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The value of long-term history of small and fragmented old-growth forests for restoration ecology

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The long-term history of small and fragmented old-growth forests can provide insights into the legacies of past environmental changes and land-use history in the surrounding landscapes, which can support nature protection and restoration ecology measures.

The value of old-growth forests

Primary and old-growth forests are of great value for sustainable forest management and restoration. By virtue of their structural and compositional complexity, they are highly biodiverse when compared with managed forests in the same ecological region, as they offer a variety of microhabitats such as large pieces of coarse, woody debris, providing shelter to a range of taxa. These naturally regenerated forests of native trees are thought to have developed dynamically for a long period of time without large stand-replacing disturbances, and show no indication of human activities (Barredo et al. 2021). They offer unique opportunities to characterize the effects of natural disturbances and the structural heterogeneity emerging from natural forest dynamics. This is important knowledge to develop close-to-nature forest management practices aimed at emulating natural processes and features in second-growth forests (Schütz et al. 2016).

In Europe, primary and old-growth forests are very rare, generally small, fragmented, and less abundant (< 3% of the total forest area) than on other continents (Sabatini et al. 2018). Currently, these forests are embedded in landscape mosaics bearing variously managed patches that are sometimes strikingly different in species composition and structure. Thus, the small and fragmented ecosystems are threatened along fragment edges by land-use activities (e.g. logging) and anthropogenic disturbances (e.g. fire ignitions) that may initiate long-term changes to the structure of the remaining fragments, thereby hindering the development or the continuity of the old-growth forest stage.

Old-growth forests are typically late-successional forests that contain structures and species that are markedly different from forests of earlier stages. Their distinguishing features include high amounts of dead-wood, presence of old trees approaching their natural longevity (which is often much higher than the management rotation cycle for a given tree species), and a patchwork of heterogeneously aged stands arising through small-scale gap dynamics (Barredo et al. 2021).

The current old-growthness is generally assessed using field-based methods, such as dendroecology and forest surveys, and remote sensing (Barredo et al. 2021). However, these methods cannot provide information on the longer-term history of an area. Paleoecology, instead, is sometimes the best, and only, tool for documenting the continuity of forest ecosystems and the legacies of land-use history, climate change, and disturbances (such as fire) on present-day forest composition. This information is critical for clarifying conservation and restoration objectives because mosaic landscapes are often the result of legacy effects arising from complex interactions between natural and human disturbances (Whitlock et al. 2018). In this context, stand-scale paleoecology can be particularly valuable as it allows us to address the history of small and fragmented ecosystems (Bradshaw and Zackrisson 1990; Foster et al. 1996).

Old-growth forests remnants in the Balkans

The causes of the current fragmented distribution of old-growth forests in Europe is a long-standing question in ecology. They are arguably remnants of formerly larger extents of "primeval forests", "virgin forests", "climax forests", or "Urwald" that have been shattered due to major human imprints on forest ecosystems over past millennia (Birks and Tinner 2016). However, primary and old-growth forests are particularly abundant in some regions, such as the Dinaric Alps, possibly due to early protection of forests and lower historical human pressure compared to other mountain ranges in Europe (Sabatini et al. 2018). Indeed, this mountain region is characterized by rugged terrain and land with low agricultural productivity (Kaplan et al. 2009). Nonetheless, detailed records documenting long-term vegetation dynamics, in conjunction with environmental changes, are lacking for the montane zone in this region (Finsinger et al. 2017).

Legacies of past land uses at an old-growth forest's fragment edge

Cagliero et al. (2021) recently presented stand-scale paleoecological records, an assessment of contemporary forest structure, and dendrochronological data from the edge of the Biogradska Gora old-growth forest (Dinaric Alps, Montenegro), one of the largest in Europe. It provides new insights into the long-term dynamics of these fragmented ecosystems. Like other old-growth

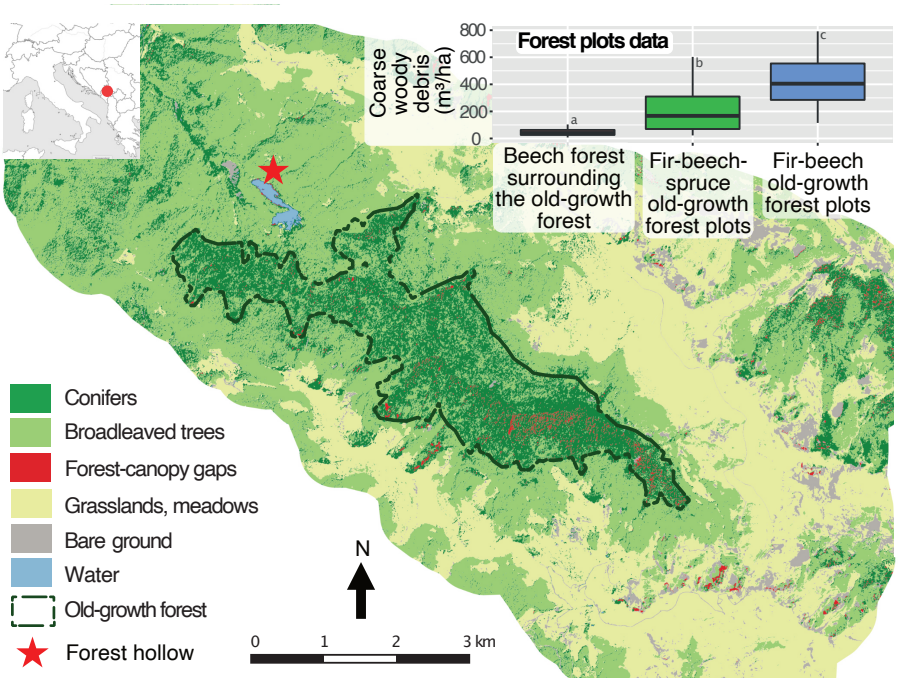

Figure 1: Distribution of land-cover types in the Biogradska Gora valley (Dinaric Alps, Montenegro). The boxplot shows the amount of coarse woody debris inside and outside of the old-growth forest (modified from Cagliero et al. 2021).

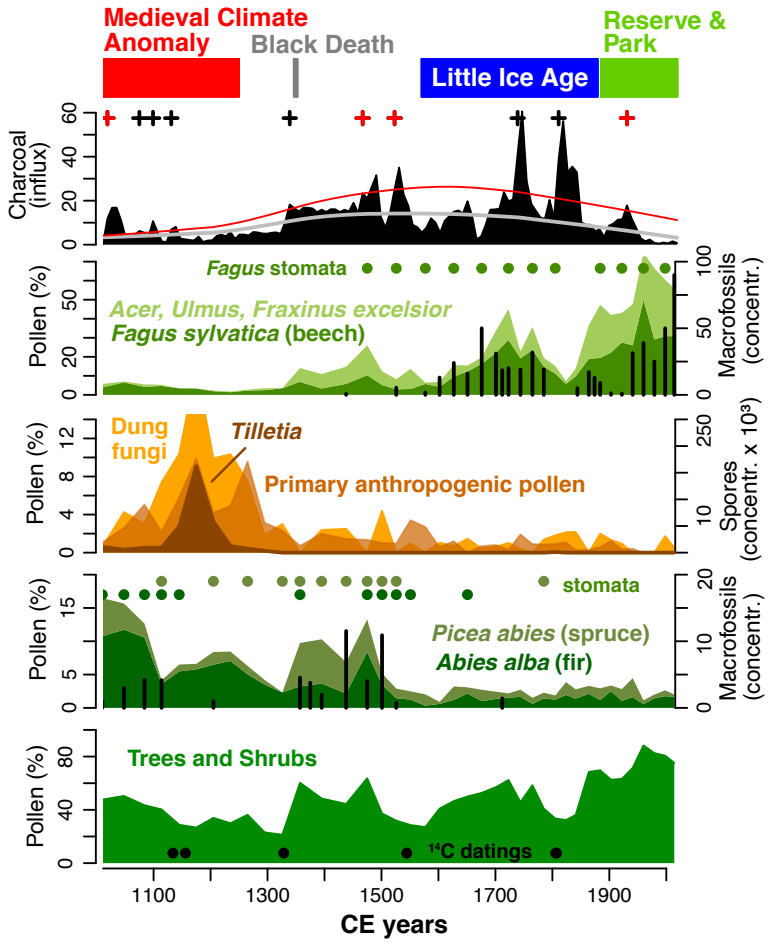

Figure 2: Local vegetation and fire-disturbance dynamics at the current edge of Biogradska Gora's old-growth forest as reconstructed with the sediments from a small forest hollow. The charcoal-influx graph includes the long-term trend of charcoal accumulation (grey line) and identified fire episodes (crosses; red crosses: higher-severity catchment fires). Pollen and spores (filled areas), stomata (full circles), and plant macrofossils (black bars) illustrate the vegetation dynamics and land-use history (primary anthropogenic pollen and *Tilletia* spores: cereal crop cultivation; cattle herding: dung-fungi spores). Full black circles (bottom) show the location of radiocarbon dates (modified from Cagliero et al. 2021).

forests in the montane zone of the Balkans, Biogradska Gora's old-growth forest is dominated by fir (*Abies alba*) and beech (*Fagus sylvatica*) with sparse spruce (*Picea abies*) (Motta et al. 2015). However, unlike many other old-growth forests, this one is surrounded by grasslands and meadows, and by almost pure beech stands. These stands are characterized by small, mostly multi-stemmed trees, the amount of coarse woody debris is negligible (Fig. 1), and charcoal kilns are present. By contrast, the fir-beech-spruce dominated old-growth forest has a mixed and multilayered structure shaped by gaps of different sizes, a large amount of coarse woody debris, and very large and old trees (> 500 years old), indicating that this part of the forest developed dynamically for a long period of time without human and natural stand-replacing disturbances.

The well-dated pollen, spore, stomata, plant-macrofossil, and charcoal records from a small forest hollow at the current edge of the old-growth forest (Fig. 1) document the reduction of fir and spruce during the Middle Ages, when the land was used for cereal crop cultivation and cattle herding, and after local, higher-severity catchment fires occurred (Fig. 2). This evidence supports the notion that historical land-use pressure reduced the extent of old-growth forests.

After intensive local land use ceased (in the mid-14th century, approximately at the time of the Black Death pandemic) and during the cooler Little Ice Age, beech-dominated stands developed in the area surrounding the old-growth (Fig. 2). The legacy of past land use is still visible as the almost pure beech stands show less old-growthness than other European beech-dominated old-growth forests. Conversely, the formal protection of the Biogradska Gora forest as a royal hunting reserve and as a national park since the late 19th century prevented intensive land use, and has strongly reduced biomass burned in recent times, which has allowed for the persistence of the beech stands in the buffer zone. This protected zone may offer a habitat for adaptation to future environmental changes, such as the expansion of the fir old-growth, as fir has more potential than spruce and beech under warmer and drier conditions (Vitasse et al. 2019).

Outlook

Old-growth forests have captured the attention of foresters and conservationists alike (Fröhlich 1930). However, there are still substantial conservation and restoration gaps, as primary and old-growth forests are only partially representative of the full range of European forest types (Sabatini et al. 2018).

Paleoecology, in conjunction with structural and dendrochronological research, can unfold the history of Europe's primary and old-growth forests. Thereby, their responses to past environmental changes, as well as legacy effects of past land use and of disturbances in surrounding landscapes, can be assessed. This may be important as strategies for the preservation and restoration of old-growth forests should acknowledge past environmental changes, including land-use history, and anticipate future environmental changes.

Although primary and old-growth forests are generally included in protected areas (Sabatini et al. 2018), they may be vulnerable to climate change and associated changing disturbance regimes (wind, pathogens, or fire; Seidl et al. 2017). For instance, several of the smaller old-growth forests that bear fire-sensitive species such as *Abies alba* may be at risk if fire-frequency becomes excessive. In this context, identifying and protecting primary and old-growth areas and their buffer zones, as well as protecting and restoring secondary forests that may represent future primary and old-growth ecosystems (Barredo et al. 2021; EU's Biodiversity Strategy for 2030: ec.europa.eu/environment/strategy/biodiversity-strategy-2030_en) could be of paramount importance to promote native forests. Such actions may likely increase ecosystem resilience to future climate change and be helpful to anticipate environmental changes (Henne et al. 2015).

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