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Establishment constraints of an alien and a native conifer in different habitats

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Abstract Alien plants are subjected to different biotic and environmental barriers that limit their establishment success in the introduced range. *Pseudotsuga menziesii* (Douglas fir), a native conifer from Northwest America, is considered one of the most invasive forestry conifers in Europe. However, little is known about the ecological filters that constrain plant establishment at early life-cycle stages and differences in habitat invasibility to this species. We conducted field experiments to compare the establishment potential (i.e. post-dispersal seed removal, seed germination, seedling survival and growth) of Douglas fir in beech forests, holm-oak forests and heathlands; and compared it with the taxonomically close native conifer *Abies alba* (Silver fir). Douglas fir seeds were more removed than Silver fir in holm-oak and in heathlands. In all habitats, seed germination was significantly higher for Douglas fir compared to that of Silver fir and, seedling mortality was extremely high in both species due to soil disturbance by wild boars and drought stress. Douglas fir mortality was only lower than Silver fir in beech forests. However, species did not differ in seedling growth. Overall, the probability of invasion success of Douglas fir decreased along the sequential stages of plant establishment in all habitats. Only high seed germination rates of Douglas fir would predict its high invasive capacity but these advantages are counterbalanced by high seedling mortality. Results showed a mismatch between invasibility and current pattern of Douglas fir invasion in the study area. Therefore, future research focused on seed production and on different components of biotic resistance is recommended to elucidate which processes are favoring its establishment success.

Keywords *Abies alba* · Germination · Invasibility · *Pseudotsuga menziesii* · Seed removal · Seedling survival

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Introduction

Alien plants are subjected to different biotic and environmental barriers that limit their establishment success in the introduced range (Lonsdale 1999). Many of these barriers have an effect on early life-cycle stages. For example, by limiting the supply of seeds due to seed consumption by native fauna (McCay and McCay 2009), or also, by controlling seedling establishment either caused by unfavorable climatic conditions (Lambrinos 2002) or by

competition with native plants (Dietz et al.1999). As in native plants, these ecological barriers vary spatially and temporally (Schupp 1988; Vilà and Lloret 2000; Traveset et al. 2003). For instance, post-dispersal seed removal varies among habitats, which can be more intense in areas far from alien conifer plantations than in others close to them (Nuñez et al. 2008).

There are studies that have compared differences in the establishment traits between alien and native congeners in the introduced range (Shafroth et al. 1995; Lambrinos 2002; Ferreras and Galetto 2010) to better understand the invasion potential of the alien species (i.e. invasivenesss), and to determine differences in habitat susceptibility to invasion (i.e. invasibility) (Pyšek and Richardson 2007). For this purpose, experiments are the best approach to disentangle the mechanisms of invasion (Sol et al. 2008). Furthermore, these experiments need to link the causal relationships of invasion, from seed dispersal to seedling establishment, in the introduced range (Vilà et al. 2006; Vilà and D'Antonio 1998) and compare them to that of native species.

Several conifer species are invasive in many regions of the world, mainly in the Southern Hemisphere (Richardson and Rejmánek 2004). There has been a fair amount of research on seed and seedling traits concerning conifer invasiveness (Grotkopp et al. 2002; Richardson and Rejmánek 2004), but differences in the ecological barriers that constrain their establishment have been less explored, with the exception of biotic resistance through herbivory by native fauna (Lombardero et al. 2008; Nuñez et al. 2008; Carrillo-Gavilán et al. 2010). *Pseudotsuga menziesii* Mirb. Franco, the Douglas fir, is considered one of the most invasive forestry conifer species of the world (Richardson and Rejmánek 2004). Douglas fir is reported as invasive in areas close to plantations in New Zealand (Kay 1994), South Africa (Richardson and Higgins 1998), Argentina and Chile (Simberloff et al. 2010). For instance, Douglas fir invasion is facilitated by deer browsing on native plants (Relva et al. 2009) and by the presence of below ground mutualisms (Nuñez et al. 2009) in Argentina. In Europe, it is naturalized in several countries (Carrillo-Gavilán and Vilà 2010). According to previous studies (Richardson and Bond 1991; Sarasola et al. 2006), the most suitable habitats to be invaded by this sort of alien conifers would be grasslands and shrublands followed by open forests and, finally, by closed forests.

To assess how Douglas fir establishment is modulated by its interaction with the host community, we conducted field manipulation experiments during the early life-cycle stages (i.e. post-dispersal seed removal, seed survival, seed germination, seedling survival and growth) and compared them with a taxonomically close native conifer *Abies alba* (Silver fir) as a baseline species. Our main objectives were: (a) to know which habitats, close to Douglas fir plantations, have the highest invasibility, (b) to assess the main ecological barriers limiting Douglas fir establishment, (c) to determine how different these patterns are compared to a taxonomically close, coexisting native conifer species. Given the current wide distribution of Douglas fir plantations in Europe, this study can contribute to habitat risk assessment to invasion when this species is introduced for afforestation.

Materials and methods

Study area

The study area is located in the Montseny Natural Park in Barcelona-Spain (latitude 41°42′–41°52′N, longitude 2°16′–2°33′E), a 40,000 ha mountainous area declared a UNESCO Biosphere Reserve in 1978. Montseny encompasses a wide climatic gradient, from a Mediterranean to a subalpine climate, and consequently a large phytogeographic range (Peñuelas and Boada 2003). At medium and high altitudes (800–1,700 m.a.s.l.), the mean annual rainfall is 1,148 mm and mean annual temperature is 8.7°C (means for the 2007/10 period, Can Lleonart meteorological station). This area hosts the most extensive southern European distribution areas of *Fagus sylvatica* (beech) forests and the western distribution of *Calluna vulgaris* heathlands (Bolòs and Vigo 1990). Also, Montane *Quercus* ilex (holm-oak) forests occur at the lowest altitudinal ranges (<800 m.a.s.l.), with a mean annual rainfall of 943 mm and mean annual temperature of 11.7°C (means for the 2007/10 period, Fontmartina meteorological station).

The experiments were conducted in the following habitat types: beech forests, holm-oak forests and heathlands (n = 4 sites/habitat). We chose these types of habitat because of their close proximity to Douglas fir plantations and therefore potentially vulnerable to invasion. Sites were 0.2–3 km apart. These habitats differ in vegetation structure and light availability, and

seed remover community (Torre and Arrizabalaga 2009). In each habitat, 3 plots of 10 × 10 m were randomly chosen to measure the diameter at breast height (DBH, cm) in all individual trees, and light availability was measured at the soil surface as photosynthetically active radiation (PAR, $\mu mol\ s^{-1}\ m^{-2}$) using a portable light meter (Sunfleck Ceptometer, Decagon, Pullman, USA). The main seed remover in all three habitats is *Apodemus sylvaticus,* followed by *A. flavicollis.* Other less frequent seed removers are *Myodes glareolus* (beech and holm-oak forests), *Mus spretus* (holm-oak), *Microtus agrestis (*heathlands) and *Glis glis* (beech) in the Montseny (I. Torre, personal communication).

Study species

Pseudotsuga menziesii var. *menziesii* (Mirb.) Franco (Pinaceae) (Douglas fir, hereafter) is a conifer of Northwestern American origin and an invasive species in many parts of the world where it has propagated from plantations (Richardson and Rejmánek 2004). The first published records of Douglas fir introductions in Europe were in the Czech Republic (1842), Germany (1900), Denmark and the U.K (1940) (Carrillo-Gavilán and Vilà 2010). In Montseny Natural Park, it was introduced during the 1950s and throughout the following decades, when marginal croplands were transformed to tree plantations of mainly fast growing alien conifers (Boada 2000). Douglas fir was one of the most planted species in Montseny with 230 scattered plantations (Boada and Broncano 2003) with a total area of 250 ha. At present, Douglas fir is considered a naturalized species (sensu Pyšek et al. 2004; Hulme 2011) in adjacent heathlands but not in beech or holm-oak forests in Montseny, which are also adjoined to plantations (Broncano et al. 2005). According to Broncano et al. (2005), an incipient expansion of Douglas fir is observed in one of the 230 plantations, which approximately covers an area of 22 ha. Therefore, observational surveys suggest that invasibility might be low in these forest types.

Abies alba P. Mill (Silver fir, hereafter) is a native conifer in Montseny where it represents the southern-most European distribution site for this species. In Montseny, the presence of *Abies alba* is a relict since the last glaciations. According to historical records this species was more abundant in the past, but intensive exploitation up to the beginning of the

twentieth century reduced and fragmented its distribution (Llobet 1990). In the present there are only three relict natural populations of Silver fir occupying a total of 28.5 ha surrounded by beech forests and heathlands (Boada and Broncano 2003), where recruitment of seedlings is observed in tree fall gaps and areas with bare soil (Carrillo-Gavilán, personal observation). Although other native Pinaceae species exist, either in natural woodlands or in plantations, such as *Pinus pinaster*, *P. nigra spp salzmanii*, *P. pinea*, *P. sylvestris* and *P. halepensis* (Boada and Broncano 2003), we chose to compare *A. alba* with Douglas fir because both species are grouped in the subfamily Abietoideae. Furthermore, according to Wang et al. (2000) and Besendorfer et al. (2005), the genus *Abies* is more closely related to *Larix* and *Pseudotsuga* than to *Picea* and *Pinus*. For this reason, they have similar dispersal mechanisms, reproductive phenology and climatic requirements (López-González 2002). For instance, Douglas and Silver fir seeds are primarily dispersed by wind and gravity in autumn while in second stage, dispersal could be promoted by mice, chipmunks or squirrels (Hemstrom et al. 1987; Wolf 2003).

To conduct our study, we purchased seeds from the Intersemillas nursery, Spain (http://www.intersemillas.es) because field collection attempts in previous years provided few viable seeds. However, this was of little concern since our focus was to compare the potential for seedling establishment between the two species under a range of different ecological conditions rather than documenting actual local rates of establishment.

For each species, 20 seeds were randomly chosen to measure fresh seed mass. Coat strength was also estimated following Rogerdson's (1998) protocol with a Chatillon Universal Force Tester (Amtek/Chatillon, Largo, Florida, USA).

Seed removal

To test differences in post-dispersal seed removal (seed removal, hereafter) in Autumn 2008, we delimited a 100 × 100 m plot at each site where we placed five 50 m long transects. In each transect, we placed 20 seeds of each species randomly chosen from a pool of seeds. Each seed was glued to a piece of nylon fishing line, tied to a wire stake (Schupp 1988) and placed on the ground surface keeping a distance of

approximately 3 m between each other. A total of 1,200 seeds (50 seeds × 2 species × 3 habitats × 4 sites) were surveyed for seed removal after 2, 6, 13, 20 and 27 days. Since conifer seeds are more successfully dispersed through their primary dispersal—wind and gravity—(Hemstrom et al. 1987; Wolf 2003), and less so through secondary dispersal (Ordóñez and Retana 2004), we considered either missing seeds or the presence of seed coat remnants as evidence of seed removal. We finished the experiment when after two consecutive visits the seed removal curves did not vary. After that day all remaining seeds were removed from the field.

We conducted two analyses. First, we tested for differences in percentage of removed seeds at the end of the experiment among habitats and between species using a Generalized Mixed Lineal analysis on SAS macro GLIMMIX (Littell et al. 2006) applying a binomial error and a *logit* link function. Habitat (n = 3), species (n = 2) and habitat × species inter-action were considered as fixed effects. Site and site × habitat interaction were considered as random factors. Second, as in many other studies (e.g. Aerts et al. 2006), seed removal time was analyzed using a time to event approach (Altman and Bland 1998). In our study the event is seed removal, which is linked to escape from predation and therefore, this data is conventionally called seed survival time (Aerts et al. 2006). Differences in mean seed survival time among habitats and between species were compared with the Gehan-Wilcoxon test (Pyke and Thompson 1986). The software SPSS 13.0 was used for survival analysis (SPSS Inc., Chicago, Illinois, USA).

Seed germination

In November 2008 we buried 10 metallic bags of 10 × 10 cm and 0.2 cm fine mesh per species, at a 2 cm depth in each site. Each bag contained 10 seeds per species. Bags rested flat, so that all seeds were in direct contact with the soil. In total 2,400 seeds were buried (10 seeds × 10 bags × 2 species × 3 habi-tats × 4 sites). In July 2009, 240 days after sowing, we retrieved the bags, and seeds were checked in the laboratory. They were considered to have germinated when the radicle and/or the cotyledon had emerged from the seed coat.

Differences in the percentage of germinated seeds in each bag among habitats and between species were

analyzed using SAS macro GLIMMIX applying a binomial error and *logit* link function. Habitat (n = 3) and species (n = 2) were considered as fixed factors while site (n = 4) and site × habitat interaction were considered as random factors.

Seedling survival and growth

In February 2009, we transplanted 1 year old seed-lings grown at a nursery (Centre de Jardineria Sils, http://www.jardineriasils.com, Girona, Spain) to each site, and thirty seedlings per species were randomly planted 3 m apart from each other along transects. In total, 720 seedlings were planted (30 seedlings × 2 species × 3 habitats × 4 sites) in this way. Seedlings were examined 1 month after being planted and those that had died from transplant shock were excluded from the experiment. Seedling survival was recorded every month until June 2010. Plant height was mea-sured before summer drought (July 2009 and June 2010, i.e. 5 and 16 months after transplanting, respectively) and after the first autumn rains (October 2009, i.e. 8 months after transplanting).

Seedling survival time was calculated through Kaplan–Meier estimations and differences in mean survival time among habitats and between species were compared with the Gehan-Wilcoxon test (Pyke and Thompson 1986).

Differences in seedling relative growth rate (i.e. relative increase in height of surviving seedlings between two consecutive monitoring times) were also analyzed with the macro GLIMMIX with the same fixed and random factors as mentioned in the seed germination analysis above, but applying a normal error and *identity* link function instead. Due to high seedling mortality in the holm-oak stands at the beginning of the experiment (see results), we per-formed comparisons of seedling growth between beech forests and heathlands at 5 months after trans-plantation, and only between species within beech forests at 10 months and at the end of the experiment.

Probability of transition from seed to seedling

In order to link the different stages of the early life-cycle, we estimated the probability of a seed becoming an established seedling, for each habitat type, in both conifer species (i.e. probability of recruitment). The model assumed that the probability of a seed achieving

recruitment can be estimated as the product of the previous elemental transition probabilities (Herrera et al. 1994; Vilà and D'Antonio 1998). We assumed that this model is independent of propagule pressure (i.e. seed production); the sequential recruitment stages considered were seed survival, seed germination and seedling survival.

Results

Habitat and conifer species characterization

Diameter at breast height of trees was significantly bigger in beech than in holm-oak forests (16.7 ± 0.8 and 9.4 ± 0.36 cm, respectively; t test: $t = 9.3$, $df = 627$, $P < 0.0001$). Heathlands were dominated by shrubby shaped *Juniperus communis*, whereas beech and holm-oak forests had a low understory cover. Light availability (PAR, $\mu mol \; s^{-1} \; m^{-2}$) at soil surface was significantly different among habitats (Kruskal–Wallis test; $\chi_2^2 = 118.7$, $P < 0.0001$), being much higher in heathlands (928 ± 28) compared to holm-oak (51 ± 11) and beech forests (53.8 ± 13).

On the other hand, the two conifer species differ in seed mass (t test: $t = 12.04$, $df = 38$, $P < 0.0001$) and seed coat thickness (t test: $t = 12.18$, $df = 38$, $P < 0.0001$). Seed mass is larger in Silver fir (0.03 ± 0.001 g) than in Douglas fir (0.01 ± 0.0006 g). Seed coat strength is also greater in Silver fir (16.7 ± 0.97 g) than in Douglas fir (4.1 ± 0.33 g).

Seed removal

Overall, seed removal was not very intense in all three habitats. At the end of the experiment, of the 1,200 seeds deployed per species, only 20.5% were removed. There were significant differences between species ($F_{1,9} = 6.56$, $P = 0.03$) but not among habitats ($F_{1, 6} = 0.84$, $P = 0.47$). There was a significant habitat × species interaction ($F_{2,9} = 4.15$, $P = 0.05$) indicating that Douglas fir seeds were removed more frequently than Silver fir seeds in holm-oak and heathlands, whereas in beech forests this difference was not significant (Fig. 1a).

There were differences in seed survival time among habitats ($\chi^2 = 16.48$, $df = 2$, $P = 0.0002$) and between species ($\chi^2 = 9.19$, $P = 0.002$), being significantly longer in beech forests, followed by
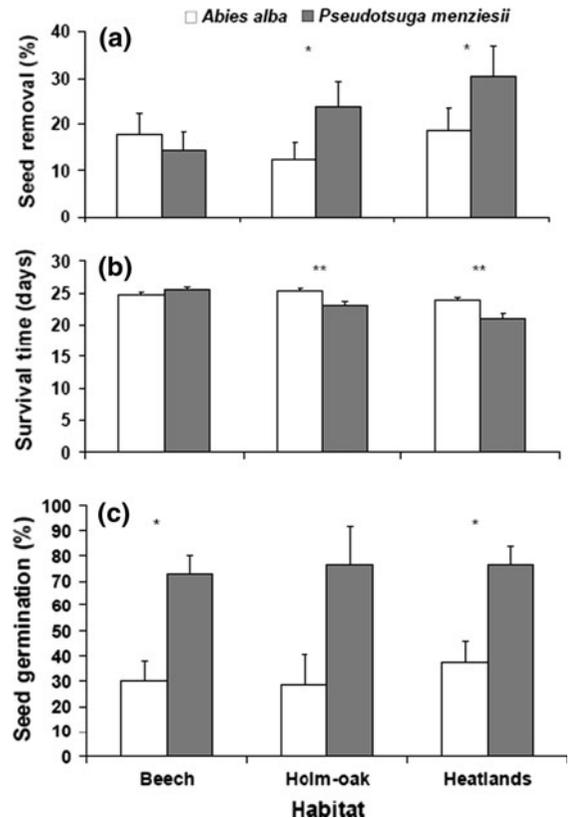

Fig. 1 (**a**) Post-dispersal seed removal (LS means + SEM), (**b**) seed survival time (mean + SE) and (**c**) seed germination (LS means + SEM) for *Abies alba* and *Pseudotsuga menziesii* in three habitat types. *Asterisks* indicate significant differences between species (* $P < 0.05$ or ** $P < 0.005$) within habitats

holm-oak forests and heathlands. Also, seed survival time of Silver fir was longer than Douglas fir (Fig. 1b). Referring to differences within habitats, seed survival time was significantly shorter in Douglas fir than in Silver fir in heathlands ($\chi^2 = 8.17$, $P = 0.004$) and in holm-oak forests ($\chi^2 = 9.38$, $P = 0.002$) but not in beech forests ($\chi^2 = 1.07$, $P = 0.3$) (Figs. 1b, 2).

Seed germination

There were significant differences in germination rates between species ($F_{1, 8} = 19.05$, $P = 0.002$), yet none were found among habitats ($F_{2, 6} = 0.22$, $P = 0.80$). Also, habitat × species interaction was not significant ($F_{2, 8} = 0.07$, $P = 0.93$). In all habitats, the percentage of seed germination was significantly higher in Douglas fir than in Silver fir (Fig. 1c).
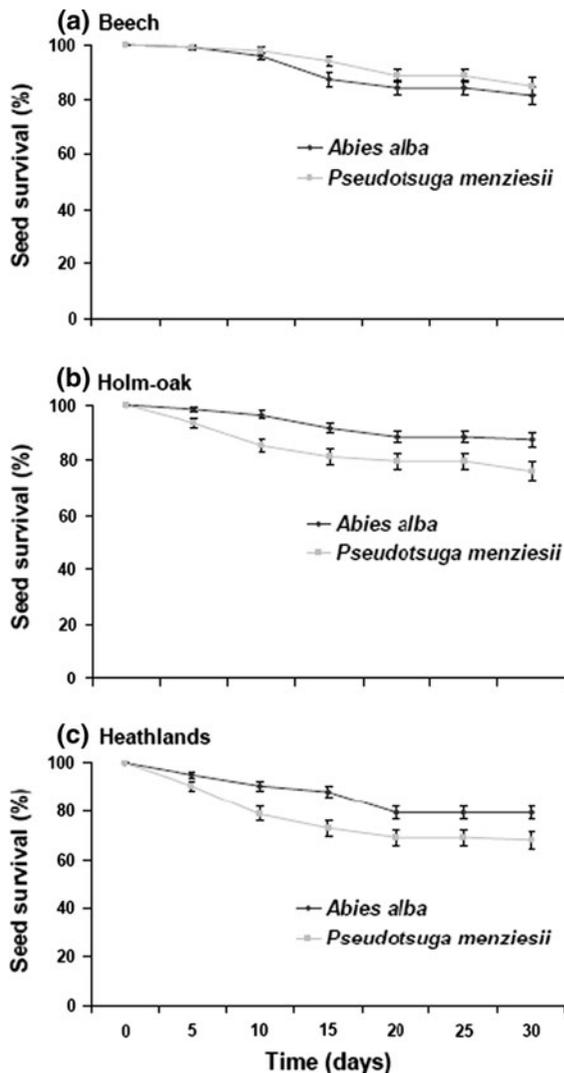
Fig. 2 Seed survival curves (mean ± SE) of *Abies alba* and *Pseudotsuga menziesii* in (**a**) beech forests, (**b**) holm-oak forests and, (**c**) heathlands

Seedling survival and growth

Seedling survival was very low in holm-oak forests due to soil disturbance by native fauna. In this habitat, wild boars pull up more than 50% of seedlings 3 months after transplantation, and by the end of the experiment all seedlings had died.

In heathlands and beech forests drought stress seemed to be the main barrier against seedling survival. In heathlands, only 4% of seedlings survived after the summer, while, in beech forests, seedling survival were less than 40% (Fig. 3).
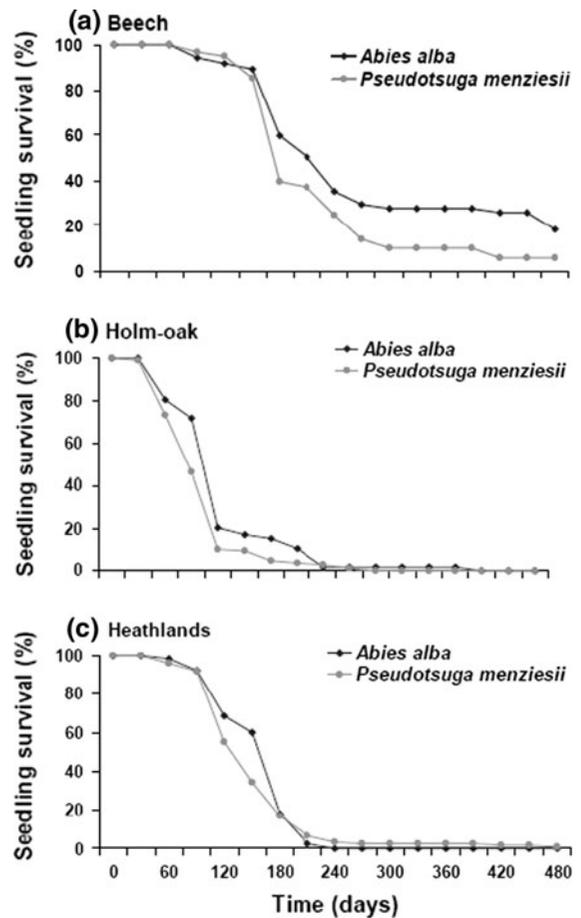

Fig. 3 Seedling survival curves of *Abies alba* and *Pseudotsuga menziesii* in (**a**) beech forests, (**b**) holm-oak forests and, (**c**) heathlands

Overall, at the end of the experiment, seedling survival time was significantly different among habitats ($\chi^2 = 319.8$, $df = 2$, $P < 0.0001$). Survival time was longer in beech forests and shorter in holm-oak forests (Fig. 4). There were differences between species ($\chi^2 = 25.4$, $P < 0.0001$) with Silver fir seedlings having longer survival time than Douglas fir. Likewise, these differences between species were also observed within habitats (beech: $\chi^2 = 8.77$, $P = 0.003$; holm-oak: $\chi^2 = 11.6$, $P = 0.0006$; and heathlands: $\chi^2 = 6.05$, $P = 0.013$) (Fig. 4).

Due to high seedling mortality, seedling relative growth rate could not be analyzed in holm-oak forests. Overall, 5 months after transplantation, relative growth rate was very low in both species (Douglas fir: 0.009 ± 0.01; and Silver fir: 0.022 ± 0.01 cm). There were no significant differences between species
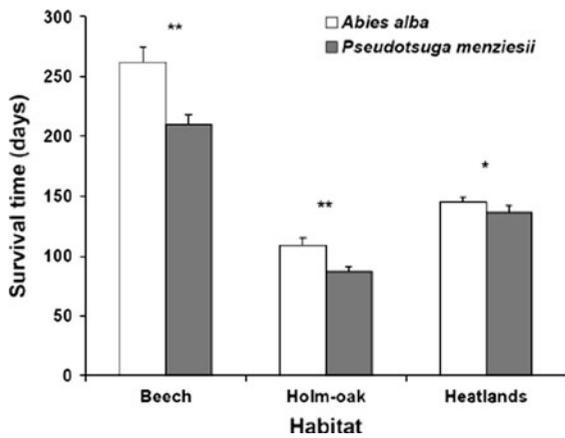
Fig. 4 Seedling survival time (mean + SE) of *Abies alba* and *Pseudotsuga menziesii* in three habitat types. *Asterisks* indicate significant differences between species (*$P < 0.05$, **$P < 0.005$) within habitats

($F_{1, 468} = 0.75$, $P = 0.38$) or between beech forests and heathlands ($F_{1, 6} = 0.4$, $P = 0.55$). In beech forests, relative growth rate was not significantly different between species, both 8 months after transplantation ($F_{1, 234} = 0.68$, $P = 0.41$) and at the end of the experiment ($F_{1, 237} = 2.36$, $P = 0.12$).

Transition from seed to seedling

Overall, the probability of one seed becoming an established seedling was very low for both conifer species (Fig. 5). In beech forests, approximately 4% of Douglas fir seeds and 5% of Silver fir seeds of initial seed sets become established seedlings (Fig. 5a). In heathlands, Douglas fir showed a higher probability of survival than Silver fir (0.4 and 0%, respectively) due to a higher germination rate, while in holm-oak forests, survival was null for both species.

Discussion

The probability of invasion success of Douglas fir decreased along the sequential stages of establishment in all habitats, showing the best performance in beech forests. The higher germination capacity of Douglas fir seemed to predict a better establishment success compared to Silver fir. However, pressures by native fauna and drought stress are potential mechanisms behind seedling mortality limiting their establishment of both conifer species.
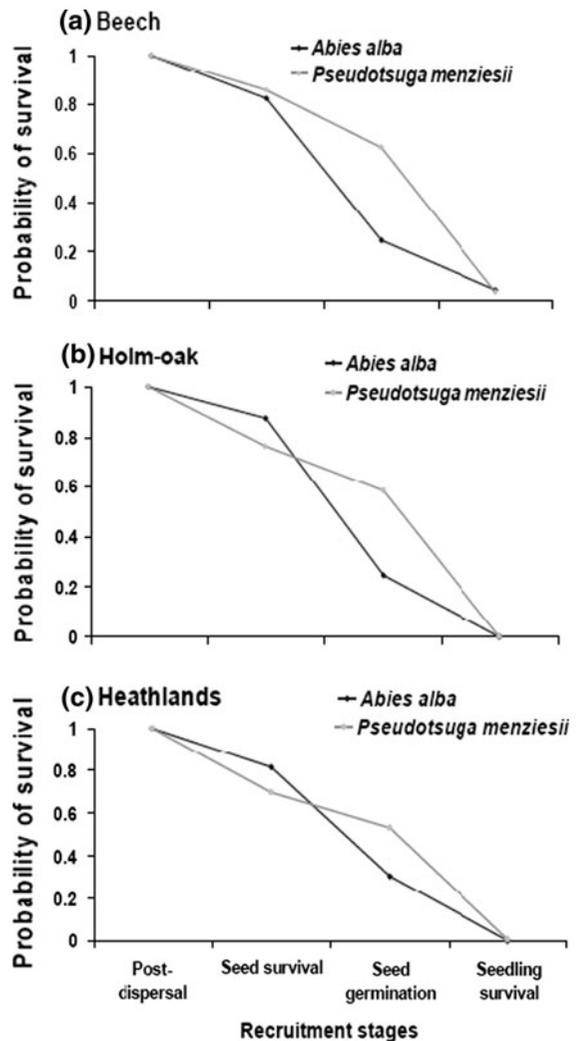

Fig. 5 Probability of survival along each establishment stage of *Abies alba* and *Pseudotsuga menziesii* in (**a**) beech forests, (**b**) holm-oak forests and, (**c**) heathlands

In Douglas fir, seed removal was not very intense in any habitat compared to its native range (Huggard and Arsenault 2009) or with other conifer species (Borchert et al. 2003; Peters et al. 2004; Carrillo-Gavilán et al. 2010). Seed removal was similar among habitats despite of the fact that the three habitat types analyzed were located at different altitudes. These results do not match with previous studies, which have observed that small mammal abundance decreases with altitudinal gradients (Torre and Arrizabalaga 2009). The low seed removal rates might be due to seed satiation (Stowe et al. 2000) as the experiment coincided with seed dispersal of many native plant

species. Moreover, seed removers might have a higher preference either towards holm-oak acorns (Gómez 2004; Espelta et al. 2009) or beech nuts, which are larger than fir seeds.

Douglas fir germination rates were high and did not differ between habitats despite large differences in vegetation structure and light availability. This is in accordance with other field studies where Douglas fir seedling emergence was very homogeneous under different microsites (Dunne and Parker 1999). In spite of this, our seed germination rates should be considered with caution. Since they come from a nursery, our seed sample might be causing an overestimation of this parameter attributable to a higher quality of seeds. Nonetheless, seed germination was higher in Douglas than in Silver fir. Silver fir's sensitivity to other environmental stresses such as drought (Gradečki and Poštenjak 2001), might be the cause of its low germination rates. In this context, a recent review by Pyšek and Richardson (2007) reveals that alien species are generally reported to germinate earlier, better and in a wider range of conditions than native species.

Since many seedlings disappeared in holm-oak forests due to soil disturbance by wild boars, native fauna might be a potential mechanism limiting the establishment of seedlings in this forest type. In contrast, in beech forests and in heathlands, seedling mortality due to summer drought stress (Alpert et al. 2000) was a prominent ecological filter for both native and alien plant species as has been reported in other Mediterranean regions (Dunne and Parker 1999; Rey and Alcántara 2000; Domènech and Vilà 2006).

The higher seedling survival in beech forests compared to other habitats might suggest a better establishment success of Douglas fir in this habitat, and therefore a higher invasibility in comparison to the other habitat types. However, Douglas fir is considered a pioneer species that prospers in partial shade, but once established it requires strong light availability (Hermann and Lavender 1999). As with most alien conifers, non-disturbed forests are resistant communities to invasion (Richardson and Bond 1991; Sarasola et al. 2006). Simberloff et al. (2002) observed that Douglas fir did not establish itself into closed forest plantations. Therefore, we would expect invasibility to decrease in beech forests in subsequent stages (Caccia and Ballaré 1998), except in natural gaps (Spies and Franklin 1989) or if forests are intensively managed. If disturbance occurs and resources fluctuate (Davis et al.

2000) this species might naturalize, even if currently there is no evidence of seedling establishment in this forest type.

Conifer traits such as a short juvenile period, a short interval between large seed crops, a small seed mass (Rejmánek and Richardson 1996; Richardson and Rejmánek 2004) and fast relative growth rate (Grotkopp et al. 2002) are correlated with high invasion success. Differences in seedling survival time between conifer species might be explained by the seed-seedling conflict (Schupp 1995), for which small seeded species have better dispersal capacity but low seedling survival due to lower investment in reserves than large seeded species. Small seeded species such as Douglas fir tend to produce large seed crops to counterbalance the low survival probability from seed to adulthood, which would be expect due to small seed mass (Moles and Westoby 2004).

According to Greene and Johnson (1999), seed production in trees is inversely proportional to seed mass. Large Douglas fir seed crops in the UK are produced every 4–6 years (Wilan 1985). Hermann and Lavender (1999) estimate that seed production is about 2.2 kg/ha, which varies widely among years; Gashwiler (1969) estimates annual mean seed dispersal to be around 3×10^5 seeds/ha in the northwest of the United States. While seed production of Silver fir seems to be lower than Douglas fir, it also varies highly among years. For example, seed production varied markedly in two consecutive years from 59.6 to 118.8 seeds/m^2 in the French Alps (Sagnard et al. 2007).

In conclusion, our results showed that the probability of establishment of both fir species decreased along the early life-cycle stages in all habitats. Soil disturbance by native fauna in holm-oak forests and drought stress in heathlands might be the mechanisms controlling seedling establishment. Douglas fir performed better in beech forests where seed survival, seed germination and seedling survival were higher than in the other habitats. Only the higher germination capacity of Douglas fir seemed to predict a better establishment success compared to Silver fir. Currently, Douglas fir is only naturalized in heathlands (Broncano et al. 2005). This indicates that there is a mismatch between the degree of invasion observed in Montseny by Douglas fir and our invasibility assessment. This mismatch might predict that the Douglas fir establishment observed in heathlands is a consequence

of a higher seed rain from adjacent plantations which, coupled with its high germination capacity, might predict its invasion success. This is in accordance with the importance that propagule pressure has on invasion success (Lockwood et al. 2005; Colautti et al. 2006, but see Nuñez et al. 2011). Many conifer species that escape from plantations and become invasive are often those that have been cultivated the most widely and for the longest time (Křivánek et al. 2006). However, a recent study reveals that propagule pressure in 80-year old woody species' plantations is not the key to predict invasion (Nuñez et al. 2011). In this sense, climate and biotic resistance seem to be two of the most important components to predict the invasion success of conifer species in the introduced range (Haugo 2010; Essl et al. 2011; Nuñez and Medley 2011). Therefore, we highlight the need for future research to focus on seed production and on other components of biotic resistance, that were not explored in this study (Nuñez and Medley 2011), to determine the invasiveness of Douglas fir and the invasiblity of different habitats to this conifer.

References

Aerts R, Maes W, November E, Negussie A, Hermy M, Muys B (2006) Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp cuspidata seeds. For Ecol Manag 230:23–31

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect Plant Ecol Evol Syst 3:52–66

Altman DG, Bland JM (1998) Statistics notes—time to event (survival) data. Br Med J 317:468–469

Besendorfer V, Krajačić-Sokol I, Jelenić S, Puizina J, Linarec J, Sviben T (2005) Two classes of 5S rDNA unit arrays of the silver fir, *Abies alba* Mill.: structure, localization and evolution. Theor Appl Genet 110:730–741

Boada M (2000) El Montseny. Fifty years of landscape evolution. Publications de l'Abadia de Montserrat, Barcelona

Boada M, Broncano M (2003) Estudi sobre la distribució d'espècies forestals al.lòctones al Parc Natural del Montseny. Evidències de la naturalització de l'avet de Douglas (P*seudotsuga menziesii)* al Parc Natural del Montseny. ICTA-

Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Barcelona

Bolòs O, Vigo J (1990) Flora Dels Països Catalans. Barcino Press, Barcelona

Borchert M, Johnson M, Schreiner D, Vander Wall S (2003) Early post-fire seed dispersal, seedling establishment and seedling mortality of *Pinus coulteri* (D. Don) in central coastal California, USA. Plant Ecol 168:207–220

Broncano M, Vilà M, Boada M (2005) Evidence of *Pseudotsuga menziesii* naturalization in montane Mediterranean forests. For Ecol Manag 211:257–263

Caccia FD, Ballaré CL (1998) Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (*Pseudotsuga menziesii*) in southwestern Argentina. Can J For Res 28:683–692

Carrillo-Gavilán MA, Vilà M (2010) Little evidence of invasion by alien conifers in Europe. Divers Distrib 16:203–213

Carrillo-Gavilán MA, Hadrien L, Vilà M (2010) Comparing seed removal of 16 pine species differing in invasiveness. Biol Invasions 12:2233–2242

Colautti R, Grigorovich I, MacIsaac H (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Dietz H, Steinlein T, Ullmann I (1999) Establishment of the invasive perennial herb *Bunias orientalis* L.: an experimental approach. Acta Oecol 20:621–632. doi:10.1016/S1146-609X(99)00104-6

Domènech R, Vilà M (2006) The role of successional stage, vegetation type and soil disturbance on *Cortaderia selloana* invasion. J Veg Sci 17:591–598

Dunne JA, Parker VT (1999) Species-mediated soil moisture availability and patchy establishment of *Pseudotsuga menziesii* in chaparral. Oecologia 119:36–45

Espelta JM, Bonal R, Sánchez-Humanes B (2009) Pre-dispersal acorn predation in mixed oak forests: interspecific differences are driven by the interplay among seed phenology, seed size and predator size. J Ecol 97:1416–1423

Essl F, Mang T, Dullinger S, Moser D, Hulme PE (2011) Macroecological drivers of alien conifer naturalizations Worldwide. Ecography 34:1–9

Ferreras AE, Galetto L (2010) From seed production to seedling establishment: important steps in an invasive process. Acta Oecol 36:211–218

Gashwiler JS (1969) Seed fall of three conifers in west-central Oregon. For Sci 15:290–295

Gómez JM (2004) Bigger is not always better: conflicting selective pressures on seed size in *Quercus* ilex. Evolution 58:71–80

Gradečki M, Poštenjak K (2001) Relation between laboratory and nursery germination of silver fir seed (*Abies alba* Mill.). In: Matić S, Krpan APB, Gračan J (eds) Znanost u potrajnom gospodarenju hrvatskim šumama: znastvena knjiga. Šumarski fakultet Sveučilišta u Zagrebu, Šumarski institute, Zagreb, pp 191–200

Greene DF, Johnson EA (1999) Estimating the mean annual seed production of trees. Ecology 75:642–647

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and

life-history strategies of 29 pine (*Pinus*) species. Am Nat 159:396–419

Haugo RD (2010) Causes and consequences of conifer invasion into Pacific Northwest grasslands. PhD, Thesis. University of Washington

Hemstrom MA, Logan SE, Pavlat W (1987) Plant association and management guide: Willamette National Forest. R6-Ecol 257-B-86. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, p 312

Hermann RK, Lavender DP (1999) *Pseudotsuga menziesii* (Mirb.) Franco. In: Burns R, Honkala BH (eds) Silvics of North America, vol 1. Conifers. USDA Forest Service. Washington, D. C., pp 540–557

Herrera CM, Jordano P, López-Soria L, Amat JA (1994) Recruitment of a mass-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecol Monogr 6:315–344

Huggard DJ, Arsenault A (2009) Conifer seed predation in harvested and burned dry Douglas fir forests in southern British Columbia. Can J For Res 39:1548–1556

Hulme PE (2011) Addressing the threat to biodiversity from botanic gardens. Trends Ecol Evol 26:168–174

Kay M (1994) Biological control for invasive tree species. N Z For 39:35–37

Křivánek M, Pyšek P, Jarošik V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv Biol 20:1487–1498

Lambrinos JG (2002) The variable invasive success of *Cortaderia* species. In a complex landscape. Ecology 83:518–529

Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberber OD (2006) SAS for mixed models, 2nd edn. SAS Press Series, Cary

LLobet S (1990) El medi i la vida al Montseny. Museu de Granollers

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228

Lombardero MJ, Vázquez-Mejuto P, Ayres MP (2008) Role of plant enemies in the forestry of indigenous vs. nonindigenous pines. Ecol Appl 18:1171–1181

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

López-González G (2002) Guía de los árboles y arbustos de la Península Ibérica y Baleares. Ediciones Mundi-Prensa, Madrid

McCay TS, McCay DH (2009) Processes regulating the invasion of European buckthorn (*Rhamnus cathartica*) in three habitats of the northeastern United States. Biol Invasions 11:1835–1844

Moles AT, Westoby M (2004) Seedling survival and seed size: as synthesis of the literature. J Ecol 92:372–383

Nuñez MA, Medley KA (2011) Pine invasions: climate predicts invasion success; something else predicts failure. Divers Distrib. doi:10.1111/j.1472-4642.2011.00772.x

Nuñez MA, Simberloff D, Relva MA (2008) Seed predations as a barrier to alien conifer invasions. Biol Invasions 8:1389–1398

Nuñez MA, Horton TR, Simberloff D (2009) Lack of belowground mutualisms hinders Pinaceae invasions. Ecology 90:2352–2359

Nuñez MA, Moretti A, Simberloff D (2011) Propagule pressure hypothesis not supported by an 80-year experiment on woody species invasion. Oikos 120:1311–1316

Ordóñez JL, Retana J (2004) Early reduction of post-fire recruitment of *Pinus nigra* by post-dispersal seed predation in different time-since-fire habitats. Ecography 27:449–458

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Glob Change Biol 9:131–140

Peters SH, Macdonald SE, Boutin S, Moses RA (2004) Post-dispersal seed predation of white spruce in cutblocks in the boreal mixedwoods: a short-term experimental study. Can J For Res 34:907–915

Pyke DA, Thompson JN (1986) Statistical analysis of survival and removal rate experiments. Ecology 67:240–245

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwing W (ed) Biological invasions, ecological studies 193. Springer, Berlin, pp 97–126

Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661

Relva MA, Nuñez MA, Simberloff D (2009) Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biol Inv. doi:10.1007/s10530-009-9623-0

Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J Ecol 88:622–633

Richardson DM, Bond WJ (1991) Determinants of plant distribution: evidence from pine invasions. Am Nat 137:639–668

Richardson DM, Higgins SI (1998) Pines as invaders in the Southern Hemisphere. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp 450–470

Richardson DM, Rejmánek M (2004) Conifers as invasive aliens: a global survey and predictive framework. Divers Distrib 10:321–331

Rodgerson L (1998) Mechanical defence in seeds adapted for ant dispersal. Ecology 79:1669–1677

Sagnard F, Pichot C, Dreyfus P, Jordano P, Fady B (2007) Modelling seed dispersal to predict seedling recruitment: recolonization dynamics in a plantation forest. Ecol Modell 203:464–474

Sarasola MM, Rusch VE, Schlichter TM, Ghersa CM (2006) Invasión de coníferas forestales en áreas de estepa y bosques de ciprés de la cordillera en la Región Andino Patagónica. Aust Ecol 16:143–156

Schupp EW (1988) Seed and seedling predation in the forest understory and in treefall gaps. Oikos 51:71–78

Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am J Bot 82:399–409

Shafroth PB, Auble GT, Scott ML (1995) Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *Monilifera*) and the exotic

Russian-olive (*Elaeagnus angustigolia* L.). Conserv Biol 9:1169–1175

Simberloff D, Relva MA, Nuñez M (2002) Gringos en el bosque: introduced tree invasion in a native *Nothofagus/Austrocedrus* forest. Biol Invasions 4:35–53

Simberloff D, Nuñez MA, Ledgard NJ, Pauchard A, Richadson DM, Sarasola M, wan Wilgen BW, Zalba SM, Zenni RD, Bustamante R, Peña E, Ziller SR (2010) Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. Aust Ecol 35:489–504

Sol D, Vilà M, Kühn I (2008) The comparative analysis of historical alien introductions. Biol Invasions 10:1119–1129

Spies SE, Franklin J (1989) Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology 70:543–545

Stowe KA, Marquis RJ, Hochwender CG, Simms EL (2000) The evolutionary ecology of tolerance to consumer damage. Annu Rev Ecol Evol Syst 31:565–595

Torre I, Arrizabalaga A (2009) Species richness and abundance of small mammals along an elevational gradient of a Mediterranean mountain. Vie Milieu 59:203–212

Traveset A, Gulias J, Riera N, Mus M (2003) Transition probabilities from pollination to establishment in a rare dioecious shrub species (*Rhamnus ludovici-salvatoris*) in two habitats. J Ecol 91:427–437

Vilà M, D'Antonio CM (1998) Fitness of invasive *Carpobrotus* (Aizoaceae) hybrids in coastal California. Ecoscience 5:191–199

Vilà M, Lloret F (2000) Seed dynamics of the mast seeding tussock grass *Ampelosdesmos mauritanica* in Mediterranean shrublands. J Ecol 88:479–491

Vilà M, Bartomeus I, Gimeno I, Traveset A, Moragues E (2006) Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. Ann Bot 97:1055–1062

Wang X-Q, Tank DC, Sang T (2000) Phylogeny and divergence times in Pinaceae: evidence from three genomes. Mol Biol Evol 17:773–781

Wilan RL (1985) A guide to forest seed handling with special reference to the tropics. FAO Forestry Paper, no. 20/2. FAO, Rome (Italy)

Wolf H (2003) EUFORGEN technical guidelines for genetic conservation and use for silver fir (*Abies alba*). International Plant Genetic Resources Institute, Rome