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FOREST ECOSYSTEMS AND GLOBAL CHANGE: THE CASE STUDY OF INSUBRIA

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ABSTRACT – Forest ecosystems face multiple challenges due to climate change, invasive species, urbanization, land use change and the interactions between these global change drivers. This review provides an overview of such challenges for the case study of Insubria. Insubria is a region on the Southern side of the European Alps, famous for its stunning lakes (e.g., Como, Garda, Lugano, Maggiore), blessed by a relatively mild and humid climate, and shaped by the geologic fault line between the African and European plates. Global change impacts in Insubria pose a threat to its biodiversity and chestnut woodlands, particularly through modified winter forest fire regimes. Insubric biodiversity conservation, in turn, is essential to counteract the effects of climate change. Sustainable management of Insubric forests is made more difficult by rural abandonment, air pollution and invasive exotic species. There is a need to develop reliable long-term bio-indicators and to predict the shift of Insubric species, ecosystems and treelines due to rapid climate changes. Insubric studies on forests and global change call for enhanced international collaboration in forest management and research. Interdisciplinary approaches are needed to move from studies of single global change drivers to experiments, scenarios and models taking into account their combination and our responses to global change.

KEYWORDS: *CASTANEA SATIVA*, ECOSYSTEM MANAGEMENT, FOREST CANOPIES, HUMAN POPULATION IMPACTS, ITALY, LANDSCAPE ECOLOGY, OZONE POLLUTION, SWITZERLAND

INTRODUCTION

Forest ecosystems are challenged worldwide by a series of concomitant processes (e.g., climate shifts; land use change including urbanization; water, air and soil pollution; habitat fragmentation and degradation; increased long-distance trade and the associated introduction of exotic species). These processes and their interactions can be summarized under the umbrella term of 'global change' (Vitousek, 1994; Ayres & Lombardero, 2000; Lascar, 2012). Just as with climate change, global change is and will be affecting not only forests, but also other ecosystems and the eco-boundaries between them (Beaumont et al., 2011). Forests are particularly vulnerable to these processes, due to the long-term nature of their main structural components (trees). Trees are generally long-lived organisms that live their entire life at a certain location (Lanner, 2002; Petit & Hampe, 2006; Bertogliati & Conedera, 2012; Di Filippo et al., 2012). Tree species, populations and individuals can thus only slowly catch up with rapid shifts in climate, fire frequencies and human use of the land (Breed et al., 2011; Zhu et al., 2012; Bräutigam et al., 2013). There is evidence that, worldwide, forests are already suffering due to global changes, as suggested by increasing tree mortality rates associated to drought in various regions (Allen et al., 2010; Carnicer et al., 2011; Zeppel et al., 2013) and by increased impacts of wind, bark beetles and wildfires on forests in Europe (Seidl et al., 2011b) and bark beetles in North America (Bentz et al., 2010).

There is a consensus that the various global change drivers and their interactions are posing a severe threat to biodiversity worldwide. Biodiversity conservation, in turn, is fundamental to safeguard the resilience of ecosystems to environmental changes. This follows from the relationship between biodiversity and the provision of ecosystem

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services without genetic, specific and ecosystem diversity, landscapes lose their capacity to provide clean water and air, safe food and other primary resources, as well as recreation potential and other services. There is thus a growing recognition that landscape, ecosystem, forest, plant, soil, crop and animal health are not independent of each other (Borer et al., 2011; Döring et al., 2012; Pautasso et al., 2012a), and may well be ultimately related to human well-being (Eriksson et al., 2012; Gòmez et al., 2013; Schirpke et al., 2013).

Many studies on the effects of the single global change factors on forest ecosystems are appearing (Pautasso et al., 2010; Beier et al. 2012; Wang et al., 2012). Given the amount of the literature produced, there is a tendency of global change scientists to be aware only of the slice of the literature relevant to the factor they are studying, despite the many potential interactions with other global change drivers (Lavorel et al., 1998; Brook et al., 2008; Ibáñez et al., 2013). Some studies are starting to consider the interactions among global change drivers, although this is often achieved by focusing on a single species, rather than on whole ecosystems or on species interactions (Tylianakis et al., 2008; Eastburn et al., 2009; Matesanz et al., 2009). Given that global change drivers are not likely to act in isolation, there is the need to consider their potential interrelations (Pías et al., 2010; Seidl et al., 2011a; Standish et al., 2012).

The aim of the present review is thus to provide an overview of the potential effects on forest ecosystems of global change factors and their interactions, focusing on Insubria as a case study. The rest of this paper introduces the essential features of the Insubric region, summarises historic human impacts on Insubric forests, and provides an overview of the current threats to the biodiversity of the region, with special emphasis on chestnut woodland and winter forest fires. The review then describes how climate change is likely to affect Insubric forests, alone and in combination with air pollution and species introductions. The paper concludes with the need for enhanced international collaboration in the study of global change drivers, and with research gaps and opportunities for global change research in Insubric forests and beyond.

The Insubric region

The Insubric region is a multiple interface. Geographically, Insubria connects the Southern side of the European Alps with the Po Valley and the Mediterranean. It thus juxtaposes long Alpine winters on its mountains with luxurious vegetation on the shores of lakes repeatedly carved during the ice ages. Geologically, the Insubric fault line provides a dynamical boundary between African and European plates. Hence, Insubria shows a diversity of parent materials, most importantly both calcareous and siliceous substrates (Furrer, 1950; Fig. 1a). Politically, the region is subdivided by a convoluted boundary between Italy and Switzerland.

Insubria is characterized by a climate which is peculiar enough to have received the name of Insubric. The essential features of Insubric climate are:

- high annual precipitations (more than 1800 mm in its Western part; Fig. 1b),
- humid summers,
- relatively mild winters due to the thermal buffer capacity of the lakes,
- and spells of a dry and warm catabatic wind (the föhn) blowing from the North especially in winter (Paul & Holdenrieder, 2000; Spinedi & Isotta, 2004).

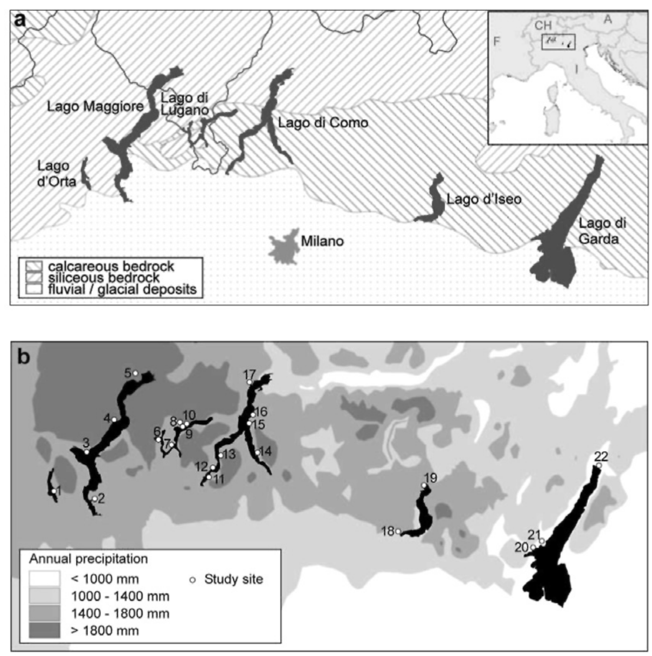

Fig. 1. Two maps of Insubria (from Berger & Walther, 2006; with kind permission of Springer). Panel (a) shows the major N-S division in geological substrates, panel (b) shows the W-E gradient in precipitation. The location of study sites shows a focus of attention towards the Western part of Insubria.

Although some of these climatic features are present in other Alpine regions, the combination is rather unique to Insubria. Given its mild climate, Insubria is often a region of preferential colonization by exotic species and a hotspot of first reports of new species (Bolay & Mauri, 1988; Martini, 1991; Germann et al., 2008; Forster et al., 2009; Prospero & Rigling, 2012). Although the contributing role of factors such as urbanization, maturing of garden/park trees, and forest fires should not be overlooked (Walther, 2000), many exotic species are facilitated by the relatively mild and wet climate

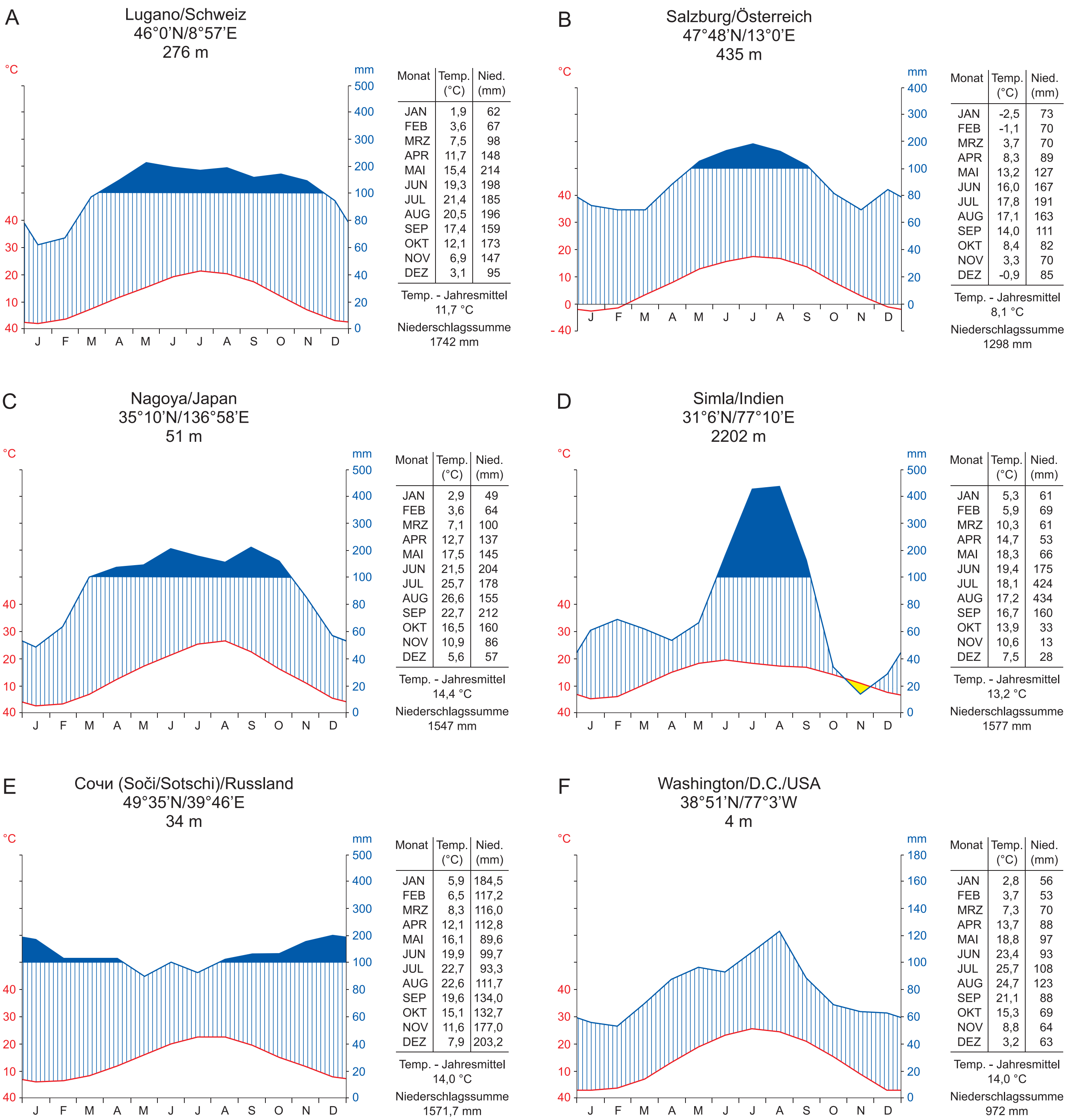

Fig. 2. Climate diagrams (with kind permission of Wikimedia Commons) for (A) Lugano (Insubric region, Switzerland) in comparison with (B) Salzburg (Austria, North of the Alps - similar summer peak in precipitation, but colder climate), (C) Nagoya (Japan - similar precipitation distribution and amount, but warmer climate), (D) Simla (India, Himachal Pradesh - precipitation concentrated in the summer monsoon, mountain subtropical climate), (E) Sotschi (Russia, on the Black Sea at the foot of the Caucasus - precipitation peaking in winter, rather than summer), and (F) Washington, DC (USA - similar precipitation pattern, but lower amount; warmer summers).

encountered in the Insubric region and limited by the markedly colder winter still found on the Northern side of the Alps. Exotic evergreen species may also be particularly successful in Insubria due to the absence in this region of many Mediterranean plant species (possibly due to the barrier posed by the intensively cultivated Po plain (Viaroli et al., 2010), which features a sub-continental climate). Some sub-Mediterranean plant species, however, are present in

Insubria; they may have arrived in previous centuries during spells of warmer climate (Parolo et al., 2005). The issue of whether such chance effects may play a role in current impacts of invasive species emphasizes the importance in global change research of historic legacies (Essl et al., 2011).
Insubria is not only characterised by a climate combining Mediterranean (absence of strong winter frost) and oceanic features (rarity of summer drought) (Maggini & Spinedi, 1996), but also by steep gradients typical of mountain regions. The Insubric region switches from Alpine conditions to mild lakeshores in a matter of a few kilometres. This results in a marked small-scale topographical heterogeneity, which in turn implies a mosaic of different expositions. Small-scale variation in exposition may have an important role in the resilience of mountain ecosystems to the predicted rapid climate warming (Randin et al., 2009; Wiens & Bachelet, 2010; Scherrer & Körner, 2011). The question arises of whether the peculiar Insubric climate (Fig. 1b, 2a) will still be recognizable at the end of the 21st century. Prediction of and preparation to climate change in Insubria is complicated by this region showing a high uncertainty of models about the direction of future climate shifts (Shaw & Osborne, 2011).

A short history of human impacts on Insubric forests

Human impacts on ecosystems in Insubria have been pervasive long before the arrival of global change. This legacy may make Insubric forests more resilient to further human pressures, but it might also be hypothesized that the historic impacts have made ecosystems more fragile to future destabilization. The second hypothesis is more likely to pertain if rural abandonment and urban densification continue unabated. Insubria was indeed characterized for centuries by a human density higher than what the local resources could sustain. Insubric farmers did not have to cope with summer drought as much as farmers in the more continental inner Alps (e.g. Valais) had to do (Ambrosetti, 1995; Kissling-Näf et al., 2002), but the narrow valleys were a limiting factor for agricultural production also in Insubria. This resulted over the last centuries in intensive land use (particularly on sunny slopes), the use of marginal alpine resources (e.g. pastures above the tree-line, which was generally lowered by human impacts), substantial emigration of young people (mainly to Northern Europe, America and Australia), seasonal migration of men (e.g. to work in towns in the plains), and a tendency to an endogamous system, which made it difficult for foreigners to immigrate (Lorenzetti, 2003).
Human influences on Insubric forests reach the most remote valleys (Boller et al., 2010) and go back to prehistoric times (Burga, 1988). After the last ice age, human beings quickly recolonized Insubric lakeshores and valleys, as documented by archaeological and palinological evidence (Antognini et al., 2008; Gobet et al., 2010). A similar process happened for lakes on the Northern side of the Alps, with phases of forest clearance and intensified land use along lakeshores taking place at the same time North and South of the Alps (ca. 1450-1250 BC, 650-450 BC, 50 BC-100 AD and 700 AD; Tinner et al., 2003). However, given that at any point in time the climate in Insubria is likely to have been warmer than on the other side of the Alps, human impacts on Insubric vegetation are likely to have been more intense than for Northern Switzerland (Tinner et al., 2005). The hypothesis that, regionally, human impacts on biodiversity are more intense with increasing temperatures has been confirmed using contemporary data for a number of regions and taxa (Barbosa et al., 2010b). A potential consequence of this pattern is that human impacts on Insubric biodiversity will become even more pronounced with the rising temperatures predicted over the next decades.
At about 7-6000 years BP, *Abies alba* (a tree species which is little resilient to fires, cutting and wood grazing) declined and then disappeared from lowland forests in Insubria, as documented by palinological evidence (Gobet et al., 2000, 2010). The reason for the local extinction of lowland *A. alba*, which is still present in the Insubric mountains, is thought to have been a combination of low genetic diversity, reduced moisture availability, calcareous soil, forest fires and human exploitation (Zoller, 1960; Wick & Möhl, 2006). The loss of *A. alba* from lowland Insubric forests is thought to be reversible (Tinner et al., 1999). The same point has been made for Tuscany (Colombaroli et al., 2007). Indeed, *Abies alba* still shows a wide altitudinal range in the Southern French Alps and foothills (Muller et al., 2007).
Despite the current dominance in Insubric mountain forests of *Fagus sylvatica*, which is less disrupted by human fires and forest use than *A. alba* is (Tinner et al., 2000; Van der Knaap et al., 2005; Valsecchi et al., 2010), for climatic reasons Insubric forest ecosystems are still richer in species than forests on the Northern side of the Alps. For example, Insubric forests commonly host *Quercus pubescens*, *Fraxinus ornus, Celtis australis* and *Ostrya carpinifolia*, tree species which are rare or absent in Northern Switzerland (Oberdorfer, 1964; Antonietti, 1968). The absence of long spells of winter frost enables Mediterranean species such as *Laurus nobilis* and *Quercus ilex* to grow in sheltered locations in Insubria (Filibeck, 2006). Frost-sensitive tree species now widespread and fully integrated in local traditions such as *Juglans regia* and *Castanea sativa* were introduced into Insubria in Ancient Roman times (Tinner & Conedera, 1995; Bradshaw, 2004) or even before, as suggested by ^{14}C dating of charcoal from soils of Southern

Switzerland (Hajdas et al., 2007). Both empirical and modelling evidence suggest that chestnut would not be able to compete with native species, if forests were allowed to follow their natural development (Conedera et al., 2001; Dionea, 2001; Mathis et al., 2003). Such natural development of forests is now increasingly occurring in many European regions, but is still affected by historical legacies and may be distorted by anthropogenic climate change and further species introductions.

More recent additions to the dendrological flora of Insubric ecosystems include *Ailanthus altissima*, *Robinia pseudoacacia*, *Prunus serotina* and *Quercus rubra* (Ceschi, 1992; Conedera et al., 2004b; Digiovinazzo et al., 2010). Both native and exotic tree species richness and abundance of ancient trees appear to be higher in Insubria than in other Italian and Swiss regions, a result which is probably a mixture of climatic and human influences (Pautasso & Chiarucci, 2008). The relatively high diversity of tree species in Insubric ecosystems is important, because it makes it possible for many other taxa to be species-richer than elsewhere. The underlying hypothesis is that high species richness of trees is concurrent with high species richness of tree-associated organisms, e.g. wood-decaying fungi (Küffer & Senn-Irlet, 2005; Schmit et al., 2005; Küffer et al., 2008; Lonsdale et al., 2008; but see Römer (2001) for the mycoflora of plantations of exotic tree species in Ticino).

Global change and the biodiversity of Insubric ecosystems

The generality of the spatial congruency of variation in biodiversity among taxa is a key issue in conservation biogeography because, if species-rich regions tend to be rich not just for one taxonomic group, but for most of them, then bio-indicators which are easier to sample can be used to establish conservation priorities (Barbosa et al., 2010a; Cantarello et al., 2010; Pecher et al., 2010; Pearman et al., 2011). Given their role as ecosystem engineers, trees are likely to remain important bio-indicators for a variety of other taxa, but we know little about whether trees will be able to track the predicted rapid climate shifts (Walther, 2003, 2010; Petit et al., 2008; Pautasso, 2009; Magri, 2010; Pignatti, 2011). The issue of finding reliable long-term bio-indicators under global change is further complicated in Insubria by the presence of several endemic species (e.g. *Gentiana insubrica*, *Ophrys benacensis, Primula longobarda, Ranunculus bilobus, Saxifraga tombeanensis*) (Pitschmann & Reisigl, 1959; Arietti & Crescini, 1971, 1976, 1978; Langer & Sauerbier, 1997), which need to be preserved in spite of the many threats posed by human beings (e.g., Cerabolini et al., 2004; Rossi et al., 2004; Pierce et al., 2006, 2010; Müller et al., 2010). Models based on the commendable Swiss Biodiversity Monitoring Programme are likely to be more reliable if predicting future occurrences of currently widespread species (Pearman et al., 2011), but ideally we would also need to be able to understand how rare species will behave.

The longitudinal gradient in Insubric mean annual precipitation (Conedera et al., 2001; Fig. 2a) has not only important consequences for the current biodiversity of the region, but also shows how Insubric ecosystems may develop depending on whether the future climate will shift towards drier or more humid conditions (Moretti et al., 2006a). On the one hand, drier conditions in future summers would make the Insubric region more similar to the Mediterranean. On the other hand, more humid winters would change the Insubric climate into a sub-Atlantic one. Evergreen hygrophilous broad-leaved species such as *Ilex aquifolium* and *Prunus laurocerasus* thrive in the Western part of Insubria (Carraro et al., 1999; Conedera et al., 1999). The invasion of the exotic palm *Trachycarpus fortunei* in Ticino may be rather associated with a decrease of frost days (Walther et al., 2002). Other evergreen species more resilient to summer drought (e.g. *Quercus ilex*, *Viburnum tinus* and, in cultivation, *Olea europaea*) tend to be present towards the drier Eastern end of the region (lake Garda only receives about 1000 mm of precipitation per year; Berger & Walther, 2006). In general, the rarity of water deficits during Insubric summers has enabled the cultivation of many evergreen broad-leaved species in parks and historic gardens (e.g. Orto Botanico of Brissago, Villa Carlotta at Tremezzo, Villa Este at Cernobbio and Villa Serbelloni at Bellagio) (Frey & Tramer, 1982; Remotti, 2002; Scariot et al., 2007; Erdnüss, 2011). Some of these species have gone on to become naturalized in and around urbanized areas (Klötzli et al., 1996), confirming the role of private and historic gardens as hotspots of invasive species introduction (Heywood, 2010).

Global change effects on chestnut woodland

The biodiversity of Insubria has been greatly affected by the introduction in (or before; Hajdas et al., 2007) Ancient Roman times of *Castanea sativa* (~2000 years BP, Conedera & Krebs, 2008). The species is thought to have survived the last ice age in refuges not far away (~ 200-300 km) from Insubria (Colli Euganei and Monti Berici, Emilia-Romagna) (Krebs et al., 2004). It was then propagated and diffused throughout many European countries to the limits of its ecological potential (Adua, 1999; Mattioni et al., 2008). Research on global change and chestnut in Insubria is thus likely to be of interest (*mutatis mutandis*) throughout the current distributional range of chestnut, from Galicia to Greece, from the Caucasus to Kent (Tokar & Kukla, 2005; Gondard et al., 2006, 2007; Martins et al., 2011; Martín et al., 2012; Pezzi et al., 2012; Fig. 3). Although chestnut was (and still is) often cultivated as a mono-culture, both for pole and fruit production, many varieties were developed differing in e.g. altitudinal distribution, ripening time, storage length and suitability for human vs. animal feed (Conedera & Krebs, 2008). More research and participatory projects are needed to make sure that local varieties and the knowledge associated with them are preserved through in situ cultivation and exchange networks (Bardsley & Thomas, 2006; Galluzzi et al., 2010; Martín et al., 2010; Portis et al., 2012; Pautasso et al., 2013).

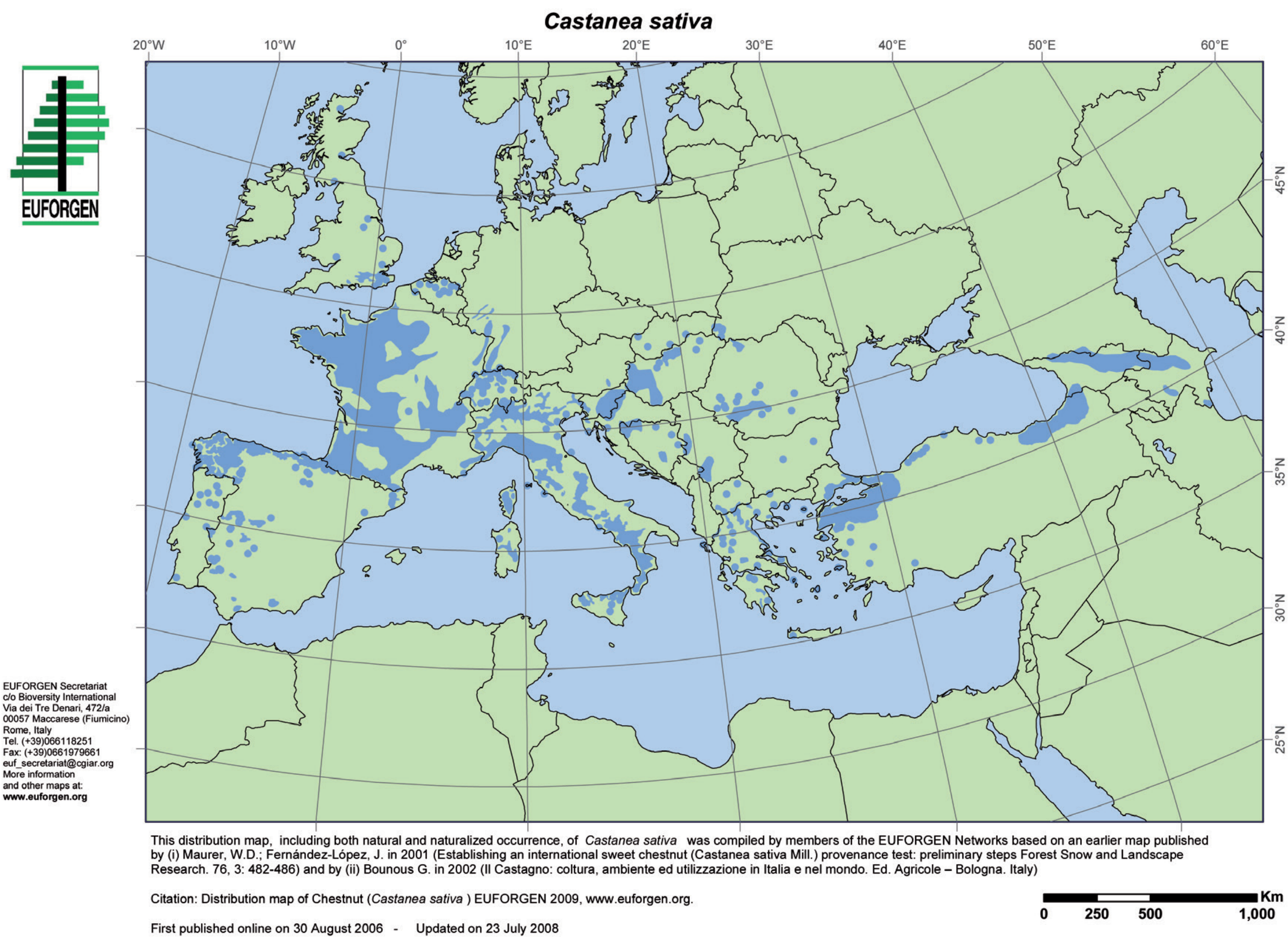

Fig. 3. The current distributional range of Castanea sativa (with kind permission of EUFORGEN). Although chestnut has a patchy distribution, the influence of Ancient Roman introductions can still be seen in the coincidence with the Roman limes. On the other hand, the boundary of the Roman Empire may well have been set by climatic features, thus emphasizing the interactions among global change drivers.

Palinological and archaeological data suggest that Insubria was already in early medieval times a hotspot of chestnut cultivation because of the suitable climatic conditions (chestnut requires summer irrigation in case of natural water deficit for a copious fruit production) and also due to the good network of waterways to reach markets outside of the production area (Conedera et al., 2004c). Just as in other regions in Southern Europe, rural abandonment following the 2nd World War was coincident with the onset of chestnut diseases (*Phytophthora* spp., *Cryphonectria parasitica*) (Maresi & Turchetti, 2009; Prospero & Rigling, 2012). Although it is an open question how much the decline of chestnut health caused rural abandonment (and vice versa), there is little doubt that global change will facilitate outbreaks of new pathogens and pests (Heiniger, 2003; Engesser et al., 2008; Dehnen-Schmutz et al., 2010), as shown by the recent introduction to Italy (and Ticino) from China through the chestnut sapling trade of the chestnut gall wasp *Dryocosmus kuriphilus,* which may end up in facilitating new infections of *C. parasitica* (Prospero & Forster, 2011).

Chestnut cultivation was and in part still is fundamental for Insubric people, as it provides a range of essential products (Arnaud et al., 1997; Prospero et al., 2006; Gullino et al., 2010; Mellano et al., 2012). The dependence of Insubric civilization on chestnut had as a side-effect that this tree species became dominant in Insubric woodlands. Uniform woodlands are in turn often impoverished in their biodiversity, although the traditional regular cutting of chestnut coppice contributed to some canopy and forest herb heterogeneity. Today's abandonment of chestnut coppices can be on the short-term detrimental to biodiversity (given the resulting uniformity in the canopy; Fuller & Moreton, 1987), but can be beneficial in the long term as absence of cultivation allows uprooting of chestnut stumps, the colonization of other species and a more dynamic ecosystem development (Fonti et al., 2006; Vogt et al., 2006).

Genetic studies of chestnut varieties are improving our understanding of the traditional cultivated varieties both in Southern Switzerland (e.g. Conedera, 1994; Gobbin et al., 2007) and in Italy (Pigliucci et al., 1990; Martín et al., 2010). Chestnut trees are central to Insubric ecosystems, as documented by research on the effects of forest fire on chestnut growth (e.g. Brugger et al., 2007), soil erosion (e.g. Marieni, 2000; Conedera et al., 2003; Marxer, 2003) and other ecosystem processes (e.g. Wütrich et al., 2002; Moretti et al., 2009). Whilst the wide variety of moulds, weevils and moths spoiling chestnut fruits was a matter of serious concern for people depending on these fruits for their livelihood, this issue can now be considered also from the point of view of the biodiversity sustained by chestnuts (Sieber et al., 2007). As is the case for most other tree species (e.g. Collado et al., 1999; Gore & Bucak, 2007; Albrectsen et al., 2010), chestnut trees are colonized by fungal endophytes, a hidden component of biodiversity (Bissegger & Sieber, 1994; Tellenbach et al., 2010). However, there is still limited knowledge on the role of these fungi in regulating plant health of various tree species in different regions, so that we have an inadequate understanding of how global change drivers will affect endophytes.

Today, chestnut cultivation is concentrated in Insubria as far as Switzerland is concerned, but for Italy the regions of foremost chestnut fruit production are Calabria, Campania, Latium, Piemonte and Tuscany (Martín et al., 2010). Climate change may result in shifts in the main regions of chestnut production, but it should not be forgotten that human management of chestnut will remain an important factor behind the future species distribution, productivity and associated biodiversity.

People, deadwood and winter forest fires

In addition to a range of ecosystem services (e.g. carbon sequestration, chestnut fruits, honey, mushrooms, pasture, recreation, timber, water, wild berries; Bounous, 2005; Gallardo & Hernandez, 2008; Baptista et al., 2010), chestnut cultivation can provide an insurance against Insubric winter forest fires. Cultivated chestnut groves can be less prone to fire than other types of woodland, as they lack a thick understory, which tends to be removed or prevented by grazing, in order to facilitate chestnut harvesting. On the other hand, chestnut stands tend to occur close to human settlements, thus increasing the likelihood of forest fire start (Reineking et al., 2010), but also of fire control (Pezzatti et al., 2009). This is often the case throughout the distributional range of chestnut, given its human introduction and cultivation.

Winter forest fires are a peculiarity of Insubric ecosystems. In the Mediterranean, winter is normally the rainy season, when fires are thus not common (e.g. Bajocco et al., 2010). In Insubria, summer is generally not as dry as in other parts of the Alps, and also winter can often be rich of precipitation (in form of snow up from a given altitude). However, the arrival of föhn can rapidly turn a humid winter into a fire-risk situation, as this dry and relatively mild wind is able to melt snow in a matter of days. Most fires in canton Ticino are started by people, either accidentally or intentionally (Pezzatti et al., 2009). Although not all fires are started in winter, the majority of the forest fire area of canton Ticino is burnt during föhn events in the cold season, when atmospheric perturbations arriving from W-NW-N produce dry and occasionally strong winds on the Southern side of the Alps, thus increasing the risk that fires will get out of control (Conedera & Pezzatti, 2005). A similar situation is found in the Italian part of Insubria, in other regions of the Southern Alps (Bovio, 1996) and, partly, in California (e.g. Santa Ana Winds; Keeley & Fotheringham, 2001).

Winter forest fires affect all components of Insubric ecosystems, from fauna to flora, from fungi to soil, from invasive species to native ones (Delarze et al., 1992; Hofmann et al., 1998; Moretti & Conedera, 2005). Despite the centuries of fire use (and abuse) by the local population (which is frequently documented in the soils (Eckmeier et al., 2010) and toponymy of canton Ticino; Conedera et al., 2007b), Insubric ecosystems have generally not co-evolved with fire as much as other ecosystems e.g. in Western North America have. However, it is now recognized by the scientific community that a non-null presence of forest fires could play an ecological role as forest disturbance also in present-day Insubria. For example, forest fire can contribute in creating a mosaic of different forest ages and in increasing the amount of deadwood. These structural features are important for many species of a wide range of taxa (e.g., spiders, beetles and fungi; Moretti et al., 2002, 2004, 2006b, 2008b, 2009, 2010; Moretti & Barbalat, 2004; Conedera et al., 2007a; Lachat & Bütler, 2009). Although fire has been shown to facilitate the invasion of many exotic species e.g. in Mediterranean ecosystems (Keeley, 2006), fires may provide a tool to control the invasion of some exotic evergreen species in Insubria, wherever this is felt as unwelcome by landscape managers, the local population and other stakeholders (Grund et al., 2005). Nonetheless, when fires occur repeatedly, the flora may be impoverished compared to Insubric ecosystems where fires do not occur or return after a long time (Moretti & Conedera, 2008).

Given the generally high human population densities of the Insubric region, an increase in the occurrence of forest fires may create problems at the interface between rural, residential and urbanized areas. A diverse age-class and size-structure may be obtained also by managing forests rather than burning them (Barbalat & Gétaz, 1999). Nonetheless, felling may need subsidies and might not provide a satisfactory amount of deadwood (Guby & Dobbertin, 1996), unless measures are taken to make sure this requirement for biodiversity is taken into account by foresters (Lonsdale et al., 2008). Throughout the Alps, deadwood volumes have recently increased thanks to increased awareness of its importance for biodiversity, but also due to lack of recent forest management (Bohl & Brändli, 2007; Pradella et al., 2010; Brändli et al., 2011).

From 1960 to 2000, the number of forest fires in Southern Switzerland has increased (from an average of 30 to about 90 events per year; Providoli et al., 2002). Most of these fires have occurred in low- to middle-altitude Insubric ecosystems, as sub-alpine forests are rarely affected (Telesca et al., 2010). Forest fires can increase the amount of deadwood in forests, if post-fire salvage logging is avoided, but can also decrease it in case of high fire intensity. The question arises as to whether the recent increase in forest fires in Southern Switzerland is causally linked to changes in (i) the behaviour of the population, (ii) the structure and dynamics of forests and the countryside, (iii) the feedback between fire occurrence and development of fire-prone vegetation, (iv) climate, or any of these factors in combination (Conedera et al., 1996a; Rebetez, 1999; Conedera & Tinner, 2000; Krivtsov et al., 2009; Catry et al., 2010; Hessl, 2011). A comparative analysis (1951-2010) of the inner Alpine area, the Northern, Western and Southern Alps found for the latter region a recent increase in meteorological fire danger but a decrease in anthropogenic ignitions (Wastl et al., 2012). In turn, a comparison of fire regimes and socio-economic conditions (1904-2008) for Valais and Ticino found that the reduction since the 1990s in fire ignitions for the Insubric part of Ticino can be mainly explained by the banning of burning garden debris in the open and of fireworks and bonfires during the Swiss National Day (August, 1st; this ban is only effective in the presence of fire danger) (Pezzatti et al., 2013).

CLIMATE CHANGE AND ITS INTERACTIONS WITH OTHER GLOBAL CHANGE DRIVERS

Management of ecosystems within the historic range of disturbances to which they are adapted makes ecological, evolutionary and social sense (e.g. Cissel et al., 1999; Conedera et al., 2009; Keane et al., 2009), but may become hardly achievable in the presence of rapid climate change. Climate change is occurring together with other anthropogenic processes such as invasion of novel species, air pollution and urbanization, thus further complicating both prediction and management efforts (Smith et al., 2009; Baeten et al., 2010; Pautasso et al., 2010; McDougall et al., 2011; Webber & Scott, 2012). Research has established that ecosystem changes due to climate warming are already ongoing in the Alps, at various altitudinal levels and both for mobile and sessile organisms (e.g. Körner, 1992; Parolo & Rossi, 2008; Bergamini et al., 2009; Frei et al., 2010; Maggini et al., 2011). When trying to predict further effects of climate change on ecosystems, it is nonetheless advisable to distinguish among species with different traits and life forms and among different stages of the altitudinal landscape continuum (Theurillat & Guisan, 2001; Seastedt et al., 2004; Díaz-Varela et al., 2010; Scheidegger et al., 2010; Marini et al., 2012).

At the subalpine level, the upward migration of tree-lines may be due to the effects of climate change on mountain ecosystems, but also to concomitant factors such as decreased grazing pressure (Leonelli et al., 2009, 2011). A Swiss-wide study showed that much of the recent upward shift in tree-lines is likely to be due to land abandonment rather than climate warming (Gehrig-Fasel et al., 2007). However, possibly because of an insufficient amount of data from this region, little attention was paid to whether patterns may differ on the Southern side of the Alps. Other things being equal, tree-lines tend to be located at higher altitude in central parts of mountain ranges, due to the protection given by the outer mountains, which results in higher summer temperatures (Körner, 2007; Pecher et al., 2011). High-altitude tree-lines due to climate (and not, e.g., land use) are associated in temperate regions with a mean ground temperature during the growing season of about 7-8 °C (Körner & Paulsen, 2004). An open question is whether tree-line upward shifts will occur to the same degree in peripheral and inner mountain ranges (Caccianiga et al., 2008). Any such divergence may have implications for the conservation of endemic mountain species. That the upward shift of vegetation will pose problems for the conservation of endemics is also likely to be an issue for mountain regions other than Insubria (Dirnböck et al., 2011; Pearman et al., 2011).

However, with exception of the many studies on evergreen broad-leaved species (e.g. Walther et al., 2007) and on a potential link between climate change and increase in forest fires (e.g. Reinhard et al., 2005), relatively little knowledge is available on whether current and potential effects of climate change on Insubric ecosystems (will) differ from other parts of the Alps, Europe, or the world. For example, research at 14 long-term monitoring sites throughout Switzerland (of which three in Ticino) showed the mitigating effect of forest canopies on the abnormally hot summer temperatures experienced in 2003 (Renaud & Rebetez, 2009). However, there were not enough data points from the Southern side of the Alps to test for any significant differences in the heat wave mitigation in Insubric vs. non-Insubric ecosystems. Forest canopies are an important factor to consider, not just in relation to heat wave mitigation (particularly in urbanized landscapes such as lowland Insubria), but also as far as watershed runoff regulation is concerned.

Comparative models of climate change effects on watershed runoff for the rivers Thur and Ticino (North and South of the Alps, respectively) predict in both cases time-shifts and decreases in the runoff peak (Jasper et al., 2004). It would be interesting to know whether this result can be consistently generalized to other watersheds North and South of the Alps, given that the record of floods in Switzerland since 1850 shows a pattern of floods on the Northern side excluding them from the Southern side of the Alps in the same year, and vice versa (Schmocker-Fackel & Naef, 2010). A further question is whether (Insubric) lakes (including the extensive dam systems) and forests will provide a perceivable buffer effect to a diminution of average runoff/increase in flood frequency due to more common extreme precipitation events (Molnar et al., 2002; Pianosi & Ravazzani, 2010; Alewell & Bebi, 2011; Beniston et al., 2011; Castelli, 2011). There are also concerns about the viability of hydropower schemes under changed climatic conditions, but this topic is beyond the scope of a review on global change and ecosystems (although a decrease in the production of hydro-electricity may have indirect effects on ecosystems by making it necessary to switch to other energy sources). These are issues not only relevant to the European Alps, but also to many other mountain ranges in the world, including Western North America, South-Eastern Australia, and the Himalayas (Xu et al., 2009; Richard et al., 2010; Beniston, 2011).

At the valley floor level, already observed climate warming in Insubria is making it possible for new risks to public health to arise, e.g. bluetongue disease vectors (Casati et al., 2009). A warmer climate may imply that Insubria would become again a region with malaria, but there is evidence that human use of the land is more important than climate alone in shaping the spatial distribution of this disease in (sub)tropical regions (Gething et al., 2010). Moreover, current Insubric climate is already humid and warm enough for the establishment of some exotic diseases to be possible, provided that disease propagules are introduced through trade and disease control does not take place early enough. There is a need to prepare for such emerging diseases with interdisciplinary collaboration among public health officials, urban ecologists and climatologists. Climate change will not only affect human and animal diseases (Semenza & Menne, 2009; Stark et al., 2009; Vineis, 2010; Guidi et al., 2011), but also plant health (Ayres & Lombardero, 2000; Pautasso et al., 2012b; Juroszek & von Tiedemann, 2013). Nonetheless Insubric ecosystems are already likely to be at risk to the introduction of *Phytophthora ramorum*, the oomycete causing Sudden Oak Death in California and Sudden Larch Death in the British Isles (Garbelotto, 2008; Brasier & Webber, 2010; Moslonka-Lefebvre et al., 2011), given the combination of humid, mild climate, the presence of susceptible (*Castanea sativa*, *Fagus sylvatica*) and sporulating hosts (*Robinia pseudoacacia,* exotic *Rhododendron* species in historic gardens), as well as nurseries and garden centres trading ornamental species susceptible to this and other *Phytophthora* pathogens (Prospero et al., 2013).

Pollution as a threat to Insubric forest health

Of relevance to both plant and public health is also air pollution in Insubria (Matyssek & Innes, 1999; Künzli, 2002; Braun & Rihm, 2012). For example, it is widely appreciated that atmospheric nitrogen pollution can result in shifts in vegetation composition by (i) favouring nitrophilous species, (ii) leading to long-term soil acidification (particularly on siliceous parent material; Bobbink et al., 1998), and (iii) causing eutrophication of aquatic ecosystems (Wade et al., 2002). Nitrogen pollution also represents a public health threat (Brunekreef & Holgate, 2002; Townsend et al., 2003). Research on air pollution in Insubric ecosystems is partly a consequence of the closeness of Insubria to the urbanized area of Milan, a major source of air pollutants for Northern Italy and Southern Switzerland (Lehning et al., 1998; Cherubini & Moretti, 1999; Pisoni & Volta, 2009; Cattaneo et al., 2010). The traffic and factories around Milan, combined with the climatic and topographical features of the region, result in critical levels of e.g. ozone concentrations being regularly exceeded (Vecchi & Valli, 1999; Gerosa & Ballarin-Denti, 2003). This is an issue relevant to many mountain ranges close to densely populated regions in the world, from California and the Mediterranean to the Andes and China (Bussotti & Ferretti, 1998; Skelly et al., 1999; Benham et al., 2010; Romero-Lankao et al., 2013).

Given the importance of the pollution load for the Insubric region, the foliar sensitivity to ozone of seedlings of tree, shrub and herbaceous species growing in Insubria has been repeatedly assessed in open-top experimental chambers located in the forest nursery of Lattecaldo, Ticino (e.g., Cherubini et al., 2002; Novak et al., 2003, 2007, 2008; Gravano et al., 2004; Cascio et al., 2010). The assumption is here that the same species will show a similar sensitivity as mature individuals under natural growth conditions and a similar climate (e.g., Cozzi et al., 2000). However, the mismatch among elevated ozone concentrations and absence of widespread vegetation damage in Mediterranean ecosystems has led to the hypothesis that there might already be adaptation to elevated ozone concentrations in such ecosystems (Paoletti, 2006). Whether such adaptation can be expected to be present also in Insubric forests is an open question.

For Insubric vegetation even more than in other situations, (i) site-specific conditions and plant species composition, (ii) local-scale variation in ozone concentrations, as well as (iii) differences in stomatal behaviour of plants due to variation in microclimate, may lead to differences in ozone-induced injury (Rogora et al., 2006; Waldner et al., 2007; Gottardini et al., 2010). Moreover, the assessment of ozone injury to various plant species is not straightforward. A study of potential observer bias in such procedure is an interesting example of research carried out across the Insubric political divide (at the forest nursery in Lattecaldo, Ticino, and in open-field conditions at Moggio, Italy; Bussotti et al., 2006).

Research on ozone pollution and its impact on plant health in Insubria showed that foliar injury can occur at pollutant levels below current legislative thresholds (VanderHeyden et al., 2001). This is a result important for other regions in Europe and in the world, wherever smog concentrations are comparable to those of the Po valley (e.g. Los Angeles, some parts of India and China), and calls for practical improvements in air quality as well as collaboration among political borders (Schenkel et al., 1997; Bergin et al., 2005; Augustin & Achermann, 2012). For example, the commendable new, low-altitude railway tunnels of the Lötschberg and Gotthard go in the right direction because they will allow moving goods crossing the Alps with electric trains rather than with petrol-powered and exhaust-producing lorries (Zuber, 1997; Clement & Darmon, 2001; Caminada, 2011). However, for the scheme to succeed there needs to be more support from the Italian side of the border towards this currently essentially Swiss infrastructure project, with a strengthened access to the new tunnels (i.e. between Bellinzona and Novara, Chiasso and Milan, Domodossola and Turin) (Fuglistaler, 2011).

The importance of research across borders

Making biodiversity conservation work across political and cultural boundaries is one of the most pressing challenges in global change biology, given that climate change, urbanization, invasive species, emerging diseases and air pollution do not recognize human administrative subdivisions of the planet (Pullin et al., 2009; Margles et al., 2010; De Sousa, 2013). Insubria is a relatively small region, but is administratively split between two countries and various provinces. This is a common situation throughout the world due to the arbitrary choices of political boundaries. For example, there are many cases where an ecoregion is managed by different states in Africa, due to the colonial past of that continent (Linder et al., 2012). Artificial boundaries among states and counties of the USA also subdivide in capricious ways mountain ecosystems in the Rocky Mountains and the Appalachians (Huber et al., 2010). Such subdivision can affect the effectiveness of conservation measures (Moilanen et al., 2013) and can result in puzzling situations. For example, *Laurus nobilis* is reported to be considered native "at least" in the Italian part of Insubria (Berger & Walther, 2006). This implies that individuals of this species growing at a short distance from each other could be managed and studied as exotic or native just because of a political boundary. The recent improvements in collaboration between Italy and Switzerland (e.g. Bilateral Agreements of Switzerland with the European Union, Schengen Agreement on the free movement of people, collaboration on regional public transport (Sciarini & Tresch, 2009; Wichmann, 2009)), are a step forward towards enhanced international collaboration in research on and management of Insubric ecosystems (Lezzi, 2000; Gianoni & Carraro, 2004; Zanelli et al., 2006, 2007; Balsiger, 2012).

Traditionally, Swiss scientific environmental projects involving canton Ticino have not considered Lombardy (e.g. Innes, 1995; Laternser & Schneebeli, 2003; Gremaud et al., 2004; Krebs et al., 2007, 2008, 2012; Müller et al., 2010; Von Arx et al., 2012). Similarly, Italian research in Insubria has typically overlooked Ticino and the Southern valleys of Graubünden, in spite of the cultural, climatic, economic, historic and linguistic ties between Southern Switzerland, Lombardy, Piemonte and other Italian regions (e.g. Digiovinazzo & Andreis, 2007; Forte et al., 2007; Costantini & L'Abate, 2009; Coli et al., 2010; Wessendorf, 2010; Bottero et al., 2013). Praiseworthy exception to the lack of pan-Insubric studies is made by Europe-wide analyses, when these involve both Southern Switzerland and Insubric Italy (e.g. Schnitzler et al., 2007), or by research carried out across the whole Alps in spite of the linguistic and administrative hurdles (e.g. Ozenda & Borel, 1991; Bätzing, 2003; Rogora et al., 2006; Ozenda, 2009).

If bridged by collaboration, political subdivision can become

a blessing in disguise by providing inadvertent long-running landscape-scale experiments on the effect of human activities on ecosystems with similar climate (Fig. 2). Many factors affecting Insubric forests operate both in Switzerland and Italy (e.g. urbanization, air and water pollution, invasive species such as *Robinia pseudoacacia* and *Ailanthus altissima* (Viegi et al., 1974; Arnaboldi et al., 2002; Kowarik & Säumel, 2007; Celesti-Grapow et al., 2009), introduced tree pathogens such as *Cryphonectria parasitica* (Cortesi et al., 1998; Nicolotti et al., 2005), although to varying degrees. However, the two distinct administrative environments may have unwittingly produced differences in resource management, potentially mediated by a different dominance of private vs. public land property (Kuemmerle et al., 2006; Fulé et al., 2012; Kaeser et al., 2013). For example, forest cover protection has been mandatory by law for over a century in Switzerland, whereas in Italy any such protection has not been so strictly enforced (Schmithüsen & Zimmermann, 2002; Falcucci et al., 2007; Angst, 2012).
It is possible that Swiss incentives towards agriculture in marginal areas may have halted or even reversed the emigration from at least parts of the Sottoceneri region of Ticino, whereas depopulation in many Insubric mountains in Italy over the last half century has been substantial (Fig. 4). In both cases, however, there has been a general abandonment of the chestnut culture, due to chestnut blight and the decreasing use of marginal areas (Conedera, 1996). Also a (mainly spontaneous) reforestation of hay meadows on steep slopes has often occurred irrespective of the side of the political boundary (Walther, 1980; Stampfli & Zeiter, 1999; Fava et al., 2010). Rural abandonment and the concurrent urban sprawl have effects on ecosystems not only because of the associated shifts in land use (Muster et al., 2007; Zimmermann et al., 2010; Monteiro et al., 2011), but also because of potentially altered regimes of forest fires started by people. Migration towards urbanized areas is a common phenomenon in many regions, but in developing countries there is still a trend towards more intensive exploitation of rural areas, not towards abandonment as is happening for some marginal areas in Insubria and, more in general, European mountain regions (Bakker et al., 2011; Hatna & Bakker, 2011; Pellissier et al., 2013). Forest ecosystems in both the Swiss and Italian part of Insubria are likely to benefit from the re-colonization of large carnivores;

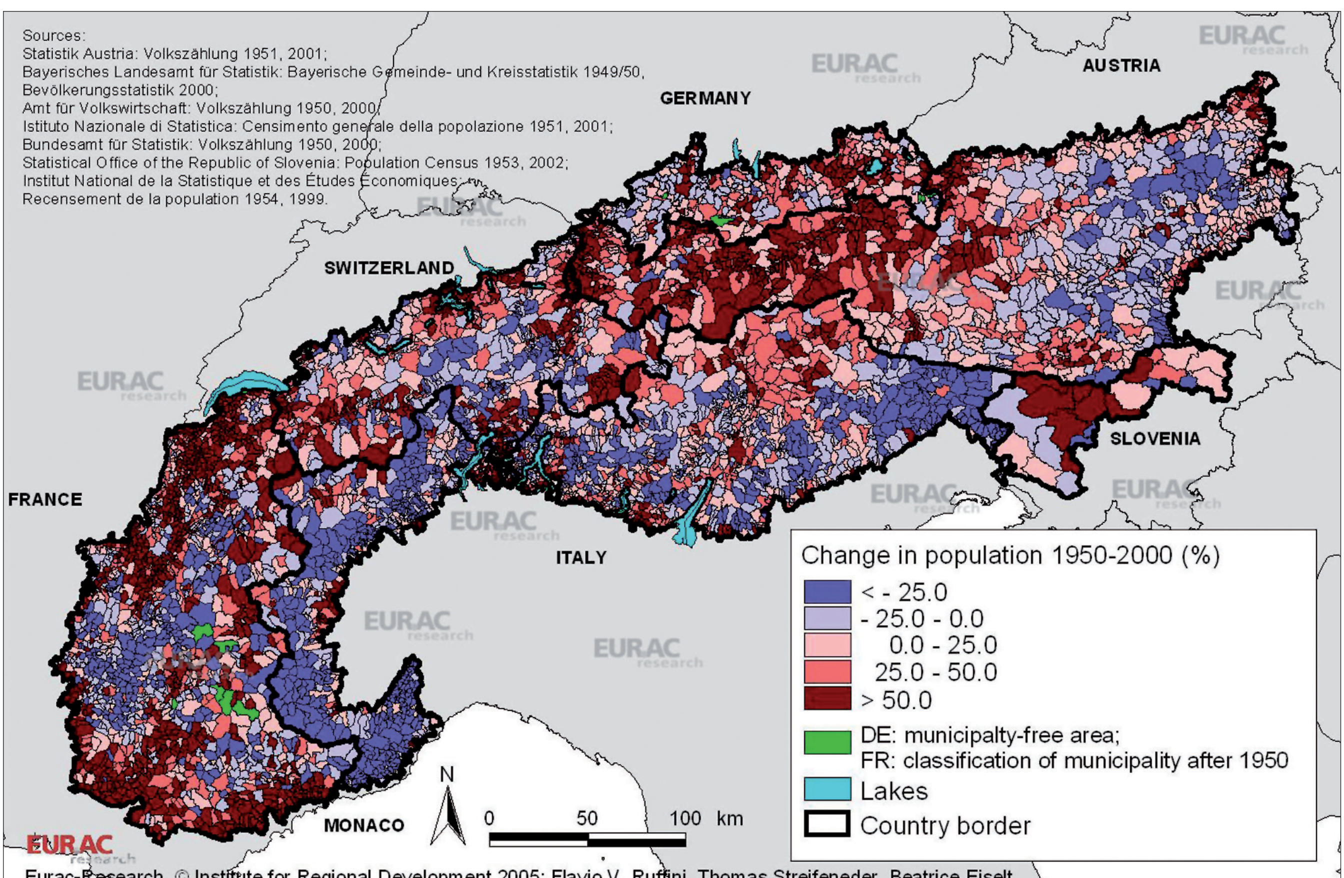

Fig. 4. Change in population from 1950 to 2000 in municipalities across the Alps (with kind permission of EURAC Research).

given the large and dynamic home ranges of wolves, their management will need fine-tuned collaboration across administrative and disciplinary borders (Kelson & Lilieholm, 1999; Bauer et al., 2009; Falcucci et al., 2013).

Research gaps and perspectives

Global change research is developing rapidly, given its importance to address the multiple threats to biodiversity and human civilization in each ecoregion (Fig. 5). This research is not centrally planned (despite attempts at horizon scanning and identification of research priorities; Lavorel et al., 1998; Sutherland et al., 2010; Gurung et al., 2012): it is the result of the more or less independent decisions on what to study/publish/fund of individual scientists, students, peer reviewers, journal editors and funding bodies. This implies that available resources to fund research on global change drivers are not evenly distributed among various problems: researchers tend to focus their attention on some issues while neglecting others. This may be because certain issues are perceived to be of more pressing importance (or easier investigation) for a certain region compared to other research questions.

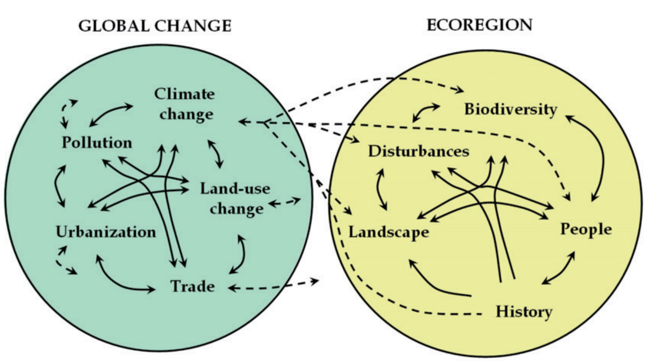

Fig. 5. Global change factors and their interactions with some key features of an ecoregion. Predicting the effects of global change factors on the forest ecosystems of an ecoregion is made difficult by the interactions among global change drivers. At the same time, ecoregions are dynamic entities with an equally complex series of interactions among their components (people, landscape structure, historical legacies, disturbances and biodiversity) (modified from Pautasso, 2012).

Based on this literature survey, forest fire appears a research area that has received more attention in Insubria than in other regions of the European Alps. There has indeed been a long tradition in observation of and research on changing forest fire regimes in Insubria (Pohl, 1938; Gutzwiller, 1962; Ceschi, 1975-76; Zuber, 1979; Conedera et al., 1996b, 1999, 2004a, 2007a, 2011; Herzog, 1998; Pezzatti et al., 2005; Tinner et al., 2005; Bigio et al., 2010; Zumbrunnen et al., 2011), particularly in Ticino (possibly because 90% of the area burnt in Switzerland since 1940 has been in that Canton; Moretti et al., 2008a). Conversely, despite the rapid economic development and associated urbanization over the last decades, urban ecology has received relatively limited attention in Insubria (Germann et al., 2008; Sattler et al., 2010a, b, 2011; Fontana et al., 2011; Vilisics et al., 2012; Tobias, 2013). This limited attention is of concern, given the rapid urbanization of the valley floors that occurred over the last decades, both in Switzerland and Italy. Moreover, urbanization has the potential to interact with each of the other global change factors (Fig. 5), thus confounding the response of ecosystems and the effects of management (Carreiro & Tripler, 2005; Tasser et al., 2008; Ramalho & Hobbs, 2012). In some regions of the Southern Alps (Trentino, and the provinces of Bergamo and Brescia), positive regional correlations between the presence of biodiversity and human beings have been reported (Marini et al., 2008, 2012). If such a correlation is present also in Insubria, it would make its biodiversity conservation more difficult, because the local detrimental impacts of human activities are magnified if species-rich areas also tend to be densely populated (Kühn et al., 2004; Pautasso, 2007; Barbosa et al., 2010b).

A key research gap related to Insubric ecosystems is the issue of future climate change. There has been research on Insubric vegetation history and past trends in climate (Tinner et al., 2003; Tinner & Ammann, 2005; Vescovi et al., 2007; Valsecchi & Tinner, 2010). Observed recent climate warming has been associated with Insubric phenological trends (Defila & Clot, 2001) and the invasion by exotic evergreen species (e.g. Walther, 2002). Scenarios of future climate change effects on inner-Alpine mountain forests have also been built (Schumacher & Bugmann, 2006). However, little attention has been paid to the impacts of future climate change in combination with other global change drivers (e.g., air pollution) on Insubric ecosystems, plant health and biodiversity (Wohlgemuth et al., 2008; Nobis et al., 2009; Dobbertin et al., 2012; Messerli, 2012). Predicting the future climate of Insubria is particularly difficult because the region is located between the Mediterranean (where models forecast increased frequency of summer droughts) and Central Europe (where winter precipitation is expected to increase; Bindi & Olesen, 2011). Given that current Insubric ecosystems are used to humid summers, they may be particularly sensitive to droughts such as the one observed in 2003 (Fink et al., 2004; Conedera et al., 2010; Ciordia et al., 2012), with potential repercussions for the conservation of Insubric biodiversity. On the other hand, increased winter precipitations may reduce the challenge posed by winter forest fires. Part of the challenge of climate change is that it makes it even harder to predict future climate. It would help to know in advance with a certain probability whether the climate in Insubria (or any other region) will get drier or wetter in future summers or winters, but (given that uncertainties on future climates will not disappear no matter the amount and refinements of modelling), applied research should make sure that land managers are prepared to cope with a variety of climate scenarios.

Research on global change and Insubric forests delivers a number of take-home messages. First of all, understanding how global change factors are likely to affect the forests of a certain ecoregion requires knowledge on historic and current human impacts. Second, predictions about how climate change will affect the region need to integrate the likely impacts of other global change drivers. Management, in turn, needs to span a variety of approaches, from prevention to mitigation, from the development of reliable long-term bio-indicators to adaptive monitoring under uncertainty. For many ecoregions of the world, there is a research gap on the interactions among global change drivers, including the human responses to each driver. In the case of Insubria, as in many other regions, there is e.g. a dearth of knowledge on how biological invasions, forest fires and land use/abandonment will interact under climate warming (Jactel et al., 2012; Maringer et al., 2012; Wastl et al., 2012; Fernandes, 2013). Similarly, we know little about future land use and forest management scenarios if the main energy sources were to shift from fossil fuels to renewable ones (MacKay, 2008; Dale et al., 2011; Miyake et al., 2012; Scarlat et al., 2013). In order for forest managers, mountain ecologists and conservation biologists to be able to successfully cope with the challenges posed by global change, it is important to consider the impacts on particular ecoregions of the various global change drivers, their interactions and multifunctional human uses of the land.

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