al fuego de la diversidad taxonómica y funcional

Son variados los estudios que han documentado los efectos del fuego sobre la estructura y composición taxonómica (DT) de artrópodos, mostrando diversas y, en ocasiones, contradictorias respuestas al fuego (Anjos et al., 2016; Apigian et al., 2006; Collett, 2003; Haugaasen et al., 2003; Manwaring et al., 2015; New, 2014; Newton et al., 2016; Uehara-Prado et al., 2010). Como vimos en el **capítulo 1**, el efecto del fuego sobre la composición taxonómica de las comunidades de hormigas de Belver ayudó a descartar la idea de que el fuego no tuviera realmente un efecto sobre la riqueza de especies y demás índices taxonómicos propios de la estructura de la comunidad, sino más bien, la pérdida de especies por el fuego se vio compensada por la entrada de nuevas especies mejor adaptadas a zonas abiertas de vegetación.

No obstante, la diversidad taxonómica solo es una de las dimensiones que conforman la diversidad biológica o biodiversidad, y para comprender de forma más completa la respuesta al fuego de la variabilidad de la vida en todas sus formas, es necesario hacer uso de más dimensiones de la diversidad. La diversidad funcional (DF), por ejemplo, refleja la diversidad de rasgos morfológicos, fisiológicos y ecológicos que se encuentran en un lugar dado (Petchey & Gaston, 2006). Sin embargo, en comparación con la DT, esta dimensión de la diversidad se ha enfrentado a un menor escrutinio y sus propiedades actualmente son menos conocidas (Pausas & Parr, 2018; Pavoine & Bonsall, 2011). Para comprender los patrones de biodiversidad en la ecología de comunidades y la biología de la conservación es de suma importancia tener en cuenta la DF además de la DT, ya que la DT por si sola trata a todas las especies como funcionalmente equivalentes (Swenson, 2011), ignorando así el hecho de que la pérdida de ciertas especies puede tener un mayor impacto en el funcionamiento del ecosistema.

Los cambios en el DF de un sitio en particular pueden estar relacionados con cambios en la DT, como la riqueza de especies, o la proporción de especies raras que son funcionalmente únicas (Bihn et al., 2010; Lohbeck et al., 2012). Además, después de una perturbación, como por ejemplo un incendio forestal, durante las etapas de sucesión ecológica, cambios en la composición de las especies pueden inducir a cambios en la composición de rasgos funcionales de las especies afectando a los procesos y servicios ecosistémicos (Butterfield & Suding, 2013; Cardinale et al., 2012).

Estaríamos ante la hipótesis de la complementariedad de nicho funcional en la que la relación entre DT-DF es positiva y lineal cuando la adición de una nueva especie a la comunidad de estudio contribuye a un conjunto de rasgos funcionales complementarios aún no presentes en la comunidad (Díaz et al., 2011). La mayor parte de la literatura que analiza esta relación hasta la fecha respalda una relación positiva y lineal entre DT-DF (Bihn et al., 2010; Lohbeck et al., 2012), tal y como ocurre con los resultados obtenidos en el **capítulo 2** para las comunidades de hormigas y arañas y en el **capítulo 3** para las comunidades de abejas. El fuego tuvo un efecto negativo significativo tanto a nivel taxonómico como funcional en las comunidades de hormigas, pero no tuvo efecto sobre ambas dimensiones de la diversidad en las comunidades de arañas y abejas.

Sin embargo, se han encontrado otros patrones de relación DT-DF. Uno de ellos sería representado por una relación logarítmica DT-DF, cuando los rasgos funcionales de las especies son redundantes y la adición de una nueva especie proporciona algunos atributos funcionales que ya están presentes en la comunidad (Petchey & Gaston, 2002). Esta relación es justamente la encontrada para la comunidad de hormigas del **capítulo 3** de la presente tesis doctoral en los que, si bien el fuego tuvo un efecto sobre la DT de las comunidades, concretamente sobre la abundancia, riqueza y diversidad, la riqueza funcional de las zonas quemadas no difirió significativamente de las zonas no quemadas, indicando una aparición y/o reemplazo de especies, pero funcionalmente redundantes. Esta redundancia funcional puede resultar especialmente relevante después de un cambio ambiental provocado por una perturbación, como pueden ser los incendios forestales, donde la disminución o incluso extinción de especies puede ser compensada por la presencia de especies funcionalmente similares (Rosenfeld, 2002). Por lo tanto, la redundancia funcional aumenta la estabilidad general del funcionamiento del ecosistema ya que las funciones descansan en más especies (Walker et al., 1999).

Una tercera opción nos ofrecería un escenario en el que la relación DT-DF podría ser exponencial en el caso de que el rendimiento funcional dependiera tanto de los rasgos complementarios de las especies como del grado de especialización de los atributos funcionales particulares de cada especie (Blüthgen & Klein, 2011), independientemente de si las especies presentan una abundancia rara o común (Díaz et al., 2011) (Figura 2).

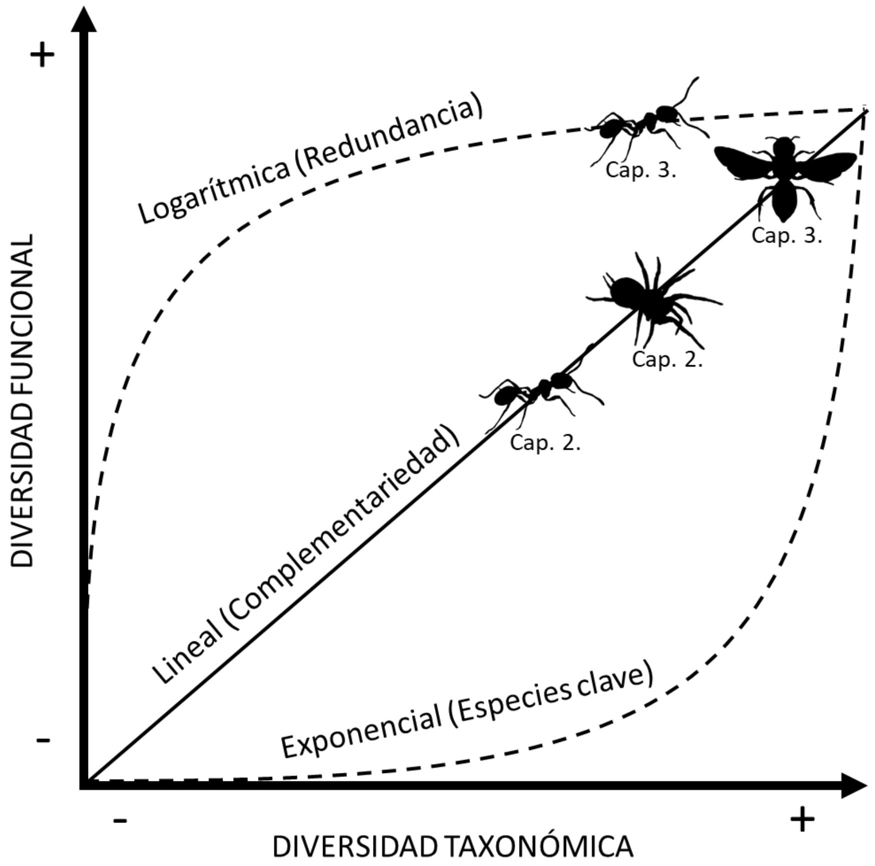

Figura 2. Posibles relaciones entre la diversidad taxonómica (DT) y la diversidad funcional (DF) según Díaz et al. (2011); Petchey and Gaston, (2002) y Blüthgen and Klein, (2011); y cómo podemos integrar los resultados encontrados en la presente Tesis Doctoral. Cap. 2: 0-4 años post-fuego; Cap. 3: 0-41 años post-fuego.

Por lo tanto, con la presente tesis doctoral queremos enfatizar la necesidad de combinar la DT con la DF en el estudio de las respuestas al fuego por parte de las comunidades animales principalmente por tres razones. En primer lugar, el estudio combinado de diferentes dimensiones de la diversidad es una idea que se está reconociendo cada vez más, ya que puede arrojar nueva luz sobre los cambios temporales y espaciales en la estructura y composición de las comunidades (Pavoine & Bonsall, 2011). La DF puede ayudarnos a comprender cómo interactúa la biodiversidad con los procesos del ecosistema y las limitaciones ambientales durante los procesos de sucesión ecológica tras un cambio ambiental (Díaz et al., 2013; Lohbeck et al., 2012; Mouchet et al., 2010). Segundo, comprender cómo se correlacionan FD con TD puede proporcionar información sobre el papel de los procesos deterministas o estocásticos en las comunidades (Pavoine & Bonsall, 2011; Purschke et al., 2013). Finalmente, en la biología de la conservación, es esencial preservar tantos tipos de diversidad biológica como sea posible (Devictor et al., 2010), pero como es difícil preservar de manera óptima todos los tipos de biodiversidad a la vez, es crucial comprender cómo los componentes de la diversidad se relacionan entre sí (Zupan et al., 2014).

Estudios futuros deberían encaminarse a estudiar las respuestas combinadas al fuego de las distintas dimensiones de la biodiversidad. Esto contemplaría otra dimensión, además de las estudiadas en la presente tesis, como es la diversidad filogenética (DP) la cuál puede reflejar la capacidad de un sistema para generar nuevas soluciones evolutivas frente a los cambios ambientales o para persistir a pesar de esos cambios (Faith, 2008; Forest et al., 2007). Arnan et al. (2016) resalta la utilidad de estudiarlas en conjunto, ya que este enfoque nos permite probar explícitamente las predicciones sobre los efectos diferenciales de la competencia y el filtrado ambiental en la biodiversidad.

La necesidad de estudiar las respuestas al fuego en el tiempo.

La gran variedad de respuestas al fuego por parte de los artrópodos se puede agrupar en una serie de estrategias generales enumeradas por Danks & Foottit. (1989) como: 1) Una supervivencia in situ, 2) una colonización tras el evento de fuego, después de la mortalidad local o escape inducido por el incendio y 3) una invasión en alguna etapa posterior al incendio. La supervivencia in situ, o la colonización tras el evento desde zonas no afectadas por el fuego, va a depender de la existencia de refugios. El concepto de refugio es un tema a considerar a la hora de estudiar los impactos del fuego sobre los organismos que solo puede entenderse en su totalidad desde una escala espaciotemporal. El tiempo puede ser un refugio cuando se considera la estación del año en la que se produce el evento de fuego y la fase del ciclo de vida en la que se encuentra el taxón objeto de estudio. Por otro lado, el espacio está relacionado con la presencia de áreas no quemadas que sirven de refugio a los organismos que allí habitan o a aquellos que huyen de las áreas que están siendo quemadas. Incluso las zonas que han sido afectadas por el fuego pueden presentar refugios, como aquellos recursos que no hayan sido objeto de las llamas, o, bien otros que han resistido el paso de este. Con todo, es de gran importancia tener en cuenta la escala espaciotemporal en el estudio de las respuestas de los artrópodos al fuego.

En relación al tiempo, uno de los principios generales de los impactos ecológicos del fuego, es la rápida recuperación de las poblaciones de la mayoría de artrópodos tal y como lo revela (Panzer, 2002) en un estudio realizado en el norte de Illinois. Trabajos llevados a cabo con los taxones objetos de estudio de la presente tesis mostraron una recuperación de entre 1-2 años para las comunidades de arañas (Polchaninova et al., 2016; Vasconcelos et al., 2009), entre 2-3 años para las comunidades de abejas (Bogusch et al., 2015; Mason et al., 2021), y entre 1-8 meses para la completa recuperación de las comunidades de hormigas (Parr et al., 2004; Verble & Yanoviak, 2013; Verble-Pearson & Yanoviak, 2014) describiendo incluso a las hormigas como las primeras colonizadoras después de los incendios forestales (Antunes et al., 2009). La recuperación para arañas y abejas encontrada en los **capítulos 2 y 3** de la presente tesis doctoral apoyan las respuestas encontradas en los trabajos citados. Sin embargo, en el **capítulo 2**, el estudio a corto plazo de las respuestas al fuego de las hormigas reveló un efecto general y negativo del fuego que se mantuvo durante los cuatro años de estudio.

Por otro lado, los estudios a medio y largo plazo de las respuestas de los artrópodos al fuego son más escasos en la literatura, siendo una de las grandes limitaciones de los estudios que persiguen ver el impacto del fuego en los artrópodos (New et al., 2010). Resultados a largo plazo pueden estar relacionados con la prevalencia de comunidades vegetales influenciadas por el fuego. Estos cambios generalizados en las comunidades vegetales a largo plazo pueden tener un impacto en las comunidades de artrópodos conforme se modifique el historial de incendios de un área determinada. Por lo tanto, los estudios a largo plazo pueden ser muy útiles para determinar el alcance y las tasas de rotación de especies, y la naturaleza de la adaptabilidad local que puede permitir que algunas especies persistan. Por este motivo, decidimos estudiar a corto, medio y largo plazo (0-41 años) las respuestas al fuego de las comunidades de hormigas y abejas en el **capítulo 3** de la presente tesis. A diferencia del **capítulo 2**, el efecto del fuego sobre la estructura de las comunidades de hormigas fue positivo e independiente del tiempo transcurrido tras el incendio (0-41 años), presentando las áreas quemadas de las zonas de estudio, mayores valores de abundancia, riqueza de especies y diversidad de hormigas que las zonas no quemadas.

Los resultados para las arañas del **capítulo 2** y para hormigas en el **capítulo 3** sugieren que el fuego puede actuar como un agente promotor de la riqueza, una idea ya concebida en el ámbito de las quemas controladas (Kelly & Brotons, 2017). Sin embargo, para llegar a comprender en su totalidad las respuestas de las hormigas y otros artrópodos al fuego también hay que tener en cuenta el papel que representa la recuperación de la vegetación y la cobertura vegetal (Seidl & Turner, 2022). Las coordenadas geográficas en las que se lleva a cabo el estudio determinan lugares que pueden albergar diferentes tipos de hábitats. Si bien la definición de hábitat para artrópodos es frecuentemente discutida en el campo de la ecología del fuego, una buena definición es la proporcionada por Dennis (2010), en la que se define hábitat como conjunto de recursos que necesita una especie para prosperar. El fuego puede afectar a cualquiera de esos recursos, desde el más evidente, como es la vegetación, a otros derivados de esta y relacionados con el microclima como la temperatura del suelo o la humedad. Centrándonos en el primero, la vegetación natural tiene una gran influencia en la respuesta de las comunidades de artrópodos al fuego, tanto como combustible como caracterizando el ambiente post-incendio y la recuperación de la zona afectada. Los bosques, a diferencia de las praderas y áreas con menos biomasa vegetal, presentan tiempos de recuperación más largos y muchos artrópodos característicos de bosques pueden estar excluidos del área quemada durante muchos años hasta que los recursos adecuados son recuperados. De esta manera, los bosques nos ofrecen un escenario ideal para el estudio de las respuestas de los artrópodos a largo plazo.

La vegetación define el hábitat para gran diversidad de especies de hormigas, abejas y arañas, las cuales recogen recursos alimenticios procedentes de las plantas o asociados a ellas, o bien utilizan la vegetación para construir sus nidos o telas de captura. Los bosques quemados cuyos hábitats han sido simplificados, reflejan una gran diversidad florística intercalada con zonas abiertas y soleadas en las primeras etapas de la sucesión ecológica. En estos escenarios post-fuego, en los que la estructura de la comunidad vegetal ha cambiado, anteriores trabajos recogen comunidades más ricas de hormigas (Andersen et al., 2009), arañas (Langlands et al., 2011; Moretti et al., 2002) y abejas (Moretti et al., 2009) y con mayor abundancia de especies con rasgos de la historia de vida propios de zonas abiertas expuestas a una mayor insolación. Estos estudios se encuentran apoyados en gran medida por los resultados obtenidos en la mayoría de capítulos de la presente tesis sobre el efecto del fuego en la estructura y composición taxonómica y funcional de hormigas, abejas y arañas (Figura 3). Asimismo, en el proceso de recuperación de un bosque tras un incendio, la estructura de la comunidad vegetal también puede verse afectada por la recurrencia del incendio y por la capacidad de recuperación de las especies de árboles que se quemaron con el fuego. En el **capítulo 3** de la presente tesis trabajamos en sistemas de coníferas de cuatro provincias andaluzas cuyas zonas de muestreo presentaban diferentes especies de pinos. Sin embargo, no todas las especies de pinos presentan adaptaciones al fuego y se regeneran igual después de un evento de fuego (Keeley, 2012; Keeley et al., 2011). De esta manera, en las áreas quemadas muestreadas más antiguas, las especies *Pinus pinaster* y *Pinus halepensis* desarrollaron nuevamente un bosque de pinos debido a su capacidad de regeneración tras el fuego, mientras que, aquellas áreas quemadas antiguas donde originalmente hubo un bosque de pinos de *Pinus pinea*, permanecieron como áreas abiertas con los estratos vegetales más o menos desarrollados, ya que, si bien esta especie puede soportar bajas intensidades de fuego gracias al grosor de su corteza, no tiene la capacidad de rebrotar tras el fuego (Madrigal et al., 2019).

Los diversos, y a veces opuestos, resultados obtenidos en los diferentes capítulos de la presente tesis, sobre la respuesta al fuego de las comunidades de hormigas respaldan la importancia de tener en cuenta la escala temporal en este tipo de estudios. En el **capítulo 1**, la estructura taxonómica de la comunidad de hormigas de un sistema de coníferas dominado por *Pinus pinaster* no se vio afectada por el fuego en el momento elegido para el estudio (cuatro años después del incendio de Belver de 2017), no presentando diferencias significativas en los valores de ocurrencia, riqueza y diversidad taxonómica entre zonas quemadas y no quemadas. Sin embargo, en el **capítulo 2**, cuando evaluamos la respuesta de la comunidad de hormigas de un sistema de coníferas dominado por *Pinus nigra* (Salo), durante cuatro años, y desde el momento en el que la zona se ve afectada por el incendio, observamos como el fuego tiene un efecto negativo sobre los diferentes índices de diversidad taxonómica que se preservan en el tiempo. Por último, en el **capítulo 3**, llevado a cabo en 35 sistemas de coníferas de diferentes especies de pino (Andalucía) y con diferente edad de antigüedad del incendio, encontramos que el fuego vuelve a tener un efecto sobre la estructura de la comunidad de hormigas, pero en este caso positivo, revelando mayores valores de abundancia, riqueza y diversidad taxonómica en las zonas quemadas frente a las no quemadas. Podemos concluir, por tanto, diciendo que nuestros resultados no son extrapolables a cualquier hábitat sometido a un incendio forestal, ni a un mismo hábitat que haya sufrido los efectos del fuego en otro momento diferente a los estudiados, ya que, tanto la escala temporal, como las condiciones locales en la que se haya llevado a cabo el estudio son fundamentales para entender las respuestas al fuego de las comunidades de organismos.

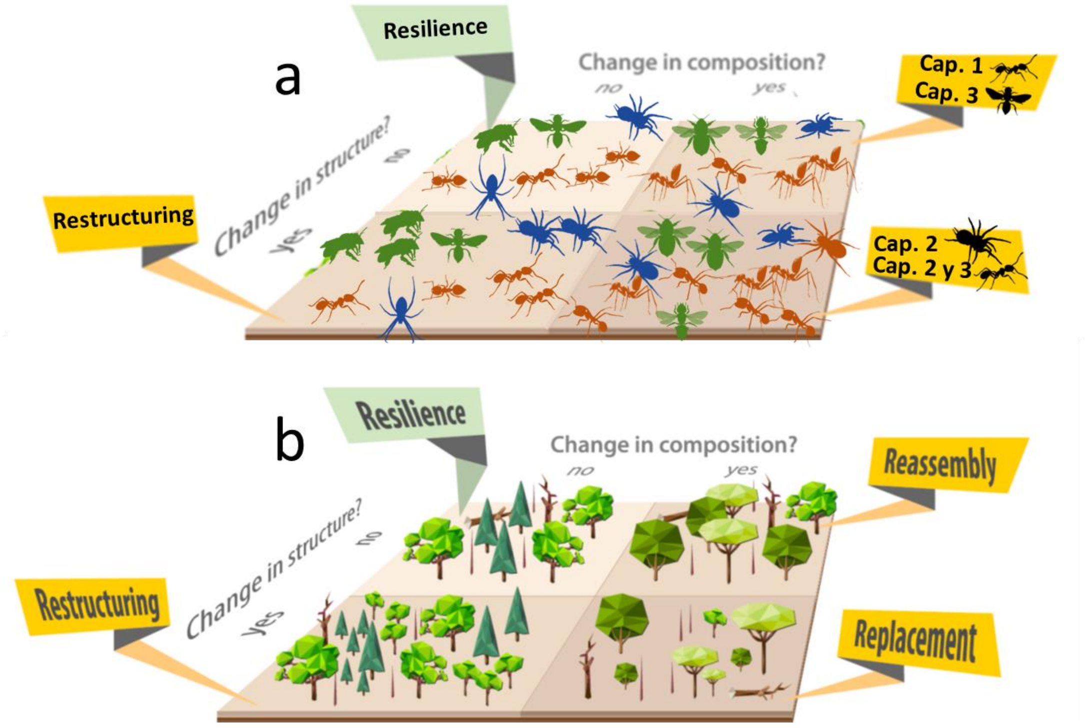

Figura 3. Vías de respuesta de la reorganización de las comunidades de artrópodos (a) tras los incendios forestales, basada en las vías de la reorganización forestal (b) según Seidl & Turner (2022). La respuesta se puede caracterizar a lo largo de las dos dimensiones de las comunidades, su estructura y su composición: resiliencia (sin cambios en la estructura y composición), reestructuración (cambios de estructura), reensamblaje (cambios de composición) y reemplazo (cambio de estructura y composición). La integración de los resultados de la presente Tesis Doctoral se ha hecho colocando los capítulos y cómo variaría cada taxón estudiado (abejas, arañas y hormigas) en cada una de las vías de respuesta.

Un inciso en el uso de hormigas como bioindicadores.

El uso de artrópodos como bioindicadores está bien documentado en la literatura (Beiroz et al., 2014; Jerez-Valle et al., 2014; Maleque et al., 2009; Nakamura et al., 2007; Paoletti et al., 1999; Van Straalen, 1998). Algunos de los grupos de artrópodos que predominan en los trabajos científicos pueden categorizarse, según del hábitat que ocupan, en epigeos (en el suelo o cerca de la superficie de este) y asociados a la vegetación y voladores. El primer grupo incluye trabajos protagonizados fundamentalmente por formícidos, coleópteros, colémbolos y arañas, mientras que el segundo incluye lepidópteros, hemípteros, algunos coleópteros y ortópteros. El predominio de estos grupos en la literatura es reflejo de una gran diversidad taxonómica, pero también de una "accesibilidad" tanto en términos de muestreo como en conocimiento ecológico y taxonómico disponible para interpretar las muestras obtenidas (New, 2014).

De entre los artrópodos más utilizados como indicadores biológicos se encuentran las hormigas, el grupo focal de la presente tesis doctoral. La familia Formicidae reúne una serie de características que sumadas, hacen de esta, una familia ideal como indicadora de la salud de los ecosistemas que ocupan. Algunas de ellas, citadas por Vanderwoude et al. 1997 para comunidades de hormigas, son: 1) la gran abundancia y diversidad; 2) la importancia funcional en los ecosistemas; 3) la sensibilidad a los cambios ambientales y 4) la posibilidad de clasificarlas dentro de grupos funcionales. Todas ellas permiten una buena interpretación de los cambios observados tras las perturbaciones. Esta fue una de las razones por las que se usó la familia Formicidae como objeto de estudio central de la presente tesis doctoral. Los **4 capítulos** de la presente tesis demuestran un efecto global del fuego en la estructura y/o composición taxonómica y/o funcional de las comunidades de hormigas de nuestras zonas de estudio. De hecho, la estructura taxonómica de la comunidad de hormigas estudiada en el **capítulo 2** no se recuperó en los cuatro años de estudio apoyando la idea de nombrarlos como grupo sensible a los cambios ambientales.

Asimismo, el estudio paralelo del efecto del fuego sobre la composición de sus comunidades reveló cambios taxonómicos (**capítulos 1-4**) en dicha composición. Asociadas a parcelas no quemadas de nuestras zonas de estudio se encontraron especies de hormigas del género *Temnothorax* spp, especies crípticas en su mayoría, y otras especies que viven asociadas a estratos vegetales más desarrollados (ej. *Crematogaster* *scutellaris, Camponotus lateralis, Lasius grandis*), como los árboles y arbustos altos, propios de una fase de sucesión ecológica más avanzada tras un incendio forestal. Por otra parte, las zonas quemadas de nuestras diversas y numerosas zonas de estudio presentaban una comunidad de hormigas compuesta por especies típicas de zonas abiertas expuestas a una mayor insolación. Ejemplo de estas especies son *Iberoformica subrufa*, *Crematogaster auberti*, *Camponotus foreli*, las hormigas del desierto del género *Cataglyphis,* o las especies de hormigas de hábitos fundamentalmente granívoros, como las diferentes especies del género *Messor*, *Goniomma* y *Oxyopomyrmex*. Apoyando los resultados obtenidos para la perspectiva taxonómica, en el **capítulo 3,** además, revelamos cómo el fuego también actuó como un mecanismo de filtrado de nichos con la mitad de los rasgos funcionales de hormigas analizados, con un efecto a largo plazo para algunos rasgos funcionales y a corto plazo para otros rasgos, y sugerimos cómo este conocimiento sobre estos rasgos puede ayudar a generar predicciones sobre cómo responderán las especies después de un incendio.

También hallamos especies de hormigas que podían encontrarse con una probabilidad similar tanto en zonas quemadas como en zonas no quemadas. Algunos ejemplos de ellas son *Aphaenogaster ibérica*, *Pheidole pallidula*, *Tapinoma nigerrimum* o las especies del género *Tetramorium*. El carácter más generalista de estas especies fue respaldado por los resultados obtenidos en el **capítulo 4**, entre los cuales, si bien se observaban cambios en la jerarquía de dominancia comportamental y ecológica de las especies de hormigas entre parcelas quemadas y no quemadas en los diferentes años posts-incendios, estos cambios no siguieron un patrón claro resaltando ese carácter generalista de la mayoría de especies presentes en las zonas de estudio. Por lo tanto, podemos concluir afirmando que no todas las especies de hormigas son buenas indicadoras de la salud de los ecosistemas o del estado de sucesión de éstos después de un incendio. El uso de hormigas como bioindicadores de sistemas forestales perturbados por el fuego debería enfocarse principalmente sobre aquellas especies más susceptibles a esta perturbación como consecuencia de una historia de vida más dependiente de la vegetación.

La conservación de las hormigas, abejas y arañas y la regeneración de los ecosistemas forestales incendiados

Como ya se ha comentado a lo largo de la presente tesis doctoral, la biodiversidad es un concepto multidimensional que engloba tres componentes fundamentalmente: La dimensión taxonómica, la funcional y la filogenética. De manera que, preservar tantos tipos de biodiversidad como sea posible debe ser esencial en la disciplina de la biología de la conservación (Devictor et al., 2010). No obstante, pueden existir otros argumentos para la preservación de la biodiversidad. En primer lugar, un argumento ecológico sostiene que las pérdidas de diversidad pueden afectar a servicios ecosistémicos vitales que los humanos necesitamos para nuestra existencia (Bengtsson et al., 2000). Las hormigas, y otros insectos sociales, presentan una serie de características como, por ejemplo, una alta biomasa y abundancia numérica, una diversidad de asociaciones mutualistas, la presencia de castas y división del trabajo, la comunicación eficiente y cooperación, la capacidad de almacenar alimentos, etc.) que hacen que sean tolerantes al estrés y fáciles de manejar, lo que aumenta los servicios ecosistémicos que proporcionan (Elizalde et al., 2020). Matias et al., (2016) descubrieron que la mayoría de los servicios y beneficios de las abejas silvestres están relacionados con la alimentación, la medicina y la polinización, siendo este último el más conocido (Kremen et al., 2007). Asimismo, no debemos olvidar el importante papel que ejercen las arañas como depredadoras (Yip, 2014) con pruebas sólidas de que son muy eficaces en el control natural de plagas y mejoran el rendimiento de los cultivos (Michalko et al., 2019a, 2019b).

En segundo lugar, un argumento de carácter económico correspondería al cierto grado de control y ganancias de la diversidad biológica inexplorada en los trópicos que quieren tener muchos países desarrollados (Bengtsson et al., 2000).

En la presente tesis doctoral se ha trabajado con dos de los tres componentes de la biodiversidad: La diversidad taxonómica (DT) y la funcional (DF). Adoptar una visión integrada de estos dos componentes es todo un desafío en la planificación de la conservación de la biodiversidad porque, como ya hemos visto en los **capítulos 2 y 3**, cambios en una dimensión no tienen por qué ir acompañados de cambios significativos en la otra. Esto nos puede llevar a un dilema de conservación caracterizado por la falta de coincidencia entre DT y DF, ya que, si las comunidades con diferentes niveles de cada componente de diversidad se encuentran en lugares diferentes, las áreas con alta DT pueden excluir altos niveles de DF (Forest et al., 2007; Naidoo et al., 2008). No obstante, la conservación de forma simultánea de varios componentes de la biodiversidad puede alcanzarse en teoría maximizando la protección de la DT, pero en la práctica este sistema es inviable y las estrategias de conservación pasadas y actuales solo invierten en taxones o áreas raras, endémicas y/o características (Myers et al., 2000).

El **capítulo 2** de la tesis presentó una menor diversidad taxonómica y funcional de hormigas en parcelas quemadas que en no quemadas a corto plazo. Esta menor riqueza y diversidad se debió fundamentalmente a la desaparición de especies crípticas (género *Temnothorax*) que se encontraban más asociadas a la vegetación que se vio afectada por el fuego. Sin embargo, al estudiar las respuestas de las hormigas al fuego a largo plazo en el **capítulo 3**, se observó de forma general una mayor riqueza y diversidad taxonómica en zonas quemadas frente a pinares inalterados, paralelamente a la creación de zonas abiertas con un cambio en la estructura de las comunidades vegetales durante el proceso de sucesión ecológica. De esta manera, los nuevos hábitats post-incendio propiciaron el asentamiento de especies mejor adaptadas a vivir en zonas abiertas, como son aquellas especies de hormigas, arañas y abejas silvestres (Underwood & Quinn, 2010) que nidifican en el suelo. Además, la madera muerta generada también puede ser utilizada como material de nidificación en determinadas especies de abejas silvestres y el crecimiento de herbáceas con flores a corto plazo constituye un recurso alimentario para la comunidad de abejas silvestres (Bogusch et al., 2015).

Por tanto, esto nos lleva a reflexionar sobre unos esfuerzos de conservación más centrados en preservar el hábitat en vez de determinadas especies por separado. La creación de zonas abiertas dentro de bosques maduros de coníferas, donde el predominio del estrato arbóreo es patente, sería una forma de maximizar la protección de la diversidad taxonómica de hormigas, arañas y abejas generando nuevos nichos ecológicos en combinación con los ya existentes. En este camino, las quemas controladas pueden ser una valiosa herramienta de gestión de los ecosistemas forestales. Estudios multidisciplinares con quemas prescritas en espacios protegidos avalan su uso en ecosistemas adaptados al fuego para mejorar el estado de conservación o favorecer taxones concretos vegetales o animales (Madrigal et al. 2022), ya que un uso rotativo de estas permitiría la creación de ecosistemas forestales con distintos hábitats característicos de cada etapa de la sucesión ecológica (Fernandes et al., 2013). Asimismo, la labor que presentan las quemas prescritas en la reducción del peligro de grandes incendios de alta severidad y/o recurrencia que comprometa la resiliencia de los ecosistemas también debe ser tenida en cuenta en la protección de áreas y la conservación de la biodiversidad (Madrigal et al. 2022).

Conclusiones generales

1.- Los efectos de los incendios forestales sobre las comunidades de artrópodos en ecosistemas mediterráneos de pinares de la Península Ibérica pueden variar en su signo atendiendo a 1) el grupo taxonómico objeto de estudio, 2) la dimensión de la variable respuesta (taxonómica o funcional) y 3) la escala temporal en la que se analicen las respuestas.

2.- Respecto a las diferencias en las respuestas al fuego según los grupos taxonómicos estudiados, los efectos son más acusados sobre las comunidades de hormigas que sobre las de abejas y arañas.

3.- El fuego aumenta la riqueza de especies de abejas en las zonas quemadas siendo la composición taxonómica y funcional de las zonas quemadas diferente de las zonas no quemadas. Los dos rasgos funcionales de las abejas afectados por los incendios (sitio de anidación y especialización floral) se recuperan a largo plazo.

4.- El fuego disminuye la abundancia y riqueza de arañas en los dos primeros años tras el incendio, pero ambas variables se recuperan a corto plazo (3-4 años). La composición taxonómica y funcional cambia tras el fuego, con especies de arañas en las zonas quemadas que son predominantemente diurnas, cazan al acecho, excavan madrigueras, y tienen dietas especializadas; mientras en las zonas no quemadas hay especies más nocturnas y que para cazar usan telarañas.

5.- La riqueza y diversidad taxonómica de las comunidades de hormigas siempre se ve afectada tras el incendio, pero presenta una gran variación de la respuesta. Así, el fuego no tuvo efecto sobre estas variables a los cuatro años en Belver (Portugal); pero redujo la ocurrencia, riqueza y diversidad de especies, en los cuatro años que siguieron al incendio de Salo (Cataluña); o bien las aumentó de forma permanente en los incendios de Andalucía. Probablemente los factores locales que afectan a la recuperación de la vegetación deben influir en esta variación.

6.- El efecto del fuego sobre la estructura y composición funcional de las comunidades de hormigas, es menos acusado o no existe. La divergencia funcional y la riqueza funcional fueron más bajas en las zonas quemadas que en las no quemadas en Andalucía y Salo, sin embargo, la dispersión funcional, aun siendo más baja en las zonas quemadas, se recuperó en los 4 años.

7.- Los rasgos funcionales de las hormigas asociados a la supervivencia, persistencia y colonización permiten predecir la respuesta tras el incendio sobre las especies que serán filtradas, y las que podrán colonizar o aumentar su abundancia en las zonas quemadas.

8.- El aumento de la temperatura en las zonas quemadas –por la desaparición del estrato arbóreo– favorece el éxito de las interacciones tanto de las especies subordinadas como de las dominantes; aunque las subordinadas tienen éxito a temperaturas más altas. La jerarquía de dominancia cambia en mayor medida justo después del incendio, y conforme pasa más tiempo desde el incendio se van dando menos cambios. En las zonas quemadas, las especies que descubren antes los cebos son especies termófilas y subordinadas, y el descubrimiento es más rápido que en las zonas no quemadas, donde las descubridoras son especies dominantes.

General conclusions

1.- The effects of forest fires on arthropod communities in the Mediterranean pine forest ecosystems of the Iberian Peninsula may vary in their sign depending on 1) the taxonomic group under study, 2) the dimension of the response variable (taxonomic or functional) and 3) the time scale on which the responses are analysed.

2.- Regarding the differences in the responses to fire according to the taxonomic groups studied, the effects are more pronounced on the ant communities than on the bee and spider communities.

3.- Fire increases bee species richness in burned areas. The taxonomic and functional composition of burned areas is different from that of unburned areas. The two functional traits of bees affected by fire (nest site and floral specialisation) recover in the long-term.

4.- Fire decreases spider abundance and richness in the first two years after, but both variables recover in the short-term (3-4 years). The taxonomic and functional composition changes after fire: the spider species in burned areas are predominantly diurnal, hunt by stalking, burrow, and have specialised diets; while the species in unburned areas are predominantly nocturnal and use webs for hunting.

5.- The richness and taxonomic diversity of ant communities is always affected after a fire, but there is great variation in the response. For example, fire had no effect on these variables after four years in Belver (Portugal). It reduces the occurrence, richness and diversity of species in the four years following the fire in Salo (Catalonia), but had the opposite effect by increasing these variables permanently in the fires in Andalusia. Local factors affecting vegetation recovery must influence this variation.

6.- The effect of fire on the structure and functional composition of ant communities is less pronounced or non-existent than expected. Functional divergence and functional richness were lower in burned areas than in unburned areas in Andalusia and Salo. However, functional dispersion, although lower in burned areas, recovered in all four years.

7.- The functional traits of ants associated with survival, persistence and colonisation help predict how filtered species will respond to the fire, and also which species will be able to colonise or increase their abundance in the burned areas.

8.- The increase in temperature in burned areas –due to the disappearance of the tree layer– favours the success of the interactions of both subordinate and dominant species, although subordinate species are more successful at higher temperatures. The dominance hierarchy changes most immediately after the fire, with less change occurring as time passes after the fire. In burned areas, baits are discovered earlier by thermophilic and subordinate species, while in unburned areas, it is the dominant species that arrive first.

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"¿Qué sería de nuestras tragedias si un insecto nos presentara las suyas?". EMIL CIORAN.

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