

Shade tolerance of *Ailanthus altissima* revisited: novel insights from southern Switzerland

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Abstract The tree of heaven (*Ailanthus altissima* (Mill.) Swingle) is considered to be an early-successional, gap-obligate pioneer species with vigorous height growth, low shade tolerance, early fecundity and large seed production. It is a highly invasive species in many temperate and Mediterranean ecosystems outside its natural range, especially after disturbance. Due to its low shade tolerance, the potential of *A. altissima* to colonise undisturbed forests is thought to be low. In this study we analysed the potential of juvenile *A. altissima* to grow and survive in sweet chestnut (*Castanea sativa* Mill.) forests in southern Switzerland. We used hemispherical photography to assess the light conditions of 204 individuals of *A. altissima* (31 % generative, 69 % vegetative) aged between 1 and 7 years (median: 3 years) in six sites. Generative (seed-borne) and vegetative (clonal ramet)

offspring of *A. altissima* are able to grow in light conditions well below the requirements of shade-intolerant tree species such as European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.). The relatively low light conditions found to be sufficient for the growth and survival of generative regeneration of *A. altissima* suggest a higher shade tolerance for this species than previously stated, at least for early regeneration. Consequently, the colonisation frontier of *A. altissima* should be intensively monitored in both forest openings but also in closed canopy forests in the vicinity of seed-bearing *A. altissima*.

Keywords Shade tolerance · Light requirement · Invasive tree · Colonisation

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Introduction

The spread of non-native species into new environments is considered one of the most significant human-driven ecological processes (Chytrý et al. 2008; Simberloff et al. 2013). Among non-native species, woody plants and trees in particular gained increasing attention during the last years since they may severely change processes and functioning of ecosystems and hence the goods and services they provide (Lamarque et al. 2011; Richardson et al. 2014). Therefore, it is important to understand the ecological traits of non-native trees for an informed and sound management (Alpert et al. 2000; Walther et al. 2009).

An example of a non-native tree species is the tree of heaven (*Ailanthus altissima* (Mill.) Swingle) that is currently showing invasive behaviour on all continents except Antarctica (Kowarik and Säumel 2007). *A. altissima* is native to northeastern China and colonizes a broad range of environments, from raw and poor to rich soils. It is largely known to colonize habitats subjected to natural or human disturbances (Fotiadis et al. 2011; Kowarik and Säumel 2007). As a consequence, *A. altissima* is usually referred to as an early-successional, gap-obligate and shade-intolerant tree species with low competitive fitness in undisturbed, closed forest ecosystems (Grime and Jeffrey 1965; Knapp and Canham 2000; Kowarik and Säumel 2007). However, clonal ramets are known to be able to survive in low light conditions below intact forest canopies owing to the assimilates provided by the adult parent trees (Kowarik 1995).

Since about the 1950s the formerly cultivated sweet chestnut (*Castanea sativa* Mill.) forests in southern Switzerland tend to be invaded by other species (Conedera et al. 2001; Knüsel et al. 2015; Radtke et al. 2013). Several of these forests are increasingly colonized by *A. altissima*. Recent observations suggest that generative regeneration of *A. altissima* is more shade tolerant than initially expected (De Boni 2013). Generative regeneration of *A. altissima* has already been found and studied in small gaps of old-growth forests (Knapp and Canham 2000) or even below closed forest canopies (Martin et al. 2010) in the northeastern US. However, *A. altissima* is still largely addressed as a highly shade-intolerant tree species.

This short note reports on the findings of a shade tolerance study in southern Switzerland based on the assessment of light conditions using hemispherical

photography and discusses the shade tolerance of juvenile *A. altissima* and their potential to spread into low light forest patches in broadleaved temperate forests.

Materials and methods

Study sites and sampling

We selected six sites within the low-elevation *C. sativa* belt in southern Switzerland that is increasingly invaded by *A. altissima* (Knüsel et al. 2015). The sites were previously cultivated as chestnut orchards or coppice forests, but were not managed within the last ca. 60 years alike many other chestnut stands in the study region (Conedera et al. 2001). Elevation ranges from 270 to 460 m a.s.l. and inclination from 30 to 120 ° (Table 1). Mean annual temperature is 12.4 °C, mean annual precipitation sum is 1476 mm, as measured at the meteorological station in Grono GR (324 m a.s.l., 5–30 km from the study sites; 1981–2010, MeteoSwiss National Weather Service). The field work took place in early autumn 2013 (sites Claro, Pollegio, San Vittore I) and in summer 2015 (sites Locarno, San Vittore II, Sementina).

The sites Claro, Pollegio and San Vittore I were colonized by *A. altissima* in the late 1950s and feature established populations (henceforth referred to as ‘late invasion stage sites’). They are characterized by adult *A. altissima* (including seed-bearing females) ranging from 20 to 50 cm in diameter at breast height. Regeneration of *A. altissima* is abundant in varying light conditions beneath a closed forest canopy.

The other sites (Locarno, San Vittore II, Sementina), in contrast, are close to the colonization frontier (henceforth referred to as ‘early invasion stage sites’). Thus, adult canopy trees are sparse in Locarno and Sementina and generative regeneration of *A. altissima* dominates. In San Vittore II, however, many adult trees grew along the road intersecting the site. Most of these adult trees had been girdled in 2010 and were felled in winter 2014, with only few remaining in the canopy.

The regeneration density of *A. altissima* in the study sites reflects the differences between the early- and late invasion stage sites (Table 1). To be able to sample enough plants in the sparsely populated early invasion stage sites we applied two different sampling methods:

Table 1 Analysed regeneration of *A. altissima* differentiated in generative and vegetative plants

Site	Coordinates (WGS 84) altitude (m a.s.l.)	Aspect	Generative regen (n)	Vegetative regen (n)	Total regen (n)	Average density ^a (n/ha)
Late invasion stage						
Pollegio	8.947°E 46.365°N 328	SW	17	44	61	10200
Claro	9.024°E 46.261°N 285	E	0	36	36	2300
San Vittore I	9.092°E 46.238°N 268	SE	24	61	85	2300
Early invasion stage						
San Vittore II	9.078°E 46.239°N 460	SE	6	0	6	400
Locarno	8.773°E 46.175°N 450	SW	10	0	10	350
Sementina	8.965°E 46.180°N 430	SE	6	0	6	200
Total			63	141	204	

Given are numbers of individuals ranging from 40 to 450 cm in height and growing in low light conditions ($\leq 30\%$ diffuse light)

^a Average regeneration densities of *A. altissima* were either estimated by tallying all plants along the transects (late invasion stage sites), or by tallying all plants in an area of 100 m² around the sampled individuals (early invasion stage sites) and extrapolating them to conventional hectare values

Late invasion stage sites: Abundant regeneration of *A. altissima* was sampled along a transect with a maximum length of 40 m covering a large light gradient. Two to five clusters of regeneration intersecting the transect were identified. For all individuals of *A. altissima* with heights ranging from 40 to 450 cm the regeneration type, light condition and growth characteristics were determined—resulting in a total sample size of 36–85 individuals per site (Table 1).

Early invasion stage sites: Sparse regeneration of *A. altissima* was sampled based on a regular grid with a mesh size of 50 m. At each grid point one juvenile *A. altissima* closest to the plot centre and inside an 800 m² area around the grid point was sampled. Only plants with a height ranging from 40 to 450 cm were selected. For each sampled plant the regeneration type, light condition, age and growth characteristics were assessed. The sites cover an average area of 8 ha.

Regeneration type

Ailanthus altissima can regenerate vegetatively via clonal ramets (root suckers) and generatively via seeds (Kowarik 1995). The here investigated individuals of

A. altissima were classified either as vegetative or generative plants (Table 1). To this end, a hole was dug next to the stem of each juvenile plant to check for connecting roots with parent trees. In case no connecting root was found, the entire individual was excavated to confirm the regeneration type. In almost all cases the distinction was clear. However, there is the possibility that a small root connection to a parent tree may have been detached during the excavation.

Light conditions

Digital hemispherical photographs were taken at the top of each of the 204 individuals of *A. altissima* using a Canon EOS 50D camera, with a Sigma EX DC 4.5 mm fisheye lens, mounted on a tripod. The hemispherical photographs were processed with the ‘Hemisfer’ software (www.schleppi.ch/hemisfer; Schleppi et al. 2007). The light condition at the top of each plant was characterised by the diffuse light index (DLI) and the gap light index (GLI) over a growing season. DLI is defined as the average transmission of diffuse (indirect) radiation and was chosen because it allows for comparisons with studies on other tree

species, whereas GLI represents the weighted average of diffuse and direct light (e.g. Canham 1988). GLI was used for comparison with other species where available. To assess the potential of juvenile *A. altissima* to grow in low light conditions, only individuals growing at a DLI ≤ 30 % were retained for further analysis (88 % of all sampled plants). This threshold was also applied to data from other studies on four native tree species used for comparison (cf. Fig. 1).

Age and growth characteristics

The age of each selected *A. altissima* individual was either estimated by counting the apical growth scars or the annual tree rings at the root collar. Tree height was identified as the vertical distance between the highest lignified tissue of the tree and the stem base. Annual tree height increment was measured between the terminal bud scars and averaged for the three most recent years (for plants >3 years) or for the entire individual (plants ≤ 3 years).

All statistical analyses were performed using R, a language and environment for statistical computing (R Core Team 2016).

Results

Regeneration type

Of the 204 analysed juvenile *A. altissima*, 141 (69 %) were identified as vegetative and 63 (31 %) as generative plants (Table 1). In the late invasion stage sites Pollegio and San Vittore I the proportion of generative plants was the same (28 %), while in Claro no generative plants were found. In the early invasion stage sites all analysed plants were generative.

Light conditions

Regeneration of *A. altissima* grew at sites with a median DLI of 5.3 (vegetative plants) and 10.6 % (generative plants, Fig. 1). Vegetative regeneration grew in significantly lower light conditions compared to generative individuals ($P < 0.01$, two-sample Wilcoxon test). The median DLI of generative regeneration (10.6 %) was smaller than for regeneration of European larch (*Larix decidua* Mill.: 28.2 %; Krebs 2001), regeneration of Scots pine (*Pinus sylvestris* L.:

22.5 %; Perren et al. 1992), regeneration of Norway spruce (*Picea abies* (L.) Karst.: 15.2 %; Frehner 2000) and similar to the one reported for regeneration of European silver fir (*Abies alba* Mill.: 9.4 %; Cadotsch 2011).

Growth performance

The median age of the sampled juvenile *A. altissima* was three years with a maximum of seven years, irrespective of the regeneration type (Table 2). Vegetative plants had a median height of 146 cm, while generative plants were smaller with a median height of 120 cm. The median annual height growth over the three most recent years was significantly higher ($P < 0.01$) for vegetative (53 cm) as compared to generative regeneration (38 cm).

Discussion

Ailanthus altissima is largely mentioned as an early-successional, highly shade-intolerant species whose successful establishment depends on disturbed areas with full light (Fotiadis et al. 2011; Kowarik 1995). While it was found to be able to germinate in low light conditions (Gonzalez-Munoz et al. 2011; Kota et al. 2007), most seedlings were reported to die within the first 2 years (e.g. Gómez-Aparicio and Canham 2008). Yet, in few cases generative regeneration of *A. altissima* has been found to grow for several years in very small gaps or in closed-canopy forests (Knapp and Canham 2000; Martin et al. 2010). Our results are in line with these observations and show that *A. altissima* is able to survive and even grow substantially for up to seven years in low light conditions, suggesting a higher shade tolerance for *A. altissima* than previously stated, at least for early regeneration.

Interestingly, we found generative regeneration of *A. altissima* germinating and surviving in similar light conditions as regeneration of *P. abies* (Frehner 2000) and regeneration of the late-successional *A. alba* (Cadotsch 2011; Fig. 1). Clearly, the latter species are known to persist several decades in such low light conditions (median age of *A. alba* in Cadotsch 2011: 22 years), while the maximum age of seed-borne regeneration of *A. altissima* in our study was only seven years. Further, it should be kept in mind that the DLI can be sensitive to site aspect, generally showing

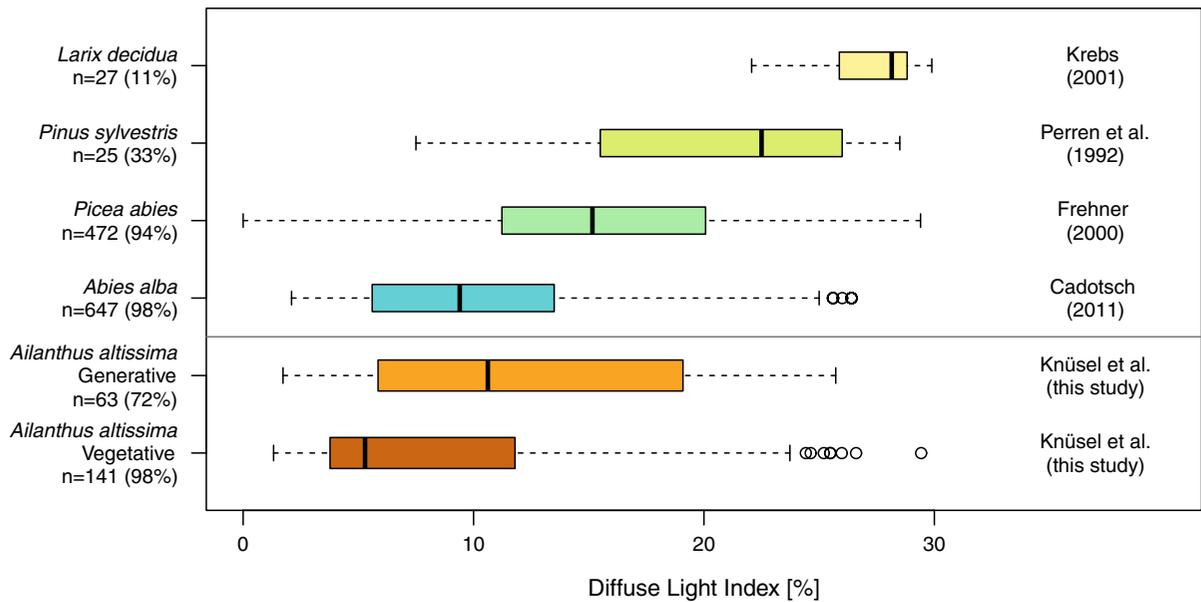


Fig. 1 Boxplots of diffuse light index [DLI: average transmission of diffuse (indirect) radiation over a growing season] of regeneration of *A. altissima* growing in low light conditions ($\leq 30\%$ DLI) with heights ranging from 40 to 450 cm. Regeneration of *A. altissima* is compared to regeneration of four native tree species *L. decidua*, *P. sylvestris*, *P. abies* and *A. alba* also growing in low light conditions ($\leq 30\%$ DLI) in near-natural forests in Switzerland. Percentages in brackets denote

the proportion of plants growing in low light conditions ($\leq 30\%$ DLI) compared to all measured plants in the respective studies. Right column refers to data sources. Boxplots: the 'box' covers the first and third quartile of the data and the median is marked with a bold line; 'whiskers' are extended to the most extreme data point between the box and 1.5 times the box length (R Core Team 2016)

Table 2 Age and height growth of generative and vegetative regeneration of *A. altissima*

	Generative regeneration	Vegetative regeneration
Age (years)	3 (1/7)	3 (1/7)
Height (cm)	120 (29/408)	146 (28/392)
Height growth (cm)	38 (9/109)	53 (20/161)

Median values (min/max in brackets) for individuals ranging from 40 to 450 cm in height and growing in low light conditions ($\leq 30\%$ diffuse light). Height growth is defined as the mean growth over the three most recent years

the highest values on north-facing and lowest values on south-facing slopes. In case of *L. decidua* (Cadotsch 2011; GLI data available), where regeneration was sampled on two north-facing slopes, the DLI was on average 5.8 % (± 1.7 median absolute deviation, MAD) higher as compared to the GLI. In contrast, the DLI of regeneration of *A. altissima* sampled on south-facing slopes was on average 2.8 % (± 4.0 MAD) lower than the respective GLI. Additionally, the studies used for comparison were conducted at higher altitudes (1000–1800 m a.s.l.), where a certain amount of direct light may be required for heat (particularly soil warming) besides photosynthesis per se (Imbeck and Ott 1987).

Niinemets and Valladares (2006) classified the shade tolerance of *A. altissima* as 2.4 on a scale from 1 (no tolerance) to 5 (maximal tolerance) in their global review on 806 temperate northern hemisphere trees and shrubs and therefore as less shade tolerant than *A. alba* (4.6) and *P. abies* (4.5). Consistent with our study, *A. altissima* was classified as more shade tolerant than *L. decidua* (1.5) and *P. sylvestris* (1.7). Yet, they used data from East Asia to classify the shade tolerance of *A. altissima*. Further, generative regeneration of *A. altissima* in the northeastern US (Knapp and Canham 2000; Martin et al. 2010) was found to grow in similar light conditions as measured in our study, but was described as a shade-intolerant

species. This may partly be owed to the fact that both studies viewed shade tolerance as a continuum between high light growth and low light survivorship (see Kobe et al. 1995), such that the minor low light survivorship of *A. altissima* placed the species near the extreme shade-intolerant border of the continuum. The minor low light survivorship may, however, be compensated to a certain degree by the enormous amounts of seeds produced by female *A. altissima* (Bory and Clair-Maczulajtys 1980). Even more importantly in our opinion, *A. altissima* was studied in forests lacking highly shade-intolerant species such as *L. decidua*, *P. sylvestris* or Black locust (*Robinia pseudoacacia* L.; Boring and Swank 1984). Thus, it was classified as a highly shade-intolerant species relative to the canopy dominants. For these reasons, and based on our observation that seeds of *A. altissima* can germinate, grow and persist below a forest canopy for up to seven years, we view *A. altissima* as an early successional species with a low to intermediate shade tolerance in early regeneration.

Generative regeneration of *A. altissima* exhibited mean annual growth rates of 38 cm year⁻¹ in the three most recent years, indicating substantial growth in low light conditions. These values lie between those reported by Knapp and Canham (2000; 11 cm year⁻¹) and Martin et al. (2010; 68 cm year⁻¹). The slightly higher mean growth rates of vegetative regeneration (53 cm year⁻¹) and also their occurrence in the lowest light conditions indicate an assimilate support via the root system by the mother plant, as already suggested by Kowarik (1995).

To further evaluate our findings, follow-up studies should focus on the long-term survival capability of generative regeneration of *A. altissima* in low light conditions. In addition, the longevity of the seed bank, another factor potentially extending the ‘waiting’ time of *A. altissima* in the understory, remains a question to be resolved (Kota et al. 2007).

Conclusion

In this short note, we argue for attributing a higher shade tolerance to juvenile *A. altissima* than previously stated, since they can grow and survive in closed canopy forests in low light conditions. *A. altissima* may thus have a higher competitive fitness in the regeneration phase as compared to highly shade-intolerant

competitors such as *P. sylvestris* or *R. pseudoacacia*. Our findings further indicate that the colonization frontier should be intensively monitored, and the monitoring should include undisturbed, closed canopy forests in the vicinity of known *A. altissima* populations, rather than just disturbed sites.

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References

- Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect Plant Ecol Evol Syst* 3:52–66
- Boring LR, Swank WT (1984) The role of black locust (*Robinia pseudo-acacia*) in forest succession. *J Ecol* 72:749–766
- Bory G, Clair-Maczulajtys D (1980) Production, dissemination and polymorphism of seeds in *Ailanthus altissima*. *Rev Gen Bot* 88:297–311
- Cadotsch D (2011) Untersuchung zum Höhenwachstum der Weisstanne (*Abies alba*)—Vergleich zwischen Nord- und Südbünden. School of Agricultural, Forest and Food Sciences HAFL. Bern University of Applied Sciences BFH, Zollikofen, p 90
- Canham CD (1988) An index for understory light levels in and around canopy gaps. *Ecology* 69:1634–1638
- Chytrý M, Maskell LC, Pino J et al (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *J Appl Ecol* 45:448–458
- Conedera M, Stanga P, Oester B et al (2001) Different post-culture dynamics in abandoned chestnut orchards and coppices. *For Snow Landsc Res* 76:487–492
- De Boni A (2013) Analisi del comportamento della rinno-vazione di ailanto (*Ailanthus altissima* (Mill.) Swingle) in funzione della luce. School of Agricultural, Forest and Food Sciences HAFL. Bern University of Applied Sciences BFH, Zollikofen, p 82
- Fotiadis G, Kyriazopoulos AP, Fraggakis I (2011) The behaviour of *Ailanthus altissima* weed and its effects on natural ecosystems. *J Environ Biol* 32:801–806
- Frehner M (2000) Untersuchung über den Einfluss unterschiedlicher Kleinstandorte und der Pflanztechnik auf Fichtenpflanzungen in subalpinen Lawinenschutzwäldern. *Beih Schweiz Z Forstwes* 92:339–556
- Gómez-Aparicio L, Canham CD (2008) Neighbourhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. *J Ecol* 96:447–458
- Gonzalez-Munoz N, Castro-Diez P, Fierro-Brunnenmeister N (2011) Establishment success of coexisting native and

- exotic trees under an experimental gradient of irradiance and soil moisture. *Environ Manag* 48:764–773
- Grime JP, Jeffrey DW (1965) Seedling establishment in vertical gradients of sunlight. *J Ecol* 53:621–642
- Imbeck H, Ott E (1987) Verjüngungsökologische Untersuchungen in einem hochstaudenreichen subalpinen Fichtenwald mit spezieller Berücksichtigung der Schneeablagerung und der Lawinenbildung. *Mitt Eidg Inst Schnee Lawinenforschung* 42:202
- Knapp LB, Canham CD (2000) Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. *J Torrey Bot Soc* 127:307–315
- Knüsel S, Conedera M, Rigling A et al (2015) A tree-ring perspective on the invasion of *Ailanthus altissima* in protection forests. *For Ecol Manag* 354:334–343
- Kobe RK, Pacala SW, Silander JA et al (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecol Appl* 5:517–532
- Kota NL, Landenberger RE, McGraw JB (2007) Germination and early growth of *Ailanthus* and tulip poplar in three levels of forest disturbance. *Biol Invasions* 9:197–211
- Kowarik I (1995) Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *J Veg Sci* 6:853–856
- Kowarik I, Säumel I (2007) Biological flora of central Europe: *Ailanthus altissima* (Mill.) swingle. *Perspect Plant Ecol Evol Syst* 8:207–237
- Krebs B (2001) Untersuchungen zum Höhenwachstum des Lärchenaufwuchses in Abhängigkeit vom direkten und diffusen Licht im Engadin. Department of Forest Sciences, ETH Zürich, Zürich, p 98
- Lamarque LJ, Delzon S, Lortie CJ (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. *Biol Invasions* 13:1969–1989
- Martin PH, Canham CD, Kobe RK (2010) Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. *J Ecol* 98:778–789
- Niinemets U, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecol Monogr* 76:521–547
- Perren B, Rigling A, Walthert L (1992) Verjüngungsökologie und -dynamik der waldföhrenreichen Wälder im Gebiet Brienz-Wiesen (GR) - mit besonderer Berücksichtigung des Standortes, der Verjüngungsökologie und der Entwicklungsdynamik. Department of Forest Sciences. ETH Zürich, Zürich, pp 269
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Radtke A, Ambrass S, Zerbe S et al (2013) Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. *For Ecol Manag* 291:308–317
- Richardson DM, Hui C, Nunez MA et al (2014) Tree invasions: patterns, processes, challenges and opportunities. *Biol Invasions* 16:473–481
- Schleppi P, Conedera M, Sedivy I et al (2007) Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agric For Meteorol* 144:236–242
- Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* 28:58–66
- Walther GR, Roques A, Hulme PE et al (2009) Alien species in a warmer world: risks and opportunities. *Trends Ecol Evol* 24:686–693