

Differences between structural and functional environmental heterogeneity caused by seed dispersal

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Summary

1. This paper explores the idea that functional heterogeneity (variability of a system property affecting ecological processes) is only a fraction of the available structural heterogeneity (variability of a property measured without reference to ecological effects) caused by non-random propagule dispersal. We report the effect of acorn dispersal by jays on the light environment experienced by Holm Oaks (*Quercus ilex* L.) during early recruitment in a Mediterranean montane forest.

2. Four light variables were estimated by studying hemispherical photographs: direct site factor (DSF); indirect site factor (ISF); and potential direct radiation during April (PDR_{April}) and August (PDR_{August}). Means and variances of these variables were compared before and after the dispersal of acorns by jays.

3. The landscape occupied by Holm Oaks was very heterogeneous, which translated into differences in the available light among microhabitats of up to one order of magnitude.

4. Because of the spatial pattern of acorn dispersal, the light environment of the oaks during their establishment was much more homogeneous than that in the whole landscape.

5. This demonstrates that the heterogeneity relevant for plant recruitment is not necessarily that of the landscape as a whole.

Key-words: light environment, *Quercus ilex*, seed dispersal, spatial heterogeneity, structural vs functional heterogeneity

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Introduction

Organisms live in habitats that are heterogeneous in space and time. Spatial heterogeneity in resource supply and abiotic conditions strongly influences individual performance in most species (Hutchings *et al.* 2000, 2003). However, it is still unclear how heterogeneity should be quantified (Dutilleul & Legendre 1993; Sparrow 1999; Wiens 2000; Turner *et al.* 2001). Following Kolasa & Rollo (1991) and Li & Reynold (1995), two sorts of environmental heterogeneity, structural and functional, can be defined. Structural heterogeneity is the complexity or variability of a system property measured without reference to any ecological effect. Functional heterogeneity is the complexity or variability of a system property that affects ecological processes (Li & Reynold 1995). Despite this distinction, environmental heterogeneity has seldom been partitioned in this way in practice.

Light availability plays a crucial role in plant regeneration in many terrestrial ecosystems by influencing the recruitment and performance of many plant species (Turton & Duff 1992; Watling & Press 2000; Valladares 2003; Beckage & Clark 2003). The strong

interactions between light and water availability, together with the potential for photoinhibition and overheating of strong radiation loads, mean light is a limiting resource not only when scarce, but also when overabundant (Valladares 2003). Among the resources essential for plants, light is particularly heterogeneous in time and space (Bazzaz 1996; Pearcy 1999; Watling & Press 2000). At a regional scale, vegetation pattern is the main cause of variability in light availability, whereas at a local scale heterogeneity in the overstorey canopy structure is the primary factor causing the great spatial variability in light environment (Caldwell & Pearcy 1994; Watling & Press 2000). Due to the uneven distribution of light in nature and its importance for plant recruitment and performance, light intensity is a primary factor explaining the spatial heterogeneity of plant regeneration (Beckage & Clark 2003). In terms of light availability for plants, the landscape can be regarded as a cost–benefit surface (Wiens 1997), with peaks corresponding to high-quality patches allowing successful recruitment, and valleys corresponding to low-quality patches precluding recruitment. However, no information currently exists about how much of the observed structural heterogeneity is actually relevant to the functioning of plant populations (that is, how much of the structural heterogeneity translates to functional heterogeneity).

The main goal of this study is to quantify the difference between structural and functional heterogeneity in an ecosystem where light heterogeneity was hypothesized to be a key ecological factor (Valladares 2003). We used a habitat dominated by the Holm Oak (*Quercus ilex* L.), a sclerophyllous evergreen tree dominant in many western Mediterranean habitats. Light influences the recruitment of *Q. ilex* and significantly affects its photosynthesis, water relations, pigment composition, biomass allocation, survival and relative growth rate (Gratani 1997; Faria *et al.* 1998; Staudt & Bertin 1998; Retana *et al.* 1999; Valladares *et al.* 2000, 2002; Zavala *et al.* 2000; Oliveira & Peñuelas 2002; Gómez 2003, 2004). We determined (i) the structural heterogeneity occurring in the landscape inhabited by *Q. ilex* estimated as the range of light environments available before acorn dispersal; and (ii) the functional heterogeneity in light conditions estimated as the range of light environments actually occupied by *Q. ilex* after acorns were dispersed by jays and after seedling emergence. Our main hypothesis was that *Q. ilex* perceives only a portion of the overall heterogeneity available in their environment, functional heterogeneity being just a fraction of the structural heterogeneity.

Materials and methods

STUDY SITE AND SPECIES

The study site is a 12 ha area located 1700 m a.s.l. in the Sierra Nevada Protected Area (south-east Spain, 37°5' N, 3°28' W). The landscape is a mosaic of small patches of mixed oak–autochthonous Scots Pine (*Pinus sylvestris nevadensis* Christ.) woodlands coexisting with several/many afforestation stands (*Pinus sylvestris iberica*, *Pinus nigra* Arnold, *Pinus pinaster* Aiton). *Quercus ilex* acorns are dispersed mainly by the European Jay, *Garrulus glandarius* L., and to a lesser extent by rodents (Gómez 2003; personal observations; Gómez *et al.* 2003). However, rodents appear to act mainly as postdispersal seed predators as most acorns transported by these animals are consumed, either directly beneath the oaks or later in caches (Gómez *et al.* 2003).

STRUCTURAL HETEROGENEITY: LANDSCAPE AND MICROHABITAT STRUCTURE

The landscape of the study site is differentiated into two main habitats or patch types: (1) oak–pine woodlands, small fragments of oak woodlands composed of large oaks and many reproductive resprouts, intermingled with isolated pines; and (2) afforestations, medium-to-large patches of old, autochthonous Scots Pine forests and oak woodlands which have been reforested with non-native pines (Gómez 2003). For the present study, six types of microhabitat were considered in oak–pine woodlands (see Gómez 2003 for a more detailed study): (1) ‘Holm Oak’, under the canopy of adult and juvenile *Q. ilex* (covering 6% of the landscape surface);

(2) ‘pines’, under the canopy of adult trees belonging to any of the three species of pine occurring at the site (covering 7%); (3) ‘shrubs’, under the canopy of shrub species >0.5 m tall (5%); (4) ‘brooms’, beneath fabaceous, tall shrubs (2%); (5) ‘subshrubs’, under the canopy of stunted shrubs ≈30 cm high (15%); (6) ‘open’, including rocky areas, bare soil with small gravel and cobble and sparse herbaceous cover (mainly annuals and short-lived perennials) and deep soil with thick herb cover (24%). The remaining 41% of the landscape surface was covered by a seventh microhabitat, afforestation (Gómez 2003).

FUNCTIONAL HETEROGENEITY: OAK SPATIAL PATTERN AFTER JAY DISPERSAL AND SEEDLING EMERGENCE

Functional heterogeneity was quantified at two early stages of the *Q. ilex* life cycle: after acorn dispersal and after seedling emergence. The spatial pattern of acorns produced by jay dispersal was quantified in 2001–02 by directly observing jays transporting and caching acorns in the study plots (see Gómez 2003 for details). The results showed that 86% of the acorns were moved to afforestation stands (or autochthonous pine woodlands), 8% to the pine microhabitat from oak woodlands, 1% to the Holm Oak microhabitat, 2% to shrubs, 2% to subshrubs, 0% to brooms and 1% to open microhabitats (Gómez 2003).

The probability of emergence was quantified in 2000–01 by directly seeding 200 fresh acorns within each microhabitat from both oak woodlands and afforestations (see Gómez 2004 for details). After controlling for the proportion of acorns arriving at each microhabitat, the estimated proportion of acorns emerging as seedlings in each microhabitat was 87% in afforestation, 6% under pine from oak woodlands, 1% under Holm Oak, 3% under shrubs, 3% under subshrubs, 0% under brooms and 0% in open sites.

DETERMINATION OF LIGHT AVAILABILITY

In October 2003 light availability was estimated from hemispherical photographs (Rich 1990; Chen *et al.* 1991; Roxburgh & Kelly 1995) taken at 50 randomly chosen points belonging to each of the six microhabitats considered in the oak–pine woodlands and at 100 points in the afforestation plots (400 points in total). Photographs were taken at a height of 0.25 m using a horizontally levelled digital camera (CoolPix 995 digital camera, Nikon, Tokyo, Japan) and aimed at the zenith, using a fish-eye lens of 180° field of view (FCE8, Nikon). All photographs were taken either before dawn, after sunset, or at other times of the day when the sun was blocked by clouds to ensure homogeneous illumination of the overstorey canopy and a correct contrast between canopy and sky.

Photographs were analysed using HEMIVIEW canopy-analysis software ver. 2.1 (1999, Delta-T Devices Ltd, Cambridge, UK), estimating the following variables

used in all standard studies of light effects on plants. (1) Direct site factors (DSF) and indirect site factors (ISF), which are defined as the proportion of direct and diffuse radiation received below the canopy as a fraction of that received above the canopy (Rich 1990). (2) Effective leaf area index (LAI) estimated as half the total leaf area per unit ground surface area (Chen & Black 1992), based on the ellipsoidal leaf angle distribution (Campbell 1986). (3) Ground cover, defined as the vertically projected canopy area per unit ground area. (4) Potential direct radiation reaching each point during April (PDR_{April}) and August (PDR_{August}), expressed in mol photons $\text{m}^{-2} \text{month}^{-1}$ and calculated as the monthly integration of the direct daily radiation reaching each spot, assuming a clear sky. We chose these two dates as they represent, respectively, the month when germination of *Q. ilex* is at its mid-point and that when summer drought is most severe (personal observation).

DATA ANALYSIS

We examined the differences in light environment among the seven microhabitats using one-way ANOVA after log-transformation of the data (Proc GLM, SAS Institute Inc., 1997). We also studied the relationship between ISF and DSF using linear regression. To test whether the ISF–DSF relationship held within each microhabitat, we first conducted the analysis by pooling the data across microhabitats, then segregating it across microhabitats.

To compare the structural light heterogeneity (SH) to the functional light heterogeneity after dispersal (FH_d) and emergence (FH_e), we generated 50 random data sets of hemispherical photographs (100 photographs per data set) for each of these three groups. For this, from the original pool of 400 photographs taken in the study site, we extracted at random a number of photographs per microhabitat to match the proportional contribution of that microhabitat to the acorn environment during each stage (predispersal or SH, dispersal or FH_d , emergence or FH_e). For each of the 150 data sets we obtained the mean value, the standard deviation (SD) and coefficient of variation (CV) of our target light parameters. With this resampling technique, a confidence interval was generated for each of the three previous statistics. The comparisons between mean values across the three groups of heterogeneities were made by one-way ANOVA (Proc GLM, SAS Institute Inc., 1997); SD and CV were compared by Levene and Brown–Forsythe tests which allow for differences in dispersion parameters.

Results

DIFFERENCES AMONG MICROHABITATS IN THE LIGHT ENVIRONMENT

There were significant differences among microhabitats in all the variables used to characterize the light environ-

ment ($F_{6,260} > 65.9$, $P < 0.0001$ in all cases, one-way ANOVA; Fig. 1) as a consequence of the large variations in vegetation structure and development in the patchy landscape. Ground cover and LAI were greatest in afforestation and under oaks, and smallest under shrubs and in open sites (Fig. 1). This pattern was reversed for light availability, ISF and DSF, and the PDRs were smallest in pines from afforestation and under oaks, and largest in open sites (Fig. 1).

Potential direct radiation also exhibited significant seasonal variation. There were significant between-microhabitat differences in PDR every month ($27.98 < F < 158.23$, $df = 6255$, $P < 0.0001$ in all cases), being always highest in open sites and lowest in afforestation and under oaks. Differences in PDR among microhabitats were greater during the summer ($F > 100.0$ and $R^2 > 0.7$ in the comparisons from May to September) than during winter ($F < 100.0$ and $R^2 < 0.5$ in the comparisons from October to April).

As expected there was a highly significant and positive relationship between DSF and ISF ($DSF = 0.986 \times ISF - 0.001$, $P < 0.0001$, $R^2 = 0.84$). This positive relationship was maintained within each microhabitat ($P < 0.0001$ in all cases, $0.40 < R^2 < 0.79$). However, in high light environments (e.g. pines, open sites and shrubs) there was a 1 : 1 relationship (linear regression slopes ranging from 0.97 to 1.07). In the low light environments the slope of the regression varied from 0.5 under brooms or 0.72 under shrubs to 2.0 under adult Holm Oaks. Thus, while potentially harmful direct light increased abruptly with slight increases of indirect light under adult Holm Oaks, only a moderate increase of direct light was observed under brooms and, to a lesser extent, shrubs. The microhabitat specificity of the relationship between direct and indirect light contributed to the measured heterogeneity of the light environments at the site.

CHANGES IN LIGHT ENVIRONMENT AFTER ACORN DISPERSAL AND EMERGENCE

The mean values of the light parameters differed statistically between structural heterogeneity and the two functional heterogeneities. Whereas average ISF and DSF were $\approx 40\%$ before dispersal, they were below 20% after dispersal (Fig. 2). Similarly, the average PDR_{April} and PDR_{August} for the whole landscape exceeded $550 \text{ mol m}^{-2} \text{ month}^{-1}$, whereas it was below $350 \text{ mol m}^{-2} \text{ month}^{-1}$ for both variables after acorn dispersal by jays (Fig. 2). This difference between pre- and post-dispersal light environments was maintained throughout the year ($14.05 < F < 39.50$, $df = 2306$, $P < 0.0001$ in all months), with the largest differences occurring during summer.

Not only the mean values, but also the range of variation of the four variables used to characterize the light environment, were significantly reduced after acorn dispersal (Fig. 2). Although the SD and CV of both light variables were large for the SH group, they were much smaller for the FH_d and FH_e groups (Fig. 2).

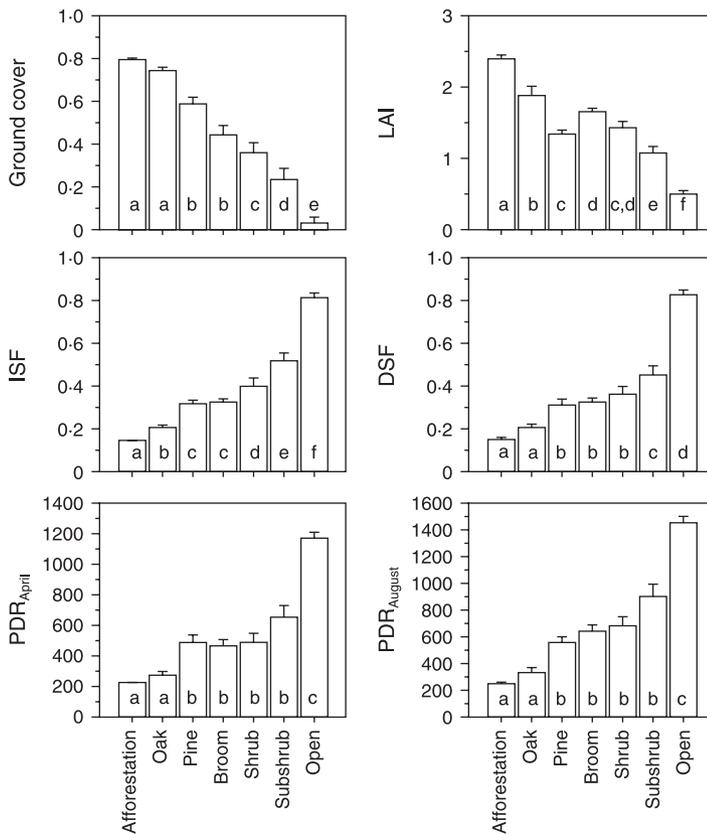


Fig. 1. Between-microhabitat differences in light parameters. Values are mean \pm SE. Letter code indicates significant differences between microhabitats (ANOVA, Tukey's test, $P > 0.01$).

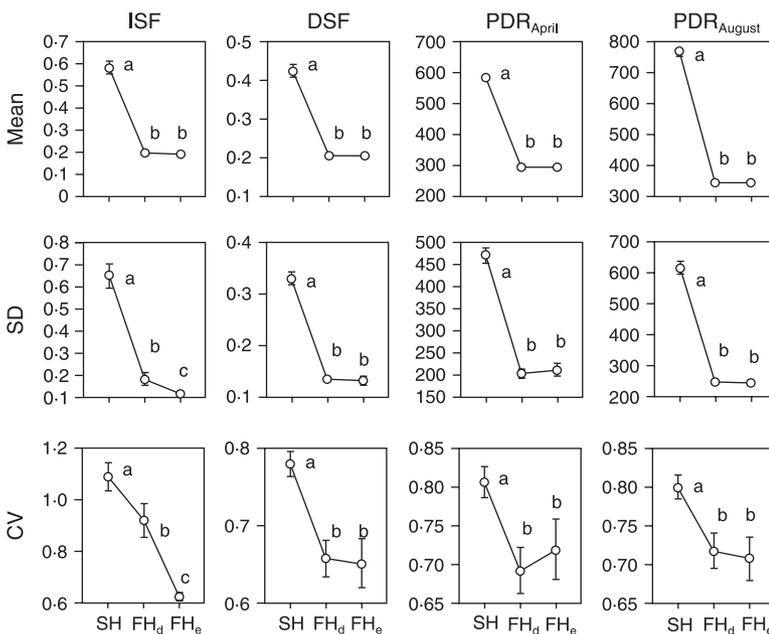


Fig. 2. Mean, standard deviation and coefficient of variation ($\pm 95\%$ confidence interval for each statistic) of the indirect site factor (ISF), direct site factor (DSF), and potential direct radiation in April (PDR_{April}) and August (PDR_{August}) for structural heterogeneity (SH), functional heterogeneity after dispersal (FH_d) and functional heterogeneity after emergence (FH_e). Values followed by different letters are statistically different at $\alpha < 0.05$ after Bonferroni's correction (mean was tested by ANOVA; SD and CV were tested by Brown–Forsythe and Levene tests).

Discussion

Light showed a remarkably high spatial, between-microhabitat heterogeneity in the study site. Open sites and sites located under subshrubs had high light availability; those located in afforestations, under oaks and under pines from oak woodlands had low mean irradiance. Light availability under the canopies of pines inhabiting the oak–pine woodlands was significantly greater than that under the canopies of pines in afforested stands. Similarly, the light available under the shrub canopies depended not only on cover and LAI, but also on the kind of shrub, being higher under subshrubs than under brooms and shrubs. The relative increase of direct light with increasing indirect light was also quite different for each kind of canopy, and was presumably due to species-specific architectural features. These specific influences of the canopy on understorey light, coupled with the patchy nature of the vegetation, were the two main causes for the great spatial heterogeneity of light at the site.

Quercus ilex is shade-tolerant during its early life cycle. It is unable to recruit when exposed to full sunlight and high temperatures because its survival and relative growth rate are lower at high irradiance than in moderate shade (Espelta *et al.* 1995; Broncano *et al.* 1998; Retana *et al.* 1999; Zavala *et al.* 2000; Gómez 2004). One consequence of light heterogeneity could be a concomitant spatial variation in the probability of *Q. ilex* germination, emergence and survival is significantly higher in shaded microhabitats than in open ones at the study site (Gómez 2004). No more than 0.02% of acorns dispersed to an open microhabitat produce seedlings that survive for at least 2 years. For acorns dispersed to an afforested habitat, the corresponding figure is 0.7–10% (Gómez 2004). The recruitment probability is more than two orders of magnitude higher in afforestation than in open microhabitats. Nevertheless, the positive effect of shade during early stages can become a negative one during late stages of the *Q. ilex* life cycle, when growth becomes more dependent on irradiance (Retana *et al.* 1999).

STRUCTURAL VS FUNCTIONAL HETEROGENEITY

There was a significant difference between the light heterogeneity in the overall landscape occupied by *Q. ilex* (structural heterogeneity) and the actual heterogeneity encountered by an acorn or seedling (functional heterogeneity). Acorns and seedlings exist in environments in which the average irradiance is less than that for the whole landscape (ISF and DSF were below 20% after acorn dispersal compared with at least 40% before; Fig. 2). The difference between structural and functional heterogeneity involves decreases not only in the mean value, but also in the range of variation of the irradiance experienced by acorns.

The main process accounting for this difference between structural and functional heterogeneity was the non-random dispersal of acorns by jays. In these Mediterranean environments, jays transport acorns mostly to shaded microhabitats such as afforestations and pines within the oak–pine woodlands (Gómez 2003), and that behaviour decreases the probability of an acorn germinating in a microhabitat receiving strong irradiance. In the Iberian Peninsula *Q. ilex* is also dispersed by rodents, which cache acorns preferentially in shaded microhabitats (Pulido 1999; Gómez *et al.* 2003). For this reason it is probable that *Q. ilex* will always experience only a portion of the overall spatial heterogeneity occurring in the landscapes in most of its geographical range. It is often assumed that spatial heterogeneity directly affects the behaviour of individuals (Kawata & Agawa 1999). In the case of *Q. ilex*, the landscape heterogeneity determines the pattern of seed dispersal indirectly, by influencing the movements of dispersers. The result is that the actual light environment experienced by acorns and seedlings is more homogeneous than predicted from measurements of structural heterogeneity. Some processes occurring during early stages of the plants' life cycle, such as seed dispersal, can significantly alter the actual heterogeneity experienced by mature plants.

Most of the relatively few studies on the effects of dispersal on plant populations in heterogeneous environments have concluded that dispersal amplifies the heterogeneity encountered by organisms (Rees *et al.* 2000; Snyder & Chesson 2003). Strikingly, our results have found the opposite effect. Dispersal diminished the potential spatial heterogeneity that an oak propagule was likely to encounter. We suggest that this disperser-mediated decrease in functional heterogeneity may be more common than has been reported for plant species dispersed by animals that move non-randomly across the landscape. Seed dispersal by animals is spatially contagious in many plant species, as seeds are transported mostly to the few microhabitats preferred by dispersers (Jordano & Godoy 2002; Schupp *et al.* 2002). It might be difficult to find any decrease in functional heterogeneity in plants that are dispersed by a range of animals differing in their microhabitat preferences. However, when seeds are dispersed just by one or few species sharing a similar habitat preference, a decrease in functional heterogeneity will probably result. Although it is widely accepted that organisms can influence abiotic heterogeneity in a variety of ways, and create heterogeneity in otherwise relatively uniform environments (Pickett *et al.* 2000; Wilson 2000), our results suggest that organisms can sometimes decrease the heterogeneity experienced by a plant population.

Our findings could have important consequences for the ecology and evolution of *Q. ilex*. For example, in contrast to the general assumptions of many ecophysiological studies, photoinhibition and heat stress might be unimportant for *Q. ilex* recruitment because acorns are dispersed by jays or other animals with similar

behaviour. This result could also explain the inability of *Q. ilex* to respond physiologically and morphologically to different light regimes (Valladares *et al.* 2000, 2002). Jays and rodents could have exerted indirect selection against such phenotypic plasticity by restricting the light heterogeneity to which *Q. ilex* individuals are exposed. *Quercus ilex* acorns and seedlings experience a relatively homogeneous light environment, and a highly plastic response to light could involve a non-conservative use of resources and perhaps compromise fitness (Valladares *et al.* 2002).

Our results urge caution when investigating ecological heterogeneity, as we have shown that measured heterogeneity does not always match that experienced by organisms *in situ*. Understanding how heterogeneity affects ecological systems requires an understanding not only of environmental patterns, but also of how organisms respond to different forms of heterogeneity (Kolasa & Rollo 1991; Wiens 1997). Distinguishing structural from functional heterogeneity can help overcome some of the difficulties

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