

# Counteracting gradients of light and soil nutrients in the understorey of Mediterranean oak forests

L. V. García, S. Maltez-Mouro, I. M. Pérez-Ramos, H. Freitas, and T. Marañón

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The forest canopy modifies the availability of resources (light, water, and soil nutrients) in the understorey. In this paper we analyze the relationships between woody canopy density, litter accumulation, and topsoil N and P availability in the understorey of two oak forests: one in southern Portugal and the other in southern Spain. Both forests persist on low-nutrient soils, particularly poor in P. We hypothesize that direct and indirect effects of the canopy overstorey cause opposite gradients in the availability of essential resources (light and key soil nutrients) in the understorey. In both studied forests we found significant relationships between the overall canopy density, light availability, topsoil litter accumulation, and the availability of N and P, which frequently limit plant growth. Path analysis (by Shipley's d-sep method) showed that the available data were consistent with the proposed causal model. The average values of soil variables at the end quartiles of the light-availability gradient were compared. Results showed large differences in litter accumulation (~30×) and available-N and -P topsoil concentrations (~3×) in the Spanish forest (with the wider environmental gradient). Furthermore, P increased from the 'very low' range to the 'low' or even the 'optimum' range of availability (according to standard plant growth criteria), which suggests potential effects on the growth of the understorey plant species. We conclude that the counteracting gradients of the essential resources -light and nutrients- in the forest understorey resulted from direct and indirect effects of the canopy overstorey, respectively. We suggest that these counteracting effects of the woody canopy on essential resources of different nature must be considered when interpreting the patterns of understorey plant populations and communities.

*L. V. García (ventura@cica.es), I. M. Pérez-Ramos and T. Marañón, Depto. de Geoecología, Instituto de Recursos Naturales y Agrobiología (CSIC), P.O. Box 1052, E-41080 Sevilla, Spain. – S. Maltez-Mouro and H. Freitas, Dept. of Botany, Univ. of Coimbra, Calçada Martim de Freitas, 3000 Coimbra, Portugal.*

The tree canopy modulates the availability and variability of some key resources for the organisms living in the understorey, thus affecting its own regeneration (Binkley & Giardina 1998, Washburn & Arthur 2003, Maltez-Mouro et al. 2005a, 2005b). Several recent studies have documented the direct effects of the Mediterranean forest canopy on the growth and survival of tree seedlings in the

understorey through changes in the availability of light and water (Sack et al. 2003, Quero et al. 2006, Sánchez-Gómez et al. 2006). However, the indirect effects such as those mediated by soil and litter have also been proven to be important for plant growth in the understorey (Rossi and Villagra 2003, Broncano et al. 2004, Puerta-Piñero et al. 2006).

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The spatial and temporal heterogeneity of different resources may induce uncoupled responses by understorey plants. Tree seedlings can grow faster during spring in open microsites with higher light availability, but will suffer a higher mortality during the summer (with lower water availability) in comparison with seedlings in moderately shaded microsites (Marañón et al. 2004). We expect that seedlings in forest gaps will find higher light levels (direct effect) but lower leaf litter and, in consequence, lower availability of soil nutrients (indirect effect).

Detection and evaluation of the indirect effects of the canopy mediated by litter accumulation and soil changes on the growth and survival of understorey plants are not easy. Firstly, the complex and multivariate nature of the understorey – and soil in particular (Binkley and Giardina 1998, Washburn and Arthur 2003) – makes it difficult to distinguish which changes are related to the direct effects of litter accumulation (e.g. limiting seedling emergence), which changes result from the indirect effects of litter on soil properties (e.g. affecting soil chemical composition), and which changes result from other factors that may affect soil properties such as changes in the parent material. Secondly, covariation exists between gradients of different essential resources that relate to changes in canopy density. This covariation may lead to the attribution of all the changes in the understorey to a few well-known and easily measurable direct effects (e.g. light availability), while ig-

norning the role of other more-subtle indirect effects (e.g. changes in soil nutrient availability related to litter accumulation).

We analyze the relationships between woody canopy density and understorey conditions, in particular light availability, litter accumulation, and changes in soil N and P concentrations. The aims of our study are 1) to test the hypothesis that the tree overstorey may induce counteracting gradients of available key resources, such as light and soil nutrients in the understorey, and through some direct and indirect effects; 2) to evaluate the potential impact of the hypothesized canopy indirect effects on the understorey plants; and 3) to analyze the covariation between direct (light) and indirect (nutrient availability) effects associated to changes in the canopy density.

## Methods

### Study sites

We studied *Quercus* forests located in two protected areas in the south of the Iberian Peninsula (Fig. 1): the *Sudoeste Alentejano e Costa Vicentina* Natural Park, in southern Portugal (SP, hereafter), and *Los Alcornocales* Natural Park, in southern Spain (SS, hereafter). Both forests are dominated

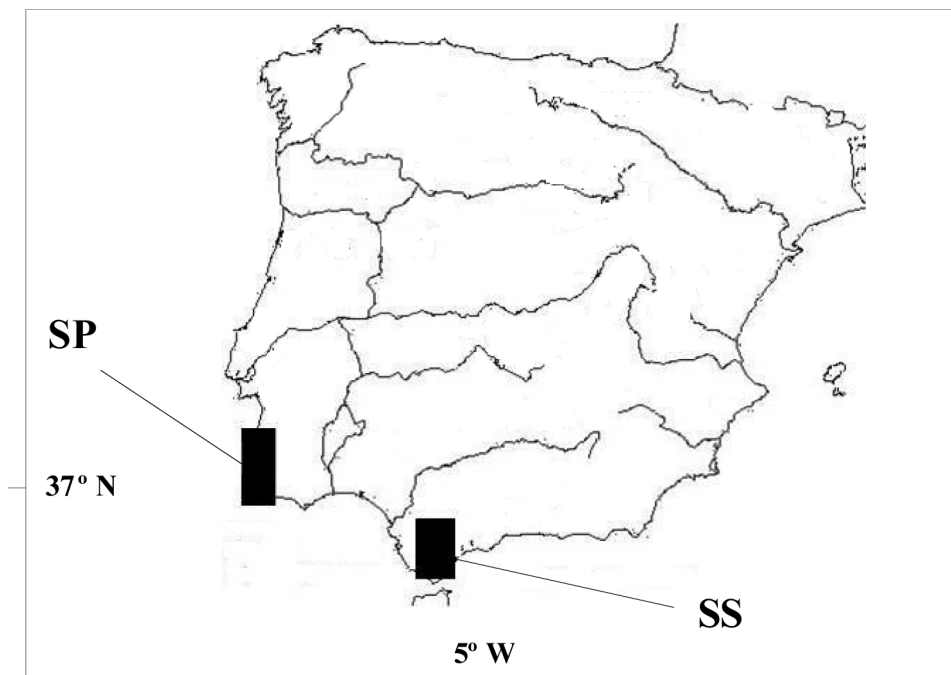


Fig. 1. Location of the study areas in the Iberian Peninsula. SS = Spanish site at *Los Alcornocales Natural Park*; SP = Portuguese site at *Sudoeste Alentejano e Costa Vicentina Natural Park*.

by an evergreen oak species (*Quercus suber*) mixed with a deciduous one (*Q. faginea* or *Q. canariensis*, respectively).

The climate is Mediterranean-type, with wet winters and dry summers. Mean annual rainfall is higher in SS (ca. 1200 mm) than in SP (ca. 600 mm). Average annual temperatures are ca. 16 °C and 15 °C, respectively. Dominant soils are acidic and usually poor in nutrients in both SP (Maltez-Mouro et al. 2005a) and SS (Jordan et al. 1998, Quilchano, C., pers. comm.).

## Canopy, litter, and soil measurements

We sampled 25 plots (4×4 m<sup>2</sup>) in SP and 60 plots (3×3 m<sup>2</sup>) in SS distributed along gradients of canopy density in late fall and beginning of winter (November–December) of yrs 2003 and 2005, respectively. In each plot we gathered information about three different groups of variables: canopy density (closely related with light availability), litter accumulation, and soil nutrients.

To quantify the canopy density variables, a spherical densimeter was used in SP to measure the percent of the overhead area not covered by the canopy. In the SS plots, digital hemispherical photographs were analyzed using the *Hemiview* software (Anon. 1998) to calculate the Global Site Factor (GSF, the proportion of total radiation under a plant canopy relative to that in the open), Leaf Area Index (LAI, surface area of leaves per ground area unit), and Ground Cover (GC, vertically projected canopy area per unit ground area). For comparison purposes, GSF values for the SP forest were roughly estimated from the GC values using the GSF-GC regression from SS data ( $R^2 = 0.65$ ).

Litter accumulation was evaluated by visual estimates (percent of the soil surface covered by litter, with agreement of three observers). In the SS plots, litter layer depth was estimated as the average of ten random measurements using a metric tape. Litter dry mass accumulation was estimated by collecting all the litter included inside a randomly placed quadrat of 30×30 cm; that litter was dried at 70 °C for three days and weighed to the nearest 0.1 g.

In each of the studied forests, topsoil (< 25 cm depth) was sampled using an auger (3 cm in diameter) at 3–7 points located inside each plot, and mixed to produce one composite soil sample per plot. The soil samples were dried, crushed, passed through a sieve (2 mm), and then analyzed for organic N (Kjeldahl method), available P (Olsen method), and NH<sub>4</sub>-N (extracted with 2M KCl) contents. To estimate P availability for plants in leached, very-poor-in-P, and acidic soils, the Bray and Kurtz method is recommended (Frank et al. 1998, Anon. 2000) instead of the most frequently used Olsen's method (Olsen et al. 1954). Therefore, values of the Bray-1 P-availability index (besides the Olsen values) were obtained for the SP samples. All soil analyses were performed according to the methods prescribed in Sparks (1996).

## Data analysis

Relationships between canopy density, litter accumulation, and topsoil nutrient content were analyzed by correlation analyses. To test whether the available data were consistent with the hypothesis of higher canopy density causing increased accumulation of litter – which decomposes and is responsible for the increase of N and P availability in the soil – a d-sep method of path analysis (Shipley 2000, 2003) was used. For both studied nutrients (N and P) and sites, two separate and one general causal model were tested. For the general model, two alternatives were considered: 1) litter accumulation is the immediate cause that simultaneously explains N and P changes, and 2) litter influence on N and P availabilities is mediated by soil processes, which can be summarized considering an unmeasured (latent) factor (labeled as 'soil processes'). Although the d-sep method is not designed for testing models including unmeasured (latent) variables (Shipley 2000), in this special case the d-sep test is still applicable assuming that N and P have correlated (instead of independent) errors (Shipley 2003).

We compared the average values of litter and soil variables at the end quartiles of the light-availability gradients to evaluate the magnitude of the increment of the variables related to litter accumulation and nutrient availability.

When necessary, variables were transformed to conform to the assumptions of the parametric analysis. Corrections for multiplicity were performed according to García (2004). All statistical analyses were performed using the *Statistica* (Anon. 2001) and *Causal Toolbox* (Shipley 2000) packages.

## Results

Descriptive values (mean, standard deviation, maximum, and minimum) of the three groups of forest variables are shown in Table 1. Ranges of variation were particularly high in the SS dataset, where the light availability range was 8–89% of the radiation at an open site. The litter accumulation gradient was also very wide: 0.8–3400 g m<sup>-2</sup> that covered 0.5–100% of the soil surface. Phosphorus availability ranged from the 'very low' (0–3 mg kg<sup>-1</sup> Bray 1-P or 0–6 mg kg<sup>-1</sup> Olsen-P) to the 'optimum/normal' level (8–20 mg kg<sup>-1</sup> Bray 1-P or 13–18 mg kg<sup>-1</sup> Olsen-P) – considering rank values of southern Spanish loamy-textured soils (Anon. 1992). Ammonium availability increased about 25-fold along the same gradient. The variation ranges for all measured variables were narrower in the SP forest (Table 1).

The high frequency of soils having P shortage in both sites is remarkable. In the SS forest, more than 80% of the studied soils were in the 'very low' range, with only 10% having 'low availability' levels (4–7 mg kg<sup>-1</sup> Bray 1-P or 7–12 mg kg<sup>-1</sup> Olsen-P), and another 10% having the so-

Table 1. Mean, standard deviation, minimum, and maximum values for the canopy density, litter accumulation, and topsoil variables measured in the two studied forests (SS = southern Spain site at *Los Alcornocales Natural Park*; SP = southern Portugal site at *Sudoeste Alentejano e Costa Vicentina Natural Park*). Data estimated using linear regression (see text) are in italics.

	SS				SP			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
<i>Canopy density / light availability</i>								
Global Site Factor (GSF, 0–1)	0.32	0.23	0.08	0.89	<i>0.11</i>	<i>0.06</i>	<i>0.05</i>	<i>0.27</i>
Leaf Area Index (LAI, m <sup>2</sup> m <sup>-1</sup> )	1.69	0.71	0.38	3.02	–	–	–	–
Ground Cover (GC, %)	49	34	0	90	85	10	62	95
<i>Litter accumulation</i>								
Covered soil (%)	63	38	0.5	100	47	28	5	90
Thickness (cm)	3.1	2.7	0.1	13.7	–	–	–	–
Dry weight (g litter m <sup>-2</sup> )	557	643	0.8	3399	–	–	–	–
<i>Soil properties</i>								
Total N (Kjeldahl, %)	0.33	0.12	0.12	0.75	0.37	0.04	0.23	0.43
Available P (Olsen, mg kg <sup>-1</sup> )	3.1	2.6	0.0	14.9	3.5	1.3	1.6	5.9
Available N (N–NH <sub>4</sub> , mg kg <sup>-1</sup> )	3.2	2.9	0.7	16.1	4.4	2.5	1.6	11.1
Available P (Bray 1, mg kg <sup>-1</sup> )	2.0	1.8	0.2	8.9	–	–	–	–

called ‘normal’ or ‘optimum’ range for most plant species (Anon. 1992). In the case of the SP forest, all the studied soil samples had ‘very low’ values of P availability.

The light availability (measured as GSF) was very heterogeneous in the SS forest but slightly more homogeneous in the SP forest, where the estimated GSF (overstorey canopy density) ranged from 0.05 to 0.27, with an average value of 0.11.

## Relationships between canopy, litter, and soil

In both forests, there were highly significant relationships between variables related to canopy density and variables related to litter accumulation (Table 2, Fig. 2). Litter accumulation variables were significantly correlated to topsoil concentrations of available N and P (Table 2, Fig. 3). In addition, canopy density variables were significantly correlated with topsoil available-N and -P concentrations

(Table 2). Finally, as an expected result of the indirect effects of the canopy on soil enrichment, available N and available P were highly intercorrelated in both studied forests (Fig. 4).

The results of path analyses (using Shipley’s d-sep method) are shown in Table 3. All the separate (single-nutrient) linear models tested for both nutrients and sites were found to be consistent with the observed data ( $p = 0.35$  to  $0.96$ ). In contrast, the general (two-nutrient) models assuming that the litter accumulation is the direct and immediate cause of the conjoint observed change in the concentrations of available N and P in the studied forests soils were rejected for both sites (Table 3).

However, the general model assuming that an unmeasured latent factor (‘soil processes’) is the immediate common cause for the observed conjoint increase of N and P availabilities along the canopy-density/litter-accumulation gradients was consistent with the empirical data ( $p > 0.70$ , Table 3). In this model, errors of N and P are correlated.

Table 2. Summary of the correlation values between canopy density, litter accumulation, and topsoil parameters in the two studied forests. For litter accumulation and canopy density, only the highest correlation found is shown. The per-test significance of the results is indicated by ns  $p > 0.05$ , \*  $p \leq 0.05$ , \*\*  $0.05 < p \leq 0.005$ , \*\*\*  $p < 0.005$ . Values in italics did not remain significant after controlling the familywise error rate (FWER) in the entire correlation matrix at the 0.05 level. SS = Spanish site at *Los Alcornocales Natural Park*; SP = Portuguese site at *Sudoeste Alentejano e Costa Vicentina Natural Park*.

	Canopy density		Litter accumulation	
	SS	SP	SS	SP
Litter accumulation	0.77***	0.85***	–	–
P availability	0.49***	0.56***	0.51***	0.70***
N availability	0.47***	0.49*	0.47***	0.59***
Total N	0.41***	0.24 ns	0.32*	0.12 ns

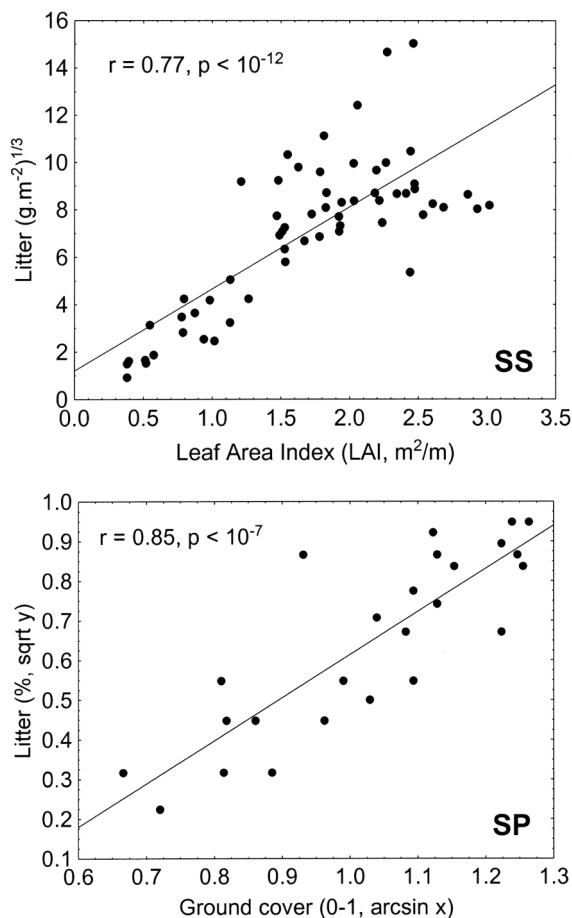


Fig 2. Scatterplots illustrating the closest linear relationships found between the measured canopy density variables and the litter accumulation variables in the soil of the forest sites located in southern Spain (SS, upper graph) and southern Portugal (SP, lower graph).

Overall, these results are consistent with the hypothesis that the overstorey canopy indirectly affects the topsoil N and P availability through litter accumulation.

There were marked differences in litter accumulation and soil nutrient contents between the plots in contrasting light environments (end quartiles,  $Q_1$ – $Q_4$ , of the light-availability gradients) in both studied sites (Table 4). In the SS forest, the decrease in light availability along the gradient (5.6 times) was paralleled by a notable increase in LAI ( $\times 3.5$ ). This change in canopy density was amplified by its direct effects on the proportion of soil covered by litter ( $\times 15$ ), litter thickness ( $\times 19$ ), and accumulated litter mass ( $\times 29$ ). The consequent increase in soil nutrient concentrations (indirect effects) was notable for both the available N ( $\times 2.7$ ) and Bray 1-P ( $\times 3.2$ ). A similar pattern was found in the SP forest, where a moderate increase in the canopy

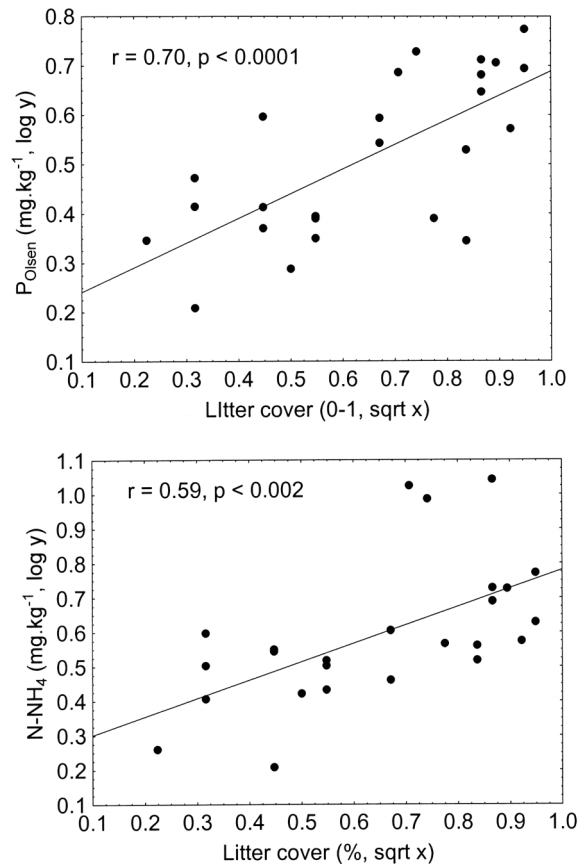


Fig 3. Scatterplots illustrating the closest linear relationships found between litter cover (%) and concentration of available P (upper graph) and available N (lower graph), in the site of southern Portugal.

density ( $\times 1.4$ ) was paralleled by marked increases in soil litter cover ( $\times 4.7$ ) and, to a lesser extent, soil P ( $\times 1.9$ ) and N-NH<sub>4</sub> ( $\times 1.7$ ) availabilities (Table 3).

## Discussion

Conjoint analysis of the canopy density gradients and changes in litter accumulation and nutrient availability showed that these variables covariate. Moreover, the results support the hypothesis of counteracting effects from the woody canopy on two different resources – light and nutrients – that are essential for plants living in the understorey.

The direct limitation of light availability in the understorey is the best-known and most-conspicuous effect of increased canopy density, and plays a major role in structuring the understorey communities in Mediterranean forests (Pérez-Ramos et al. 2006, Sánchez-Gómez et al. 2006, Valladares and Guzmán 2006). Therefore, light must be the most-limiting ecological factor at the darkest end of the

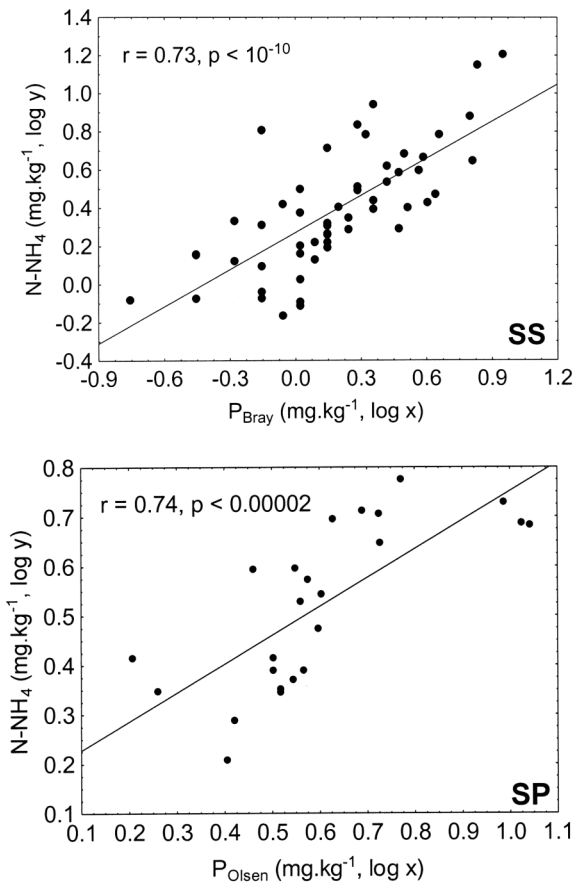


Fig. 4. Relationships between P and N available concentrations in topsoil of the forest sites located in southern Spain (upper graph) and southern Portugal (lower graph).

light gradient (with values about 1/10 of full sun) in both studied forests.

At the same time, except in very low light conditions, forest plants usually respond positively to soil nutrient increases, especially in poor soils (Walters and Reich 2000). Therefore, soil nutrients may condition plant growth and survival in the SS forest, where a significant proportion of microsites have enough light availability (Table 4).

In both forests, there is correlational support for the existence of counteracting trends between nutrient and light availability. This pattern is particularly significant for P availability, which reached extremely low values of available concentration at the brightest end of the canopy density gradient, while increasing to 300% and reaching non-limiting levels for most plant species at the darkest end.

The patterns for P and N availability in relation to light were similar: both reached very low values for the sparsest canopy and increased towards the darker end of the light gradient. In semi-arid ecosystems, isolated trees induce a joint decrease in light availability and an increase in organic matter and nutrients under the canopy (Mordelet et al. 1993). However, Gallardo (2003) found that N and P were differentially affected by the oak canopies in a Spanish *dehesa*: only the N distributions were coincident with the tree canopies, while P was distributed beyond the oak canopies due to geochemical processes.

The plants' growth and survival along these counteracting gradients depend on their ability to cope with limiting light *versus* soil nutrient availability. At intermediate positions of the illumination gradient (i.e. in sites without severe light limitations) one would expect that the increased nutrient availability – related to the accumulation of moderate amounts of litter – would have significant effects on the composition of the understorey communities. In fact, understorey plants having a certain degree of shade tolerance may take advantage of the soil enrichment in essential nutrients such as N and P as the canopy density increases. In contrast, plants being more efficient in the use of N and

Table 3. D-sep test results of different causal models explaining the observed covariation between canopy density ("Cover"), litter accumulation ("Litter"), and nutrient (N and/or P) availability in the two studied sites (SS = Spanish site, SP = Portuguese site). The upper panel shows the results related to models including only one nutrient (N or P). The lower panel refers to models including both nutrients (N and P). These models consider either litter accumulation the immediate cause of their variation (upper line, corresponding to a model with independent errors) or assuming that litter influence on the availability of the two nutrients is mediated by an unmeasured, latent factor related to soil processes (lower line, corresponding to a model with correlated errors).

	Chi-sq	SS DF	p	Chi-sq	SP DF	p
<i>One-nutrient models</i>						
Cover – Litter – N availability	0.11	2	0.94	0.08	2	0.96
Cover – Litter – P availability	2.09	2	0.35	0.78	2	0.67
<i>Two-nutrient models</i>						
Cover – Litter – N & P availabilities	41.35	6	0.00	13.01	6	0.04
Cover – Litter – (Soil) – N & P availabilities	2.20	4	0.70	0.86	4	0.93

Table 4. Comparison of litter accumulation and soil properties between the end quartiles of the studied light-availability gradients. For each variable, the value of Mean±Standard Deviation and of the ratio between means of end quartiles ( $Q_1/Q_4$ ) are shown.

	Light availability in the understorey		
	Low ( $Q_1$ )	High ( $Q_4$ )	$Q_1/Q_4$
<b>South Spain's forest (SS)</b>			
<i>Litter layer</i>			
Covered soil (%)	91 ± 10	6 ± 8	15.3
Thickness (cm)	5.6 ± 2.1	0.3 ± 0.4	18.6
Dry weight (g litter m <sup>-2</sup> )	917 ± 720	31.8 ± 36.7	28.8
<i>Soil properties</i>			
Total N <sub>Kjeldahl</sub> (%)	0.43 ± 0.16	0.29 ± 0.10	1.5
Available N (N-NH <sub>4</sub> ) (mg kg <sup>-1</sup> )	5.1 ± 4.7	1.9 ± 1.6	2.7
Available P <sub>Olsen</sub> (mg kg <sup>-1</sup> )	5.4 ± 3.9	3.0 ± 1.0	1.8
Available P <sub>Bray</sub> (mg kg <sup>-1</sup> )	2.9 ± 2.4	0.9 ± 0.7	3.2
<b>South Portugal's forest (SP)</b>			
Litter cover (%)	75 ± 17	16 ± 9	4.7
Total N <sub>Kjeldahl</sub> (%)	0.38 ± 0.06	0.35 ± 0.03	1.1
Available N (N-NH <sub>4</sub> )	4.7 ± 1.0	2.7 ± 0.8	1.7
Available P <sub>Olsen</sub> (mg kg <sup>-1</sup> )	4.3 ± 1.3	2.3 ± 0.4	1.9

P may be favored in sites having higher light availability (Walters and Reich 2000).

Interactions between light, soil resources, and the overstorey canopy species will affect regeneration dynamics of the forest ecosystem. Therefore, the complex covariation of different resources must be fully understood to optimize management or conservation actions in Mediterranean forests. In particular, some soil chemical properties with ecological relevance (such as soil N and P availabilities) in forest regeneration may change in a close relationship with other better-known ecological factors (such as light, moisture, and temperature). Thus, attention should be given to separating direct (e.g. light limitation) *versus* indirect (litter and soil mediated) effects of the woody canopy on ecosystem processes.

Covariation of different essential resources depending (direct or indirectly) on canopy density tends to obscure the role of more-complex, indirect, and subtle effects (e.g. soil nutrients) against those that are more conspicuous and direct (e.g. light) when interpreting the patterns of understorey plant populations and communities. The indirect effects may influence (in some sites or moments) regeneration processes as much as those directly depending on canopy density (e.g. light). Based on our results, it can be predicted that the understorey communities at the recent gaps (natural or artificially opened) in dense canopies will include new species with higher light requirements than those formerly living in deep shade, but also with higher nutrient requirements than those usually living in the N- and P-depleted older gaps. Thus, periodic disturbances would reduce the usual negative correlation between light and nutrients (typical of unmanaged forests), inducing higher habitat and species diversity (Spies and Turner 1999).

There are marked changes in density, composition, and diversity of the understorey communities growing along the studied combined gradients of light and nutrients (Maltez-Mouro et al. 2005a, 2005b, García, unpubl.). For a mechanistic explanation, we must know the response of existing species to light and nutrient gradients, or at least some index of their ecological preferences such as the indices defined by Ellenberg (1988) for Central Europe. Further studies on the ecophysiology of Mediterranean species, together with field manipulative experiments, will allow evaluating the relative importance of these covarying factors for forest regeneration and dynamics.

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