***Quercus suber* dieback alters soil respiration and nutrient availability in Mediterranean forests**

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Summary

1. An increase in tree mortality rates has been recently detected in forests worldwide. However, few works have focused on the potential consequences of forest dieback for ecosystem functioning.

2. Here we assessed the effect of *Quercus suber* dieback on carbon, nitrogen and phosphorus cycles in two types of Mediterranean forests (woodlands and closed forests) affected by the aggressive pathogen *Phytophthora cinnamomi*. We used a spatially-explicit neighbourhood approach to analyse the direct effects of *Q. suber* dieback on soil variables, comparing the impact of *Q. suber* trees with different health status, as well as its potential long-term indirect effects, comparing the impact of non-declining coexistent species.

3. *Quercus suber* dieback translated into lower soil respiration rates and phosphorus availability, whereas its effects on nitrogen varied depending on forest type. Coexistent species differed strongly from *Q. suber* in their effects on nutrient availability, but not on soil respiration rates. Our models showed low inter-annual but high intra-annual variation in the ecosystem impacts of tree dieback.

4. *Synthesis*. Our results support that tree dieback might have important short- and long-term impacts on ecosystem processes in Mediterranean forests. With this work we provide valuable insights to fill the existent gap in knowledge on the ecosystem-level impacts of forest dieback in general and *P. cinnamomi*-driven mortality in particular. Because the activity and range of this pathogen is predicted to increase due to climate warming, these impacts could also increase in the near future altering ecosystem functioning worldwide.

Key-words: carbon cycle, drought, forest disease, invasive species, neighbourhood, nutrient availability, plant-soil (below-ground) interactions, *Phytophthora cinnamomi*, soil pathogen, tree mortality.

Introduction

In the last decades, an increase in tree mortality rates (forest dieback *sensu* Allen (2009)) has been detected in forests worldwide (e.g. van Mantgem *et al.* 2009; Allen *et al.* 2010; Carnicer *et al.* 2011). Causes underlying this phenomenon are complex and uncertain, but they are

frequently associated with global change drivers such as increasing temperatures and droughts, invasive pests and pathogens, or interactions between these factors (Martínez-Vilalta, Lloret & Breshears 2012; McDowell *et al.* 2013). The process of tree defoliation and mortality can have strong direct impacts on ecosystem functioning, causing a reduction in primary productivity and changes in the circulation of nutrients (Lovett *et al.* 2006; Hicke *et al.* 2012; Wang *et al.* 2012). Moreover, increased tree mortality rates could indirectly affect the function of the whole ecosystem in the long term if species replacements occur due to differences among species in their vulnerability to mortality factors (Ellison *et al.* 2005; Lovett *et al.* 2010). Despite the potential for large direct and indirect ecosystem-level impacts, our current understanding of the consequences of forest dieback on biogeochemical cycles is still limited (see reviews by Hicke *et al.* 2012; Wang *et al.* 2012; Anderegg, Kane & Anderegg 2013).

Soil CO_2 fluxes –including autotrophic (root and rhizosphere) and heterotrophic (microbes) respiration– are a key component of the terrestrial carbon cycle that might be dramatically altered by an increase in tree mortality rates (Kurz *et al.* 2008; Hicke *et al.* 2012; Anderegg, Kane & Anderegg 2013). Tree defoliation and mortality has been frequently found to cause a reduction in soil respiration rates, explained by a decrease in root activity (Nuckolls *et al.* 2009; Nave *et al.* 2011). However, other studies have found no changes (Morehouse *et al.* 2008; Brown *et al.* 2010) or even increments (Barba *et al.* 2013; Lloret, Mattana & Curiel Yuste 2015) in soil respiration rates as a consequence of higher microbial respiration due to post-mortality increases in litter inputs or changes in microclimate. Therefore, the implications of forest dieback for soil respiration are complex and depend on the balance of its effects on root and microbial respiration (e.g. Morehouse *et al.* 2008; Hicke *et al.* 2012). Given that forest dieback usually implies a reduction in gross primary productivity - at least in the short-term (i.e. weeks to years scale, following Hicke *et al.* 2012)

- assessing its impact on soil respiration rates is key to foresee potential changes in the role of forests in the terrestrial carbon cycle, which might change from a carbon sink to a carbon source as tree mortality increases (Kurz *et al.* 2008; Hicke *et al.* 2012).

Tree defoliation and mortality could also have pervasive effects on nitrogen (N) and phosphorus (P) cycles, two of the most important limiting nutrients in terrestrial ecosystems (e.g. Attiwill & Adams 1993). However, the number of existing studies addressing the effect of forest dieback on soil nutrients is low, particularly for P (Block, Knoepp & Fraterrigo 2013). The few N studies available have found mainly increases in soil N after tree mortality due to a reduction in vegetative uptake or changes in litter quantity and quality and its mineralization (e.g. Kizlinski *et al.* 2002; Morehouse *et al.* 2008). The case of P is however more complex. P availability might increase due to lower plant uptake after tree death (Block, Knoepp & Fraterrigo 2013). However, tree mortality also implies a reduction in root phosphatase activity (responsible of the mineralization of organic P, Schneider *et al.* 2001; George *et al.* 2011) and in the exudation of organic acids (responsible of the solubilization of mineral P, Jurinak *et al.* 1986; Hinsinger 2001). Therefore, the result of a decrease in root exudations (i.e. rhizodeposition) could translate into reductions in P availability underneath declining trees. Understanding the effects of tree mortality on N and P cycles is of paramount importance, since any change in the availability of these limiting nutrients might impact multiple processes after forest dieback such as forest productivity or vegetation recovery (e.g. Mladenoff 1987; Edburg *et al.* 2012).

In the long-term (at decades scale, following Hicke *et al.* 2012), the impacts of forest dieback on ecosystem function as a consequence of species replacements during secondary succession might be even more severe than the direct effects of tree defoliation and mortality (Hancock *et al.* 2008; Lovett *et al.* 2010; Barba *et al.* 2013). This situation would occur when the affected species is dominant (or co-dominant) in the forest and functionally different from

coexistent non-affected species susceptible to increase in abundance and eventually substitute the declining species. For example, in Californian forests affected by sudden oak death, Cobb, Eviner and Rizzo (2013) found that the strongest impact of this disease on the N cycle was not directly caused by the death of the affected *Notholithocarpus densiflorus*, but indirectly due to its substitution by *Umellularia californica*, a species with a higher litterfall %N. In order to predict the long-term effects of forest dieback on biogeochemical cycles, it is essential to compare the 'footprint' of affected and not affected (potentially replacement) species on ecosystem processes (Adams *et al.* 2010).

The aim of this study was to assess the impact of *Quercus suber* dieback on soil respiration rates and N and P availability in Mediterranean forests of southern Spain. Specifically, we measured *in situ* soil respiration, and ammonium, nitrate and phosphate availability during three consecutive years in six mixed oak forests affected by the decline of its dominant species, *Q. suber*. In the last decades, a severe decline of evergreen *Quercus* species (*Q. suber* and *Quercus ilex*) in southern Europe has been related to the attack by the exotic pathogen *Phytophthora cinnamomi,* very likely in combination with other stress sources such as climate change-type drought (Brasier 1996; Camilo-Alves, da Clara & Ribeiro 2013; Corcobado *et al.* 2013). We explored the direct effects of dieback, comparing the impact on soil variables of *Q. suber* trees with different health status, as well as its potential long-term indirect effects, comparing the "footprint" of *Q. suber* and coexistent late-successional species not affected by dieback (i.e. *Quercus canariensis* and *Olea europaea* var. *sylvestris*). The study was conducted in two contrasted seasons (i.e. spring and summer), given the large intra-annual variation in soil water content typical of Mediterranean ecosystems and its role on biogeochemical cycles (Sardans & Peñuelas 2005; Asensio *et al.* 2007). We developed spatially-explicit neighbourhood models that predicted the observed variation in ecosystem processes as a function of the size, identity, health status, abundance

and distribution of adult trees in the immediate neighbourhood. This is a novel approach for the study of ecosystem impacts of forest dieback, which is usually conducted at the stand level (e.g. Kizlinski *et al.* 2002; Orwig *et al.* 2008; Lovett *et al.* 2010). The neighbourhood models allowed us to characterize and compare the per capita effects of individual trees with different health status and of different species growing closely intermingled in the canopy. We tested the following three hypotheses. First, we predicted that *Q. suber* dieback would cause reductions in soil respiration rates and P availability given previous works showing reductions in belowground C allocation following disturbance (e.g. Edburg *et al.* 2011; Nave *et al.* 2011; Hicke *et al.* 2012). However, we expected an increase in N availability after dieback due to a reduction in N uptake, as suggested by published studies on other disease and insect-caused tree mortality (e.g. Hobara *et al.* 2001; Morehouse *et al.* 2008; Edburg *et al.* 2011). Second, we predicted different 'footprints' of coexistent species on the studied soil variables given their differences in relevant functional traits such as leaf litter chemistry (e.g. Aponte, Marañón & García 2010; Aponte *et al.* 2011), which would lead to long-term impacts on ecosystems. Third, we predicted that the effects of *Q. suber* dieback on soil processes would be of larger magnitude in spring than in summer, as spring represents the season of higher plant activity in Mediterranean systems (Bonilla & Rodà 1992; Tang & Baldocchi 2005). With this work we aim to provide valuable insights that contribute to fill the existent gap in knowledge on the ecosystem-level impacts of tree dieback in Mediterranean forests.

Material and methods

STUDY SITE

This study was conducted in Los Alcornocales Natural Park (Southern Spain), considered one of the largest *Quercus suber* L. forests within the Mediterranean Basin (Urbieta, Zavala & Marañón 2008). The climate is sub-humid Mediterranean, with mild and humid winters and

warm and dry summers. Annual mean temperature ranges from 15.4 to 17.3 ºC and annual mean rainfall varies from 720 to 1100 mm (period 1951-1999, Ninyerola, Pons & Roure 2005). The hydrological years of the study (i.e. 2010-2012) had contrasting rainfall conditions: the year 2010 was a wet year, with higher than average annual rainfall (1917 mm; 381 mm in spring and 43 mm in summer), the year 2011 was an average year (1145 mm; 363 mm in spring and 9 mm in summer), and 2012 was an extremely dry year (559 mm; 127 mm in spring and 0 mm in summer - data from a meteorological station located at the study area: 5°27′20′′W, 36°26′00′′N). These forests occur on acidic, nutrient-poor, sandy soils, derived from Oligo-Miocene sandstone, but sometimes they are interspersed with clayish soils derived from layers of marl sediments. The flora in the Alcornocales Natural Park is dominated by mixed sclerophyll forests, with *Q. suber* as the main species. In drier lowlands of the park with clayish soils, *Q. suber* coexists with the evergreen *Olea europaea* var. *sylvestris* Brot. forming open woodlands. In moister habitats with sandy soils, *Q. suber* appears intermingled with the deciduous *Quercus canariensis* Willd. forming closed forests. Structurally, open woodlands show lower tree densities and higher solar radiation in the understory than closed forests (Ojeda, Marañón & Arroyo 2000).

Quercus suber forests within the Natural Park suffer from severe problems of dieback driven by the soil-borne oomycete pathogen *Phytophthora cinnamomi* Rands, one of the most aggressive invasive pathogens on earth (Brasier 1992; Gómez-Aparicio *et al.* 2012). This pathogen destroys the root systems, killing fine roots and occasionally producing necrotic bark lesions in large roots (Weste & Marks 1987). The effect of *P. cinnamomi* in root systems can interact with drought stress and lead to a severe decrease in tree survival (Brasier 1996; Camilo-Alves, da Clara & Ribeiro 2013; Corcobado *et al.* 2013).Trees may die suddenly but death often takes several years (Weste & Marks 1987). No other tree or shrub species in the study area showed evident symptoms of dieback.

SAMPLING DESIGN AND NEIGHBOURHOOD CHARACTERIZATION

We selected 6 sites within the Natural Park, three situated in open woodlands of *Q. suber* and *O. europaea* and the other three in closed forests dominated by *Q. suber* and *Q. canariensis*. This selection allowed us to explore the ecosystem implications of *Q. suber* dieback in the two main mixed forest types of the region, covering an ample gradient of climate and soil conditions. At each site, a permanent 70 x 70 m plot was established and subdivided into a grid with 49 10 x 10 m subplots. At the centre of each subplot we established a sampling point, with 147 points per forest type (a total of 294).

To characterize local neighbourhoods, we mapped and identified all live and dead trees and shrubs around each sampling point. We determined a neighbourhood as a 15-m radius circle around each sampling point (Gómez-Aparicio *et al.* 2012; Ibáñez *et al.* 2015). In each neighbourhood we identified and mapped all trees taller than 1.5 m and with a diameter at breast height (d.b.h.) > 2 cm using a total station Leica TC 407 (Leica Geosystems, Heerbrugg, Switzerland). We measured the d.b.h. of each of the trees mapped (n = 1341 trees). In addition, we classified *Q. suber* trees into three different health categories: healthy, defoliated and dead (Gómez-Aparicio *et al.* 2012; Ibáñez *et al.* 2015). Although information on the time of death for *Q. suber* trees was not available, the decline of the species at the study plots is a relatively recent and progressive process, so dead trees (most of them still standing) can be considered to have occurred in the short term (< 10 years).

BIOGEOCHEMICAL MEASUREMENTS

Soil respiration rates were estimated using an alkali trap absorption method (Singh & Gupta 1977). We chose this static method because it allows extensive replication, and thus could be applied simultaneously in all the 294 sampling points of the study (Singh & Gupta 1977; Pumpanen, Longdoz & Kutsch 2010). Absorption methods have been effectively used in

previous studies and can be reliable for field measurements when they are implemented with due care minimizing possible errors (e.g. Joshi *et al.* 1991; Gallardo & Schlesinger 1994; Keith & Wong 2006; Barba *et al.* 2013). During spring (May) and summer (August) of 2011 and 2012 we located an alkali trap of 45 ml of NaOH 1.5N placed in a plastic vial of 60 ml (height 66 mm, top diameter 44.2 mm) at each sampling point. Each trap was covered with a cylindrical metal tin (height 153.5 mm, diameter 155 mm) that was turned upside down and pushed into the soil to a depth of 2 cm (Froment 1972). After 6 days, traps were closed with a cap and transported to the lab, where the carbon dioxide production was estimated by a titration of the excess of NaOH remaining in the trap with HCl, previous precipitation of carbonates with $BaCl_2$ (Froment 1972). Soil respiration rates were expressed in gCm^2 $year^{-1}$.

Nutrient availability was also measured at each sampling point using ionic exchange membranes (IEMs, types I-100 and I-200, Electropure Excellion, Laguna Hills, California). This method has been demonstrated to provide a useful alternative to traditional soil extraction for estimating soil inorganic N and P availability (Qian & Schoenau 2002; Durán *et al.* 2013). Moreover, nutrient concentrations measured by this method are strongly correlated to plant uptake of those nutrients (Schoenau & Huang 1991; Ziadi *et al.* 1999). We estimated soil N and P availability (NH_4–N, NO_3–N and PO_4–P) following the method developed by Durán *et al.* (2008) and Rodríguez *et al.* (2009). Both, anion and cation exchange membranes (2.5 x 2.5 cm) were positioned at a depth of 10 cm with a metal spatula and we ensured good contact between the membranes and the soil. The membranes were incubated for 30 days at each sampling point in spring (May) and summer (August) during 2010, 2011 and 2012. In the lab, the adsorbed nutrients in the membranes were extracted using 25 ml of 2 M KCl in 125ml flasks by orbital spinning for 1h at 200 rpm. We estimated nutrient concentration of the extracts by colorimetry, using a microplate reader (Asys Jupiter–Asys Hitech, Austria). Inorganic N concentration (NH_4–N and NO_3–N) was assessed

with the indophenols blue method (Sims, Ellsworth & Mulvaney 1995) and phosphate

concentration (PO_4–P) by the molybdenum blue method (Allen, Grimshaw & Rowland

1986). N and P availability were expressed as μgN(or P) $dm^{-2}day^{-1}$.

DATA ANALYSIS

Neighbourhood models of soil respiration and nutrient availability - For the analysis of our

data we applied likelihood methods and model selection (Johnson & Omland 2004; Canham

& Uriarte 2006; Gómez-Aparicio & Canham 2008). We fit separate models for each

combination of soil variable (soil respiration rates and ammonium, nitrate and phosphate

availability), forest type (woodland and closed forest) and season (spring and summer). Our

full model estimated two terms: 1) the average soil variable at each combination of study site

and year in the absence of specific effects of neighbouring trees ($a_{Site\text{-}Year}$ in equations 1 and

2), and 2) tree neighbourhood effects on soil variables, which are assumed to vary as a

function of a neighbourhood index (NI). We included these neighbourhood effects using both

a linear (1) and an exponential (2) model framework (for a similar approach, see Baribault &

Kobe 2011; Gómez-Aparicio *et al.* 2012):

Soil variable = $a_{Site\text{-}Year} + b_{Year}$ x NI $\hspace{3cm}$ (eqn 1)

Soil variable = $a_{Site\text{-}Year}$ x exp (b_{Year} x NI) $\hspace{2.5cm}$ (eqn 2)

The parameter b_{Year} defines the steepness of the variation in the soil variables due to

an increment in NI and was allowed to vary among years to account for inter-annual

differences in tree effects. The NI quantifies the net effect of *j=1,…,n* neighbouring trees of

i=1,…,s species on the soil variable and it is related directly to the size (d.b.h.) of the

neighbouring trees and inversely to the distance to neighbours (Gómez-Aparicio & Canham

2008; Boyden *et al.* 2012):

$$NI = \sum_{i=0}^{s} \sum_{j=0}^{n} \lambda_i \frac{dbh_{ij}^{\alpha}}{dist_{ij}^{\beta}} \hspace{3cm} \text{(eqn 3)}$$

where dbh_{ij} is the diameter at breast height of each of the jth neighbouring tree of the ith species and $dist_{ij}$ is the distance of the jth neighbouring tree of the ith species to the sampling point. The parameters α and β estimated by the model determine the shape of the effect of the tree size (α) and the distance to the neighbour (β) on the index.

In order to explore differences between neighbours of different species or health status on their effects on soil variables, we multiplied the net effect of each individual tree by a per capita coefficient (λ) that ranged from -1 to 1. We tested three different candidate models of decreasing complexity (i.e. decreasing number of λ parameters) to assess the effects of the tree community on the studied soil variables. First, we fit a model that explicitly considered the effect of trees of different health status and species on soil properties ('Health + Tree species' model). This model calculated 4 different λ values (healthy, defoliated and dead *Q. suber* in both forest types, and *O. europaea* in woodlands or *Q. canariensis* in closed forests). Second, we fit a model that ignored the health status of *Q. suber* and only considered differences among tree species on their impacts on soil variables ('Tree species' model). This model calculated 2 λ values, one for *Q. suber* and one for the coexisting tree species (*O. europaea* or *Q. canariensis* depending on the forest type). And third, we fit a null model that ignored tree effects on soils ('No tree' model) and therefore calculated soil variables just as a function of the site and year of study. Moreover, we compared models that considered variability among sites and/or years in 1) background values of soil variables ($a_{Site-year}$ parameter) and 2) tree effects (b_{Year} parameter) with simpler models that ignored these sources of spatio-temporal variability in soil variables.

Parameter estimation and model selection - Soil variables were modelled with maximum likelihood using a simulated annealing algorithm (Goffe, Ferrier & Rogers 1994). Model comparisons were conducted following information theory principles and Akaike Information Criterion corrected for small sample size (AICc, Burnham & Anderson 2002). Lower AIC_c values indicate best model performance. Asymptotic two-unit support intervals were calculated for each estimated parameter. The goodness-of-fit of the best models was determined with the R^2 of the regression between observed and predicted data. The slope of that regression was used to measure model bias, with an unbiased prediction having a slope ~1. Spatial autocorrelation in the residuals was analyzed with Mantel tests (Legendre & Fortin 1989), whereas temporal correlation was analyzed exploring lack of patterns in the plots of residuals against year. However, it is important to highlight that likelihood-based inference is very robust even in cases of lack of independence, with deviations from independence mostly resulting in underestimates of variance terms but not in biased parameters values (Hubbell *et al.* 2001; Uriarte *et al.* 2004). All statistical analysis were performed using R 3.0.2 (R Core Team 2013) and the 'likelihood' package (Murphy 2012).

Results

SOIL RESPIRATION RATES

All models produced unbiased estimates of soil respiration rates (i.e. slopes of observed vs. predicted were close to 1) and explained from 25 to 68% of the data variation. Models did not show spatial or temporal autocorrelation in their residuals with one exception (the null model in closed forests in spring, see Table S1 and Fig. S1 in Supporting Information). Most of the best models (3 of 4) included the effects of the tree community (i.e. 'Health + Tree species' or 'Tree species' models) on respiration rates. Differential effects of *Q. suber* trees depending on their health status were detected in the two forest types, but only in summer (i.e. the 'Health +

Tree species' model had the lowest AIC$_c$, Table 1). Neighbourhoods dominated by healthy *Q. suber* trees had higher soil respiration rates than those dominated by defoliated or dead *Q. suber* trees (Figs. 1b,d). We detected similar soil respiration rates in neighbourhoods dominated by healthy *Q. suber* compared to neighbourhoods dominated by the coexistent species (see overlapping values of λ parameters in Tables S2 and S3 in Supporting Information) (Fig. 1). No inter-annual differences were found in the tree effects (no differences in parameter b_{Year} among years, Tables S2 and S3).

We found important variation among seasons and forest types in the characteristics of the footprint of individual trees on soil respiration rates. In woodland sites, a large α value (>2) in spring indicated neighbour effects that were disproportionally large relative to the tree size, whereas a α~0 in summer indicated effects that scaled with neighbour density, regardless of the size of individual trees (Table S3). The decay in the tree effect in woodlands (controlled by parameter β) was steeper in spring than in summer (Fig. 2a, Table S3). In closed forests (where tree effects were only detected in summer), the footprint of individual trees on soil properties increased strongly with tree size and decreased steeply with distance (Fig. 2a, Table S3).

SOIL N AVAILABILITY

Models produced unbiased estimates of NH_4^+ and NO_3^- availability (slope ~ 1) and accounted from 8 to 43% of the variation in the data. Model residuals did not show temporal or spatial autocorrelation (Table S1, Fig. S1). For all combinations of nitrogen variable, season and forest type, models that considered the effects of the tree community offered a much better fit to the data than models that ignored these effects (Table 1). Most of those models (6 of 8) also included differential impacts of *Q. suber* trees varying in health status (i.e. the 'Health + Tree species' model had the lowest AICc). In woodlands, NH_4^+ and NO_3^- availability was

lower in neighbourhoods dominated by dead and defoliated trees than in neighbourhoods dominated by healthy *Q. suber* trees (Figs. 3b and 4b). However, the opposite pattern was detected in closed forests: NH_4^+ and NO_3^- availability was higher in neighbourhoods dominated by dead trees than in those dominated by healthy trees (Figs. 3c,d and 4c,d). Differences in the effects of neighbours with different health status were detected in both seasons, but more consistently in summer. Among species, our results showed differential impacts of healthy *Q. suber* and the coexistent tree species on N variables, as indicated by non-overlapping λ values in most situations (Tables S2 and S3). In woodlands, NH_4^+ and NO_3^- availability was higher in *Q. suber* than in *O. europea* neighbourhoods in most cases (Figs. 3a,b and 4a,b). In closed forests, on the contrary, *Q. suber* neighbourhoods had lower NH_4^+ and NO_3^- availability than neighbourhoods dominated by the co-existent *Q. canariensis*, but these differences disappeared in summer (Figs. 3c,d and 4c,d). In general, no differences among years were detected in tree effects.

The influence of neighbour size (α parameter in the NI function (equation 3)) on N availability was quite variable among forms of nitrogen, seasons and forest types. The effect of neighbour size on N availability varied from disproportionally large effects relative to tree size (e.g. NO_3^- in summer in woodlands) to virtually null (e.g. NO_3^- in spring in woodlands) for which N availability was only proportional to tree density (Tables S2 and S3). The values of the β parameter (which controls the decline in neighbour effects with distance from the tree) were always higher in spring than in summer, indicating much more localized tree effects on N availability in spring. Among forest types, the decay of tree effects with distance was steeper in woodlands than in closed forests for NO_3^-, but not for NH_4^+ (Figs. 2b,c).

All models produced unbiased estimates of PO_4^{3-} availability (slope ~ 1) and explained from 17 to 31% of its variation (Table 1). Model residuals did not show temporal or spatial autocorrelation, except for a slight spatial autocorrelation for closed forests in summer (Table S1, Fig. S1). Most of the best models (3 of 4) included the effects of the tree community on PO_4^{3-} availability. However, differences among *Q. suber* trees of different health status were only found in summer (i.e. lowest AICc for the 'Health + Tree species' model, Table 1). In both forest types, neighbourhoods dominated by defoliated and dead trees had lower PO_4^{3-} availability than neighbourhoods dominated by healthy *Q. suber* trees (Figs. 5b,d). Among species, healthy *Q. suber* neighbourhoods had generally higher levels of PO_4^{3-} availability than *O. europaea* (woodlands) and *Q. canariensis* (closed forests) neighbourhoods, but this effect varied between seasons (Fig. 5, see λ in Tables S2 and S3). No differences in the tree effects were detected among years, except for woodlands in summer (see b_{Year} in Tables S2 and S3).

The influence of neighbour size on the effect of trees on PO_4^{3-} availability varied among seasons and forest types. In woodlands, the effect of neighbour size on the influence of trees was larger in spring (α~1.5) than in summer (α~0.5) (Table S2). In closed forests, where the effect of trees was detected just in summer, tree size had a strong effect on PO_4^{3-} availability (Table S3). The decay of tree effect in distance was always steeper in summer than in spring and in woodlands than in closed forests (Fig. 2d, Tables S2 and S3).

Discussion

Our study provides compelling evidence that *Q. suber* dieback leads to important alterations in biogeochemical cycles of Mediterranean oak forests. We found a strong spatial concordance among the distribution and health status of individual trees and the soil variables

studied (i.e. soil respiration rates and nutrient availability) consistently across space (i.e. different forest types) and time (i.e. different years and seasons). To our knowledge this study represents the first attempt to connect complex neighbourhoods (i.e. composed by trees of different species, sizes and health status) with the spatiotemporal variability of soil processes, allowing the estimation of per-capita tree effects on ecosystems in a context of tree dieback.

DIRECT EFFECTS OF *Q. SUBER* DIEBACK ON BIOGEOCHEMICAL CYCLES

Our results indicate that the decline and death of *Q. suber* translate into an important reduction in soil respiration rates, in agreement with our first hypothesis. In fact, our models predicted reductions in soil respiration rates as high as 20% in neighbourhoods dominated by dead trees compared to neighbourhoods dominated by healthy trees (Fig. 1). These findings might be linked to a decrease in root and rhizosphere respiration in the first years following disturbance (Nuckolls *et al.* 2009; Edburg *et al.* 2011; Flower, Knight & Gonzalez-Meler 2013). Root pathogens as *P. cinnamomi* destroy the root system and reduces tree productivity (Cherubini *et al.* 2002). This attack could lead to lower belowground C allocation and autotrophic respiration, as it has been demonstrated in girdling experiments simulating pathogen attacks (Högberg & Read 2006; Nuckolls *et al.* 2009; Levy-Varon, Schuster & Griffin 2012; Levy-Varon, Schuster & Griffin 2014). Recent literature on insect-driven tree mortality has suggested that forest dieback might result in large alterations in forest-atmosphere C exchange, shifting the role of forests from a C sink to a C source (Kurz *et al.* 2008; Hicke *et al.* 2012). However, our results suggest that in forests affected by pathogen-driven mortality a decrease in total soil respiration rates might attenuate C losses, at least in the short term, weakening the impact of pathogen-induced tree mortality on the net C exchange between the forest and the atmosphere.

Quercus suber dieback altered both N and P availability, but the impacts on P were of larger magnitude than on N. Our models predicted reductions in P as high as 50% in neighbourhoods dominated by dead *Q. suber* trees compared to healthy neighbourhoods (Fig. 4),

Therefore, these results confirm our first hypothesis and are consistent with a mechanistic explanation based on a reduction in root exudation and rhizodeposition after mortality (Högberg *et al.* 2001; Xiong *et al.* 2011). The decrease in P availability as a consequence of a reduction in root activity after *Q. suber* dieback would support the idea that root phosphatase plays a key role in P availability for plants and microorganisms in Mediterranean forest systems (Schneider *et al.* 2001). Our results also agree with those obtained by the only previous study that has analysed the implications of *P. cinnamomi*-induced plant mortality on P availability (Shearer *et al.* 2009). The reductions in P caused by dieback are of particular relevance in Mediterranean systems, where P is usually considered the main limiting nutrient (e.g. Sardans, Rodà & Peñuelas 2004; Morillas *et al.* 2012) and has been shown to constrain microbial biomass, tree growth and seedling performance (Sheriff, Nambiar & Fife 1986; Gallardo & Schlesinger 1994; Gómez-Aparicio *et al.* 2008). Therefore, a decrease in P availability as a consequence of tree dieback would limit even further demographic and ecosystem processes in Mediterranean forests.

Unlike P, the sign of the effect of *Q. suber* dieback on N availability varied among forest types (i.e. woodlands vs. closed forests). Our first hypothesis of positive effects of tree mortality on N availability was supported only in closed forests. This hypothesis was based on previous studies that showed a reduction in N uptake following insect outbreaks or drought-induced mortality (e.g. Kizlinski *et al.* 2002; Clow *et al.* 2011; Wang *et al.* 2012). The fact that our hypothesis was not supported in open woodlands suggests that mechanisms other than plant uptake were driving N availability in these systems. In particular, post-

mortality alterations of microclimatic conditions could explain the results found in woodlands. In these forests, gaps opened after tree death were of higher extent than in closed forests due to their lower tree density, leading to much stronger changes in microclimate (i.e. higher light and lower moisture availability, J.M. Ávila *et al.* unpublished data). These microclimatic alterations in large gaps could bring a reduction in N mineralization rates and N availability (Zhang & Zak 1995). Overall, an important implication of our results is that the sign of the effect of tree dieback on essential nutrients such as N and P can be opposite, depending very much on forest structure. This decoupling between the N and P cycles might in turn impact the C cycle, with important negative effects on primary productivity and organic matter decomposition (Finzi *et al.* 2011).

Our neighbourhood approach allowed us to assess the effect of tree size and distance to neighbour trees on the studied soil variables. Previous studies have highlighted the strong influence of tree size in explaining the spatial patters of soil respiration or nutrient availability (Ludwig *et al.* 2004; Søe & Buchmann 2005). Although we found a high variability in the effects of neighbour size on soil respiration rates and nutrient availability, our results make a case for the disproportionately large effect of big trees on the studied variables ($\alpha > 2$). This finding, together with the fact that *Phytophthora*-driven mortality usually affects medium to large size canopy trees (Cobb *et al.* 2012), implies that *Q. suber* dieback is a disturbance with a large capacity to alter ecosystem function. Regarding the role of distance, we found a strong variability in the shape of the tree footprints on soil variables among forest types and seasons (Fig. 2). Tree effects on the studied soil variables extended generally further in closed forests than in woodlands and in spring than in summer. The strong spatial (forest type) and temporal (seasonal) variability in the spatial extension of tree effects confirms for Mediterranean forests the inherent complexity of the spatial component of tree effects on ecosystems

(Gómez-Aparicio & Canham 2008), and suggests that it should be considered in future studies in order to gain a solid understanding of dieback impacts on ecosystem functioning.

INDIRECT EFFECTS OF *Q. SUBER* DIEBACK ON BIOGEOCHEMICAL CYCLES

In the long term, the process of secondary succession after tree mortality might induce species replacements that could lead to indirect impacts on ecosystem processes (e.g. Lovett *et al.* 2006; Loo 2009; Lovett *et al.* 2010). In agreement with our second hypothesis, we found differences among species in their effects on soil variables that could translate into important indirect changes in biogeochemical cycles due to the substitution of *Q. suber* by non-declining coexistent species. However, our models also indicated that the direction of such changes might vary strongly among ecosystem processes. Thus, we did not detect species-specific differences in soil respiration rates, likely influenced by similar root maintenance respiration rates among species (Martínez *et al.* 2002), but found important differences in nutrient availability (i.e. N and P). Such differences might be related to contrasting litter quality between species. Neighbourhoods dominated by *O. europaea* - a species characterized by its low litter quality (Rodríguez Pleguezuelo *et al.*, 2009, J.M. Ávila *et al.*, unpublished data) - had soils with lower N and P availability than *Q. suber* neighbourhoods, whereas neighbourhoods dominated by *Q. canariensis* - with a nutrient-rich litter (Aponte *et al.* 2011) - had soils with higher N availability than *Q. suber* neighbourhoods. A relevant implication of this result is that the indirect effects of the mortality of a given tree species will be strongly dependent on the identity of the replacement species, leading to different long-term ecosystem implications that can vary from acceleration to deceleration of nutrient cycles.

TEMPORAL VARIATIONS IN THE EFFECTS OF *Q. SUBER* DIEBACK ON

BIOGEOCHEMICAL CYCLES

In Mediterranean ecosystems, the strong inter- and intra-annual variability of soil water

availability have a profound effect on ecosystem functioning since water is the main factor

controlling above- and belowground processes such as photosynthesis, decomposition or soil

respiration (Asensio *et al.* 2007; Galmés, Medrano & Flexas 2007). However, how the

temporal variation of water availability affects the impacts of forest dieback on ecosystems

has not been explored yet. Our models showed low inter-annual but high intra-annual

variation in the ecosystem impacts of tree dieback. We detected no substantial differences in

the impacts of tree dieback among the studied years, even though they had contrasting

climatic conditions (see Study site). However the impacts of *Q. suber* dieback varied strongly

within the year. In fact, the effects of tree health status on soil variables were detected mainly

in summer, contrary to our third hypothesis. The differences in the effects between seasons

could be explained by the fact that during spring not only the tree activity is high, but also the

activity of microbes and herbaceous vegetation (Jackson *et al.* 1988). For instance, a previous

study conducted in a Mediterranean oak savanna ecosystem found that an increase in grass

cover during spring caused a reduction in the spatial variation of soil respiration rates,

weakening the differences in soil CO_2 fluxes among soils under and outside oak canopies

(Tang & Baldocchi 2005). Therefore, the likelihood to detect differences in C and nutrient

cycling between healthy and declining or dead trees would be much lower during spring than

during summer. Tree neighbourhood effects might also be weaker in spring as a consequence

of the high soil moisture content in this season, which can keep the soil well connected

hydrologically leading to high respiration and mineralization rates in the whole system

(Gallart *et al.* 2002). The strong seasonal variability of the ecosystem consequences of *Q.*

suber dieback highlights the importance of considering the temporal component of these processes to obtain a comprehensive understanding of the implications of this disturbance for Mediterranean systems.

CONCLUSIONS

Forest dieback is a concerning issue worldwide and particularly in water-limited Mediterranean regions, where several forests are affected by pathogen-induced and/or drought-induced tree mortality (Carnicer *et al.* 2011; Garbelotto & Pautasso 2012). This study provides novel evidence on the effects of the spatial distribution of intermingled trees of different species and health status on three of the most important biogeochemical cycles (i.e. C, N and P). Moreover, to our knowledge this is the first study that assesses the impacts of tree dieback on C, N and P cycles simultaneously. Our results support that the decline and mortality of a particular species in a mixed forest might have important short- and long-term impacts on different biogeochemical cycles that do not always go in the same direction (i.e. varying from positive to negative effects), leading to potential decoupling among cycles. Our neighbourhood models also suggested that large trees - which are those more frequently affected by decline and mortality (Griffin, Turner & Simard 2011; Cobb *et al.* 2012) - had disproportionate impacts on soil respiration and nutrient availability, conferring to the process of forest dieback an extremely high capacity to modify biogeochemical cycles.

The findings of this study are of special relevance in a context of tree dieback induced by *P. cinnamomi*. This pathogen, considered one of the most aggressive invasive species on earth, has invaded most temperate and subtropical regions in the world (Hansen 2015) and has already devastated important areas in Australia (Cahill *et al.* 2008) and Europe (Brasier 1996). The negative effects of this pathogen are expected to increase in the near future due to the positive effects of warming temperatures on pathogen activity and to the expansion of its

potential range to higher latitudes where low temperatures currently limit its establishment (Brasier 1996; Sturrock *et al.* 2011). Therefore the spatial extension and the magnitude of the ecosystem impacts of tree mortality detected in this work might be expected to increase in future years, which could have profound implications for ecosystem functioning in forests worldwide.

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Data accessibility

Data available from the Dryad Digital Repository doi:10.5061/dryad.6nd4k (Avila *et al.* 2016)

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Supporting information

Additional supporting information may be found in the online version of this article:

Table S1 Results of Mantel tests for spatial autocorrelation.

Figure S1 Plots of the residuals against the sequence of data collection (years).

Table S2 Parameter estimates and support intervals for the best model selected for each combination of soil variable and season in woodlands.

Table S3 Parameter estimates and support intervals for the best model selected for each combination of soil variable and season in woodlands and closed forests.

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Table 1. Comparison of alternative models for soil respiration rates and N and P availability in the two forest types (woodlands and closed forests) and seasons (SPR, spring; SUM, summer) using the Akaike Information Criterion corrected for small sample sizes (AIC_c). ΔAIC_c represents the differences between the AIC_c of the model and the AIC_c of the best model (i.e. the model with the lowest AICc, indicated in bold). 'Health + Tree species' models include differences among tree species and health status in their effects on soils, 'Tree species' models consider only differences among tree species, and 'No tree' models do not consider any tree effects. b_{Year} (eqn. 1 and 2 in the text) shows the existence of inter-annual differences in tree effects on soil variables (Y, YES; N, NO). 'Mod' indicates a linear (Lin) or an exponential (Exp) relationship between soil variables and tree effects. 'Par' is the total number of parameters in the best model. The slope ('SL') and R^2 for the relationship between predicted and observed values are also given.

| Type of forest	Soil variable	Season	ΔAICc			b_{Year}	Mod	Par	SL	R^2
			Health + Tree species	Tree species	No tree					
Woodlands	CO_2	SPR	4.89	**0.00**	3.48	N	Exp	12	1.00	0.25
		SUM	**0.00**	2.24	12.64	N	Lin	14	0.97	0.68
	NH_4^+	SPR	7.59	**0.00**	2.88	N	Lin	12	0.96	0.43
		SUM	**0.00**	41.91	113.20	Y	Lin	19	1.06	0.36
	NO_3^-	SPR	6.27	**0.00**	8.33	N	Lin	12	0.96	0.08
		SUM	**0.00**	13.34	22.00	N	Lin	11	0.99	0.18
	PO_4^{3-}	SPR	7.58	**0.00**	1.91	N	Exp	15	1.00	0.31
		SUM	**0.00**	5.91	19.67	N	Exp	17	0.94	0.17
Closed forests	CO_2	SPR	13.25	8.94	**0.00**	-	-	7	0.99	0.42
		SUM	**0.00**	50.95	61.20	N	Lin	14	0.97	0.67
	NH_4^+	SPR	**0.00**	17.99	22.20	N	Lin	17	0.92	0.18
		SUM	**0.00**	12.63	13.71	Y	Lin	19	0.97	0.29
	NO_3^-	SPR	**0.00**	65.70	105.32	N	Lin	14	1.09	0.30
		SUM	**0.00**	26.45	58.46	N	Lin	17	0.99	0.13
	PO_4^{3-}	SPR	8.00	5.71	**0.00**	-	-	10	1.00	0.18
		SUM	**0.00**	66.53	136.15	Y	Lin	19	0.97	0.17
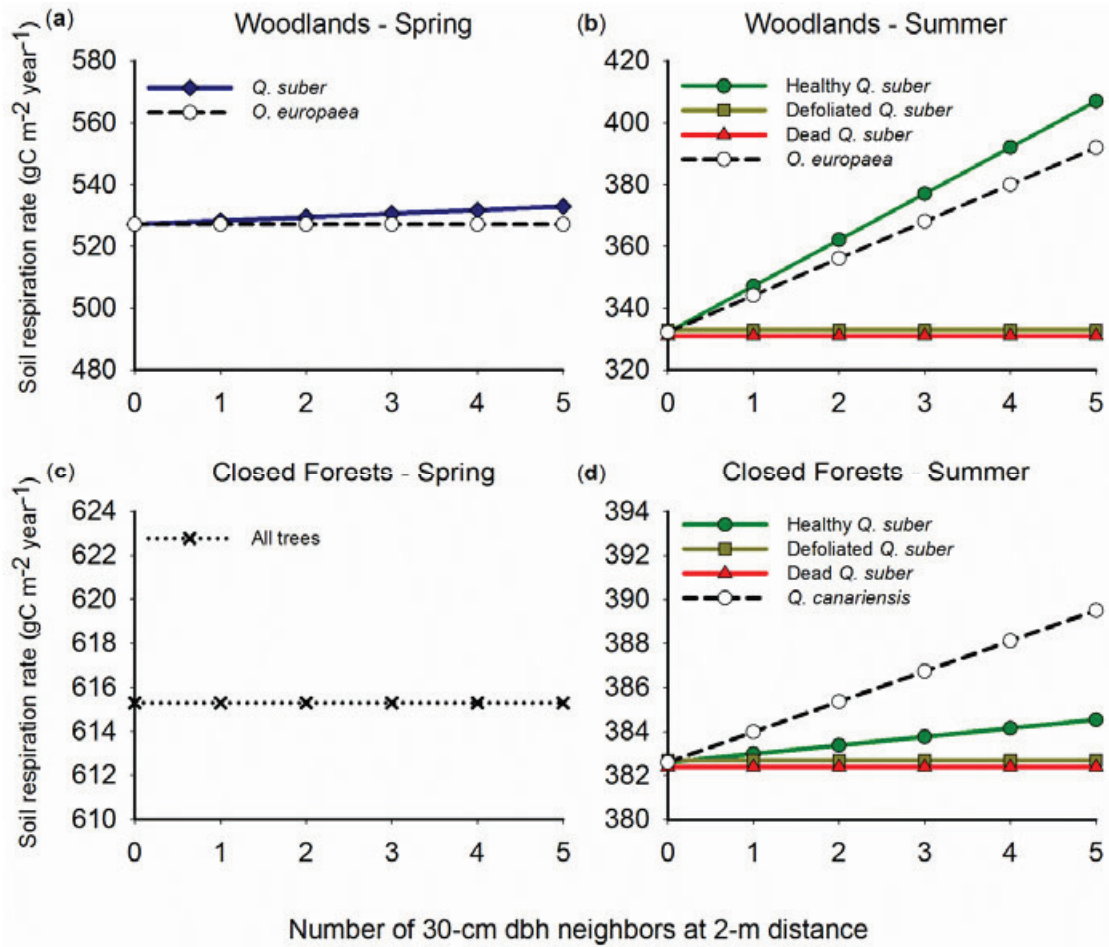
Fig. 1. Predicted effects of variation in neighbour identity and quantity on soil respiration rates in woodlands during spring (a) and summer (b), and in closed forests during spring (c) and summer (d). Predictions were done using parameter values from best models (Supporting Information Tables S2, S3). The number (0-5) of average-sized neighbours (i.e. d.b.h. = 30 cm) at 2-m distance represent the range of neighbour abundance found in our forests for that distance.
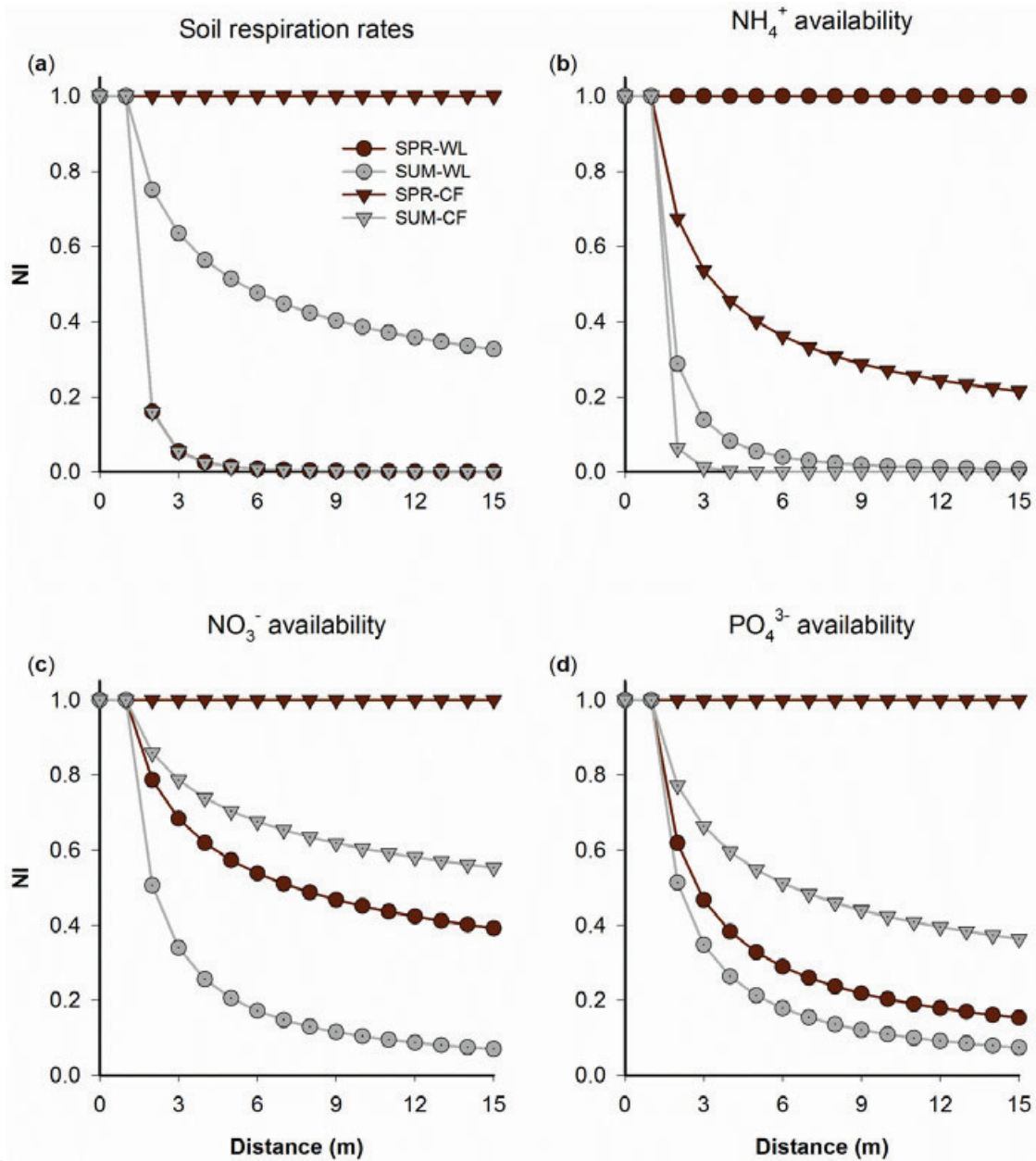
Fig. 2. Predicted decline in the neighbourhood index (NI) as a function of distance to a neighbour for the soil respiration rates (a) and NH_4^+ (b), NO_3^- (c) and PO_4^{3-} availability (d). NI is calculated using equation 3 and values of β parameter given in Supporting Information Table S2 and S3 for best models ($\alpha = 0$ and $\lambda = 1$ for simplicity of presentation of results). Season: SPR = spring and SUM = summer. Forest type: WL = woodlands and CF = closed forests.
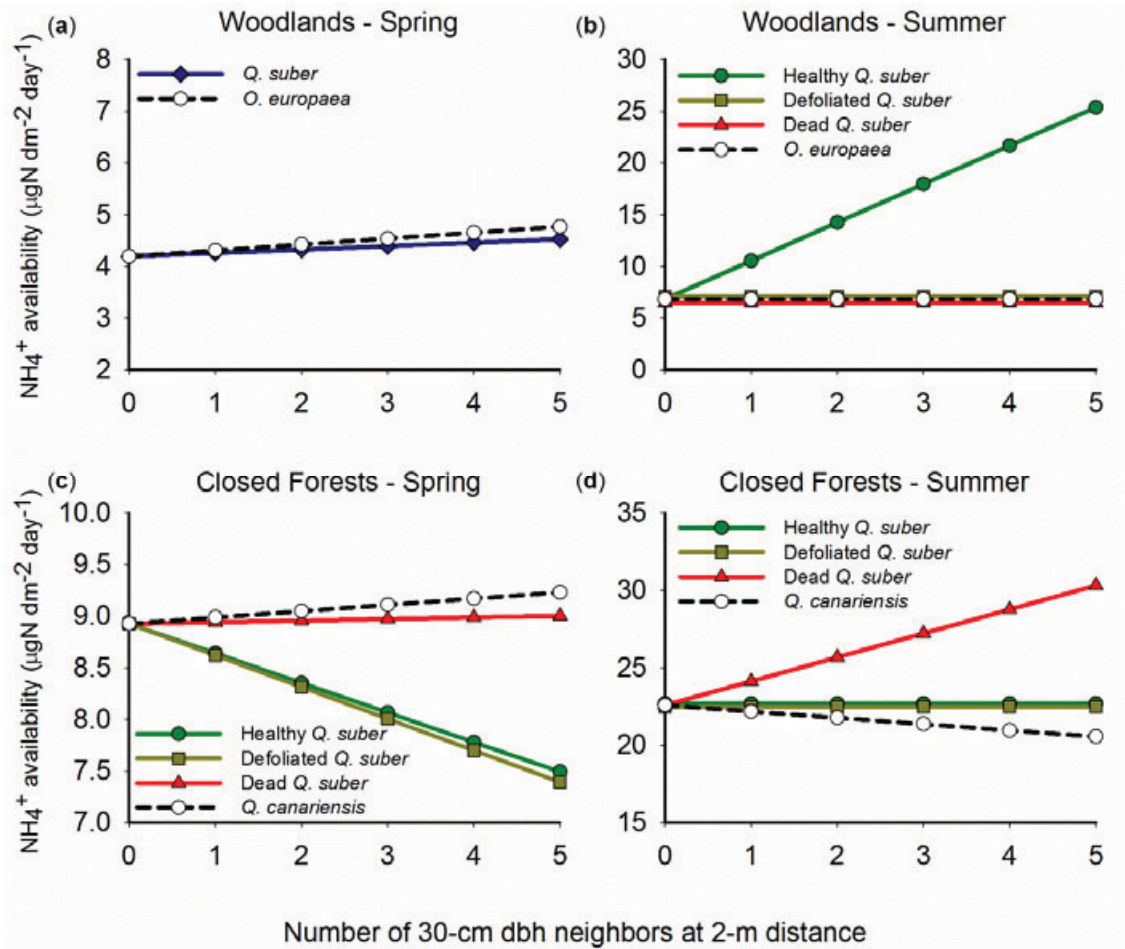
Fig. 3. Predicted effects of variation in neighbour identity and quantity on NH_4^+ availability in woodlands during spring (a) and summer (b), and in closed forests during spring (c) and summer (d). Predictions were done using parameter values from best models (Supporting Information Tables S2, S3). The number (0-5) of average-sized neighbours (i.e. d.b.h. = 30 cm) at 2-m distance represent the range of neighbour abundance found in our forests for that distance.
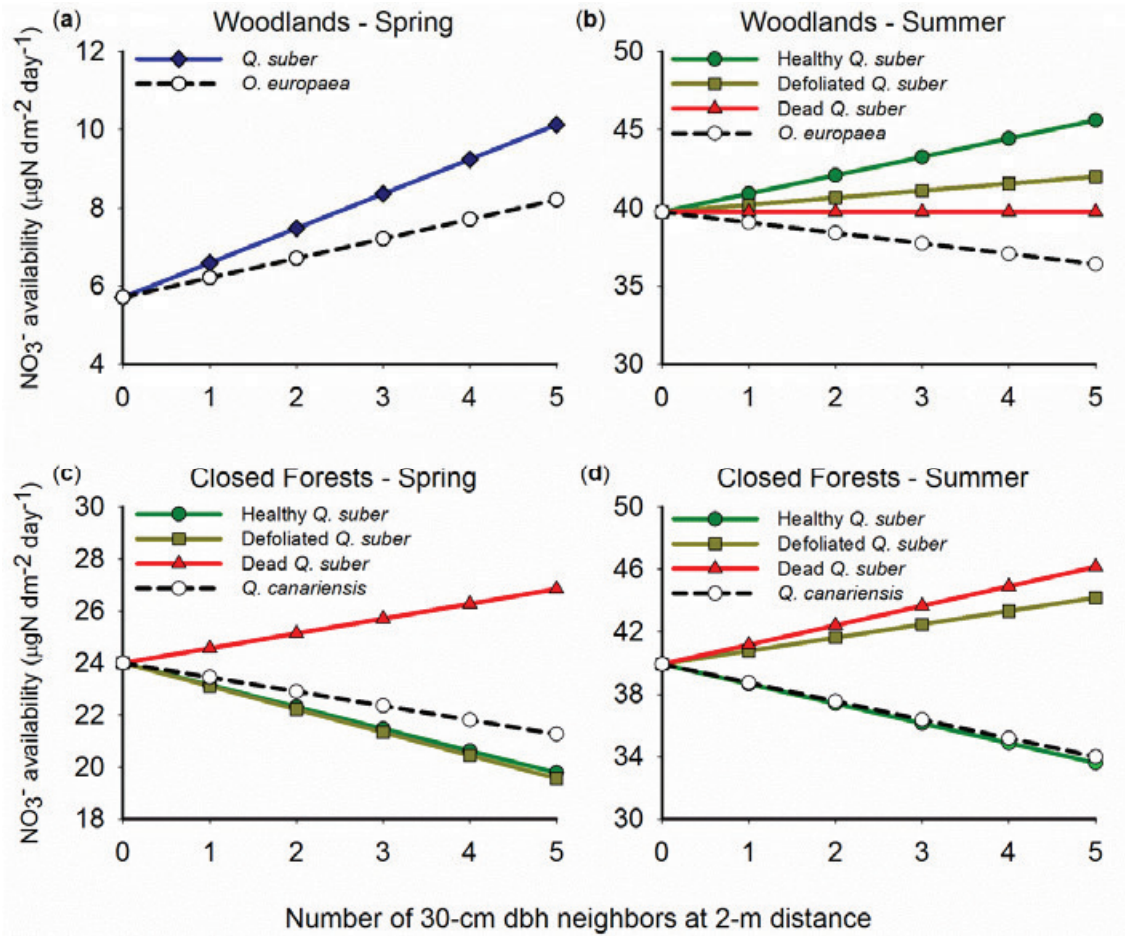
Fig. 4. Predicted effects of variation in neighbour identity and quantity on NO_3^- availability in woodlands during spring (a) and summer (b), and in closed forests during spring (c) and summer (d). Predictions were done using parameter values from best models (Supporting Information Tables S2, S3). The number (0-5) of average-sized neighbours (i.e. d.b.h. = 30 cm) at 2-m distance represent the range of neighbour abundance found in our forests for that distance.
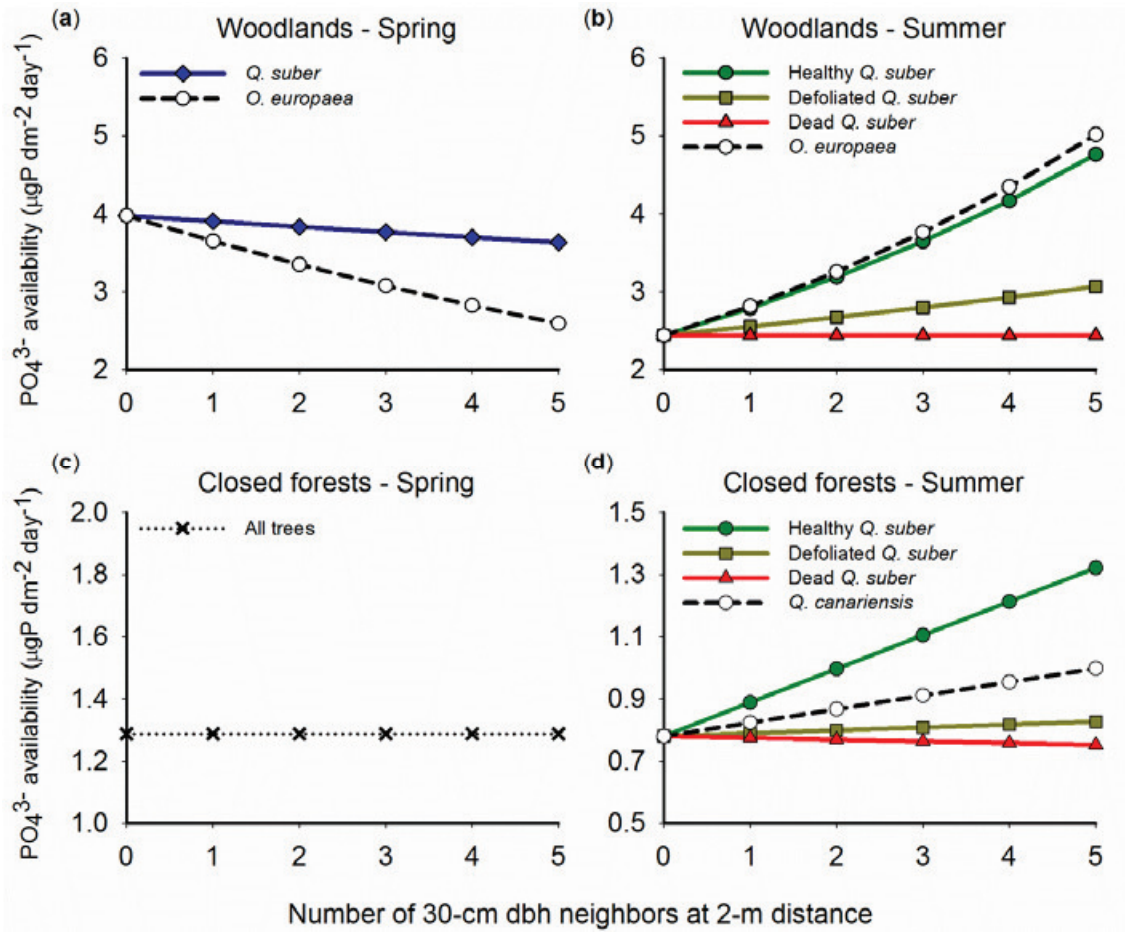
Fig. 5. Predicted effects of variation in neighbour identity and quantity on PO_4^{3-} availability in woodlands during spring (a) and summer (b), and in closed forests during spring (c) and summer (d). Predictions were done using parameter values from best models (Supporting Information Tables S2, S3). The number (0-5) of average-sized neighbours (i.e. d.b.h. = 30 cm) at 2-m distance represent the range of neighbour abundance found in our forests for that distance.