

Research Article

Do good neighbours compensate for bad climate? The case of sessile oak *Quercus petraea* in phylogenetically distant neighbourhoodsKeliang Zhang^{1,2}, Vincent Jung², Maud Deniau², Benjamin Yguel², Benoît Béchade³, Soumen Mallick^{2,4}, Miguel Verdú⁵ and Andreas Prinzing²¹College of Horticulture and Landscape Architecture, Yangzhou University, Yangzhou, China²Research Unit “Ecosystem, Biodiversity, Evolution”; Université de Rennes/Centre National de la Recherche Scientifique; Campus de Beaulieu, Rennes, France³Department of Biology, The University of Texas at Arlington, Arlington, TX, USA⁴Field Station Fabrikshleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Rauhenebrach, Germany⁵Department of Ecology, Centro de Investigaciones sobre Desertificación (CIDE-CSIC), Moncada, Valencia, Spain

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Oikos

2026: e12734

doi: 10.1002/oik.12734

Subject Editor: Dylan Craven

Editor-in-Chief: Pedro Peres-Neto

Accepted 15 August 2026



www.oikosjournal.org

Stressful climates threaten the performance of individuals and the survival of species, but individual performance also depends on biotic interactions with neighbours, so that ‘good’ neighbours might in theory compensate for ‘bad’ climates. However, what makes a good neighbour, and why, has been little studied. We hypothesize that phylogenetically proximate neighbours either interact positively (by sharing mutualists), thereby helping to resist climate stress, or they interact negatively (by sharing enemies or competing), thereby reducing resistance. We studied seed germination, juvenile growth, and adult phenology of sessile oaks *Quercus petraea* and how they respond to microclimatic stress in phylogenetically proximate and distant neighbourhoods, manipulating offspring-density, the presence of insects and fungi, and spatial proximity to oaks. We found that juvenile oaks were more resistant to drought stress when growing in phylogenetically distant neighbourhoods. Also, the budburst delay in adults in phylogenetically distant neighbourhoods disappeared under drought. In contrast, under drought, seeds germinated better in the presence of conspecific adults. Most importantly, under humid or cold conditions, phylogenetically proximate neighbours were more favourable in multiple ways. Differences in resistance to microclimate-stress among phylogenetically proximate and distant neighbourhoods reflect the activity of fungi, insects, or the interaction with conspecific adult neighbours, i.e. differences disappear once the pertinent factor is experimentally excluded. These interactive effects were mostly stronger than the main effects of microclimatic variables and phylogenetic distance. Effects of phylogenetic distance were partly replaceable by the percentage of gymnosperms. We suggest that under the increased temperature and decreased precipitation due to climate change, oak regeneration may profit from a phylogenetically distant neighbourhood, partly in the presence of a spatially proximate conspecific. At the same time, such warmer and drier conditions eliminate the advantages that oaks

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have from a phylogenetically proximate neighbourhood, potentially contributing to an erosion of phylogenetic niche conservatism under climate change.

Keywords: climate change, mutualist, phenology, phylogenetic isolation, tree regeneration in temperate forests

Introduction

Global climate change translates into increasingly stressful microclimates that threaten the performance of individual plants and the survival of species (Corlett and Westcott 2013, for forest trees: Cheaib et al. 2012, Mina et al. 2022, Xu et al. 2023). Besides microclimate, individual performance also depends on biotic interactions – such as competition with neighbouring plants, pressure from enemies and support from mutualists – all of which are influenced by or shared with neighbours (Kennedy 2010, Deniau et al. 2017, Lebrija-Trejos et al. 2023). In theory, microclimatic stress might be compensated by neighbours that favour positive, or prevent negative, biotic interactions. Such neighbourhood effects could, in theory, help to maintain native tree species under climate change. However, it has been little studied what makes such a ‘good’ neighbour, and through which interactions it may compensate for microclimatic stress.

Biotic interactions might be more frequent among neighbours characterised by similar functional traits (Prinzing et al. 2017, Ploughe et al. 2019). In forests, traits related to biotic interaction are often evolutionarily conserved (Prinzing et al. 2021, see also Tucker et al. 2018), such as traits related to interactions with competitors (Yang et al. 2014, but see Kunstler et al. 2012), traits enabling interactions with mycorrhizal fungi (Strullu-Derrien et al. 2018), and traits involved in defences against herbivores (Gilbert et al. 2015). Trees in a phylogenetically proximate neighbourhood (i.e. composed of conspecifics or phylogenetically proximate species) might hence benefit from stronger mutualist support than in a phylogenetically distant neighbourhood (e.g. reversed Janzen–Connell effect, Zahra et al. 2021), or suffer from stronger enemy or competition pressure (e.g. phylogenetic Janzen–Connell effect, Liu et al. 2012, Staab et al. 2021). Thus, our overall alternative hypotheses are that resistance to microclimatic stress increases in a phylogenetically proximate neighbourhood due to increased mutualist support, or, alternatively, decreases due to increased competition or enemy pressure. We develop this overall hypothesis below.

On the one hand, trees in a phylogenetically proximate neighbourhood might interact positively by sharing mutualists, thus improving the trees’ ability to resist a stressful microclimate. For a given host, mycorrhizae can significantly improve its water uptake (Smith and Read 2008), increase its water use efficiency (Garcia et al. 2016), bolster its anti-oxidant defences (Smith and Read 2008), and induce its systemic resistance to pathogens and herbivores (Koricheva et al. 2009, Cameron et al. 2013). These benefits are particularly pronounced under microclimatic stress (i.e. stress gradient hypothesis) (Compant et al. 2010, Tedersoo et al. 2020).

Trees or seedlings might share common mycorrhizae through an extended network of hyphae that connect several different host plants (Yguel et al. 2014a, Laliberté 2017, Tedersoo et al. 2020), especially among phylogenetically proximate adults (Tedersoo et al. 2013, Hoeksema et al. 2018, Rog et al. 2020) and seedlings (Deniau et al. 2018). Therefore, our first hypothesis (H1) is that phylogenetically proximate tree neighbours interact positively by sharing mutualists, which may help trees in such a neighbourhood to better resist climate stress (Fig. 1).

On the other hand, phylogenetically proximate tree neighbours are usually more similar in ecological requirements than phylogenetically distant neighbours (Prinzing et al. 2017, 2021). As a result, phylogenetically proximate neighbours might compete strongly (Violle et al. 2011, Montesinos-Navarro et al. 2019). Trees in a phylogenetically proximate neighbourhood might, for example, have access to less soil water (Pretzsch et al. 2013, Manoli et al. 2014, Deniau et al. 2017) or soil nutrients (Deniau et al. 2018), increasing their vulnerability to microclimatic stress. In other words, there may be a trade-off between investment into competition and into resistance against microclimatic stress (Grime 2001, Prinzing et al. 2017). In addition, compared to phylogenetically distant neighbours, phylogenetically proximate neighbours are more likely to share enemies and diseases, including phytophagous insects and fungal pathogens (Yguel et al. 2014b, Jactel et al. 2021, but see Molleman et al. 2022). Pressure from enemies can reduce the resistance of a host to various types of stress, including stress from climatic change (Prinzing et al. 2017, Vanhellemont et al. 2019), by triggering direct or indirect defences against enemies (Cusumano et al. 2015, Erb 2018, Gely et al. 2020), which may often be costly (Koricheva et al. 2009, Tack et al. 2012, Prinzing et al. 2017). Therefore, our second hypothesis (H2) is that phylogenetically proximate tree neighbours interact negatively through competition and shared antagonists, which may reduce the ability of trees in such a neighbourhood to resist climate stress (Fig. 1).

Overall, H1 predicts increased climate-stress resistance in a phylogenetically proximate neighbourhood, while H2 predicts the inverse. Both effects should disappear when biotic interactions are suppressed. To our knowledge, these hypotheses on the effect of phylogenetic neighbourhood on resistance to microclimatic stress have only partly been tested so far. What is well established is that plants may facilitate each other (Bertness and Callaway 1994, Gómez-Aparicio et al. 2004, Valiente-Banuet and Verdú 2007, Verdú et al. 2009), including by reducing pressure from (rather than resistance to) microclimatic stress or enemies (Gómez-Aparicio et al. 2008, Graff and Aguiar 2011). Also, the fact that the

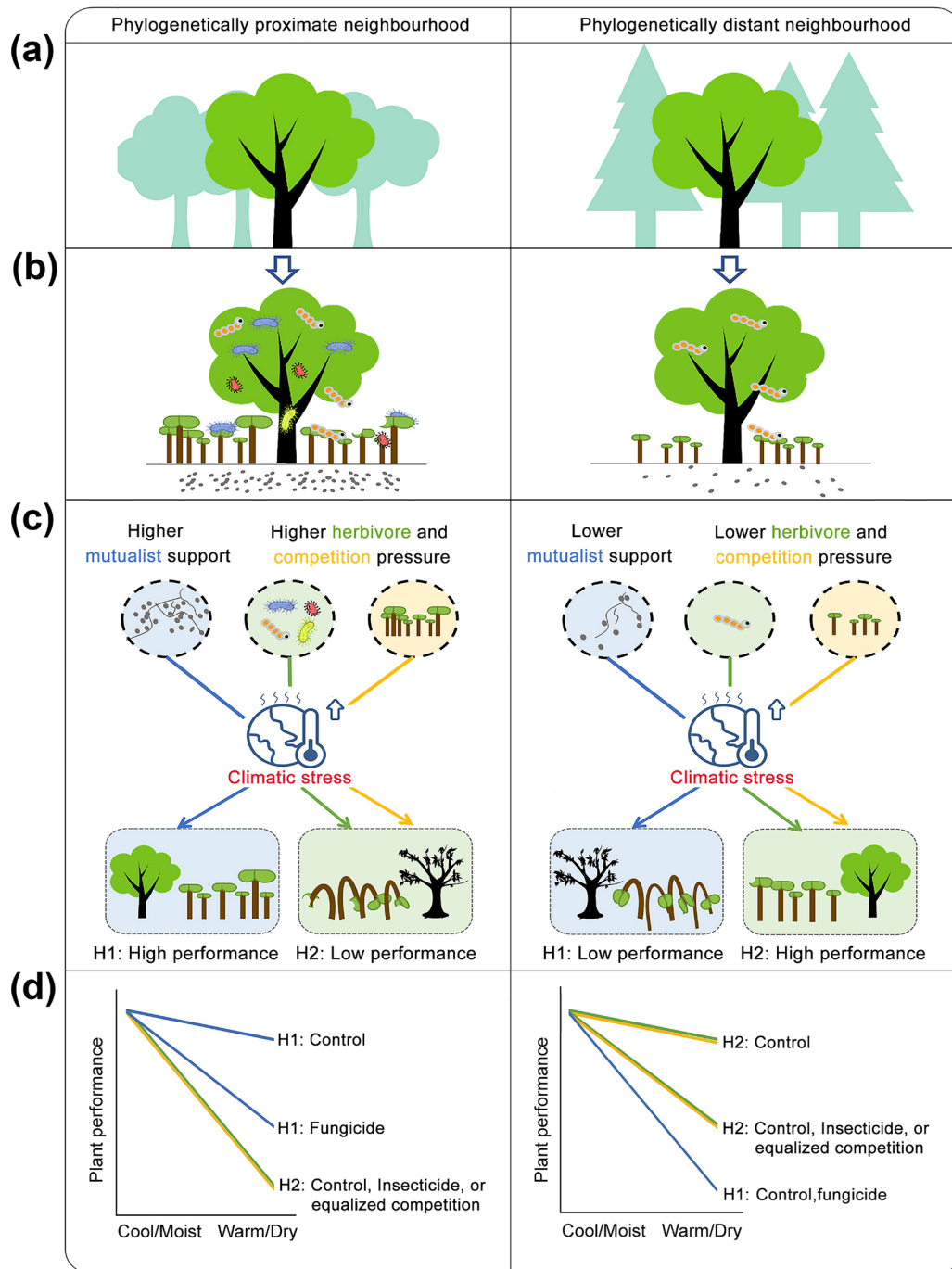


Figure 1. How (a) phylogenetic distance of neighbourhoods affects (b) biotic interactions; (c) adult and seedling performance under climate change (our hypotheses); and (d) our predictions. (a) Illustrates phylogenetically proximate and distant neighbourhoods. (b) A phylogenetically proximate neighbourhood increases support from mutualists such as mycorrhizae, pressure by insect herbivores, and competition from close relatives. (c) We hypothesize that under H1, a focal tree and seedlings might benefit from a conspecific or phylogenetically proximate neighbourhood due to shared mutualists, which may help them to better tolerate harsh and changing environments. Under H2, however, a focal tree and seedlings might also suffer from a conspecific or phylogenetically proximate neighbourhood due to high competition pressure from such neighbours, and likely an extensive sharing of enemies and diseases, which may reduce the tolerance of the host to climatic stresses. (d) We predict that under H1, increased support from mutualist mycorrhizal fungi in phylogenetically proximate neighbourhoods will permit increased performance under climatic stress effects than in phylogenetically distant neighbourhoods. Fungicide application will reduce this relative advantage under climatic stress in a phylogenetically proximate neighbourhood. Inversely, for H2, we predict that under control conditions, reduced pressure from insect herbivores or competitors in phylogenetically distant neighbourhoods will permit increased performance under climatic stress compared to phylogenetically proximate neighbourhoods. Equalized competition or insecticide application will reduce this relative advantage under climate stress in a phylogenetically distant neighbourhood.

performance of plants may depend on phylogenetic neighbourhood is established (Webb et al. 2002, Valiente-Banuet and Verdú 2007, Hill and Kotanen 2009, Castillo et al. 2010, Liu et al. 2012, Montesinos-Navarro et al. 2012, Navarro-Cano et al. 2016). However, it remains unknown whether the performance of a given species in the field under the same microclimatic stress depends on the phylogenetic proximity of its neighbours, and whether biotic interactions might explain this biotic resistance.

We tested the above hypotheses on one of the major forest trees across much of Europe, sessile oak *Quercus petraea*. Sessile oak often suffers from climatic stress and the sustainability of growing oaks is discussed in multiple regions (Cheaib et al. 2012). In addition, sessile oak is attacked by numerous enemies (Southwood et al. 2004, Yguel et al. 2011), faces competition (Ligot et al. 2013, Deniau et al. 2017), and strongly depends on mycorrhizal associations (Yguel et al. 2011, 2014a), all of which depend on the phylogenetic proximity of the neighbourhood (Yguel et al. 2011, 2014a, Deniau et al. 2017, 2018, 2021). We benefit from the fact that, at a given moment, microclimates may vary in space across a forest to a similar extent as predicted variation in time across the next decades (Lal and Stewart 2018), to some extent allowing the replacement of space with time (Blois et al. 2013, Roberts et al. 2017). We measured the performance of sessile oak across a gradient of soil temperature and humidity at three crucial developmental stages: 1) at the seedling stage: high seed germination, 2) at the juvenile stage: low leaf herbivory (ca one-year-old seedlings), a major predictor of juvenile survival (Wada et al. 2000, and in our study system: Deniau et al. 2017), and 3) at the adult stage: a long vegetation period, and an early timing of budburst, which may increase competitiveness (Chapin et al. 2011) and possibly decrease herbivore attack (Tikkanen and Julkunen-Tiitto 2003, but see Mallick et al. 2025). To assess these performances, we experimentally exposed standard seeds and juveniles to canopies dominated by species phylogenetically proximate or distant from sessile oak, and recorded the phenological performance of adult oaks growing with phylogenetically proximate or distant neighbours. We also manipulated the biotic interactions by which neighbourhoods affect performance: 1) intraspecific competition (seed density) and vulnerability to such competition (seed size), 2) abundance of insect herbivores, and 3) availability of fungi (Fig. 2). In adults, manipulation of biotic interactions was not feasible; we therefore quantified these interactions in the field and accounted for them in further analyses. Finally, we also explored the extent to which the effect of phylogenetic proximity in our study is lineage-specific, i.e. reflects a high percentage of gymnosperms (an important determinant of phylogenetic distance in temperate forests, Yguel et al. 2011), or can be explained by other environmental variables.

We predicted that the effect of microclimate on tree performance would depend on its phylogenetic neighbourhood (i.e. significant 2-way interaction terms between neighbourhood and heat or drought). We also predicted that differences in resistance to microclimatic stress would depend on biotic

interactions (i.e. significant 3-way interaction terms between neighbourhood, heat/drought, and biotic interactions). More specifically, we predicted in H1 that interactions with mutualistic mycorrhizal fungi in phylogenetically proximate neighbourhoods would compensate for the negative effects of drought or heat on performance (Fig. 1d). In other words, oaks growing in a phylogenetically proximate neighbourhood would be less vulnerable to drought or heat, resulting in higher seed germination, lower juvenile herbivory damage, earlier adult budburst and a longer adult vegetation period. If the effect of phylogenetically proximate neighbourhood was indeed due to mycorrhizal fungi, the application of fungicide would make the performance of seeds/seedlings decline under heat and drought even in a phylogenetically proximate neighbourhood (Fig. 1d). Conversely, we predicted in H2 that interactions with insect herbivores or competitors in a phylogenetically proximate neighbourhood would amplify the negative effects of drought or heat on tree performance (Fig. 1d). In other words, oaks growing in a phylogenetically proximate neighbourhood would suffer more from drought or heat, resulting in lower seed germination, greater juvenile herbivory damage, delayed adult budburst, and a shorter adult vegetation period. Application of insecticides or imposing equal competition in all neighbourhoods would make this difference between neighbourhoods disappear (Fig. 1d).

Material and methods

Study site

We studied the forest of Rennes, Brittany, France (3000 ha, 48°12'N, 01°33'W, ca 90 m a.s.l.). The area has an oceanic climate with a mean annual temperature of 11.3°C. The entire forest is located on the same acidic bedrock (shale) and spans a small total altitudinal range of 60 m (Supporting information). Differences in canopy composition are likely related to forest disturbances and management legacies dating back at least 80 years (Supporting information). Importantly, with an average annual precipitation of 660 mm, the site is towards the dry end of the macroclimatic distribution of sessile oak (644 mm, Bergès et al. 2005). Locally, humidity is further limited by a dense drainage system (Préfecture d'Ille-et-Vilaine et al. 2010). As elsewhere, in the study area, temperatures increased during recent decades, increasing hydric deficits continuously (Centre Régional de la Propriété Forestière Bretagne – Pays de la Loire 2019), resulting in signs of stress of sessile oak from heat and drought (CNPFF and CRPF 2018–2021).

We selected a total of 11 pairs of focal adult oak trees (*sensu* Petit et al. 2004) from across the forest in 2012, according to availability at short within-pair distance (these paired oaks were separated by spatial distances of <150 m) and spread across the forest (also used by Yguel et al. 2011, 2014a, 2014b, Deniau et al. 2018, 2021) (see the Supporting information for the detailed locations). All focal trees were in a continuous forest canopy. The diameter at breast height of focal trees was 14–32 cm (mean: 22 cm, SD: 5.8 cm),

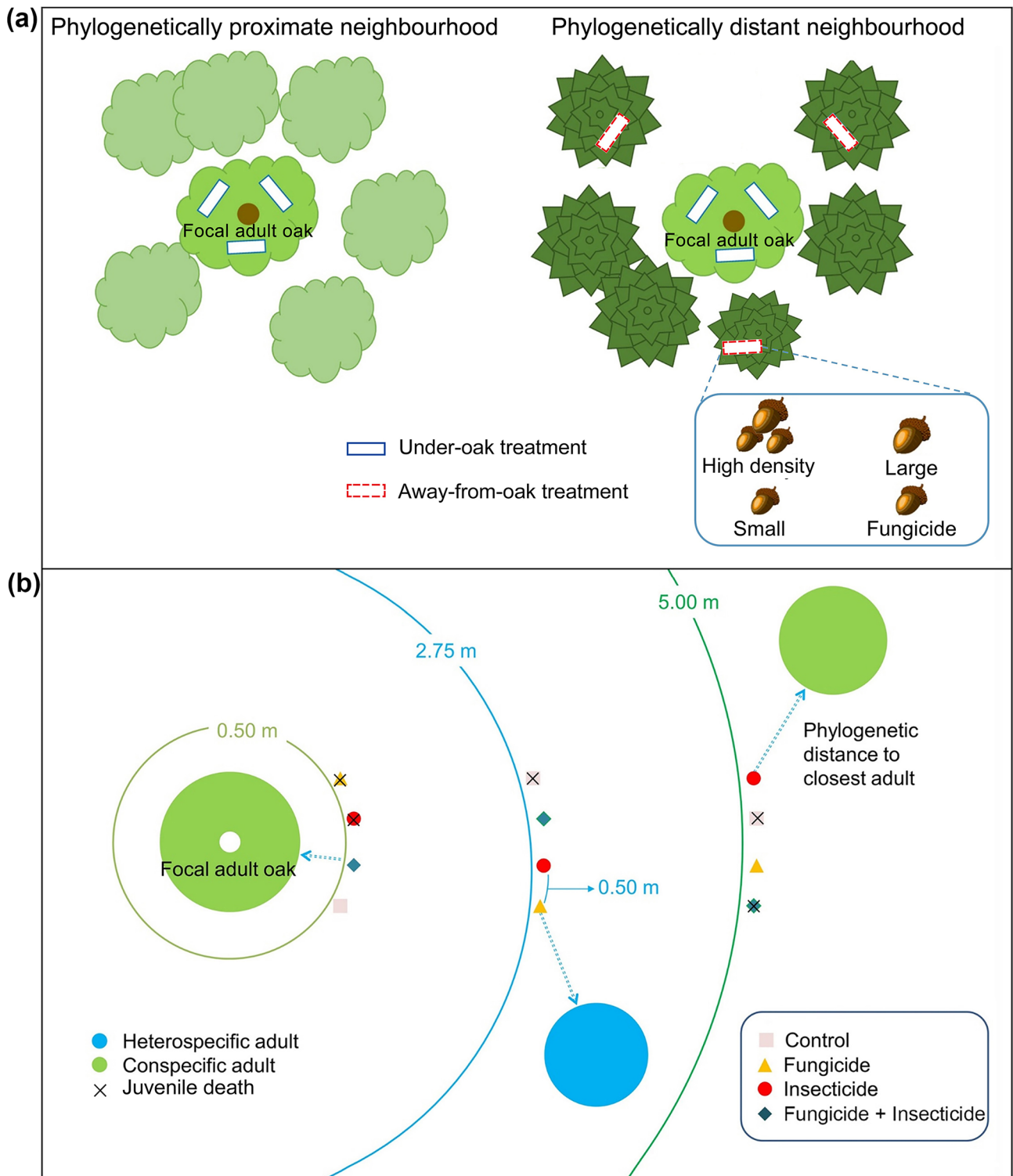


Figure 2. Experimental design for: (a) seed germination, and (b) juvenile growth, established for 22 and 20 focal oaks, respectively, in neighbourhoods ranging from phylogenetically proximate to distant (see the Supporting information for species names of neighbouring trees). (a) Seed germination: germination stages were recorded across four months. To avoid pseudoreplication, multiple seeds undergoing the same treatment for the same tree were averaged. (b) Juvenile growth: herbivory was recorded across 4.5 months. An initial treatment of spatial distance to the focal oak failed due to large immediate mortality ('juvenile death'), and resulted in some juveniles being closer to a tree other than the focal tree. We hence recorded the phylogenetic distance to the closest tree. Note that the focal trees in (a) and (b) were those used for the (non-experimental) study of adult phenology.

equivalent to adult age (Steele et al. 2007). In each pair, the focal oaks had similar size, age and circumference. In each pair of oaks, one tree had more phylogenetically proximate neighbours while the other had more phylogenetically distant neighbours (see the Supporting information for the species names of neighbouring trees). This blocked design helped to control for variation among pairs due to different macro-environments (Legendre et al. 2004).

We took phylogenetic distances between tree species from Vialatte et al. (2010, also used by Deniau et al. 2017, 2018, 2021 and Yguel et al. 2011, 2014a, 2014b). We calculated the mean phylogenetic distance to all neighbouring trees in direct contact with the focal oak's crown, following Yguel et al. (2011) and Deniau et al. (2021) (Supporting information). We note that calculating phylogenetic distance to trees within a larger radius (e.g. all tree species within 10–30 m of the focal oak's trunk) does not yield better model fit and results (Supporting information), as also supported by previous studies (Zhang et al. 2025). Overall, mean phylogenetic distance between a tree and its in-contact neighbours ranged from 10 to 125.66 million years (Myr, median = 51.0278).

As explained, within a pair of focal oaks the mean phylogenetic distances from respective neighbours were very different. Nevertheless, across all focal oaks, the mean phylogenetic distance from neighbours covered a continuous gradient, with focal trees having more phylogenetically proximate and distant neighbours showing mean ($\pm$ SD) phylogenetic distances of 23.04 ± 13.16 Myr (range: 10.00–54.56 Myr) and 87.49 ± 25.14 Myr (range: 47.50–125.67 Myr), respectively. So, in a given pair, the focal oak with more phylogenetically distant neighbours could still be relatively phylogenetically proximate across all focal oaks (i.e. phylogenetic distance $\leq$ overall median), and vice versa. The 'spatial distance' treatment was therefore available across a wide range of phylogenetic distances.

Field studies

We studied seed germination, juvenile growth, and adult phenology through three discrete experiments (Fig. 2). Note that the protocols for different life stages were inevitably partly inconsistent. The overall aim was not to make direct comparisons among life stages or among treatments; instead, we searched for consistent patterns in the effects of phylogenetic distance on seed, juvenile and adult performance depending on microclimate variables and biotic interactions.

Seed germination

Seed collection and pre-treatment

In late October 2012, freshly matured acorns (hereafter 'seeds') of oak trees were collected from two mature neighbouring trees (as they produce more seeds than trees inside forests). Because oak seeds typically have epicotyl physiological dormancy at maturity (Baskin and Baskin 2014 for sessile oak), the collected seeds were cold-stratified at 5°C for two months before sowing on 31 January 2013. All seeds used for sowing were viable: they showed signs of initial germination

with the root visibly emerging below but not yet penetrating the pericarp.

Exposure of seeds and experimental treatment in the field

We exposed 540 available seeds to field conditions in late January 2013. For each of the chosen focal adult oaks, three sets of six seeds were placed on the litter under the crown of each focal oak (Fig. 2a), 1–2 m away from the trunk. Each six-seed set was covered by a plastic cage (size $33 \times 14 \times 6$ cm; closed on the sides, with 2 cm wire mesh on top) fixed to the ground to minimise access by ungulates and rodents, as ungulates can destroy such an experiment within seconds and rodents can remove all seeds from our study site within a few days (Deniau et al. 2021, Zhang et al. 2025). In addition, for the focal tree in a phylogenetically more distant neighbourhood within each pair, another three sets of 6 seeds were placed on the litter, i.e. outside the area covered by the focal oak-crown at 7 m distance from the focal tree (Fig. 2a), but still under the crown of phylogenetically distant species (spatial distance treatment). This spatial distance treatment permitted us to separate the effects of phylogenetic distance and spatial distance from an adult oak (Janzen–Connell effect, Liu et al. 2012, Deniau et al. 2018) and to determine how the two interacted. For the focal oak with more phylogenetically proximate neighbours within each pair, such a spatial distance treatment was not possible, because moving away from the focal oak would have resulted in moving closer to a non-focal oak. Nevertheless, for the oaks in the phylogenetically more distant neighbourhood, phylogenetic distances of neighbours still ranged from intermediate to maximum, allowing us to tease apart phylogenetic distance from spatial distance to oak in later analyses. Seeds (and older seedlings, 'juveniles' as defined below) exposed in different neighbourhoods had been collected from the same sources, so that neighbourhood was not confounded with genetic identity of the seeds (and juveniles).

Within each group of six seeds, three alternative treatments were applied (Fig. 2a): 1) density treatment (three seeds in direct contact across ca 25 cm² for high density versus one seed for low density), to assess the effect of competition (high seed density may increase the likelihood of pathogen infestation and inhibit seed germination through allelopathic compounds released by seeds, Baskin and Baskin 2014). We note that the natural density gradient ranges from 0 seeds to full coverage in a masting year (Zhang et al. unpubl.). Our design hence captures a broad range of density conditions relevant to competition and seed germination; furthermore, previous studies (Zhang et al. 2025) and the later analysis of the present study indeed found a negative effect of high density (three seeds) on seedling survival. 2) Fungicide treatment (one seed received 10 ml 1% Bordeaux-mixture solution based on the operating instructions of the manufacturer versus all other seeds receiving 10 ml water), to assess the effect of mutualistic or pathogenic fungi (Dalla Rosa et al. 2017 found that such a low concentration will not affect seedling survival). 3) Seed-size treatment, i.e. one relatively large seed (mean $\pm$ SD:

4.5443 $\pm$ 0.4352 g) versus one small seed (mean $\pm$ SD: 3.0472 $\pm$ 0.5609 g). Seed-size treatment permitted us to assess the effect of seed storage reserves, which increase the seed germination success, and subsequent competitiveness (Leck et al. 2008, Baskin and Baskin 2014). Note that precise seed masses ($\pm$ 0.001g) were recorded for all seeds and used in further analyses. For each tree, a given treatment (e.g. 'below crown-high density') within each of the three groups was averaged to avoid pseudoreplication in the subsequent analyses (Fig. 2a).

We applied no insecticide treatment in the present study of seed germination as studying the effects of insects on the advancement of germination is hardly practical: Insect-attacked seeds seldom germinate (Baskin and Baskin 2014), and those that do would be too few to permit sufficient statistical power to identify a signal of microclimate variables, phylogenetic distance, treatments, or their combination in insect-attacked seeds. We hence selected only unattacked seeds.

Monitoring of seed performance and microclimate variables

For each seed, we recorded germination stage every two weeks over four months. The scale of germination stages was designed to reflect the biological significance and progression of each stage (Baskin and Baskin 2014). Clearly defined stages are: 0, no germination, i.e. as deposited (root developing below the pericarp but not yet penetrating); 1, germination, i.e. root fixed in the soil; 2, stem established. Additionally, we assigned a transitional stage of 0.5 when the root had penetrated the pericarp but had not yet reached the soil (Baskin and Baskin 2014).

In addition, we measured the soil humidity and soil temperature within 1 m from the trunk of each focal oak using a WET sensor (WET-2, AT-Delta-T Devices) from March to April before budburst of adults (averages in the Supporting information). This early timing of measurements reduced the risk of abiotic conditions just being an indirect effect of neighbourhood budburst and ensured that humidity conditions rather reflected the microrelief of the soil surface, which remained constant throughout the study period. We also measured soil pH (pH-H₂O) using a hand-held pH meter 3110 Set2 and a sensor SenTix FET-D (WTW GmbH-Xylem), as gymnosperm neighbours tend to decrease soil pH (Augusto et al. 2015). Measurements taken at one instant obviously did not capture the seasonal or diurnal variation in precise levels of humidity or temperature at a given locality, but they did permit us to characterize spatial patterns in relative variation of humidity and temperature, as these patterns remained relatively stable through time (Kang et al. 2000). Moreover, variation among tree pairs could be accounted for in later analyses by including tree pair as a random factor. We note that among these three variables during the germination study, only soil humidity was partially related to phylogenetic distance ($r = -0.195$, $p < 0.05$). However, subsequent regression models testing effects of phylogenetic isolation were not biased by this minor covariation with microclimate (Supporting information).

Juvenile growth

Juvenile harvesting and pretreatment

In early March 2014, we harvested 240 oak juveniles (ca one-year-old) from the more phylogenetically proximate neighbourhoods (as juveniles were rare in the more phylogenetically distant neighbourhoods), following established procedures of Deniau et al. (2021). The harvested juveniles were about the same height, morphologically similar, without a seed attached, lacked visible damage, and had intact buds. Harvested juveniles were gently washed to remove any insect eggs or potential infestations. All fine roots of juveniles were cut as close as possible to the taproot to avoid importing fungi and soil residues from the site where the juvenile was harvested (pre-experiments had found that such fine roots can be rapidly re-established by the juvenile within days).

Exposure of juveniles and experimental treatment

The harvested juveniles were planted ≥ 30 cm apart around the trunk of each focal adult oak immediately after harvesting. Juveniles were initially planted at three distances (0.5, 2.75 and 5 m) (Fig. 2b); however, survival was too low to exploit the combined and interacting effects of spatial distance, treatments, microclimate variables, and phylogenetic distance (but we explored the effect of spatial distance as explained below). Because the closest tree was occasionally not the focal oak, phylogenetic distance was recorded as the phylogenetic distance of a given juvenile to the closest tree (defined as height > 2 m).

Four treatments were applied simultaneously at each of the above-mentioned three distances (Fig. 2b), with the aim of determining the effects of fungi and insect herbivores on juvenile growth: 1) control, 2) insecticide, 3) fungicide and 4) fungicide+insecticide (Supporting information).

In contrast to the study of seed germination, we conducted no treatment for density, juvenile size, or proximity to conspecific adults. We, however, recorded the natural juvenile density, the spatial distance of focal juveniles to the closest conspecific or heterospecific adult, and the circumferences of those adults. In later analyses, we explored whether the effect of phylogenetic distance on juvenile herbivory could ultimately be explained by these variables; we did so by replacing phylogenetic distance with either of these variables.

Monitoring of juvenile performance and microclimate variables

Insect herbivory is a major determinant of juvenile survival, and even low levels of insect herbivory can substantially increase juvenile mortality (Wada et al. 2000, and in our study system: Deniau et al. 2017). Furthermore, herbivory is much easier to study within a short time window and across a continuous scale than mortality, albeit mortality and herbivory do not fully replace each other. We therefore recorded leaf-area loss caused by chewing insects as a proxy for juvenile performance, with higher leaf-area loss indicating lower performance. Herbivores may entirely consume certain leaves, leaving no trace for a later evaluation of herbivory.

We therefore monitored juvenile herbivory roughly every week from the day of transplantation and ceased after four months, in mid-July, when most damage by herbivores had occurred (Supporting information). In late July, the leaf-area loss on the remaining leaves of each juvenile was visually estimated by the same observer, using a grid of points (1 cm², for the largest leaves, 0.25 cm² for intermediate leaves, and 0.0625 cm² for smallest leaves, following Yguel et al. 2011, Giffard et al. 2012).

To determine the effects of microclimate on leaf herbivory, we measured soil humidity and temperature in March/April, immediately before juvenile budburst (averages in the Supporting information), a particularly important period for leaf development (Visser and Holleman 2001). These measurements were recorded as snapshots using a reader HMobile Moisture Meter and a sensor Trime-pico64 TDR Technology (IMKO-Micromoduletechnik). We also measured soil pH at the same positions using the same equipment as that used in the seed germination experiment. Measurements were made close to each juvenile, at approximately 5 cm depth on a single day in March 2014 (taken from Deniau et al. 2017, who studied different juveniles and questions). Snapshot measurements may be vulnerable to noise from temperature and humidity fluctuations. However, microclimatic conditions in soil fluctuate much less than at the surface, and relative variation in humidity and temperature remains relatively stable through time (Kang et al. 2000). Moreover, measurements for a given pair of trees were taken within 40 minutes, and variation among tree pairs could be accounted for in later analyses by including tree pair as a random factor. We note that, in this experiment, the phylogenetic distance of neighbourhoods did not affect microclimate variables, except for soil pH ($r = -0.1807$, $p < 0.05$) (Supporting information).

Adult phenology

As explained in the Introduction, we inferred the high phenological performance of trees from the capacity to burst early and to maintain a long duration of the vegetation period. For each of the selected 22 focal adult oaks, we recorded the timing of budburst starting in March 2010 when all buds were entirely closed and ceased when all the focal trees had developed small, unfolded leaves (details in Supporting information). We also recorded the timing of leaf shedding every three days from July and ceased recording when the tree had lost 50% of its leaves (Gill et al. 2015). We then calculated the duration of the vegetation period as the date when 50% of leaves were shed minus the date when budburst finished (i.e. the date when all 20 buds had developed small, unfolded leaves).

In contrast to the above studies of seed germination and juvenile growth, no experimental treatments of biotic interactions were conducted for adult trees. Spatial proximity to adults was of no interest here as there were always other adults in contact, and the density of neighbourhood canopy was almost constant compared to the massive variation in seeds and juveniles (no clearings or canopy gaps). Fungi and insects are likely pertinent for adult trees, but their experimental

treatment at the level of entire trees was impracticable and forbidden at the study site. We, however, did explore in later analyses whether the effect of phylogenetic distance can be explained by the activity of insect herbivores (see the Supporting information for detailed methods of measuring adult herbivory) or by the enzymatic activity of mycorrhizal fungi (Supporting information) of adult focal trees by replacing phylogenetic distance with either of these variables. Enzymatic activity was quantified in terms of laccase activity, which reflects the mycorrhizal investment in extracellular oxidative enzymes involved in breaking down lignin and other recalcitrant organic matter, thereby facilitating nutrient mobilization for the host tree, and has been shown to be particularly responsive to the phylogenetic neighbourhood of oaks (Courty et al. 2006, Yguel et al. 2014b). Activities were measured based on the decomposition of phenolic substrates by laccase, using high-throughput microplate assays for each root tip (Supporting information).

We measured air temperature and humidity every day from April to August (averages in the Supporting information). Temperature and relative humidity were measured with a sensor placed in a mesh bag in the middle of each crown, at a position sheltered from precipitation as well as sunlight (DS1923 Hygrochron Temperature/Humidity Logger iButton, 8KB Data-Log Memory), and recorded hourly. We also measured soil pH from March to April (taken from Yguel et al. 2014a) as pH might influence budburst in the slightly acidophilic sessile oak (Arend et al. 2016). Effective temperature sum (i.e. degree-days above a lower developmental threshold) is commonly used in studies of tree phenology, as in many temperate biomes, trees require a mean temperature above a threshold of 0–6°C for budburst (Man and Lu 2010, Rossi and Isabel 2017). Therefore, we calculated the effective temperature sum per month following Man and Lu (2010) by using the threshold of 0°C. Humidities were averaged per month. We selected the climate of April to statistically explain the date of budburst, because budburst usually occurs in late April, and the climate of July and August to statistically explain the duration of the vegetation period, because summer stress caused by high temperatures and drought had a direct effect on leaf senescence (Zani et al. 2020). Note that in later analyses, July and August had similar results overall, we hence present the results of August only. We note that, in this experiment, temperature sum, humidity, soil pH and phylogenetic distance showed no significant pairwise correlations, and additional diagnostics indicated no problematic multicollinearity among these variables (Supporting information).

Statistical analyses

We performed all statistical analyses using R ver. 4.1.1 (www.r-project.org). Generalised linear mixed-effects models (GLMM) ('lme4' package ver. 1.1-35.5, Bates et al. 2015) were used to test the effects of phylogenetic distance of neighbourhood (PD), microclimate variables, and treatment of biotic interactions (e.g. fungicide, insecticide) on oak performance. The response variables (performance)

were germination stage for seeds, leaf herbivory for juveniles, and the date of budburst, as well as the duration of the vegetation period for adults. Rankings of germination stage were averaged across seeds for each treatment within each of the three seed sets per tree to avoid pseudoreplication within environment/treatment, given that the hypotheses are across environment/treatment and the design was balanced (Murtaugh 2007). The resulting averages of germination stage rarely reached the lower bound of 0 and never approached the upper bound of 2 (Fig. 3). As a result, these averages and all other response variables were continuous and de facto unbounded. Only one variable was bounded between 0 and 1: herbivory. For this variable, beta regression or a binomial model with a logit link may be more appropriate than a Gaussian model, and the DHARMA package retained beta regression as the best based on residual uniformity, quantile diagnostics and AIC (and a Gaussian model with an identity link for the remaining, continuous, unbounded variables, Supporting information). The model structure included all possible full factorial 3-way interactions among PD, one biotic interaction treatment (e.g. one of the four treatments in seed germination: fungicide, density, spatial distance, seed size), and the two microclimatic variables (temperature and humidity). Including all interaction terms involving all biotic interaction and microclimate variables (temperature and humidity) would have resulted in up to 28 interaction terms, i.e. complete overparameterisation, and would have sacrificed statistical power. Classical variable selection procedures starting from an overparameterized model may be unstable (Burnham and Anderson 2002). Moreover, in our case variable selection resulted in exclusion of main effects and left interaction terms, while our hypotheses are on interactions modifying main effects e.g. of climate, and so main effects have to be kept. As an alternative approach we conducted preliminary analyses in each of which we included the interaction terms with temperature and humidity only for a given treatment of biotic interaction (all climatic variables and all treatments were entered as main effects), i.e. for example, germination stage = PD $\times$ temperature $\times$ fungicide + PD $\times$ humidity $\times$ fungicide + all other treatments (i.e. density + spatial distance + seed size). We always included tree pair (i.e. 'Site') as a random effect to account for variation caused by the spatial component. We also included 'tree' nested within pair as a random effect to avoid pseudoreplication of seeds planted in the same focal tree in analyses of the performance of seeds. Finally, we included soil pH as a covariate (Augusto et al. 2015, Arend et al. 2016).

In the final analysis, we retained all main effects and the interaction terms that were significant in the preliminary analysis. We note that including non-significant 2-way interactions would neither have changed the results (any significant term remains at least marginally significant, no non-significant becomes significant) nor improved the model fit (marginal R^2 increases by only 0.009). This final analysis allowed us to compare the retained variables while the initial analyses served only to retain a manageable number

of variables (Burnham and Anderson 2002, Engqvist 2005, Zuur et al. 2010).

For Gaussian mixed models, p-values for fixed-effect coefficients were calculated using Satterthwaite's approximation for degrees of freedom ('lmerTest' ver. 3.2.1, Kuznetsova et al. 2017), whereas Wald z-tests were used for the beta-regression model fitted using 'glmmTMB' ver. 1.1.9 (Brooks et al. 2017). Marginal R-squared with the delta method using the pseudo-R-squared function (*MuMIn*) was used to quantify the variance explained by the fixed effects. We recall that microclimatic conditions were mostly not correlated with PD (Supporting information). Even in the case of such a correlation, the structure of our GLMM avoids bias from microclimates (Supporting information). Studying up to two dependent variables for a given stage implies an up to 2/20 risk of finding by chance a relationship of $p=5\%$ for one single of these variables. Such chance effects therefore cannot explain our observation of significant effects for every single dependent variable, often at $p < 0.01$.

As stated in the hypotheses, our study focuses on interaction terms, i.e. whether phylogenetic distance in neighbourhoods can compensate for climate stress and whether in seeds and juveniles this is modulated by biotic interactions (a 3-way interaction between phylogenetic distance, climate stress and biotic interactions). Whenever such a 3-way relationship was found to be significant, we visualised it using simple regressions on subsets of the data. Both climatic variables and phylogenetic distance are continuous. To avoid difficult-to-grasp three dimensional plots, we chose to represent, for each treatment, the effect of phylogenetic distance as distinct two dimensional plots of microclimate against performance for phylogenetic neighbourhoods smaller ($\leq$) versus larger ($>$) than the overall median across all focal oaks.

As explained above, some biotic interactions could not be manipulated by experimental treatment in the study of juvenile growth, and none could be manipulated in the study of adult phenology. Instead, we conducted supplementary analyses for juvenile growth, replacing PD by either juvenile density, or spatial distance to conspecific/heterospecific adults and their circumferences. The same approach was used for adult phenology, replacing PD of the adult tree by its insect herbivory or mycorrhizal enzymatic activity (laccase) (Supporting information).

We also explored to what extent phylogenetic distance of trees was related to other characteristics of the focal trees or their neighbourhoods. We found that the phylogenetic distance was neither correlated with tree size [measured as breast diameter ($R^2 < 0.0001$, $p=0.9777$) and crown diameter ($R^2=0.0068$, $p=0.7154$)], nor with species diversity indices (species richness: $R^2=0.0032$, $p=0.8040$; Shannon index: $R^2=0.0223$, $p=0.5070$; Simpson index: $R^2=0.0493$, $p=0.3210$; Pielou's evenness: $R^2=0.0969$, $p=0.1580$) or with the number of neighbouring trees ($R^2 < 0.0001$, $p=0.9880$). Inevitably, phylogenetic distances were correlated with the percentage of gymnosperm neighbours ($R^2=0.9687$, $p < 0.0001$). We hence determined in later analyses the extent to which the effect of phylogenetic

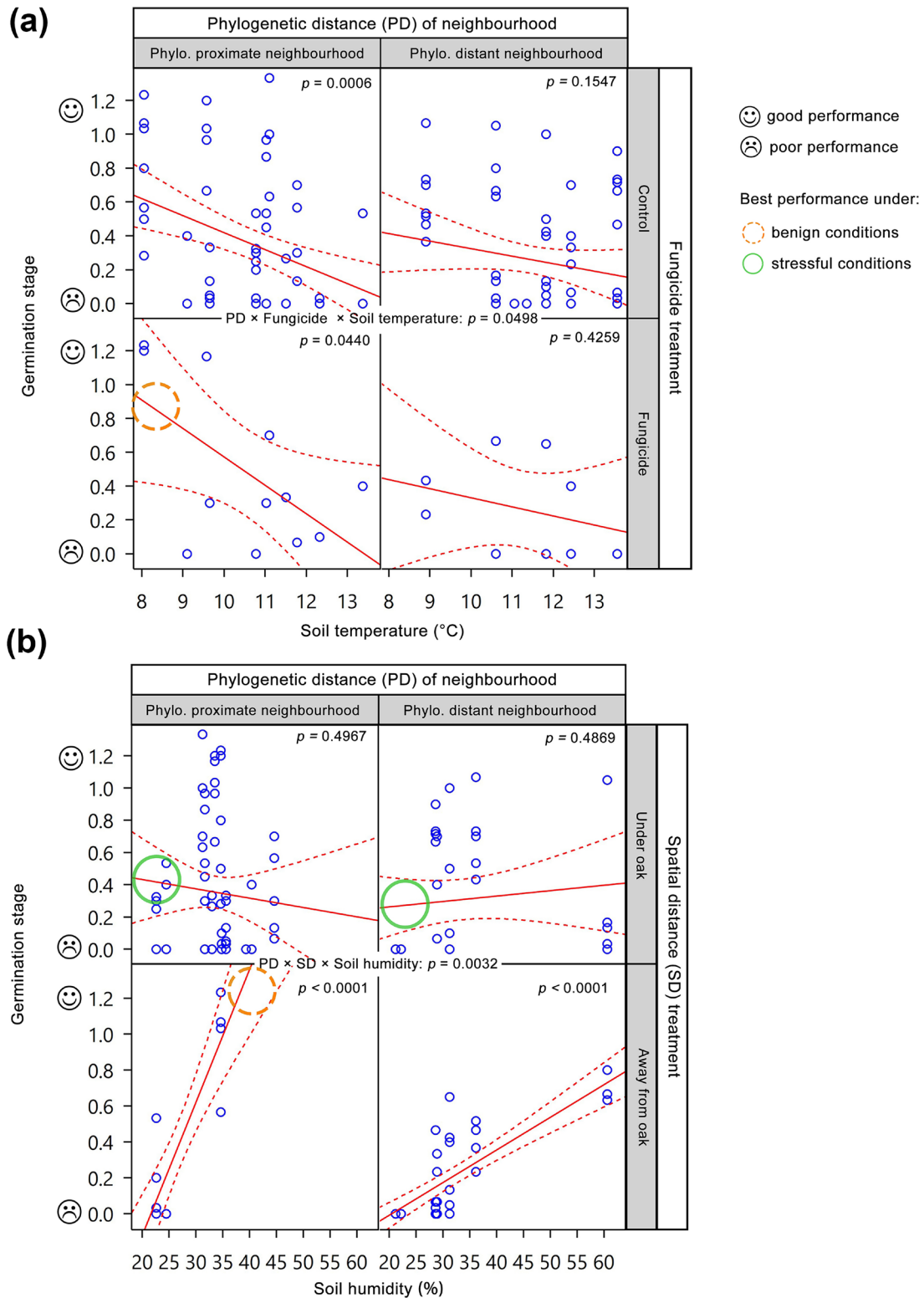


Figure 3. Seed germination. Graphical representation of the statistically significant three-way interactions among phylogenetic distance of neighbours, (a) soil temperature and fungicide treatment, and (b) soil humidity and spatial-distance treatment on seed performance. Note that the focus is on the statistically significant three-way interactions (as indicated in Table 1), i.e. differences between slopes in different subfigures, not on the slopes individually. All slopes in the subfigures are hence illustrated using simple regression lines with 95% confidence intervals, even if a given slope itself is non-significant. Phylogenetic distance is presented as a binary variable in the figures but is continuous and was treated as such in the statistical analyses. Taken together, the differences in p-values from simple regression for the different subsets are consistent with the 3-way interaction terms across the entire data set (Table 1).

proximity in our study is lineage-specific. For this purpose, we replaced PD by the percentage of gymnosperms. If the effect of phylogenetic distance was entirely due to the presence of gymnosperms (e.g. through soil acidification or shading in winter), then the percentage of gymnosperms should perform better than does phylogenetic distance.

We used the 'Dharma' package ver. 0.5.0 (Hartig 2022) including residuals- versus fitted values plot and QQ-plot of the residuals to check the adequacy of the model in explaining the data (see the Supporting information for details). Residual outliers were highly influential individual data points that were far from fitting the expected residual distribution, and biased the entire analysis by producing significant (or non-significant) relationships that were not representative of the remaining data points (Warton 2022). We hence excluded a maximum of three out of 160, two out of 117, and one out of 22 data points for seed germination, juvenile growth, adult phenology, respectively (further exclusion of less distinct outliers would then not change the results). Residuals always approached normality (in the case of Gaussian models) and homoscedasticity apart from the mentioned occasional outliers (Supporting information).

Results

Seed germination

Germination was significantly affected by fungicide treatment ($t=2.006$, $p=0.0469$) and spatial distance treatment ($t=4.132$, $p=0.0001$), but not by density treatment, seed mass treatment, phylogenetic distance, microclimate variables, or their 2-way interactions ($p > 0.0675$, Table 1). In addition, we also observed two statistically significant 3-way interactions affecting seed germination stage (Table 1): 1) phylogenetic distance $\times$ soil temperature $\times$ fungicide treatment ($t=1.980$, $p=0.0498$, Fig. 3a), and 2) phylogenetic distance $\times$ soil humidity $\times$ spatial distance treatment ($t=3.006$, $p=0.0032$, Fig. 3b). Specifically, 1) at low temperatures, seeds germinated best in a phylogenetically proximate neighbourhood, especially when fungi were excluded, whereas as temperature increased, germination decreased in both neighbourhoods (Fig. 3a). 2) under high humidity, seeds away from an oak crown exhibited higher germination (Fig. 3b), especially in a phylogenetically proximate neighbourhood. However, with decreased humidity, seed germination away from an oak crown declined to zero, whereas those under an oak crown maintained their performance in either neighbourhood (Fig. 3b).

Note that the statistical effect of phylogenetic distance and microclimate variables in those 3-way interactions was more significant than the main effects of both ($p=0.0032$ and 0.0498 versus each single term at $p=0.079$ – 0.906), suggesting that microclimate is more likely to affect how neighbours change performance than to directly affect performance. The effect of phylogenetic distance in those 3-way interactions could not be replaced by the percentage of neighbouring gymnosperms (Supporting information), suggesting that

Table 1. Seed germination: Statistical effects of phylogenetic distance of adult neighbours, treatment (fungicide, seed density, seed mass and spatial distance from focal oak), microclimate variables (soil temperature and humidity), and their interactions on germination of oak seeds (accounting for soil pH). Effects were calculated using Wald z-tests and the corresponding t values are given. The variance explained by the fixed effects was quantified by marginal R-squared (R^2_m). Bold values represent statistical significance ($p < 0.05$), and italics marginal significance ($0.05 \leq p < 0.1$). See Methods for selection of interaction terms entered into a model, and Fig. 3 for a graphical representation of the statistically significant 3-way interactions. The models include Site and Tree (nested in Site) as random factors (not shown).

	Germination stage	
	t statistics	p
Phylogenetic distance (PD)	<i>-1.9310</i>	<i>0.0791</i>
Fungicide treatment	2.0060	0.0469
Density treatment	-1.3680	0.1737
Spatial distance treatment (SpD)	4.1320	0.0001
Seed mass treatment	0.4210	0.6742
Soil pH	<i>-1.7710</i>	<i>0.0990</i>
Soil temperature	-0.8790	0.4025
Soil humidity	-0.1210	0.9061
PD $\times$ Fungicide	-2.0340	0.0440
PD $\times$ Soil humidity	1.6880	0.1149
Fungicide $\times$ Soil temperature	-2.0230	0.0451
Density $\times$ Soil temperature	1.0010	0.3189
SpD $\times$ Soil humidity	-4.7630	<0.0001
PD $\times$ Fungicide $\times$ Soil temperature	1.9800	0.0498
PD $\times$ SpD $\times$ Soil humidity	3.0060	0.0032
PD $\times$ Seed mass $\times$ Soil humidity	-1.3220	0.1885
R^2_m	0.3021	

the effect of phylogenetic distance was not resulting from the presence of gymnosperms.

Juvenile growth

Leaf herbivory was significantly affected by the 2-way interaction term between phylogenetic distance and soil humidity ($z=1.9954$, $p=0.0460$), but not by treatment, or microclimate variables ($p > 0.2274$, Table 2). In addition, we also observed two 3-way interaction terms (Table 2): 1) phylogenetic distance $\times$ treatment $\times$ soil humidity ($\chi^2=9.8302$, $p=0.0201$, Fig. 4), and 2) phylogenetic distance $\times$ treatment $\times$ soil temperature ($\chi^2=12.0511$, $p=0.0170$, Supporting information). Specifically, 1) Under high soil humidity, juveniles had lower leaf herbivory in a phylogenetically proximate neighbourhood, except after fungicide treatment. By contrast, under low humidity, herbivory was lower in a phylogenetically distant neighbourhood, especially after fungicide treatment (Fig. 4). 2) Under low soil temperature, juveniles had the lowest leaf herbivory in a phylogenetically proximate neighbourhood after fungicide treatment. By contrast, at higher soil temperatures, herbivory in both neighbourhoods decreased, except in a phylogenetically proximate neighbourhood after fungicide treatment and in a phylogenetically distant neighbourhood after insecticide treatment or fungicide + insecticide treatment (Supporting information).

Table 2. Juvenile growth. Statistical effects of phylogenetic distance of adult neighbours, treatment (control, fungicide, insecticide or fungicide+insecticide), microclimate variables (soil temperature and soil humidity) and their interactions on leaf herbivory of oak juveniles (accounting for soil pH). Effects were evaluated using Wald z-tests, and the corresponding z values are given. The variance explained by the fixed effects was quantified by marginal R-squared (R^2_m). Bold values represent statistical significance ($p < 0.05$), and italics marginal significance ($0.05 \leq p < 0.1$). See Methods for selection of interaction terms entered into a model, and Fig. 4 and the Supporting information for a graphical representation of the statistically significant 3-way interactions. The models include Site and Tree (nested in Site) as random factors (not shown). [†] Tested by ANOVA (the corresponding χ^2 -value is given instead of z-value).

	Leaf herbivory	
	z statistics	p
Phylogenetic distance (PD)	1.7089	0.0875
Treatment	2.0349 [†]	0.5652
Control	0.5392	0.5898
Fungicide	1.0230	0.3063
Insecticide	0.3602	0.7187
Soil humidity	-1.2070	0.2274
Soil pH	0.2544	0.7992
Soil temperature	-0.3992	0.6898
Treatment × PD	0.3664 [†]	0.9471
Control × PD	-0.8571	0.3914
Fungicide × PD	-1.2440	0.2135
Insecticide × PD	-1.0230	0.3063
Soil temperature × Treatment	4.9097 [†]	0.1785
Soil temperature × Control	-0.2722	0.7855
Soil temperature × Fungicide	1.2579	0.2084
Soil temperature × Insecticide	-0.0582	0.9536
Soil humidity × PD	1.9954	0.0460
Soil humidity × Treatment	4.3252 [†]	0.2284
Soil humidity × Control	1.0969	0.2727
Soil humidity × Fungicide	2.4940	0.0126
Soil humidity × Insecticide	-0.3972	0.6912
Soil temperature × Treatment × PD	12.0511[†]	0.0170
Soil temperature × Control × PD	1.0593	0.2895
Soil temperature × Fungicide × PD	-2.0949	0.0362
Soil temperature × Insecticide × PD	2.1543	0.0312
Soil humidity × Treatment × PD	9.8302[†]	0.0201
Soil humidity × Control × PD	-1.2318	0.2180
Soil humidity × Fungicide × PD	-1.9397	0.0524
Soil humidity × Insecticide × PD	-0.2987	0.7652
R^2_m	0.4032	

Note that the statistical effect of phylogenetic distance and microclimate variables in those 3-way interactions were as strong as the main effects of phylogenetic distance and microclimate variables ($p=0.0312$ – 0.7652 versus $p=0.0875$ – 0.6898), suggesting that phylogenetic distance and microclimate variables influence juvenile herbivory through their interactive effects no less than through their direct main effects. The effect of phylogenetic distance in those 3-way interactions with fungicide treatment and soil humidity or temperature could not be replaced by the percentage of neighbouring gymnosperms (Supporting information) nor by the distance to the closest hetero- or conspecific adults and their circumferences, or the density of oak juveniles

(Supporting information), suggesting that the effect of phylogenetic distance was not resulting from those factors.

Adult phenology

The date of budburst was significantly affected by phylogenetic distance, and its interaction with April air-humidity ($t=2.682$, $p=0.0179$, Table 3). Specifically, under high air humidity, adults in a phylogenetically proximate neighbourhood tended to burst their buds at least a week earlier than those in a phylogenetically distant neighbourhood (Fig. 5a). However, under low air humidity, bud-burst timing of adults hardly differed between neighbourhoods (Fig. 5a).

In addition, the duration of the vegetation period was significantly affected by phylogenetic distance, August air-humidity, and their interaction ($t=-4.0711$, $p=0.0046$, Table 3). Specifically, under high humidity conditions, adults in a phylogenetically proximate neighbourhood exhibited longer vegetation periods than those in a phylogenetically distant neighbourhood, but under low humidity conditions, both neighbourhoods showed reduced vegetation period lengths.

Note that the statistical effect of phylogenetic distance in those 2-way interactions was as strong as the main effect of phylogenetic distance ($p=0.0179$ and 0.0046 versus $p=0.0199$ and 0.0049), suggesting that phylogenetic distance and microclimate variables influence adult phenology no less through their interactive effects than through their direct main effects. The effect of phylogenetic distance on budburst phenology (i.e. the date of budburst) in 2-way interactions with April air-humidity and on the duration of the vegetation period in interaction with August air-humidity could be entirely or partly replaced by the percentage of neighbouring gymnosperms (Supporting information), but not by the laccase activity of mycorrhizae, nor by leaf herbivory (Supporting information), nor by tree size or circumference (drastic decline in R^2 in the Supporting information), suggesting that the effect of phylogenetic distance could be entirely explained by neighbouring gymnosperm dominance, but not by mycorrhizal laccase activity, herbivory or tree size.

Discussion

Our study shows that ‘good’ neighbours do, at least to some extent, compensate for a ‘bad’ climate. Notably, under dry conditions, juvenile oaks performed best (measured as low herbivory) in phylogenetically distant neighbourhoods (Fig. 4), consistent with hypothesis 2 (close relatives decrease and distant relatives increase performance under stress). Also, in adults, the poor performance (measured as budburst delay) observed in benign, humid conditions in such distantly related neighbourhoods partially disappeared under less benign conditions (Fig. 5a). In addition, we also observed strong and consistent patterns under benign conditions: in phylogenetically proximate neighbourhoods, oak performance tended to be highest, as measured through: 1) seed germination (under cold or high humidity conditions,

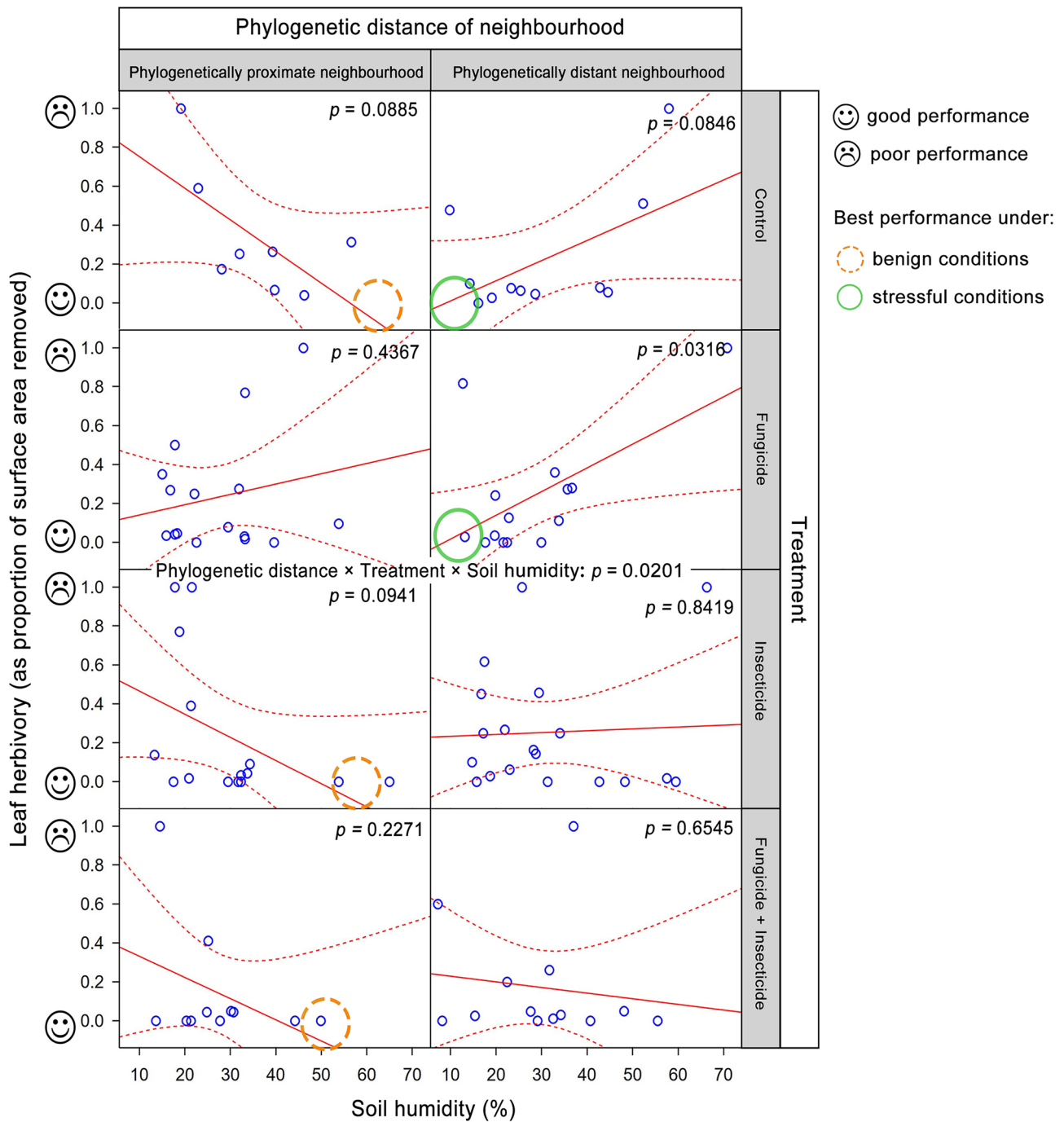


Figure 4. Juvenile growth. Graphical representation of the statistically significant three-way interaction among phylogenetic distance of neighbours, treatment (control, fungicide, insecticide, or fungicide + insecticide), and soil humidity (March/April) on juvenile performance in terms of low herbivory. Note that the focus is on the statistically significant three-way interaction (as indicated in Table 2), i.e. differences between slopes in different subfigures, not on the slopes individually. All slopes in the subfigures are hence illustrated using simple regression lines with 95% confidence intervals, even if a given slope itself is non-significant. Phylogenetic distance is presented as a binary variable in the figures but is continuous and was treated as such in the statistical analyses. Taken together, the differences in p values from simple regression for the different subsets are consistent with the 3-way interaction terms across the entire data set (Table 2).

when fungi were excluded or adult oak neighbours were distant, respectively, Fig. 3); 2) juvenile herbivory (under high humidity, Fig. 4); and 3) timing of adult budburst and duration of adult vegetation period (under humid conditions,

Fig. 5). Differences in resistance to microclimatic stress among phylogenetically proximate and distant neighbourhoods reflect the activity of fungi, insects, or the interaction with conspecific adult neighbours, i.e. differences disappear

Table 3. Adult phenology. Statistical effects of phylogenetic distance of adult neighbours, climate variables (air temperature-sums and humidity of April or August), and their interactions on date of budburst, and duration of vegetation period of oak adults (accounting for soil pH). Effects were calculated based on Satterthwaite's approximation, and the corresponding *t* values are given. The variance explained by the fixed effects was quantified by marginal R-squared (R^2_m). Bold values represent statistical significance ($p < 0.05$), and italics marginal significance ($0.05 \leq p < 0.1$). See Fig. 5 for a graphical representation of statistically significant 2-way interactions. The model includes Site as a random factor (not shown). ¹ Independent variables that are biologically little pertinent for the respective dependent variable as explained in Methods. Those independent variables were hence not included into the model to avoid overparameterisation.

	Date of budburst		Duration of vegetation period	
	<i>t</i> statistics	<i>p</i>	<i>t</i> statistics	<i>p</i>
Phylogenetic distance (PD)	-2.6282	0.0199	4.0309	0.0049
Soil pH	-0.5850	0.5678	1.9590	0.0706
April air temp-sums	-0.4416	0.6655	Not entered ¹	
April air humidity	-1.8464	0.0861	Not entered ¹	
PD × April air humidity	2.6817	0.0179	Not entered ¹	
August air-temp. sums	Not entered ¹		2.8461	0.0219
August air humidity	Not entered ¹		4.4727	0.0026
PD × August air humidity	Not entered ¹		-4.0711	0.0046
R^2_m	0.6567		0.4235	

once the pertinent factor is experimentally excluded. The interactive effects of phylogenetic distance with microclimate variables and treatments on performance in multiple regression models were robust: they were confirmed by simple regression models for subsets of data (Tables 1–3 versus Fig. 3–5). These interactive effects were mostly stronger than the main effects, suggesting that the combined effect of microclimate variables and phylogenetic distance impacts oak performance more than these variables alone. Effects of phylogenetic distance were mostly partly, but not entirely, replaceable by the percentage of gymnosperms, suggesting that the effect of phylogenetic distance was not entirely resulting from the presence of gymnosperms.

Limitations

We acknowledge that our study has some limitations. First, we only studied a single focal species and found that the effects of phylogenetic distance in the interaction with microclimatic conditions and treatment could, albeit seldom, be fully replaced by the percentage of neighbouring gymnosperms. This indicates that the effects of phylogenetic isolation in our study system are sometimes lineage-specific and may yield different results when gymnosperms are used as the focal species, which should be studied in the future. However, for whatever focal species, phylogenetic isolation will mostly increase the functional dissimilarity from neighbouring species in forests (Prinzing et al. 2021). Second, as all the experiments were carried out in the natural environment, there might be some covariates that we have missed – albeit

the ones we considered mostly did not replace the effect of phylogenetic distance, and the specificities of the study species and forest strongly limit the extent of such variation. Greenhouse experiments might come closer to causality, but are farther from reality and not practicable for adult trees. Third, to manipulate fungi, we utilised fungicide, which inevitably may also affect non-target organisms (albeit only to a limited extent). Alternative approaches like sterilisation or inoculation (Gibson 2015) would not have permitted us to study the entire fungal community in the field, and therefore fungicide remains extensively used in ecological studies (Bagchi et al. 2014, Deniau et al. 2018, Huang et al. 2022). Fourth, we ignored the effects of microclimate on interacting biota (Gely et al. 2020), effects that might partly explain the observed interaction terms of microclimate and biota on oak performance. Fifth, we studied climatic stress only to the extent to which it varies in space at present. While this spatial variation is as large as the worst temporal variation predicted to occur across the next 80 years (IPCC 2022), it obviously does not cover the higher, more severe end of the predicted temporal variation. During future severe drought, the herbivory of juveniles and budburst of adults might be impaired in both neighbourhoods (Gely et al. 2020). Sixth, we used space to partly replace time, while acknowledging that species interactions in existing conditions are shaped by adaptations to the current climate. Future climate change may select for new genotypes, alter the strength of biotic interactions, or create new interactions adapted to future conditions (Pihain et al. 2019, Åkesson et al. 2021). These changes could alter species' responses to new climatic stress, complicating direct comparisons between spatial and temporal scale. In that case, our study would still serve to describe the local selection pressures, for instance, for increased abiotic stress tolerance in a 'bad' neighbourhood. Finally, we admit that some of our mechanistic discussions below are highly speculative. Regardless of the underlying mechanisms, across three essential life stages, we found a strong shift in performance under climatic stress when offspring were exposed to a phylogenetically proximate and distant canopy and to controlled biotic interactions.

Explanations

We did not observe any pattern entirely consistent with hypothesis 1, i.e. a relative increase in performance under stress in a phylogenetically proximate neighbourhood. There was no significant negative interaction term between phylogenetic distance and microclimatic stress on any of the performance variables (except, in part, if natural interactions with insects or fungi were suppressed in juveniles). We, however, observed one pattern roughly consistent with hypothesis 1, if we consider being under an oak as being close to the most phylogenetically proximate neighbours: oak seeds beneath oak crowns did not suffer from reduced germination under drought (Fig. 3b). This relationship, however, was independent of phylogenetic distance of the surrounding canopy trees. This result might result from 1) the decrease of cover by the very competitive grass *Molinia caerulea* beneath

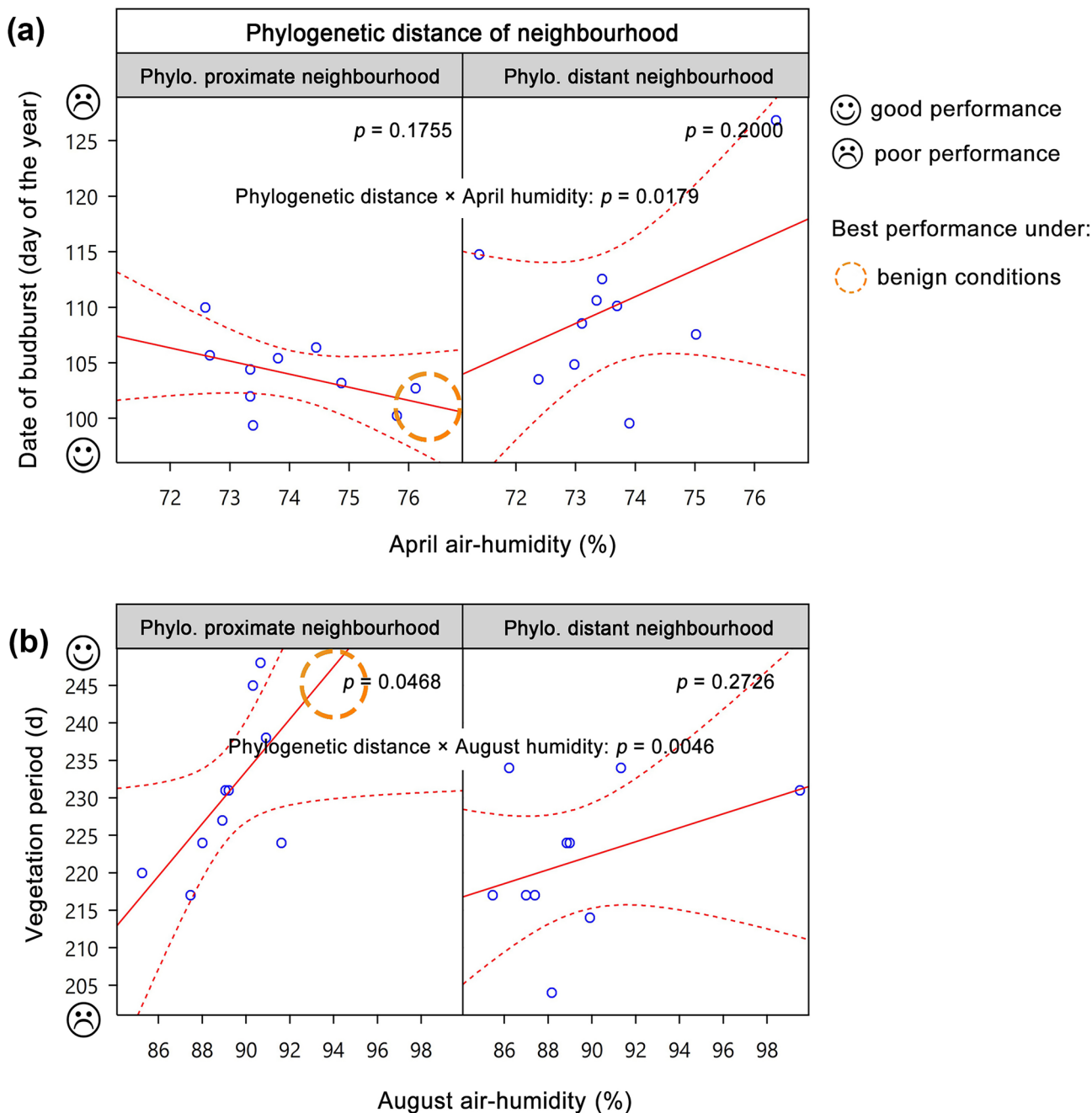


Figure 5. Adult phenology. Graphical representation of the statistically significant two-way interactions between (a) phylogenetic distance of neighbours and April air humidity, and (b) phylogenetic distance of neighbours and August air humidity, on adult phenology. DOY denotes day of the year. Note that the focus is on the statistically significant two-way interactions (as indicated in Table 3), i.e. differences between slopes in different subfigures, not on the slopes individually. All slopes in the subfigures are hence illustrated using simple regression lines with 95% confidence intervals, even if a given slope itself is non-significant. Phylogenetic distance is presented as a binary variable in the figures but is continuous and was treated as such in the statistical analyses. Taken together, the differences in p values from simple regression for the different subsets are consistent with the 2-way interaction terms across the entire data set (Table 3).

an adult oak (Deniau et al. 2017) and 2) conspecific neighbours facilitating each other under stressed abiotic environments, such as through shared effects on microclimates (stress gradient hypothesis, Bertness and Callaway 1994), as demonstrated in many studies (Valiente-Banuet and Verdú 2007, Castillo et al. 2016).

We observed two patterns entirely consistent with hypothesis 2, i.e. a relative increase in performance under stress in a phylogenetically distant neighbourhood. 1) Juveniles in a phylogenetically distant neighbourhood did not suffer from an increase in herbivory under heat and, to a lesser extent, drought, notably in the presence of fungi (Fig. 4). We

speculate that heat and drought stress juveniles and thereby decrease their resistance to the numerous herbivores in a phylogenetically proximate neighbourhood. However, we did not find 2-way interaction effects of neighbourhood with insecticide treatment, which is surprising given the higher herbivory in a phylogenetically proximate neighbourhood (Deniau et al. 2018). One possible explanation is that in a phylogenetically proximate neighbourhood, insecticide effects are more rapidly compensated by local re-immigration (contributing to the weak effect of insecticide overall). 2) Under dry conditions, adults in a phylogenetically distant neighbourhood burst their buds somewhat earlier than under moist conditions contrary to the tendency in phylogenetically proximate neighbourhoods (Fig. 5a). We find it difficult to explain this pattern. Whatever the reasons, in oaks, such an earlier budburst under drought among phylogenetically distant neighbours is advantageous in gaining a competitive advantage over other individuals (Tikkanen and Julkunen-Tiitto 2003, Chapin et al. 2011).

We also observed patterns that are significant, but inconsistent with either hypothesis. In particular, in three cases, phylogenetically proximate neighbours increased performance under lack of stress, but not under stress. First, in a phylogenetically proximate neighbourhood, cold and humidity increased seed performance (germination) provided fungi were excluded or an adult oak neighbour was far (Fig. 3). We speculate that cold triggers germination and humidity maintains it (Baskin and Baskin 2014), and that this germination benefits from the improved litter quality in phylogenetically proximate neighbourhoods (Pan et al. 2015, Santonja et al. 2025). However, these advantages might be negated by pathogenic fungi accumulated around an adult tree (Yu et al. 2022), so that application of fungicide or distancing from an adult oak might be needed to benefit from the phylogenetically proximate neighbourhood. Second, in a phylogenetically proximate neighbourhood, herbivory on juvenile oaks overall declined with increasing humidity (Fig. 4). Fungi appeared to favour the decline of herbivory with an increase in humidity (albeit preventing the decline of herbivory with a decline in temperature). High humidity might enable plants to outgrow herbivores provided sufficient availability of nutrients and beneficial mycorrhizae – which have been shown to be more available in a phylogenetically proximate neighbourhood (Deniau et al. 2018, Santonja et al. 2025). Third, we found that in a phylogenetically proximate neighbourhood, budbursts tended to occur earlier in high humidity in April (in significant contrast to phylogenetically distant neighbourhoods) and the duration of the vegetation period increased at similarly high humidity levels in August (Fig. 5). We speculate that in a phylogenetically distant neighbourhood oaks can only slightly benefit from increased humidity due to other limiting factors that might induce senescence, which might include low soil nutrients (Fu et al. 2019, Santonja et al. 2025) and shading (Wu et al. 2021). Also, in a phylogenetically distant neighbourhood, the vegetation period starts late (Fig. 5), and delayed leaf senescence due to a moist month of August increases the chance of leaves being

exposed to autumn storms, which will tear leaves off, with little net gain in vegetation period.

Implications

Our results have direct application to the adaptation and restoration of temperate forest ecosystems under threat of increasing heat and drought (Cheaib et al. 2012, Mina et al. 2022, Xu et al. 2023). While ecologists have proposed assisted migration or managed relocation as a possible adaptation measure, this approach sometimes fails (Montwé et al. 2018) and carries multiple risks, such as the spread of parasites and diseases, the introduction of maladaptive alleles into focal populations, and potential invasiveness in the introduced range (Ricciardi and Simberloff 2009). We showed that under drought stress, juvenile oaks tend to be more resistant in phylogenetically distant neighbourhoods. These statistical effects seem to be mediated by the biotic interactions with insects and fungi, interactions that could emerge during tree ontogeny and during forest succession, and ultimately increase the resistance of the entire forest. On the other hand, seed germination may continue to benefit from the presence of conspecific adults. Therefore, in the context of predicted climate change scenarios (increased temperature and decreased precipitation), foresters may facilitate oak regeneration by nursing/planting oak seedlings among phylogenetically distant neighbours while maintaining individual oaks to favour seedling development below them. Importantly and unexpectedly, we found several cases where phylogenetically proximate neighbours improved performance under more benign abiotic conditions, which is consistent with the hypothesis that biotic interactions are relatively more important at the less stressful ends of environmental gradients (Louthan et al. 2015). This is bad news for forestry as it suggests that with ongoing climate change, trees will suffer the double burden of climatic stress and the loss of favourable biotic interactions with close relatives in classical planting schemes. This double burden could, however, be mitigated by avoiding monoculture plantings and promoting diverse, phylogenetically distant forest plantings, which may both improve oak performance and support biodiversity across trophic levels.

Our results may also have implications for understanding niche evolution. Evolutionary lineages often show major conservatism of ancestral niches (Ackerly 2003), including in the flora considered in our study (Prinzing et al. 2001), albeit numerous cases of niche convergence also occur. Such niche convergence suggests that species from one lineage perform better when growing in the niche dominated by another lineage (Ackerly 2003). We found cases of such increased performance among distantly related neighbours under drought, suggesting that drought might trigger niche convergence, whereas niche conservatism might be maintained under benign conditions when performance was highest when surrounded by close relatives. Future studies might test these hypotheses using growth-ring series in different neighbourhoods or macroevolutionary reconstructions of niches and their possible convergence between tree lineages during periods of climatic stress.

Acknowledgements – We thank Sara Kada, Valérie Gouesbet, Frédéric Jean, Thierry Fontaine, Freerk Mollemen, Amaury Brault, Charlene Briard, Cynthia Gauthier and Fouad Nassur for help in the field, Office National des Forêts for logistic support and access to their field sites.

Funding – KZ was funded by the National Natural Science Foundation of China (32471591); MD by a PhD fellowship from the French Ministry of Education; BY by a doctoral grant from Région Bretagne and the CNRS.

Conflict of interest – The authors declare no conflict of interest.

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Data availability statement

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.19766749> (Zhang et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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