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Delineating limits: confronting predicted climatic suitability to field performance in mistletoe populations

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Authors contributions: G. Sangüesa-Barreda and J.J. Camarero performed the sampling design and collected the data. S. Pironon and A. Gazol carried out the Species Distribution Models and the germination and establishment analysis, respectively. G. Sangüesa-Barreda, J.J. Peguero-Pina and E. Gil-Pelegrín did the cold tolerance analysis. G. Sangüesa-Barreda and J.J. Camarero took and prepared the samples for the iWUE analysis. G. Sangüesa-Barreda led the writing of the manuscript. All authors contributed critically to the writing and the discussion and gave final approval for publication.

Abstract

1. Biotic stressors such as hemiparasites have a profound impact on forest functioning. However, predicting the future incidence of these stressors on forests remains challenging because climate-based distribution do not consider tree-hemiparasite interactions or the impacts of extreme climate events on stressors' performance.

2. We use Species Distribution Models (SDMs) and ecophysiological and demographic field data to assess whether climatic suitability is a proxy for the performance of the hemiparasite mistletoe (*Viscum album*) in two forests with contrasting climatic conditions. Two host-tree species representing wet-cold (Scots pine) and dry-warm (Aleppo pine) conditions were selected. We fitted SDMs based on climate variables, and measured different ecophysiological variables capturing cold- (photoinhibition) and drought-tolerance (intrinsic water-use efficiency, iWUE). We also assessed demographic variables related to seed germination and establishment rates of mistletoe through a translocation experiment.

3. SDMs showed a high climatic suitability of mistletoe in both forests. Mistletoes living in the Scots pines site presented a higher cold tolerance, whilst those inhabiting the Aleppo pine site showed a higher iWUE. Seedlings coming from local seeds showed a lower mortality than seedlings coming from translocated seeds. Germination and seedling establishment showed temporal mismatches when comparing local and translocated seeds.

4. *Synthesis:* Habitat suitability predicted by SDMs based on climate data and field performance were related in this mistletoe species. However, ecophysiological and demographic variables indicated a lower fitness of mistletoe in the dry-warm site associated with drought stress. In conclusion, predicted climate suitability based on SDMs forecasts should be refined using field data on actual performance and considering plant-to-plant interactions and extreme climate events.

Introduction

The geographical distribution and population dynamics of forest biotic stressors such as parasites, herbivores and pathogens are related to climate variability (Ayres & Lombardero, 2000; Miller & Stephenson, 2015). The most recent climatic models forecast rapid rises in temperature, more frequent extreme events such as dry spells and cold/heat waves and local reductions of precipitation during the 21st century (IPCC, 2014). These major environmental changes could shift the interactions between trees and their biotic stressors, resulting in a range expansion of biotic stressors and making some forests more vulnerable to the resulting stress (Sturrock et al., 2011).

How forests will be affected by biotic stressors is therefore a relevant and challenging question for ecologists (Kurz et al., 2008; Lantschner, Atkinson, Corley, & Liebhold, 2016). However, so far, predictions have often been based solely on climatic suitability by Species Distribution Models (hereafter SDMs; Guisan & Zimmermann, 2000; Elith & Leathwick, 2009) but several concerns have been raised. Firstly, there is a debate about the appropriateness of using climate suitability in order to predict key processes for the

persistence and performance of populations (Kearney & Porter, 2009; Wittmann, Barnes, Jerde, Jones, & Lodge, 2016; Pironon et al., 2017b). Secondly, it is expected that climate alone cannot properly predict species performance because biotic interactions (biotic stressor - host) play a determining role (Araújo & Luoto, 2007). Third, it is questioned whether climatic suitability based on climatic averages across decades is able to determine the response of populations and individuals to extreme climatic events (e.g., droughts and cold spells). These events can accelerate shifts in species composition and distribution (Jentsch, Kreyling, & Beierkuhnlein, 2007). Therefore, increasing the reliability of SDM predictions regarding population performance, species interactions, and extreme events is a priority task.

Suitable model species to evaluate these questions include the European mistletoe (*Viscum album* subsp. *austriacum*; hereafter mistletoe), which is a hemiparasitic plant that obtains water and minerals from its tree hosts (conifers) but it is also able to photosynthesize (Zuber, 2004). This mistletoe constitutes an ideal species due to the variety of tree hosts and their wide ecological range (Zuber, 2004). In this study we focus on two major host conifers of mistletoe representing northern or wet-cold (the Eurosiberian Scots pine, *Pinus sylvestris* L.) and southern or dry-warm (the Mediterranean Aleppo pine, *Pinus halepensis* Mill.) limits of mistletoe (Zuber, 2004).

Mistletoe has perennial leaves and photosynthetic stems and it is very sensitive to low winter temperatures which determine its cold tolerance and thus its northernmost or uppermost distribution limits (Iversen, 1944, Jeffree & Jeffree, 1996). Currently, mistletoe does not reach the cold-distribution limits of its host species (e.g. treeline), the Scots pine, leading to a mismatch between the distribution of the hemiparasite and the host tree species (Tubeuf, 1923), although this mismatch may be reduced by the increase in temperature. This uncoupling suggests that the actual mistletoe distribution is not only constrained by climate and also by the absence of seed-dispersing birds that act as vectors (Mellado & Zamora,

2014a). Therefore, the current mistletoe distribution is the result of a suitable climate, host presence, seed-vector abundance and their interactions (Overton, 1996).

A higher environmental suitability and field performance is often expected at the center of species' distributions than at their limits (i.e. so-called "centre-periphery" hypothesis; see Pironon et al., 2017a for a review). However, this prediction may be challenged in the case of mistletoes due to their interactions with other species having different ranges and physiological tolerances. Thus, it is particularly important to improve the knowledge of the ecology of biotic stressors to improve SDMs' predictions, especially in their distribution limits where responses to climate may be magnified (Hampe & Petit, 2005; Louthan, Doak, & Angert, 2015).

In addition to cold stress, water deficit may also contribute to the poor performance of mistletoe in drought-prone sites. Water shortage and mistletoe infection induce stomatal closure in the host tree but mistletoes are xylem-tapping hemiparasites which continue transpiring which exacerbates drought stress in the host tree (Fischer, 1983; Zweifel, Bangerter, Rigling, & Sterck, 2012). In addition, mistletoe traps nutrients from the host and this also contributes to amplify drought stress (Mutlu, Osma, Ilhan, Turkoglu, & Atici, 2016; Sangüesa-Barreda, Linares, & Camarero, 2012). A positive feedback between mistletoe infection and drought stress can lead to decline in growth, reduce the host´s performance and cause canopy dieback or trigger tree death (Dobbertin et al., 2005; Rigling, Eilmann, Koechli, & Dobbertin, 2010; Sangüesa-Barreda, Linares, & Camarero, 2012, 2013). Furthermore, warmer and drier conditions are expected in relatively humid forests from central Europe and these trends are related to increasing mistletoe abundance and forest dieback (Dobbertin et al., 2005; Varga et al., 2014). Therefore, warmer conditions may favor the mistletoe´s expansion in humid-cold areas whereas in dry-warm zones drought and mistletoe may induce host dieback.

Seed germination and establishment are among the most critical stages for the development of mistletoe populations within the hosts' canopies (Zuber, 2004). Mistletoe recruitment may depend on the microclimatic features inside the tree canopy (i.e. radiation levels, branch size or bark thickness; Norton & Carpenter, 1998). Its seeds are capable of germinating onto the host canopy without being ingested by birds so deposition of seeds by gravity is frequent (Aukema, 2004). Nonetheless young seedlings usually show high mortality rates (Sallé, 1983) and therefore, it is critical to consider the first life stages of mistletoe to assess the species' actual niche and dynamics. Here we address this issue by translocating seeds between the two study sites and then following seed germination and seedling establishment and development.

In this study, we assess whether climatic suitability is controlling mistletoe population performance, i.e. we related climate-based projections of suitability and field data of mistletoe performance. Climatic suitability and mistletoe performance may be uncoupled because other factors such as biotic interactions or drought stress drive mistletoe performance. To achieve this goal we confront SDMs outcomes and relevant ecophysiological and demographic traits: (i) photoinhibition as proxy of low-temperature tolerance, (ii) intrinsic water-use efficiency (iWUE hereafter) as surrogate of drought tolerance, and (iii) mistletoe recruitment as a bottleneck of its lifecycle. These three sets of variables are compared between a wet-cold Scots pine stand and a dry-warm Aleppo pine stand. We expect a high climatic suitability of mistletoe in both pine stands but contrasting ecophysiological and demographic performances including: higher cold tolerance in the Scots pine site, higher iWUE in the Aleppo pine site, and lower mortality of seedlings from local seeds as compared with seedlings proceeding of translocated seeds.

Material and methods

Host tree species and study sites

We selected two host species corresponding to northern and southern host tree species of mistletoe European distribution, the Eurosiberian Scots pine (*Pinus sylvestris* L.) and the Mediterranean Aleppo pine (*Pinus halepensis* Mill.), respectively. We selected a wet-cold Scots pine site situated in the Iberian System mountains (Puerto de Gúdar, Teruel; 0.71º W, 40.36º N; 1490 m a.s.l.), and a dry-warm Aleppo pine site situated in the Middle Ebro Basin (Vedado de Peñaflor, Zaragoza; 0.72º W, 41.78º N; 379 m a.s.l.). Both sites are located in north-eastern Spain (see Fig. 1 and Fig. S1, Supporting Information). The wet-cold Scots pine experiences continental Mediterranean conditions, whereas the dry-warm Aleppo pine site is subjected to semi-arid Mediterranean conditions (see Fig. S2). In the wet-cold Scots pine the minimum and maximum mean temperature are 3.1 and 15.3 ºC, and the mean precipitation is 550 mm. In the dry-warm Aleppo pine the minimum and maximum mean temperature are 8.2 and 19.3 ºC, and the mean precipitation is 472 mm. In both study sites, temperatures have increased since the 1950's, whilst precipitation showed no trend (Fig. S2).

The Scots pine stand constitutes the southernmost continuous forests for the current distribution of one of the most widespread conifers worldwide (Fig. S1). Here, the infested pines often have abundant mistletoe clusters in their crowns (see Fig. S1; Sangüesa-Barreda, Linares, & Camarero, 2013). On the other hand, the Aleppo pine stand represents the xeric limit of the current mistletoe distribution (Zuber, 2004). Aleppo pine forms open forests highly suitable for mistletoe infestations due to high radiation levels and the abundance of seed-dispersing birds (Sangüesa-Barreda, Linares, & Camarero, 2012). In both stands, mistletoe populations are located near their southernmost species-distribution limit (Zuber, 2004).

Climatic suitability for mistletoe and the two host species

We gathered occurrence records across Europe for the mistletoe and the two studied host pine species from the international network ICP Forests program (www.icp-forests.org) and the Global Biodiversity Information Facility (http://www.gbif.org/). We reviewed thoroughly every record to detect for incorrect or imprecise observations.

For the three species (mistletoe, Scots pine and Aleppo pine), we calibrated and projected species distribution models (SDMs) based on 1960-1990 climatic information retrieved from the Worldclim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a 2.5 arc-minutes resolution. We reduced multicollinearity among the 19 bioclimatic variables provided by Worldclim by using Principal Component Analysis (PCA) and correlation matrix analyses (*results not shown*). We selected the following five variables: temperature seasonality (BIO4), mean temperature of the wettest (BIO8) and coldest (BIO11) quarters, precipitation of the driest (BIO17) and coldest (BIO19) quarters.

As the accuracy of species distribution models can vary from one statistical technique to another, we used a consensus method (Araújo & New, 2007; Marmion, Parviainen, Luoto, & Heikkinen, 2009) by considering four different probabilistic models from the *biomod2* package in the R statistical software (R development Core Team 2017): Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Random Forest (RF), and MaxEnt. Each model run was carried out using 1,000 pseudo-absence/background points selected randomly across Europe and, in order to account for the variability resulting from this sub-selection, we repeated the process 10 times. Furthermore, we used 75% of the original data for the model calibration and the remaining 25% for model evaluation. To ensure that this random-splitting strategy did not impact the model accuracy, we also repeated it 10 times. Finally, we evaluated such accuracy with two different metrics: the True Skill Statistics (TSS) (Allouche, Tsoar, & Kadmon, 2006) and the area under the Receiver Operating

Characteristic curve (ROC) (Hanley & McNeil, 1982). In total, we ran 800 models per species by using four different statistical models, ten pseudo-absence selections, ten repetitions, and two evaluation metrics.

Species' distributions were then projected across Europe under current climatic conditions according to the different models calibrated previously. To obtain a single map representing the distribution of the probability of occurrence of each species, we finally computed a mean of all projections weighted by their respective model predictive accuracy (i.e. TSS scores). Models exhibiting TSS and ROC scores below 0.6 and 0.8, respectively, were discarded.

Finally, we assessed each variable contribution to the predictions of each model by using a randomisation procedure implemented in the *biomod2* package (Thuiller, Lafourcade, Engler, & Araújo, 2009) in R statistical software (R development Core Team, 2017). This procedure, which allows a direct comparison across the different statistical models used, is based on a Pearson correlation between the standard predictions of the models and those for which the variable considered has been randomly permutated. We repeated this procedure four times for each variable and kept the mean correlation coefficient. The importance of the variable is finally calculated as one minus the correlation, so that higher values indicate more important variables for the model.

Mistletoe tolerance to low temperatures

In the spring of 2013, we selected a total of 27 mistletoe individuals from Aleppo pine and 48 from Scots pine. We collected equally distributed female and male mistletoe individuals, as well as non-reproductive (< 5 years old) and reproductive individuals (> 5 years old; Zuber, 2004). In each mistletoe individual, we cut apparently healthy leaves from the last year. They were exposed to various freezing temperatures between –5 and –30 ºC, with 5 ºC intervals, and during 1h using an industrial controller to establish cooling rates in the laboratory (FP50-

HE Refrigerated/Heating Circulator, Julabo, Seelbach, Germany). This device provides a constant thermal stability (± 0.01 ºC) on set temperature along the whole thermal profile (from -50 to +200 ºC). At least 6 mistletoe individuals (3 leaf cohorts per shrub) were analyzed per freezing temperature and host.

We used the fluorometry method to quantify the changes in efficiency of the photosystem II of plant tissues (leaves) subjected to different temperatures as the dark-adapted chlorophyll fluorescence ratio (F_v/F_m) which was used as an indicator of photoinhibition induced by low temperatures (Peguero-Pina, Morales, & Gil-Pelegrín, 2008). We measured the photosynthetic efficiency of mistletoe leaves before the experiment and after freezing.

Water-use efficiency

To compare the changes in iWUE of mistletoe and host tree species, (i.e. the ratio of net assimilation (*A*) to stomatal conductance (*g*)), we measured $^{13}C/^{12}C$ isotope ratios in mistletoe leaves and tree needles in two climatically contrasting years, 2012, a very dry year (cf. Trigo et al., 2013; Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015a) and 2013, a normal year according to precipitation records (see Fig. S2). We selected apparently healthy needles and leaves from sunny branches of dominant trees and mistletoe shrubs.

Leaves and needles were carefully homogenized and milled using an ultra-centrifugation mill (Retsch ZM1, mesh size of 0.5 mm). An aliquot of 0.6 mg of each wood sample was weighed on a balance (Mettler Toledo AX205) and placed into a tin capsule for isotopic analyses. The isotope ratio $^{13}C/^{12}C$ ($\delta^{13}C$) was determined on an isotope ratio mass spectrometer (ThermoFinnigan MAT 251) at the Stable Isotope Facility (Univ. California, Davis, USA). The results were expressed as relative differences in the $^{13}C/^{12}C$ ratio of plant material with respect to the Vienna Pee-Dee Belemnite (V-PDB) standard. The estimated precision of the measurements was ±0.1‰.

Isotopic discrimination between the carbon of atmospheric CO_2 and plant carbon (Δ; see Farquhar & Richards, 1984) was defined as:

$$\Delta = (\delta^{13}C_{atm} - \delta^{13}C_{plant}) / (1 + \delta^{13}C_{plant} / 1000) \qquad (1),$$

where $\delta^{13}C_{atm}$ and $\delta^{13}C_{plant}$ are the isotope ratios of carbon ($^{13}C/^{12}C$) in atmospheric CO_2 and plant material (mistletoe leaves or pine needles) respectively, expressed in parts per thousand (‰) relative to the standard V-PDB; Δ is linearly related to the ratio of intercellular (c_i) to atmospheric (c_a) CO_2 mole fractions, by (see Farquhar et al., 1982):

$$\Delta = a + (b-a) \, c_i/c_a \qquad (2),$$

where a is the fractionation during CO_2 diffusion through the stomata (4.4‰), and b is the fractionation associated with reactions by Rubisco and PEP carboxylase (27‰; Farquhar & Richards, 1984). The c_i/c_a ratio reflects the balance between A and g. Thus, the linear relationship between c_i/c_a and Δ may be used to calculate iWUE as follows:

$$iWUE = (c_a / 1.6) \, [(b-\Delta) / (b-a)] \qquad (3)$$

Mistletoe germination and establishment

In January 2014, we performed a translocation experiment of mistletoe seeds to assess germination and seedling establishment. We collected mature mistletoe berries from the two study sites and host species. We gathered berries in the field that were visually viable and with no external signs of predation or damage. We selected 11 healthy trees from Aleppo pine and 14 trees from Scots pine with similar size (*dbh*, diameter at breast height measured at 1.3 m; tree height), age (estimated by taking cores at 1.3 m using a Pressler increment borer) and topographic features (aspect, slope). In each tree, we randomly selected one or two accessible, sunny and healthy tree branches with a diameter between 3 and 12 cm. In 5-7 trees and 10-12 branches (Aleppo and Scots pine respectively), we placed 25-30 local berries

per branch and in the other 6-7 trees and 12-10 branches; we placed non-local berries coming from the other site and pine host species. A total of 430 berries were placed in Aleppo pine (160 local and 270 translocated berries) and 550 in Scots pine (300 local and 250 translocated berries). We removed the exocarp and placed the mature berries onto the tree branch surface and inside a metallic-open mesh cage of size 0.5 cm to avoid predation. The mucilaginous layer (viscin) keeps the berry stuck onto the branch, and then, seeds are able to germinate and develop an haustorium (Zuber, 2004). We assumed that the metallic-open cages did not alter the microclimate conditions of branches (radiation, air temperature) used for seeding.

Every two weeks during the whole year, we recorded the germination status of each seed following Frochot and Sallé (1980). We considered 4 different stages: 1) non-germinated; 2) germinated (the seed produces an haustorium); 3) established (haustorium enters the branch); 4) dead (see Fig. S3 Supporting Information).

In this experiment, the germination status of mistletoe seeds represents a typical example of longitudinal and clustered ordinal response data, because the germination rates of the same individuals (clusters) are observed through time. Thus, the outcome of the study is an ordinal ordered variable that represents different status of the life cycle of mistletoe seeds. For that reason, we used ordinal generalized linear mixed models (Agresti, 2010) to study the temporal dynamic of mistletoe seeds.

The response variable measures the status of mistletoe seeds and is an ordered factor with four different levels. A separate model was constructed for each site. In each model, we used as response variables the sampling time, the origin of the mistletoe seeds and the *dbh* of the tree in which the seeds were located. In particular, we were interested in studying the cumulative probability of the *ith* seed falling in the *jth* status at time *t* considering the influence of the covariates (i.e. origin of the seeds and tree *dbh*). Thus, we proposed a random

intercept logit link model in which the status of the seeds depends on sampling time, the origin of the seed and tree *dbh*.

We fitted five competing models: (i) containing only the intercept and no covariates; (ii) containing only sampling time as covariate; (iii) containing sampling time and the site of seed origin as covariates; (iv) containing sampling time, seed origin and their interaction as covariates; and (v) containing sampling time, seed origin, their interaction and tree *dbh* as covariates. For each site, the model showing the lowest Akaike Information Criterion (AIC) value was selected as the best model (Burnham & Anderson, 2002). Statistical analyses were performed using the *vcrpart* package in R (Bürgin & Ritschard, 2015).

Results

Climate suitability for mistletoe and host pine species across Europe

SDMs performed well for the mistletoe (TSS = 0.79 ± 0.06; ROC = 0.94 ± 0.02) and its two host species (Scots pine, TSS = 0.69 ± 0.08, ROC = 0.90 ± 0.03; Aleppo pine, TSS = 0.86 ± 0.07; ROC = 0.96 ± 0.04 respectively; Fig. 1). SDMs predicted a high climatic suitability for the mistletoe in the two studied sites. The probabilities of occurrence at the Scots pine and Aleppo pine sites were 0.90 and 0.83, respectively. The predicted southernmost distribution limit (rear edge) of mistletoe in Europe was situated in southeastern Spain, whereas the northernmost limit (leading edge) was predicted to occur in southern Sweden (Fig. 1). On the other hand, Scots pine showed a high climatic suitability in northern and central Europe but also in the Iberian mountains; the probability of occurrence at the study site was 0.76. Aleppo pine exhibited a high climatic suitability across the Western Mediterranean Basin; we found a probability of occurrence of 0.95 at the study site.

Regarding the mistletoe, temperature seasonality was identified as the main driver of its European distribution, followed by the mean temperature of the coldest quarter and the

precipitation of the driest quarter (Table 1). For Scots pine, temperature seasonality was the most important variable, followed by the mean temperatures of the coldest and wettest quarters. Finally, the mean temperature of the coldest quarter and temperature seasonality were the main drivers of the Aleppo pine distribution.

Low-temperature tolerance of mistletoe

We found a higher resistance to low temperatures in mistletoes from the wet-cold Scots pine site than in those from the dry-warm Aleppo pine site (Fig. 2). Mistletoes hosted by Scots pine showed a decrease in the PSII efficiency (reduction of the F_v/F_m ratio) below -22.3ºC, while mistletoes hosted by Aleppo pine showed a sharp decrease in the F_v/F_m ratio below -17.5 ºC. We also found lower F_v/F_m ratios in the case of Scots pine mistletoes than Aleppo pine mistletoes at relatively soft temperatures (-5 and -10 ºC). Finally, we only found significant ($P < 0.001$) differences in F_v/F_m between mistletoe age classes in the Aleppo pine site, being higher in old (>5 years) individuals (Fig. S4).

Water-use efficiency and drought stress

We observed significant lower iWUE values in the two mistletoe populations than in their respective host pine species (Table 2). Furthermore, iWUE in mistletoes on Aleppo pine was higher than in mistletoes on Scots pine.

Regarding the two years with contrasting climatic features, in the two populations and years, mistletoe showed similar iWUE trends. Additionally, we did not find a significant difference in iWUE between the very dry 2012 and the normal 2013 in both populations (Table 2).

Mistletoe regeneration: seed germination and recruitment

The selected models for the two sites included as covariates: sampling time, the origin of the seeds and their interaction (Table 3). Nevertheless, we only found a significant influence of tree *dbh* on mistletoe seed germination and seedling establishment in the case of the Aleppo pine stand.

In the Scots pine site the probability of mistletoe seeds to germinate was zero until week 12, after that most of the seeds germinated and established while 27-1% (translocated and local berries respectively) were not able to germinate (Figs 3 and 4). There was a marked increase in the probability of mistletoe seedling establishment starting around week 20, which peaked in week 30 and began declining afterwards. Finally, mistletoe seedling mortality started increasing after week 30.

Mistletoe seeds and seedlings translocated from the Aleppo pine site to the Scots pine site germinated and started declining and dying later than local seeds and seedlings. Furthermore, we found a higher mortality in the local seedlings than in the translocated seedlings. A similar pattern was observed in the Aleppo pine site, despite the peak of mistletoe establishment being lower. The establishment was realized during a shorter time and mortality was higher than in the Scots pine site (Figs 3 and 4). Moreover, the delayed response of seeds coming from the Aleppo pine site as compared to Scots-pine was less pronounced than vice versa. In this case, we found 15% and 26% of translocated and local seeds, respectively, that did not germinate.

Discussion

We provide novel evidences at the yet little-explored connection between climatic suitability and species fitness-related traits (ecophysiological or demographic variables). SDMs predicted a noteworthy climatic suitability for the two mistletoe populations and their tree

hosts. We found positive relationships between SDMs outcomes and the mistletoe performance and thus links between climatic variability and key processes. However, our results also indicated important constraints on mistletoe dynamics due to drought impact not completely captured by the models, and probably magnified by the host-mistletoe linkage. The very low iWUE of mistletoe (Table 2) and the high seedling mortality rates (Figs 3 and 4) suggest a low ability to cope with droughts in the dry-warm Aleppo pine site and a lower fitness than the wet-cold Scots pine site. This partially agrees with the relatively lower climatic suitability predicted for the Aleppo pine site, but it was not so low to fully capture the fitness-related drought impact. Other studies have also pointed out how the mistletoe uses water inefficiently (see Griebel, Watson, & Pendall, 2017). The resulting interpretation of correlative approaches, and the potential improvement of new avenues such as biotic interactions and the role of extreme climate events, open new mechanistic approaches and process-explicit SDMs, especially in biotic stressors, as it has been pointed out before in previous research (Guisan & Thuiller, 2005; Kearney & Porter, 2009; Dormann et al., 2012; Wittmann, Barnes, Jerde, Jones, & Lodge, 2016; Pironon et al., 2017b).

Both, SDMs and physiology- and demography-based analysis pointed out the importance of minimum temperatures and precipitation for mistletoe performance as has been previously reported. Firstly, the high sensitivity of the mistletoe to low winter temperatures which probably determines its northernmost (leading edge) and uppermost distribution limits has been previously widely recognized (Jeffree & Jeffree, 1996; Zuber, 2004; Dobbertin et al., 2005). Secondly, extreme cold events ("winter droughts") may induce local mortality and dieback even in southern Mediterranean populations of host trees as has been documented in Scots pine (Camarero, Gazol, Sancho-Benages, & Sangüesa-Barreda, 2015b). Such growth decline and vitality loss thus influence the long-term mistletoe-tree dynamics. Finally, drought stress can induce dieback events in trees already infested by mistletoe in different

host species and forest types (Dobbertin & Rigling, 2006; Sangüesa-Barreda, Linares, & Camarero, 2012; Gea-Izquierdo, Viguera, Cabrera, & Cañellas, 2014).

Previous results have also shown that habitat suitability predicted by SDMs was highly correlated to local abundance and performance (VanDerWal, Shoo, Johnson, & Williams, 2009; Huntley et al., 2004; Wittmann et al., 2016). However, this relationship may be highly variable and dependent on the species and/or trait considered (Thuiller et al., 2014; Pironon, Villellas, Morris, Doak, & García, 2015; Pironon et al., 2017b). Moreover, differences between SDMs predictions and observed local fitness have often been linked to the lack of equilibrium conditions with the environment due to constrained dispersal or disturbances (e.g. Thuiller, Albert, Dubuis, Randin, & Guisan, 2010; Nagaraju et al., 2013).

The higher cold tolerance in mistletoes on the wet-cold Scots pine site than in the dry-warm Aleppo pine site may be mainly explained by phenotypic plasticity and genetic diversity related to a long-term local adaptation process to the local climatic conditions (Loveless and Hamrick, 1984). These differences were also found in the germination and establishment experiment (Figs 3 and 4). Nonetheless, we lack genetic data to verify this hypothesis; therefore further research is needed. We also found similar F_v/F_m values (0.4-0.5) to those observed in 1-year old *Viscum album* subsp. *album* leaves by Míguez, Fernández-Marin, Hernández, Becerril, and García-Plazaola (2014) in northern Spain in spring. Furthermore, we detected significant lower F_v/F_m values in mistletoes living on Scots pine than in mistletoes hosted by Aleppo pine at relatively cold temperatures (-5º and -10ºC). This may be associated to a seasonal variation of photochemical efficiency of PSII due to winter stress (loss of vigour due to lower chlorophyll concentrations and consequent lower F_v/F_m). This reversible process has also been cited on trees and it should be reverse during spring (Ottander, Campbell, & Öquist, 1995; Míguez, Fernández-Marin, Hernández, Becerril, & García-Plazaola, 2014).

Mistletoe showed lower iWUE than their hosts pine species (Table 2). Mistletoes show similar or inferior photosynthesis rates than their hosts (Lüttge et al., 1998; Strong et al., 2001), but much higher transpiration rates (Marshall, Dawson, & Ehleringer, 1994; Urban, Gebauer, Nadezhdina, & Čermák, 2012) due to poor stomatal regulation (Zweifel, Bangerter, Rigling, & Sterck, 2012; Urban, Gebauer, Nadezhdina, & Čermák 2012). As a result, mistletoes show a wasteful use of water compared with pines which may amplify the drought stress in host trees (Sangüesa-Barreda, Linares, & Camarero, 2013). In declining tree populations, mistletoe infestation may lead to carbon starvation in the long-term as consequence of stomata closure by the host to compensate the water loss through the mistletoe leaves (Galtzel & Geils, 2009; Zweifel, Bangerter, Rigling, & Sterck, 2012). Therefore, we argue that mistletoe infestation can contribute to drought-triggered forest dieback in xeric regions (Dobbertin & Rigling, 2006; Sangüesa-Barreda, Linares, & Camarero, 2012).

Mistletoe and their two host pines did not show differences in the iWUE in two climatically contrasting years (Table 2). The year 2012 has been reported as one of the most extreme winter drought years in Iberia of the last decades (Trigo et al., 2013), and it was the starting point for forest-dieback events in many Spanish forests (Camarero, Gazol, Sangüesa-Barreda, Oliva, & Vicente-Serrano, 2015a). Pine species tend to show long legacy effects on growth (Peltier, Fell, & Ogle, 2016), and it is expected that a more severe drought would prolong legacy effects (Anderegg et al., 2015). On the other hand, long-term mistletoe impacts on performance in drought-prone forests may be cumulative (Sangüesa-Barreda, Linares, & Camarero, 2012) because mistletoe infestation leads to crown defoliation in very infested hosts (Rigling, Eilmann, Koechli, & Dobbertin, 2010), leading to growth loss (Noetzli, Müller, & Sieber, 2003; Shaw et al., 2008), and reducing the concentration of non-structural carbohydrates (Sangüesa-Barreda, Linares, & Camarero, 2012). Hence, we argue

that the lack of differences between 2012 and 2013 may be explained by a drought-legacy effect which interacts with mistletoe-induced decline (Sangüesa-Barreda, Linares, & Camarero, 2013). We would probably need longer iWUE series to fully test the impact of drought on mistletoe and their host trees, but we found strong evidences of the important role of droughts on the performance and persistence of mistletoe.

Seeds and seedlings from the wet-cold Scots pine site germinate, establish and die earlier than seeds and seedlings coming from the dry-warm Aleppo pine site (Figs 3 and 4). Therefore, the mistletoe may locally adapt and increase its fitness and enhance range expansion. Previous research agree with our results and indicated that local climate conditions play a major role in the germination and establishment of mistletoe seeds and seedlings on the host (Norton & Carpenter, 1998), and have also been shown in other mistletoe species (López de Buen & Ornelas, 2002).

Mistletoe seeds show high mortality rates which depend on local climatic conditions as highlighted by the high mortality rates in the wet-cold Scots pine site (around 40-80 % depending on the seed origin) and the observed extremely high mortality rates in the dry-warm Aleppo pine site (around 100% of seeds died after the first year; Fig. 3). In both sites, seedlings started declining after week 28 (July), when drought started (Fig S2b). These results highlight the possible limitation of mistletoe recruitment by droughts, especially in dry-warm sites where drought stress might be a major constraint. Other authors have pointed out high mortality rates in the first life stages of mistletoe species (Forchot & Sallé, 1980; Sallé, 1983). Similar patterns were found in a sowing experiment of mistletoe seeds in a *Pinus nigra* forest located in southern Spain, where only 5-8 % of seedlings established by the end of the experiment (Mellado & Zamora, 2014a). Norton et al. (2002) showed a high germination of two New Zealand mistletoe species, whereas they also observed low establishment rates (2-13%). On the contrary, seedling establishment of the mistletoe

Phragmanthera dschallensis on *Acacia sieberana* in a savannah in Zambia was notably higher and varied from 18% to 39% three years after seed sowing (Roxburgh & Nicolson, 2007). Some limitations of our approach should be mentioned since we considered host branches with slightly wider diameters, and thus thicker barks, than in previous studies (Roxburgh & Nicolson, 2007; Mellado & Zamora, 2014a). Lower seedling mortality would have been found on smaller twigs where mistletoe haustorium may penetrate more easily to reach the host xylem (Mellado & Zamora, 2014b). However, we used these branch-size classes because we have previously observed a high recruitment of mistletoes individuals in branches of several diameter classes including stems (Sangüesa-Barreda, Linares, & Camarero, 2012). A caveat is that we did not assess seed viability prior to sowing in the field. These potential limitations might be considered in further experimental studies.

Several studies have detected an upward shift of mistletoe distribution in response to the increase of winter temperatures in central Europe (Dobbertin et al., 2005; Varga et al.*,* 2014). We go a step further by demonstrating additional important constraints of mistletoe expansion in dry-warm Mediterranean sites. Drought stress might represent an important constraint for mistletoe dispersal close to its ecological or thermal distribution limits when high infestation levels are reached and when mistletoe infestation amplifies drought stress and contributes to forest dieback processes (Sangüesa-Barreda, Linares, & Camarero, 2012, 2013). Conversely, in cold sites, mild winter temperatures and warm spring temperatures might reduce photoinhibition, and thus promote the establishment and expansion of the species.

In conclusion, climate habitat suitability and local performance were related in the mistletoe, signifying the current prevalence of climatic variability in the persistence and dynamics of mistletoe. However, drought stress magnified by the host-mistletoe interaction negatively impacted the mistletoe performance and demographic rates especially in the driest

site. In the last decades, little attention has been paid to the refinement of SDMs' predictions using field data. Here we show that this is a mandatory approach to fully understand climate- and plant-plant interactions in a changing world.

Data accessibility

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.5943136.v1 (Sangüesa-Barreda et al., 2018)

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Figures and tables

Table 1. Relative importance of the five climatic variables used to model the three species' distributions (mean values ± standard deviations across the 800 models considered). Different letters show significant differences among variables ($P < 0.05$; Tukey HSD tests).

	Viscum album	*Pinus sylvestris*	*Pinus halepensis*
Mean Temperature of Wettest Quarter (BIO 8)	0.082 ± 0.003 a	0.496 ± 0.006 b	0.111 ± 0.004 a
Precipitation of Coldest Quarter (BIO 19)	0.182 ± 0.005 b	0.295 ±0.010 a	0.196 ± 0.005 c
Precipitation of Driest Quarter (BIO 17)	0.246 ± 0.003 c	0.316 ± 0.010 a	0.179 ± 0.003 b
Mean Temperature of Coldest Quarter (BIO 11)	0.268 ± 0.003 d	0.509 ± 0.008 b	0.330 ± 0.003 e
Temperature Seasonality (standard deviation *100) (BIO 4)	0.573 ± 0.003 e	0.607 ± 0.006 c	0.287 ± 0.003 d

Table 2. Intrinsic water use efficiency (iWUE) of mistletoe and the two studied host species (Scots pine, *Pinus sylvestris*; and Aleppo pine, *Pinus halepensis*). The iWUE values are presented for a drought year (2012) and a year (2013) with average precipitation (see also Fig. S2 in Supporting Information). Different letters show significant differences between $\delta^{13}C$ and iWUE values for each year (2012 and 2013) regarding the mistletoe from the two tree hosts (*Viscum album* on *Pinus sylvestris*, and *Viscum album* on *Pinus halepensis*; $P < 0.05$; Tukey HSD tests).

Forest type	Species	2012		2013	
		$\delta^{13}C$ (‰)	iWUE (μmol mol^{-1})	$\delta^{13}C$ (‰)	iWUE (μmol mol^{-1})
Scots pine	*Pinus sylvestris*	-25.8 ± 0.4	103.5 ± 4.4	-25.1 ± 0.5	108.4 ± 5.7
	Viscum album	-31.0 ± 0.4b	43.1 ± 5.0a	-31.2 ± 0.5b	41.1 ± 5.5a
Aleppo pine	*Pinus halepensis*	-25.4 ± 0.2	107.5 ± 2.7	-25.9 ± 0.1	103.3 ± 2.3
	Viscum album	-29.9 ± 0.1a	56.1 ± 0.9b	-29.9 ± 0.1a	57.2 ± 0.4b

Table 3. Summary of the best ordinal model selected in each site. The variables included in the Scots pine (*Pinus sylvestris*) and Aleppo pine (*Pinus halepensis*) final models are shown. In addition, we show the increase of the AIC (ΔAIC) of the presented model as compared to the best of the four remaining models. The coefficients associated with each covariate, as well as with the intercepts for each class, and the Z statistic are shown. The intercepts refer to the transitions between the four mistletoe seed stages (1, non-germinated seed; 2, germinated seed; 3, established seed; 4, dead seed).

| Host tree species	Factors	Coefficient ± SE	Z value	ΔAIC
Pinus sylvestris	Time	-8.04 ± 0.17	-47.75	528.56
	Origin	-12.73 ± 0.52	-24.62	
	Time* origin	0.94 ± 0.08	11.09	
	1|2 intercept	38.85 ± 0.82	47.65	
	2|3 intercept	39.97 ± 0.84	47.76	
	3|4 intercept	54.35 ± 1.11	49.08	
Pinus halepensis	Time	-10.73 ± 0.54	-20.04	101.28
	Origin	-19.85 ± 1.92	-10.37	
	Dbh	-0.14 ± 0.01	-16.74	
	Time* origin	3.88 ± 0.38	10.11	
	1|2 intercept	55.73 ± 2.69	20.71	
	2|3 intercept	56.08 ± 2.70	20.74	
	3|4 intercept	62.71 ± 2.90	21.65	
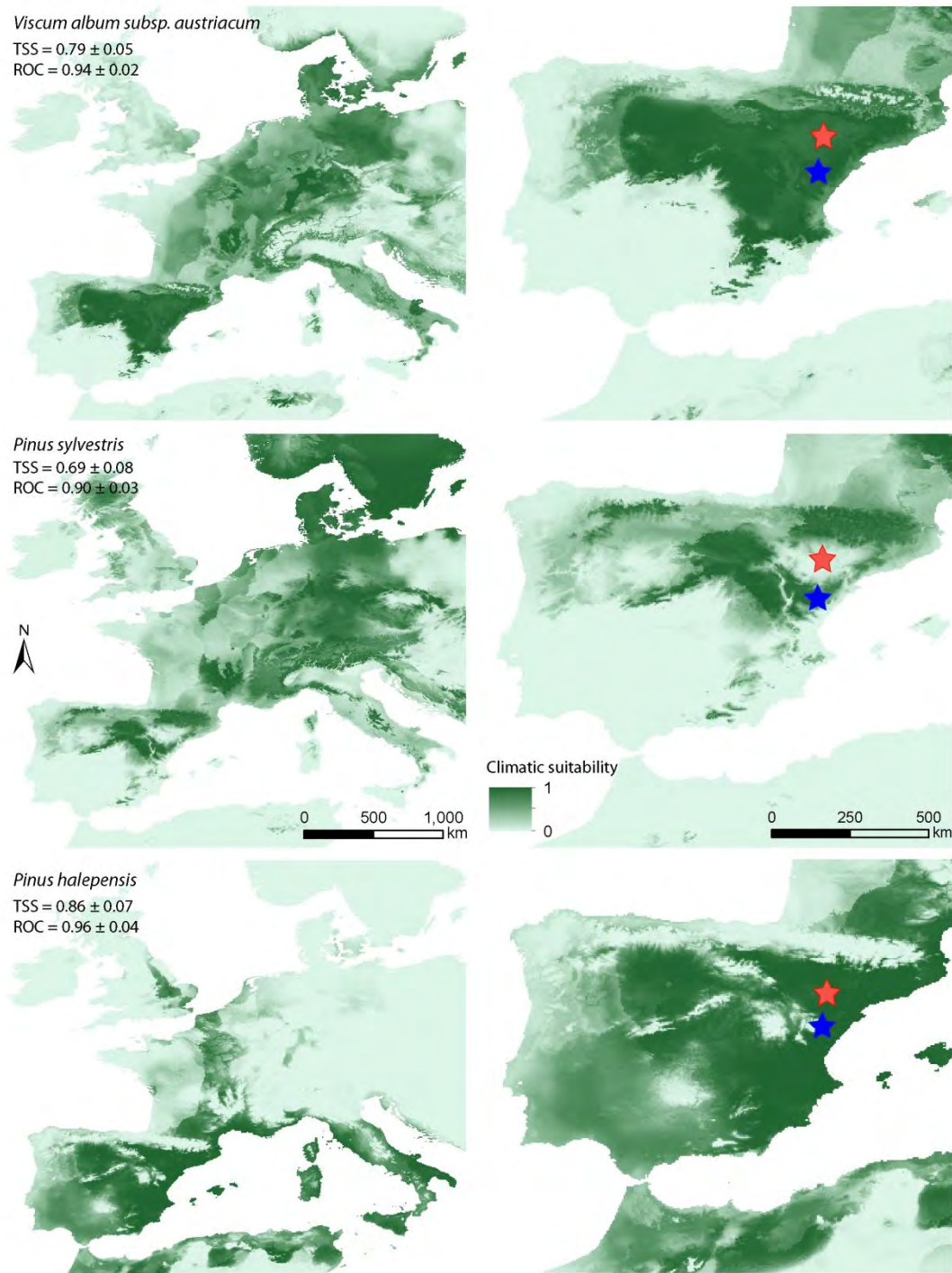
Fig. 1. Modelled climatic suitability for mistletoe and their two host tree species (Scots pine, *Pinus sylvestris*, and Aleppo pine, *Pinus halepensis*) across Europe and the Iberian Peninsula. Two statistics showing the fit (TSS, True Skill Statistics; ROC, area under the Receiver Operating Characteristic curve) are shown for each model (values are means ± standard deviations). The two stars show the sites with physiological data (Scots pine stand, blue star; Aleppo pine stand, red star) studied in NE Spain.
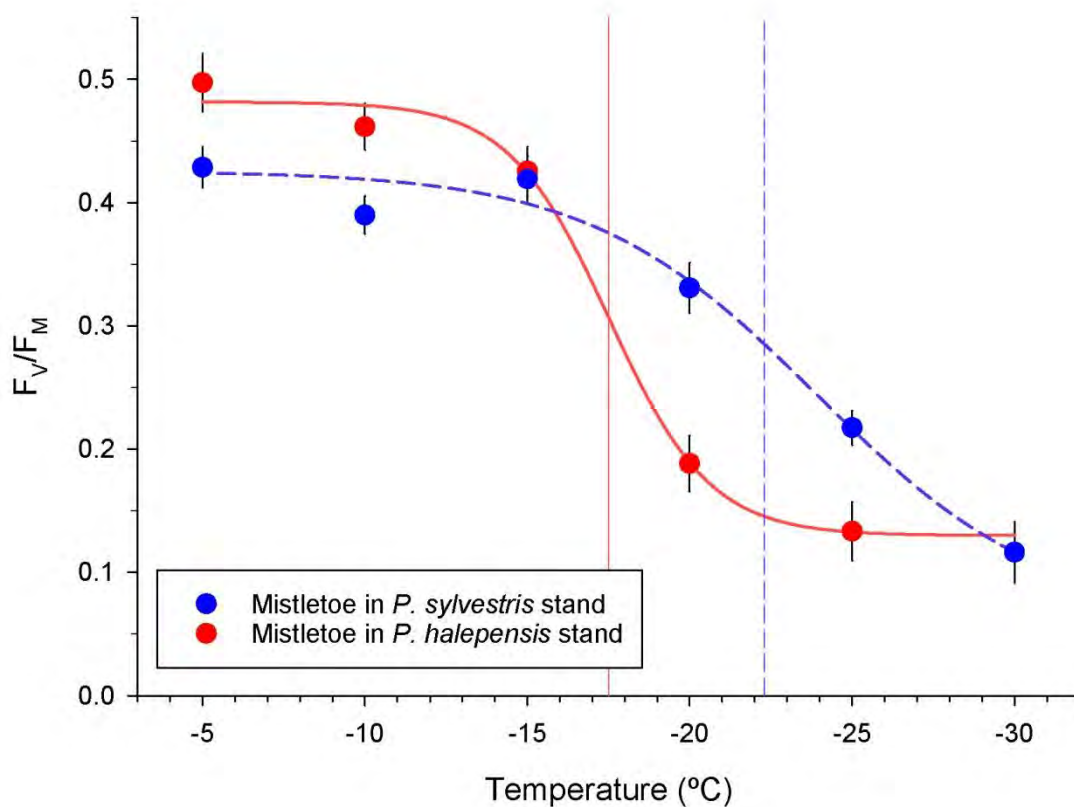
Fig. 2. Relationships between air temperature and maximum potential PSII efficiency (F_v/F_m) in mistletoe leaves from a wet-cold Scots pine (*Pinus sylvestris*) forest and a dry-warm Aleppo pine forest (*Pinus halepensis*). Note the change on x-axis in order to indicate the increase in low temperatures. Error bars indicate the standard error of the mean values. Fitted lines show the long-term tendency of F_v/F_m values. Vertical lines represent the threshold of PSII efficiency reduction.
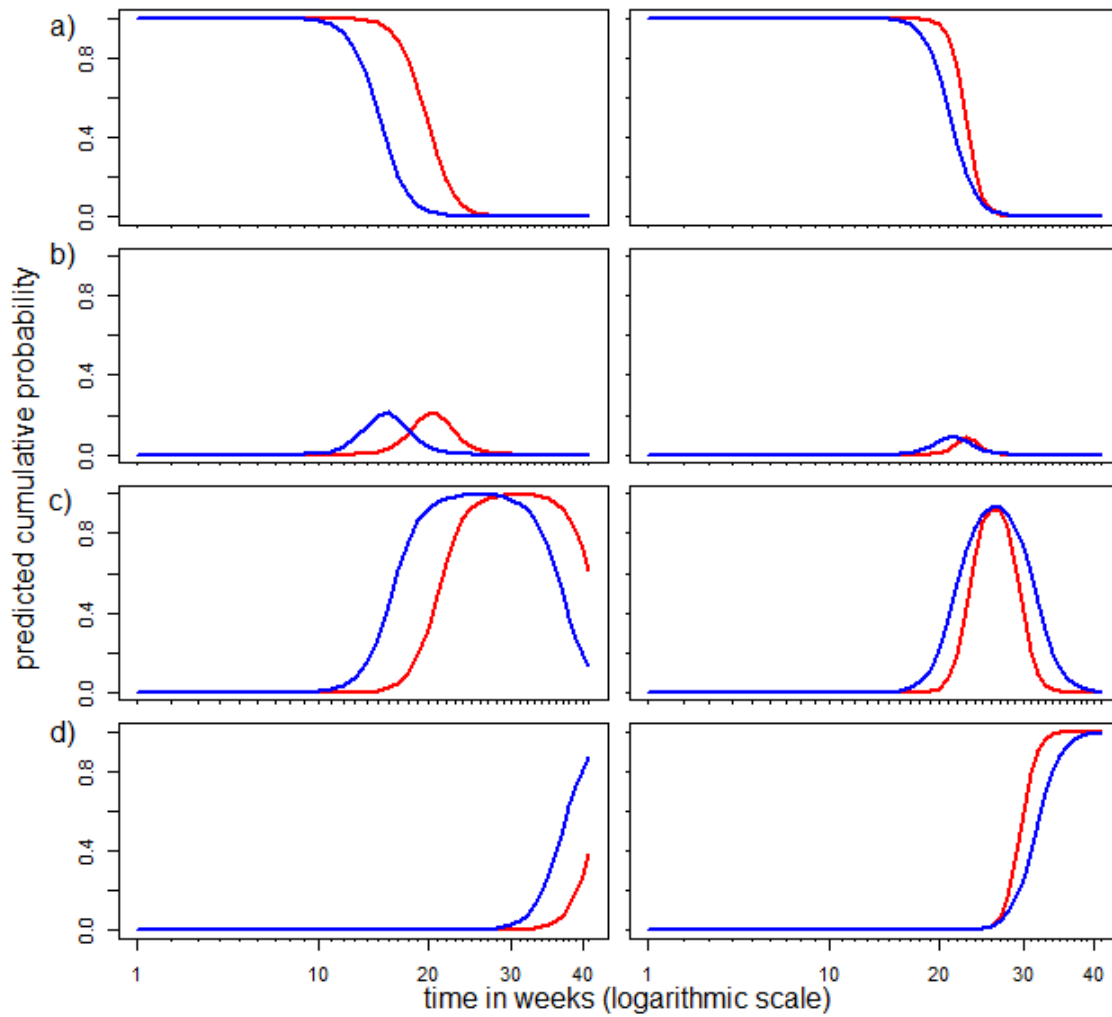
Fig. 3. Predicted cumulative probability for mistletoe seed germination and seedling establishment and dead through time in the Scots pine (*Pinus sylvestris*, left-column plots) and Aleppo pine (*Pinus halepensis*, right-column plots) sites. For each site, the cumulative probability to find a seed in a stage across time is shown. The different stages are: a) non-germinated seed; b) germinated seed; c) established seedling; and d) dead seedling (see stages in Fig. S3, Supporting Information). The two colours indicate the origin of the seeds: Scots pine (blue lines) and Aleppo pine (red lines) sites.
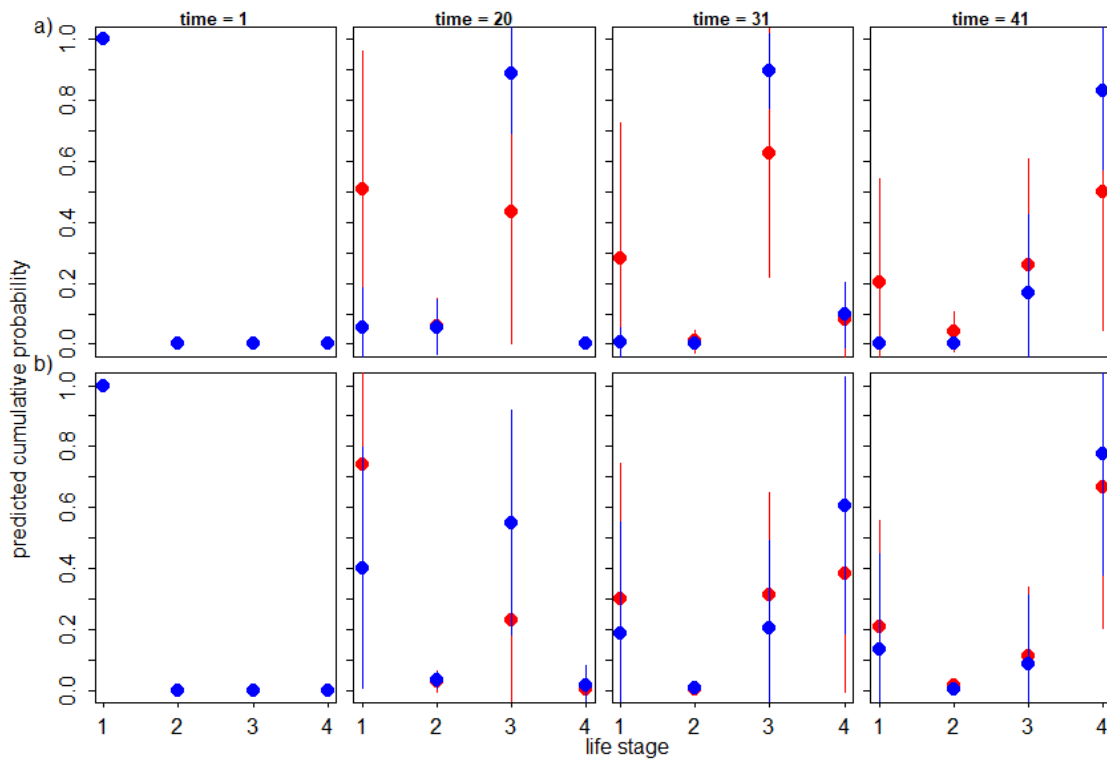
Fig. 4. Predicted cumulative probability for seed germination and seedling establishment and dead through time (weeks) in the (a) Scots pine (*Pinus sylvestris*) and (b) Aleppo pine (*Pinus halepensis*) sites. The cumulative probability to find a seed in a stage across four particular sampling times (weeks 1, 20, 31 and 40) is shown. The different seed stages are: 1) non-germinated; 2) germinated; 3) established; 4) and dead (see stages in Fig. S3, Supporting Information). The two colours indicate the origin of the seeds: Scots pine (blue symbols) and Aleppo pine site (red symbols). Vertical bars correspond to the standard error.