Spatial patterns of soil pathogens in declining Mediterranean forests: implications for tree species regeneration

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Main body: 6461 words

Introduction: 885 words

Material and Methods: 2507 words

Results: 945 words

Discussion: 2048 words

Number of figures: 5

Number of tables: 2

Supporting information: 3 appendices

Summary

- Soil-borne pathogens are a key component of the belowground community due to the significance of their ecological and socio-economic impacts. However, very little is known about the complexity of their distribution patterns in natural systems. Here we explored the patterns, causes and ecological consequences of spatial variability in pathogen abundance in Mediterranean forests affected by oak decline.
- We used spatially-explicit neighborhood models to predict the abundance of soil-borne pathogen species (*Phytophthora cinnamomi*, *Pythium spiculum* and *Pythium* spp.) as a function of local abiotic conditions (soil texture) and the characteristics of the tree and shrub neighborhoods (species composition, size and health status). The implications of pathogen abundance for tree seedling performance were explored by conducting a sowing experiment in the same locations where pathogen abundance was quantified.
- Pathogen abundance in the forest soil was not randomly distributed, but exhibited spatially predictable patterns influenced by both abiotic and particularly biotic factors (tree and shrub species). Pathogen abundance reduced seedling emergence and survival, but not in all sites or tree species.
- Our findings suggest that heterogeneous spatial patterns of pathogen abundance at fine spatial scale can be important for the dynamics and restoration of declining Mediterranean forests.

Key words: forest decline, neighborhood models, *Quercus suber*, regeneration dynamics, soil-borne pathogens, soil texture, species coexistence

Introduction

Soil-borne pathogens are a key component of the belowground community due to the significance of their ecological and socio-economic impacts. For instance, several species of *Phytophthora* and *Pythium*, two well-known genera of soil-borne oomycete pathogens, are common causes of agricultural diseases (Erwin & Ribeiro, 1996; Martin & Loper, 1999) and are involved in the massive decline of *Quercus*, *Castanea*, *Eucalyptus* and other trees in forests worldwide (Brasier *et al*., 1993; Brasier, 1996; Rizzo *et al*., 2005; Romero *et al*., 2007; Cahill *et al*., 2008). Not surprisingly, understanding when and where soil-borne pathogens are more likely to cause destructive epidemics has long been an important topic of agricultural research. In natural systems, however, much less is known about the complexity of their distribution patterns, which remains as one of the most challenging aspects of studying belowground organisms (Ettema & Wardle, 2002; Reinhart & Clay, 2009).

The pathogen landscape can be affected by a variety of abiotic and biotic factors (Martin & Loper, 1999; Agrios, 2005). Among these factors, vegetation is a major determinant of the spatial distribution of soil pathogens both across and within plant species (Wardle, 2002). Plant species can affect soil-borne pathogen populations directly by providing living host tissue, or indirectly by generating environmental conditions that affect their reproductive activity (Augspurger, 1990). In forest ecosystems, for example, pathogen populations can benefit from the wetter microclimatic conditions found in the shaded understory compared to open environments (Gómez, 2004; Matías *et al*., 2011). On the other hand, understory environments tend to have more fertile soils than gaps and sustain a larger microbial community, which could negatively affect soil-borne pathogens through competition for resources and colonization space (Weste *&* Marks, 1987; Aponte *et al*., 2010).

74 Depending on the relative importance of the different mechanisms, the net effect of a
75 given woody species on soil pathogen abundance might range from highly positive to
76 largely negative. Species-specific effects could be obscured by intra-specific variation
77 in plant traits such as size or tolerance to infection (Packer & Clay, 2000, 2003;
78 Reinhart & Clay, 2009). Clearly, further research is needed in order to determine
79 whether and how the mosaic of plant species and gaps in the forest canopy translate into
80 a mosaic of soil pathogen abundance and composition.

81 Just as adult plants can drive the abundance and activity of soil-borne pathogens
82 in forests, pathogens can in turn shape regeneration dynamics of the plant community,
83 because seedlings are particularly vulnerable to pathogens when roots are still
84 structurally simple and poorly lignified (Packer & Clay, 2003; O'Hanlon-Manners &
85 Kotanen, 2006). Moreover, because pathogens vary in pathogenicity of different tree
86 species (Augspurger & Wilkinson, 2007; Moralejo *et al*., 2009; Reinhart *et al.,* 2010),
87 they can affect the composition of the seedling bank. For example, it has been proposed
88 that shade-intolerance tree species are more susceptible to soil-borne diseases than
89 shade-tolerant species, and that such susceptibility might be a key mechanism excluding
90 them from the understory (Vaartaja 1962, O'Hanlon-Manners & Kotanen, 2004;
91 McCarthy-Neumann & Kobe, 2008). If differential responses to soil pathogens exist,
92 then interactions with soil-borne pathogens may contribute to species coexistence across
93 heterogeneous forests.

94 The objective of this paper was twofold. First, we aimed to advance the
95 understanding of the pathogen landscape by developing spatially-explicit neighborhood
96 models that explain the importance of abiotic (soil texture) and biotic (tree and shrub
97 community) drivers of soil-borne pathogen abundance in Mediterranean forests affected
98 by cork oak (*Quercus suber*) decline. We built upon established methods for

characterizing neighborhood processes (Canham & Uriarte, 2006), and applied these methods for the first time on soil organisms in close association with plants. A main advantage of the neighborhood approach is that it allows linking soil pathogen abundance with the distribution of neighboring individuals of the whole woody community. It therefore captures the complexity of natural plant communities, where a particular volume of soil is not necessarily occupied by just one host species.

The second objective of our study was to explore the consequences of soil-borne pathogen abundance on seedling emergence and survival of dominant tree species with varying shade-tolerance (*Quercus canariensis* > *Q. suber* > *Olea europaea* var. *sylvestris*). For this, we conducted an *in-situ* field experiment where seeds of the three tree species were sown and monitored in the same locations where pathogen abundance was quantified. To the best of our knowledge, this is the first study that simultaneously analyzes the spatial relationship among abiotic soil properties, adult plants (trees and shrubs), and the pathogen and seedling community in a multi-species natural context.

Material and Methods

Study site and species

The study was conducted in Los Alcornocales Natural Park, a hotspot of biodiversity in southern Spain (Médail & Quézel, 1999). The climate is sub-humid Mediterranean, with most rainfall (95%) occurring from October to May. Soils are generally sandy, acidic and nutrient poor, derived from a bedrock dominated by Oligo-Miocene sandstones, but appeared interspersed with soils richer in clay derived from layers of marl sediments. The Alcornocales Natural Park contains the largest and best conserved *Q. suber* forests of Europe (Anonymous, 2005). In the drier lowlands of the park, *Q. suber* forms mixed open woodlands with the evergreen and shade-intolerant *Olea europaea* var. *sylvestris*,

124 whereas in wetter areas *Q. suber* coexists with the deciduous shade-tolerant *Quercus*
125 *canariensis* forming closed forests. The shrubby understory is diverse and rich in
126 endemic taxa (Ojeda *et al*., 2000).

127 A severe decline affecting *Quercus* species (especially evergreen oaks *Q. ilex*
128 and *Q. suber*) has been reported since the early 1990s in the park and throughout the
129 Mediterranean Basin (Brasier, 1992, 1996). Several abiotic (e.g. drought) and biotic
130 (e.g. insects and pathogens) factors are potentially involved in this decline (Tuset &
131 Sánchez, 2004). However, in the study area, two main oomycete soil-borne pathogens
132 (*Phytophthora cinnamomi* and *Pythium spiculum*) have been isolated from symptomatic
133 *Q. suber* trees and are suggested to be the main drivers of the decline of the species
134 (Brasier, 1996; Sánchez *et al.*, 2002, 2006; Romero *et al*., 2007).

135

136 ## Field sampling of soils and plants

137 We selected six study sites, three in open woodlands of *Q. suber* and *O. europaea* var.
138 *sylvestris* (hereafter woodland sites) and three in closed forests of *Q. suber* and *Q.*
139 *canariensis* (hereafter forest sites), distributed across the whole Natural Park (see sites
140 description in Appendix 1). At each site, we established a 60 x 50 m permanent plot in a
141 topographically uniform area. Topography was kept constant in order to avoid
142 confounding effects for the analysis of impacts of soil texture and plants on pathogens.
143 Each plot was subdivided in 30 10 × 10 m subplots. During the spring of 2010 (April-
144 May), we took two soil samples (0-20 cm) at the center of each subplot, one for texture
145 and another for pathogen analysis. Soil samples were taken within 1 m of where seeds
146 were planted for the sowing experiment (see *Seed sowing experiment* below), rapidly
147 put in a cooler, and transported to the lab for assessment of texture and pathogen
148 abundance (see *Lab methods* below).

149 To characterize local neighborhoods, we identified and mapped all live and
150 standing dead trees (including stumps) with a diameter at breast height (d.b.h.) > 2 cm
151 and all shrubs in the 60 x 50 m permanent plots, as well as in a buffer zone 15-m (for
152 trees) or 5-m (for shrubs) wide around each plot, using a total station Leica TC407. Tree
153 neighborhoods of similar size have been shown to capture the most important aspects of
154 tree neighborhood interactions in temperate forests (Gómez-Aparicio *et al*., 2008a;
155 Coates *et al*., 2009). Although we did not have any reference to choose the maximum
156 shrub neighborhood, we considered a size of 5 m to be big enough based on the small
157 size of most shrubs in these forests (height usually < 3 m). We measured the d.b.h. of
158 each of the trees mapped (n = 1341 trees). Due to its multi-stem growth form, shrub size
159 was characterized measuring the two diameters of the elliptical projection of its crown
160 (n = 3005 shrubs). In addition, we evaluated the health status of *Q. suber* individuals by
161 a visual estimation of crown defoliation on a standardized semi-quantitative scale
162 widely used in the region for monitoring purposes of oak decline (e.g. García *et al*.,
163 2011): (1) healthy reference trees, (2) slightly defoliated trees (< 50 % crown
164 defoliation), (3) highly defoliated trees (> 50% defoliation), and (4) dead trees
165 (including stumps). No other tree or shrub species in the study area showed symptoms
166 of decline.
167
168 ## Lab methods
169 *Soil texture.*- Soil samples were air dried and sieved through a 2-mm mesh sieve to
170 remove root material and stones. Particle size analysis was undertaken using the
171 Bouyoucos hydrometer method (Gee & Bauder, 1986). Total sand (i.e. fine + coarse
172 sand, 0.05-2 mm) was used as a representative measurement of the soil texture (see a
173 similar approach in Gómez-Aparicio *et al*., 2008b).

174

175 *Pathogen abundance*.- Soil samples were air dried and sieved (2-mm mesh). Aliquots of
176 10 g from each soil sample were processed as described in Romero *et al*. (2007),
177 preparing soil suspensions in 100 ml Water-Agar 0.2%. Aliquots of 1 ml taken from the
178 soil suspensions were plated on NARPH Petri dishes (20 dishes per sample, Romero *et*
179 *al.*, 2007). Colonies growing on the plates were morphologically identified and counted.
180 As soil samples were previously dried, it was assumed that each colony obtained
181 resulted from the germination of, at least, one resistant spore (oospore or
182 chlamydospore). Results were expressed as colony forming units per gram of dry soil
183 (cfu/g).

184 Identification of the isolated colonies was carried out by microscope
185 observations after incubation on carrot-agar medium (Dhingra & Sinclair, 1995) at 24º
186 C in the dark for 4-6 days and staining with acid fuchsine in lactophenol. Colonies were
187 classified in three groups: *Phytophthora cinnamomi*, characterized by clustered hyphal
188 swellings and smooth cell walled chlamydospores (Erwin & Ribeiro, 1996; Romero *et*
189 *al*., 2007); *Pythium spiculum,* which has characteristic ornamented oospores (Paul *et al*.,
190 2006; Romero *et al*., 2007); and *Pythium* spp., characterized by the absence of septa in
191 narrow branched hyphae (less than 4 μm thickness). *Phytophthora cinnamomi* and *Py.*
192 *spiculum* are the main soil-borne pathogens involve in the decline of *Quercus* species in
193 southern Spain (Sánchez *et al.*, 2006; Romero *et al*., 2007; Jiménez *et al*., 2008). The
194 *Pythium* spp. group represents a mix of *Pythium* species of unknown pathogenicity, and
195 therefore it can include both virulent and avirulent (i.e. saprophytic) species (see a
196 similar approach in Reinhart & Clay, 2009 and Reinhart *et al*., 2010). Although this
197 group does not necessarily have to cause any pathogenic effect on trees, we will refer to
198 the three different oomycete categories considered as "pathogen species" for simplicity.

199

200 ## Seed sowing experiment

201 During winter 2009-2010 (December-January), we conducted a sowing experiment in
202 the six study sites. Surface sterilized seeds of the two dominant tree species were sown
203 at the center of each of the 30 subplots. Seeds were sown at 2 cm depth in two adjacent
204 30 × 30 cm quadrats per subplot. Each quadrat contained three lines of seeds separated
205 7.5 cm from each other and from the border of the quadrat. Each line was randomly
206 assigned for sowing either three *Quercus* or six *Olea* seeds. The larger number of *Olea*
207 seeds was chosen based on their lower probability of germination (Goyiatzis &
208 Porlingis, 1987; Rey *et al*., 2004). Sowing quadrats were protected with 1-cm mesh
209 hardware to exclude seed predators. As a whole, we sowed 1620 seeds of *Q. suber*,
210 1620 seeds of *O. europaea*, and 810 seeds of *Q. canariensis*. Seedling emergence was
211 monitored in early June 2010 to ensure that most seedlings had emerged (Pérez-Ramos
212 & Marañón, 2011). Seedlings were revisited in early October 2010 to record survival
213 after the first summer in the field, the main period of seedling mortality in
214 Mediterranean systems (Gómez-Aparicio, 2008; Pérez-Ramos *et al*., 2011).
215 Unfortunately, emergence of *O. europaea* was virtually nil in all sites (data not shown),
216 which precluded us from testing the effect of pathogen abundance on emergence and
217 survival of this tree species.

218

219 ## Statistical analysis

220 *Neighborhood models of soil pathogen abundance.*- We used likelihood methods and
221 model selection for analysis of our data (Johnson & Omland, 2004; Canham & Uriarte,
222 2006). Following the principles of likelihood estimation, we estimated model

parameters that maximized the likelihood of observing the pathogen abundance measured in the field given a suite of alternate neighborhood models.

We fit separate models for each combination of forest type (Qs-Ol and Qs-Qc) and pathogen species (*P. cinnamomi*, *Py. spiculum* and *Pythium* spp.). Our analyses of soil-borne pathogen abundance estimated four terms: 1) average potential pathogen abundance (PPA, in cfu/g) at each of the three sites, and three multipliers that quantified the effects on average potential pathogen abundance of 2) local abiotic conditions (expressed in terms of soil texture), 3) the characteristics of the tree neighborhood (expressed in terms of the size, spatial distribution, species and health status of the trees), and 4) the characteristics of the shrub neighborhood (expressed in terms of shrub size). Our *full model* had the following form:

$$\text{Pathogen abundance} = PPA_{Site} \times \text{Abiotic effect} \times \text{Tree effect} \times \text{Shrub effect} \quad (1)$$

We also tried a linear model framework where the different effects were summed (see Baribault & Kobe, 2011, for a similar approach), but it showed in general poorer performance than the multiplicative model framework (data not shown). *Potential pathogen abundance* (PPA_{Site}) is a parameter estimated by the model that represents the expected pathogen abundance at each site when texture is at its optimal value (i.e. Abiotic effect = 1) and in the absence of neighboring trees or shrubs (i.e. Tree effect and Shrub effect = 1). The three effects in Eq. 1 were modeled using Weibull functions:

$$\text{Abiotic effect} = \exp(b\ \text{Sand}) \quad (2)$$

$$\text{Tree effect} = \exp(c\ NI_{Tree}) \quad (3)$$

$$\text{Shrub effect} = \exp(d\ NI_{Shrub}) \quad (4)$$

where b, c and d are parameters estimated by the analyses determining the sign and

247 magnitude of the abiotic, tree, and shrub effects, respectively.

248 The *abiotic effect* was modeled as a function of soil texture quantified as the
249 proportion of sand content. Texture was chosen to represent the abiotic drivers of
250 pathogen abundance because it is a relatively stable soil property that influences key
251 environmental variables for pathogens (e.g. water availability) and it is not easily
252 modified by plants, being therefore independent of the biotic effects in the equation.

253 The *tree effect* was modeled as a function of a tree neighborhood index (NI_{Tree}).
254 This index quantifies the net effect of *j=1,...,n* neighboring trees of *i=1,...,s* species on
255 pathogen abundance, and was assumed to vary as a direct function of the size (d.b.h.)
256 and an inverse function of the distance to neighbors following the form:

257 $$NI_{Tree} = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \, dbh_{ij}^{\alpha} \exp\left(-\gamma \, distance_{ij}^{\beta}\right) \quad (5)$$

258 where α, β and γ are parameters estimated by the analyses, and that determine the shape
259 of the effect of the d.b.h. (α) and the distance to neighbors (β and γ) on pathogen
260 abundance. Instead of setting α, β and γ arbitrarily, we tested two different versions of
261 Eq. 5, fixing α to values 0 or 1 and letting β and γ to vary. We could not let α, β and γ
262 vary simultaneously due to difficulties in estimation caused by parameter trade-offs. A
263 value of α = 1 implies that the effect of a neighbor is proportional to its d.b.h. and
264 therefore to its crown radius, whereas a value of α = 0 means that the tree influence on
265 soil pathogen varies as a function of tree density, regardless of size.

266 We were particularly interested in exploring whether tree effects varied between
267 individuals of different species or health status. For this purpose, we multiplied the net
268 effect of an individual tree by a *per-capita* coefficient (λ) that ranged from -1 to 1 and
269 allowed for differences between neighbors in their effects (negative or positive) on a
270 target pathogen. We tested four different groupings of neighbor species in Eq. 5 with

increasing complexity: 1) a model in which all trees were considered equivalent (i.e. fixing $\lambda = 1$); 2) a species-specific model that calculated two separate λ, one for *Q. suber* and another for the coexisting tree species (either *O. europaea* or *Q. canariensis*); 3) a model that also took into account the health status of *Q. suber* trees, and therefore calculated four separate λ (healthy *Q. suber*, slightly defoliated *Q. suber*, highly defoliated *Q. suber*, and the coexisting tree species); and 4) a model that not only considered alive trees of different species and health status, but also the legacy effect of dead *Q. suber* trees, calculating five separate λ.

The *shrub effect* was modeled as a function of a shrub neighborhood index (NI_{Shrub}). This index is a simplified version of the tree neighborhood index, and quantifies the net effect of $j=1,...,n$ neighboring shrubs of $i=1,...,s$ species on pathogen abundance following the form:

$$NI_{Shrub} = \sum_{i=1}^{s} \sum_{j=1}^{n} area_{ij} \quad (6)$$

The NI_{Shrub} was assumed to vary just as a direct function of the size (crown area) of neighbor shrubs in a 5-m radius neighborhood. We decided not to include distance in the calculation of the index given the already restricted area over which shrubs were mapped and to keep the number of parameters in the models manageable.

Finally, in order to test whether any of the three effects studied (i.e. texture, trees and shrubs) varied among sites of a given forest type, we tried variations of the full model in which the slopes of each effect (i.e. parameters *b, c* or *d*) were allowed to vary among sites.

Effect of soil-borne pathogens on seedling emergence and survival.- We fit models that estimated seedling emergence or survival at each node of the plots as a direct function of the pathogen abundance in the soil. We tried both a multiplicative and a linear model

framework, this last offering a better fit to the data. Thus, for each combination of forest type, tree species, and pathogen species, seedling emergence and survival were predicted as:

$$\text{Seedling emergence} = PSE_{Site} + b * \text{Pathogen abundance} \quad (7)$$

$$\text{Seedling survival} = PSS_{Site} + b * \text{Pathogen abundance} \quad (8)$$

where PSE_{Site} and PSS_{Site} are the potential seedling emergence and survival (respectively) at each site in the absence of pathogens, and *b* is the slope of the regression determining the pathogen effect. We explored the existence of site-dependent pathogen effects by fitting models that allowed the parameter *b* to vary among sites of a given forest type.

Parameter estimation and model selection.- Following the principle of parsimony, we followed the strategy of systematically reducing the number of distinct parameters in the full model to the simplest model that is not a significantly worse fit than any more complicated model. We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to select the best model, with lower AIC_c values indicating stronger empirical support for a model (Burnham & Anderson, 2002). Pathogen abundance values were modeled using a Poisson error distribution, and seedling emergence and survival using a binomial error distribution. We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e., the parameters that maximize the log-likelihood) given our observed data (Goffe *et al*., 1994). The slope of the regression (with a zero intercept) of observed on predicted pathogen abundance was used to measure bias (with an unbiased model having a slope of 1) and the R^2 of the regression was used as a measure of goodness-of-it. We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum

likelihood parameter estimates (Edwards, 1992). Neighborhood analyses were performed using software written specifically for this study using Java (Java SE Runtime Environment v6, Sun Microsystems Inc., California, USA, 2010).

Results

Neighborhood models of soil pathogen abundance

All of the models produced unbiased estimates of soil-borne pathogen abundance (i.e. slopes of predicted vs. observed abundance were all very close to 1.0) and explained a percentage of the variation in the data that ranged from 0.07 to 0.43 (Table 1). The full model (i.e. including the effect of texture, trees and shrubs) was the best fit in 5 of the 6 forest type-pathogen species combinations. The only exception was *Py. spiculum* in Qs-Qc forests, for which a simpler alternate model that ignored the effect of texture and shrubs ("No Texture + Shrub model" in Table 1) had a much lower AIC_c score (i.e. was much better supported statistically) than the full model. Site-dependent models were never a better fit to the data than more simple site-independent models (results not shown for simplicity), which implies that soil and plant effects on pathogen abundance can be considered consistent across sites of the same forest type.

The proportion of sand in the soil always had a negative effect on pathogen abundance (i.e. negative *b* parameter, Appendix 2). The magnitude of the texture effect (indicated by the magnitude of the *b* parameter) was larger in Qs-Ol than on Qs-Qc forests for all three pathogen species (Fig. 1). Within forest types, the texture effect also varied among pathogen groups (i.e. support intervals for the *b* parameter did not overlap), being larger for *Pythium* spp. > *P. cinnamomi* > *Py. spiculum* (Fig. 1).

Much of the variation in soil-borne pathogen abundance was explained by the tree neighborhood from which the soil was sampled. Thus, excluding the tree effect

346 from the full model ("No Tree" model in Table 1) always caused a much larger increase
347 in AIC_c than excluding either the texture or shrub effect (Table 1). In all models, $\alpha = 1$
348 offered a better fit to the data than $\alpha = 0$, indicating that the tree influence on pathogen
349 abundance was proportional to its size. The effect of distance to neighbors on pathogen
350 abundance (controlled by parameters β and γ in Eq. 5, Appendix 2) was however not
351 consistent among pathogen species. The decline in distance varied from very steep in *P.*
352 *cinnamomi* to virtually null in *Pythium* spp., for which abundance was only proportional
353 to host density (Fig. 2).

354 For *P. cinnamomi* and *Pythium* spp. in both forest types, models that
355 discriminated among living trees of different species and health status and included the
356 legacy effect of dead trees (i.e. calculated 5 different λ values) provided a much better
357 fit to the data (i.e. had lower AIC_c) than simpler models that ignored species or health
358 differences (Table 1). In Qs-Ol forests, λ values varied from very positive in highly
359 defoliated *Q. suber* trees to largely negative in *O. europea* (Appendix 2). This is
360 because neighborhoods dominated by healthy *Q. suber* trees had lower abundance of *P.*
361 *cinnamomi* and *Pythium* spp. than those dominated by symptomatic *Q. suber* trees, but
362 higher abundance than neighborhoods dominated by dead *Q. suber* and *O. europaea*
363 trees (Fig. 3). Similarly, in Qs-Qc forests, neighborhoods dominated by healthy *Q.*
364 *suber* trees had lower *P. cinnamomi* and *Pythium* spp. abundance than those dominated
365 by symptomatic *Q. suber* trees. In this forest type, on the contrary, healthy *Q. suber*
366 neighborhoods also had lower pathogen abundance than neighborhoods of the
367 coexisting species *Q. canariensis* (Appendix 2, Fig. 3). Finally, for *Py. spiculum*,
368 models that grouped all tree species as equivalent always had the largest empirical
369 support (i.e. lower AIC_c, Table 1). It is likely that the substantial lower abundance of
370 *Py. spiculum* compared to the other two pathogen groups limited the capacity of the

models to detect complex spatial patterns for this species. In both forest types, the abundance of *Py. spiculum* varied positively with tree abundance in its neighborhood (Appendix 2, Fig. 3).

The effect of shrubs on pathogen abundance varied strongly among forest types, being negative in Qs-Ol forests but positive (*P. cinnamomi* and *Pythium* spp.) or neutral (*Py. spiculum*) in Qs-Qc sites (Fig. 4). The magnitude of the effect did not vary among pathogen species in most cases, as indicated by the overlapping values of the *d* parameter (Appendix 2).

Effect of soil-borne pathogens on seedling emergence and survival

Among the nine combinations of forest type-seedling species-pathogen species tested, we only found support for an effect of *P. cinnamomi* on the emergence of *Q. suber* seedlings in Qs-Ol forests (Table 2). This effect varied among sites, as indicated by the fact that a site-specific model was a better fit to the data than a simpler linear model (Table 2). Thus, *P. cinnamomi* had a large negative effect on *Q. suber* emergence in two sites (Cinchao and Picacho) and a neutral effect (i.e. support interval for the *b* parameter overlaps zero, Appendix 3) in one site (Ahumada, Fig. 5).

We found support for an effect of *P. cinnamomi* on survival of *Q. suber* seedlings in Qs-Ol forests, but not in Qs-Qc forests (Table 2). The model that incorporated site-effects had a lower AIC_c score than a simpler model omitting those effects. Thus, *P. cinnamomi* had a negative effect on *Q. suber* survival in just one of the three Qs-Ol sites (Ahumada), which happened to be the only site where *P. cinnamomi* effects on seedling emergence were not found (Appendix 3, Fig. 5). Although models incorporating pathogen effects were the most parsimonious fit in two other situations - effects of *P. cinnamomi* and *Pythium* spp. on *Q. canariensis* survival- the differences in

396 AIC_c with the null model were < 2 units (Table 2), and therefore do not provide strong
397 support for a pathogen effect on survival of this species.
398
399 **Discussion**
400 Our results indicate that pathogen abundance in the forest soil is not randomly
401 distributed, but exhibits spatially predictable patterns influenced by both abiotic (soil
402 texture) and particularly biotic factors (tree and shrub species). The relative importance
403 of each factor on soil-borne pathogen abundance varied among forest types and/or
404 pathogen species, revealing the complexity of the pathogen landscape. We also found
405 that the spatial variability in the pathogen community had significant ecological
406 consequences by affecting the performance of tree seedlings under natural field
407 conditions, but only for particular combinations of species and sites. Our findings
408 suggest that heterogeneous spatial patterns of pathogen abundance at fine spatial scale
409 can have important implications for the dynamics and restoration of declining
410 Mediterranean oak forests.
411
412 Drivers of soil-borne pathogen abundance: the role of soil texture
413 Our models showed a consistent negative effect of soil sand content on pathogen
414 abundance, presumably due to the direct influence of texture on water availability.
415 Sandy soils have low water-holding capacity, high percolation rates and are less prone
416 to suffer temporal waterlogging than poorly drained clayish soils (Brady & Weil, 2008),
417 conditions that strongly benefit pathogen abundance and disease development (Hendrix
418 & Campbell, 1973; Weste & Marks, 1987). The texture effect was much larger in Qs-Ol
419 than in Qs-Qc forests for the three pathogen species, probably because the Qs-Qc forests
420 soils were all very sandy (Appendix 1). In fact, the sandier soils of closed Qs-Qc forests

421 could also explain why they showed lower loads of all pathogen species than Qs-Ol
422 forests (Fig. 3). Our results therefore suggest that texture is an important abiotic driver
423 of soil-borne pathogen variation at both the local and landscape scale.
424
425 Drivers of soil-borne pathogen abundance: the role of the tree community
426 A main finding of this paper is the strong empirical support found for a spatial
427 concordance among the distribution and health status of trees of different species and
428 the abundance of soil-borne pathogens in the soil. *P. cinnamomi* and *Pythium* spp. were
429 much more abundant under declining *Q. suber* trees, particularly those already showing
430 a high defoliation level (>50%), than under healthy *Q. suber* trees. Although our
431 observational approach does not allow separating cause and effect in the tree-pathogen
432 interaction, the finding of a concomitant increase in the abundance of pathogens in the
433 soil and defoliation in the canopy is consistent with the predictions of the *hypothesis of*
434 *decline development* in oak forests, which propose a tree-pathogen feedback process
435 (Brasier, 1996). According to this hypothesis, the loss of fine roots by soil-borne
436 pathogens may translate into a loss of leaf area aboveground. The opening of the canopy
437 trigger a series of environmental changes (e.g. higher soil temperature, reduced organic
438 matter content and microbial activity) that might in turn favor pathogen development,
439 giving rise to a feedback loop where pathogens under the trees produce changes at the
440 canopy level that favor the build-up of larger pathogen loads, eventually killing the tree.
441 On the other hand, the fact that our models supported a negative effect of dead trees on
442 soil pathogen abundance (negative λ, Appendix 2) suggests that once a tree dies, its
443 legacy is a gap with lower pathogen abundance than the surrounding forest matrix.
444 These gaps could play a role of refuge for the establishment of susceptible species as
445 reported for canopy gaps in tropical and cool temperate forests (Augspurger, 1984;

446 O'Hanlon-Manners & Kotanen, 2004, 2006; Reinhart *et al*., 2010).

447 Our neighborhood approach allowed us to compare the effect of different
448 coexisting tree species on pathogen abundance. We found that tree species can play very
449 different roles in the pathogen landscape. Thus, among the species co-existing with the
450 susceptible *Q. suber* in our study sites, *O. europaea* neighborhoods seem to suppress
451 pathogens (pathogen abundance was lower under *O. europaea* than in neighborhoods
452 without trees), whereas *Q. canariensis* seem to act as a reservoir without showing any
453 apparent disease symptom (Fig. 3). These results help to understand the nature of plant-
454 plant interactions mediated by pathogens in these forests. Specifically, they suggest that
455 whereas *O. europaea* trees could indirectly benefit *Q. suber* by acting as refuges for its
456 recruitment, the presence of *Q. canariensis* could result in apparent competition (Cobb
457 *et al*., 2010) by promoting a pathogen that harm *Q. suber* more strongly than itself.
458 These complex indirect heterospecific effects, although largely ignored in the literature,
459 show the need to use a community approach when trying to explain patterns of spatial
460 variation in disease dynamics (e.g. Janzen-Connell effects; Mordecai, 2011) of tree
461 species.

462 Another important advantage of using spatially-explicit neighborhood models is
463 that it allows gaining valuable insights into the role of tree size and distance as
464 determinants of pathogen abundance. This type of information is extremely rare in the
465 literature on plant-pathogen interactions, since most studies do not quantify pathogen
466 abundance but measure disease expression directly, which can be affected by additional
467 factors such as host susceptibility or environmental conditions (e.g. Augspurger &
468 Kelly, 1984; Gilbert *et al*., 1994; Packer & Clay, 2000, 2003; but see Reinhart & Clay,
469 2009). First, our models indicate that the tree effect on pathogen abundance is not
470 independent of its size, with larger trees hosting larger pathogen communities. This

result provides empirical support for the hypothesis of the importance of d.b.h. as a source of intra-specific variation in plant-pathogen interactions (Reinhart & Clay, 2009), and calls for the inclusion of this plant trait as a covariable in experimental and observational studies of pathogen abundance and disease. Second, our models showed that the decline of the net effect of a neighbor tree within the 15-m neighborhood vary strongly among pathogen species, from rather sharp for *P. cinnamomi* (tending to zero within 5-6 m) to virtually null for *Pythium* spp. (Fig. 2). This result suggests that pathogen species can vary strongly in their scale of spatial variation, with some of them showing heterogeneous patterns at smaller scales than others.

Drivers of soil-borne pathogen abundance: the role of the shrub community

We found that not only the tree community, but also the shrub community had a strong effect on soil-borne pathogen abundance, supporting previous studies that have emphasized the relevance of the understory as a driver of the soil microbial community (Nilsson & Wardle, 2005; Wu *et al*., 2011). However, the sign of the shrub effect was not consistent among forest types, being negative in Qs-Ol forests but positive in Qs-Qc forests. A likely explanation for this difference would be that the net effect of the understory was driven by the identity of the dominant shrub species, which differed among forest types. Thus, despite their similar species composition, species relative abundance changed from dominance of *Pistacia lentiscus* in Qs-Ol forests to dominance of *Erica* spp. in Qs-Qc forests. These two species vary strongly in their litter quality and effects on soil fertility: *P. lentiscus* forms islands of fertility rich in organic matter (Armas & Pugnaire, 2009), whereas *Erica* spp. produces low-quality litter and is indicative of acidic nutrient-poor soils (Van Vuuren & Berendse, 1993; Zas & Alonso, 2002). Because an acidic pH, low nutrient content and low organic matter favor soil-

borne pathogen growth and disease expression (Weste & Marks, 1987; Jönsson *et al*., 2003; Serrano *et al*., 2011), soils under *Erica* spp. could be expected to provide more favorable conditions for pathogen build-up than soils under *P. lentiscus*. Although this hypothesis remained to be tested, our results highlight the strong variability in the understory effects on pathogen populations that can be expected even in forests with similar shrub species composition.

Pathogen effects on seedling emergence and survival: implications for regeneration dynamics

Our models of seedling emergence and survival indicate that, under natural field conditions, the spatial variability of soil-borne pathogen abundance does translate into spatial variation in seedling performance, but not for all species or forest types. In fact, we only found support for a negative effect of *P. cinnamomi* on emergence and survival of *Q. suber* seedlings in Qs-Ol forests. The fact that we detected negative effects of *P. cinnamomi* but not of *Py. spiculum* or *Pythium* spp. on seedling performance is probably influenced by its much larger abundance in the studied forests, but could be also indicative of the larger aggressiveness of this species (Romero *et al*., 2007). Differences in *P. cinnamomi* abundance, much larger in *Qs-Ol* than in *Qs-Qc* forests, could also explain its stronger effects in the former forests. These findings therefore suggest that certain thresholds in pathogen abundance need to be overcome before they translate into measurable effects on seedling performance in the field. Interestingly, these thresholds seem to be higher than those expected based on pathogenicity trials, where much lower *P. cinnamomi* abundances (<500 cfu/g) are lethal for Mediterranean *Quercus* seedlings (Sánchez *et al.*, 2002; Serrano *et al.*, 2011).

Our results do not support our initial hypothesis of higher pathogen resistance in

521 shade-tolerant than shade-intolerant species. Unfortunately, the lack of emergence of *O.*
522 *europaea* in Qs-Ol sites did not allow reaching conclusions on inter-specific differences
523 in pathogen effects in this forest type. However, in Qs-Qc forests, neither *Q. suber* nor
524 *Q. canariensis* seedlings were negatively affected by pathogens, despite their
525 differences in shade-tolerance. A question that remained to be answered is whether
526 differences among the two *Quercus* species would emerge at larger pathogen
527 abundances such as those found in Qs-Ol forests, where *Q. suber* emergence and
528 survival was severely impaired by *P. cinnamomi* (Fig. 5). To date, our results do not
529 support a significant role of pathogens as promoters of species coexistence through
530 species-specific effects at the seedling level. On the contrary, because adults of *Q. suber*
531 are much more susceptible to pathogen attack than adults of *Q. canariensis*, soil-borne
532 pathogens seem more likely to play a role for species exclusion than for coexistence in
533 the studied forests.

534 While our results point out important net impact of pathogens on tree seedlings
535 under natural conditions, the rather low explanatory power of the emergence and
536 survival models should be taken as evidence that pathogens are just one of many other
537 relevant abiotic and biotic drivers of natural patterns of recruitment. These drivers could
538 also interact with each other, a given abundance of soil-borne pathogens having
539 implications for seedling performance only under specific environmental situations such
540 as low light availability or low mycorrhizal abundance (Hood *et al*., 2004; Morris *et al*.,
541 2007). Further studies that simultaneously explore the effect of multiple abiotic and
542 biotic drivers of seedling performance are clearly needed to improve our understanding
543 of the factors affecting the expression of disease in forest ecosystems.

544

545 ## Concluding remarks

546 This study provides new insights into the highly complex spatial distribution of soil-
547 borne pathogens and reveals the extent that soil characteristics and the woody plant
548 community explain pathogen abundance in forest soils. Because we have shown that the
549 spatial variability in soil-borne pathogen abundance can have important implications for
550 recruitment of susceptible species such as *Q. suber*, these findings might be useful in
551 the restoration of forests affected by pathogen-driven decline, which frequently involves
552 planting seeds or seedlings of susceptible species to replace dead trees in the future
553 (Tuset & Sánchez, 2004). Specifically, our results could help to choose those planting
554 microsites where seedling emergence and survival would have lower probability of
555 being impaired by soil-borne pathogens, hence maximizing the economic and ecological
556 benefits of restoration efforts.
557

558 **Acknowledgements**

559 We thank the director and technicians of the Alcornocales Natural Park for facilities and
560 support to carry out the field work. We are also indebted to Pierre Callier, Eduardo
561 Gutiérrez and Ana Pozuelos for invaluable lab and field assistance. This study was
562 supported by the MICIIN project INTERBOS (CGL2008-4503-C03-01), the
563 OAPN/MIMARM project DECALDO (091/2009), and European FEDER funds. B.I.
564 was supported by a FPI-MEC grant, JMA by a JAEpre-CSIC grant, and I.M.P.R. by a
565 JAEdoc-CSIC contract.
566

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Table 1. Comparison of the alternate models for the three pathogen species in the two forest types using AIC_c. The full model includes the effect of texture, tree neighbors and shrub neighbors on each pathogen species. The "No Texture", "No Tree", "No Shrub" and "No Texture+Shrub" models ignore the effect of these factors, respectively. The "Type of tree effect" column indicates whether the best model considered all tree species as equivalent ("Equiv."), differentiated among species ("Sp") and health status ("H"), or considered the legacy effect of dead trees ("D"). The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. *NP* is the total number of parameters in the best model, and *n* the sample size. The slope and R^2 for the relationship between predicted and observed pathogen abundance is also given.

Forest type	Pathogen species	AIC_c						Type of tree effect	NP	n	Slope	R^2
		Full	No Texture	No Tree	No Shrub	No Texture + Shrub	Null					
Q. suber-O.europaea	*P. cinnamomi*	**16597**	17576	18910	17735	17758	18914	Sp+H+D	12	90	1.00	0.35
	Py. spiculum	**614**	639	650	619	642	654	Equiv.	7	60	1.00	0.07
	Pythium spp.	**2035**	2472	2510	2194	2486	2565	Sp+H+D	11	60	0.96	0.43
Q. suber-Q. canariensis	*P. cinnamomi*	**4241**	4476	6020	5813	5911	6038	Sp+H+D	11	90	1.08	0.36
	Py. spiculum	128	126	131	121	**118**	129	Equiv.	5	60	1.07	0.18
	Pythium spp.	**1789**	2237	2270	2070	2253	2298	Sp+H+D	11	60	1.01	0.28

Table 2. Comparison of alternate models analyzing the effect of pathogens on seedling emergence and survival. The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. The Site-specific model considers differential pathogen effects among sites, the Linear model a homogeneous pathogen effect among sites, and the Null model the absence of pathogen effects. *NP* is the total number of parameters in the best model, and *n* the sample size. The slope and R^2 for the relationship between predicted and observed emergence/survival are given for best models other than the null.

Forest type	Seedling species	Pathogen species	AIC_c			NP	n	Slope	R^2
			Site-specific	Linear	Null				
Emergence									
Q. suber-O.europaea	*Q. suber*	*P. cinnamomi*	**363.01**	368.56	369.13	6	90	1.00	0.12
		Py. spiculum	244.34	242.65	**240.65**	3	60		
		Pythium spp.	259.53	256.24	**255.72**	3	60		
Q. suber-Q. canariensis	*Q. suber*	*P. cinnamomi*	392.02	388.01	**386.19**	3	88		
		Py. spiculum	258.01	255.47	**251.97**	2	58		
		Pythium spp.	296.66	292.25	**290.25**	2	58		
	Q. canariensis	*P. cinnamomi*	423.27	416.38	**414.48**	3	88		
		Py. spiculum	293.34	291.79	**289.88**	2	58		
		Pythium spp.	277.07	275.80	**273.84**	2	58		
Survival									
Q. suber-O.europaea	*Q. suber*	*P. cinnamomi*	**190.68**	194.81	195.33	6	86	1.04	0.16
		Py. spiculum	145.89	142.23	**140.60**	2	57		
		Pythium spp.	121.55	119.29	**117.31**	2	56		
Q. suber-Q. canariensis	*Q. suber*	*P. cinnamomi*	230.42	226.33	**224.60**	3	81		
		Py. spiculum	143.98	141.00	**139.06**	2	51		
		Pythium spp.	159.03	156.00	**154.02**	2	56		
	Q. canariensis	*P. cinnamomi*	282.49	**278.44**	279.27	3	82	0.98	0.14
		Py. spiculum	181.08	178.67	**176.69**	2	52		
		Pythium spp.	192.79	**190.59**	191.77	3	56	0.97	0.04

Figure legends

Fig 1. Predicted effect of soil texture (proportion of sand) on potential abundance of *Phytophthora cinnamomi*, *Pythium spiculum*, and *Pythium* spp. in a) *Quercus suber-Olea europaea* and b) *Quercus suber-Quercus canariensis* forests. The texture effect on potential abundance is calculated using Eq. 2 and values of the *b* parameter reported in Appendix 2.

Fig 2. Predicted change in the tree Neighborhood Index (NI_{Tree}) as a function of distance to a neighbor for the three studied pathogen species in *Quercus suber-Olea europaea* (Qs-Ol) and *Quercus suber-Quercus canariensis* (Qs-Qc) forests. The NI_{Tree} is calculated using Eq. 5 and values of the γ and β parameters given in Appendix 2 (λ=1 and α=0 for simplicity of presentation of results). To facilitate comparison among pathogen species, NI_{Tree} values are shown standardized (i.e. divided by the maximum value for the species).

Fig 3. Predicted effects of variation in neighbor identity and quantity on abundance (measured in colony forming units per gram of dry soil) of a) *Phytophthora cinnamomi* in *Quercus suber-Quercus canariensis* (Qs-Qc) forests, b) *P. cinnamomi* in *Quercus suber-Olea europaea* (Qs-Ol) forests, c) *Pythium spiculum* in Qs-Qc forests, d) *Py. spiculum* in Qs-Ol forests, e) *Pythium* spp. in Qs-Qc forests, and f) *Pythium* spp. in Qs-Ol forests. Neighbor types are given by the best model for each pathogen species (Table 1). For *Py. spiculum*, the best model considered all trees as a single group. Pathogen abundance is calculated using Eq. 1-6 and optimum texture values, standard 30-cm tree neighbors (the average tree size across study sites) at 2-m distance from target soils, and no shrubs. For each combination of pathogen species and forest type, only the site with

the largest potential pathogen abundance (PPA_{Site} in Appendix 2) is represented. The dotted line indicates the background pathogen abundance without neighboring trees.

Fig 4. Predicted effect of variation in the shrub Neighborhood Index (NI_{Shrub}) on potential abundance of *Phytophthora cinnamomi*, *Pythium spiculum*, and *Pythium* spp. in a) *Quercus suber*-*Olea europaea* forests and b) *Quercus suber*-*Quercus canariensis* forests. The shrub effect on potential abundance is calculated using Eq. 4 and values of the *d* parameter reported in Appendix 2.

Fig. 5. Probability of a) emergence and b) survival of *Quercus suber* seedlings in the three woodland sites as a function of the abundance (colony forming units per gram of dry soil) of *Phytophthora cinnamomi*.

Fig 1.

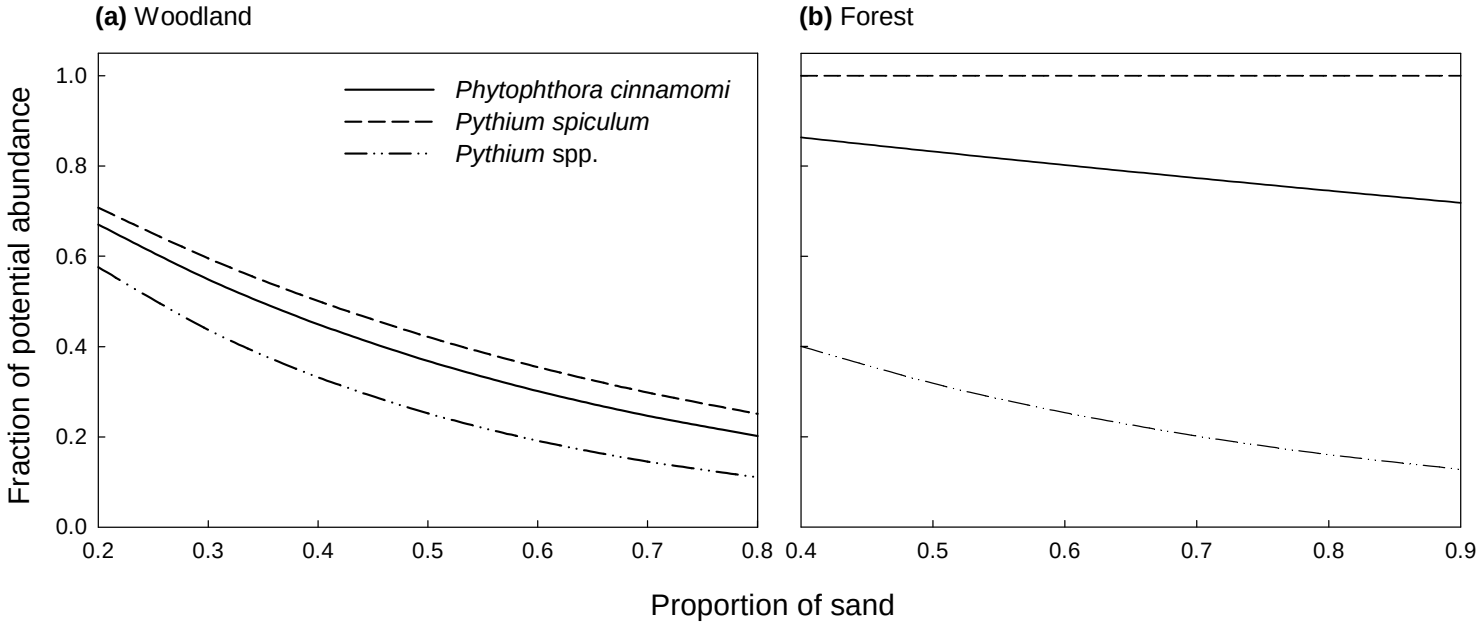

(a) Woodland
(b) Forest
Phytophthora cinnamomi
Pythium spiculum
Pythium spp.
Fraction of potential abundance
Proportion of sand
0.0
0.2
0.4
0.6
0.8
1.0
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9

Fig 2.

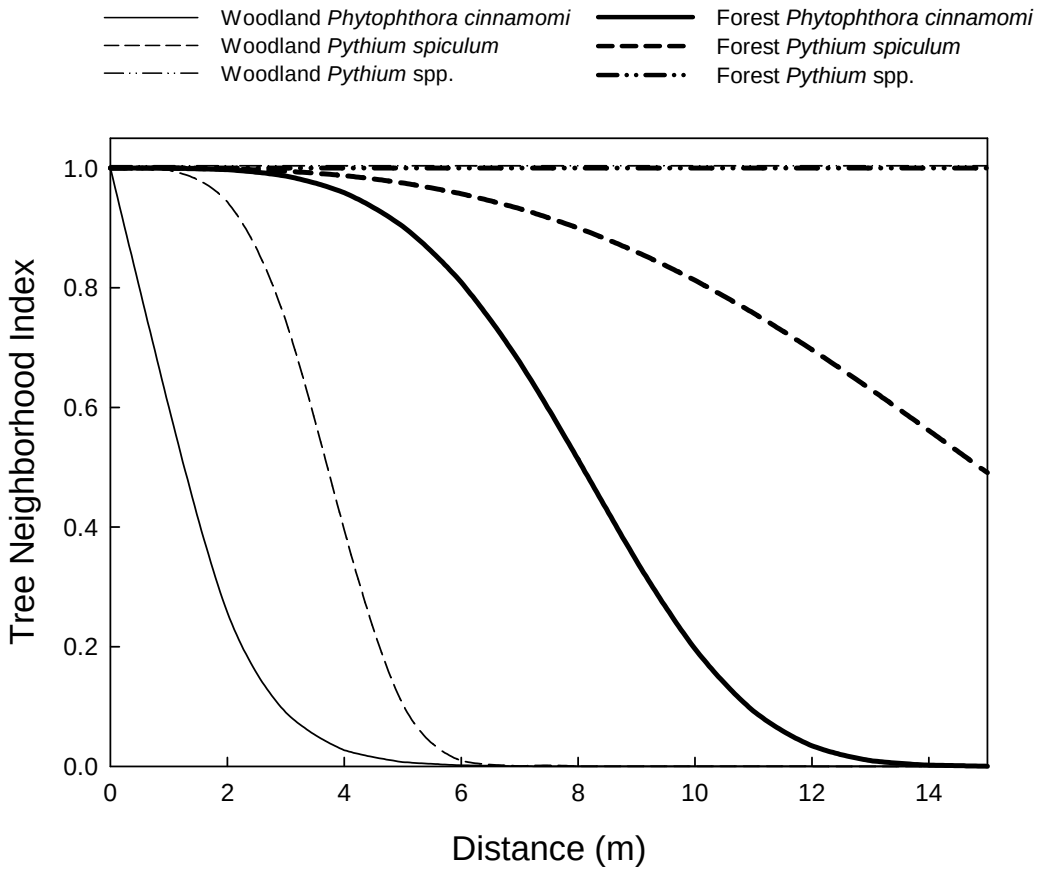

Woodland *Phytophthora cinnamomi*
Woodland *Pythium spiculum*
Woodland *Pythium* spp.
Forest *Phytophthora cinnamomi*
Forest *Pythium spiculum*
Forest *Pythium* spp.
Tree Neighborhood Index
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
Distance (m)

Fig 3.

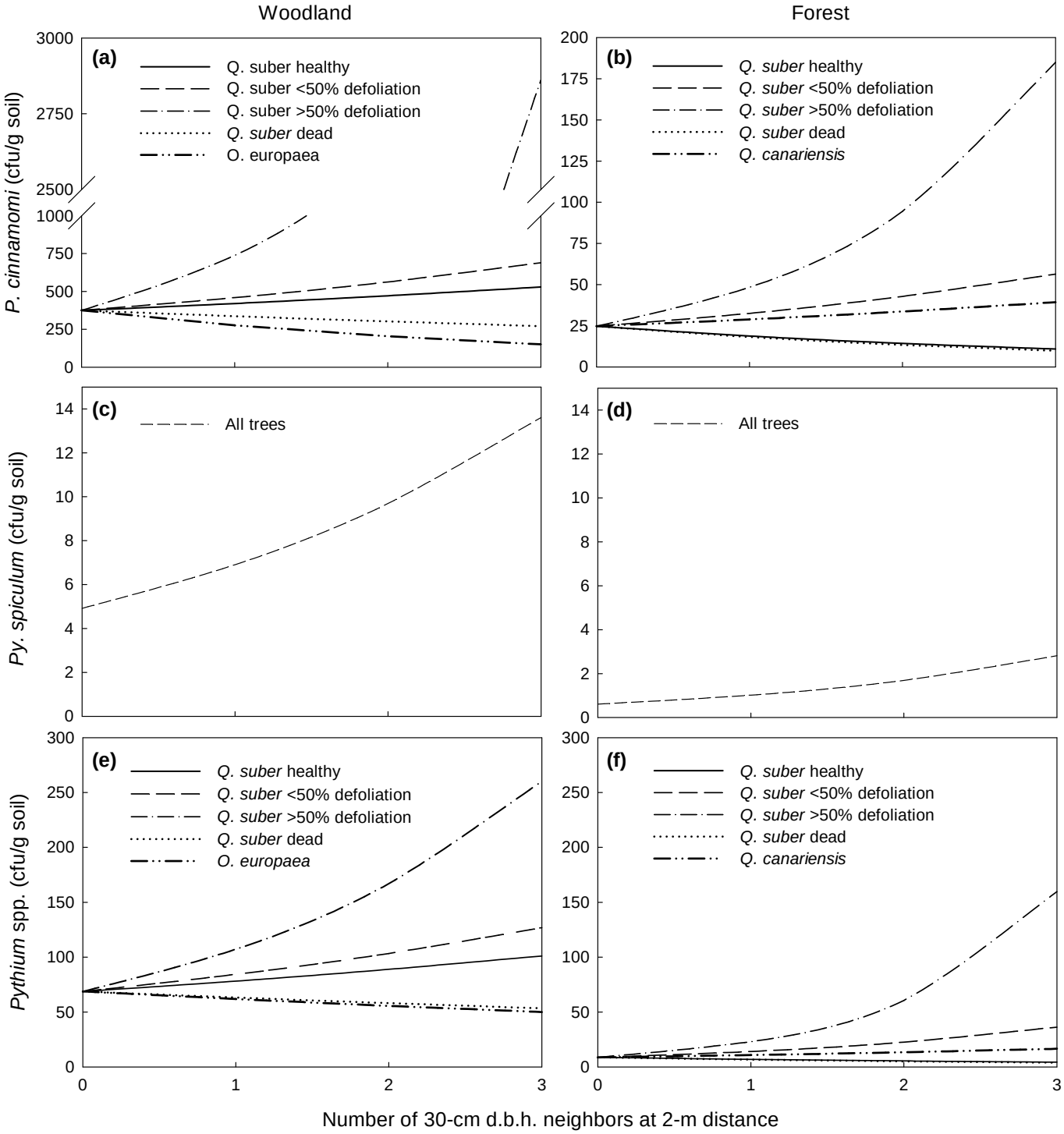

Woodland
Forest
(a)
(b)
(c)
(d)
(e)
(f)
Q. suber healthy
Q. suber <50% defoliation
Q. suber >50% defoliation
Q. suber dead
O. europaea
Q. canariensis
All trees
P. cinnamomi (cfu/g soil)
Py. spiculum (cfu/g soil)
Pythium spp. (cfu/g soil)
Number of 30-cm d.b.h. neighbors at 2-m distance

Fig 4.

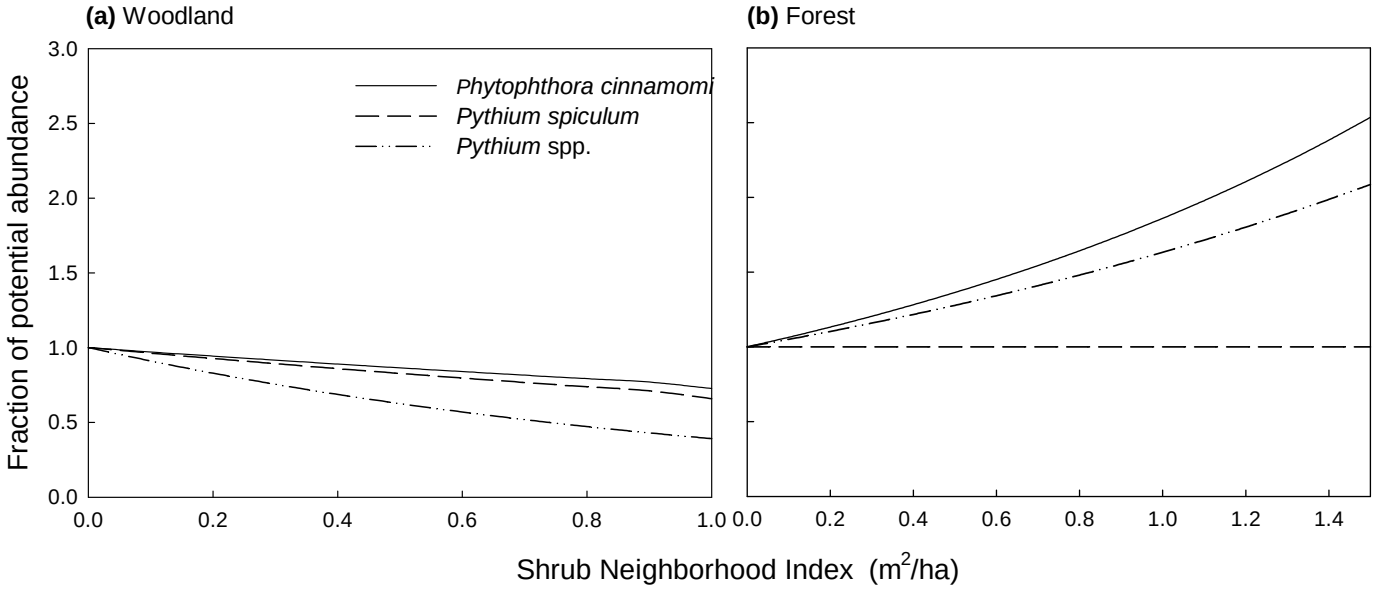
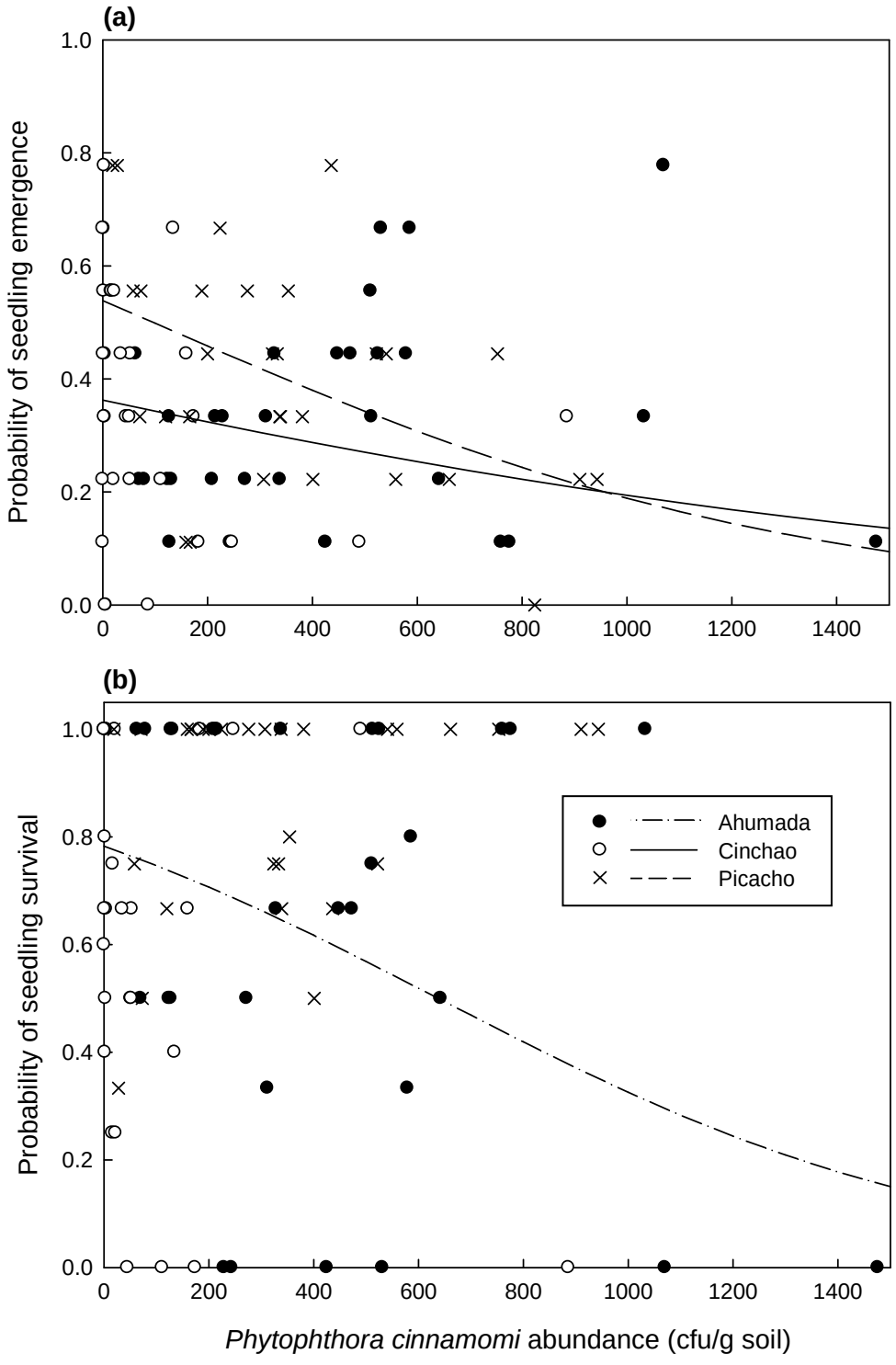

(a) Woodland
(b) Forest
Phytophthora cinnamomi
Pythium spiculum
Pythium spp.
Fraction of potential abundance
Shrub Neighborhood Index (m2/ha)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0.2
0.4
0.6
0.8
1.2
1.4

Fig 5.


(a)
Probability of seedling emergence
1.0
0.8
0.6
0.4
0.2
0.0
0
200
400
600
800
1000
1200
1400
(b)
Probability of seedling survival
Ahumada
Cinchao
Picacho
Phytophthora cinnamomi abundance (cfu/g soil)

Appendix 1. Description of main characteristics of the six study sites located in the South (S), Center (C) and North (N) of the Alcornocales Natural Park. Values of texture (proportion of sand), tree basal area (m^2/ha) and shrub crown area (m^2/ha) represent median [P10 – P90, 10th and 90th percentiles] for the 30 sampled neighborhoods at each site. Neighborhoods are circles of 15-m (for trees) and 5-m (for shrubs) radius around each sample point. Shrub crown area is given for the most common species across the six study sites.

	Quercus suber-Olea europaea forests			*Quercus suber-Quercus canariensis* forests		
	Ahumada (S)	Cinchao (C)	Picacho (N)	Comares (S)	Jimena (C)	Tala (N)
Latitude (N)	36º 04' 38"	36º 18' 37"	36º 31' 69"	36º 06' 09"	36º 23' 10"	36º 28' 13"
Longitude (W)	05º 33' 05"	05º 41' 14"	05º 38' 08"	05º 30' 53"	05º 31' 52"	05º 35' 31"
Annual rainfall (mm)	948.9	726.4	973.1	1067.1	1022.6	1097.0
Mean annual T (ºC)	16.3	16.9	16.3	15.4	17.3	15.9
Texture	0.47	0.67	0.54	0.72	0.66	0.75
	[0.24-0.61]	[0.56-0.77]	[0.36-0.63]	[0.65-0.79]	[0.55-0.76]	[0.69-0.82]
Tree basal area						
Olea/*Q. canariensis*	3.49	4.09	3.73	16.99	10.21	11.34
	[0.10-7.47]	[0-23.41]	[0.34-17.49]	[6.14-32.14]	[0-21.19]	[3.31-23.03]
Q. suber $_{\text{Healthy}}$	0.82	14.08	0.82	2.22	2.06	5.37
	[0-10.98]	[3.88-25.37]	[0-10.98]	[0-16.27]	[0-9.97]	[0-14.77]
Q. suber $_{<50\% \text{ defoliation}}$	3.29	2.37	15.74	3.09	2.18	0.09
	[0-4.92]	[0-9.91]	[3.76-35.69]	[0.21-4.48]	[0-12.32]	[0-5.76]
Q. suber $_{>50\% \text{ defoliation}}$	1.76	------	2.54	1.92	0.00	0.00
	[0-6.59]		[0-5.53]	[0.23-4.85]	[0-2.43]	[0-0.00]
Q. suber $_{\text{Dead}}$	3.76	0.00	0.00	3.46	0.00	0.44
	[0-17.75]	[0-0.64]	[0-3.64]	[1.68-8.50]	[0-3.90]	[0-2.54]
Shrub crown area						
Pistacia lentiscus	0.00	0.08	0.14	------	0.00	------
	[0-0.06]	[0-0.47]	[0-0.25]		[0-0.07]	
Erica spp.	0.00	------	------	0.02	0.36	0.00
	[0-0.01]			[0-0.21]	[0.08-1.08]	[0-0.03]
Phillyrea latifolia	0.03	0.00	0.02	0.00	0.00	0.00
	[0-0.09]	[0-0.00]	[0-0.09]	[0-0.09]	[0-0.04]	[0-0.29]
Crataegus monogyna	0.03	0.00	0.05	------	0.00	------
	[0-0.13]	[0-0.01]	[0-0.16]		[0-0.01]	

Appendix 2. Parameter estimates and 2-unit support intervals (in brackets) for the best model selected for each combination of soil pathogen species and forest type. See text for a description of the parameters.

Parameter	*Quercus suber-Olea europaea forests*			*Quercus suber-Quercus canariensis* forests		
	Phytophthora cinnamomi	*Pythium spiculum*	*Pythium* spp.	*Phytophthora cinnamomi*	*Pythium spiculum*	*Pythium* spp.
PPA_{South}	1002.35	-----	305.11	4.20	0.40	-----
	[1002.34-1002.36]		[305.10 -305.12]	[3.63-5.15]	[0.39-0.41]	
PPA_{Center}	383.74	12.52	89.51	5.35	0.61	3.61
	[383.73-383.75]	[12.51-12.53]	[89.43-89.89]	[4.19-6.01]	[0.60-0.62]	[2.58-4.84]
PPA_{North}	1133.24	8.17	-----	31.87	-----	44.35
	[1133.23-1133.25]	[8.16-8.18]		[30.23-32.90]		[41.76-47.27]
b (texture)	-2.05	-1.73	-2.76	-0.37	-----	-2.29
	[-2.17 to -1.96]	[-1.91 to -1.56]	[-2.77 to -2.75]	[-0.38 to -0.36]		[-2.30 to -2.28]
c (tree)	0.72	1.22	2.78	2.23	3.98	3.23
	[0.71-0.73]	[1.21-1.23]	[2.77-2.79]	[2.22-2.24]	[3.99-3.97]	[3.22-3.24]
d (shrub)	-0.29	-0.38	-0.94	0.62	-----	0.49
	[-0.45 to -0.12]	[-0.58 to -0.21]	[-1.09 to -0.79]	[0.54-0.71]		[0.33-0.63]
α	1	1	1	1	1	1
γ ($\times 10^{-3}$)	510.62	3.63	0.00	0.21	0.17	0.00
	[470.71-550.73]	[0.45-13.63]	[0-10]	[0.12-5.22]	[0.05-6.13]	[0-10]
β	1.41	3.99	1.60	3.99	3.03	3.67
	[1.35-1.46]	[3.72-4]	[0.50-4]	[3.76-4]	[2.75-3.11]	[0.50-4]
λ *Olea*/*Q. canariensis*	-0.45		-0.24	0.23		0.22
	[-0.46 to -0.44]		[-0.25 to -0.23]	[0.22-0.24]		[0.22-0.24]
λ *Q. suber* Healthy	0.17		0.29	-0.41		-0.28
	[0.16-0.18]		[0.28-0.30]	[-0.42 to -0.40]		[-0.29 to -0.30]
λ *Q. suber* <50%	0.30		0.46	0.41		0.49
	[0.29-0.31]		[0.45-0.47]	[0.40-0.42]		[0.48-0.50]
λ *Q. suber* >50%	1		1	1		1
	[0.99-1]		[0.99-1]	[0.99-1]		[0.99-1]
λ *Q. suber* Dead	-0.16		-0.19	-0.46		-0.24
	[-0.17 to -0.15]		[-0.12 to -0.17]	[-0.47 to -0.45]		[-0.25 to -0.23]

Appendix 3. Parameter estimates and 2-unit support intervals (in brackets) for the best models of *Phytophthora cinnamomi* effects on emergence and survival of *Quercus suber* and *Quercus canariensis* seedlings. Because emergence and survival were modeled with a binomial distribution, parameter values predict the logit(emergence) and logit(survival). See text for a description of the parameters.

		Quercus suber-Olea europaea forests	*Quercus suber-Quercus canariensis* forests	
Variable	Parameter	*Q. suber*	*Q. suber*	*Q. canariensis*
Emergence	PSE_{South}	-0.83 [-1.12 to -0.59]	0.27 [0.02-0.52]	-0.22 [-0.46 to 0.04]
	PSE_{Center}	-0.56 [-0.80 to -0.27]	-0.01 [-0.25 to 0.25]	-0.31 [-0.55 to -0.05]
	PSE_{North}	0.15 [-0.12 to 0.40]	-0.67 [-0.93 to -0.41]	-1.07 [-1.36 to -0.79]
	b_{South}	0.03 [-0.02 to 0.08]		
	b_{Center}	-0.09 [-0.27 to -0.01]		
	b_{North}	-0.16 [-0.23 to -0.09]		
Survival	PSS_{South}	1.28 [0.84-1.85]	1.20 [0.83-1.66]	1.08 [0.73-1.46]
	PSS_{Center}	0.35 [0.84-1.85]	1.36 [0.92-1.83]	1.31 [0.91-1.73]
	PSS_{North}	0.93 [0.84-1.85]	0.36 [-0.05 to 0.82]	0.15 [-0.20 to 0.52]
	b_{South}	-0.20 [-0.29 to -0.11]		
	b_{Center}	-0.19 [-0.68 to 0.06]		
	b_{North}	0.12 [-0.02 to 0.27]		