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Research

Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain)

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Altitudinal upward shifts of species' ranges have occurred across a wide range of taxonomic groups and geographical locations during the twentieth century in response to current climate warming. However, actual data of plant species' altitudinal shifts are still scarce and not always clear. Here we provide a more detailed investigation of a previously reported European beech *Fagus sylvatica* forest altitudinal shift in the Montseny Mountains (Catalonia, NE Spain) now based on field photographic survey and on the population age structure and the recruitment patterns in the high *Fagus* limit (HFL), the central forest area (CFA) and the low *Fagus* limit (LFL). Monitoring of the lowest altitudinal range shows that beech forest is being progressively replaced by Mediterranean holm oak forest. Holm oaks are characterized by recruitment rates more than three times higher than those of beech in the LFL in the last decades. The percentage of young individuals in the LFL is only half that in the HFL and CFA. In the highest altitudinal range, present day and early 20th century photographs show that the HFL has gained density and has shifted altitudinally upwards, advancing with establishment of new, vigorous outpost trees (13 individuals per each 100 m of tree-line). They are mostly (89%) younger than 35 yr old and mostly (97%) located up to 70 m (with a few up to 105 m) ground surface distance above the current tree line (36–51 m altitude) at the highest altitudes (1600–1700 m). The beech forest upward shift is a likely consequence of warming, but land-use practice changes (cessation of burning by shepherds) have made it possible. These changes in vegetation distribution and population structure constitute a new indication of the complex global change effects on life in mountain ecosystems.

As a result of past climate warming events, plant species and biomes have shifted towards the poles or higher altitudes (Gates 1993). It is increasingly accepted that, across a wide range of taxonomic groups and geographical locations, species' distributions have changed during the twentieth century in response to current climate warming (IPCC 2001a, Walther et al. 2002). Numerous studies have reported shifts of species altitudinal ranges in response to recent warming (Wardle and Coleman 1992, Grabherr et al. 1994, Meshinev et al. 2000, Kullman 2001, 2002, 2003, Sturm et al. 2001, Lloyd and Fastie 2003, Peñuelas and Boada 2003, Sanz-Elorza et al. 2003) although some studies failed to find such changes (Camarero and Gutiérrez 2004, Wang et al. 2006). Exact and detailed measurements to document altitudinal shifts in woody species, however, are rare.

We recently reported an upward altitudinal shift of the temperate beech forest during the 20th century in response to climate and land use changes in the Montseny Mountains in Catalonia (NE Iberian Peninsula) (Peñuelas and Boada 2003). The European beech forests at medium and highest altitudes (800–1700 m a.s.l.) of the Montseny Mountains constitute one of the ecotonic southernmost distribution areas of *Fagus sylvatica* (beech) forest in western Europe (Bolòs

1983, Bolòs and Vigo 1990). At lower altitudes of these mountains (< ca 800 m a.s.l.) the vegetation is typically Mediterranean, with dominance of the *Quercus ilex* (holm oak) forests. As the beech forests of Montseny represent an extreme of the distribution of this species (Fig. 1), they are especially sensitive to environmental changes such as climate and land use change.

Average annual temperatures in Montseny have increased by ca 1.5°C since 1950 while the total amount of annual precipitation remained unchanged (Boada 2001, Peñuelas et al. 2002, Peñuelas and Boada 2003, Jump et al. 2006a) (Fig. 2). As a consequence, the flora and fauna of this region have shown significant alterations in their life cycles during the last five decades (Peñuelas and Filella 2001, Peñuelas et al. 2002), and apart from the above mentioned beech forest shift, northward shifts in geographical ranges of its butterfly species have been reported (Parmesan et al. 1999). The Montseny Mountains have also been subjected to important land use changes during the last decades, including their declaration as a Natural Park in 1977 and a UNESCO Biosphere Reserve in 1978. This declaration, together with the decrease in firewood demand due to its substitution by fossil fuels (1960s–1970s) represented the cessation of traditional management practices such as burning by shepherds and coppicing for charcoal.

Population structure at the tree-line ecotone is a good indicator of climate change (Payette and Filion 1985, Weisberg and Baker 1995). Upper tree lines often respond to climate warming with increases in

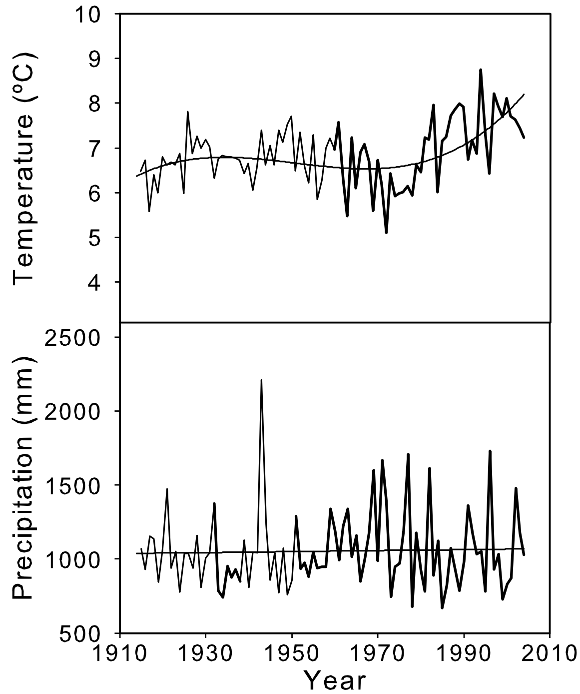

Fig. 2. Mean annual temperature and total annual precipitation during the period 1914–2003 for Turó de l'Home, the highest peak of the Montseny Mountains (bold solid lines: data from climate records, non-bold solid lines: interpolated data from climate records from neighbouring meteorological stations). Temperatures show a significant warming trend beginning in the mid-1970s whereas no trend is seen for precipitation.

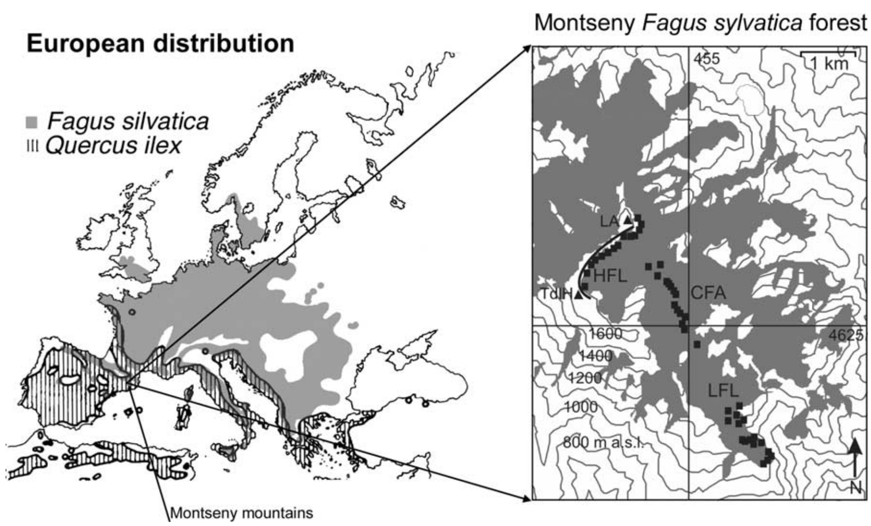

Fig. 1. The distribution of European beech *Fagus sylvatica* (wet temperate biome), and holm oak *Quercus ilex* (Mediterranean biome) in Europe (Bolòs and Vigo 1990) and location of the plots in the three sites: high *Fagus* limit, HFL, central forest area, CFA, and low *Fagus* limit, LFL, in the Montseny Mountains, Catalonia, NE Spain. The bold line represents the area studied for outpost trees. The symbols used to represent the plots (20 × 20 m) are not to scale in the figure.

recruitment (Kullman 1986, 1990, Payette and Lavoie 1994) or tree-density (Szeicz and Macdonald 1995, Camarero and Gutiérrez 2004) as well as upward advances (Bradley and Jones 1993, Camarero and Gutiérrez 2004). We aimed to further explore the upward altitudinal biome shift previously described in the Montseny Mountains. We hypothesized that the warmer current climate translates into better conditions for recruitment and growing of beech at its upper limit and facilitates the upward expansion of its population, while at lower limit decline in growth and regeneration is to be expected resulting in replacement of beech trees with more warm-loving Holm oak trees. With the aim of testing these hypotheses, we conducted an intensive study of the population age structure and recruitment patterns in the high *Fagus* limit (HFL) at 1600 m (1591–1626 m), the central forest area (CFA) at 1200 m (1196–1241 m) and the low *Fagus* limit (LFL) at 950 m (858–1063 m), and assessed size and distribution of outpost trees above the upper tree-line. These data were supplemented with newly available photographic evidence from the 20th Century and visual monitoring and description of current upper tree-line and lower beech forest limit.

Materials and methods

Study site and meteorological data

This study was conducted at the southern edge of the distribution of *F. sylvatica* in Europe in the Montseny Mountains, 50 km north-northwest of Barcelona (Catalonia, NE Spain) (Fig. 1). The study area, the Montseny Mountains, (longitude 2°16′–2°33′E, and latitude 41°42′–41°52′N), is sited in the Mediterranean region. However, the climate at the highest altitudes (from 1000 to 1700 m) is wet temperate. The average rainfall is ca 1000 mm, and the mean annual temperature is ca 7°C at the top of these mountains (1712 m a.s.l.; Fig. 2). *Fagus sylvatica* forest occurs in the wet temperate zone of the mountains, typically above 1000 m a.s.l. Below this, the vegetation is Mediterranean, dominated by *Quercus ilex* (holm oak) forest. *Fagus sylvatica* forms the tree line on the highest peaks of the region (Turó de l'Home and Les Agudes 1712 and 1706 m a.s.l. respectively). The *F. sylvatica* forest is a naturally occurring, uneven-aged high forest that has been managed at low intensity by the selective removal of large trees, coupled with natural regeneration from seed. However, the impact of forest management on the upper and lower limits of the *F. sylvatica* forest has been low (Peñuelas and Boada 2003). A detailed description of the vegetation of Montseny and its altitudinal zonation is presented by Bolòs (1983). Soils of the Montseny *F. sylvatica* forest are typically Dystric Regosols and Dystric Cambisols established over schist and granodiorite lithology.

Climate data (mean annual temperature and total precipitation) were obtained from the Turó de l'Home meteorological station (1712 m a.s.l.), directly above our HFL and outpost trees study site (1600–1700 m a.s.l.). Mean annual temperature and total annual precipitation records were available for the period 1952–2003 (Fig. 2). Climate data from 1910–1951 were interpolated from monthly climate records from neighbouring meteorological stations (Jump et al. 2007).

Past and current distribution of the European beech forest. Population age-size structure and recruitment and current outpost trees

We studied three sites identified here as the upper treeline (high *Fagus* limit or HFL), central forest area (CFA) and low *Fagus* limit (LFL) (Fig. 1). These sites were in closed forest in areas without signs of recent disturbance and situated at the upper tree line, a central area of the forest interior and the low limit of *F. sylvatica* respectively. The HFL and LFL sites were on steep rocky slopes whereas the CFA site was predominantly on level ground with deeper, less stony soils around the Santa Fe river. The reason for doing this originally was to pick a site where there was no immediately obvious climatic limitation – i.e. water availability could have been low if we had chosen a steep rocky section of central altitude. In fact although the soils are deeper in the CFA the plant community is still the same and the plant community is a good indicator that the environmental conditions (particularly soils) are fairly similar.

We measured population size-age structure and recruitment in the HFL, CFA and LFL by sampling 15 plots (20×20 m^2) randomly located throughout 2 km of forest at each site (Fig. 1). The diameter of each tree at 10 cm height was measured and all trees of each species were grouped into 5-cm diameter interval size classes in every plot. Finally, we also measured the distances of the outpost trees to the tree-line between Les Agudes and Turó de l'Home peaks and their stem diameter at 10 cm. Owing to the uneven form of the tree-line (higher in some places, lower in others), we measured any distances directly down slope to the tree-line. We used an age-diameter relationship calculated from previously developed tree-ring chronologies (Jump et al. 2006a) to approximate tree ages.

We used non-parametric Kolmogorov-Smirnov tests to compare population size and age structures at the HFL, CFA and LFL sites, and ANOVAs and Bonferroni post-hoc tests to test differences in recruitment and tree frequencies of the different size-age classes at each one of these altitude-sites. The percentage distribution of stem diameter classes (standardisation of the number of individuals of each class by the number of censused trees) of *Fagus sylvatica* population on the different altitudinal sites, the HFL, CFA and LFL, were also calculated and statistically analysed. Statistical analyses were conducted using Statistica (StatSoft, Tulsa, OK, USA).

We also present here rediscovered old photographic evidence of tree-line position and forest structure at the tree-line during the 20th and early 21st century and visual monitoring and description of current upper tree-line and lower limit for documenting spatial shifts of beech forest limits.

Results and discussion

Warming in the last decades

During the last fifty years mean annual temperatures have increased ca 1.5°C both at the top and the base of the Montseny mountains (Fig. 2, Peñuelas and Boada 2003, Jump et al. 2006a). The main temperature increase occurred during the last thirty five years, as it also has occurred worldwide (IPCC 2001b, 2007). Linear trend analysis did not reveal a significant change in rainfall during the observation period (Fig. 2, Jump et al. 2006a). Therefore the increased temperatures and consequent increased potential evapotranspiration rates have led to progressively more arid conditions.

Beech forest replacement by holm oak forest at medium altitudes

At medium altitudes of Montseny Mountains (800–1200 m), and especially on south-facing slopes with higher solar irradiation and temperature, beech is being replaced by holm oak, an evergreen Mediterranean species better adapted to cope with the currently warmer and drier conditions. We here found further evidence to that reported in the previous study (Peñuelas and Boada 2003). Visual inspection shows that individual beech trees suffering crown damage and death of major limbs are common and both, visual inspection and population structure measurements show a displacement of the beech understory by holm oak at the lowest altitudinal range of distribution (Fig. 3–4). A similar impact is seen on *Quercus petraea* (sessile oak) forest located at ca 800–1200 m (Panareda 1996) whose understory has now been occupied by dense holm oak short tree canopies.

In the population size-age structure and recruitment survey in the HFL, CFA and LFL, we censused 1349 trees (787 beech trees), split among 45 plots over the three sites. HFL plots had 211 beech individuals, CFA 420, and LFL 156. In this survey of population structure, the distribution of individuals over the range of tree sizes represents the change in the rate of tree recruitment and mortality over time (Harcombe 1987). Following relatively high numbers of individuals in the youngest size class, beech sample plots at the CFA show a relatively stable size structure until the 50 cm size class is reached when mortality increases (whether through

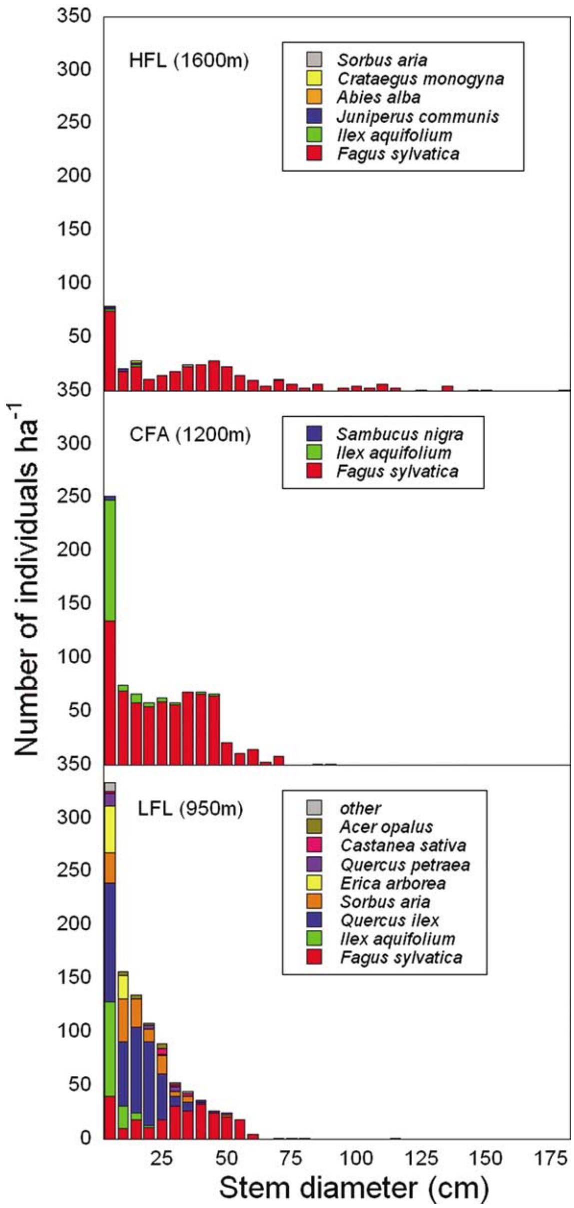

Fig. 3. Size structure of forest population. Number of individuals of the different species present in the high *Fagus* limit (HFL), central forest area (CFA) and low *Fagus* limit (LFL) as a function of the stem diameter.

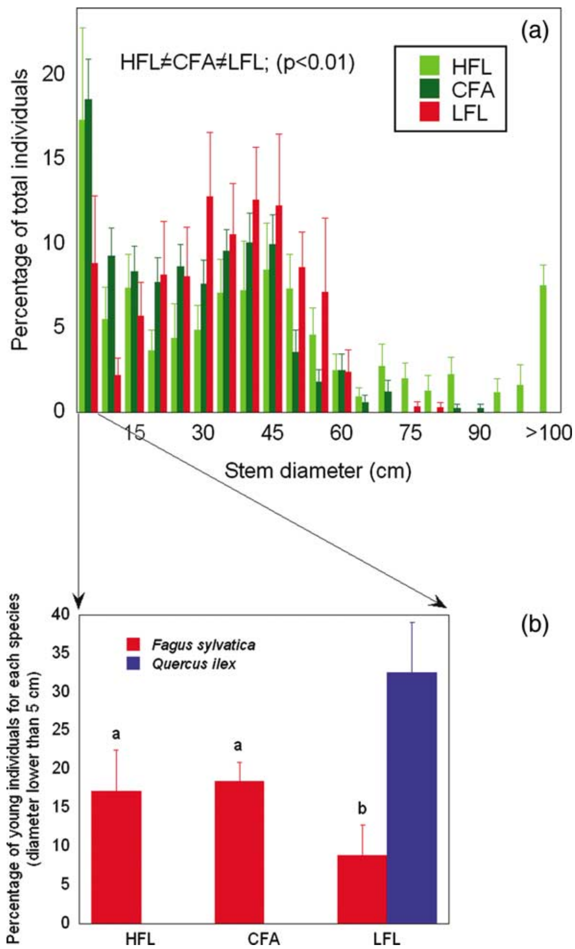

Fig. 4. (a) The percentage distribution of stem diameter classes of *Fagus sylvatica* population on the different altitudinal sites, the high *Fagus* limit (HFL), central forest area (CFA) and low *Fagus* limit (LFL). (b) Percentage of young individuals relative to the total number of censused individuals (diameter lower than 5 cm – younger than ca 20 yr) in the HFL, CFA, and LFL. (a) Compared with the CFA, the size and age structure of LFL and HFL transects were significantly different ($p<0.05$, Kolmogorov-Smirnov test). (b) Different letters indicate significantly different percentages ($p<0.05$) in Bonferroni post-hoc test ANOVA.

natural causes or selective removal of large trees) leading to a substantial reduction of the number of individuals in larger size classes. This stable size structure following initially high mortality of juvenile trees in the smallest size class is typical of long-lived tree populations growing under near optimum conditions (Wang et al. 2004). At the LFL and HFL however, a bell-shaped size distribution follows the early period of high juvenile mortality. This abnormal size structure is indicative of the impacts of limiting factors (such as unfavourable climate, pest and pathogen outbreaks) causing a dramatic reduction in recruitment success during particular historical periods (Wang et al. 2004). Compared with the CFA, the size and age structure of LFL and HFL transects were significantly different ($p<0.05$ in all comparisons, Kolmogorov-Smirnov test). The relative abundance of new beech individuals (diameter lower than 5 cm – younger than ca 20 yr) in the LFL is half that in the CFA and the HFL ($p<0.05$, Bonferroni post-hoc test ANOVA) (Fig. 4). It should also be noted that whereas in larger size classes (20–55 cm) the relative abundance of trees at the LFL was generally higher than at the HFL, this situation is reversed in smaller size classes, indicating a substantial drop in abundance at the LFL in more recent years. In addition to reduced relative beech recruitment, very high recruitment of holm oak is seen in small size classes at the LFL (Fig. 3 and 4). Holm oaks present relative recruitment rates more than three times those of beech in the LFL in the last decades (Fig. 4). There has also been a very high recent recruitment of *Ilex aquifolium* in the CFA and in the LFL.

This shift towards reduced recruitment at the LFL can be partly explained by the impacts of high temperature on recruitment success at the lower limits of the *F. sylvatica* distribution linked to recent temperature changes (Peñuelas and Boada 2003, Jump et al. 2006a, 2007). Lower beech recruitment in these lower-altitude stands is likely to be linked to less adequate environmental conditions for germination and seedling survival and development in recent decades. Inadequate environmental conditions here also explain the growth decline reported in adult trees (Jump et al. 2006a, 2007). These inadequate environmental conditions in the LFL include not only climatic factors (warming and increased aridity) but also competition of lower altitude zonal vegetation (particularly *Q. ilex* and *I. aquifolium*, Fig. 3). But altogether warming and increasing aridity seem to play a stronger role than land use changes in all these processes at the LFL (Jump et al. 2006a, 2007). Grazing should favour beech, as sheep and goats feed on holm oak and not on beech (Bartolomé et al. 1998). Forestry practices never discriminated beech in favor of oak since these two species had similar economical value (Boada 2001). Moreover, the influence of management change should be negligible at the LFL since these lower altitude stands, like the HFL trees, have not been much managed given the low economical value beech individuals at the forest margins. Furthermore, there was neither recent harvesting or fires (there were no important fires in the beech forests and much less in the last three decades of park administration) that might have accounted for the previously reported decrease in the beech distribution area (Peñuelas and Boada 2003).

Beech forest upward shift.

The photographs show an upward shift of beech forest of several meters at the highest altitudes (1600–1700 m) in the last decades (Fig. 5). In these last decades, beech forests have replaced heathlands and grasslands (and a few coniferous trees, likely spruce *Abies alba* trees) and have reached some of the summits as shown by photographs taken in the 1920s, 1940s, and 2003 (Fig. 5). The older photographs show isolated trees, which may have been existing for more than a century at the upper limit of survival of beech, and now these trees are to be found in closed forest. In other words, the historic out-post trees have now largely become the current tree-line while outpost trees are now establishing upper the current tree-line. The recent establishment of beech both above the current tree-line and in uninhabited areas within it demonstrates that both the elevational response and particularly the density response are ongoing. In both of the first half 20th century photographs, scattered "outpost trees" can be seen well above the 1920s–1943 tree-line in both slopes, which were not sharp boundaries in 1943. Now there is a forest stand, most probably, a consequence of altitudinal shift of its upper limit. An alternative explanation might be that the forest was clear-cut when taking the early photographs and now we see a regenerated part. However, this would require that the majority of the trees in the areas that appear as forest expansion should be similar in age – either re-sprouts from stumps or even-aged stands from seed, which is not the case (Fig. 3–4). There was also a slight warming trend from 1910 to 1950 (Fig. 2). However, the old photos of Fig. 5 are not very clear and it is difficult to discern where the tree-line was. It seems the same in the 1920s than in the 1940s, except for the disappearance of the spruce trees.

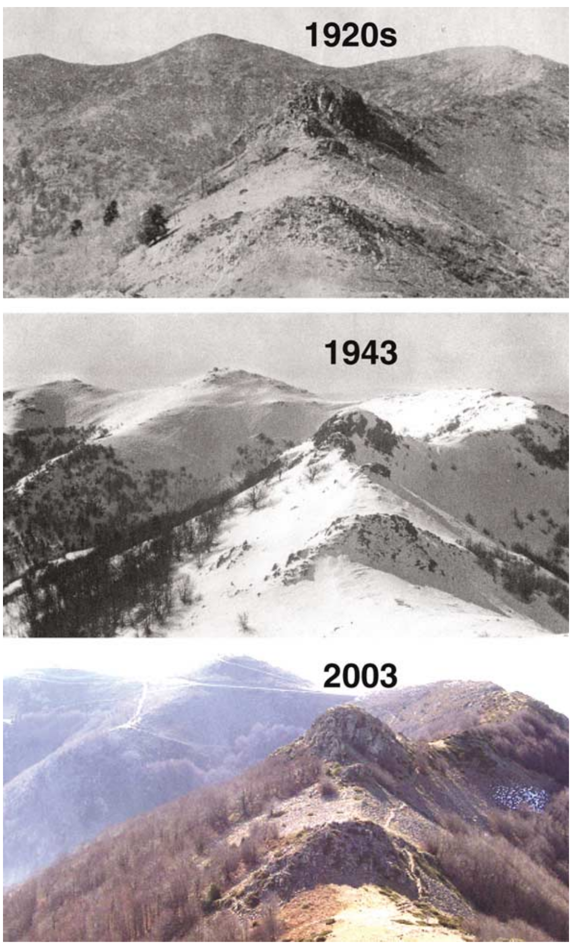

Fig. 5. Altitudinal upward shift of European beech forest towards the top (ca 1700 m) of the highest summits in the Turó de l'Home-Les Agudes ridge in the last century. The most evident change is the increase in tree size and density across the tree-line ecotone together with an upward shift of several meters in some areas. Another evident change is the disappearance of the few coniferous trees, likely *Abies alba*, remaining at the beginning of the century.

The current dense tree-lines include some fairly old multi-stemmed individuals (Fig. 6), but also young straight trunked, single stemmed individuals with trunk diameter at base of <10 cm (Fig. 6). Behind these tree-lines, the canopy is quite open in places and includes similar areas of recent recruitment and many areas with young straight-trunked trees (Fig. 6). In advance of any tree-line, outpost trees may have existed for many years and with the advance of the tree-line, these are now found within a closed forest stand. Tree-line advances include 1) an increase in density of canopy – through growth of old individuals with ameliorating climate and establishment of new individuals in areas between them, and 2) the establishment of new outpost trees beyond the tree-line and the current outpost trees. The historical photographs (Fig. 5), and the survey of the population structure and recruitment (Fig. 3–4, 7–8) indicate that the largest part of the response over the last 60 yr is a density increase. However, there is also establishment of new, vigorous outpost trees (currently 13 individuals per each hundred meters of tree-line), 97% of which located up to 70 m (distance on the ground corresponding to 31 m altitude) above the current tree-line at the highest altitudes (1600–1700 m) (Fig. 8). There are outpost trees exceptionally up to 105 m on the ground (corresponding to 52 m altitude) (Fig. 8). Therefore there has also been a major increase in the elevation at which the trees occur. Most of these outpost trees are newly established beech trees, 67% are estimated to be younger than 30 yr old, 89% younger than 35 yr old, and 93% younger than 40 yr old (Fig. 8).

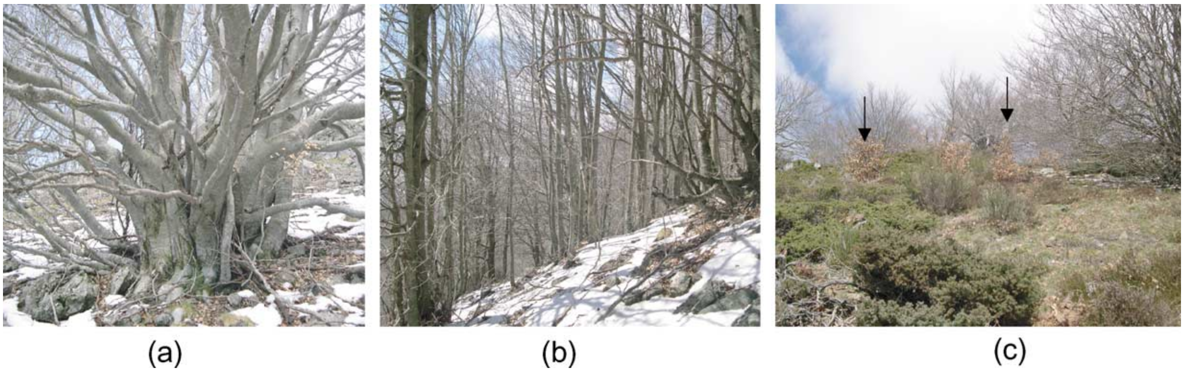

Fig. 6. In some ridges, both the tree-line and the area directly behind it include several old trees, sometimes multi-stemmed individuals (a), but they also include many much younger straight-trunked individuals (b). Behind the high forest line, in the open treeless areas, many young beech trees <10 cm diameter at base are now becoming established (c).

The ca 1.5°C increase in annual temperature seems a strong driver of this shift, particularly given the evidence of a positive response of tree growth and recruitment to high temperatures at the HFL reported by Jump et al. (2007). Grazing, which is another possible driver, has not changed in the last decades. There are now a lower number of herds but similar number of heads, and neither sheep nor goats feed on beech (Bartolomé et al. 1998). However, grazing associated activities such as shrub clearing and burning have decreased, as the area is now a natural park, thus facilitating the beech upward shift in response to climate change. Finally, the cessation of forestry practices does not seem to have had much influence in this area of the forest. Forestry practices favoring beech growth were not applied to this upper border of the forest since the typically very branchy individuals were always considered of bad quality and therefore of

Fig. 7. Current tree-line below the Turó de l'Home-Les Agudes ridge (a) and new recruits (outpost trees) above it (b).

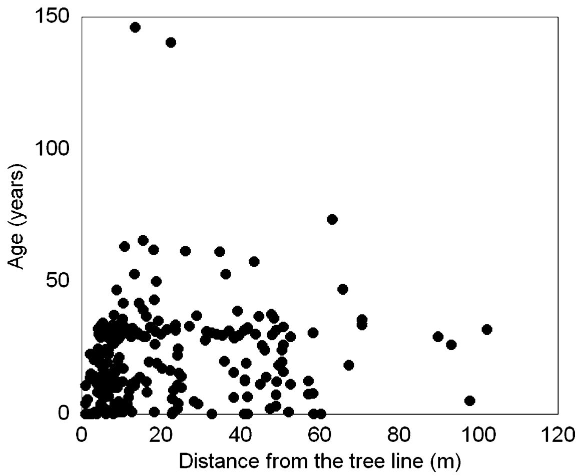

Fig. 8. Age and distance of the outpost trees above the current tree-line below the Turó de l'Home-Les Agudes ridge.

low economical value, analogous to the low value trees at the LFL. Therefore, of these possible driving factors, the most clear and convincing one is the progressive warming with a complementary favoring role of cessation of burning and shrub clearing by shepherds.

Plant species upward shifts like this one of beech in the Montseny Mountains have been reported in other studies (Wardle and Coleman 1992, Grabherr et al. 1994, Meshinev et al. 2000, Kullman 2001, 2002, 2003, Sturm et al. 2001, Lloyd and Fastie 2003, Sanz-Elorza et al. 2003) but there are also several studies that did not find obvious upward tree-line shifts in the past several decades (Camarero and Gutiérrez 2004, Wang et al. 2006). A tree-line ascent implies several processes: production of viable seeds, dispersal, availability of adequate regeneration sites, germination, seedling survival and persistence until individual adulthood. Climate change affects all these sequential stages, but not necessarily in the same direction, which may explain some of these different results. It has also been hypothesized that the different results may be the result of episodic recruitment/survival patterns at the tree-line. Tree-line would remain static until the climatic threshold is surpassed, which would result in sharp boundaries between the old and the new tree-lines (Camarero and Gutiérrez 2004, Wang et al. 2006). These varied responses to 20th century warming suggest that in addition to temperature, tree-line dynamics are mediated by species-specific traits and environmental conditions at landscape and local scales (Danby and Hik 2007). Tree-line advances since the early-20th century in other areas such as the southern Scandes of Sweden have been also observed to vary depending on species and site (Kullman 2006). Subalpine/alpine plant species have shifted upslope by average 200 m. Nevertheless, plants have migrated upslope with widely different rates, producing non-analogous alpine plant communities, i.e. peculiar mixtures of alpine and silvine species (Kullman 2006).

Final remarks

The changes in forest size structure and distribution that we report here are associated with negative responses to high temperature at the LFL, resulting in declining beech growth in the last decades (Jump et al. 2006a, 2007) and even changes in the forest genetic composition (Jump et al. 2006b); and conversely with positive responses of beech growth to temperature in the HFL. The beech replacement by holm oak at the LFL and the upward shift of beech forest at higher altitudes seem strongly linked to regional warming, but land-use changes (reduced burning and clearing by shepherds) have facilitated these changes in this species' distribution. It is likely that the other mountainous areas of the Mediterranean region will present similar shifts and species/biome replacements in response to climate and land use changes. Altogether, this accumulating evidence of rapid changes in the vegetation of Montseny Mountains provides a new indication of complex effects of global change on life in mountain ecosystems.

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