Coexistence of *Abies alba (Mill.*) - *Fagus sylvatica (L.*) and climate change impact in the Iberian Peninsula: a climatic-niche perspective approach.

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ABSTRACT

Abies alba Mill. (European silver fir) and *Fagus sylvatica L*. (beech) are Eurosiberian species dispersed over the Iberian Peninsula. Climate change predictions indicate a rise in temperature and a decrease in precipitation in this region, threatening the future existence of these species. In the present study we analyzed the future topo-climatic suitability of *Abies alba* and *Fagus sylvatica* and the mixed forests of these two species, using the General Linear Models technique and data from the third National Forest Inventory (Ministerio de Agricultura PyA 2007). We considered two modeling approaches based on niche theory: modeling community (*Abieti-Fagetum*) and overlapping individual species models. General trends showed an overall decrease in both species' topo-climatic suitability and indicated that the Pyrenees will play a crucial role as a climatic refuge. The modeling approaches markedly differed, however, in their current and future spatial agreement. Despite good accuracy results, community modeling through co-occurrence do not encompass the environmental space of individual species prejudicing future assessments in new environmental situations, suggesting a need for future studies in community modeling.

Keywords: species distribution, co-occurrence, *Abies alba*, *Fagus sylvatica*, climate change.
Abreviations: Fundamental niche (FN), realized niche (RN), pseudo-fundamental niche (PFN), community model (CM), individual species model (IM), species distribution models (SDM).

INTRODUCTION

The effects of global climate change on vegetation and forests might induce deep transformations in natural resources and landscape structure, posing a challenge to biodiversity and habitats (Thomas et al., 2004; Botkin et al., 2007; Nogués-Bravo et al., 2007). The implications of climate warming for vegetation have therefore been widely studied on different scales, ranging from the physiological responses of plants (Peñuelas et al., 2002; Walther et al., 2002) to regional plant distribution (Thuiller et al., 2005), using various modeling approaches (Guisan and Zimmermann, 2000, Elith et al., 2006).

Species distribution models (SDM) refer to the whole set of statistical correlative approaches that extrapolate the environmental data associated with a species' presence and/or absence and project its relationship with these data onto a different site and/or time period. As they are easy to implement, these models are now widely used to address various issues in ecological research, while also providing guidance for applied research (Franklin, 2009).

The theoretical basis for most species distribution models is the niche theory, which establishes the existence of a whole set of conditions and resources in which a species can live (*sensu* Hutchinson, 1957; see Holt, 2009). The niche theory makes it possible to use current patterns of distribution to characterize the realized niche (RN), whereas the fundamental niche (FN) concept indicates the whole range of conditions in which a species may survive.

There has been great debate on the scientific scene over what these SDMs are really modeling (Hirzel and Lay, 2008; Kearney, 2006) and many studies point out that the proximity of a modeled niche to either a realized or a fundamental is dependent on the techniques used, the selection of absences and whether the model's construction is built on presence-absence data or presence data alone (Jiménez-Valverde et al., 2008). Furthermore, it has often been argued that the processes involved (e.g.: growth, reproduction, competition and migration) are not evaluated directly, thus hampering both the interpretation and application of these models (see Guisan and Thuiller, 2005; Thuiller et al., 2008 for an extended review).

These models have usually treated species distribution on an individual basis, although vegetation units have also been considered (Miller and Franklin, 2002). Community assemblies may be modeled via a number of different strategies: (1) assemble first, predict species later; (2) predict species first, assemble later; or (3) assemble and predict at the same time (Ferrier and Guisan, 2006). Modeling communities (several species simultaneously) may provide a faster way to model diversity and examine different patterns of co-occurrence. Although community-based models may render accurate results, species may respond differently to variations in climate (Williams and Jackson, 2007) and are subject to differences in plasticity (Valladares et al., 2007), prejudicing these models' ability to predict various situations in space and time (Guisan and Zimmermann, 2000) and therefore be extrapolated (Elith and Leathwick, 2009). Previous studies investigated the effect of individual models versus community models (Baselga and Araújo, 2009) using a community approach based on patterns of co-occurrence and

co-exclusions (Canonical Quadratic Ordination). Their results pointed out some shortcomings, due to the generality of the model and species interactions in such community models.

In fact, by applying SDMs to model community distribution, we would expect the projection of the current conditions in which a community appears (realized niche of the community; RNC) to result in smaller areas than the overlap of the projections of single species. If this is true, models of future communities may overestimate species assemblages if produced by Boolean intersection (overlap) from the performance of individual species. Such an overlap could be interpreted as the niche space lying between the realized niche of the community and the fundamental niche, corresponding to the pseudo-fundamental niche of a community (PseudoFNC; Figure 1). Although the fundamental niche of any species or community is difficult to estimate, the pseudo-fundamental niche represents combinations of the environmental space in which the species in a community currently occur, projecting a niche close to the fundamental niche. Therefore, the degree of disagreement between both niches (realized to pseudo-fundamental) may elucidate whether a community's current realized niche meets the whole set of current conditions met by species comprising the target community (RealizedNiche$_{sp1}$ $\cap$ RealizedNiche $_{sp2}$).

[INSERT FIGURE 1]

In the Iberian Peninsula, the distributions of silver fir (*Abies alba* Mill.*)* and European beech (*Fagus sylvatica* L.*)* and Abieti-Fagetum community are restricted to some areas of the Eurosiberian bioregion (Figure 2). Therefore, here both species are located on the southwest boundary of its European distribution, making them more vulnerable to changes in climate and management (Jump et al., 2006; Aitken et al., 2008). Although both species show similar distribution patterns within this region, the community *Abieti-Fagetum* is relatively scarce and the two indicator species often occur separately. Fir is mainly distributed at higher altitudes than beech, which requires greater humidity and shows a more continental distribution in the European context (European Flora Atlas: Lahti and Lampinen, 1999). Climate Change scenarios (IPCC WPG 2007) predict a rise in temperature and changing patterns of precipitation in the Iberian Peninsula, resulting in increased water deficit. The relatively high water requirements of these species therefore reduce the viability of the community of *Abies alba* and *Fagus sylvatica*. All these elements make the case of the *Abies alba-Fagus sylvatica* a good study-system for analyzing the performance of species-based distribution models when building community assembly models. Previous studies already presented community models results in Abieti-Fagetum community in Switzerland (Brzeziecki et al., 1993,Brzeziecki et al., 1995), but did not directly considered different modeling approaches.

[INSERT FIGURE 2]

In the present research we aim to assess the future distribution and the reliability of predictions about the community formed by the co-occurrence of *Abies alba* and *Fagus sylvatica* in the Iberian Peninsula, by considering and comparing both the individual-species approach (OIM, strategy 2) and the community-based approach (CM, strategy 1), under climate change scenarios A1FI an d A2 (IPCC, 2007).

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MATERIAL AND METHODS

We used a Generalized Linear Model to map the suitability of *Abies alba*, *Fagus sylvatica* and mixed forests of these species based on presence/absence plots from the third National Forest Inventory (Ministerio de Agricultura PyA, 2007). The National Forest Inventory uses a regular sampling of all 1x1 UTM grid intersections matching forest areas. A presence of the target-species was selected only when dominant (first or second more abundant species according to their Basal Area [BA]).

Data on absences may influence model accuracy (Chefaoui and Lobo, 2008, Lobo et al., 2010), so we built 250 different data sets and run models for each dataset to obtain robust results, i.e. results not dependent on absences. Prevalence was kept constant ($N_{absence}=N_{presence}$) in each dataset and we imposed a distance constraint on absence selection: plots within a buffer zone of 5 kilometers around presences were not considered. By imposing these criteria we restricted the selection of absences in suitable climatic conditions.

We followed two approaches to project community suitability: (1) overlapping individual-species modeling (OIM), and (2) community-based modeling (CM) of the co-occurrence of both species on the same forest inventory stand.

Selection of variables

Firstly, a correlation analysis was conducted between several climatic and topographic variables that explain, *a priori*, the distribution of *Abies alba* and *Fagus sylvatica* (Benayas et al., 2002: Thuiller et al., 2003): minimum, maximum and mean temperature and precipitation on a seasonal and yearly time scale, and water availability, computed as precipitation minus evapotranspiration (Thornwaite, 1948).

Climatic variables were derived from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al., 2000; available at: http://opengis.uab.es/WMS/acdc/index.htm). This cartography consists of 65 monthly maps of mean air temperature (minimum, mean and maximum), precipitation and solar radiation derived from 1000 to 2000 meteorological stations, depending on the variable. These climatic grids are built using multiple regression and interpolation techniques, such as inverse distance weighting and kriging, coupled with a residual error correction method implemented in a GIS environment. Data from meteorological stations have been combined with altitude, latitude, distance from coast, solar radiation and terrain curvature to obtain 180 m spatial resolution grids of every climatic variable. Cross validation results show a root mean square error (Root Mean Square Error, RMSE) of 6-20 mm, for annual precipitation, and 0.8-1.5 ºC for annual mean temperatures. Topographic variables such as slope, terrain curvature, solar radiation and continentality (cost-distance to coast) were derived from a 200 m spatial resolution Digital Elevation Model (DEM).

Highly correlated variables were removed for subsequent species distribution modeling. We preferred this procedure to the use of factors extracted from Principal Components Analysis, as when many

variables are used it is often difficult to interpret the extracted components in biological terms. Correlation analysis was performed using R 2.11.1 software (R Development core team, 2010) and correlations above 0.70 led to the elimination of one of the correlated variables. To decide which variables should be selected, we used the rule of the most comprehensive and integrative variable. For example, water balance is obviously highly correlated with precipitation and temperature but since it is also the most integrative variable, we would then remove precipitation and temperature from further analysis. The variables used in each model are shown in Table 1.

Generalized Linear Models for *Abies alba*, *Fagus sylvatica* and *A.alba-F.sylvatica* co-occurrence.

A stepwise GLM was performed using R software (R Development Core Team, 2010) based on an Akaike Information Criterion (AIC; Akaike, 1974). This procedure was run separately for *Abies alba*, *Fagus sylvatica* (OIM) and the community *Abies alba-Fagus sylvatica* (CM), with presence and absence considered on a scale of 1 km^2. In each approach 250 iterations (runs) of a GLM were performed, using different selections of absences. For each run, the GLM algorithm chose the best combination of variables that minimize the input information in the model (AIC), and the most repeated set of variables in the 250 models was chosen to run the final model. The final model consisted of a regression using averaged regression coefficients from the 250 GLM iterations, using the selected formula.

Model calibration was performed by using 80% of the plots from each dataset (250 in total), with 20% of the plots reserved to calculate the accuracy of the model using the area under the ROC curve parameter (Fielding and Bell, 1997). The final model accuracy for each approach was computed using the mean of the 250 runs.

Suitability models for each species and CM produced an output (suitability index), ranging from 0 to 1, which can be mapped. A threshold needs to be set in order to differentiate a suitable location from unsuitable ones (binary response). We calculated this threshold as a compromise between maximizing the correct predicted presences and minimizing unpredicted presences, thus optimizing model sensitivity and specificity (see examples in Pearce and Ferrier, 2000; Randin et al., 2009).

Future scenarios: Downscaling GCM

The IPCC socioeconomic analysis (IPCC, 2007) proposes several scenarios of CO2 emissions. Different scenarios and climate variability may achieve quite different results (Beaumont et al., 2007), so we used two climatic projections (A1FI, A2) derived from the coupled atmosphere-ocean general circulation model (AOGCM) HadCM3 simulation, developed at the Hadley Centre-UK (Gordon et al., 2000, Pope et al., 2000). Each scenario represents a storyline in green house gasses emissions, taking into account demographic and social frameworks. In our study we selected two scenarios from the A1 and A2 storylines family. The former forecasts a future of rapid economic growth and intensive fuel use (A1FI), whereas the latter describes growth, albeit limited to a regional level and free of any rapid technological development (IPCC, 2007). In the Iberian Peninsula these scenarios describe varying degrees of severity: A1FI predicts an increase of 4.5 °C in mean annual temperature and a drop of 111 mm in annual

precipitation, whereas A2 represents a milder change, with an increase of 3.2°C and an average decrease in annual precipitation of 95mm.

These General Circulation Models (GCM) were applied to obtain the mean annual temperature and precipitation for the period 2050-2080 on a grid with a 4000 m spatial resolution. We downscaled these values by adding the predicted mean increase or decrease in temperature and precipitation (2050-2080) to the Digital Climatic Atlas of the Iberian Peninsula, which offers a finer resolution for mountainous areas (Randin et al., 2009). The topographic variables remained constant for the two scenarios. The new values for the models' variables resulted in new suitability maps in the predicted scenarios, making it possible to determine future increases or decreases in suitability.

RESULTS

Individual-species models present positive evaluation results with AUC values of 0.98 for *Abies alba* and 0.96 for *Fagus sylvatica* (Table 1). The geographic pattern of topo-climatic area suitable for *Abies alba* is restricted to the northern mountain regions of the Iberian Peninsula, although some remnants of suitable area may also be found in the mountainous central areas of Spain (Figure 3 A). Curiously, large suitable areas can be found in the northeastern mountains, where the species is not currently present, although it has been reported to exist during the Quaternary (Peñalba, 1994; Benito Garzón et al., 2007).

[INSERT TABLE 1]

[INSERT FIGURE 3]

With respect to the present time, the models predict larger suitable area of *Fagus sylvatica* compared to *Abies alba* (Table 2). Even though the range of *Fagus sylvatica* is narrow, but larger than *Abies alba*, the variability of climatic situations within current presences provide suitable areas in other locations, such as the central mountain areas of Spain, the mountain regions in the east of the Iberian Peninsula and even the southern mountain region (Figure3 D).

Future scenarios predict a large decrease for both species. This decrease is stronger for *Fagus sylvatica* than for *Abies alba* but the suitable area for *Abies alba* remains smaller in both the climate change scenarios (see Figure 3 B, 3E-F and Table 2). Suitable area decrease is linked to the aridity of the scenario and, as expected, a larger loss of suitable area is predicted for both species under the A1FI scenario than under then A2 scenario. No net gain in suitable area is observed in any of the scenarios considered.

[TABLE 2]

The geographic pattern of suitable area loss is similar for both species: the western Iberian peninsula and forests at lower altitudes are much more affected while the Pyrenean range (North-East) remains stable, with the exception of the west side, where losses are forecasted to be large (Figure 3 B-E).

The Community Model (CM) also showed good accuracy results (Table 1) and correctly identified the 77.2% of the stands in which both species were present. A ROC curve cannot be calculated for the overlap of individual models (OIM) approach since it is a simple GIS overlap function, although it correctly classified the 88.2% of co-occurrences (Table 5).

As expected, the suitable area for mixed forests obtained by the OIM is larger than that obtained by the CM approach, regardless of the climate change scenario considered (Table 3). Both the CM and the OIM predict that the co-occurrence of these two species will undergo a large decrease in suitable area but the percentage of area reduction is higher in the OIM than in the CM (Table 3). Of the climate change scenarios, the CM is more sensitive than the OIM, predicting a larger reduction of suitable area in the A2 scenario. The CM suitable area represents 70% of the OIM area suitable for current conditions, and this figure drops to 50% and 40% in the A1FI and A2 scenarios, respectively (Table 3).

[TABLE 3]

Geographically, both approaches project the most suitable area for the community in the Pyrenees under present conditions (Figure 4). Despite this common tendency, there are differences between the two approaches as regards the spatial distribution of the suitable area: the OIM forecasts the occurrence of mixed forests in the Cantabrian mountain range system (northwest Iberian Peninsula), whereas the CM locates small patches of suitable area along the southern face of the Pyrenees (Figure 4).

In both the climate change scenarios considered, the Cantabrian mountains and inland mountain ranges are sites where the decrease in suitable area is predicted to be more severe, whereas it will remain fairly stable in the Pyrenees , especially in places at higher altitudes (Figure 4 , A1FI and A2).

[FIGURE 4]

The degree of spatial disagreement, calculated as the area predicted to be suitable by only one of the approaches, increases when the models are projected onto climate change scenarios (Table 4). As expected, the RNc (modeled by the CM) is geographically included in the PFNc (modeled by the OIM) for the current environmental conditions, i.e. the suitable area predicted only by the OIM is 30% compared to 0.6% in the CM (Table 4). This geographical inclusion of the modeled niche also occurs in the A2 scenario, with a 6% disagreement in the CM, although the spatial disagreement increases in both approaches for both climate change scenarios. In the case of the most severe scenario, A1FI, the geographical inclusion effect of the CM in the OIM disappears because spatial disagreement rises up to 50%.

[TABLE 4]

The spatial differences between the modeling approaches become more relevant when assessing the future of the current plots of mixed forests of *Abies alba* and *Fagus sylvatica*. The OIM predicts a loss of between 73% and 80% of the current stands depending on the scenario, whereas the CM increases this

loss to between 92% and nearly 99% of the current co-occurrences of the forest inventory for these species (Table 5). In many cases, the OIM predicts that losses of mixed forests are the result of a decline in *Fagus sylvatica*, while *Abies alba* would remain on these sites (Table 5). Remnants of future suitable plots are to be found on the northern slopes of Pyrenees and at higher altitudes (Table 6), which suggests an upwards shift in its distribution. Likewise, more threatened forest are those located at lower altitudes.

[TABLE 5]

[TABLE 6]

DISCUSSION

The present study highlights a decline in the climatic suitability of *Fagus sylvatica* and *Abies alba* and its present co-occurrence. This trend can be appreciated in both the future climatic scenarios and the two modeling approaches for co-occurrence assembly (individual overlapping and community). This pattern concurs with modeling studies on a European (Bakkenes et al., 2002; Thuiller et al., 2006) and at Iberian Peninsula scale (Benito Garzón et al., 2008). Furthermore, indications of this downward trend are already being detected in fir and beech forests in the region. For instance, Macias et al. (2006) documented a die-back of Pyrenean forests of *Abies alba* in recent decades, associated with the interaction of climate tendencies and management history. Likewise, Puddu et al. (2003) detected vulnerability of *Abies alba* to fungi in less suitable climatic conditions, while canopy defoliation of *Fagus sylvatica* forests on a regional scale was detected by remote sensing during a drought episode that affected Western Europe in 2003 (Lloret et al., 2008). Xeric conditions have also been reported as affecting the physiological performance of *Abies alba* (Peguero-Pina et al., 2007). These episodes, and overall water stress, are likely to increase with climate change (Meehl and Tebaldi, 2004; Schar and Jendritzky, 2004), reducing the regional climatic fitness of the species. In keeping with our predictions, an upward shift in the altitudinal distribution of *Fagus sylvatica* has been detected in the region (Peñuelas and Boada, 2003; Jump et al., 2006), similarly to the cases reported for other species and regions (Parmesan and Yohe, 2003; Beckage et al., 2008; Kelly and Goulden, 2008), including latitudinal changes (Jump et al., 2009).

Both the approaches to co-occurrence modeling (CM and OIM) indicate that the Pyrenees will be the most stable suitable area for the maintenance of these mixed forests. For this reason, it is important to consider the Pyrenees as a future potential refuge for these species and a reservoir for mixed silver fir-beech forests in the Iberian Peninsula. Interestingly, this mountain range has been a climate refuge in the past for these two species (Terhurne-Berson et al., 2004). Nevertheless, a significant portion of the flora currently present in this mountain range may be in danger (Thuiller et al., 2005; but see Scherrer and Körner, 2011).

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SDMs are not free from the limitations and uncertainties widely discussed in the literature (Thuiller 2004; Jiménez-Valverde et al., 2008; Thuiller et al., 2008). In addition to management, some important factors involved in species' resistance to changes in distribution ranges are interactions between climate and resource availability (for instance, CO_2, see Keenan et al 2011), phenotypic and genetic adaptation (Visser, 2008; Valladares et al., 2007), dispersal ability across fragmented landscapes (Opdam and Wascher, 2004), and biotic interactions, such as pathogens (Negrón et al., 2009). These factors may produce an under- or overestimation of the future species suitability obtained from current climatic suitability. There is great uncertainty, however, about the ultimate effect of all these factors, and the resultant adaptation to new conditions is still subject to controversy (Davis and Shaw, 2001; Hamrick and Godt, 1996; Rehfeldt et al., 2002; Jump and Peñuelas 2005, Kramer et al., 2010).

The extent of the distribution range considered in modeling may affect local estimations of extinction (Barbet-Massin et al., 2010; Thuiller et al., 2004). In our case, both species present a wide European distribution (Lahti and Lampinen, 1999) and the use of this expanded territory in the model would involve profiling a colder niche; more extinction would therefore be predicted in the Pyrenees. We argue that the use of our regional data is appropriate because of the importance of local adaptations (Hamrick and Godt, 1996; Sork et al., 2010), particularly in the case of beech (Kramer et al., 2010). Also, it could be argued that the use of constant variables over time (i.e. terrain) may lead to an overestimation of species persistence. It is common to explicitly ignore terrain variables in climate change in order to achieve a strict assessment of climatic effects on distribution (Araújo et al., 2006; Araújo and Luoto, 2007; Araújo and Guisan, 2006; Thuiller et al., 2006), but terrain variables play a key role in species distribution (Franklin, 1998; Leathwick, 1998; Austin and Van Niel, 2011). Other terrain variables not available for this study may significantly enhance the accuracy to our results. Soil cover, for example, is particularly important in mountain areas since mountain soils are often not sufficiently developed to sustain tree growth. The absence of this variable in the model may result in an overestimation of species persistence or an unrealistic upward altitudinal shift. For instance, Scherrer and Körner (2011) found that terrain induced mosaic of environmental conditions buffers Alp's flora against climate change.

Co-occurrences do not track the whole environmental space of the species composing the community, and the CM is therefore a less general model than the OIM. In general, a major argument for selecting the overlapping of individual models (OIM) is its greater capacity to model different situations (Guisan and Zimmerman, 2000; Baselga and Araujo 2009). Although the CM's performance may achieve good results, it seems less informative in terms of future niche differentiation than the OIM, which can assess future fitness at the level of an individual species. The analysis of niche differentiation, even across large regional scales, may provide information that enhances our understanding of local coexistence across environmental gradients (Silvertown, 2004).

On the other hand, profiling the RNc allows for a comparison between the environmental space of the observed co-occurrence and the environmental space of combinations (overlap) of the current individual species distributions. Similar concepts appear at the species level with equations such as the range/potential range ratio (Gaston, 2003), which has been used to evaluate species range filling on the

European scale (Svenning and Skov, 2004). At the individual species level, it has been observed that current distribution of *Abies alba* and *Fagus sylvatica* is smaller than the potential realized environmental niche (RN). Some authors state that low migration rates or even beech forest would have hampered the spread of *Abies alba* in this area during Holocene (Peñalaba 1994). However, despite the historical component, much of the differences between realized distribution and its potential environmental space may be attributed to biotic interactions, namely competition and facilitation processes.

According to our expectations, the RNc (modeled by the CM) is spatially included in the PFNc (modeled by the OIM) under present conditions, but this pattern differs in all the climate scenarios studied. Although both approaches predict similar declines in suitability, there is a relevant spatial disagreement. Although such differences are rooted in model parameterization, it highlights the relevance of the modeling approach (CM or OIM) in climate change analysis of the distribution of species co-occurrence. Further research should be undertaken, using different modeling techniques and ensembles of forecasts in order to achieve more general results (Thuiller et al., 2009; Araújo and New, 2007).

We conclude that the climatic suitability of *Abies alba*, *Fagus sylvatica* and their mixed forests will experience a significant decline in their climatic fitness as a result of climate change, whichever modeling approach is chosen. Accuracy measures and future scenario trends are similar in both the CM and the OIM, but spatial projections differ, resulting in variations in the future assessment of climate-change effects on present distributions. We argue that the OIM is preferable for future scenarios, because of its broader generality, but the CM approach may provide information that determines the current shape in the environmental space occupied by co-occurrence, especially if compared to the full range of conditions in which the two species occur, either jointly or separately.

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Table 1. Summary of the GLMs. Variables: WA (Water Availability), MinWiT (minimum winter temperature), CURV (Terrain curvature), SLP (Slope), RA (Solar radiation). AUC refers to the Area Under the Receiver Operating Characteristics curve (ROC), a measure of accuracy calculated with the 20% of points in each dataset. Data correspond to the mean values of 250 datasets with different absence locations.

MODELING APPROACH	VARIABLES	MEAN EXPLAINED VARIANCE	AUC
IM *Abies alba* (individual model)	WAsummer WAwinter MinWiT Curvature Slope RAsummer	74 %	0.98
IM *Fagus sylvatica* (individual model)	WAspring MinWiT Continentality Slope RAsummer	65%	0.96
CM *Fagus sylvatica+ Abies alba* (community model)	WAfall MinWiT Curvature Slope	84%	0.98

Table 2. Total suitable area of *Abies alba* and *Fagus sylvatica* obtained from present and two future (A1FI and A2) climatic scenarios.

SPECIES	Suitable area (km^2)			Change in suitable area	
	PRESENT	A2	A1FI	PRESENT-A1FI	PRESENT-A2
Abies alba	19418	8625	7735	-60 %	-56 %
Fagus sylvatica	56024	9287	6241	-88 %	-83 %

Table 3. Differences in suitable area and predicted changes for each modeling approach: OIM (Overlapped Individual Models) and CM (Community model).

Model Approach	Suitable area (km^2)			Change in suitable area	
	PRESENT	A1FI	A2	PRESENT-A1FI	PRESENT-A2
OIM	16105	1787	2722	-91.8 %	-90.2 %
CM	11238	927	1096	-88.9 %	-83.1 %

Table 4 Agreement between the community model (CM) and overlay individual model (OIM) for the climate change scenarios considered. Percentages in brackets indicate the degree of disagreement in suitable areas (Area of disagreement under approach X/Total suitable area under approach X).

	PRESENT (km^2)	A1FI(km^2)	A2(km^2)
Suitability agreement (OIM and CM)	11 170	464	1 030
Disagreement OIM (suitable only in OIM)	4 935 (30%)	1 323 (74%)	1 692 (62%)
Disagreement CM (suitable only in CM)	68 (0.6%)	463 (50%)	66 (6%)

Table 5. Percentage of predicted suitable/non-suitable topo-climatic conditions for current NFI plots of mixed forest (*Abies alba*-Fagus sylvatica) for the two model approaches (OIM: overlap individual model; CM: community model) under A1FI and A2 scenarios. Not suitable areas in the case of OIM are divided, depending on the source of the loss of the co-occurrence. Shaded cells correspond to present climate plots (model accuracy in OIM).

%	NOT SUITABLE	SUITABLE	NOT SUITABLE	SUITABLE

		FOR MIXED FORESTS	FOR *Fagus sylvatica*	FOR ANY SPECIES	FOR *Abies alba*
OIM	PRESENT	15.8	7.0	0.6	8.2
CM		22.8		22.8	
OIM	A1FI	80.3	19.7	14.6	45.9
CM		98.7		98.7	
OIM	A2	73.9	24.2	8.3	41.4
CM		92.4		92.4	

Table 6. Main orientation and average elevation characteristics of current plots of mixed forests (*Abies alba-*Fagus sylvatica) according to climate scenario and future model projection. Unclear category refers to the disagreement between community model and overlap individual models´ assessment.

	ORIENTATION (% plots in main orientation)			AVERAGE ELEVATION (m)		
	Present	A1	A2	Present	A1	A2
Suitable	North (52%)	North (100%)	North (66%)	1404	1502	1470
Not Suitable	North (61%)	North (50%)	North (51%)	992	1345	1316
Unclear	North (48%)	North (56%)	North (51%)	1417	1447	1471

Fig.1.

Fig.2.

Fig.3.

Legend:
- Not suitable
- Low suitable
- Medium suitable
- High suitable

- Lost
- Maintained

Fig.4.

Suitable in CM
Suitable in OIM
Agreement
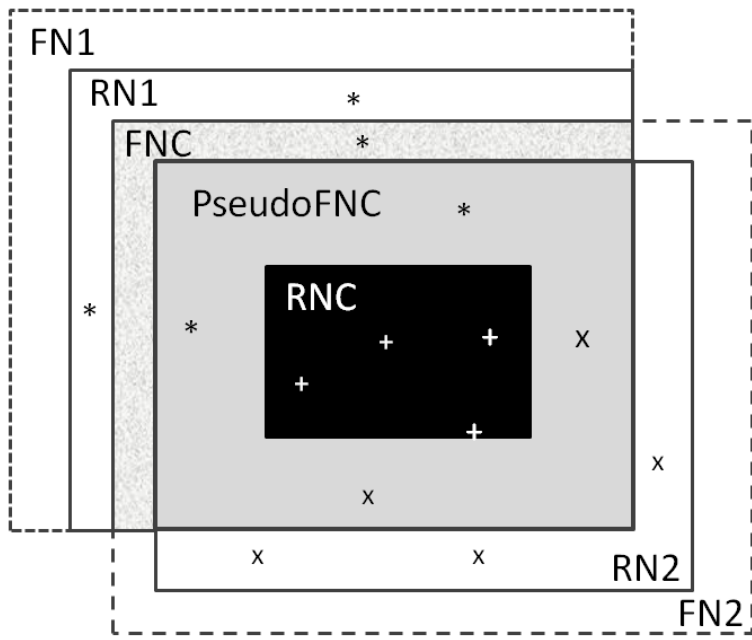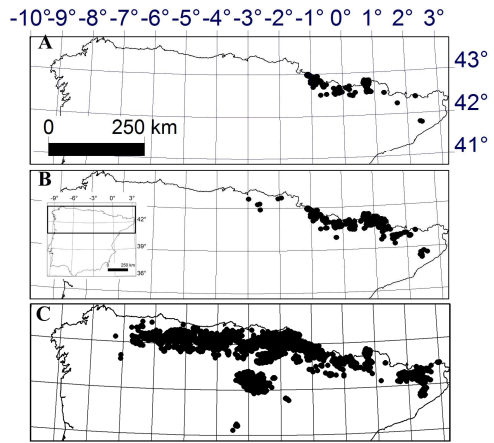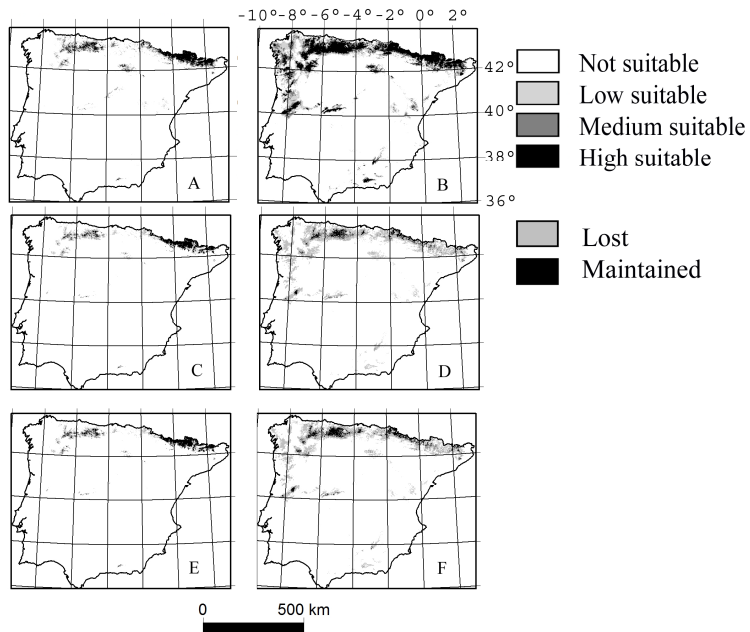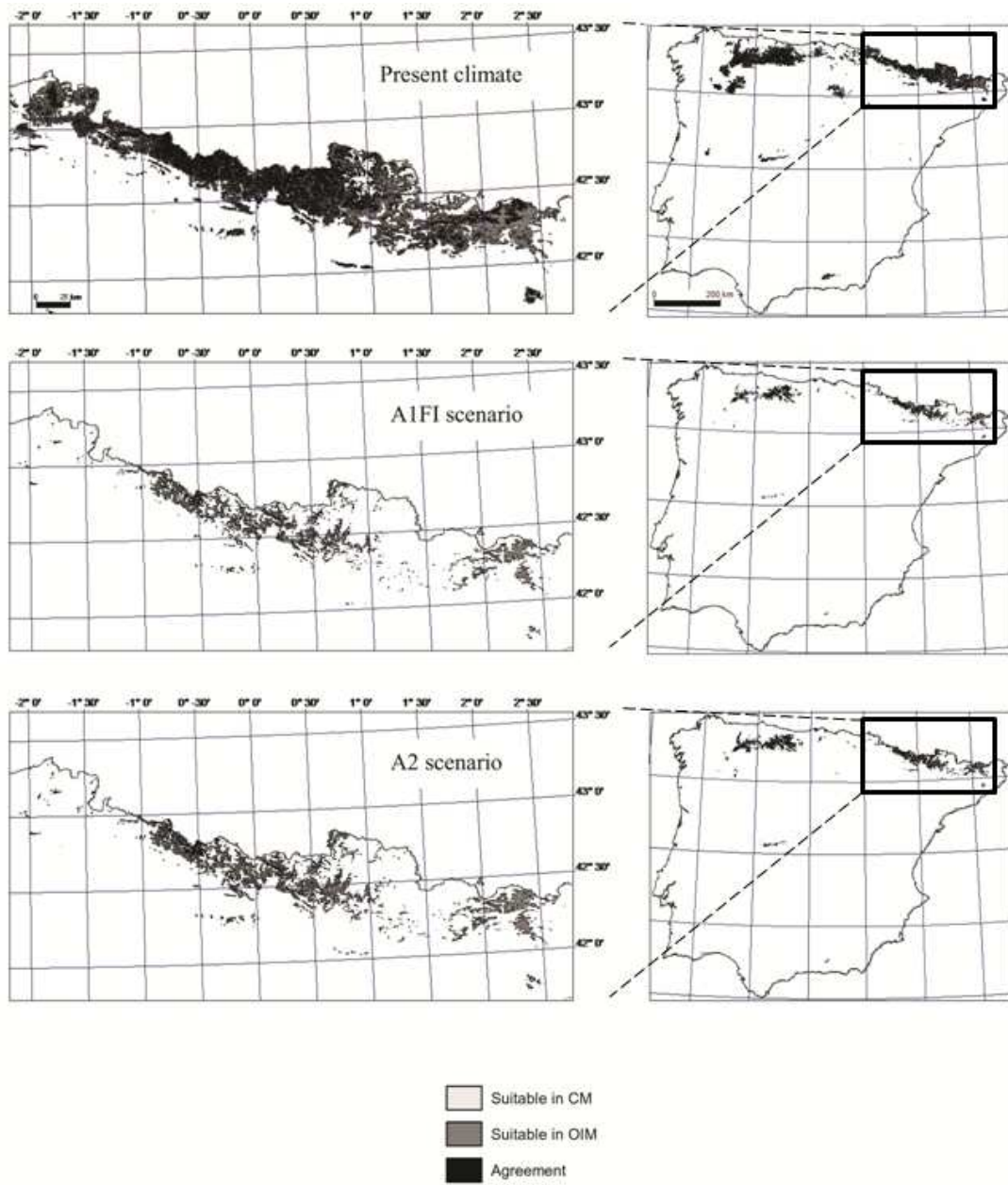
Figure 1. Framework of the niche concept. Fundamental Niche of the community (FNc) corresponds to the intersection of the Fundamental Niche of species of the community (FN1, FN2). Pseudo-fundamental niche of the community (PseudoFNC) models the intersection of the realized niches of each individual species (RN1, RN2; modeled by Overlapping Individual Models) whereas community Realized Niche (RNC) is modeled by community model approach.

Figure 2. Spanish National Forest inventory plot location of Abies alba, Fagus sylvatica and co-occurrence of the two species in the Pyrenees (A) and in the Iberian Peninsula (B).

Figure 3. Current and future suitability for Abies alba and Fagus sylvatica separately. (A) Present suitability index for Abies alba, predicted dynamics of suitable areas in scenario A1FI (C) and A2 (E). (B) Present suitability index for Fagus sylvatica, predicted dynamics of suitable areas in scenario A1FI (D) and A2 (F).

Figure 4. Agreement and disagreement between modeling Community and Overlapped IndividualModels approache (CM and OIM) for present climate and future scenarios. Agreement declines with climate chane and most suitable area is only forecasted by OIM approach. Main agreement geographical region corresponds to the central Pyrenees range.