Influence of forest structure and environmental variables on recruit survival and performance of two Mediterranean tree species (*Quercus faginea* L. and *Q. suber* Lam.)

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Abstract

We investigated the regeneration requirements of the two dominant tree species in a mixed-oak forest of SW Portugal: *Q. suber* (cork oak, evergreen) and *Q. faginea* (Portuguese oak,winter-deciduous). We hypothesized that: (1) recruits of different oak species are differentially influenced by soil and overstory variables; and (2) different factors explain the recruitment occurrence and performance of the same species. We sampled the recruits' height and diameter, and several environmental and forest structure variables of their microsites. Both recruitment occurrence and performance were modelled using generalized linear models. Our final models predicted the probability of occurrence of recruits of *Q. faginea* and *Q. suber* with 74% and 82% of accuracy, respectively, and explained about 50% of the variance of their recruitment performance. The recruits of *Q. faginea* tended to occur in microsites with higher canopy height, canopy density and litter cover, and closer to both conspecific and heterospecific adults, while the opposite was true for recruits of *Q. suber*. The performance of recruits of *Q. suber* was favoured by the higher litter cover (a good surrogate for N and P availability), but negatively affected by the higher litter depth. We concluded that: (1) there were significantly different regeneration niches for each species (*Q. faginea* and *Q. suber*), (2) the factors explaining the of recruitment occurrence differed from those explaining the recruitment performance; (3) the overstory plays a complex and important role in the regeneration process; (4) different variables apparently related with the same environmental factor (e.g. litter cover and litter depth) could affect recruits in an opposite way, (5) sensitive trade-offs must be considered for delineating management actions,

since they could favour the regeneration of *Q. suber* but, at the same time, negatively affect the regeneration of *Q. faginea*.

Keywords: Mediterranean forest, recruitment, evergreen oak, winter-deciduous oak, litter effects.

Introduction

The Mediterranean ecosystems have been recognized as one of the Earth's biodiversity hotspots (Myers *et al.* 2000). Nevertheless, natural forests throughout the Mediterranean Basin have been disturbed or destroyed by human activities, and nowadays they follow a fragmented distribution that occupies less than 10% of the area (Marchand 1990).Therefore, it has been encouraged to look for a better understanding of the natural regeneration processes in Mediterranean forests (Acácio et al. 2007), because it is essential to know the ecological requirements for recruit establishment and growth, before trying to develop management and restoration strategies (Khurana and Singh 2001). Besides, little is known about the natural regeneration of Mediterranean *Quercus* species, as long as a noticeable part of the research has been carried out in the dehesa (savannah-like) agrosytems (Pons and Pausas 2006).

Evaluating the natural regeneration is an integrative way of evaluating the fitness and give an insight into the future of the populations under study (Pons and Pausas, 2006). As any plant species, the established trees in a Mediterranean forest have succeed in a chain of processes, including dispersion, germination and emergence responses, and seedling growth and survival (Herrera et al. 1994), but the regeneration requirements can be inferred from the micro-environmental conditions associated with the successful seedlings, saplings and juveniles of each species in their natural habitats (Marañón et al. 2004).

In this study we investigated the regeneration conditions of two *Quercus* species that frequently exhibit lack of regeneration (Pérez-Ramos and Marañón 2005, Esteso-Martinez et al. 2006, Pausas et al. 2006, Acácio et al. 2007, Urbieta et al. 2008a, Urbieta et al. 2008b): the evergreen oak *Q. suber* L. (cork oak) and the winter-deciduous oak *Q. faginea* Lam. (Portuguese oak). These species occur mainly in the Mediterranean Basin (Tutin 1964), they are the dominant trees of mixed-oak Mediterranean forests on southern Portugal (Maltez-Mouro et al. 2005, García et al. 2006, Maltez-Mouro et al. 2007), and they are protected by the European Union Directives (Habitat Directive 92/43EEC).

Q. faginea does not constitute mono-specific communities and, being together with other (tree and not tree) species, promotes the higher species richness of mixed-oak forests. However, and regardless its huge ecological importance, *Q. faginea* has not been much studied, compared to the high number of references for other species more useful directly for humans – as timber, fuel, charcoal, or resin extraction (Sánchez Arroyo 2002). *Q. suber* is a tree species with socio-economic and cultural value, but very little is known about the recruitment and regeneration of this species (see review by Montero et al. 1994), and most of the research has been performed in the dehesa agrosystems. Even though, Pausas et al. (2006) have recently shown the lack of successful regeneration of *Q. suber*, and the need of land management to provide appropriate conditions for seedling or recruit establishment and growth. Therefore, studying the natural conditions prevailing in preserved forest patches with an adequate oak regeneration is of primordial importance (Khurana and Singh 2001, Acácio et al. 2007).

The published literature on oak regeneration in Mediterranean forests gives important knowledge related with the processes of dispersion (e.g. Aparicio et al. 2008), seed predation (e.g. Pérez-Ramos and Marañón 2005), establishment (e.g. Lloret et al. 2004), and seedling survival and growth (e.g. Benayas et al. 2005, Antúnez et al 2001). Most studies on the first stages of regeneration of the Mediterranean oak species have been performed on seedlings growing under controlled conditions (Espelta et al. 1995; Quero et al. 2006, Sánchez-Gómez 2007). However, some studies carried out in natural ecosystems have shown that at low-light environments, the survival of seedlings of deciduous species (related with *Q. faginea*) exceeded the survival of seedlings of the evergreen *Q. suber* (Gómez-Aparicio et al. 2008). This pattern has been explained by the tendency of the deciduous species to be more frequent in habitats with denser overstory canopy, where the availability of water and nutrients is higher (Quero et al. 2006, Urbieta et al. 2008b).

In this paper we aim to focus on the young and middle phases of the regeneration process in natural conditions. Therefore, we studied a natural Mediterranean mixed-oak forest and the oak recruits that have succeeded the first processes of regeneration, but still being part of the understory and suffering from the effects of the overstory (George and Bazzaz 1999, Maltez-Mouro et al. 2005). We analyze how several environmental factors related to the regeneration (occurrence and performance) success of *Q. suber* and *Q. faginea*, we evaluate the differences between them, and we investigate the role of the overstory structure and composition. We also show how a non-temporal approach can provide useful information on (still) well-preserved Mediterranean forests, which was urgent before any major change or disruption occurs - and as it is the case for many other endangered ecosystems.

We hypothesized that: (1) in natural conditions, recruits of the two studied oak species are differentially influenced by different soil variables (litter depth, water content, nutrient availability) and by the overstory structure and composition; (2) different factors explain the recruitment occurrence and performance of the same species, because of changes in the regenerations niches along their ontogeny. We also relate our findings on natural conditions, with those described in other studies developed on controlled conditions.

Methods

Study site

The study site is located in the Sudoeste Alentejano e Costa Vicentina Natural Park, SW Portugal (37º 40' N, 8º 43' W). It is a mixed-oak forest composed of evergreen oaks (cork oak, *Q. suber*) and semideciduous oaks (Portuguese oak, *Q. faginea*), on a north-facing slope (32º). Other frequent woody species are the strawberry tree (*Arbutus unedo* L.), the laurestine (*Viburnum tinus* L.) and the kermes oak (*Quercus coccifera* L.) (see Maltez-Mouro et al. 2005).

The climate is typically Mediterranean, with mild wet winters and warm dry summers. The mean annual precipitation is ca. 600mm, with only 10% occurring between May and September, and the mean annual temperature is ca. 15 ºC, with mean maximum and minimum annual temperatures of ca. 29 ºC and 6 ºC, respectively (PNSACV 2002). Soils are acidic (mean pH=5.0) and low in nutrients (especially in N and P, see Maltez-Mouro et al. 2005).

The studied forest site is within an area that has undergone a long history of fire and land use, but it is relatively well preserved, with no record of fire or logging since at least 1956. Management is limited to the periodic (at approximately 9-year intervals) removal of the bark from the largest cork oak trees, for cork production. The oak regeneration is good, with frequent recruits (~0.2 individuals/m^2) of the two dominant *Quercus* species (Maltez-Mouro et al. 2007).

Study species

Q. faginea is a winter-deciduous medium high tree, which may reach only a high-shrub stature, due to human-caused conditioning or ecological limitations. However, and in contrast to other *Quercus* species, *Q. faginea* can produce seeds immediately when reaching the shrub phase (Sánchez Arroyo, 2002). The seeds are dispersed mainly by gravity near the mother tree, but they can be dispersed short-distance by rodents (Pulido and Díaz 2005), or long-distance by birds (Gómez 2003). It is a slow-growing species that propagates both by seeds and sprouting from trunks and roots, and the latter produces vegetative saplings that are difficult to distinguish from old seedlings.

Q. suber is an evergreen tree rarely reaching 20 m height, and typical for its corky bark. Most cork oak trees occur in highly managed savannah-like agrosystems (designated “dehesas” or “montados”), but they also constitute rare and fragmented forests of south-western Iberian Peninsula. The dispersion strategies of this species are similar to those referred for *Q. faginea*.

The two distinct regeneration strategies (vegetative sprouts and seedlings) may have different responses to water and nutrients, and sprouts usually show higher survival and growth rates than seedlings (Pardos et al. 2005). However, both strategies were put together in the present study, since the main objective was to determine the ability of a mixed-oak Mediterranean forest to (self-) maintain the floristic and ecological characteristics, and at what extent (and how) the overstory could influence the ecosystem dynamics, independently from the strategies used by each species. Seedlings and vegetative sprouts are hereafter named recruits.

Sampling methods

We studied a forested slope of 70m length by carefully exploring two transects of 32 x 10 m located in the upper- and lower-slope, respectively. Every young individual of *Q. faginea* and *Q. suber* between 10 and 130 cm height was censused.

The recruits and the micro-environmental conditions of their habitat were sampled using plastic rings of 50 cm diameter centred in each one, for measuring (either on the forest floor inside the rings or within a vertical cylinder above them) the following micro-environmental and forest structure variables (units, classes, and sampling gear in brackets): soil moisture (% volume, using time domain reflectometry – TDR); slope (degrees, using a clinometer positioned on the floor); overstory canopy density (%, using a spherical densiometer positioned 1m above the ground); litter ground-cover (%, by direct visual estimation at increments of 5%), litter depth (cm); overlying species over each recruit (or the occurrence of canopy gaps); maximum overstory canopy height (six categories: 0, 1, 2, 4, 6, and 8 m); density of overstory canopy layers (counting one layer per each height class); distance to the nearest conspecific adult; and distance and the species name of the nearest adult of a different species (considering as an adult every plant able to reproduce).

For interpreting the observed environment-recruit relationships, we made use of a previous study (García et al. 2006) on data gathered in the same season and site, which included measurements of soil litter cover and N and P availability. According to their results, in our study we could assume that the litter cover and the overstory density were proxies for the nutrient (N,P) and light availability, respectively.

Data analysis

The statistical modelling of recruitment occurrence (i.e. presence/absence) of *Q. faginea* and *Q. suber* was performed using the generalized linear model (GLM), with binomial error and a logit link function. Akaike's information criterion (AIC) was used to select the best models, according to the Burnham and Anderson's (2002) criteria. The selected models were checked for overdispersion, residual patterns, and possible artefacts derived from extreme values (Dobson, 2002), before the final selection. The overall performance of the model fit for that dichotomous dependent variable, was expressed using the percent of success in predicting occurrence.

The recruitment performance was evaluated from the shoot number, diameter (calliper, at 10 cm) and height of each recruit. That is, we used the product between basal area (at 10 cm height) and height, as a surrogate of the recruit biomass for fitting the regression models described next. The dependent variable was modelled using the normal distribution of error. The overall goodness of fit of the model was expressed using the

R2-statistics. When necessary, variables were transformed for skewness correction. The basic assumptions for residuals of the fitted models (i.e. normality and independence) were tested (using the Shapiro-Willk's and the runs tests, respectively) before the definitive models were selected.

The non-parametric Mann-Whitney U-test was used to compare the average values of the microsite variables and the recruits' characteristics of *Q. faginea* and *Q. suber*. The overall relationships between the measured environmental variables (i.e. the structure of the micro-environmental data), was explored with principal component analysis (PCA).

For controlling the increased proportion of ''false positives'' due to repeated testing, we applied an overall FDR correction at the 5% level, as suggested by García (2003, 2004). Data analyses were performed using the Statistica (Statsoft, 2001) and the SPSS (SPSS Inc. 2004) software packages.

Results

Microsite environmental data

The PCA analysis of the microsite environmental data showed a strong underlying structure, since more than 50% of the total variance was extracted by only two underlying components (Table 1). The main component of variation (PCA1) accounted for about 35% of the overall variance, and it could be interpreted as a gradient of increased overstory density (highly correlated to canopy density, number of canopy layers and maximum canopy height) and litter cover. This gradient summarized a tendency of the darker microsites to be richer in some key nutrients, as detected in previous studies (Maltez-Mouro et al. 2005, García et al. 2006).

The second independent underlying gradient (PCA2) could be interpreted as a combined gradient of litter depth and soil moisture. Interestingly, litter cover and litter depth were related with different underlying components, the former closely related to the increased canopy density and the second to the increased soil moisture (Table 1).

Differences in the regeneration niche

A total of 93 recruits were sampled and used in the analysis: 55 belonging to *Q. suber* and 38 to *Q. faginea*. These two oak species that dominate in the overstory of the studied mixed-oak forest, but other large shrubs were also found and corresponded to their nearest heterospecific neighbours: *Arbutus unedo*, *Phylirea angustifolia*, *Erica arborea*, *Quercus coccifera*, *Viburnum tinus* and *Rhamnus alaternus*.

The average values and the results of the U-test comparing the variables measured for each species of recruits are shown in Table 2. These results showed that most of the recruits' characteristics (i.e. height, basal area and overall performance), most of the canopy density -related variables (canopy density and maximum canopy height), and the litter cover (but not litter depth), were significantly higher in the microsites where recruits of *Q. faginea* occurred. On the other hand, the distance to the closest adult of the same species, and their basal area was significantly higher for recruits of *Q. suber* (Table 2).

Modelling the recruitment occurrence and performance

Tables 3 and 4 summarize the fitted models that best explained the occurrence (presence/absence) and performance of recruits of the two studied species of *Quercus*. According to the results in Table 3, the microsites where those recruits were predicted to occur, are clearly contrasted in at least four variables: the canopy maximum height, the litter cover, the basal area of the nearest conspecific, and the distance to adults of another woody species. The model with these four predictors was able to predict the suitable microsites for *Q. faginea* and *Q. suber*, with an accuracy of 74% and 82%, respectively. The recruits of *Q. faginea* had higher probability of occurrence in microsites with higher canopy height and litter cover, and further from big heterospecifc adults, as well as their nearest conspecific adults were thinner. At the opposite, the recruits of *Q. suber* tended to occur in microsites with lower canopy and litter covers and closer from heterospecific trees, and they had bigger nearest conspecifics.

The models predicting recruitment performance (Table 4) explained 47% and 50% of the variance of recruits of *Q. faginea* and *Q. suber*, respectively (Fig. 1), and the assumptions for residuals were met (Fig. 2). The results in Table 4 showed that the factors affecting recruitment performance differed from those affecting recruitment occurrence, for the two studied species: for *Q. faginea*, no matches were found; for *Q. suber*, litter cover had significant opposite effects on recruitment occurrence and performance (i.e. the higher litter cover was associated with an increased performance, but also with a lower recruitment occurrence). Besides, different variables related with the same environmental factor, affected the recruits in a different way: the performance of recruits of *Q. suber* was favoured by higher litter cover, but negatively affected by higher litter depth (Table 4). In fact, although those two different variables for litter abundance (cover and depth) were slightly correlated, they shared only 14% of their variance. That is, they behaved as opposite environmental factors conditioning the recruitment performance of *Q. suber*.

Discussion

Our study showed that the effects of the community structure and environmental variables on the recruitment of *Q. suber* and *Q. faginea* are complex (Fig. 3). Besides, our results showed that the requirements for recruitment occurrence and recruitment performance differed. This could be explained by the changes in the regeneration niches of different tree species along their ontogeny, as it has been remarked in other studies (Cavender-Bares and Bazzaz 2000, Medavilla and Escudero 2004, Quero *et al.* 2008).

The recruits of *Q. faginea* tended to occur in microsites with higher canopy density and height and higher litter cover, compared with microsites occupied by recruits of *Q. suber*. These results are consistent with different studies in Mediterranean environments, which have suggested that the seedling survival of a winter-deciduous species (*Q. canariensis*) exceeded the survival of the evergreen *Q. suber*, in low-light environments (Gómez-Aparicio et al. 2008). On the other hand, García et al. (2006) have shown a strong relationship between the litter cover and the overstory cover, and between the litter cover and the concentration of available P and available N, in the topsoil of the same studied forest. Therefore, recruits of the winter-deciduous *Q. faginea* could take advantage of their shade tolerance (Sánchez Arroyo 2002, Benayas et al. 2005) to benefit from the higher availability of the two main limiting soil nutrients, because they grow faster (Reich et al. 1992, Antúnez et al. 2001), and have a higher efficiency in the assimilation of energy and carbon dioxide (Wright et al. 2004). Other authors have also shown that the deciduous species of *Quercus* tend to be more abundant than the coexisting evergreen species of *Quercus*, in habitats having higher water, higher nutrient availability, and denser overstory canopies (Quero et al. 2006, Urbieta et al. 2008b).

Regarding the recruitment performance, the multi-layered canopy had a positive effect on *Q. faginea*, but the favourable multi-layered canopy could not be associated with the extremely dense canopies covers, which reduced recruitment performance of *Q. faginea*. It also showed to be an important factor for the existence of suitable light supplies: the higher number of canopy layers was strongly correlated with the main gradient of overstory density (Table 1). It has been shown that some degree of canopy closure corresponds to a moderate radiation that can ameliorate (or, at least, not aggravate) the drought impact on oak seedlings during summer, and thus may be crucial for recruitment (Quero et al. 2006, Puerta-Piñero et al. 2007). High levels of radiation usually lead to increased temperatures and higher water evaporation rates, exerting a negative effect on oak seedlings (Valladares et al. 2000). In fact, the recruits exposition to high irradiance and water losses during the harsh (hot and dry) summer, are the major causes of seedling mortality of Mediterranean woody species (Herrera et al. 1994). The leaf behaviour of the studied species could explain our results, since it is related with the species strategies for responding to drought (Quero et al. 2006): the winter-deciduous oak species (*Q. faginea*) could be expected to be more dependent from the canopy cover than the evergreen species (*Q. suber*), which is able of better tolerating summer stress (Mediavilla *et al.* 2004, Quero et al. 2006, Sanz-Pérez et al. 2007, Urbieta et al. 2008b).

The average litter cover was significantly lower for the recruits of *Q. suber*, compared with the recruits of *Q. faginea*, as well as the microsites with high litter cover percentages had a significantly lower probability of occurrence of recruits of *Q. suber*. However, considering only the range of litter covers occupied by *Q. suber*, a significant positive effect of litter cover on recruit performance was observed. Rinkes and McCarthy (2007) recently reported that an adequate litter cover was needed to promote oak seedling establishment, and our results showed that the nutrient enrichment associated with litter accumulation (García et al. 2006) was also an advantage for this species, when it was not associated with strong light limitations nor increased litter depth. Sánchez-Arroyo (2002) has also reported an association between soil richness and higher regeneration rates, together with high canopy densities that preserved recruits from insolation, in a north-faced slope occupied by deciduous trees that produced high amounts of litter.

On the other hand, we detected a significant negative effect of the higher litter depth on recruitment performance of *Q. suber*. Some authors explained these negative effects as a result of the mechanical and/or chemical effects of litter (e.g. Facelly and Picket 1991), and Maltez-Mouro et al. (2007) have shown that unlike the recruits of *Q. suber*, the recruits of the winter-deciduous species *Q. faginea* are able to tolerate the thicker litter layers, which are mostly produced by their conspecific adults. Again, the deciduous behaviour of *Q. faginea*'s leaves showed to play an important role in the community structure and dynamics (Sánchez-Arroyo 2002).

The recruits of *Q. suber* tended to occur in microsites farther from conspecific adults. Other studies have shown that the distance between recruits and conspecific adults can be a major factor determining the recruitment spatial patterns (Maltez-Mouro et al. 2007) and partially reflects the dependence of recruits on their mother trees and dispersion strategies (Herrera et al. 1994). The basal area of the closest conspecific adult was significantly higher for recruits of *Q. suber*, as well as the fitted model suggested a higher probability of occurrence of recruits of this species in microsites located in the nearby of adults with higher basal area. Two reasons contribute to explaining these results. First, *Q.*

faginea can produce seeds in the shrub phase, while the trees of *Q. suber* need to be larger to produce seeds (Sánchez Arroyo 2002). Second, the recruits of *Q. faginea* need or tolerate shade in their first years of living (Sánchez Gómez 2007), while *Q. suber* may be considered an "intermediate" species, i.e. it is a transition species between winter-deciduous and other evergreen Mediterranean oaks (i.e. *Q. faginea* and *Q. ilex* L., respectively) with respect to leaf longevity and drought tolerance (David et al. 2007), and thus it needs and tolerates shaded environments but only when drought and competition for water are not much severe (Benayas et al. 2005).

The performance of recruits of the two studied species was significantly increased farther from conspecific adults. This could be explained by the higher competition for light and/or water in microsites near conspecific adults. In contrast, the recruitment performance of each studied species was affected in a different way by the heterospecific adults: the recruits of *Q. suber* were not affected by the proximity of any heterospecific adult, while the recruits of *Q. faginea* were strongly affected in the nearby of two evergreen arborescent shrub species - *Viburnum tinus* and *Q. coccifera*. The negative effect of *Q. coccifera* on recruits of *Q. faginea* is probably because the former is known to be a strong competitor for water, specially during the dry season (Castro-Diez et al, 2007). More studies would be necessary to evaluate how the adults of *V. tinus* play the detected negative influence on recruits of *Q. faginea*, and why recruits of *Q. suber* go beyond both influences.

Maltez-Mouro et al. (2007) have shown that the higher soil moisture positively correlated with the occurrence of seedlings of the two studied species of *Quercus*. Other studies have also shown that the canopy density, herbaceous ground-cover, or the litter amounts, are strongly related with the availability of water (e.g. Benayas et al. 2005, Maltez-Mouro et al. 2005). Moreover, it has been shown that the deciduous oak species are not so efficient as the evergreen oak species on relatively dry soils (Corcuera et al. 2002). However, in our study the soil moisture was not significantly different in microsites inhabited by recruits of *Q. faginea* or *Q. suber*, nor it was an important variable in explaining the recruitment occurrence/performance of these species. These unexpected results could be explained by: (1) the limited set of measurements of the water-content variable; (2) the superficial measurement (i.e. from upper soil horizons) of soil moisture – because oak seedlings depend from their deep rooting to surpass the summer drought (capturing water from the deeper soil horizons); (3) the existence of other significant and more predictable variables that correlated with soil water content – and thus gave to the latter an apparent lack of power in predicting regeneration. This was the case of the litter depth variable, which was statistically associated to the same underlying gradient (Table 1). Different studies have reported increased soil water contents with higher litter accumulation, but the corresponding effects on soil water dynamics have received scarce attention in forest ecosystems (Facelly and Picket 1991).

Conclusions

In the studied mixed-oak Mediterranean forest, there were significantly different regeneration niches for each of the dominant species, *Q. faginea* and *Q. suber*. The effects of the community structure and environmental variables on recruitment were in agreement with the ecophysiological characteristics known for each species and for the related evergreen and deciduous species of *Quercus*. However, our study showed that the factors affecting the probability of recruitment occurrence differed from those affecting the recruitment performance. Also, those factors interacted in a complex and, to a great extent, unpredictable way, and different variables of to the same environmental factor could affect recruits in a very different (even opposite) way.

The structural and environmental heterogeneity of the forest was shown to be extremely important to promote the regeneration of the two dominant oak species, and the overstory structure and composition played an important role in the regeneration process. We suggest that there is a huge risk of a negative feedback of some overstory species that usually co-dominate in these forest types - in particular *Q. coccifera* and *V. tinus* - over the dominant (*Quercus*) species trying to succeed in the understory (before reaching the overstory layers). This could ultimately lead to a completely different forest composition and structure, and the corresponding loss of diversity.

The data gathered in this study, and the models fitted to the recruitment occurrence and performance of *Q. suber* and *Q. faginea*, suggested that clearing practices would favour the regeneration of *Q. suber*, while more closed canopies with deep litter layers would favour *Q. faginea*. However, both an excessive cover of some shrub species and the complete absence of woody canopies, would negatively affect the regeneration of *Q. faginea*. Since there was no lack of regeneration of the two dominant oak species in the studied forest site, our results are relevant for threatened Mediterranean forests with serious regeneration problems. Knowing the ecological requirements and limitations of the survival and performance of different oak species is essential, for developing ecologically –based management and restoration strategies for mixed-oak Mediterranean forests.

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Table 1. Results of the PCA analysis of the measured micro-environmental predictors. Factor loadings exceeding 0.5 (in absolute value) are in bold.

Table 2. Recruits' characteristics and microsite conditions. Means and standard deviations of the measured variables are shown. The critical *p*-value for controlling the False Discovery Rate at the 5% level throughout the study was 0.0354.

Table 3. Environmental factors that significantly explained the occurrence of *Q. faginea* (1) or *Q. suber* (0) in the studied forest site. Data were modelled using a generalized linear model with binomial error and a logit link. Abbreviations: dbhNCA, diameter at breast height of the nearest conspecific adult; DNHA, distance to the nearest heterospecific adult.

Table 4. Effects of the environmental factors on the recruitment performance of *Q. faginea* and *Q. suber*. Data were modelled using a generalized linear model with normal error. Abbreviations: DNCA, distance to the nearest conspecific adult; DNHA, distance to the nearest heterospecific adult; NA, nearest adult; Qc, *Quercus coccifera* Vt, *Viburnum tinus*.

Figure 1. Observed and predicted values of recruitment performance, expressed as $\log_{10}$ (basal area x height) of recruits of *Q. faginea* (a) and *Q. suber* (b). Multiple-R values for the fitted models were 0.73 and 0.72, respectively.

Figure 2. Residuals and predicted values of the modelled performance (expressed as $\log_{10}$ (basal area x height)), for recruits of *Q. faginea* (a) and *Q. suber* (b). The assumptions of normality and independence of the residuals were tested and verified with the Shapiro Willk's (p=0.05 and 0.37, respectively) and Runs tests (p=0.29 and 0.92, respectively).

Figure 3. Diagram summarizing the effects of environmental and community structure variables on the regeneration and performance of *Q. suber* and *Q. faginea*. Each rectangle represents higher values of that variable. The solid and dotted lines represent positive and negative effects of the variable, respectively.

Table

	PCA1	PCA2	PCA3
Canopy density	**0.7**	0.3	0.1
Canopy height	**0.6**	-0.2	0.4
Canopy layers	**0.7**	0.2	0.0
Litter cover	**0.7**	0	-0.4
Soil Hum	-0.2	**-0.8**	-0.1
Litter Depth	0.4	**-0.6**	-0.5
Slope	0.2	-0.5	**0.7**
Eigenvalues	2.2	1.3	1
Total variance (%)	31.7	18.7	14.9

Table

Variables	*Q. faginea*	*Q. suber*	*U*	*P*
Recruit parameters				
Shoot number	2.9 ± 2.9	1.8 ± 1.3	795.5	0.0509
Height (cm)	57.8 ± 34.1	39.1 ± 23.1	761.0	0.0098
Basal area (cm^2)	0.7 ± 0.8	0.4 ± 1.6	707.5	0.0079
Overall performance (cm^3)	56.8 ± 74	38.6 ± 208	688.5	0.0050
Microsite parameters				
Slope (¼)	31.6 ± 8.0	29.2 ± 10.9	837.0	0.1051
Soil moisture ($m^3.m^{-3}$)	0.1 ± 0.01	0.1 ± 0.02	653.5	0.1135
Canopy density (%)	93 ± 9	89 ± 9	609.0	0.0005
Number of canopy layers (1-5)	1.7 ± 0.8	1.4 ± 0.7	791.5	0.0472
Maximum canopy he ight (m)	5.9 ± 1.9	4.3 ± 1.9	505.0	0.0000
Litter cover (%)	82.0 ± 22.4	64.5 ± 26.3	477.5	0.0000
Litter depth (cm)	5.8 ± 1.7	5.4 ± 2.7	833.0	0.0985
Distance to nearest conspecific adult (cm)	143 ± 72	289 ± 190	553.5	0.0001
dbh of nearest conspecific adult (mm)	78 ± 41	190 ± 116	536.0	0.0000
Distance to nearest heterospecifc adult (cm)	77.6 ± 38	61.2 ± 33	809.0	0.0655

Table

	Whole model		Explanatory variables			
Species occurrence	AIC	p	Factor	Influence	WaldÕs χ^2	p
Q. faginea	88.4	0.0000	Canopy height	+	7.43	0.006
			Litter cover	+	9.61	0.002
			dbhNCA	-	9.55	0.002
			DNHA	+	4.47	0.035

Table

	Whole model		Explanatory variables			
	AIC	*p*	Factor	Influence	WaldÕ χ^2	*p*
Q. faginea	94.5	0.0000	Canopy layers	+	11.75	0.0006
			Canopy density	-	5.09	0.0241
			DNCA	+	6.62	0.0101
			Litter depth	+	11.98	0.0005
			Qc/Vt NA	-	37.92	0.0000
Q. suber	98.5	0.0000	DNCA	+	46.29	0.0000
			Litter cover	+	10.46	0.0012
			Litter depth	-	12.71	0.0004

Figure
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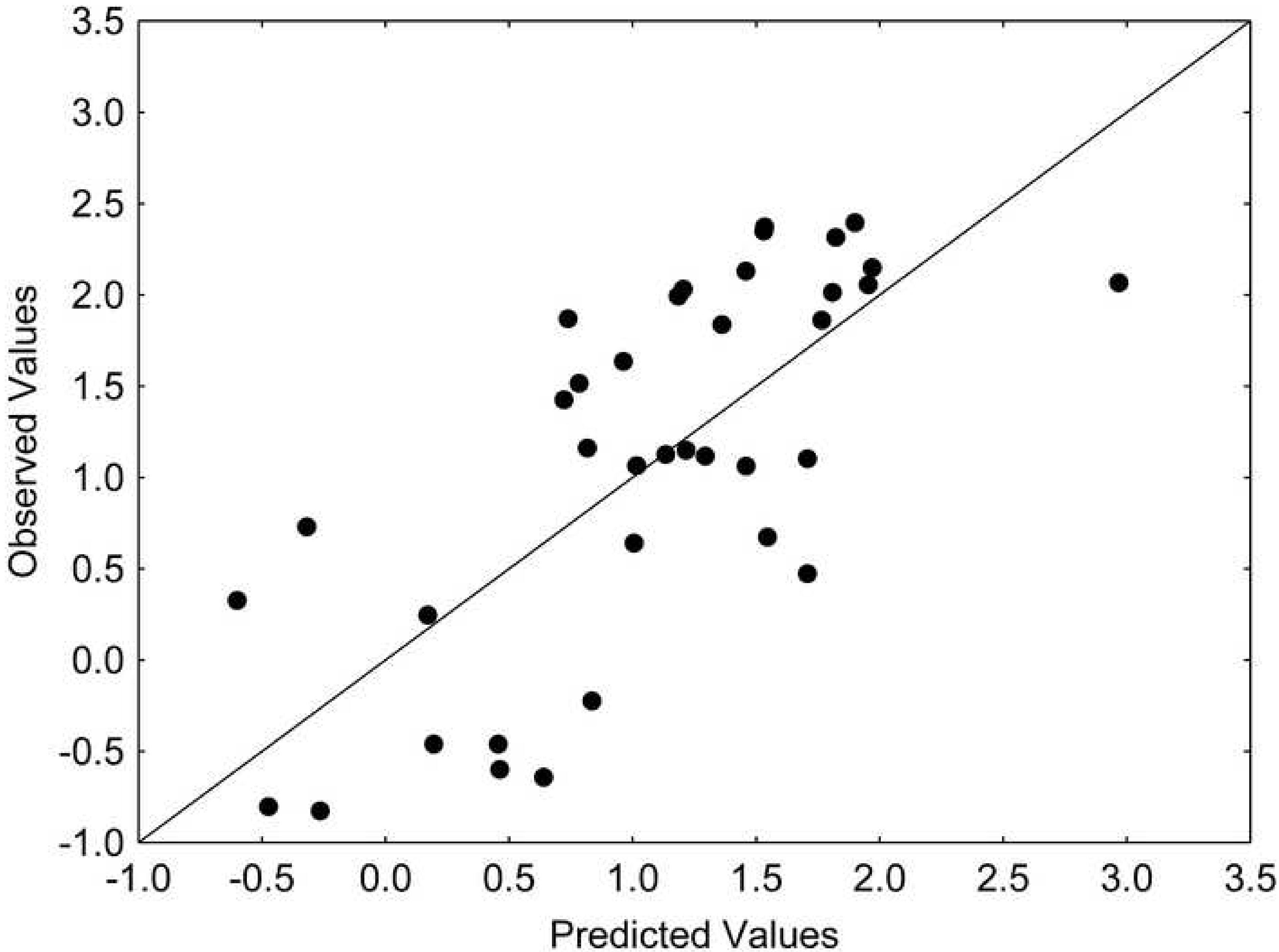

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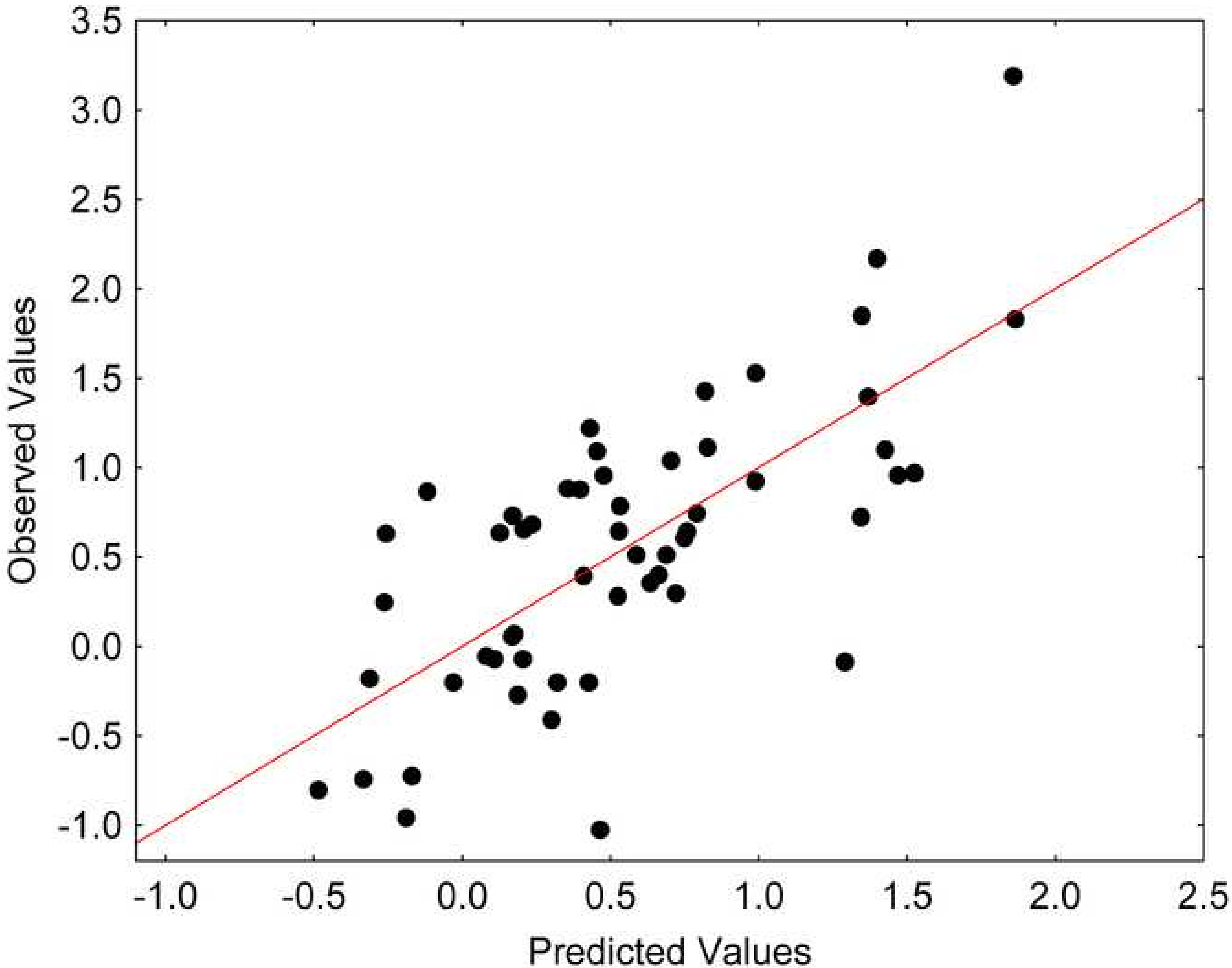

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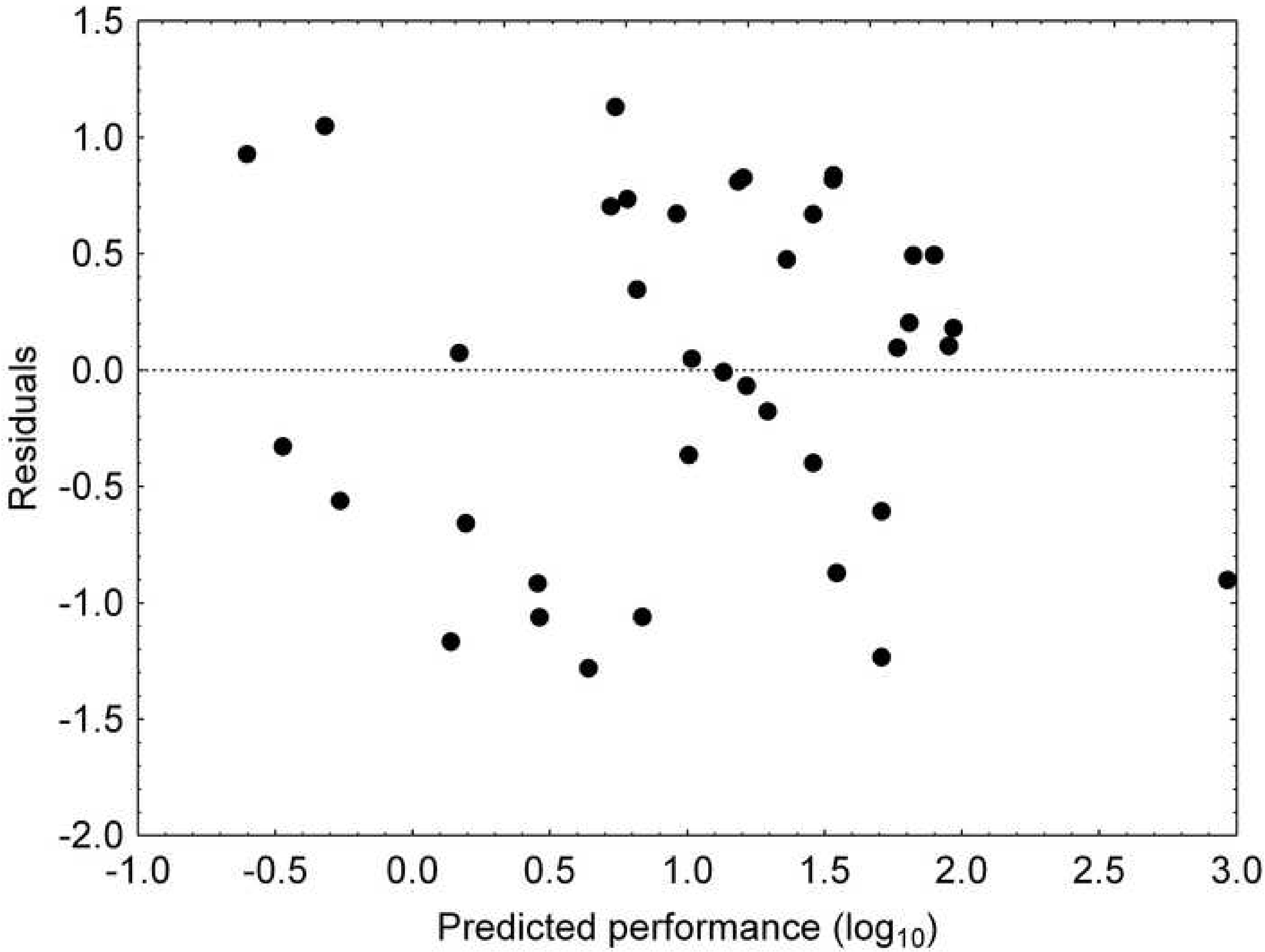

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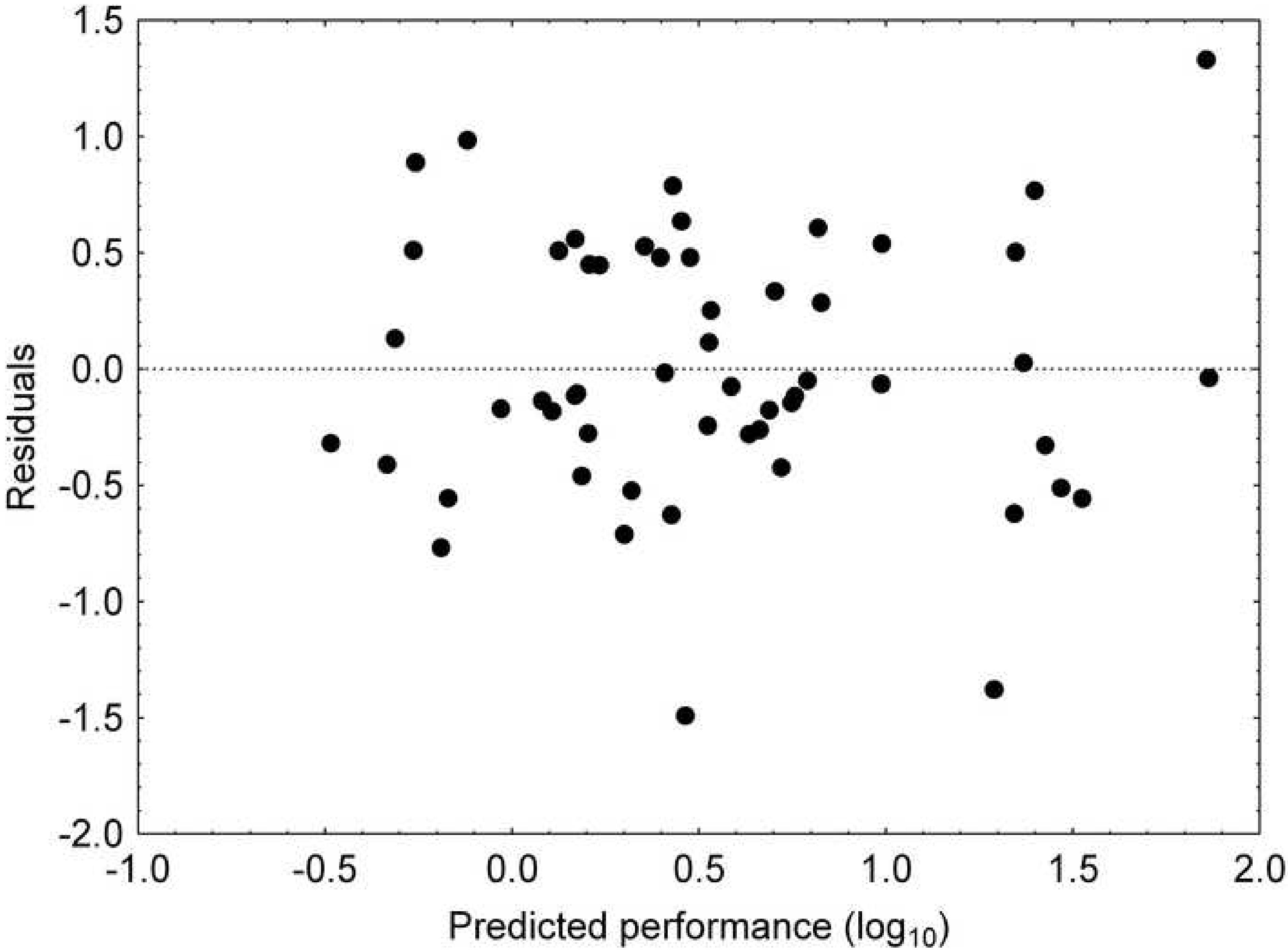

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