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Long-term dynamics of tree of heaven (*Ailanthus altissima*) in central European forests

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Abstract

Since the 1950s, the tree of heaven (*Ailanthus altissima*) has progressively invaded forests in southern Switzerland and is becoming a growing concern also north of the Alps. Recent studies have increased the understanding of the species' ecology, but its role in long-term stand dynamics remains uncertain. Therefore, we simulated the long-term dynamics of unmanaged and managed forest stands in southern and northern Switzerland under current and future climate conditions (RCP8.5) using the forest gap model ForClim. Our results indicate that *A. altissima* will increase its presence in the short term (< 100 yrs), but does not gain dominance in the long term (> 200 yrs), confirming its pioneer character. Timber harvesting led to an increasing share of *A. altissima* compared to unmanaged stands. Overall, our findings suggest that in the long run, a competitive displacement of native dominant species by *A. altissima* appears unlikely, with the exception of drought-prone sites under strong climate change. Furthermore, our findings underline the importance of the frequency and intensity of forest management for the long-term abundance of *A. altissima* in forest stands.

Keywords Invasive tree species · Dynamic vegetation model · Long-term forest dynamics · Switzerland

Introduction

Biological invasions are considered to be one of the major drivers of changes in biodiversity and ecosystem services (McGeoch et al. 2010; Sladonja, Sušek, and Guillermic, 2015; Walther et al. 2009). The invasibility of an ecosystem is influenced by a variety of factors such as climate, the disturbance regime and the competitive strength of the indigenous species (Lonsdale 1999). In view of climate change, the invasibility of native ecosystems may undergo important changes as a consequence of more frequent and intensive drought periods, reduction of the competitive fitness of

native tree species, and shifts in disturbance regimes (cf. Allen et al. 2015; Anderegg et al. 2013). Thus, the future distribution and abundance of invasive species are likely to increase (Walther et al. 2009), which may compromise ecosystem functions (Seidl et al. 2018).

The recent invasive behavior of Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle) in European forest ecosystems is a representative example in this respect. The functional traits of the species such as its high growth rate, early sexual maturity, high fecundity and sprouting capacity (Kowarik and Säumel 2007; Pyšek and Richardson 2008; van Kleunen et al. 2010) make it one of the most successful invasive tree species (Sladonja et al. 2015). In Switzerland, it has progressively invaded fallow lands and forests starting in the early 1950s, especially south of the Alps (Knüsel et al. 2020). In this region, many of the invaded forests protect settlements and infrastructure from gravitative natural hazards such as rockfall (Moos et al. 2019). Furthermore, the presence of *A. altissima* can negatively affect biodiversity and other ecosystem services (Knüsel et al. 2020). Furthermore, species distribution modeling indicates a strong expansion of *A. altissima* toward the northern Alps under warmer, drier future climatic conditions (Gurtner 2015). Thus, it is important to improve our knowledge on the role of *A. altissima* in

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the context of long-term forest dynamics. However, there are few data on the long-term dynamics of the invasion process of *A. altissima* in Central European forests.

In this situation, simulation models are suitable to better understand the role of individual species and their impact on forest dynamics (e.g., Vanhellemont et al. 2011; Morales and Perry 2017). Forest gap models are particularly pertinent as they are based on the characterization of key autecological properties of the tree species regarding regeneration, growth and mortality, while considering bioclimatic variables as well as intra- and interspecific competition (Bugmann 2001). Recent research has provided a wealth of new insights on the ecology of *A. altissima* (e.g., Wunder et al. 2016; Knüsel 2018; Moos et al. 2019), including additional information on the species traits (e.g., initial shade-tolerance).

However, in spite of these recent insights on the ecology of *A. altissima*, it remains difficult to assess its long-term potential in forest succession. For example, both its high root sprouting capability and its very high shade tolerance in the early life stage suggest a good initial invasion potential, whereas its low final tree height may indicate a limited potential to become a canopy-dominant species (Knüsel et al. 2015). Yet, there are species such as beech (*Fagus sylvatica*) that compensate for their low terminal height by high propagule pressure and thereby reach dominance or at least high abundance in many forests. Thus, a quantitative tool integrating the species' life history traits is needed to improve our understanding of the invasiveness of *A.altissima* in forests south and north of the Alps (i.e., the species potential to establish and dominate in forest stands), as well as the species response to management interventions (Knüsel et al. 2020). Although species distribution models provide projections of potential future range shifts under climate change, possible counteracting effects due to species interactions are not considered in such approaches (Elith et al. 2011), hence raising the question how *A. altissima* will perform in competition with native trees under the present and a future climate. We ask the following research questions:

(1) Under current climate, does *A. altissima* attain long-term dominance in forest stands south and north of the Swiss Alps?
(2) How does climate change and forest management affect the invasiveness of *A. altissima* in both regions?

To address these questions, we investigated the long-term development of *A. altissima* abundance using a forest gap model at two case study sites in southern and one in northern Switzerland. Since the effect of harvest interventions on *A. altissima* is of considerable interest for forest management, we furthermore investigated scenarios including typical harvest interventions and their effect on *A. altissima* long-term dynamics.

Material and methods

The model ForClim

ForClim (v4.0.1 22; Huber et al. 2020) is a forest gap model that was originally developed to study forest dynamics in the European Alps and changes in tree species composition under changing climate conditions (Bugmann et al. 1996). The model has been applied and evaluated under a wide range of environmental conditions in managed and unmanaged temperate forests in Central Europe as well as on other continents (Bugmann and Solomon 2000; Huber et al. 2018). In ForClim, the forest is represented by multiple small patches, based on the concept of patch dynamics (Watt 1947). For each patch, the establishment, growth and mortality of tree cohorts (i.e., groups of trees of the same species and age) are simulated at an annual resolution (Bugmann et al. 1996). Tree establishment is determined by a set of species-specific environmental and biotic constraints such as soil moisture, winter temperature, the sum of growing degree-days, light availability at the forest floor, and browsing pressure (Bugmann 1996; Didion et al. 2009). The effects of environmental conditions on tree growth are implemented via response functions that lead to a reduction of growth under conditions deviating from the species optimum (see also Bugmann 2001). Tree mortality is captured by a combination of age-based and stress-induced components (Bugmann 1994; Huber et al. 2020). In ForClim, more than 30 central European tree species are parameterized by a set of traits describing their ecology (for a detailed model description cf. Bugmann 1994; Bugmann et al. 1996). ForClim is capable of representing different management types, including a wide range of typical silvicultural management techniques applied in Swiss forests (Rasche et al. 2011). The user can define the timing, intensity and the type of management interventions; cf. Bugmann (1996), Didion et al. (2009) and Huber et al. (2020) for further details.

In order to consider the very pronounced capability of vegetative reproduction (stem and root sprouting) of *A. altissima*, which provides a significant competitive advantage compared to native tree species (Knüsel et al. 2020), a sprouting module was implemented in ForClim, based on the sprouting model of FORECE (Kienast 1987). Further information on the implementation and evaluation of this module is provided in Appendix A.

Study sites

Three study sites were chosen to represent low-elevation conditions in Switzerland and provide a comparison
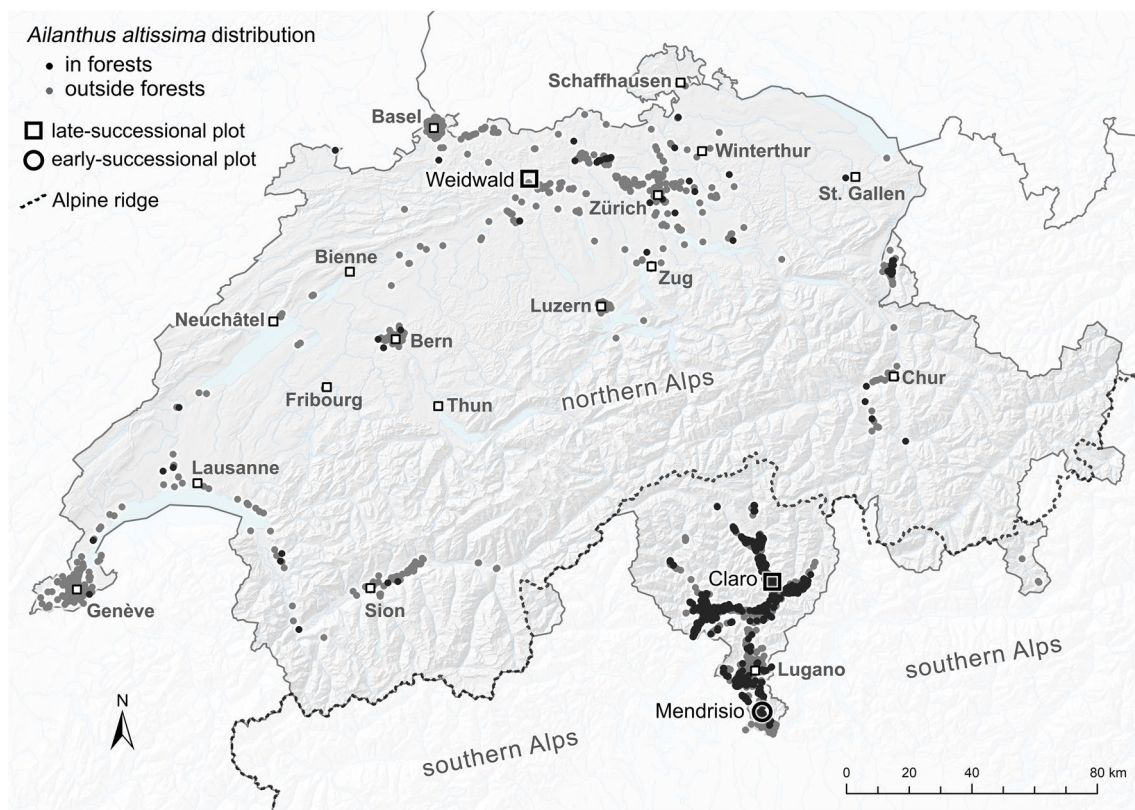
Fig. 1 Distribution of *A. altissima* in Switzerland and location of the three study sites Mendrisio, Claro, and Weidwald (data source: Gurtner 2015, Forest service of Canton Ticino; topo map © Swisstopo, 2017)

of long-term dynamics under the contrasting southern (S–CH) and northern Alpine (N–CH) settings (Fig. 1). As the invasion history of *A. altissima* in Switzerland started in the southern Alpine region (S–CH), we selected two sites in this area (Claro and Mendrisio) in order to dispose of longer stand history with *A. altissima* for model evaluation purposes. Further, the two southern sites display differences in tree species composition, stand history and successional stages: Mendrisio represents an early successional forest stage, whereas the forest stand of Claro was characterized by an open structure of mature trees, which makes it more suited for the long-term modeling approach. The study site of Weidwald in the northern Alps (N–CH) represents a late-successional stage allowing us to consider it for the long-term simulation as well.

An overview of the environmental conditions (topography, climate, soil) used in the simulation of the three case study sites is provided in Appendix B.

Mendrisio (S–CH)

The forest stand in Mendrisio (N45°53′13″, E8°58′56″) is situated on a west-facing, steep (> 25°) slope at an elevation of 360–500 m on coarse rock debris (Moos et al. 2019). The

mean annual precipitation is 1800 mm and the mean annual temperature is 11 °C. According to old aerial images, Mendrisio was largely devoid of forest in the 1930s and thus represents conditions of invasion into an early successional forest stage (© Federal office of topography Swisstopo). Today, it is a mixed forest stand with *Tilia cordata* (small-leaved linden), *Ostrya carpinifolia* (hop hornbeam), *A. altissima*, *C. sativa*, and other broadleaved tree species, such as *Acer* spp. (maples), *Fraxinus* spp. (ashes), and *Quercus* spp. (oaks).

Claro (S–CH)

The site in Claro (N46°15′41″, E9°01′27″) is comparable to the one in Mendrisio in terms of environmental conditions and climate (mean annual precipitation 1800 mm, mean annual temperature 11 °C). However, it differs regarding stand structure and successional stage. The site is situated on a west-facing gentle (< 25°) slope on coarse rock debris, at an elevation ranging from 280 to 350 m a.s.l. The stand was formerly managed as a chestnut orchard, which was abandoned in the 1950s (Knüsel et al. 2015) and represents thus mature open forest stand at time of the invasion by *A. altissima*. Today, it is composed mainly of *C. sativa*, *A. altissima*, *Robinia pseudoacacia* (black locust),

Acer pseudoplatanus (sycamore maple), *Betula pendula* (common birch) and a few other broadleaved tree species of minor abundance.

Weidwald (N–CH)

The site of Weidwald (N47°24′53″, E7°59′46″) is situated on a steep (> 30°) south-facing ridge at an elevation ranging from 580 to 670 m a.s.l., featuring shallow soils, a mean annual precipitation of ca. 1200 mm and a mean annual temperature of about 8 °C. The forest stand is a near-natural dry beech forest formerly managed as a coppice and then converted into a high forest. The forest has been declared a strict reserve in 1961, i.e., no management has taken place since then (Brang et al. 2011). Today, the stand is dominated by *Fagus sylvatica* (European beech) and a few secondary tree species such as *Quercus petraea* (sessile oak), *Taxus baccata* (European yew), *Fraxinus excelsior* (European ash) and *T. cordata*. The site was chosen as a representative site for northern Switzerland due to its aspect and soil conditions, as the distribution of *A. altissima* preferentially occurs on dry, south-facing slopes (Gurtner 2015).

History and ecology of *Ailanthus altissima*

Ailanthus altissima is a deciduous, dioecious species of the Quassia family (*Simaroubaceae*) (Brunner 2009; Hu 1979). It is commonly described as a shade-intolerant, thermophile species with a high seed production, a highly competitive growth rate and vigorous vegetative regeneration (e.g., Kowarik and Säumel 2007; Brandner and Schickhofer 2010). Its home range covers large parts of China as well as Korea. It is now being present on all continents except Antarctica (Hu 1979; Kowarik and Säumel 2007). The introduction in Europe dates back to the middle of the 18th century, when it has been planted as an ornamental, low-demanding street and park tree. As a result, its current distribution in the secondary range has a close link to urban environments (Hu 1979; Kowarik and Böcker 1984), from where it started to spread into natural ecosystems (Espenschied-Reilly and Runkle 2008; Knapp and Canham 2000; Wunder et al. 2018). Where *A. altissima* invades forests, it initially often forms nearly monospecific thicket and pole stage stands, thus raising concerns about its long-term abundance and impact on ecosystem services (Sladonja et al. 2015; Knüsel et. al, 2020).

While *A. altissima* provides various ecosystem services such as timber production, erosion control, nutrient cycling, and cultural purposes (Brandner and Schickhofer 2010; Hu 1979; Kowarik and Säumel 2007), it exerts major negative impacts on ecosystems such as altering soil properties, replacing natural vegetation and reducing biodiversity (Castro-Díez et al. 2012; Constán-Nava et al. 2015; Vilà et al.

2006). Thus, its spread is viewed skeptically by many forest managers and conservationists.

In Switzerland, *A. altissima* was introduced about 150 years ago in the southern Alps, where it started to spontaneously spread into fallow lands and chestnut forests in the 1920s (Wunder et al. 2016). Nowadays, *A. altissima* is a widespread species at low elevations in southern Switzerland, whereas the naturalization process in northern Switzerland is mostly limited to suburban areas around the main cities of Zürich, Basel, and Geneva (Fig. 1; Wunder et al. 2016).

Parameterization of *A. altissima*

The species-specific parameters of *A. altissima* that are required in ForClim (Bugmann 1996) were obtained based on a literature review. For uncertain or sensitive parameters, an additional sensitivity analysis was conducted (Isler 2019). Table 1 reports the final parameter estimates as well as the corresponding key references. For a detailed description, please refer to Isler 2019).

Simulation experiments

Experimental design

The simulation experiment comprised two sets of simulations: (1) A model evaluation by comparing model results with different empirical datasets and (2) future projections of long-term dynamics of *A. altissima* in southern and northern Alpine forests under current and future climatic conditions (see Fig. 2).

### Evaluation of model performance

For a detailed evaluation of model behavior, century-long observation datasets of several stands would be required, which, however, are not available for *A. altissima* in Switzerland. As a surrogate, we used a combination of sensitivity analyses as well as quantitative and qualitative tests against different types of empirical data (Bugmann 2001; Grimm et al. 2005).

We ran simulations in Claro and Mendrisio over a period of ca. 80 years, corresponding to the time frame between the first observation and the full-callipering data available for comparison. In Mendrisio (simulation time: 1928–2017), the simulation started from a fully developed soil profile, but without any trees ("bare ground"), as the analysis of old aerial images (early 1930s) indicated largely open conditions or early successional stage vegetation (© Federal Office of Topography Swisstopo), whereas in Claro (simulation time: 1939–2015) an open chestnut orchard (100 trees/ha, average DBH 36 cm) was used as the initial state. The influence of

Table 1 Species-specific parameter values for *A. altissima*

Parameter	Abbreviation	Unit	Value	Key references
DBH-foliage allometry	kType	–	D2	–
Maximum height	kHMax	m	31	Kowarik and Säumel (2007), Knüsel et al. (2015)
Maximum age	kAMax	yrs	132	Kowarik and Säumel (2007)
Maximum diameter	kDMax	cm	161	Kasson et al. (2013)
Growth-rate parameter	kG	cm/yr	400	Huber et al. (2020)
Minimum annual sum of degree-days	kDDmin	°C·days	1077	Gurtner (2015)
Lowest mean winter temperature tolerated	kWiTN	°C	− 10	Kowarik and Säumel (2007), Fick and Hijmans (2017)
Highest mean winter temperature tolerated	kWiTX	°C	10	Kowarik and Säumel (2007), Fick and Hijmans (2017)
Drought tolerance	kDrTol	[0…1]	0.36	Landolt (1977)
Nitrogen tolerance	kNTol	[1…5]	3	Landolt (1977), Ellenberg et al. (1991)
Browsing susceptibility	kBrow	[1…3]	1	Carter and Fredericksen (2007), Knüsel (2018)
Juvenile light requirement	kLy	%	0.1	Landolt (1977), Knüsel et al. (2017)
Adult light requirement	kLa	[1…9]	6	Knüsel et al. (2017)
Maximum reduction of height due to unfavorable conditions	kRedMax	%	48	Arnaboldi et al. (2003)
Sprouting ability	kSprTend	1 or 2	1	Kienast (1987)
Initial DBH of sprouts	kSprInitDBH	cm	1.7	Kienast (1987)

Fig. 2 Overview of all simulation experiments with their main characteristics
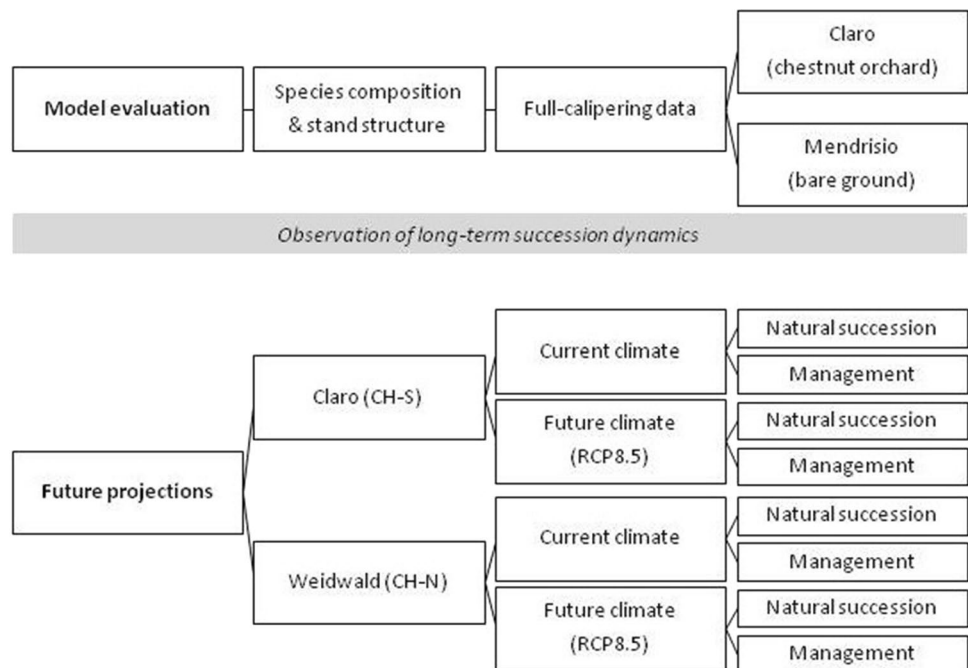
the assumptions on initial stand density and tree DBH in the chestnut orchard on the simulation results was evaluated in a sensitivity analysis and found to have a small impact on long-term (> 200 years) basal area development of the stand (Isler 2019). Further information is provided in Appendix B.

Simulated basal area and tree number data were compared to the contemporary full-callipering data, which was provided by Daniel Trappmann and Markus Stoffel (summer 2015) for Claro and by Christine Moos (winter 2017)

for Mendrisio. For the model-data comparison, simulation results (which include trees from a diameter of 1.27 cm on) were truncated to the callipering threshold of 10 cm for Claro, and 4 cm for Mendrisio. Woody species that were measured empirically, but are not represented in For-Clim were summarized in two classes: "other trees" and "other shrubs" (cf. Appendix B).

Projections into the future

Simulations into the future were conducted at Claro (S-CH) and Weidwald (N–CH), as these sites are expected to experience drier conditions in a future climate. For each site, four scenarios were simulated to combine different climatic conditions (present and future climate) with varying management scenarios (no management and a common management approach in Switzerland; cf. Figure 2). Simulations were carried out for a period of 300 years (starting in 2015 in Claro and in 2011 in Weidwald) in order to capture long-term dynamics, as in Elkin et al. (2013).

The stand initialization was based on the full-callipering data of the forest stands, following the approach of Thrippleton et al. (2020). For Claro, the same data were used as for model evaluation purposes (full-callipering, summer 2015, Trappmann and Stoffel), whereas for Weidwald, the full-callipering data of 2011 were used, kindly provided to us by the research project "Monitoring Naturwaldreservate Schweiz" (Envidat 2021). Some recorded species, which were not represented in the ForClim species list, were assigned to functionally similar species (cf. Appendix B).

For the simulation of climate change, a linear change from the current climate to a future RCP8.5 climate scenario (Collins et al. 2013) over a time period of 100 years was assumed, based on the approach of Bircher (2015). After this time, climatic conditions were assumed to remain constant until the end of the simulation (i.e., year 2300). The delta values for temperature and precipitation changes were taken from the CH2018 Report for southern (CHS) and north-eastern (CHNE) Switzerland, respectively (Croci-Maspoli et al. 2018; cf. Appendix B). The direct effect of increasing CO_2 levels on tree physiology was not taken into account in this study.

To investigate the impact of forest management on the abundance of *A. altissima*, a scenario with no management, thus representing development under natural succession, and a scenario with management were chosen. Bircher (2015) described the current best practice management in Switzerland for different elevation zones in uneven- and even-aged forests, based on recommendations by silvicultural experts. An adapted version of the approach described for the low land (colline) zone was used, i.e., a target cut (target DBH = 50 cm) with an intensity of 80%, i.e., 80% of all trees above the target DBH were harvested during an intervention, with a return period of 24 years. Using this setup allowed us to evaluate how current management interventions would affect the future behavior of *A. altissima* in these forests.

To account for stochastic variability in the model results (e.g., due to mortality), all simulations were carried out with 200 iterations.

Results

Model evaluation

In Claro, stand basal area (BA) was slightly underestimated by the model (measured: 30.6 m^2/ha, simulated: 28.8 m^2/ha), whereas simulated tree number was 43% higher than measured values (simulated: 765 trees/ha, measured: 535 trees /ha). At the species level, measured and simulated BA for *A. altissima* was in good agreement (measured: 6.1 m^2/ha, simulated: 5.5 m^2/ha; Fig. 3). Tree numbers of *A. altissima* showed larger differences, with the simulated tree number exceeding the measured data by almost 30%. In terms of the other tree species shares, *F. excelsior* and *B. pendula* were slightly overrepresented in the simulations, while the reverse was true for *Acer campestre* (field maple). *Castanea sativa* (chestnut) and *A. pseudoplatanus* (sycamore maple) were overestimated in terms of BA as well as tree number. For *C. avellana* (hazelnut) the simulation returned comparable BA values, but overestimated the number of individuals.

Similar patterns were found in Mendrisio, where simulated stand BA corresponded well with the measured data (31.5 and 30.0 m^2/ha, respectively), while simulated tree numbers were almost 25% higher than measured data (Fig. 3). At the species level, BA was overestimated for almost all tree species with the exception of *F. excelsior* und *Ulmus glabra* (Scots elm). *A. campestre* and *U. glabra* showed the best match in terms of BA. *A. campestre* and *C. avellana* showed good agreement in terms of tree numbers, while the model tended to overestimate the tree number for all other species.

Overall, the model featured satisfactory agreement with measured data at both sites, although the site Claro was matched considerably better at the species level than the site Mendrisio.

Future forest dynamics

Claro, Southern Switzerland

(a) Current climate

Under current climatic conditions (Fig. 4a, b), stand BA in Claro increased strongly over the simulation period (up to ca. 50 m^2/ha under unmanaged conditions). At the species level, the BA of *A. altissima* and *F. excelsior* decreased in the long term compared to the initial state under unmanaged conditions (Fig. 4a). The BA of *C. sativa* also showed a decrease in the long term, but increased over the first 100 years of the simulation period. Most species showed an

Fig. 3 Comparison of simulation data (dark green) with empirical stand data (light green) in terms of basal area (upper row) and tree numbers (lower row) in Claro (left column) and Mendrisio (right column). "Other deciduous" and "understorey" summarize tree species not represented in ForClim (cf. Appendix B)
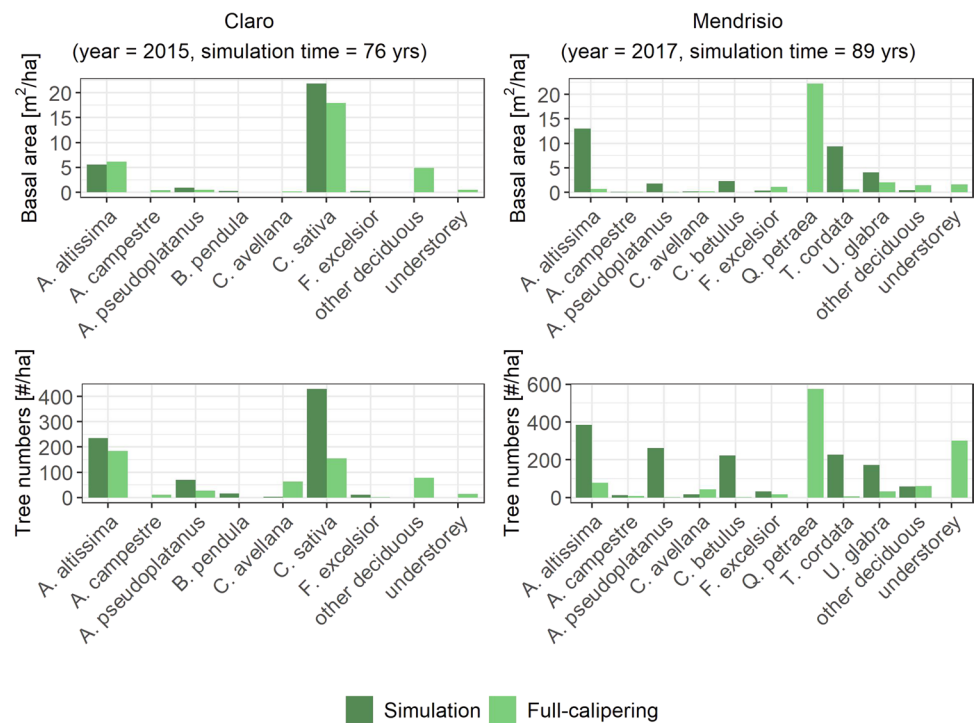
increase in BA or remained at a comparable level throughout the simulation period. In the managed simulated stand (Fig. 4b), the BA stabilized in the long term at ca. 40 m²/ha. The temporal development of *A. altissima*'s BA is comparable to the unmanaged scenario, while its share of stand BA was slightly higher in the managed than the unmanaged scenario. The development of the other tree species was largely comparable to natural succession, with a slight increase in light-demanding species (e.g., *B. pendula*).

(b) Climate scenario RCP8.5

After an initial strong increase, stand BA decreased markedly in Claro within the first 100 years of the simulation under the climate change scenario, independent of the management scenario (Fig. 4 c, d). BA thereafter stabilized in both scenarios, albeit at the very low level of ca. 11 m²/ha. Most species showed an initial increase in the short-term (< 100 yrs), followed by a subsequent decline, irrespective of the management option. Also, the temporal development of tree species composition was comparable and independent of the management, indicating the strong dominance of the climate signal. The BA of *A. altissima* showed a temporary increase in the short-term (< 100 yrs) in the managed scenario compared to the one without management, but stabilized in both cases at a level of ca. 5 m²/ha in the long term, accounting for almost half of stand BA. In contrast, the BA of *C. sativa* increased in the short-term in the

unmanaged scenario, but declined strongly in both scenarios after 100 years and remained rather constant thereafter.

Northern Switzerland

In general, simulated stand BA of the Weidwald forest increased strongly over the simulation period, independent of the management or climate scenario (Fig. 5). Furthermore, stand BA was higher in the unmanaged than in the managed scenario, irrespectively of the climate scenario considered.

(a) Current climate

Under unmanaged conditions (Fig. 5a), the BA of most tree species increased, in particular for the shade-tolerant species *A. alba* and *T. cordata*. Exceptions were *F. excelsior* and *T. baccata*, *Pinus montana* (mountain pine) and *S. aria*, whose BA decreased.

In the managed scenario (Fig. 5b), the overall pattern remained comparable to unmanaged conditions. In general, the BA of most species, particularly the shade-intolerant ones, increased compared to the unmanaged simulations. In contrast, the shade-tolerant *F. sylvatica* initially decreased in BA reaching its lowest level after about 100 years and slightly increased in the following. On the contrary, the BA of *T. baccata* and *A. altissima* reached their maximum
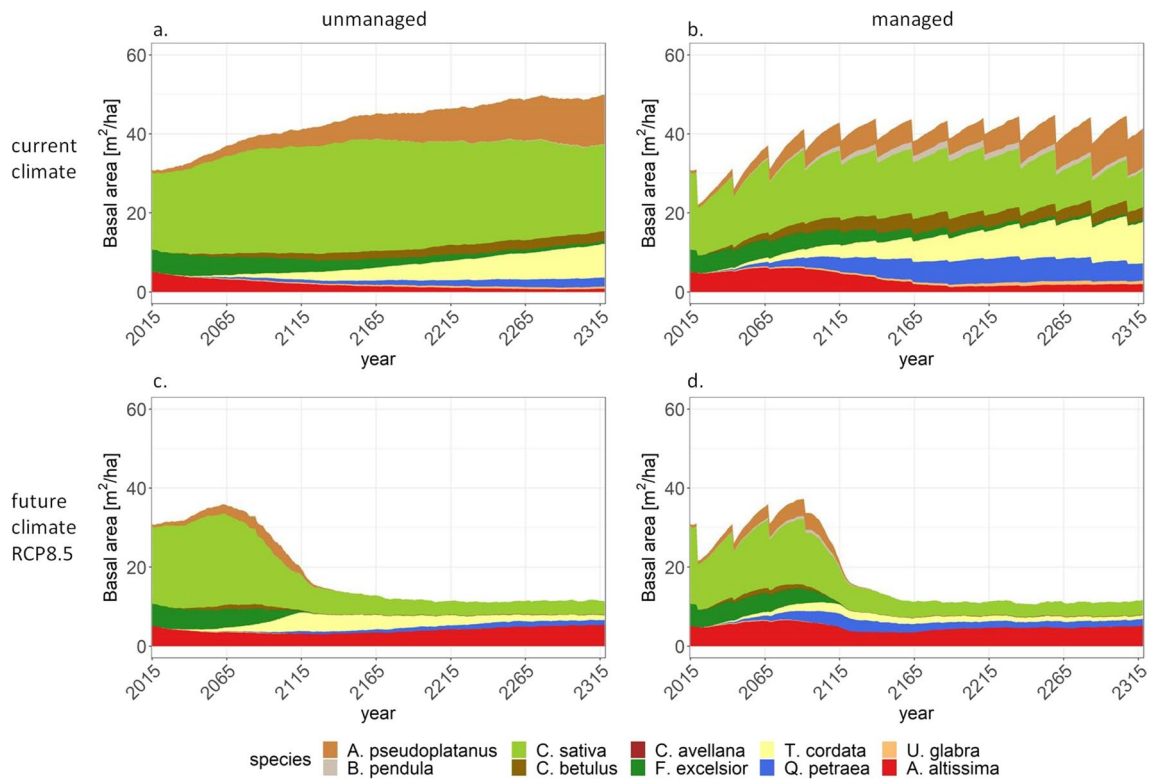
Fig. 4 Development of basal area by species under present climate (top) and the climate scenario RCP8.5 (bottom), under unmanaged conditions (left) and management (right) for the Claro forest. The full-callipering data of 2015 were used for stand initialization
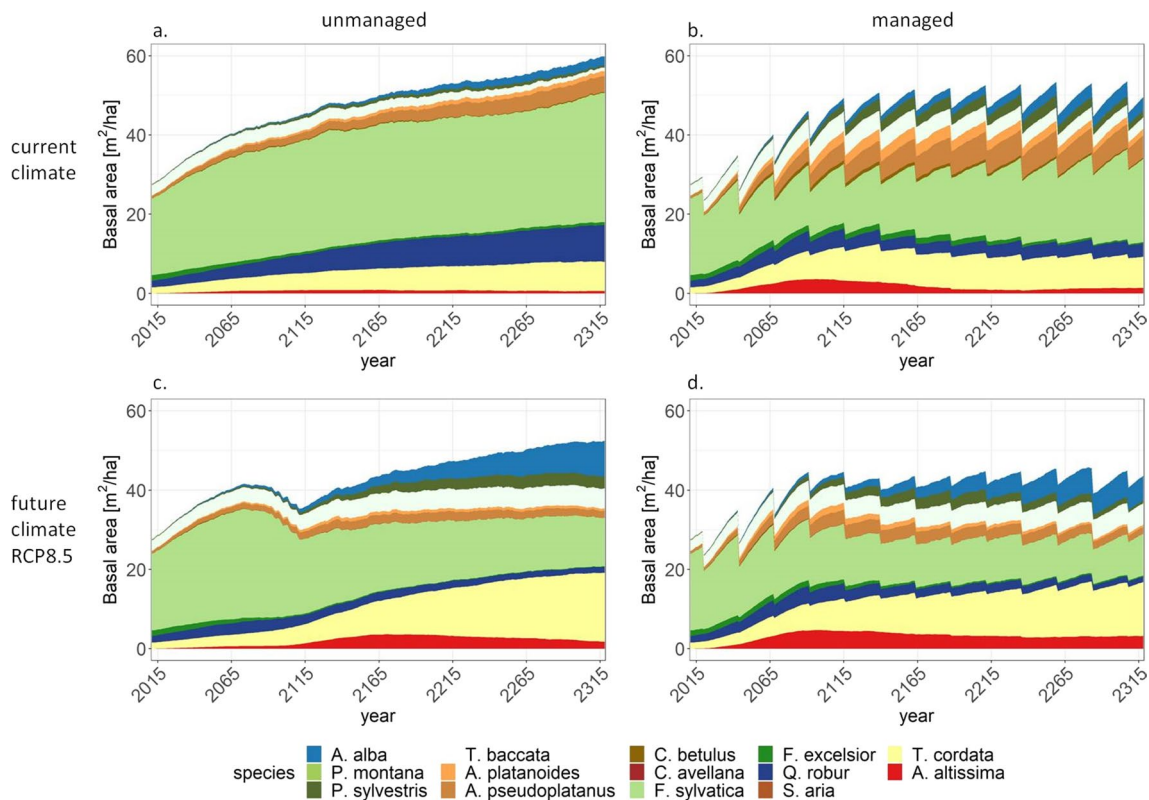

Fig. 5 Development of basal area by species under present climate (top) and the climate scenario RCP8.5 (bottom) under unmanaged conditions (left) and management (right) for the Weidwald forest. The full-callipering data of 2011 were used for stand initialization

within the same time frame of about 100 years and declined thereafter.

(b) Climate scenario RCP8.5

Under unmanaged conditions (Fig. 5c), stand BA increased over the first ca. 60 years, dropped subsequently until around year 2100, and thereafter increased again, reaching its maximum at the end of the simulation. In the managed stand (Fig. 5d), stand BA increased over the first 100 years of the simulation, despite the BA removed by management, and reached a relatively constant level thereafter. The long-term succession patterns were comparable between the two management scenarios, although in the unmanaged one *T. cordata*, *A. alba*, and *T. baccata* showed a higher BA increase with respect to the managed scenario. Similarly, the BA of *A. altissima* increased during the first half of the simulation period and decreased in the long term, but its share of stand BA was higher in the managed than the unmanaged scenario.

The largest difference between the two scenarios was found for *F. sylvatica*, which reached a maximum in BA in the unmanaged scenario after ca. 60 years and then decreased, while its BA decreased throughout the simulation in the managed stand.

Discussion

Modeling approach and model evaluation

Implementing the invasive species *A. altissima* in ForClim allowed us to elucidate a range of possible trends of the species' long-term role in Swiss forests, thus providing a better understanding of its influence on the structure and species composition of forest stands under strongly differing environmental settings. Huber et al. (2018) conducted a full-fledged parameter sensitivity analysis of ForClim that included both monospecific and mixed stands as well as the early vs. the late successional stages. It demonstrated that the most influential parameters in mixed stand settings relate to the establishment probability as well as shade casting. While *A. altissima* has a high establishment probability in the model due to its vigorous sprouting behavior, its shade-casting ability and low terminal height reduce its competitiveness. The simulation results presented here suggest that in combination, this makes it impossible for the species to come to dominance in the long term. Based on Huber et al. (2018), a small sensitivity analysis of the *A. altissima* parameters was conducted by (Isler 2019) to substantiate the choice of parameter values that were characterized by considerable uncertainty. Thus, the results on the successional behavior of *A. altissima* shown here are robust.

At the two test sites used for model evaluation, simulated stand BA was in good agreement with field measurements, while tree numbers were generally overestimated. The model showed a better match to the data in Claro than in Mendrisio, where the number of tree species not represented in ForClim was larger. Generally, all expected tree species occurred in the simulations except for *A. campestre* in Claro. This may be explained by its lower maximum height (25 m) compared to the other tree species growing at the Claro site (Huber et al. 2020), resulting in a poor growth performance in the shaded sub-canopy. The overestimation in the simulated BA of *C. sativa* in Claro may be partly caused by the uncertainty in representing the long-term survival of *C. sativa*, which is a potentially very long-lived tree if managed, but suffer strongly from competition by late-successional tree species under natural growing conditions (Conedera et al. 2021). Considering the challenges of obtaining a good match between empirical data and simulation results for longer simulation timespans (e.g., Rasche et al. 2011; Mina et al. 2017), the current results indicate that the general species dynamics are overall captured well by the model.

A major limitation of this study and especially for the simulations under future climatic conditions is the presence of tree species in these forest stands that are not parameterized in ForClim. Under the RCP8.5 climate scenario, a shift toward more Mediterranean species is expected, which is likely associated with a strong shift in species composition (e.g., Hanewinkel et al. 2013). Including further tree and shrub species from the Mediterranean region would thus be required for future, more detailed studies (e.g., Henne et al., 2013).

Another restriction is the assumption that only *A. altissima* was capable of sprouting. This approach, however, is reasonable considering that most other canopy-dominant deciduous species in central Europe are much less vigorous root or stool sprouters than *A. altissima*, perhaps with the exception of root suckers for *Populus tremula* (European aspen) and *R. pseudoacacia* (Caudullo and de Rigo 2016; Sitzia et al. 2016), and of stool resprouting for *C. sativa* (Conedera et al. 2016). A further aspect to consider is that both study sites represent rather poor site conditions and are expected to be prone to invasion by *A. altissima* due to increasing drought. An analysis of the invasion progress on sites with better-growing conditions would add to the understanding of the invasion biology of *A. altissima*. Besides gradually changing climatic conditions, it is furthermore likely that the invasion process will be significantly accelerated by increasing disturbance magnitude and intensities (Seidl et al. 2017), which open the canopy and promote the establishment of early successional pioneer vegetation such as *A. altissima* (Knüsel et al. 2020). Furthermore, it should be noted that a long-term dynamic representation of browsing pressure could not be included in the approach presented

here due to a lack of data. Instead, we assumed no strong browsing-induced competition bias in favor of *A. altissima*, which would act to the detriment of most native species as they are much more palatable for game. In the current real-world situation, high browsing levels provide a strong advantage to *A. altissima* in most parts of the southern Alps (cf. Maringer et al. 2012).

In spite of these limitations, our study demonstrates the utility of using a forest gap model such as ForClim for integrating the autecological traits of an invasive species from short-term observations or experimentation, which makes it possible to derive the long term, compound effects of all these traits in their interaction with one another and under competition with other species.

Simulated future forest dynamics

General findings

In our simulations, tall and mostly shade-tolerant tree species dominated the species composition in the long term (> 300 yrs), independent of the site, management and climate, with *A. altissima* never reaching dominance in terms of BA. In contrast to *F. sylvatica*, which compensates its lower maximum height compared to conifers such as spruce (*Picea abies*) or fir (*Abies alba*) by high shade tolerance and abundant (sexual) regeneration and hence reaches natural dominance at many mid-elevation sites (Ellenberg 1986; Brändli and Eggman, 1996), *A. altissima*'s short-term high shade tolerance in the juvenile phase (Knüsel et al. 2017) and its high sprouting ability (Kowarik 1995) do not fully compensate for its low maximum height (i.e., 25–30 m) and its presumably low longevity (< 150 yrs) compared to several native tree species. These results are in line with its pioneer character (Kowarik and Säumel 2007) and support Wunder et al. (2018), who reported the occurrence of *A. altissima* in Ticino either in admixed stands with other species such as *C. sativa*, *T. cordata* or *F. excelsior* or forming pure pole-stage stands on recently disturbed stands.

A short-term increase of *A. altissima*'s BA followed by a long-term decrease is consistent with the findings of Kasson et al. (2013), who examined the tree age structure of forests in which *A. altissima* had been planted in the late eighteenth century. In this study, no *A. altissima* exceeding an age of 120 years were found, which further underlines its pioneer character (Kowarik and Säumel 2007). Thus, individuals of *A. altissima* present in both long-term study scenarios may represent the end stage of its dominance.

A. altissima was generally more abundant in managed compared to unmanaged forests, independent of climate or site. From a modeling point of view, this is likely related to its low maximum height compared to other dominant tree

species exceeding maximal heights of 30 m. Consequently, *A. altissima* did not reach the upper canopy under unmanaged conditions, in spite of its ability to survive as a very young tree in low light (≤ 30% diffuse light; Knüsel et al. 2017) and to maintain highly competitive growth rates over longer time periods in the sub-canopy (Knapp and Canham 2000). Management inevitably opens the canopy and provides more light to the lower layers in forest stands, which thus is beneficial for the pioneer and gap-dependent *A. altissima* (Kowarik and Säumel 2007; Knüsel et al. 2017).

These findings have implications for the invasion control and management of *A. altissima*. On the one hand, if *A. altissima* indeed remains an admixed species, it may to some degree be considered as a complement to the indigenous species and contribute to providing ecosystem services (e.g., Sladonja et al. 2015), such as protection against gravitational hazards (Moos et al. 2019). Also, in terms of wood quality *A. altissima* may be a suitable replacement for *F. excelsior*, which is strongly suffering from ash dieback (Rigling et al. 2016). On the other hand, it has been shown that the species can have major negative effects on biodiversity and on ecosystem functioning (Castro-Diez et al. 2012; Constan-Nava et al. 2015; Vila et al. 2006).

Furthermore, our results emphasize the potential effect of management interventions on *A. altissima*'s share in tree species composition. Using a new girdling method, Wunder et al. (2016) showed that most treated trees died after two to four growing seasons without significant re-sprouting. Additionally, the use of natural antagonists such as the fungus *Verticillium nonalfalfae* opens new opportunities for the biological control of *A. altissima* (Maschek and Halmschlager 2018; Siegrist and Holdenrieder 2016). Overall, targeted management interventions provide an important pathway to control the distribution and abundance of *A. altissima* (but see Constán-Nava et al. 2010). Further research is required to develop spatially differentiated management strategies to meet the different demands on multifunctional forests with or without *A. altissima* (Knüsel et al. 2020).

With respect to the comparison between the southern- and northern Alpine site, *A. altissima* featured a higher share in the tree species composition in southern compared to northern Switzerland, independent of management and climate scenario. While the southern Alpine site Claro is characterized by a more open and therefore easier to colonize Chestnut orchard (Conedera et al. 2000), the northern Alpine site Weidwald is a dense, closed-canopy forest with a high species richness, and may have hence a higher resistance to invasion (Maron and Marler 2007). Nevertheless, in both stands *A. altissima* occurred for more than 300 years during the simulation, supporting the frequent expectation of a further spread of *A. altissima* (Knüsel 2018; Wunder et al. 2018).

Southern Switzerland

The pronounced decrease in stand BA under the future climate scenario (RCP8.5) occurred in southern Switzerland only. These findings are in line with other studies showing similar trends for southern Switzerland (e.g., Bircher et al. 2015; Elkin et al. 2013; Huber et al. 2021). The abrupt decline is due to the low water storage capacity of the soils in combination with the strongly reduced summer precipitation, which enhanced drought stress (e.g., Brang et al. 2008). Consequently, a shift to more thermophilous broadleaved forests or even Mediterranean macchia vegetation may occur (Gonzalez et al. 2010; Goodall et al. 1981). Indeed, the simulated forest was quite open and featured a very low BA after the year 2100. Including drought-tolerant species from the Mediterranean in ForClim could help to assess whether higher basal areas could be achieved in future with alternative species such as *Quercus ilex* (holm oak) and whether this would reduce the share of *A. altissima*. This is important especially from the perspective of biodiversity and ecosystem service provisioning, such as carbon storage and the protection function against gravitative natural hazards (e.g., rockfall; Frehner et al. 2005).

Northern Switzerland

Our results showed a slight increase in BA of *F. sylvatica* in the unmanaged scenario under current climate. On the contrary, stand data show a slight decrease of *F. sylvatica* in the Weidwald over the last forty years in favor of *T. baccata*, which is likely due to the rather poor site conditions that bring about seasonal drought (Heiri et al. 2009). Our results may be caused by an overestimation of the soil water holding capacity, which may have led to an underestimation of drought occurrence at this site. However, estimating soil water holding capacity is particularly challenging (Henne et al. 2011) and more soil-related data would be required for a better estimate. Our results further showed that *F. sylvatica* decreased with increasing management intensity, while other tree species benefited from management interventions. This is in line with general ecological expectations, with *F. sylvatica* naturally dominating large parts of the Swiss Plateau (Brändli and Eggmann 1996; Ellenberg 1986), whereas in managed forests its strong dominance is reduced by the artificially increased light availability.

Under climate change, changes in BA were much lower for Weidwald than for Claro. This is in line with Huber et al. (2021), who showed a reduction of the negative effect of climate change on stand BA at sites with higher water storage capacity. The change in stand BA was mainly caused by the decrease of the summer drought-sensitive *F. sylvatica* (van der Maaten-Theunissen et al. 2016). Subsequently, drought-tolerant species such as *A. altissima* and less drought-susceptible species such as *T. cordata* and *A. alba* profited, although shade tolerance became the predominant trait in the long term, shaping the species composition of the stand. Thus, *A. altissima* lost importance in terms of BA, whereas *T. cordata* and *A. alba* showed a steady increase throughout the simulation, which is in line with other studies (e.g., about adaptation potential of *A.alba*, Frank et al. 2017).

Conclusions

We used a dynamic forest gap model evaluated against field measurements to assess the long-term development of the invasive *A. altissima* as a function of forest management and climate change. The model evaluation revealed that this approach adequately represents the behavior of *A. altissima* and its interspecific competition over a timespan of several decades. We thus conclude that the estimates of *A. altissima*'s species-specific parameters faithfully represent the species' autecological and synecological properties.

Independent of site, climate and management, *A. altissima* did not dominate the tree species composition in the long term (> 200 yrs) in the simulated stands. In terms of BA, *A. altissima* gained importance in the managed compared to the unmanaged stands, but remained an admixed species in all scenarios. These results emphasize the high potential of management to regulate the tree species composition so as to modulate the mixture proportion of *A. altissima* and to mitigate species shifts caused by climate change.

Based on these results, it is plausible to expect an increase in the abundance of *A. altissima* and thus a change in the tree species composition in the long term, especially at managed sites. However, our results do not indicate a complete displacement of the indigenous tree species by *A. altissima*, but rather a persistence of *A. altissima* as an additional admixed tree species. This persistence may furthermore be promoted by climate change, particularly on drought-prone sites, as shown by our simulations.

Overall, the approach presented here confirms that quantitative dynamic models have an important role to play in the assessment of the future potential of invasive tree species, especially in the context of climate change.

Appendix A: ForClim sprouting module

A. Altissima (and many other deciduous tree species) rely strongly on vegetative reproduction (Bond and Midgley 2001; Caplat and Anand 2009; Dietze and Clark 2008; Price et al. 2001).

The sprouting module implemented in ForClim is based on the sprouting model of the forest succession model FORECE (Kienast 1987). It assumes that if a tree species is capable of sprouting and a dead stump (due to management or natural mortality) of a predefined diameter exists, the numbers of sprouts are determined using a random number procedure. Based on Kienast (1987), two sprouting tendencies (maximum of 2 or 3 stems per dead tree) and a higher initial DBH of sprouts compared to seedlings, due to the allocation of resources from the mother tree (Caplat and Anand 2009), were implemented. Furthermore, the distinction between root and stem sprouts was considered as unimportant, as ForClim is spatially non-explicit.

The following parameters are required in the approach by Kienast (1987):

Sprouting tendency (according to Kienast (1987)): sprouting tendency of 1 allows a maximum of two stems per stump, sprouting tendency of 2 a maximum of three stems per stump. To determine the sprouting tendency of *A. Altissima*, a sensitivity analysis was conducted and the results were compared to empirical results described by Knüsel et al. (2017), see Isler 2019) for details. Based on this analysis, the sprouting tendency of *A. altissima* was fixed to a value of 2 (cf. Isler 2019).

Minimum diameter of dead stump: *A. altissima* is known to be able to produce sprouts at a very young age (cf. Kowarik 1995; Bory et al. 1991). Thus, it was assumed that if a dead stump of *A. altissima* with a DBH > 1.27 (minimum DBH in ForClim) was present in the previous simulation year, sprouting was allowed to occur in the following year. i

Initial sprout DBH: Kienast (1987) suggested an initial sprout DBH around 0.1 cm. In ForClim, regeneration establishes with an initial DBH of 1.27 cm. Various studies characterize the difference in height between vegetative and generative regeneration of *A. altissima*, but there is a lack of literature describing the difference in DBH. Hence, a sensitivity analysis was conducted in Isler 2019) and the initial DBH for sprouts was defined as 1.7 cm (initial DBH + 33%).

The module was found to be capable of adequately representing the broad pattern of *A. altissima*'s sprouting behavior (cf. Isler 2019). In the model version used here, *A. altissima* was the only species capable of sprouting. This approach is reasonable considering that all other European deciduous species that can reach the canopy are much less vigorous sprouters than *A. altissima*.

For details of the ForClim Code of the sprouting module, see Isler (2019).

Appendix B: Simulation settings

Site conditions

Table B.1 describes the general environmental site conditions of the three study sites and provides an overview of the most important site-specific parameters used in ForClim, as well as the occurring tree species.

The weather data originate from the DAYMET data and the soil types were described by Blaser (2005) for the sites in southern Switzerland (S-CH), respectively, by Brang (2012) for the study site in northern Switzerland (N–CH).

The slope aspect was assigned according to the classification by Schumacher (2004, p.114). All four sites are located on rock debris, and thus, the water storage capacity (bucket size) and the nitrogen availability are considered low to mediate which is in line with the description of the sites in the layers "Water storage capacity" and "Nutrient storage capacity" by Swisstopo (2017). As Huber et al. (2018) showed, that the simulation output was highly sensitive to the bucket size, the same value was attributed despite the different description. Based on the fourth Swiss National Forest Inventory (2009–2013) (NFI4) (Kupferschmid et al. 2015) estimated that the browsing throughout Switzerland reaches a level 2. Browsing level 2 implies that several tree species are in the range of their browsing threshold and/or one tree species is above its threshold, which can lead to a loss of the species in the long term. Thus, the browsing pressure was set to an intermediate level at all sites.

Simulation experiments

Evaluation of model performance

For Mendrisio, the aerial image showed open areas and it was further assumed that no regeneration existed. Thus, the simulations were run from bare ground (i.e., open land, developed soil without trees).

In Claro, no information was available despite the knowledge that both sites were previously managed as chestnut orchards, but abandoned in the 1950s (Knüsel et al. 2017). According to Pezzatti et al. (2021), in southern Switzerland, the average stand density for chestnut orchard located on gentle to medium slopes is 101 trees/ha. This is in line with the observation in the field in October 2018 and the regulations for chestnut orchards, which states that the tree number of chestnut orchards has to be lower than 100 trees/ha as a prerequisite for agricultural subsidies (Art. 22 para. 1

Table B.1 Geographical and climatic characteristics of the study sites, including site-specific parameters used in ForClim

	Claro	Mendrisio	Weidwald
Geographical and climatic variables			
Elevation [m a.s.l.]	280–350	360–500	580–670
Exposition	W	W	S
Inclination [°]	27	> 30	> 30
Location	N 46°15′41" E 9°01′27"	N 45°53′13" E 8°58′56"	N 47°24′53" E 7°59′46"
Mean annual precipitation [mm/yr]	1500	1823	1173
Mean annual temperature [°C]	11.0	10.2	8.3
Mean winter temperature [max/min; °C]	6.0/-3.1	6.4/-2.8	5.6/-9.5
Soil	Haplic podzol	Haplic podzol	Rendzina
Site-specific parameters in ForClim			
Patch size(m^2)	400	400	400
Bucket size (kBs)	9	9	12
Slope Aspect (kSlAsp)	0	+1	+1
Nitrogen availability (kAvN)	60	60	80
Browsing pressure (kBrPr)	50	50	50
Establishment probability (kEstP)	0.04	0.04	0.04
Tree species	Apse, Bpen, Csat, Cave, Fexc, Aalt, Acam, Cbet, Tcor, Qpet, Ugla	Apse, Acam, Cbet, Cave, Fexc, Qpet, Tcor, Ugla, Aalt	Apse, Aalb, Pmont, Psyl, Tvac, Aalt, Cbet, Cave, Fsyl, Fexc, Qrob, Sari, Tcor, Apla

Aalb Abies alba, Aalt *Ailanthus altissima*, Acam *Acer campestre*, Apla *Acer platanoides*, Apse *Acer pseudoplatanus*, Bpen *Betula pendula*, Cave *Corylus avellana*, Cbet *Carpinus betulus*, Csat *Castanea sativa*, Fexc *Fraxinus excelsior*, Fsyl *Fagus sylvatica*, Pmont *Pinus montana*, Psyl *Pinus sylvatica*, Qpet *Quercus petraea*, Qrob *Quercus robur*, Sari *Sorbus aria*, Tbac *Taxus baccata*, Tcor *Tilia cordata*, Ugla *Ulmus glabra*

lit. h LBV (Landwirtschaftliche Begriffsverordnung), BLW (2014)). Due to the lack of information about the DBH-distribution in the chestnut orchards, it was assumed that the growing stock (336 m3 /ha, NFI2) is evenly distributed among 100 trees per ha, with a diameter of 36 cm (see Isler 2019 for further details and a sensitivity analysis of these assumptions).

In the validation, tree and shrub species not represented by ForClim, were combined in the additional groups "other deciduous" and "understorey" (basal area, resp. tree numbers). Details are provided in Table B.2.

Stand initialization for projections into the future

Although in ForClim more than 30 central European tree species are parameterized, not all of the tree species present at the two study sites are represented. Thus, the following simplifications were made.

For Claro and Weidwald, the species *P. avium, R. pseudoacacia* and *Juglans regia* (common walnut) were aggregated in *F. excelsior* as it was considered the present

tree species representing a generic tall broadleaved tree type. For Weidwald, two individuals of *Sorbus torminalis* (checker trees) were assigned to *Sorbus aria* (common whitebeam). Similarly, the understorey *S. nigra, I. aquifolium* and *Crataegus ssp.* were grouped as understorey shrubs and considered to be represented best by *C. avellana*. This simplification affected only few individuals (Table B.3) and ensured that stem numbers were maintained as observed in the measurements (rather than simply removing the species that were not present in the ForClim species set). For further details, see also Isler 2019.

Climate change scenarios

We assumed that climate change was only going to affect the mean temperature and the precipitation sum, but not the variance of these variables. Therefore, the changes of the standard deviations and the cross-correlation of temperature and precipitation were set to zero in the input data file of ForClim. See Table B.4.

Table B.2 Number of individuals and DBH of species not represented in ForClim and thus summarized as "other deciduous" (tree species) or "understorey" (shrub species) for both sites, used for evaluation purposes

DBH (cm)	≤6	10	14	18	22	26	30	34	38	42	46	50	54	58	62	66	70	74
Claro																		
Prunus avium		6	4	3	1	2		1		1		2		1				1
R. pseudoacacia		4	3	4	3	7	4	3	2	1	1							
Fraxinus spp.			1															
Juglans regia			1															
Sambucus spp.	2		1															
Laurus nobilis		2	1															
Ilex aquifolium	1																	
Crataegus spp.						1												
Mendrisio																		
Celtis australis	131	69	63	57	43	14	15	18	8	6	4	2	3	2			1	
Ostrya carpinifolia	1	8	15	13	13	20	14	10	10	5	11	4	5	1	2	1		
F. ornus	20	11	11	8	6	2	1											
R. pseudoacacia		1	4	2	2													
Ficus carica	2		1															
C. betulus	1	1																
P. avium	1																	
J. regia						1												
L. nobilis	155	51	24	3	2	1	1											
Cornus mas	68	7																
Euonymus europaeus	17																	
Sambucus ssp.	5	3																
Laburnum anagyroides	1																	

Table B.3 Number of individuals and DBH of species not represented in ForClim for both study sites. Tree species were represented as *F. Excelsior* (exception *S. torminalis* in Weidwald = *S. aria*), whereas shrub species were considered to be represented best by *C. avellana*

DBH	<6	6	10	14	18	22	26	30	34	38	42	46	50	54	58	62	66	70	74
Claro																			
R. pseudoacacia			4	3	4	3	7	4	3	2	1	1							
P. avium			6	4	3	1	2		1		1		2		1				1
Fraxinus spp.				1															
J. regia				1															
I. aquifolium	1																		
Crataegus spp.							1												
Sambucus spp.		2		1															
L. nobilis				2															
Weidwald																			
S. torminalis	1			1															
P. avium	1																		
I. aquifolium	1			1															

Table B.4 Details for the climate change scenario: Median change of temperature and precipitation under the climate scenario RCP8.5 for the year 2085 according to Croci-Maspoli et al. (2018)

Region		Winter	Spring	Summer	Fall
CHS	Absolute change in temperature (°C)	+ 3.8	+ 3.37	+ 5.04	+ 4.12
	Relative change in precipitation (%)	+ 21.8	+ 1.0	− 22.8	0
CHNE	Absolute change in temperature (°C)	+ 3.77	+ 3.28	+ 4.5	+ 3.92
	Relative change in precipitation (%)	+ 14.5	+ 8.2	− 16.9	− 2.0

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