Highlights

- Potential of successional process as tool to restore oak-woodlands was assessed.

- Compositional differences were reduced among pine and oak-habitats trough succession.

- Natural successional processes are effective for tree and ferns.

- Effective reorientation of pine plantations requires adaptive forest management practices.

Can understorey native woodland plant species regenerate under exotic pine plantations using natural succession?

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Abstract

Forestry industry in many European countries has begun to focus on sustainable forest management practices, and consequently, a greater emphasis is now being placed on the restoration and enhancement of native woodlands in places where intensive forestry is nowadays not highly profitable. In this context, we evaluate the natural regeneration of native oak woodland vegetation under cultivated stands of *Pinus radiata* in the Biscay region, Northern Iberian Peninsula. We compared vegetation composition and diversity on 60 stands representing the three commonly observed habitats: regenerating *Quercus robur* woodlands, old-growth native *Q.robur* woodlands, and their adjacent *P.radiata* plantations at different successional stages. The aim was to assess the potential of natural successional processes to restore the native oak woodland species under pine plantations, determining whether natural regeneration is sufficient or some management interventions are needed. The results reveal significant differences in understorey species composition between pine plantations and oak habitats. However, these understorey compositional differences were reduced during natural successional process (from young to old age plantations), being especially important in the case of tree and fern growth-forms. The successional trends are driven by an increase of tree, fern and native species cover during pine plantations succession, although the richness was always higher in plantations mainly by the presence of a great number of generalist and opportunistic species. Nevertheless, some typical woodland species, such as *Ulmus minor* and *Lamiastrum galeobdolon*, did not appear in plantations. Here, the natural successional process produced a slowly convergence in understorey species composition between plantations and oak habitats. However, the old pine plantations and oak habitats still differed considerably in understorey composition, suggesting that using only natural succession a much longer time frame is needed to achieve our ecological restoration objective. Natural succession could be used to achieve the restoration objectives at relatively low costs almost for tree and fern growth-forms, although in the case of ancient woodland species especial actions would be needed. The reorientation of pine plantations towards species compositional states that are more similar to native oak habitats could be faster using adaptive forest management practices (e.g. single tree selection).

Key-words: Forest management, native woodland, exotic pine plantation, *Pinus radiata*, *Quercus robur*, restoration.

1. Introduction

In many regions of Western Europe, the native forest area has diminished dramatically over the past several centuries as a consequence of human impacts (Calviño-Cancela et al., 2012). Forests are becoming increasingly fragmented, typically resulting in numerous small patches isolated by different land uses (Rudd et al., 2002), as a result, loses of biodiversity, ecological functions and ecosystem services are produced (Onaindia et al., 2013). Simultaneously, during the last decades one of the most endangered activities for native forest is the expansion of tree plantations, and specially those of fast growing exotic tree species (Bremer and Farley, 2010). Towards the end of the last century, the forestry industry in many European countries began to focus on sustainable forest management practices, and consequently, a greater emphasis is now being placed on the restoration and enhancement of native woodlands (Mason, 2007), especially in places where intensive forestry is not highly profitable.

The effect of intensive forestry practices on native species is a cause of great concern and a source of controversy. The conservation of native plant species and biodiversity for forest landscapes dominated by plantations has become an increasingly important topic, and opportunities to maintain or enhance biodiversity within these forests need to be recognised and applied (Perry et al., 2011). The expansion of intensive managed plantations has raised concerns amongst forest managers and general public over the implications of these trends for sustainable production and native species conservation (Carnus et al., 2006). Some authors consider plantations to be valuable habitats for flora and fauna, and they suggest that they can catalyse the regeneration of native understorey species and thus, contribute to biodiversity conservation (Lugo, 1997; Carnus et al., 2006). In contrast, other authors showed neutral or even negative effects of plantation on native species and biodiversity (see reviews of Stephens and Wagner, 2007; Bremer and Farley, 2010). This lack of consensus around the ecological impacts of forest plantations can arise from the scarcity of studies that examine plantations along their successional gradients (Brockerhoff et al., 2008). It is well known that age and structure of the stands (e.g. canopy closure, tree height) determine the ability of plantations to harbour biodiversity (Lindenmayer and Hobbs, 2004). At the same time, comparisons between plantations and target communities should be made considering the potential vegetation stage after natural succession. The consideration of these aspects in the analysis helps to identify the plantations potential to restore native-forest species composition and diversity.

In the Biscay region (Northern of the Iberian Peninsula), native forests have suffered substantial degradation from the fifteenth to the nineteenth century, due to wood demand for charcoal and timber productions. As a result, at the beginning of the twentieth century, native mixed-oak forests, dominated by *Quercus robur*, were highly fragmented. In the 1950s, industrialisation in the area initiated a crisis in the rural regions that resulted in farm abandonment and the spread of rapid growth and fast turnover *Pinus radiata* plantations (35-40 years rotations). Even if pine plantations were once highly profitable, the reduction in prices of timber over the last ten years has reduced their profitability. Thus, in the near future this economical change might give rise to silvicultural policies and practices that allow for increasing consideration towards native forest restoration and biodiversity conservation.

The links between succession and restoration have emphasized the potential of natural processes to achieve native forest restoration. In this context, the use of pine plantations as passive restoration tool of native oak forest, relying on natural succession, is an important aspect to be considered. Fast-growing pines represent an intermediate successional stage between the transitional shrubs communities and the mature tree communities (Gómez-Aparicio et al., 2009); as a consequence the spontaneously regenerated vegetation (most frequently shrubs and broadleaved trees) plays an important role in restoring natural conditions in plantations (Onaindia and Mitxelena, 2009). Studies from temperate zone plantations have found evidence that plantations can promote habitat conditions for establishment of mid-successional native tree species such as oaks (*Quercus* spp.) and ashes (*Fraxinus* spp.) (Truax et al., 2000; Cogliastro and Paquette, 2012), then this regeneration could be left to form a canopy after the plantation trees are harvested (Lust et al., 2001). However, since natural oak forests have been transformed into remnant patches the natural processes governing dispersal (e.g. dispersal distances) have a major influence on plant colonization (Cain et al., 2000), being fundamental factors to be considered in native forest restoration. Therefore, native woodlands close to pine plantations, which act as seed sources, produce more active recruitment and successional dynamics on plantations (Gómez-Aparicio et al., 2009), favouring the restoration of native community.

Within this context, we evaluate the natural regeneration of native oak woodland vegetation under cultivated stands of *Pinus radiata* in Northern of the Iberian Peninsula. To achieve this, we compared vegetation composition and diversity changes on three commonly observed habitats: regenerating *Q.robur* woodlands, old-growth native *Q.robur* woodlands; both acting as seed sources and their adjacent *P.radiata* plantations at different succession stages that act as seed traps. This study can determine whether natural regeneration will be sufficient for restoring the natural woodland main species or some management interventions are needed. The aim was to assess the potential of natural successional processes as an effective tool to restore oak woodlands under pine plantations. Specifically, we tested the following questions: (1) Does the course of succession on pine plantations reduce the understorey compositional differences with natural oak communities?, and (2) What are the understorey vegetation structural and diversity changes in comparison with natural oak woodlands?.

2. Methods

2.1. Study area

The study was carried out in the mountainous region of Biscay, Basque Country, Northern Iberian Peninsula (43°07'N 2°51'W). The climate is temperate Atlantic with a mean annual rainfall of 1200 mm and a mean annual temperature of 12 °C. The native vegetation in this mountainous area is composed by mixed-oak woodlands, which a canopy dominated by *Q. robur*, *Fraxinus excelsior* and *Crataegus monogyna* (Aseginolaza et al., 1988), being other characteristic tree species *Castanea sativa, Ulmus glabra* and *Ulmus minor*. In the Biscay region, many mixed-oak woodlands have been replaced by plantations of *P. radiata*, thus remnant native forests are highly fragmented occupying only 3.5% of the area (Schmitz et al., 1998). Therefore, the predominant landscape is a mosaic dominated by pine plantations with small remnants of disseminated mixed-oak woodlands with an average size of 2.20 ha (Rodríguez-Loinaz et al., 2011).

2.2. Habitat selection

The understorey plant species composition and diversity were studied in three types of habitats: (1) mixed-oak woodland (*Q. robur* and *F. excelsior*) in a regeneration process for at least 70 years (n=15, Qr), (2) old-growth native *Q.robur* woodlands older than 100 years (n=15, Qo), both considered target communities from a conservation viewpoint; and (3) their adjacent *P. radiata* plantations at different successional stages (n=30, P). The selected stands were located at an altitude of 350-400 m a.s.l. on sandstone soils with slopes lower than 30%. The oak stands were selected first, and then the nearest pine plantation to each oak stand was selected, being the average distance between pairs of forest 199±22 m (Table 1).

The sampled pine stands were sorted into four groups according to the *P.radiata* structure and age of plantation as follows: Py=young pine plantations from 1 to 10 years old (n=8); Pt =teen pine plantations from 11 to 20 years old (n=9); Pm = middle age pine plantations from 21 to 30 years old (n=7); and Po=old-growth pine plantations >30 years old (n=6). The plantation rotation is approximately 40 years, being the pine seedlings planted in a density of 1000 trees/ha. During the first half of the rotation (<20 years) different treatments such as pruning and thinning are applied, after that (>20 years) the density of the plantations is approximately 400 trees/ha, and at this stage, silvicultural activities are uncommon.

2.3. Sampling design

Sampling was performed between June and July. In each stand, one sample plot of 20×20 m was established in the centre of the stand. In each plot, 10 sub-plots of 5×2 m were used to sample plant species. The number of sub-plots was determined by calculating the species/area curve. In each sub-plot, the plant species were identified and the percentage cover for each species was calculated through visual estimation (Onaindia et al., 2004). The total species cover of each sub-plot was used to calculate the mean cover of the stands.

Species detected were classified into four growth-forms: trees, shrubs, herbs and ferns. To classify woody species as shrubs or trees the following criteria were used: woody species that usually do not reach heights higher than 3 or 4 m and that are usually branched out from the base were classified as shrubs and woody species that reach heights higher than 3 or 4 m and have a differentiated stem were classified as trees. Climbers were included within shrubs. Unidentified grasses were quantified as a single group (*Gramineae*).

2.4. Data analysis

Statistical analyses were performed in the R software environment (v.2.15.2; R Development Core Team, 2012), using the lme4 package for generalized and linear mixed models (GLMM and LMM; Pinheiro et al., 2011) and the vegan package for multivariate and diversity analyses (Oksanen et al., 2011).

The species data set was analyzed using both multivariate and univariate methods. In the multivariate analysis, the species data sets were log-transformed (log(x+1)) to reduce the influence of rare species. Analyses were performed on the entire data set and considering the four growth-form subsets: (1) trees, (2) shrubs, (3) herbs and (4) ferns.

First, Nonmetric multidimensional scaling (NMDS, 'metaMDS' function with Bray-Curtis distance; Oksanen et al., 2011) was used to identify the understorey compositional similarities between the two oak habitats (Qr, Qo) and pine plantations as a whole (P) and *versus* the four plantation groups (Py, Pt, Pm, Po). To help interpretation of the outputs the centroids for each habitat and plantation group (Qr, Qo, P or Py, Pt, Pm, Po) were overlaid ('envfit' function; Oksanen et al., 2011), followed by their standard deviational ellipses ('ordiellipse' function; Oksanen et al., 2011). The significance of these differences was tested using Permutational Multivariate Analysis of Variance (PMAV, 'adonis' function using Bray-Curtis distance; Oksanen et al., 2011).

Second, LMM were used to test the plant cover differences between oak habitats and plantation groups for all species present in more that 30% of the stands (13 species) and for fourth growth-forms. In these analyses, the woodland-plantation group (Qr, Qo, Py, Pt, Pm, Po) was treated as categorical fixed factor and sampling point was included as random factor to account for spatial autocorrelation of adjacent locations (Pinheiro and Bates, 2000). In LMM analyses all plant cover measures (%) were arcsine square root transformed. At the same time, GLMM were implemented to determine the richness differences between woodland-plantation groups using the same fixed and random structure as in LMM. GLMM were fitted using the Poisson error distribution and log-link function for count data (species richness). All model values are reported as the mean±standard error of the fixed factor, and the magnitude of the effects is calculated as the estimated difference from the Qo habitat.

Third, diversity profiles were used to compare the diversity changes between habitats (Hill, 1973). Diversity profiles provide a graphical representation of how the perceived diversity changes as the emphasis shifts from rare species (left-hand of the plot) to common species (right-hand; Leinster and Cobbold, 2012). We used the naive approach called by Leinster and Cobbold (2012) plotting a single measure of community diversity through the q parameter (for equation information see Leinster and Cobbold, 2012). The q parameter, plot as x axis in the graphs, represents the sensitivity to rare species; when $q=0$ the profile represents total richness, when $q=1$ represent Shannon diversity and when $q=2$ represents Simpson diversity. In this analysis the pine age-groups were sorted into two groups: pine stands younger than 20 years-old (P<20) and pine stands older than 20 years-old (P>20). The aim was to maintain the sampling effort since richness is a sampling dependent variable.

3. Results

Over the entire study 57 plant species were recorded (Supplementary Appendix 1) of which 26 were found in both the pine plantations and the oak woodlands; 17 and 14 species were only recorded in the pine plantations and oak woodlands, respectively. The most abundant species into the pine plantations were: *Clematis vitalba*, *Lonicera periclymenum*, *Pteridium aquilinum*, and *Ulex europaeus*, whereas in oak woodlands they were: *Fagus sylvatica*, *Helleborus viridis*, *Lamiastrum galeobdolon*, *Ulmus glabra*, *Ulmus minor* and *Saxifraga hirsuta*.

3.1. Understorey species compositional differences between habitats

Pine plantations and native oak stands showed different species composition considering all species together (pine *vs.* oak; PMAV, R^2=0.33, P<0.01, Fig. 1a). When the three habitat types (P, Qr, Qo) were considered the significant differences of pine plantations were maintained, although two oak habitats (Qo *vs.* Qr) showed no significant differences between them (P>0.05). NMDS ordination (stress: 0.18; Fig. 1a, 1b) and SD-ellipses showed clearly that the pine plantations and oak stands occupied different regions of the ordination space along the axis 1. The oak stands were located at the right hand of the axis 1 (+ve), whereas pine plantations were displayed at the left hand of the axis 1 (-ve) showing an obvious separation from oak stands. However, analyzing the pine plantations by age group there was a move of centroids on axis 1 towards oak stands related to plantations age (Fig. 1b). This movement was related with a reduction on mean Bray-Curtis dissimilarity index as plantation age increased (Py *vs*. Q habitats=0.84±0.08; Po vs. Q habitats=0.62±0.09, 22% reduction). NMDS ordination with plantation age groups illustrated that the young pine plantations (Py) were located at the most negative values of the axis 1 showing a significant separation from medium- and old-age plantations (Pm, Po). These medium- and old-pine plantations (Pm, Po) were closer to the centre of the ordination, showing less compositional differences from oak stands than young plantations (Py). Finally, teen-age plantations (Pt) were centred between these two plantation extremes with considerable overlap with them**,** and showing an intermediate composition.

The NMDS species plot (Fig. 1a) showed that gradients reflect change in the major species between habitats. Axis 1 gradient reflects change in community composition from pine plantations species (-ve; *Lonicera periclymenum*, *P.aquilinum*, *U.europaeus*) to oak woodland species (+ve; *Acer campestre*, *L.galeobdolon*, *Q.robur* and *Polystichum setiferum*), whereas, axis 2 represents the differences between groups inside the pine plantations and oak woodland respectively.

The independent analysis of the four growth-forms revealed an interesting pattern of species compositional dynamics. Two groups, shrubs and herbs (data not shown) showed the same compositional pattern derived from overall species compositional analysis. Similar pattern was found for ferns (stress: 0.10; Fig. 2a) although in this case greater movement of pine plantation centroids on axis 1 towards oak stands was produced, showing middle-age plantation (Pm) no differences from oak habitats (Qo, Qr). Here, there is a clear change in fern species composition in axis 1 from pine stands dominated by *P. aquilinum* (-ve; Py and Pt) to more diverse pine stands with oak characteristic fern species (+ve; *Blechnum spicant, A.filix-femina* or *Dryopteris affinis*). In contrast, tree compositional patterns were different to the overall pattern. The NMDS ordination for tree group (stress: 0.18; Fig. 2b) showed that there were no compositional differences between three pine age groups (Pt, Pm and Po) and old oak habitats (Qo), and between middle-age plantations (Pm) and regeneration oak stands (Qr). This is mainly for the colonization of main native tree species such as *Q.robur, F.excelsior* and *C.sativa* in pine plantations, which produced an increase of similarity between oak and pine stands.

3.2. Changes in vegetation cover between habitats

Only three growth-forms (tree, shrub and herb) showed significant differences between oak habitats and pine age groups ($P<0.05$, Table 2). First, understorey tree species cover was significantly greater in oak habitats than in all pine age groups (155% oaks *vs*. 83% pines), although the differences were reduced as pine age increased (49% Py to 93% Po). Second, shrub cover only was significantly greater than oak habitats in Pm stands (130% Pm *vs*. 81% Qo and 76% Qr), but Po and Pt pine groups showed higher values than oak stands. Third, herb cover was significantly greater in Po than in oak habitats (53% Po *vs*. 26% Qo and 29% Qr).

The plant cover analysis of the 13 most frequent species showed that seven species had significant differences between oak habitats and pine age groups (P<0.05, Table 2). In general, native woodland species had significantly greater cover values in both oak habitats than in pine plantations (tree species: *A.campestre, C.sativa* and *F. excelsior*; shrub species: *H.helix*; Fern species: *A.filix-femina*, Table 2), although when plantation age is considered there is an increase in the cover values of these species from young plantation (Py) to old plantations (Po). In contrast, generalist species as *Rubus* spp. and *Gramiane* group showed an opposing pattern with greater cover values in pine plantations. Six species, composed by generalist (*Salix atrocinerea*) and native woodland species (*B.spicant* and *Viola riviniana*), showed no differences between oak and pine habitats (Table 2), although three of these species characteristic of native woodlands (*Euphorbia amygdaloides*, *D.affinis* and *P.setiferum*) were absent in Py or Pt pine groups.

3.3. Changes in diversity between habitats

The species richness per stand in pine plantations ranged from 9 species found in a young-stand to 30 species found in an old-stand, whereas the oak habitats showed a shorted range from 11 to 21 species. Nevertheless, there were only significant differences in species richness between Po and oak habitats (P<0.05), showing old-pine stands greater richness than oak habitats (Po=23 *vs*. Qo=17 and Qr=16 species, Table 3). Considering functional groups, there were only significant differences in fern richness between Py and oak habitats, showing Py lower richness (P<0.05, Table 3).

The diversity profiles for both oak habitats and pine plantations divided in two ages (P<20 years and P>20 years) showed that the total richness in pine plantations is greater than in oak habitats (P<20=42, P>20=41vs. Qo=36, Qr=35; Fig. 3). However, the diversity profiles indicate that diversity (Shannon (q=1) and Simpson (q=2)) is greater in oak habitats than in pine plantations (Fig. 2), although Qr showed slightly greater values than pine stands. An interesting results is that pine profiles showed an abrupt dropt before q=1, indicating the presence of many rare species in the pine stands, stabilizing around 3 or 4 species that are evenly distributed. In contrast, oak habitats (Qo, Qr) are lower species rich, but showed greater asymptotic values indicating that they have more common species evenly distributed.

4. Discussion

In this study, we found that the understorey compositional differences between pine plantations and oak habitats were reduced during natural successional process, being especially important in the case of tree and fern growth forms. Moreover, this successional trend is driven by an increase of tree, fern, and native species cover during pine plantations succession. Therefore, natural succession could be used to achieve the restoration objectives at relatively low costs almost for tree and fern growth forms. In any case, these overall results are in agreement with Brockerhoff et al. (2008) who suggest that plantations must be examined along their successional gradient to identify their effect over native forest species.

4.1. Understorey species compositional differences between habitats

As expected from the literature (Fulé et al., 2005; Tarrega et al., 2011), the understorey species composition was significantly different between pine plantations, as a whole, and native oak habitats. However, when pine plantations were divided by age-groups the compositional differences were reduced as the plantations age increased. Young pine plantations showed a clear difference on species composition, whereas medium-age and old-pine plantations showed fewer compositional differences from oaks than young plantations (22% of dissimilarity reduction). The compositional difference reduction is caused by a combination of (1) a decrease in generalist species and (2) by colonization process of native understorey species. Here, there are some good dispersal generalist species over-represented in young and teen-age plantations, namely *C. vitalba, Lonicera* spp., *P. aquilinum* and *U. europaeus*, which decline as plantations grow probably caused by the stand maturation (e.g. increased shade, Pickett and White, 1985). It is well known that land preparation for pine planting (management impacts) produce perturbed areas prone to be colonized by these generalist species (Decocq et al., 2004; González-Alday et al., 2009; Alday et al., 2010). Afterward, the fast change over time in abiotic and structural conditions as *P. radiata* plantation matures facilitates the colonization of native oak-habitat forest specialist, such as *B.spicant*, *D.affinis* and *V.riviniana* more adapted to shade conditions (Calviño-Cancela et al., 2012). The high growth rate of *P. radiata* has been proposed as a cause for the relatively fast regeneration of understorey native woodland species (Cusack and Montagnini, 2004). In contrast, plantations with a low growth rate such as *Pinus sylvestris* hardly approach the species composition of native forests (Tarrega et al., 2011). This may be a general compositional trend on fast-growing plantations, since similar models of understorey community development from young to mature ages have been observed on different temperate fast growing plantations of Europe and America (Brockerhoff et al., 2008; Calviño-Cancela et al., 2012). Thus, the canopy of pines provided conditions for a progressive colonisation and establishment of native species when adequate seed sources are near (Onaindia and Mitxelena, 2009; Becerra and Montenegro, 2013).

A noteworthy result was that the colonization process was mainly seen for trees and ferns. Main native tree species, namely *A.campestre*, *F. excelsior*, *C. sativa* and *Q. robur*, early colonize pine plantations. This finding agrees the literature on recruitment in plantations, which has shown that stand structural changes, that are related with plantation age, promoted late successional native broadleaves tree species recruitment compared with low or no canopy cover (Zerbe, 2002), suggesting the existence of some facilitative interactions (Goméz-Aparicio et al., 2009). Thus, the spontaneous tree occurrences on pine plantations from an early plantation-age indicate a development towards natural oak habitats, although some management actions on pines (e.g. single tree harvesting) must be done to overcome pine-oak regeneration stage to produce a native tree canopy (Lust et al., 2001). In relation to ferns compositional dynamics, there was a clear successional process through plantations age; the more generalist *P. aquilinum* species decreased its presence from young to old plantations while the oak-habitat characteristic species, such as *B. spicant*, *A. filix-femina* and *D. affinis* (Aizpuru et al., 2000), showed an opposite trend, i.e. an increase from young to old plantations. Here, no differences were found between middle-age and old-age plantations and oak habitats suggesting that for fern species compositional regeneration at this stage is achieved.

Woodland native species, and in particular so-called ancient woodland species, are very slow to colonise recent forest patches (Jacquemyn et al., 2003), being very sensitive to local extinction under changing habitat conditions (Brockerhoff et al., 2008). As a consequence, dispersion, germination and establishment of ancient woodland species are bottlenecks in forest habitat restoration (Thomaes et al., 2011). Under these circumstances, it is not surprising that some native oak forests species in the area were not found in the sampled pine plantations. Here, this was particularly interesting in the case of (1) two important tree species, *U. minor* and *U. glabra*, endangered species in Europe (Dunn, 1999) and (2) two vernal herb species *L. galeobdolon* and *S. hirsute*, both indicators of old-growth forests (Aizpuru et al., 2000; Thomaes et al., 2011). The absence of *Ulmus* species was most likely due to the ecological conditions within plantations. The age of the oldest plantations (40 years) may not be sufficient to promote the conditions required to settle *Ulmus* tree species considering their regeneration limitations (Dunn, 1999, Biroščíková et al., 2004). In contrast, herb vernal species absence is more related with weak dispersion ability and a lack of persistent seed bank (Amezaga and Onaindia, 1997). Previous seed bank studies have demonstrated that *L. galeobdolon* and *S. hirsute* seeds disappeared from the bank when evergreen conifers are planted on formerly deciduous oak woodland (Amezaga and Onaindia, 1997). As a consequence, ancient woodland species and slow-moving native species show a slow colonization rate on these newly created habitats (Matlack and Monde, 2004). Therefore, for native oak habitat restoration it is necessary to implement management practices that develop understorey conditions that support species requiring high-quality habitats (e.g. partial harvesting to reduce stand density or gap creation, Goméz-Aparicio et al., 2009), but always maintaining habitat connections to accommodate slow-migrating species (Matlack and Monde, 2004).

4.2. Changes in vegetation structure and diversity between habitats

In general, understorey native woodland species cover was higher in oak habitats than in pine plantations. However, as plantations age increases these plant cover divergences are reduced considerably mainly for tree and fern growth forms, i.e. there is an increase of some native tree species (*A. campestre*, *C. sativa*) and ferns species cover (*A. filix-femina, D. affinis* and *P. setiferum*) as plantations matures. This is also produced in the case of *H.helix* (shrub) that prefers large and isolated trees as hosts to grow (Castagneri et al., 2013). These results are parallel to compositional responses indicating a successional process in the understorey of plantations towards the species composition of surrounding native forest. In contrast, shrub and herb species cover and richness were higher in pine plantations than in native oak habitats: these groups are dominated by pioneer and generalist species characterized by a competitive component in their plant strategy *sensu* Grime (2001). Among them highlight *Rubus* spp. and *Graminae* spp. groups that show a rapid growth, high biomass and seed production and fast lateral spread, which enable them to produce high shoot and root densities to outcompete native woodland herb layer species that colonize plantations. Similar results have also been found in native forest restoration studies on coniferous plantations in North America and Asia (Kimmins, 2004; Igarashi and Kiyono, 2008). Thus, management actions focused on reduction of species with stronger competitive ability might be an option to favour the establishment of potential herb species (Kimmins, 2004).

The understorey compositional changes produced in pine plantations as they mature were followed by increases in understorey species richness, and this agrees with the trend observed in coniferous plantations worldwide (Nagaike et al., 2006). In general, middle-age and old-pine plantations showed more richness than oak habitats, although this only was significant on old-pine plantations. In this study, the cause of these richness differences may be due to the great proportion of generalist and opportunistic species (shrubs and herb species) found in plantations. The chance of species colonization on plantations appears to be primarily driven by 'community drift' (*sensu* Hubbell, 2001); stochasticity may have partly replaced interspecific interactions in structuring colonization in these newly created ecosystems (Hubbell, 2001). Here, as plantations mature through time the understorey vegetation is expected to result in generalist species extinctions and the immigration of oak-woodland species. In any case, the diversity profiles indicate that plantations always maintained a lower diversity and more rare and dominant species relative to oak habitats, and this hinders understorey woodland species recovery, therefore it is necessary to implement management practices to reduce the dominant understorey species in plantations (Kimmins, 2004).

4.3. Implications for management

Pine plantations in the studied area provided optimal conditions for regenerating native forests because in approximately 20 years, plantations could catalyse the regeneration of most characteristic trees, ferns and some herb species of native woodlands. This understorey regeneration process is most likely facilitated by the proximity of small patches of oak-woodlands that act as seed sources (Rodríguez-Loinaz et al. 2012), providing native species propagules for colonization. At the same time, the species development improved slowly the ecological conditions under plantations assimilating them to native woodland conditions. Thus, remaining patches of native woodland near plantations are necessary to maintain adequate seed sources for restoration purposes. In these situations, the natural successional process could be used to improve restoration objectives at relatively low costs.

The progressive colonisation of native woodland species takes place thanks to the canopy of pines, which create the conditions for native species to settle, and the rapid regeneration may be caused by the fast growth-rate of *P. radiata*. Therefore, the maintenance of pine canopies during conversion of pine plantations to native broadleaved woodland may be appropriate during the first stages (here until 20 years), since it facilitates the colonization of woodland specialist species (Harmer et al., 2012). These patterns suggest that the use of management actions of different intensity (e.g. single tree harvesting, thinning) after middle age (>20 years) would enable the reorientation of pine plantations towards species compositional states that are more similar to oak habitats (Rescia et al., 2010). In base of these considerations, programmes could be implemented to restore and preserve mixed-oak woodlands using pine plantations as catalysers. Also, special care should be given to the small patches of oak-woodlands within plantations. The conservation and regeneration of native forests remnants is necessary to maintain a resilient landscape that can cope with loss of diversity. However, it should be interesting to implement supplementary management measures (e.g. target species seeding and competitive species elimination) to introduce some native woodland species that were not present in plantations such as *U. minor*, *L. galeobdolon* and *S. hirsute*, or species that were outcompeted to maintain local biodiversity.

Clearly, further investigations are needed to assess the effectiveness and the potential value of natural successional process and proposes silvicultural practices, such as single tree selection or selective harvesting, as tools to restore oak woodlands. In any case, our results point out the way for the development of multi-use management strategies to restore oak woodlands in pine plantations, where conservation of biodiversity can be integrated with the maintenance of the landscape and ecological protection functions, whilst still producing a supply of timber.

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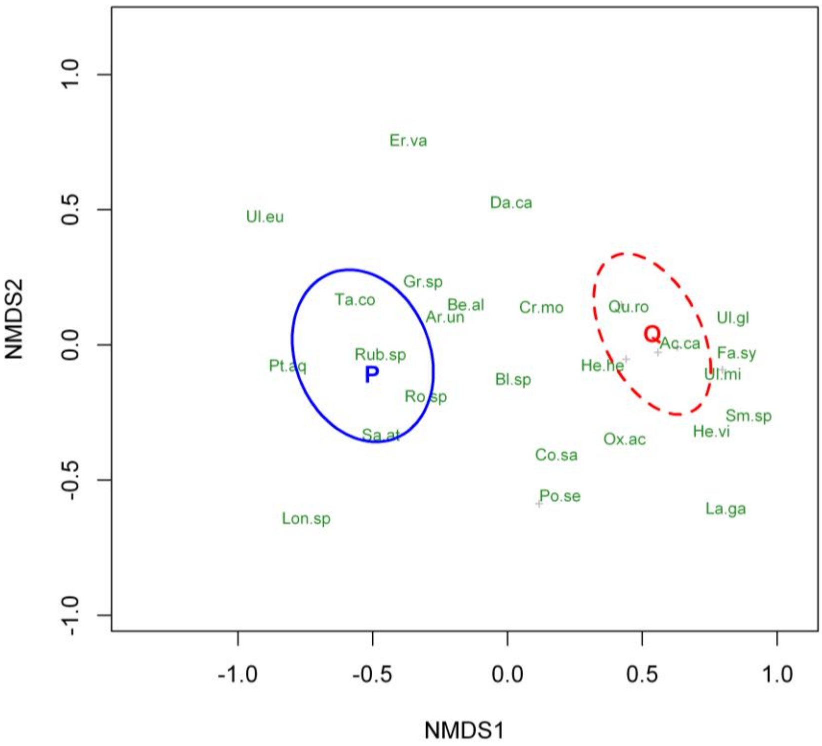
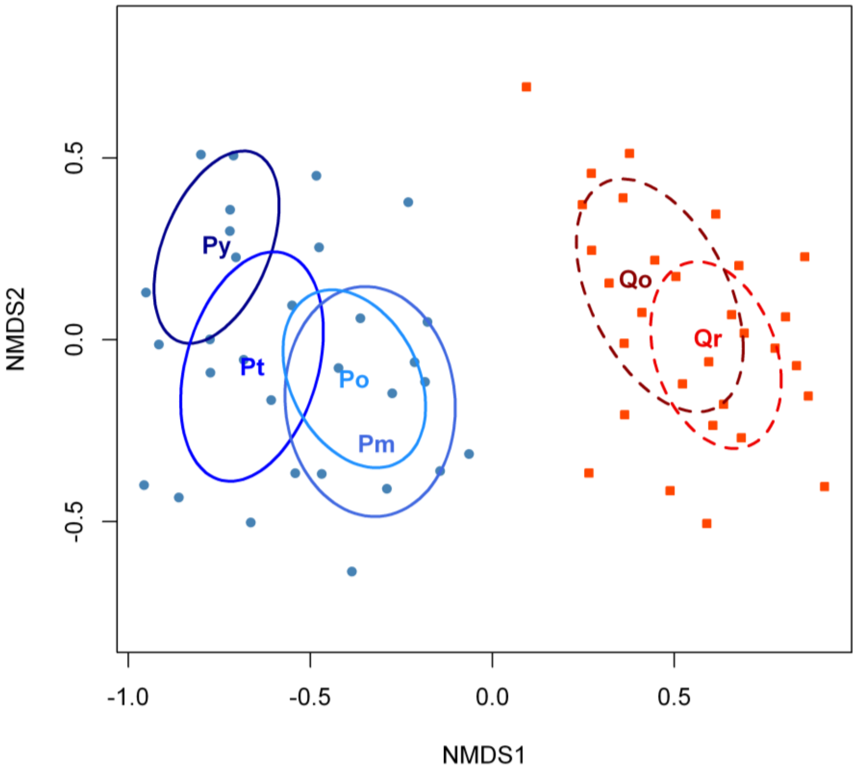


a)

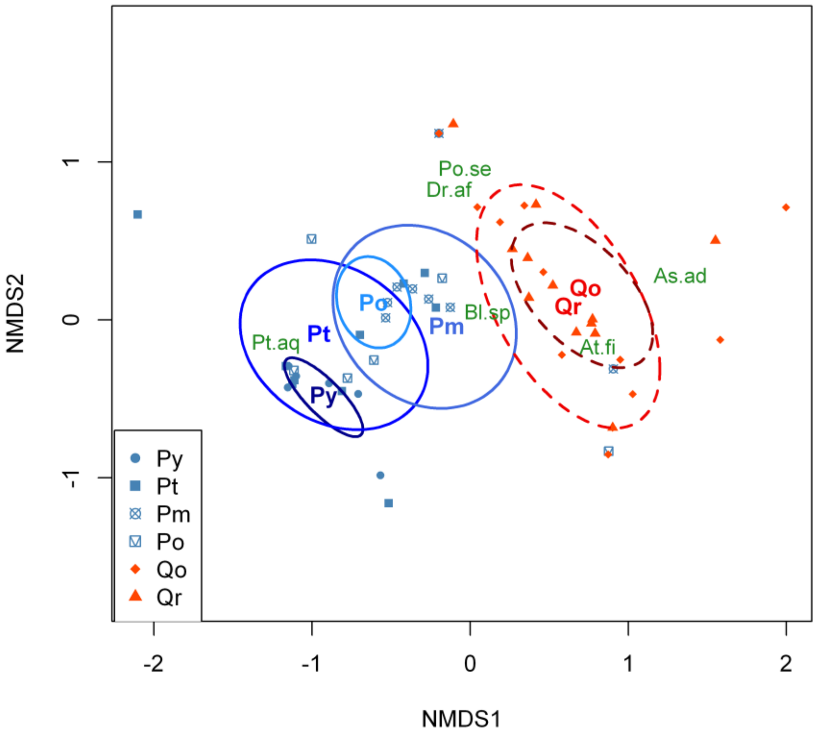


b)

Fig. 1. NMDS ordination for the first two axes of floristic composition data from the three habitats in Biscay (Northern Iberian peninsula), illustrating: (a) Species biplot with bivariate-deviational ellipses (95% confidence intervals) of the main two different habitats (blue ellipses pine plantations=P, red ellipses oak woodlands=Q); (b) Ordination biplot with deviational ellipses of each oak habitat and pine groups (blue ellipses represent pine plantations; Py=young plantations; Pt=teen plantations; Pm=middle age plantations; Po=old

plantations, and red ellipses oak woodlands; Qo=old-growth oak woodland; Qr=regenerated oak woodland). Only the most frequent species are shown. Species codes are: Ac.ca=*Acer campestre,* Ar.un=*Arbutus unedo*, Be.al=*Betula alba*, Bl.sp=*Blechnum spicant*, Co.sa=*Cornus sanguinea*, Cr.mo=*Crataegus monogina*, Da.ca=*Daboecia cantabrica*, Er.va=*Erica vagans*, Fa.sy=*Fagus sylvatica*, Gr.sp=*Graminae*, He.he=*Hedera helix*, He.vi=*Helleborus viridis*, La.ga=*Lamiastrum galeobdolon*, Lon.sp=*Lonicera periclymenum*, Ox.ac= *Oxalis acetosella*, Po.se=*Polystichum setiferum*, Pt.aq=*Pteridium aquilinum*, Qu.ro=*Quercus robur*, Ro.sp=Rosa sp., Rub.sp=*Rubus* sp., Sa.at=*Salix atrocinerea*, Sm.sp=*Smilax aspera*, Ta.co=*Tamus communis*, Ul.eu=*Ulex europaeus*, Ul.gl=*Ulmus glabra*, Ul.mi=*Ulmus minor*.

a)



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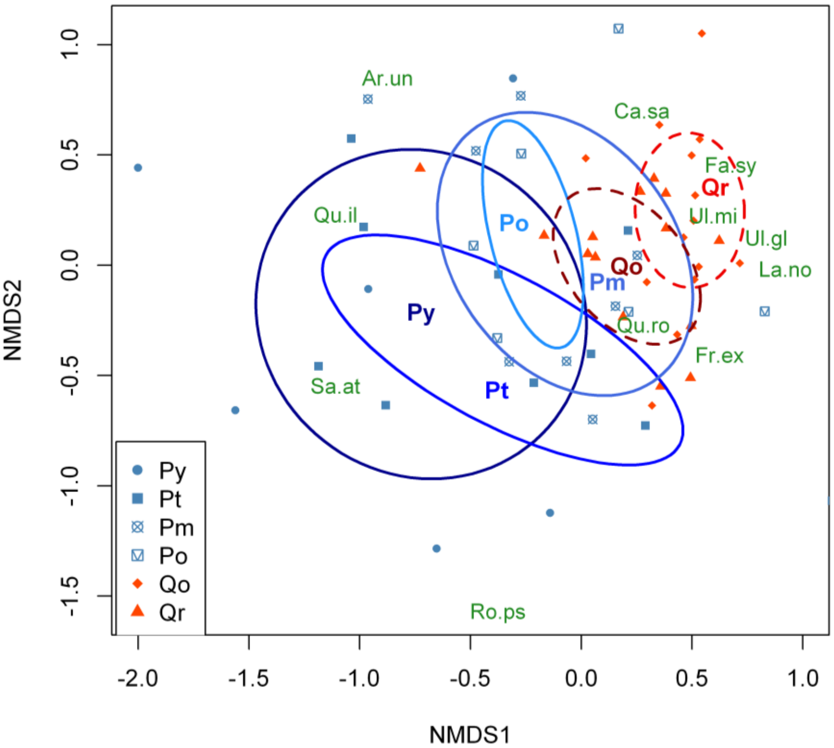


Fig. 2. NMDS ordination for the first two axes of ferns and tree species subsets data from the three habitats in Biscay (Northern Iberian peninsula), illustrating: (a) Ferns biplot; (b) Tree ordination biplot. The deviational ellipses of each oak habitat and pine groups are included,

blue ellipses represent pine plantations; Py=young plantations; Pt=teen plantations; Pm=middle age plantations; Po=old plantations, and red ellipses oak woodlands; Qo=old-growth oak woodland; Qr=regenerated oak woodland. Species codes are: Ar.un=*Arbutus unedo*, As.ad=*Asplenium adiantum-nigrum*, At.fi=*Athyrium filix-femina*, Bl.sp=*Blechnum spicant*, Dr.af=*Dryopteris affinis*, Ca.sa=*Castanea sativa*, Fa.sy=*Fagus sylvatica*, Fr.ex=*Fraxinus excelsior*, La.no=*Laurus nobilis*, Po.se=*Polystichum setiferum*, Pt.aq=*Pteridium aquilinum*, Qu.il=*Quercus ilex*, Qu.ro=*Quercus robur*, Ro.ps=*Robinia pseudoacacia*, Sa.at=*Salix atrocinerea*, Ul.gl=*Ulmus glabra*, Ul.mi=*Ulmus minor*.

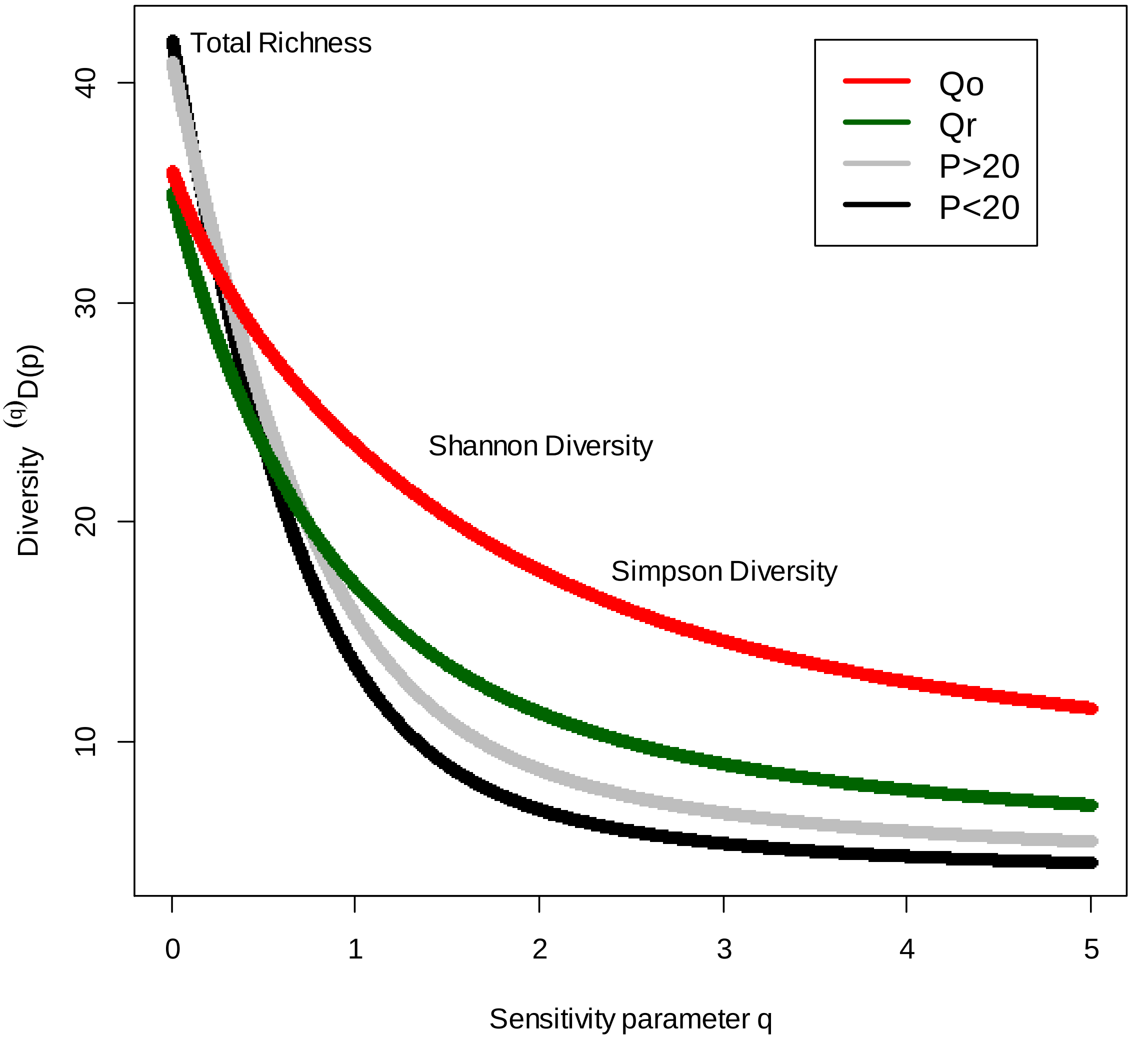


Fig. 3. Diversity profiles for both oak habitats (Qo=old-growth oak woodland; Qr=regenerated oak woodland) and pine plantations divided in two age groups (P<20=Pine plantations younger than 20 years; P>20=Pine plantations older than 20 years). Total richness, Shannon and Simpson diversity values are represented at q=0, q=1 and q=2, respectively.

Table 1. Detailed description and location of the paired native woodland and pine plantation stands in the region of Biscay (Northern Iberian Peninsula). The stand number is enclosed in parentheses. Key to oak and plantation groups: Qo=old-growth oak woodland; Qr=regenerated oak woodland; Py=young pine plantations; Pt=teen pine plantations; Pm=middle age pine plantations; Po=old pine plantations.

Type of pine plantation	X (UTM)	Y (UTM)	Type of oak native woodland	X (UTM)	Y (UTM)
Py (1)	519000	4794000	Qr (31)	518743	4794045
Py (2)	524962	4779062	Qr (32)	524962	4779062
Py (3)	512979	4772962	Qr (33)	513399	4773196
Py (4)	516010	4772971	Qr (34)	515899	4772921
Py (5)	515963	4782013	Qr (35)	515990	4782043
Py (6)	507009	4779000	Qr (36)	507036	4781817
Pt (7)	540002	4800004	Qr (37)	539797	4800177
Pt(8)	540001	4797000	Qo (38)	528260	4790793
Py(9)	533993	4779000	Qo (39)	527769	4787600
Pt (10)	521971	4778998	Qo (40)	516364	4778797
Pt (11)	528018	4806000	Qo (41)	518988	4769911
Py (12)	531020	4787992	Qo (42)	510175	4800065
Pt (13)	534000	4776000	Qo (43)	476840	4790702
Pt (14)	533991	4799994	Qo (44)	537719	4796906
Pt (15)	497968	4787998	Qo (45)	513072	4769911
Pt (16)	528001	4791001	Qr (46)	540024	4797025
Pt (17)	528054	4788011	Qr (47)	533700	4775842
Pm (18)	516011	4778986	Qr (48)	522049	4777869
Po (19)	518992	4769990	Qr (49)	528106	4805181
Pm (20)	510054	4799998	Qr (50)	530556	4787986
Po (21)	477000	4791000	Qr (51)	533701	4775844
Pm (22)	537033	4796974	Qr (52)	533936	4779068
Pm (23)	513012	4769986	Qr (53)	497640	4787705
Po (24)	521992	4794008	Qo (54)	521921	4793723
Po (25)	522015	4773016	Qo (55)	522237	4773241
Pm (26)	537007	4782032	Qo (56)	537201	4782064
Po (27)	504009	4779028	Qo (57)	503578	4779072
Po (28)	507001	4782019	Qo (58)	506647	4778889
Pm (29)	536986	4773004	Qo (59)	536851	4773051
Pm (30)	516031	4803021	Qo (60)	515573	4802518

Table 2. Differences in plant cover of most frequent species for the two oak habitats and pine plantation groups using Linear-Mixed models (LMM). Mean values (±SE) are presented followed by model estimates (±SE) in bold from the LMMs along with significance of each term, only for significant variables. Key to oak and plantation groups: Qo=old-growth oak woodland; Qr=regenerated oak woodland; Py=young pine plantations; Pt=teen pine plantations; Pm=middle age pine plantations; Po=old pine plantations. Significance: *=P<0.05; **=P<0.01. Different letters indicate significant differences.

	Qo	Qr	Po	Pm	Pt	Py
Plant Cover (%)						
Tree	153.07±19.76 **0.76±0.05a**	156.87±11.46 **-0.01±0.07a**	92.67±10.53 **-0.21±0.09*b**	96.19±6.95 **-0.20±0.08**b**	86.95±8.60 **-0.23±0.07**b**	49.27±12.88 **-0.38±0.09**c**
Shrub	80.60±10.80 **0.52±0.05a**	75.87±11.57 **-0.02±0.07a**	106.72±17.44 **0.10±0.09a**	130.38±29.88 **0.21±0.08*b**	85.84±7.55 **0.03±0.08a**	71.50±13.33 **-0.03±0.09a**
Herbs	25.87±6.82 **0.41±0.06a**	29.33±9.05 **0.05±0.09a**	53.32±10.06 **0.24±0.12*b**	27.62±8.28 **0.01±0.11a**	23.67±6.15 **-0.02±0.10a**	26.46±8.39 **0.01±0.12a**
Fern	34.33±4.17	20.40±5.66	49.16±8.81	43.68±7.31	49.44±12.89	35.86±9.53
Species Cover (%)						
Tree species						
Acer campestre L.	18.20±7.95 **0.35±0.07a**	13.67±3.10 **-0.02±0.09a**	2.56±1.67 **-0.24±0.12*b**	1.08±0.87 **-0.29±0.11*bc**	0.07±0.06 **-0.33±0.11**c**	1.50±1.50 **-0.29±0.12*bc**
Castanea sativa Miller	16.87±7.92 **0.36±0.06a**	12.33±3.04 **-0.02±0.09a**	2.93±2.01 **-0.21±0.12*b**	1.08±0.87 **-0.27±0.11*b**	0.07±0.06 **-0.31±0.10**c**	1.67±1.67 **-0.28±0.12*b**
Fraxinus excelsior L.	9.67±3.73 **0.20±0.05a**	4.73±1.77 **-0.04±0.07a**	0.08±0.07 **-0.18±0.09*b**	3.36±1.75 **-0.08±0.08a**	1.93±1.83 **-0.17±0.07*b**	0.28±0.26 **-0.17±0.09*b**
Salix atrocinerea Brot	2.06±0.94	-	0.39±0.25	0.50±0.35	7.91±7.07	3.32±2.83
Shrub species						
Hedera helix L.	28.67±10.06 **0.51±0.10a**	44.73±9.42 **0.18±0.15a**	19.32±8.79 **-0.12±0.19a**	25.71±9.52 **-0.05±0.18a**	3.95±2.67 **-0.39±0.16*b**	0.50±0.50 **-0.48±0.19*b**
Rubus spp.	5.40±1.40 **0.18±0.06a**	3.86±1.26 **-0.01±0.09a**	53.12±12.04 **0.67±0.11**b**	56.43±9.08 **0.70±0.11**b**	50.54±7.69 **0.62±0.09**b**	45.12±13.66 **0.55±0.12**b**
Herb species						
Euphorbia amygdaloides L.	1.73±0.70	4.07±1.14	2.33±1.12	1.12±0.74	-	0.67±0.49
Viola riviniana Reinchenb.	2.07±1.06	2.13±1.05	2.72±2.07	0.12±0.12	0.15±0.10	0.85±0.83
Gramineae spp.	4.53±0.89 **0.19±0.05a**	3.20±1.10 **-0.04±0.07a**	27.34±10.93 **0.30±0.10**b**	19.10±10.81 **0.19±0.09*b**	12.47±4.86 **0.12±0.08a**	14.52±4.52 **0.18±0.10a**
Fern species						
Athyrium filix-femina (L.) Roth	15.47±2.68 **0.36±0.04a**	6.33±2.03 **-0.17±0.05*b**	1.27±0.63 **-0.28±0.07**c**	2.87±1.20 **-0.24±0.06*bc**	1.29±0.87 **-0.31±0.06**c**	0.70±0.70 **-0.36±0.07**c**
Blechnum spicant (L.) Roth	7.73±2.15	3.73±1.84	3.17±1.34	5.34±1.86	3.81±2.14	0.93±0.67
Dryopteris affinis (Lowe) Fraser-Jenkins	3.73±1.84	4.33±2.11	2.81±0.85	4.80±1.96	3.00±2.09	-
Polystichum setiferum (Forsskäl) Woynar	5.07±1.97	5.00±2.12	2.81±0.85	3.16±1.48	1.90±1.08	-

Table 3. Differences in species richness for the two oak habitats and pine plantation groups using Generalized-Linear-Mixed models (GLMM). Mean values (±SE) are presented followed by model estimates (±SE) in bold from the GLMMs along with significance of each term, only for significant variables. Key to oak and plantation groups: Qo = old-growth oak woodland; Qr=regenerated oak woodland; Py=young pine plantations; Pt=teen pine plantations; Pm=middle age pine plantations; Po=old pine plantations. Significance: *=P<0.05; **=P<0.01. Different letters indicate significant differences.

	Qo	Qr	Po	Pm	Pt	Py
Richness (S)	17±0.6 **2.81±0.06a**	16±0.7 **-0.04± 0.09a**	23±2.8 **0.32±0.11**b**	18±0.9 **0.06±0.11a**	17±1.2 **0.03±0.10a**	16±1.3 **-0.01±0.12a**
Tree	5±0.4	5±0.3	6±0.8	5±0.2	4±0.7	4±0.9
Shrub	5±0.4	5±0.3	7±0.9	6±0.7	6±0.4	6±1.1
Herbs	3±0.6	4±0.4	6±1.6	3±0.5	5±0.8	5±1.3
Fern	3±0.3 **1.12±0.15a**	2±0.4 **-0.36±0.23ab**	4±0.5 **0.27±0.25a**	3±0.6 **0.10±0.24a**	2±0.6 **-0.25±0.25ab**	2±0.2 **-0.71±0.26*b**

Graphical Abstract (for review)

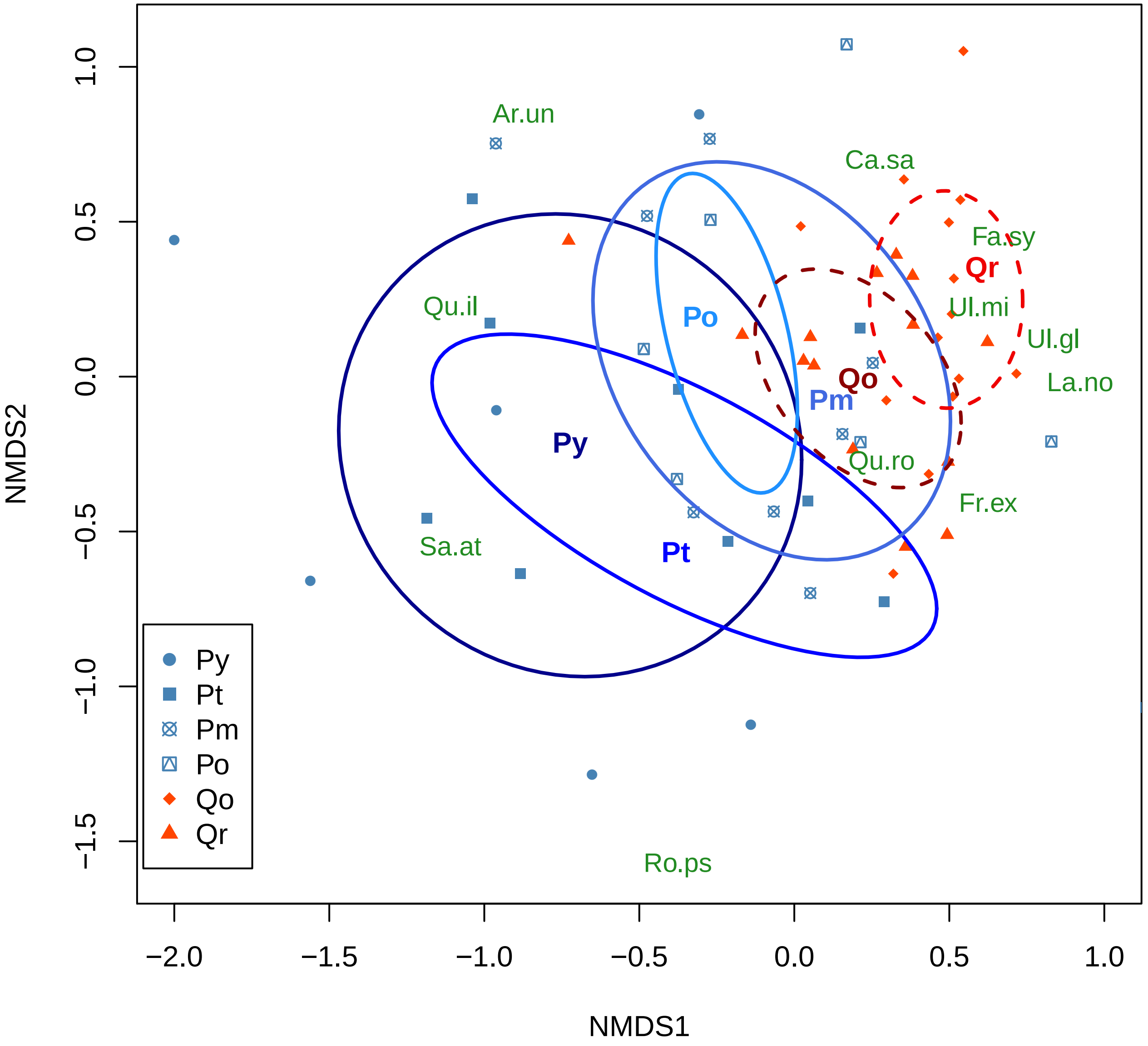


Fig1a Black$white

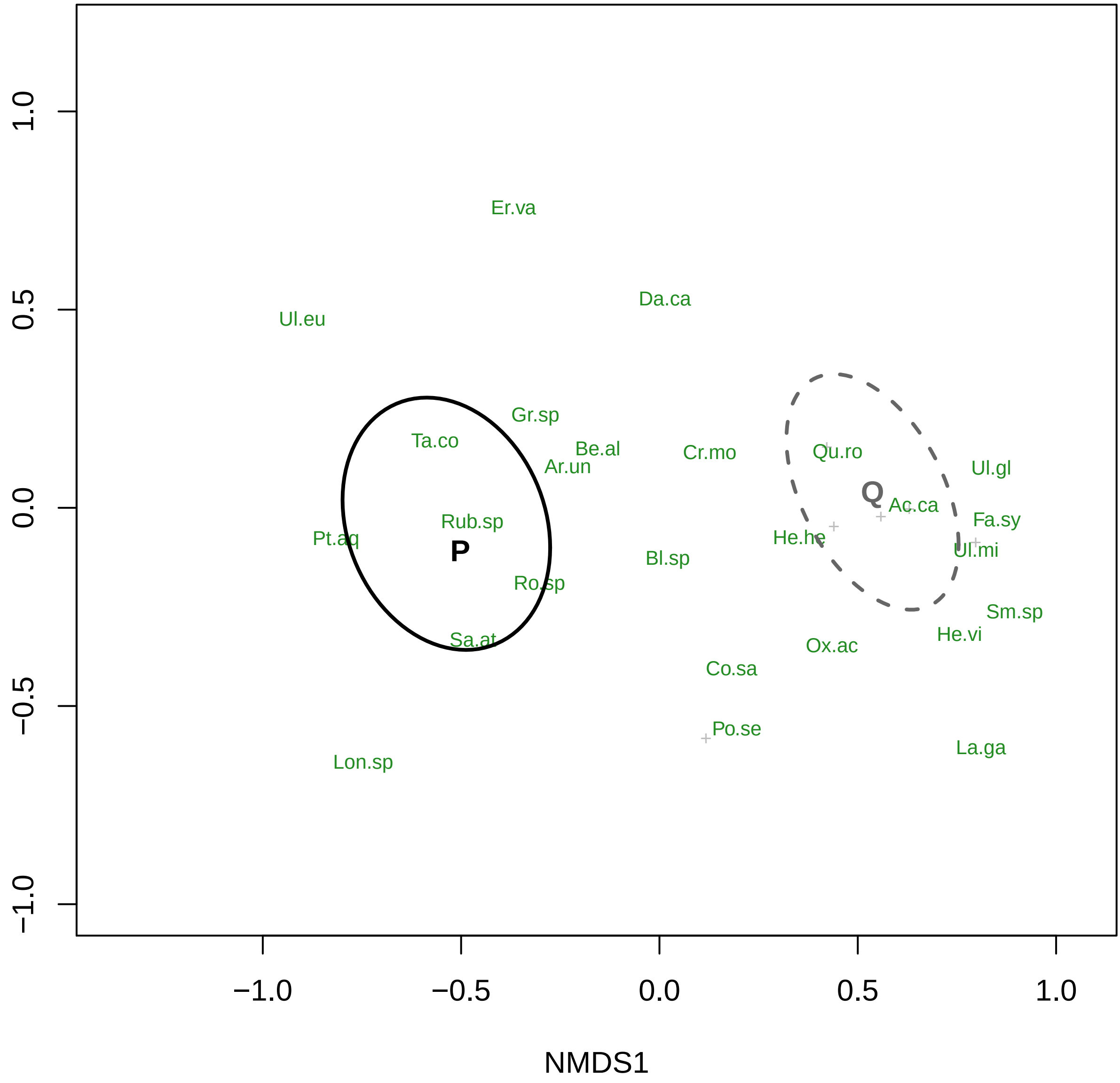
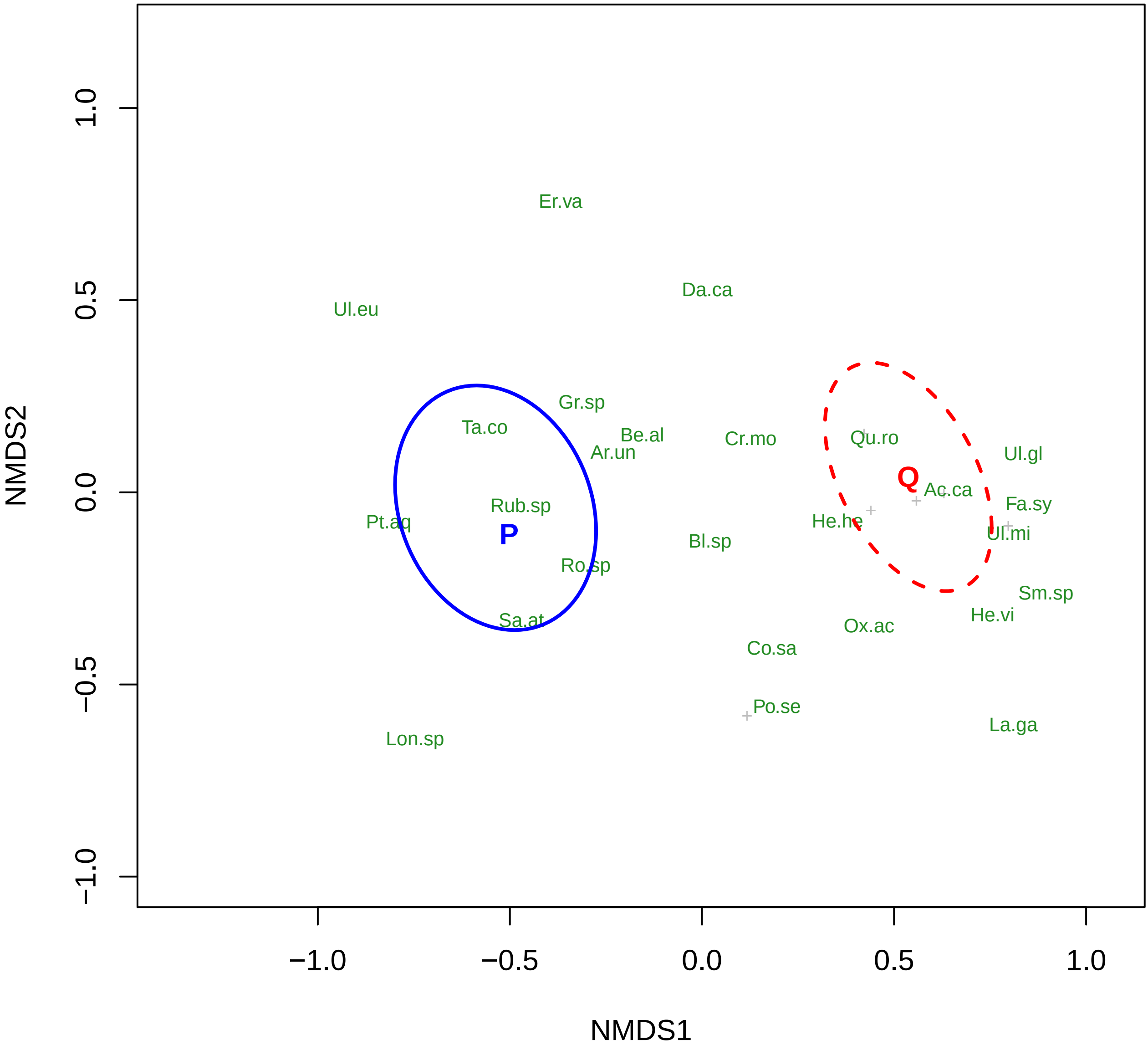


Fig1a Color



Er.va
Da.ca
Ul.eu
Gr.sp
Ta.co
Be.al
Cr.mo
Qu.ro
Ar.un
Ul.gl
Q
Ac.ca
Fa.sy
Rub.sp
Pt.aq
He.he
P
Ul.mi
Bl.sp
Ro.sp
Sm.sp
He.vi
Sa.at
Ox.ac
Co.sa
Po.se
La.ga
Lon.sp
NMDS2
1.0
0.5
0.0
−0.5
−1.0
−1.0
−0.5
0.0
0.5
1.0
NMDS1

Fig1b Black&White

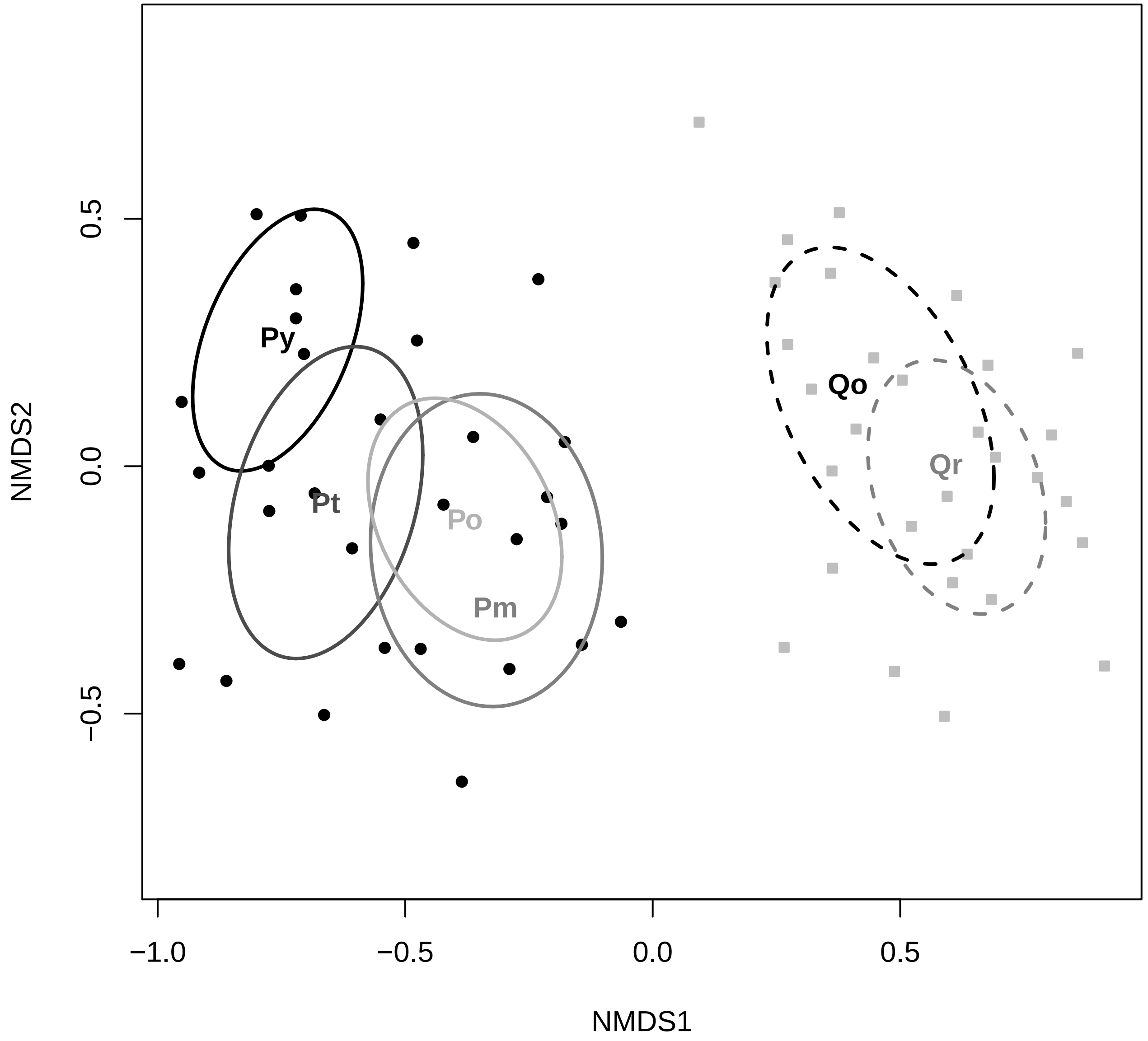


Fig1b Color

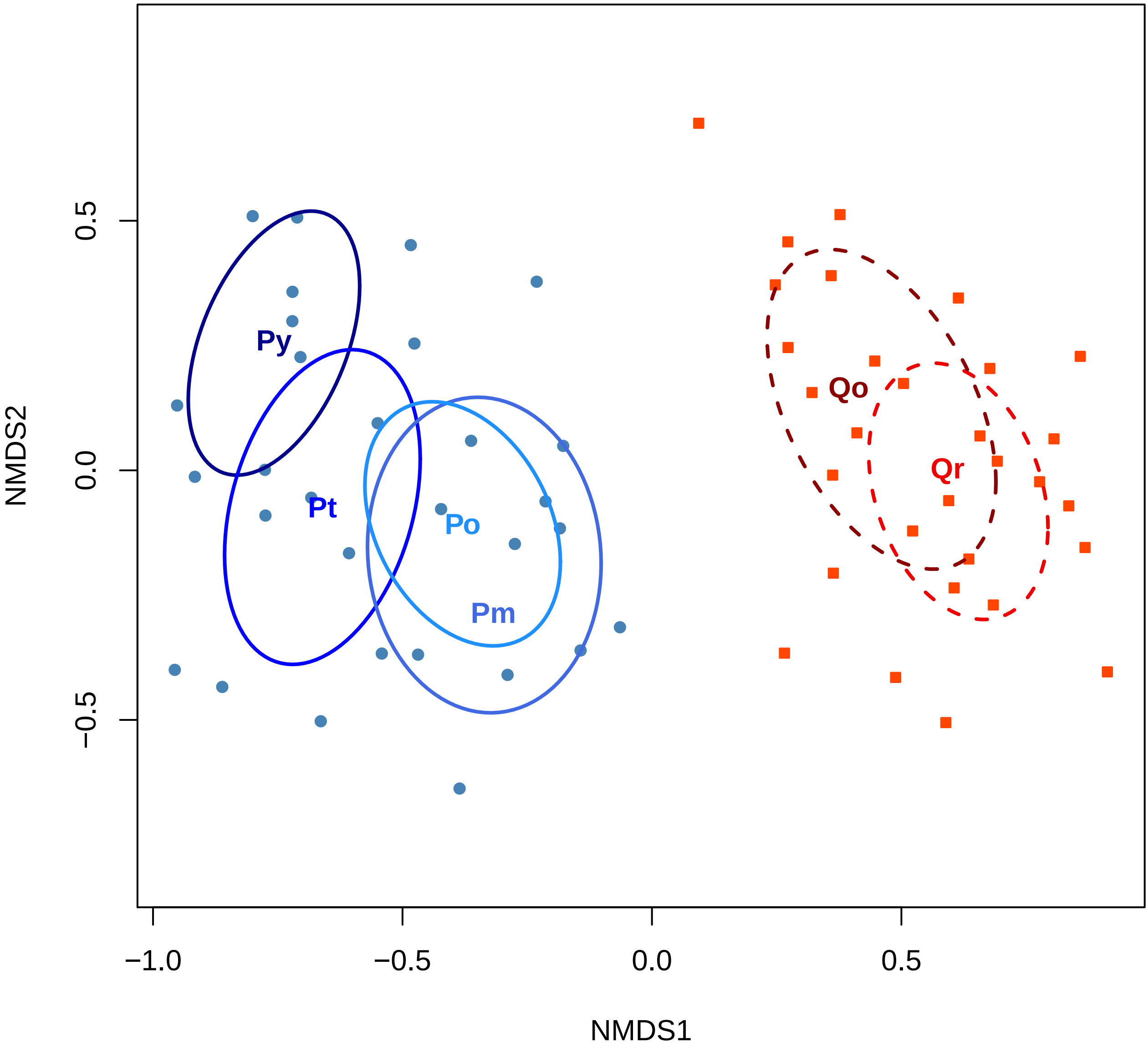


Fig2a Black&White

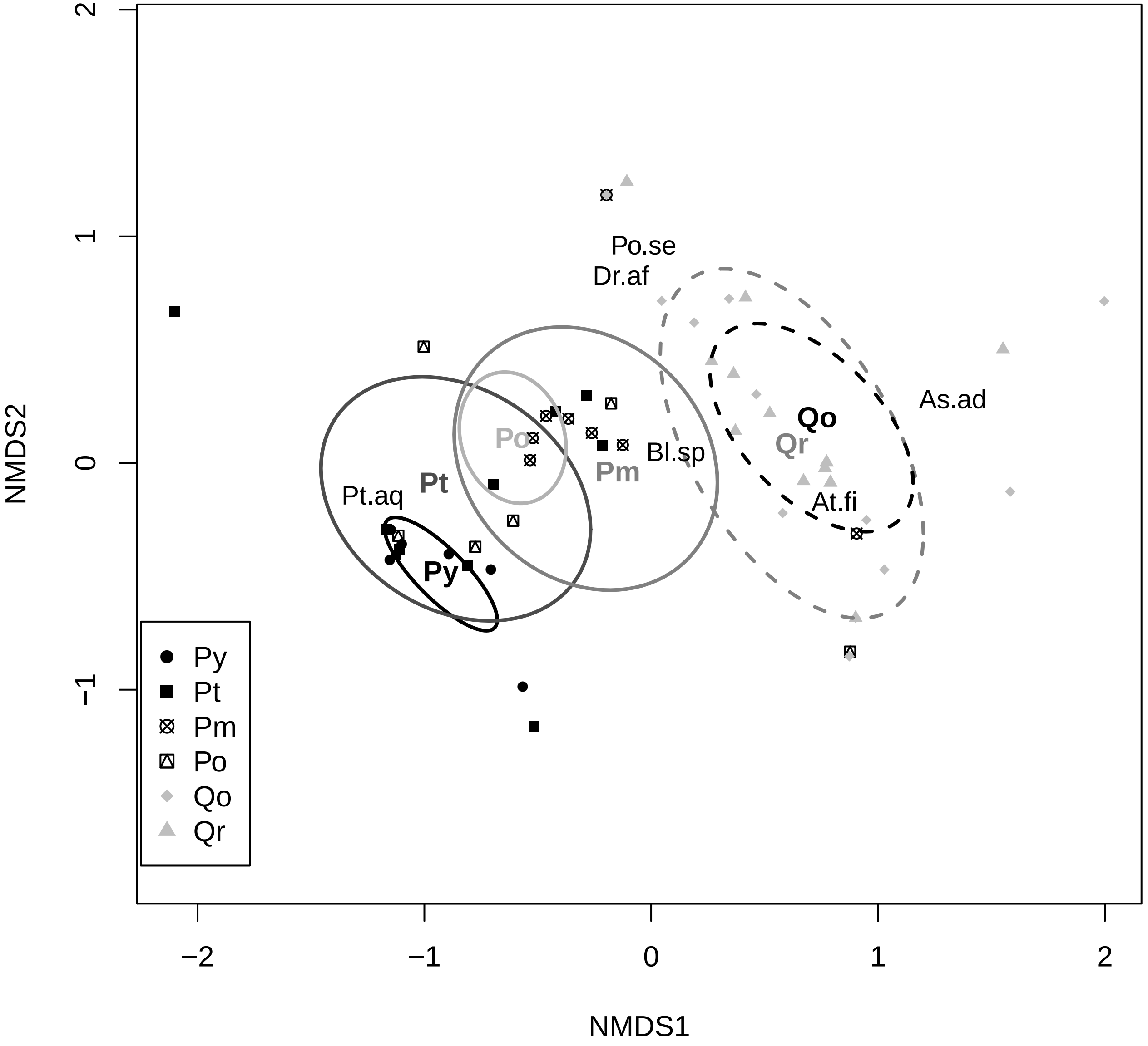
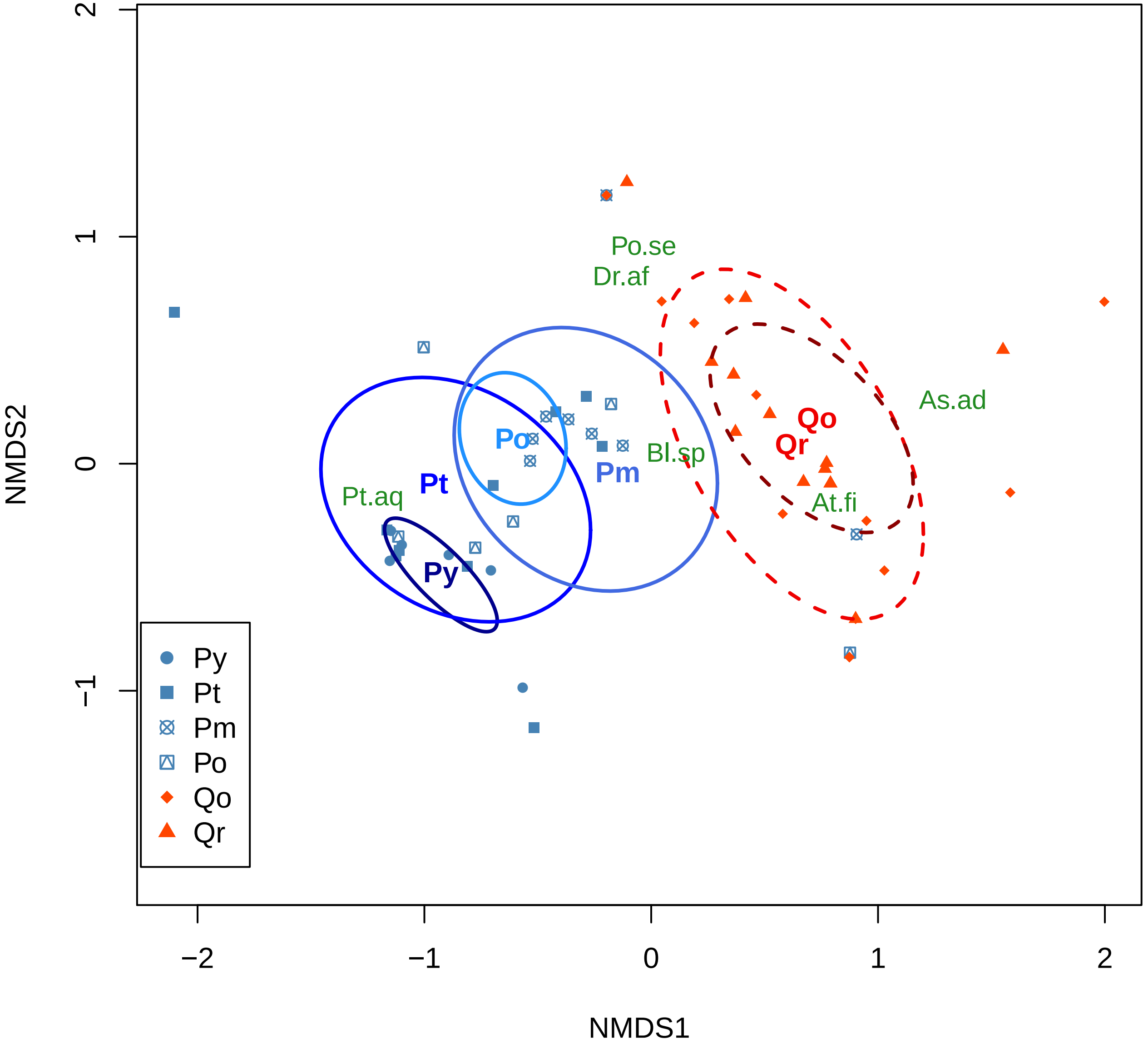


Fig2a Color



NMDS1
NMDS2
−2
−1
0
1
2
Po.se
Dr.af
As.ad
Qo
Qr
Bl.sp
Pm
Po
Pt
Pt.aq
At.fi
Py
Py
Pt
Pm
Po
Qo
Qr

Fig2b Black&White

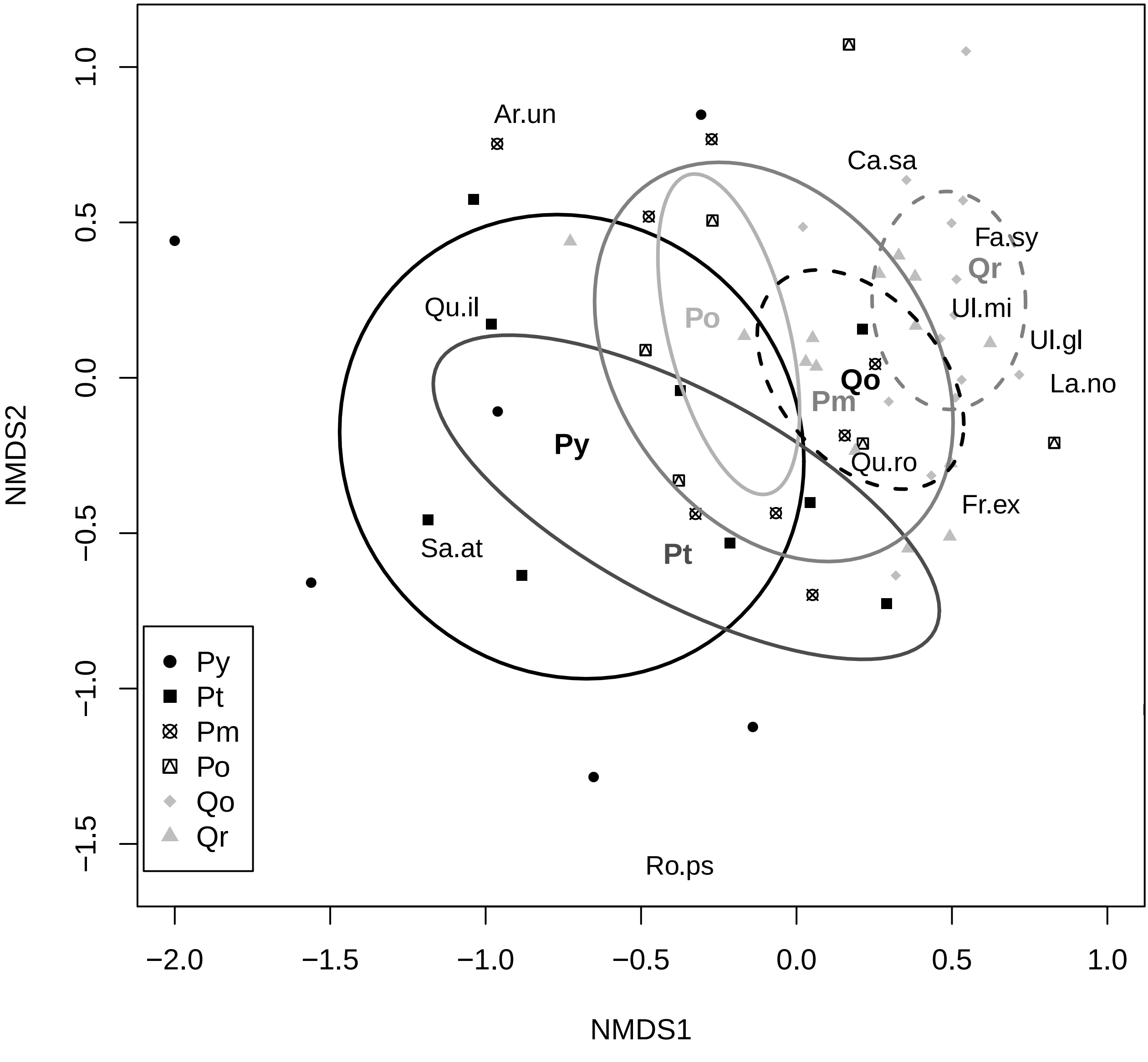
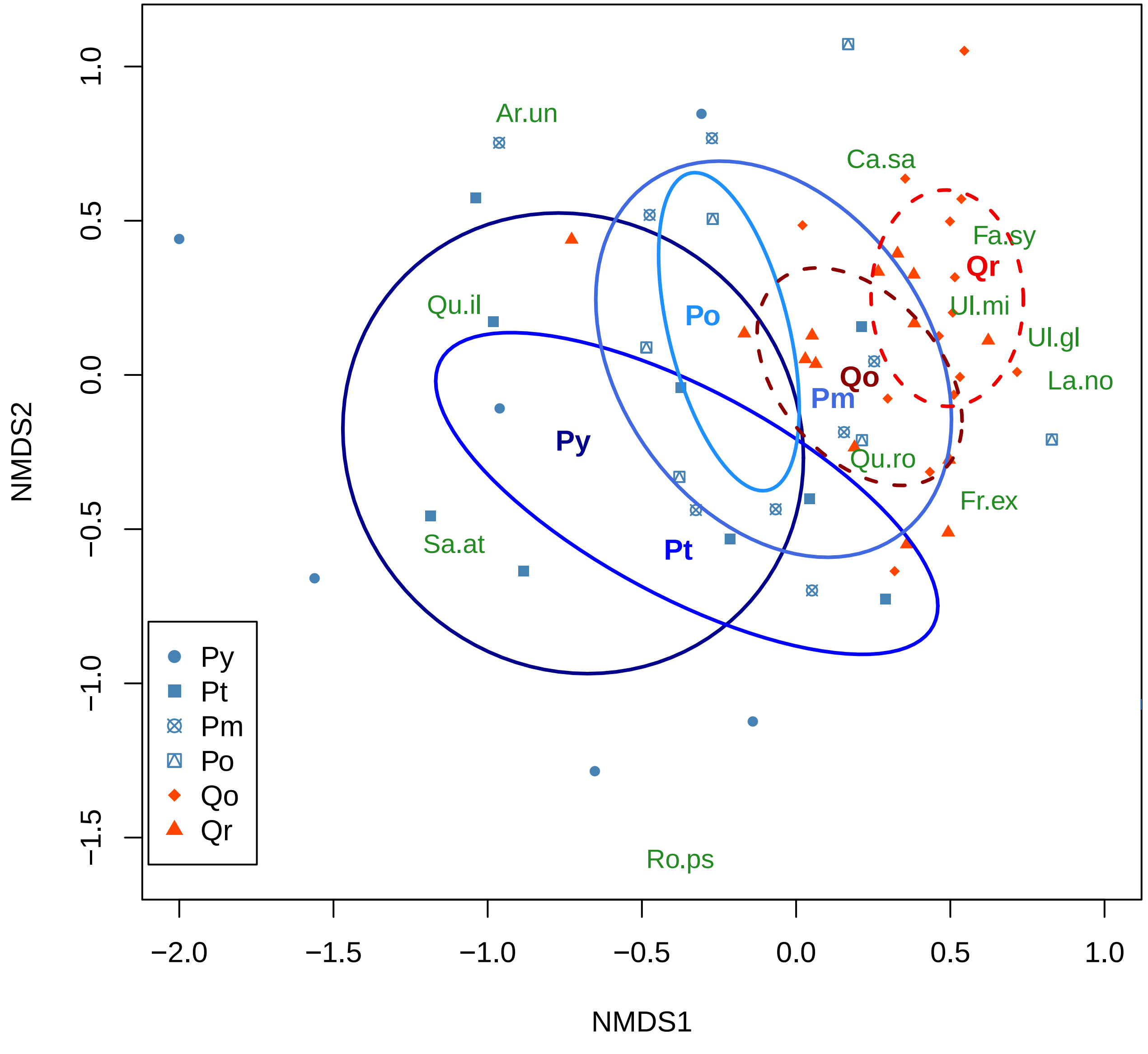


Fig2b Color



1.0
0.5
0.0
−0.5
−1.0
−1.5
NMDS2
−2.0
−1.5
−1.0
−0.5
0.0
0.5
1.0
NMDS1
Ar.un
Ca.sa
Fa.sy
Qr
Ul.mi
Ul.gl
La.no
Qu.il
Po
Qo
Pm
Py
Qu.ro
Fr.ex
Sa.at
Pt
Ro.ps
Py
Pt
Pm
Po
Qo
Qr

Fig3 Black&White

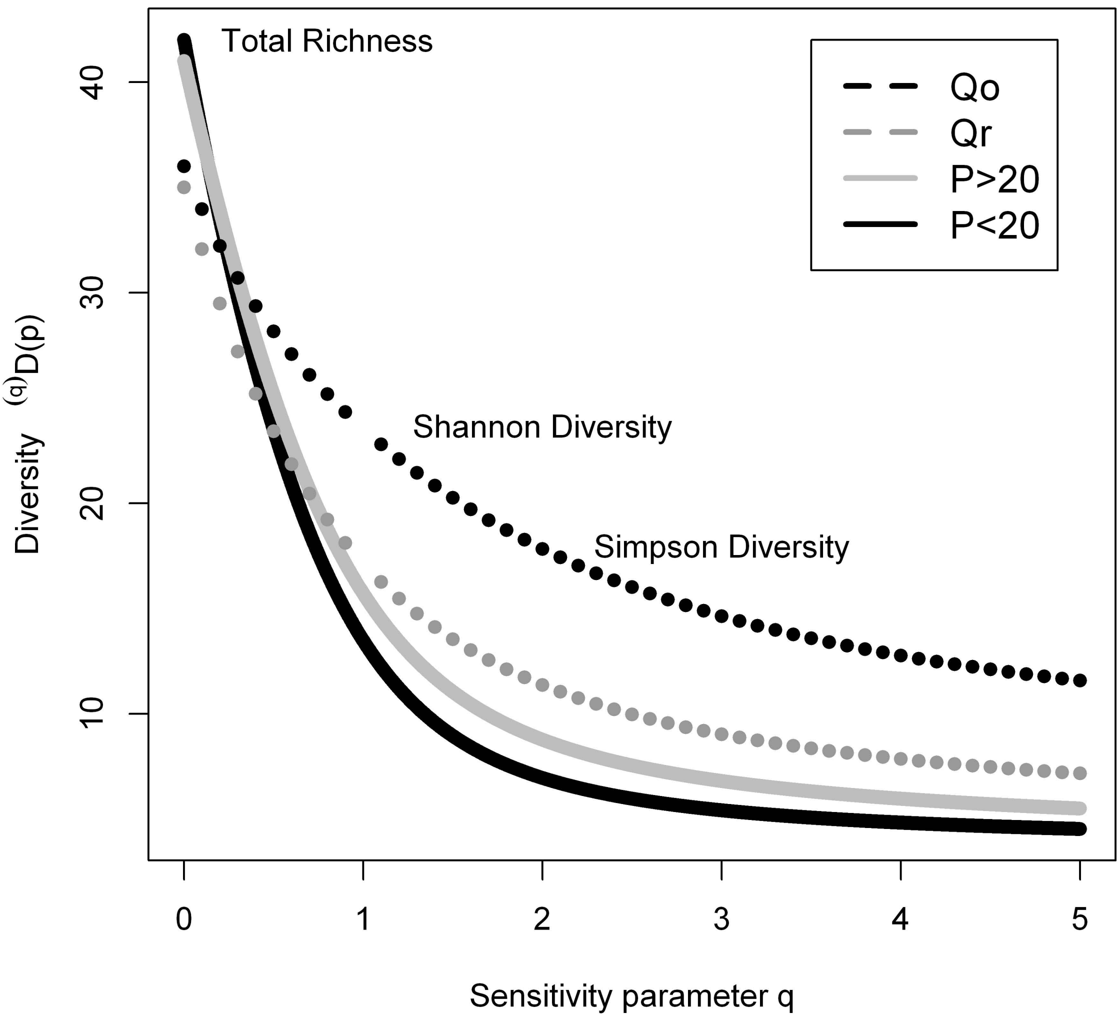
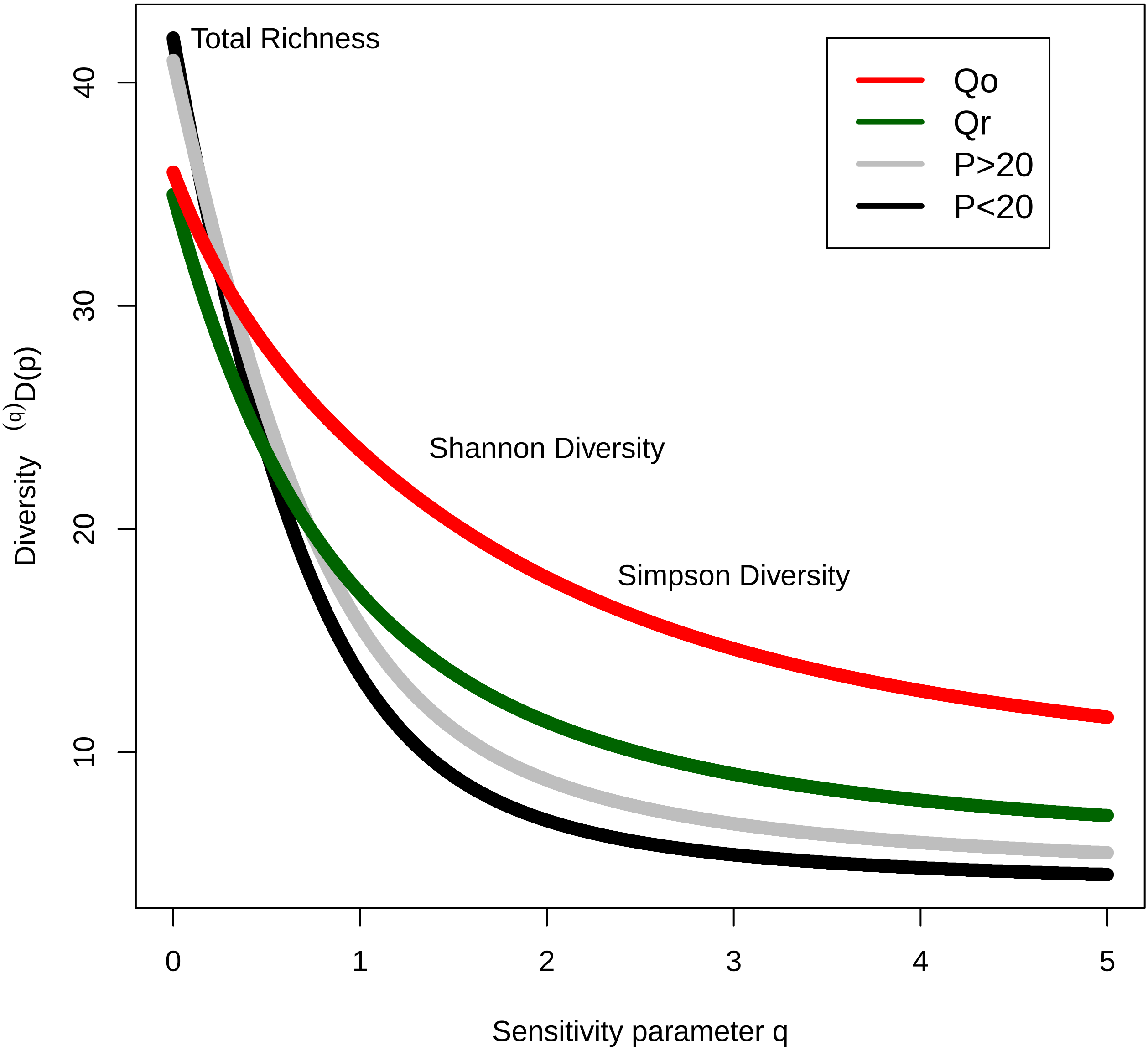


Fig3 Color


Total Richness
Shannon Diversity
Simpson Diversity
Qo
Qr
P>20
P<20
Diversity $^{(q)}D(p)$
Sensitivity parameter q
0
1
2
3
4
5
10
20
30
40

Appendix1