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Indirect Interactions Driven by Soil Effects Enable Coexistence Among Competing Plant Species

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ABSTRACT

Reciprocal effects between plants and soil have been proposed as mechanisms that promote coexistence. However, recent theoretical and empirical works have questioned their role in stabilizing coexistence within multispecies communities. In these systems, soil-mediated indirect interactions may play a pivotal but often overlooked role. We investigate these indirect interactions using an experimental system of two competing shrub species grown in soil conditioned by a mediating third tree species. Tree-induced shifts in soil microbial communities, metabolites and nutrients boost growth in the weak competitor species while reducing germination in the dominant competitor. Simulations demonstrate that these shifts in plant performance are sufficient to stabilize coexistence, producing simulated spatial distributions consistent with those observed in natural communities. Our findings underscore the role of soil effects in driving indirect interactions that sustain coexistence in diverse plant communities, highlighting the importance of indirect but also positive and negative multitrophic interactions in maintaining biodiversity.

1 | Introduction

How can plants that use similar resources coexist? The long-standing belief that species competing for the same resources cannot stably coexist has shaped ecological theory through the lens of the competitive exclusion paradigm (Hardin 1960). Yet, plants are not merely resource consumers—they actively modify soil properties and nutrient dynamics through interactions with microbial communities, mediated by processes such as nutrient uptake, litter deposition, root exudation and allelopathy (Wardle et al. 2004; Ehrenfeld et al. 2005; Lebeis et al. 2012; Fujii et al. 2018). These soil modifications can, in turn, strongly influence germination, growth and reproduction (Bonanomi et al. 2005; Veen et al. 2019; Weyens et al. 2009), ultimately shaping individual fitness (Bever et al. 2012; Lau and Lennon 2012). Moreover, plant-induced changes in soil conditions can affect the performance of neighbouring species, thereby shaping competitive and facilitative interactions within plant communities (van der Putten et al. 2013; Rodríguez-Echeverría et al. 2013; van de Voorde et al. 2011). These reciprocal interactions—known as plant–soil feedbacks—are increasingly viewed as a potential mechanism for maintaining biodiversity. However, despite their conceptual appeal, both empirical and theoretical evidence remain mixed regarding their role in promoting species coexistence. While some studies suggest that negative feedbacks

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can limit dominance and facilitate coexistence (Crawford et al. 2019; Mack et al. 2019; van der Putten et al. 2013; Teste et al. 2017; Willing et al. 2024), others indicate that interspecific plant–soil feedbacks alone may be insufficient to maintain coexistence in multispecies communities (Miller et al. 2022; Pajares-Murgó et al. 2024).

Multispecies communities are characterized by pervasive indirect interactions, which occur when the dynamics between two species are influenced by the presence of a third (Wootton 1994). These interactions significantly affect plant performance (Levine 1999, 2000), influencing competitive and facilitative processes, with far-reaching implications for community stability and species coexistence (Allesina and Levine 2011; Gibbs et al. 2022; Levine et al. 2017; Molina-Venegas et al. 2025). Despite the recognized importance of indirect interactions in community dynamics, much of the current understanding of plant–soil feedback and its role in species coexistence stems from studies that isolate single-species or pairwise interactions (Bever et al. 1997; Peay 2018; Scheublin et al. 2007; Veen et al. 2019; Willing et al. 2024). This focused approach, while informative, inherently overlooks the web of indirect effects that are intrinsic to multispecies communities, potentially contributing to the lack of consensus on the role of plant-driven soil modifications in promoting species coexistence in natural communities (Mack et al. 2019; Miller et al. 2022; Pajares-Murgó et al. 2024; Zhang et al. 2020). Stabilizing indirect interactions mediated by interspecific plant–soil feedback would entail that shifts in soil biotic and abiotic characteristics caused by one species drive demographic shifts in other plant species that foster coexistence. For instance, soil modifications by a third species may reduce the fitness of dominant competitors, thereby enhancing the persistence of weaker competitors and promoting stable coexistence. These soil modifications by a third species can also create spatial heterogeneity, which is widely recognized as an important factor promoting species coexistence (Amarasekare 2003; Holt 1984). Therefore, unravelling the role of plant–soil feedback in shaping multispecies coexistence requires a comprehensive investigation of its effects through the lens of indirect interactions.

To explore the role of indirect interactions mediated by soil shifts in promoting multispecies coexistence, we investigated an experimental system involving three woody species. Specifically, we examine how soil modifications caused by a mediating tree species (*Quercus pyrenaica* Willd.) influence the competitive dynamics between two closely related shrub species (*Cistus ladanifer* L. and *Cistus laurifolius* L.). These shrubs are broadly distributed and dominate many shrublands across the Iberian Peninsula (Fernández-Mazuecos and Vargas 2010). Throughout much of the Mediterranean region, *C. ladanifer* often dominates, forming nearly monospecific stands. In these areas, the locally rare or weak competitor, *C. laurifolius*, tends to occur in the presence of *Q. pyrenaica* (Castroviejo 2020; See Appendix S1 and Figure S1). *Quercus* species are particularly relevant in this context, as they are well known to induce strong soil modifications through root exudation and litter deposition, with extensive evidence documented for several species of the genus (Aponte et al. 2011; Lasa et al. 2019). This makes *Q. pyrenaica* an ideal focal species for studying the effects of interspecific plant–soil feedback. Hence, this system provides a relatively simple yet ecologically relevant context to investigate potential indirect mechanisms mediated by soil shifts in stabilizing species coexistence. Its simplicity allows us to perform controlled and detailed experiments while its broad natural distribution ensures that experimental findings can be validated with field observations. By leveraging this widely distributed but experimentally tractable system, our study aims to uncover the soil-mediated indirect interactions that may underpin coexistence in plant communities.

2 | Results and Discussion

2.1 | Effects of Soil Conditioning by the Mediating Species on Germination

The majority of evidence linking species coexistence to reciprocal plant–soil interactions is based on their effects on plant growth (Crawford et al. 2019; Teste et al. 2017). Yet, shifts in soil properties are also expected to influence critical demographic plant parameters that may facilitate coexistence beyond growth, such as germination (Dudenhöffer et al. 2018). Therefore, we initially investigated whether soil conditioned by the mediating species affects the germination of the two competing species. To facilitate the link between experimental and observational evidence, we used naturally occurring soils from our study system that were undoubtedly conditioned by a single target species: either *Quercus pyrenaica* (the mediating species) or *Cistus ladanifer* (the locally dominant competitor). In addition, we included soils unconditioned by woody species as control soils (see Appendix S2). The germination of the dominant species is significantly reduced in the influence of the mediating species' soil compared to its own soil ($Z = 2.55$; $p = 0.033$; Figure 1A; Table S1). Comparison with the control soil reveals that the significantly reduced germination arises from a combination of increased germination in the dominant species' soil and decreased germination in the mediating species' soil (Figure 1A). In contrast, the germination of the weak competitor remains similar across all treatments ($p > 0.05$ always; Figure 1B and Table S1). These findings show that the mediating species modifies the soil in ways that reduce the germination of the dominant competitor, without affecting the weak competitor. To determine whether these effects are primarily driven by soil biochemistry or living microorganisms, we compared germination responses in sterilized soils. Similar to above results, germination of the dominant competitor was significantly reduced in sterilized soils previously conditioned by the mediating species, compared to those conditioned by the dominant species ($Z = 3.297$; $p = 0.01$; Figure 1A). This suggests that the observed effects are likely mediated by shifts in soil biochemistry, such as the accumulation of allelochemicals produced by the mediating species (Meiners et al. 2017). Together, these findings indicate that biochemical soil modifications induced by the mediating species can suppress the dominant competitor, potentially promoting coexistence by reducing competitive asymmetries.

2.2 | Effects of Soil Conditioning by the Mediating Species on Plant Growth

Although the observed changes in germination may contribute to the coexistence of these competitors, the germination

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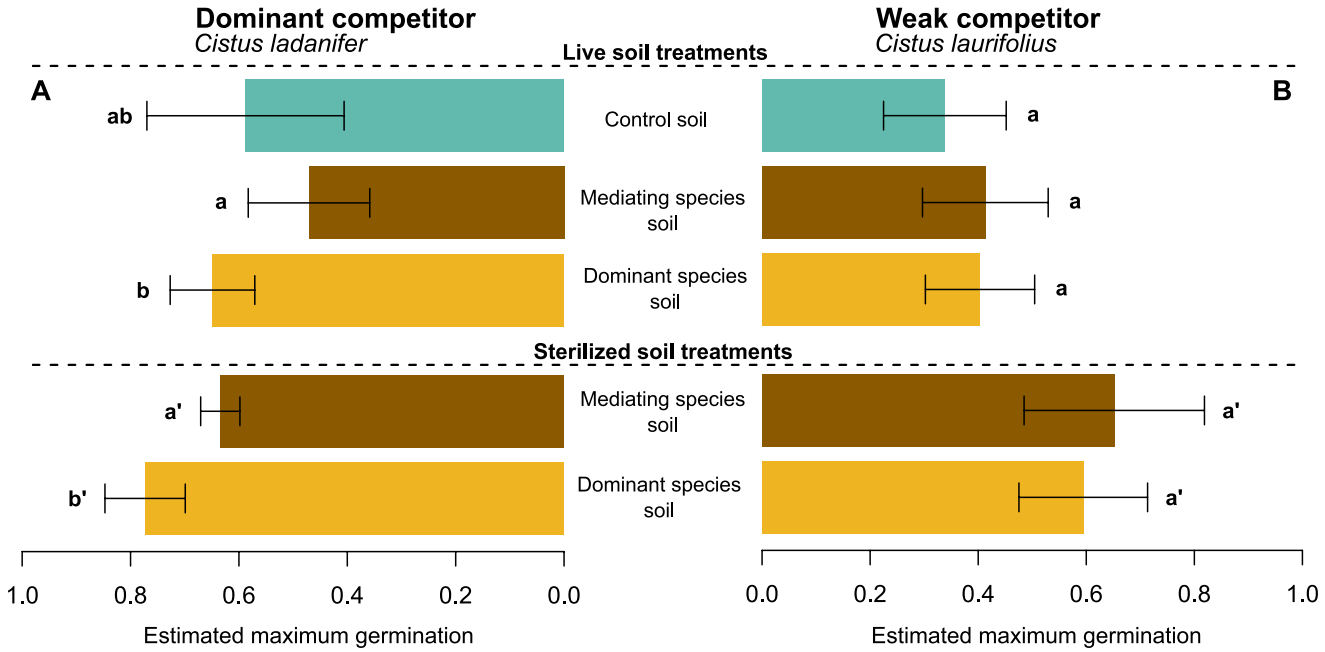

FIGURE 1 | Biochemistry of soil conditioned by the mediating species reduces the germination of the dominant competitor. The locally dominant competitor (*C. ladanifer*, A) exhibits significantly reduced germination in both live (top bars) and sterilized (bottom bars) soils conditioned by the mediating species, indicating negative effects of soil biochemistry. In contrast, the locally weak competitor (*C. laurifolius*, B) shows no significant response to soil treatments. Bars represent the estimated maximum germination (mean and 95% confidence interval) in different soil solutions, fitted using a nonlinear logistic growth mixed model (alternative models provide similar results, Appendix S3). Treatments were based on soils conditioned either by the mediating species (*Quercus pyrenaica*), the dominant species (*Cistus ladanifer*) or by none of them (control; see Methods for details). Different letters indicate statistically significant differences within sterilized and live soil treatments ($p < 0.05$, Table S1).

rates of the dominant competitor remain higher than those of the weak competitor (Figure 1B), suggesting that additional mechanisms are involved. Plant–soil feedback is well-known to affect plant growth, which might also contribute to species performance and coexistence (Crawford et al. 2019; Teste et al. 2017). We therefore investigated whether soil conditioned by the mediating species affects the growth of these closely related species. In contrast to germination, no significant differences are observed in the growth of the dominant competitor across all soil treatments ($p > 0.05$ in all cases; Figure 2A; Table S2). However, our results reveal that the growth of the weak competitor is significantly enhanced in the mediating species' soil compared to the control and dominant species' soils ($p < 0.01$ in both cases; Figure 2B; Table S2). Because larger seedlings generally experience lower mortality in semiarid environments (Andivia et al. 2021), this increase in growth likely promotes the persistence of the weak competitor under Mediterranean semiarid conditions. Taken together, these findings demonstrate that plant–soil feedback can drive demographic shifts by influencing distinct stages of plant ontogeny (Dudenhöffer et al. 2018). More importantly, the reduced germination of the dominant species, coupled with the enhanced growth of the weak competitor in soil conditioned by the mediating species, is expected to promote the coexistence of both competitors. These findings underscore how soil-mediated positive and negative interactions can support biodiversity.

To gain deeper insights, we explored whether growth changes are driven solely by soil biochemistry or also involve shifts in microbial communities. To address this, we conducted a growth experiment using sterilized soils paired with water-based microbial inoculum derived from live soils in a cross-experimental design (see Methods). In the dominant competitor, a significant enhancement in growth was observed only when plants were grown in soils conditioned by the mediating species and inoculated with the microbiome of the dominant species. This treatment produced more biomass than both treatments grown in the dominant species' soil, regardless of the microbial inoculum ($p < 0.05$ for both comparisons; Figure 2C; Table S2). Thus, the dominant competitor appears to benefit from increased nutrient availability in soils conditioned by the mediating species (see Appendix S4 and Figure S2) only when its native soil microorganisms are present. This combination is unlikely to occur under natural conditions because soils conditioned by the mediating species should also carry its characteristic microbial community, consistent with the lack of effects observed in untreated live soils. Similarly, the locally weak competitor exhibits significantly enhanced growth in soils conditioned by the mediating species when paired with microorganisms associated with the mediating species compared with all other treatments ($p < 0.05$; Figure 2C; Table S2). This experimental setup, which mimics natural conditions, reveals that the enhanced growth of the weaker competitor in soils conditioned by the mediating species arises from the combined effects of shifts in soil biochemistry and microbial communities. Hence, plant growth seems to depend not only on soil chemical properties but also on specific microbial communities to which plant species are likely adapted (Lau and Lennon 2011). Importantly, our findings suggest that shifts in both soil biochemistry and microbial communities are necessary to facilitate the coexistence of these closely related species.

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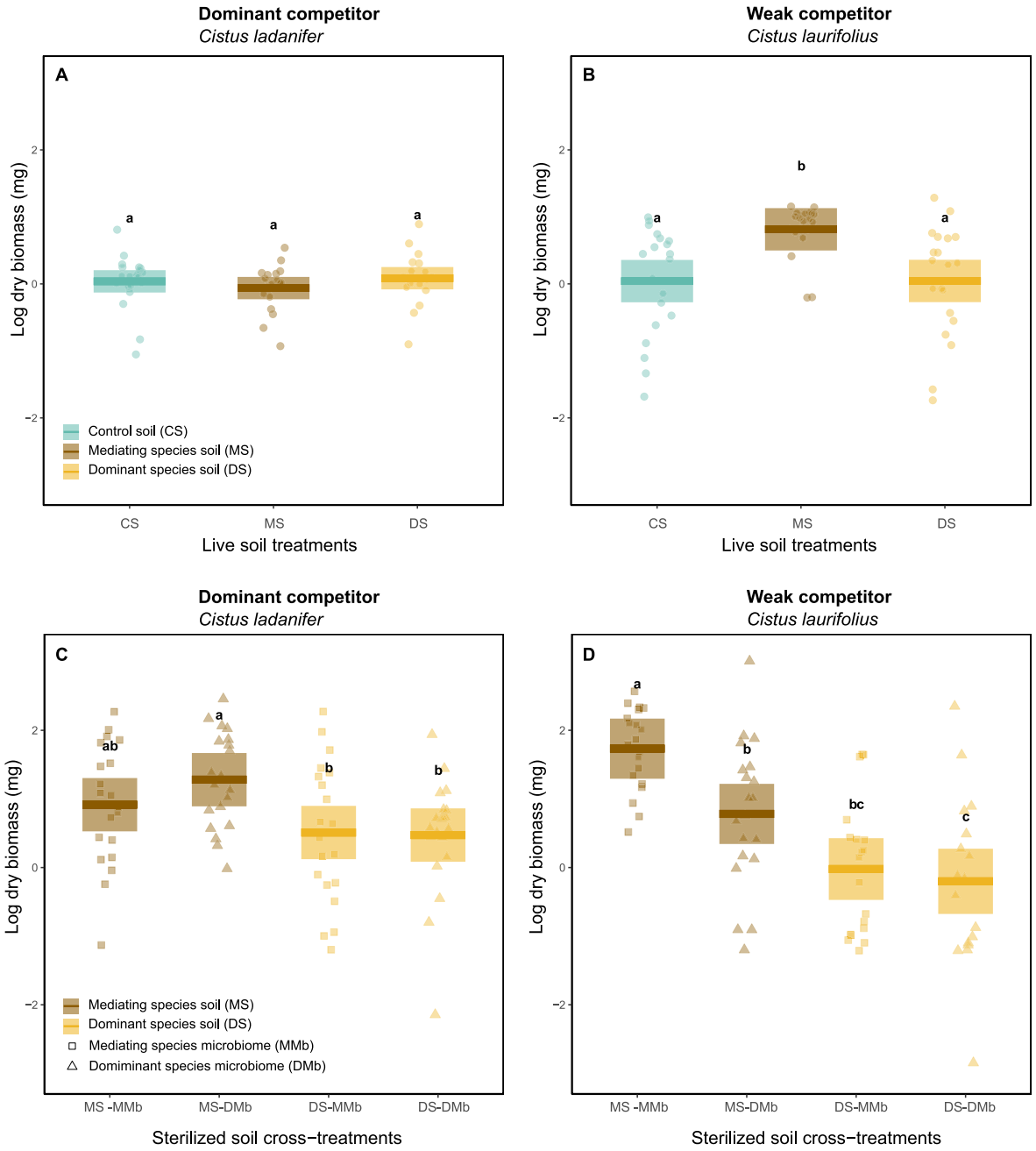

FIGURE 2 | Microorganisms and biochemistry of soil conditioned by the mediating species enhance the growth of the weak competitor. (A) Live soil treatments do not influence the growth of the locally dominant competitor (*Cistus ladanifer*) while (B) soil conditioned by the mediating species (*Quercus pyrenaica*) promotes the growth of the locally weak competitor (*C. laurifolius*). In cross-treatments using sterilized soil with microbiome inoculums, (C) the dominant competitor benefits from soils conditioned by the mediating species only when its own soil microbiome is reintroduced. Conversely, (D) the weak competitor benefits from both soil biochemistry and the associated microbiome of the mediating species. Box plots show log-transformed dry biomass (mg): Solid bars represent means, shaded areas indicate 95% confidence intervals. Soil treatments are indicated by colour, and in (C) and (D), microbiome inoculum treatments are distinguished by symbol shape. Different letters indicate statistically significant differences ($p < 0.05$, see Table S2). CS, MS and DS refer to control soils, soils conditioned by the mediating species, and soils conditioned by the dominant species, respectively. Microbiome inoculums are abbreviated as MMb (mediating-species microbiome) and DMb (dominant-species microbiome).

2.3 | Experimentally Based Expectations Align With the Spatial Organization of Natural Communities

Experimental evidence is most compelling when it directly links to patterns observed in natural communities. If the mediating species modifies soil properties in ways that influence the germination and growth of the competing shrub species, thereby shaping their coexistence, we would expect that: (i) individuals of the mediating species alter both biotic and abiotic soil properties at fine spatial scales, and (ii) at this scale, the dominant and the weak competitor species tend to segregate from and aggregate to the mediating species, respectively. Supporting the first expectation, proximity to individuals of the mediating species

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significantly shifts the composition of soil nutrients ($R^2 = 7.84\%$; $F = 4.08$; $p < 0.01$), metabolites ($R^2 = 4.06\%$; $F = 2.03$; $p < 0.01$) and bacterial ($R^2 = 5.02\%$; $F = 2.54$; $p < 0.01$) and fungal ($R^2 = 3.14\%$; $F = 1.55$; $p < 0.01$) communities. These effects are not linear but occur within short distances from the individuals, with compositional dissimilarities reaching their maximum at approximately 5.73, 6.28, 3.87 and 3.82 m for nutrients, metabolites, bacterial and fungal compositions, respectively (Figure 3A–D). The changes in soil composition at short distances from the tree trunk correspond to areas that remain largely covered by tree litter (Figure S3) throughout most of an individual's lifespan (average age 36.6 years, Appendix S5) and probably characterized by a denser root system. Such conditions strongly suggest that the combination of litter decomposition and root exudations are driving the pronounced modifications in soil composition observed near the tree individuals. This aligns with evidence showing that *Quercus* spp. strongly modify soil chemical, and biological properties (Aponte et al. 2011; Lasa et al. 2019). Our findings also support the second expectation: the abundance of the locally dominant competitor increases with distance from the individuals of the mediating species ($R^2 = 13.6\%$; $F = 24.23$; $p < 0.01$; Figure 3E), whereas the locally weak competitor follows the opposite trend ($R^2 = 3.03\%$; $F = 7.53$; $p < 0.01$). This spatial replacement pattern is evident, with the weak competitor prevailing within approximately 3 m from the mediating species and the dominant competitor dominating beyond this distance (Figure 3E). Focusing on species cover instead of individual counts yields similar results (Figure S4). Although the specific soil microorganisms and chemical compounds driving these patterns remain unidentified, the fine-scale spatial structure of soil properties and species distribution closely aligns with experimental-based expectations. This supports the idea that soil modifications by mediating species play a crucial role in promoting the coexistence of competing species.

2.4 | Simulations Predict Spatial Patterns and Stable Coexistence of the Competing Species

Definitive evidence for the role of soil-mediated indirect interactions in stabilizing coexistence would require experimental data on all relevant demographic parameters (Dudenhöffer et al. 2018). However, obtaining such data—For example, seed production—in the studied woody species is largely unfeasible due to their long-life cycles and the challenges of maintaining realistic yet fully controlled experimental conditions over extended timescales. We therefore used numerical simulations parameterized with experimental results to assess whether observed changes in germination and growth are sufficient to enable the stable coexistence of both shrub species (see Methods and Appendix S6). We used experimentally derived germination data and inferred survival probabilities from observed growth responses in conditioned soils. This inference was based on the well-supported assumption that increased growth enhances survival (Andivia et al. 2021).

Our simulations showed that the combination of measured germination probabilities and a slight increase of 0.08 in the survival probability of the weak competitor in soil conditioned by the mediating species—compared to soil conditioned by the dominant competitor—was sufficient to reproduce a spatial abundance pattern closely matching that observed in natural

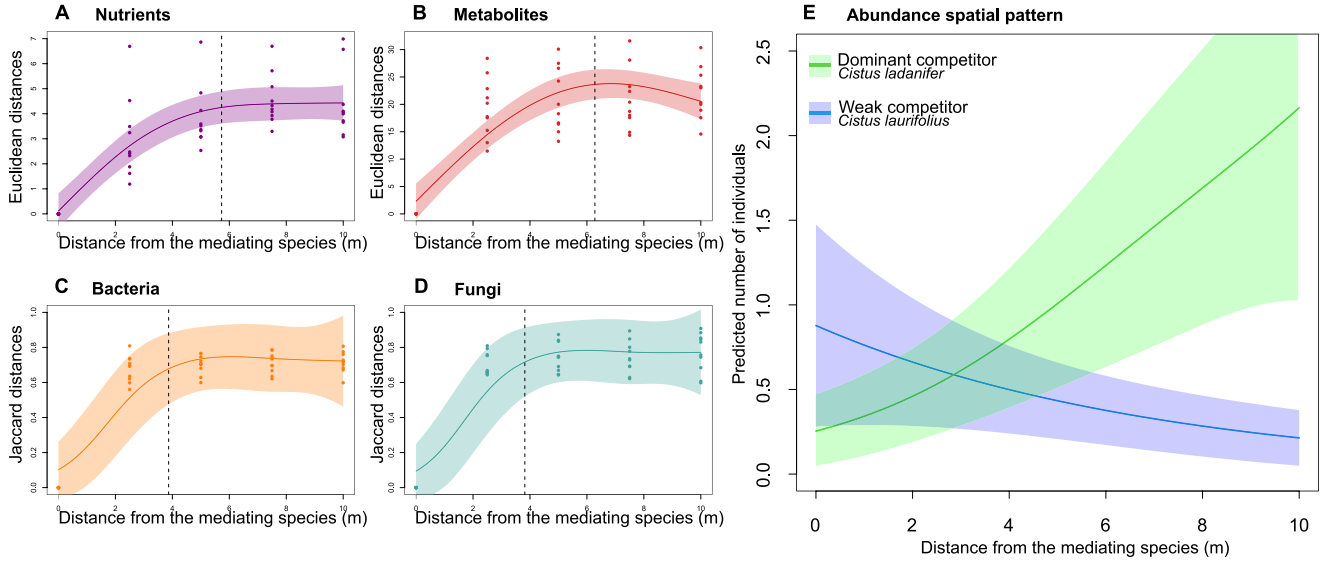

FIGURE 3 | The presence of the mediating species drastically alters the microbial communities and biochemistry of natural soils as well as the distribution patterns of the competing shrub species. The presence of the mediating species (*Quercus pyrenaica*) significantly alters the composition of (A) nutrients ($R^2 = 66.1\%$; $F = 85.24$; $p < 0.01$), (B) metabolites ($R^2 = 66.6\%$; $F = 69.12$; $p < 0.01$), (C) bacteria ($R^2 = 86.3\%$; $F = 4.76$; $p = 0.016$) and (D) fungi ($R^2 = 85.8\%$; $F = 5.17$; $p = 0.012$). Solid lines show predictions from a generalized additive mixed model of compositional dissimilarity between the sample collected at zero distance from individuals of the mediating species and samples collected farther away, as a function of distance. Shaded areas represent 95% confidence intervals. The vertical dotted lines indicate the inflection point in compositional dissimilarities. (E) Predicted spatial distribution of the number of individuals in 1 m^2 plots of the locally dominant (*Cistus ladanifer*, green) and weak (*C. laurifolius*, blue) competitor species, relative to the distance from individuals of the mediating species. The abundance of the weak competitor is replaced by the dominant competitor as distance from the mediating species increases. Predictions are based on fitted generalized additive mixed models with a Poisson error distribution and a log link function.

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communities (averaged $R^2 = 0.92$; average RMSD = 0.313; compare Figure 4A and Figure 3E, see also Figure S5 and Table S3). Under this parameterization, both species also maintained stable population sizes over time (Figure 4B, Table S3), establishing a link between the demographic effects of soil modifications by the mediating species, the spatial distribution of the shrub species, and their long-term coexistence.

Sensitivity analyses varying the soil-conditioning extent consistently yielded stable coexistence driven by relatively modest increases in survival probabilities (0.054–0.141) associated with enhanced growth (Appendix S7 and Table S4). Nevertheless, the link between plant size and survival should be interpreted with caution, as the growth experiment spanned only 60 days and therefore captured seedling responses, leaving uncertainty about how these short-term, soil-mediated growth differences translate into long-term survival. Similarly, soil modifications by the mediating species might also influence reproduction (Dudenhöffer et al. 2018) or even the competitive process itself (Willing et al. 2024). Experimental approaches spanning the complete lifespan of the shrub species and incorporating direct competition trials are required to address these questions and to fully disentangle the intricate interplay between competitive interactions and the facilitative and negative effects of soil-mediated interactions shaping species coexistence. Additionally, the mediating species could also affect competitive dynamics through other mechanisms, such as asymmetric shading or differential overlap in resource use with the shrub species. Nonetheless, our results suggest that only the combined effect of soil-mediated reductions in germination of the dominant competitor and enhanced growth in the weaker competitor is sufficient to reverse competitive hierarchies and enable coexistence. We also acknowledge that the dynamics of the mediating species were not explicitly included in our framework, and therefore the long-term coexistence of the shrub species will be conditioned by the longer-term demographic dynamics of the mediating species. However, *Quercus* trees are far more long-lived than the shrubs, with the lifespan of a single tree spanning several shrub generations, which likely explains the congruence between our simulations and the observed field patterns where living trees are present. Overall, these results highlight the role of soil-mediated indirect interactions in modulating competitive dynamics and underscore their importance in driving species coexistence.

2.5 | Implications and Future Directions

Our findings provide mechanistic insight into how competing plant species can coexist through soil-mediated indirect interactions. Acting as mediators, certain plant species can modify both biotic and abiotic soil components in ways that alter competitive dynamics, reducing the performance of dominant competitors while enhancing that of weaker ones. Together, these soil-mediated effects generate a combination of positive and negative interactions that operate beyond direct competition and can play a central role in structuring species coexistence. Such processes may underlie observational patterns in which rare species more frequently spatially aggregate with nurse plants (Soliveres et al. 2015) or cluster with other rare species (Calatayud et al. 2020), providing a mechanistic basis for general patterns observed in ecological communities that are presumably linked to species coexistence.

Several open questions remain. While our results demonstrate that soil-mediated indirect effects associated with a mediating species can facilitate species coexistence, the specific processes responsible

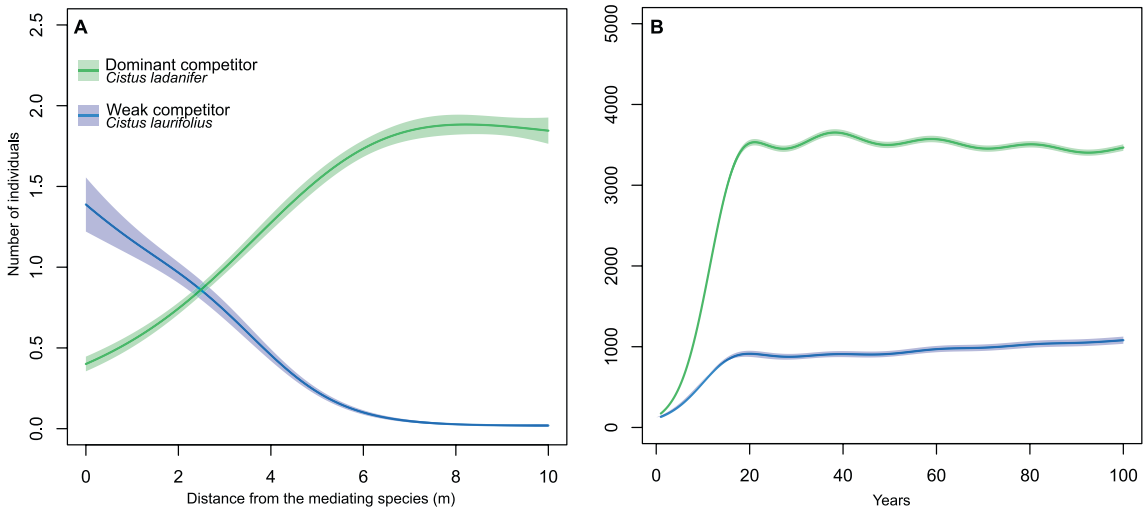

FIGURE 4 | Experimentally informed simulations reproduce natural spatial patterns of competing species relative to the mediating species, supporting also their stable coexistence. (A) Simulated spatial distribution of the number of individuals in 1 m^2 of the locally dominant (*Cistus ladanifer*, green) and weak (*C. laurifolius*, blue) competitor species as a function of distance from individuals of the mediating species (*Quercus pyrenaica*). Similar to field observations (Figure 3E), the dominant competitor increases in abundance with distance from the mediating species, while the weak competitor aggregates near it ($R^2 = 36\%$; $F = 619.5$; $p < 0.01$ for the dominant competitor and $R^2 = 22\%$; $F = 389.3$; $p < 0.01$ for the weak competitor). Model predictions (solid lines) were estimated using a generalized additive mixed model with a Poisson distribution and log link function. Shaded areas denote 95% confidence intervals. (B) Population dynamics of both competitors across the entire simulated area over 100 years of simulation. Under the observed parameterization, populations have remained stable over the last 20 years, showing no significant temporal trends for any species ($p > 0.01$). This stability supports the idea that indirect soil-mediated effects may play a key role in facilitating long-term coexistence.

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for altering soil properties—such as root exudation, litter deposition or the timescales over which soil modifications accumulate—remain unresolved. Similarly, because soils were pooled within species prior to the experiment, some among-individual or spatial variability in soil-mediated effects may have been reduced, potentially amplifying the influence of rare but strong soil biota (Clark et al. 2025; Smith-Ramesh and Reynolds 2017). In addition, the long-term demographic dynamics of the mediating species, as well as potential soil feedbacks from the weaker competitor and their effects on competitive dynamics, warrant further investigation. Our results further suggest that soil modification by the mediating species can reverse competitive hierarchies between the shrub species, a pattern characteristic of coexistence mediated by spatial heterogeneity (Amarasekare 2003; Holt 1984). However, because both shrub species appear to coexist only in soils modified by the mediating species, it remains unclear whether coexistence is primarily driven by the spatial heterogeneity generated by the mediating species or by soil shifts per se, independent of their spatial configuration. Future research should assess whether these dynamics extend to more diverse communities, explore how species differentially respond to microbial communities and soil biochemistry, and evaluate whether soil-mediated effects are maintained across species ranges and environmental conditions. Such efforts will provide deeper insight into the eco-evolutionary pathways through which plant–soil feedbacks mediate coexistence, with important implications for understanding how species interactions shape species distributions (Kissling and Schleuning 2015).

More broadly, our study highlight the need to integrate indirect and multitrophic interactions (Allesina and Levine 2011; Chesson and Kuang 2008; García-Callejas et al. 2023; Molina-Venegas et al. 2025)—such as those between plants and soil microbes—into coexistence theory, moving beyond a framework centred on direct competition (Chesson 2000). Our results further emphasize that both positive and negative indirect interactions play a fundamental role in promoting species coexistence and sustaining biodiversity (Buche et al. 2025; Calatayud et al. 2020; Molina-Venegas et al. 2025). Expanding coexistence theory to incorporate the indirect as well as positive and negative interactions will help resolve the diversity paradox, reframing species-rich communities as the expected outcome of complex ecological interactions rather than an exception (Simha et al. 2022). Overall, our findings reinforce the view that the maintenance of biodiversity is shaped not only from competition but from a web of interacting forces, where soil-mediated positive and negative indirect effects can play a central role in stabilizing species-rich plant communities.

3 | Methods

3.1 | Study Area, Soil and Seed Collection and Treatments

We used two closely related mediterranean shrub species (*Cistus ladanifer* and *Cistus laurifolius*) and a *Quercus* tree (*Quercus pyrenaica*) as our experimental system. Given their close phylogenetic relationship, *C. ladanifer* and *C. laurifolius* are expected to engage in strong interspecific competition (Violle et al. 2011). Based on local species' abundances, we define *C. ladanifer* as the dominant competitor, and *C. laurifolius* as the weak competitor. *Quercus pyrenaica* is considered the mediating species, as its presence is associated with the occurrence of *C. laurifolius* within a study area otherwise dominated by *C. ladanifer* (Appendix S1 and Figure S1). The study area is located at the south of the Sistema Central mountain range in central Spain, at an elevation of 940–1050 m a.s.l. (40°26′ 46″N, 3°42′ 36″W). It features a continental Mediterranean climate characterized by cold winters and mild, dry summers.

Fruits of wild specimens of both *Cistus* species were collected between September and October 2022 from 10 individuals per species, randomly selected across the study area. After collection, seeds were separated from the fruits, air-dried under ambient conditions and pooled by species. Immediately before experiments, seeds were exposed to a heating treatment, 100°C during 5 min (Valbuena et al. 1992). Soils were collected from three categories based on vegetation context: areas dominated by *C. ladanifer*, soils conditioned by *Q. pyrenaica*, and an area without woody vegetation for over 50 years (see Appendix S2). To separate biotic and abiotic soil effects, subsamples were sterilized by gamma irradiation, and aqueous soil inocula were prepared from both live and sterilized soils following standardized protocols. Detailed methodological procedures are provided in Appendix S2.

3.2 | Germination Experimental Design and Analysis

To investigate soil effects on the germination of both *Cistus* species we conducted a controlled germination experiment using five soil treatments. Each treatment involved a soil aqueous inoculum derived from different soil types: (i) soil conditioned by the mediating species, (ii) soil conditioned by the locally dominant species, (iii) unconditioned control soil, (iv) sterilized soil conditioned by the mediating species and (v) sterilized soil conditioned by the dominant species. For each treatment, 10 mL of the corresponding inoculum was pipetted onto the Petri dishes before seed placement. After inoculation, 20 seeds of a single *Cistus* species were evenly distributed on a moistened filter paper. We established five replicate dishes per treatment. A total of 1000 seeds were used in the experiment (20 seeds × 5 Petri dishes × 5 treatments × 2 species). Petri dishes were incubated in a phytotron under controlled conditions (20°C, 14 h light; 16°C, 10 h dark) for 30 days (April–May 2023). Germination (radicle emergence) was recorded every 3 days, distilled water was replenished as needed, and dishes were fully randomized at each census.

Cumulative germination over time was modelled for each species and soil treatment using a three-parameter logistic nonlinear mixed-effects model (see Appendix S3), with Petri dish as a random effect. Models adequately captured sigmoidal germination patterns (median pseudo-$R^2 = 83\%$; Table S5, Figure S6) and results were consistent using the Gompertz model (Appendix S3); analyses focused on the maximum germination parameter (K), with pairwise treatment comparisons conducted using Z-tests and FDR-corrected *p*-values, excluding direct comparisons between live and sterilized soils because gamma sterilization altered soil nutrient properties (McNamara et al. 2003). All models were fitted in R (R Core Team 2025) using the *nlme* package (Pinheiro et al. 2022).

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3.3 | Growth Experimental Design and Analysis

We conducted common garden experiments to explore the effects of soil on plant growth. The experiment consisted of two steps. First, we tested the influence of three provenances of live soils on growth: (i) soils conditioned by the mediating species, (ii) soils conditioned by the dominant species and (iii) control soils. Second, we designed a cross-treatment experiment to disentangle the individual and combined effects of soil biochemistry and living microorganisms. The cross-treatment experiment consisted of a total of four treatments, in which sterilized soils of the mediating and dominant species were supplemented with aqueous live-soil inoculums of the mediating and dominant species to restore microbiological activity: (i) sterilized soil of the mediating species + aqueous inoculum of the mediating species; (ii) sterilized soil of the mediating species + aqueous inoculum of the dominant species; (iii) sterilized soil of the dominant species + aqueous inoculum of the mediating species; (iv) sterilized soil of the dominant species + aqueous inoculum of the dominant species.

In common garden experiments, pre-heated seeds were sown in sterilized 3.5 × 3.5 cm pots (five seeds per 58 cc pot), with one randomly selected seedling retained after germination. Microbiome cross-treatments were applied by adding 58 mL of soil aqueous inoculum prior to sowing. We used 20 replicates per each of the seven treatment and two species (280 individuals total), grown for 60 days (April to May) under controlled greenhouse conditions (22°C, 14 h of 230 L μmol m^{-2} s^{-1} LED lighting, 46 g m^{-3} humidity) with automated nebulized irrigation (2 min 3 times daily) and periodic pot randomization. Aboveground biomass was harvested, oven-dried (60°C, 48 h, Cornelissen et al. 2003) and weighed. Treatment effects were analysed using linear models on log-transformed biomass with Tukey-corrected marginal mean comparisons as implemented in the R package *emmeans* (Lenth 2025).

3.4 | Field Observations

We further assessed whether the experimental results align with the spatial distribution patterns of the competing shrub species relative to the mediating species observed in natural communities. For this, we performed vegetation inventories around *Q. pyrenaica* individuals within a ca. 2-ha area of the study area. Ten adult trees (average age 36.6 years, average DBH 45.9 cm, Appendix S5) were randomly selected, ensuring a minimum distance of 20 m from other *Q. pyrenaica* individuals. From the base of each selected tree, a 10 × 1 m transect was established in a random direction and subdivided into ten 1 × 1 m sections, where abundance and cover of each *Cistus* species were recorded. Variation in abundance and cover with distance from *Q. pyrenaica* was analysed using generalized additive mixed models with Poisson error distribution, a log link function, and tree identity as a random effect, implemented in the *mgcv* package in R (Wood 2011).

To explore the influence of the mediating species on soil nutrients, metabolites composition and microbial communities, we collected soil samples along the same transects. Sampling was conducted at five points along each transect, beginning at the base of the trunk (0 m) and extending up to 10 m, with a separation of 2.5 m. Soil samples were subsequently analyzed to determine their nutrient, metabolite, and microbial (bacteria and fungi) composition; detailed methodological procedures are provided in Appendix S8.

To assess differences in microbial communities, nutrients and metabolites in relation to tree proximity, we first calculated compositional distances across all soil samples. For microbial communities, we computed Jaccard distances separately for bacterial and fungal ASVs, choosing this presence/absence-based dissimilarity index to mitigate issues associated with compositional data of ASV counts (Gloor et al. 2017). We excluded taxa present in fewer than five samples, though including these taxa yielded similar results (Appendix S9 and Figure S7). For nutrients and metabolite compositional differences, we used Euclidean distances. We conducted permutational multivariate analysis of variance on compositional distances as a function of spatial distance, as implemented in the *vegan* R package (Oksanen et al. 2025), incorporating tree identity as a stratification factor. Additionally, we examined where the strongest compositional differences occurred in relation to tree proximity. Specifically, we compared the compositional distances between soil sampled directly beneath tree individuals (0 m) and all the other samples. In this case, we fitted GAMMs of compositional distances as a function of spatial distances, including tree identity as a random factor. We identified turning points as locations where the first derivative of the fitted curve crossed zero.

3.5 | Individual-Based Model

We developed an individual-based model to test whether experimentally observed soil-mediated demographic differences are sufficient to enable stable coexistence of two competing *Cistus* species. The model was implemented on a 50 × 50 lattice of 1 m^2 cells. We randomly placed 20 individuals of *Quercus pyrenaica* and assumed that their soil-conditioning effects extended homogeneously within a circular area of 4 m radius around each individual, corresponding to the maximum distance at which consistent changes in microbial communities, metabolite composition and nutrient availability were observed. A sensitivity analysis using alternative influence radii yielded qualitatively similar results (Appendix S7 and Table S4). We also randomly placed 100 individuals of each competing *Cistus* species. In cells influenced by *Q. pyrenaica*, germination and size were assigned according to estimates from *Q. pyrenaica*–conditioned soils, whereas all other cells followed estimates from *Cistus ladanifer*–conditioned soils.

Reproduction was simplified by assuming that each adult individual produced one viable seed per year. Seeds were dispersed following a negative exponential kernel, mimicking the short-range dispersal of the genus (Bastida and Talavera 2002). Germination occurred only when local density did not exceed the carrying capacity (2 individuals m^{-2}), preventing unbounded population growth. Germination probabilities were

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drawn annually from species × soil–specific uniform distributions bounded by experimental 95% confidence intervals (Table S4).

We assumed that soil effects on survival are mediated through plant size following Andivia et al. (2021). Plant size values were drawn from species × soil–specific uniform distributions based on experimental measurements, using the same 95% confidence intervals. Survival was then modelled as size-dependent following a logistic function:

$$P_s(\text{size}) = \frac{1}{1 + e^{-(x+y\,\text{size})}}$$

where $x = 1.386$ yields a basal survival probability of 0.8, consistent with the observed longevity of *Cistus* species (Oria-de-Rueda et al. 2008). The parameter y modulates the effect of plant size on survival; $y = 0$ implies size-independent survival, while higher values increase the positive effect of size. Senescence was implicitly included, as individuals were removed from the lattice once annual survival draws failed. Because the size–survival relationship is unknown, we explored 21 values of y (0–2, step = 0.1). For each competing species and soil type, annual survival probabilities were drawn from uniform distributions bounded by the logistic predictions within experimentally observed size ranges (Table S3).

For each value of the size–survival parameter y, we ran 25 simulations of 100 years. All model specifications are detailed in Table S6. We selected the value of y that produced simulated spatial abundance patterns most similar to those observed in the field (Appendix S6 and Figure S5). Under this parameterization, we then assessed whether both competing *Cistus* species persisted and maintained stable population sizes, which we interpreted as evidence of stable coexistence. See Appendix S6 for a detailed explanation of the simulations and analyses of model output.

Author Contributions

E.A. and J.C. conceived the ideas and designed the experiments, with inputs from J.M.-G., E.A. and J.C. conducted the fieldwork and experiments. E.A. carried out the analyses with assistance from J.C. and input from R.B.-M., M.A.F.-M. and M.C., E.A. led the writing of the manuscript with support from J.C. All authors read and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code supporting the results are archived in Zenodo and are available at: https://doi.org/10.5281/zenodo.17347340. (Antorán et al. 2025).

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Biogeographic and landscape vegetation context of the study system. **Appendix S2:** Soil collection, sterilization and aqueous inoculum preparation. **Appendix S3:** Sensitivity analysis germination models. **Appendix S4:** Nutrient variation with distance from the mediating species. **Appendix S5:** Assignment of age values to *Quercus pyrenaica* individuals. **Appendix S6:** Specification of the Individual-Based Model and simulation parameters. **Appendix S7:** Sensitivity analysis on the soil conditioning radius. **Appendix S8:** Soil sampling design and nutrient, microbial and metabolomic analyses. **Appendix S9:** Sensitivity analysis of microbial community composition. **Table S1:**. Pairwise comparisons of the fitted K parameter for germination probability using *Z*-test with FDR correction for the Logistic growth and Gompertz models. Comparisons were conducted for *Cistus ladanifer* and *Cistus laurifolius* germination under live soil and sterilized soil treatments: (CS) control soil, (DS) dominant specie' (*C. ladanifer*) soil, (MS) mediating species' (*Quercus pyrenaica*) soil, (SDS) sterilized dominant species soil and (SMS) sterilized mediating species soil. The *Z*-stat refers to the *Z*-statistic from the pairwise comparisons of model parameters. The *P* (FDR) shows the *p*-values adjusted using the FDR correction to control for multiple testing. **Table S2:**. Post hoc Tukey comparisons from linear models assessing soil treatment effects on aboveground dry biomass of *C. ladanifer* and *C. laurifolius*. To denominate the treatments we use: (CS) Control soil; (MS) Mediating-species (*Quercus pyrenaica*) soil and (DS) Dominant-species (*Cistus ladanifer*) soil, (MMb) Mediating-species microbiome and (DMb) for Dominant-species microbiome. **Table S3:** Results of increasing the effect of size on survival probability. Simulations were conducted by varying the effect of size on survival probability (y) from 0 to 2, in increments of 0.1. Results are presented for both *Cistus laurifolius* and *Cistus ladanifer*. The root mean square deviation (RMSD) quantifies the mismatch between observed and predicted abundance patterns, averaged across both species. Stability was assessed based on the statistical significance (P) of the relationship between abundance and time over the final 20 years of each simulation. DS.Surv.Range and MS.Surv.Range indicate the ranges of survival probabilities in soils conditioned by the dominant species and the mediating species, respectively, for both shrub species. ΔSurv.Prob represents the difference between the mean survival probability in soils conditioned by the mediating species and that in soils conditioned by the dominant species. Values shown in bold correspond to $y = 0.8$, the point at which simulated spatial patterns most closely matched the observed patterns. This value—corresponding to an increase of just 0.08 in the survival probability of *C. laurifolius* in soils conditioned by the mediating species compared to those conditioned by the dominant species—was sufficient to promote stable coexistence in the simulated communities. **Table S4:** Results of the sensitivity analysis on the soil-conditioning radius. Simulations were run using conditioning radii from 1 to 6 m. For each radius, five replicate simulations were performed across values of the survival-conditioning parameter (y) from 0.1 to 2.0 (step = 0.1), except for radius = 4 m, for which we report the 25 replicates used in the main text. Δ Surv.Prob represents the difference between the mean survival probability in soils conditioned by the mediating species and that in soils conditioned by the dominant species for *C. laurifolius* (ΔSurv. Prob Weak) and *C. ladanifer* (S ΔSurv. Prob Dominant). Stab. indicates community stability (Y = stable, both *Cistus* species show no significant temporal trends during the final 20 simulated years, $p > 0.01$; N = unstable). RMSD values quantify the mismatch between observed and simulated abundance–distance patterns. Bold values denote, for each radius, the combination that achieves both the lowest RMSD and stable coexistence. **Table S5:**. Results of nonlinear regression models (Logistic growth and Gompertz model) for germination of *C. ladanifer* and *C. lauriflolius*, with all treatments: (CS) control soil, (DS) dominant-species (*C. ladanifer*) soil, (MS) mediating-species (*Quercus pyrenaica*) soil, (SDS) sterilized dominant-species soil and (SMS)sterilized mediating-species soil. The table reports the coefficient of determination (R^2), the estimated maximum germination proportion (K), the standard error (SE) of K and the 95% confidence intervals (95% CI). The 95% CIs estimated from the logistic model were used to define the range of germination probabilities in the simulations. **Table S6:** Parameters and structural assumptions of the individual-based model. **Figure S1:** Vegetation composition in shrublands and deciduous forest patches. *C. ladanifer* dominates shrublands, while *C. laurifolius* is commonly associated with *Q. pyrenaica* in deciduous forest patches. Bars represent the mean cover of woody species and the 95% confidence interval. (A) Shrublands are nearly monospecific, predominantly dominated by *C. ladanifer* (green). In contrast, (B) deciduous forest patches exhibit greater species diversity. **Figure S2:** Nutrient variation with distance from the mediating species. Panels show the variation in different soil nutrients with distance from the *Q. pyrenaica* tree. (A) Carbon, (B) Nitrogen, (C) Phosphorus, (D) pH, (E) Conductivity, (F) Nitrates, (G) Phosphates, (H) Ammonium. Adjusted R^2, F statistics and p-values are also provided. **Figure S3:** Distance-dependent shifts in soil biochemistry, microbial communities and shrub distribution around the mediating species, with associated litter cover. The presence of the mediating species (*Quercus pyrenaica*) significantly alters the composition of nutrients (A), metabolites (B), bacteria (C), fungi (D) and the spatial distribution of the competing shrub species (E) (see Figure 3). Solid lines show predictions from generalized additive mixed models of compositional dissimilarity between samples collected at zero distance from individuals of the mediating species and those collected farther away, as a function of distance. Shaded areas represent 95% confidence intervals. Litter cover was measured as the percentage of ground surface covered by leaf litter in each 1 m^2 plot, simultaneously with counts of *Cistus ladanifer* and *C. laurifolius* individuals along 10 × 1 m transects (see Methods: Field observation). Values are normalized to the maximum observed within each panel. Litter cover is shown in black, with shaded areas representing 95% confidence intervals. Predictions for litter cover are based on a generalized additive mixed model with a binomial error distribution and a logit link function ($R^2 = 65.7\%$; $F = 23.32$; $p < 0.01$). These results indicate that the areas where compositional changes occur are largely covered by tree litter. **Figure S4:** The presence of the mediating species alters the spatial distribution of the competing shrub species. Predicted spatial distribution of the cover (per 1 m^2) of the dominant (green; $R^2 = 29.3\%$, $F = 280.1$, $p < 0.01$) and the weak (blue; $R^2 = 7.64\%$, $F = 150.7$, $p < 0.01$) competitor species as a function of distance from individuals of the mediating species. Solid lines show the fitted values

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from generalized additive mixed models (GAMMs), with shaded areas indicating 95% confidence intervals. GAMMs were fitted using a Poisson error distribution and a log link function and included as a random the identity of *Quercus pyrenaica* individuals. **Figure S5:** Root mean square deviation (RMSD) between simulated and observed spatial abundance patterns as a function of increased survival probability of the weak competitor in soils conditioned by the mediating species. Each point represents the RMSD between simulated and empirical spatial abundance patterns for a given increase in the survival probability of the weak competitor (*Cistus laurifolius*) in soils conditioned by the mediating species (*Quercus pyrenaica*), relative to those conditioned by the dominant species (*C. ladanifer*), averaged across 25 simulation replicates (see ΔSurv.Prob. in Table S2). Lower RMSD values indicate a closer match between simulation outputs and observed field patterns. Red points denote parameter combinations that result in unstable species coexistence, while black points correspond to scenarios where stable coexistence is maintained. **Figure S6:** Accumulated germination proportion over time. Panels (A)–(F) represent live soil treatments, and Panels (G)–(J) represent sterilized soil treatments. Specifically: (A, B) control soil, (C, D) dominant species' (*Cistus ladanifer*) soil, (E, F) mediating-species (*Quercus pyrenaica*) soil, (G, H) sterilized dominant species' soil and (I, J) sterilized mediating-species soil. Within each pair, germination of *Cistus ladanifer* is shown on the left, and *Cistus laurifolius* on the right. Solid lines indicate the mean germination predictions from mixed-effects logistic models, while shaded areas denote the standard errors. **Figure S7:** Dissimilarities in bacterial and fungal community composition as a function of distance to the tree. Sensitivity analysis of community dissimilarities without excluding taxa occurring in fewer than five samples for (A) bacterial and (B) fungal communities. Solid lines show predictions from a generalized additive mixed model of compositional dissimilarity between the sample collected at zero distance from individuals of the mediating species and samples collected farther away, as a function of distance. Shaded areas represent 95% confidence intervals. The vertical dotted lines indicate the inflection point in compositional dissimilarities.

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