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Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests

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ABSTRACT

The non-native tree species Black Locust (*Robinia pseudoacacia* L.) from N America and Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle) from E Asia are invading both anthropogenic and near-natural habitats throughout Europe. So far, few studies have focused on their invasion into forests and none has addressed the influence of coppice management, which is characterized through regular clear-cuts. To retrace the invasion during the last 50 years, we studied the abundance in the canopy as well as the natural regeneration of these species in the coppice forest of Gargazon (South Tyrol, Northern Italy), which was ideal due to its patchy mosaic of different forest age (time since last coppicing). We analyzed which factors favor the presence and abundance of *A. altissima* and *R. pseudoacacia* regeneration. Tree saplings were sampled on 113 plots each measuring 7 m^2 in a total study area of 25.5 hectares. On each plot, the following environmental variables were recorded: canopy cover per species, total herb layer cover, distance to clearing, stone cover, slope, and aspect. Soil moisture was derived from herbaceous indicator species. Hurdle models were used for data analysis to account for the zero-inflated data structure. The results showed that *R. pseudoacacia* has established earlier in the studied forest than *A. altissima*, but *A. altissima* has been spreading with higher speed during the last 30 years. Our study exemplifies the invasion of both species synchronously to the coppice cycle, that means they colonize fresh clear-cuts, establish, and remain. We conclude that the currently applied coppice management, which consists of repeated clear cuttings each 20–30 years, favors the spread of both invasive species. Thus, an adaptation of the management system is needed to avoid further invasion.

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1. Introduction

Coppice forest management as a silvicultural system has a long history and is still practiced on over 21 million hectares in Southern and Southeastern Europe (Puumalainen, 2001). Usually, relatively small forest patches of about 0.5 hectares, depending on country and forest ownership, are clear-cut each 20–30 years (Piussi, 2006; Bartha et al., 2008). In some regions like in our study area South Tyrol, Northern Italy, coppice is favored for its rockfall protection efficiency (high number of stems), while in other regions it is maintained for its heritage and nature conservation value (Kirby and Thomas, 2000; Hedl et al., 2010). Nevertheless, each clear-cut displays a disturbance event (Roberts and Gilliam, 1995) and disturbances are generally regarded to facilitate biological invasions (Catford et al., 2012). Alien species are often good colonizers, so that early stages of secondary succession are very susceptible to invasion (Catford et al., 2012). Growth conditions are additionally facilitated on clearings, because resource availability is high and competition from native tree species is reduced (Alpert et al., 2000). In fact, non-native *Ailanthus altissima* and *Robinia pseudoacacia* occur in European forest ecosystems mainly on clearings, along the fringes of forests and in sparsely stocked woodlands (Celesti-Grapow et al., 2010; Kohler, 1963; Kowarik, 2010). In the insubric region of Switzerland, regeneration of *R. pseudoacacia* and *A. altissima* has been abundant after a forest fire and the authors concluded that few native species will be able to compete with them after stand-replacing forest fires (Maringer et al., 2012). These findings lead to the question whether coppice management facilitates their invasion in a similar way because the clearings display safe sites (*sensu* Harper et al., 1961) for the regeneration and establishment of both light-demanding pioneer species.

While the ecology of Tree of Heaven (*A. altissima* (Mill.) Swingle) and Black Locust (*R. pseudoacacia* L.) is well understood in urban-industrial ecosystems, much less is known about their invasion

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into semi-natural woodlands and how forest management activities can unintentionally favor these species (Kowarik and Böcker, 1984; Gutte et al., 1987; Celesti-Grapow and Blasi, 2004; Kowarik and Säumel, 2007; Basnou, 2009). Currently, there is hardly any information on the invasive potential of *Ailanthus* and *Robinia* in coppice systems (Hegi, 1925; Lohmeyer, 1976; Ließ and Drescher, 2008). This is a serious knowledge gap considering on the one hand the vast abundance of coppice forests especially in the Mediterranean Basin (Puumalainen, 2001) and on the other hand the high biodiversity that is found there (Cowling et al., 1996).

Biological invasions are identified as one of the major causes for biodiversity loss (Hassan et al., 2005; Kowarik, 2010; Millennium Ecosystem Assessment, 2005) and changes of ecosystem structure and function (Vitousek et al., 1996; Higgins et al., 1999; Mooney, 1999; Nentwig, 2007). Changes in plant community composition and negative impacts on the recruitment of native species were reported (Richardson, 1998). Fuentes-Ramirez et al. (2011) showed that some invasive species can form monospecific stands impeding the recolonization of native species. Consequently, managing and combating non-native species is one of the major objectives of the current European biodiversity strategy (European Commission, 2011). To develop such measures it is important to understand the invasion dynamics.

From a theoretical point of view, coppice management should favor the invasion of *A. altissima* and *R. pseudoacacia* for a second reason. Since it has been shown that mechanical control measures, which are often applied to repress invasive tree species, actually stimulate vegetative regeneration (Burch and Zedaker, 2003; Böcker and Dirk, 2008), the frequent clear-cuts in coppice forest likely enhance the vegetative regeneration of *A. altissima* and *R. pseudoacacia*. Furthermore, the vegetative offspring of *R. pseudoacacia* and *A. altissima,* which are still connected to the mother plant by roots, is considered more shade-tolerant than the generative offspring (Kowarik, 1995, 1996; Knapp and Canham, 2000). In addition to disturbance and the subsequent change in resource availability, environmental stress has been described as a major factor influencing habitat invasibility (Alpert et al., 2000). However, *A. altissima* and *R. pseudacacia* are known to be very drought-tolerant even outside their natural range (e.g. Celesti-Grapow and Blasi, 2004).

To better understand the invasion dynamics of the two alien species into coppice forest systems, we addressed the following questions:

(1) Are *Ailanthus* and *Robinia* more abundant in younger forest patches than in older ones? Do abundance in canopy and regeneration show the same pattern?
(2) Which factors favor the regeneration of *Ailanthus* and *Robinia* in coppice forests in general?
(3) Do non-native saplings occur more frequently than native saplings and do they grow faster?

2. Materials and methods

2.1. Study site

The study was carried out in the upper Etsch valley in South Tyrol, Northern Italy, south of the city of Meran (46°34′50″N, 11°12′46″E). The investigated coppice forest is located near the village of Gargazon at the eastern slope of the valley between 260 and 430 m a.s.l. The climate is sub-mediterranean with a mean annual precipitation of about 700 mm with maxima in summer and autumn. The mean annual temperature is 11.5 °C (Autonome Provinz Bozen – Südtirol, 2010). During the summer an absolute maximum temperature of 40 °C can be reached. The geology is volcanic porphyry with nutrient-poor and acidic Syrosem soil (Peer, 1995). The intensive frost shattering during the post-glacial period created stony slopes with different stone or block size (Lüth, 1993; Bosellini, 2007).

Two forest types that are well-adapted to those warm and dry slope habitats are the *Antherico liliaginis-Quercetum pubescentis* (further referred to as very dry oak forest) on the driest areas of the study area and the *Fraxino orni-Ostryetum quercetosum pubescentis* (further referred to as hophornbeam-manna ash forest) on the slightly moister areas (Peer, 1995). Additionally, *Quercus petraea* is often part of the forest as standard tree, i.e. a tree that is kept longer than one rotation period to ensure natural regeneration from seeds and high-quality timber instead of firewood only. In addition to the above mentioned species, *Acer campestre*, *Ailanthus altissima*, *Celtis australis*, *Prunus avium*, *Prunus mahaleb*, *Robinia pseudoacacia*, *Sorbus domestica*, *Sorbus torminalis, Tilia cordata*, *Ulmus glabra*, and *Ulmus minor* occur.

2.2. Sampling procedure

Considering the patchiness of different stand age and small-scale environmental variation in the municipality forest of Gargazon, tree regeneration was systematically sampled in a 45-m grid. This was laid over the total study area of 25.5 ha resulting in 126 sampling points. After exclusion of some points due to inaccessibility or man-made structures, such as trails, 113 points were inventoried. Around each point, two circles were sampled. Firstly, a circle with a radius of 1.5 m (plot size: 7 m^2) for recording natural regeneration and secondly one with a radius of 2 m (plot size: 12.6 m^2) for the inventory of herbaceous indicator species. Slope correction was taken into account. Field sampling was carried out in May and June 2011.

Natural regeneration, i.e. saplings >10 cm in height and <7 cm dbh (diameter at breast height), were counted per tree species and per height class (11–33, 34–66, 67–99, 100–199, >199 cm). Since it would have been too time-consuming to excavate all individuals, we could not differentiate between generative and vegetative saplings. The two oak species *Quercus petraea* and *pubescens*, which occur in the study area, are difficult to differentiate due to hybridisation (Salvini et al., 2009; Viscosi et al., 2009). Hence, oaks were identified as one species (*Qu. petraea et pubescens*).

As suggested by Ellenberg et al. (1991), herbaceous indicator species were used to get an estimate of soil moisture. More precise technical measurements were not possible due to the sample size and stony ground. Using indicator values of herbaceous species to retrieve site information which may influence regeneration, is an approved method (Ammer et al., 2004; Zerbe and Wirth, 2006). Based on previous vegetation data from the study site (Radtke, 2011, unpublished data), 14 relatively abundant species were chosen as indicator species, i.e. 7 indicators for dry sites and 7 for moist sites (Table 1). Plots were classified as "moist" or "dry" when only indicator species for moist or dry sites were found, respectively. Plots with both dry and moist site indicators were classified as "medium". Moisture indicator values and nomenclature of the species follow Landolt et al. (2010).

Forest stand age, i.e. time since last coppicing, was derived from a map of the forest service in ten-year classes (0–10, 11–20, 21–30, 31–40, >40 years). Canopy tree composition was visually estimated in 10% classes when standing on the plot center within a circle of app. 20 m radius. In addition we recorded the presence of single mature *Ailanthus* and *Robinia* trees (dbh >7 cm) as potential diaspore sources.

We estimated the distance to the border of the next clearing in meters to consider edge effects. Clearings are characterized by high light and resource availability as well as a specific micro-climate in general. These features clearly distinguish clearings from patches of all other age classes. The distance of sample points on clearings

Table 1
Indicator species for moist and dry sites with moisture indicator values from Landolt et al., 2010. Values range between 1 (very dry) and 5 (flooded). *Sedum* and *Sempervivum* individuals could not be identified to species level without flowers, but all species of those two genus occurring in the study site have moisture values between 1 and 2.

Indicator species for moist sites	Moisture value	Indicator species for dry sites	Moisture value
Tamus communis	3.5	*Anthericum liliago*	1.5
Dryopteris filix-mas	3.5	*Hepatica nobilis*	2.0
Hedera helix	3.0	*Hieracium pilosella*	2.0
Humulus lupulus	4.0	*Sedum spec.*	1.0–2.0
Oplismenus undulatifolius	3.5	*Sempervivum spec.*	1.0–2.0
Pulmonaria officinalis	3.5	*Stachys recta*	1.5
Salvia glutinosa	3.5	*Veronica officinalis*	2.0

Table 2
Environmental factors recorded and used for multiple regression.

Environmental factor	Unit	Scale	Method
Forest stand age classes	0–10 years old 11–20 years old 21–30 years old 31–40 years old >40 years old	Metric	Map of forest service
Dominance in canopy per tree species	10% Classes	Metric	Visual estimation
Distance to clearing	m	Metric	Visual estimation
Aspect	°	Metric	Compass
Slope	°	Metric	Compass
Stone cover	10% Classes	Metric	Visual estimation
Soil moisture	Moist, medium, dry	Categorical	Indicator species
Herbaceous cover	10% Classes	Metric	Visual estimation

was rated as zero meters. The value 50 m was assigned to plots with no clearing within sight distance.

Slope and aspect were measured with a compass in degrees. Percentage of soil skeleton, i.e. vegetation-free stones at the surface and coverage of the herbaceous layer were estimated visually in classes of 10% (Table 2).

2.3. Statistical analyses

All analyses and graphs were conducted with the free statistical software R (R Development Core Team, 2011).

Tree regeneration data typically contains many zero values, i.e. plots where the species is absent (Ammer et al., 2004). Thus, the data displays a zero-inflated count distribution. Therefore, we used a hurdle model from the *pscl* package (Zeileis et al., 2008). This is a two component model with a logistic part for the presence-absence data and a negative binomial part for the count data. The negative binomial distribution is appropriate for tree regeneration data (Zhang et al., 2012). The plots in Figs. 2a, c, d and 3a, c are spinograms, i.e. a variant of mosaic displays (see e.g., Friendly, 1994) and are closely related to stacked bar plots. The respective metric variable on the *x*-axis is broken into intervals (as in a histogram) and then stacked bar plots are created. The width of each bar is proportional to the relative frequency of the *x*-value and the height is proportional to the conditional frequency of the *y*-category, i.e. presence or absence of *Ailanthus* or *Robinia* regeneration, given the respective interval of x.

The most important factors explaining *Ailanthus* and *Robinia* regeneration in the study area were selected by a multiple regression approach for each species separately. Since R offers no automatic model simplification function (step) for hurdle models yet, a logistic generalized linear model (GLM) and a negative binomial GLM were calculated for the presence-absence part and the count part of the data, respectively. The build-in functions ‘step’ (logistic GLM) and ‘stepAIC’ (negative binomial GLM) were used for automatic model simplification. This means backward selection is applied to select only the most important from all eight recorded variables (Table 2) by choosing the model with the lowest AIC (Akaike Information Criterion). Due to a relatively low number of observations in the count model (*Ailanthus* $n = 26$; *Robinia* $n = 20$), eight variables were too many to start the model simplification with. Therefore, the variables, which were selected in the logistic model, were used as starting point for the count models. In the results section, we do not present all the steps of this variable selection, but only the results of the hurdle model, which was calculated using the selected variables.

We used the non-parametric Kruskal–Wallis Test to compare the non-native/native sapling proportions between forest stand age classes (Crawley, 2007).

3. Results

3.1. Ailanthus and Robinia abundance in forest patches of different age

Robinia was much more established in the study area than *Ailanthus*, accounting for 14% of the total canopy cover whereas only 3% were made up by *Ailanthus*. However, *Ailanthus* was widespread over the study area but often with single mature trees only (Fig. 1a), which suggests that its invasion is still in an earlier stage than that of *Robinia*. This latter dominated about one third of the 31–40-years-old patches already (Fig. 1b). *Ailanthus* regeneration was found on 26 and *Robinia* on 20 of the 113 surveyed plots. Whereas 9% of all saplings were *Ailanthus*, only 2% were *Robinia*. The progressive invasion in time and space becomes clearly visible in the stairs-like pattern of the regeneration spinograms (Figs. 2c and 3c), i.e. the younger the forest patch was, the more often *Ailanthus* and *Robinia* saplings were found. This pattern was clearer for *Ailanthus* (steeper stairs) than for *Robinia* (flatter stairs) indicating higher invasion speed for *Ailanthus* than for *Robinia*.

3.2. Factors favoring Ailanthus and Robinia regeneration in coppice forests

The presence of *Ailanthus* regeneration was explained by ‘distance to clearing’, forest stand age, presence of mature *Ailanthus* trees, and soil moisture class. However, from these four variables

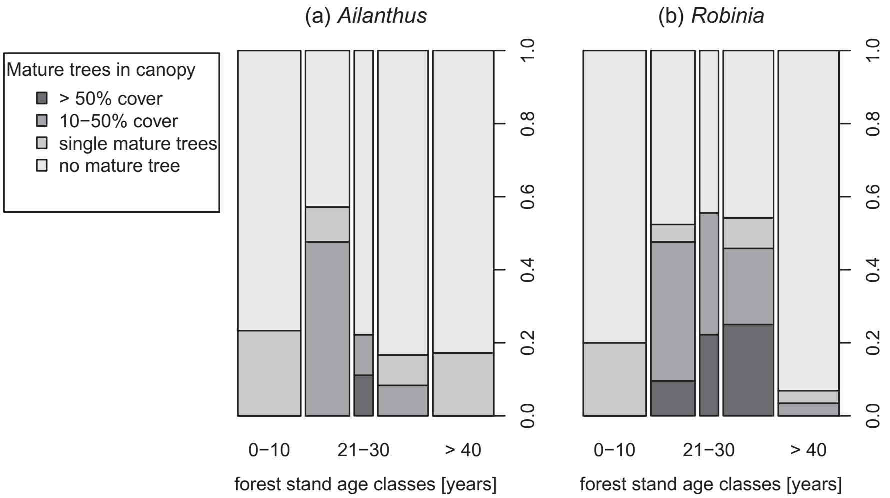

Fig. 1. Abundance of mature *Ailanthus* (a) and *Robinia* (b) trees in the canopy (in classes) per forest stand age class. Spinograms show the frequency of cases over all 113 plots. For more explanation see methods section.

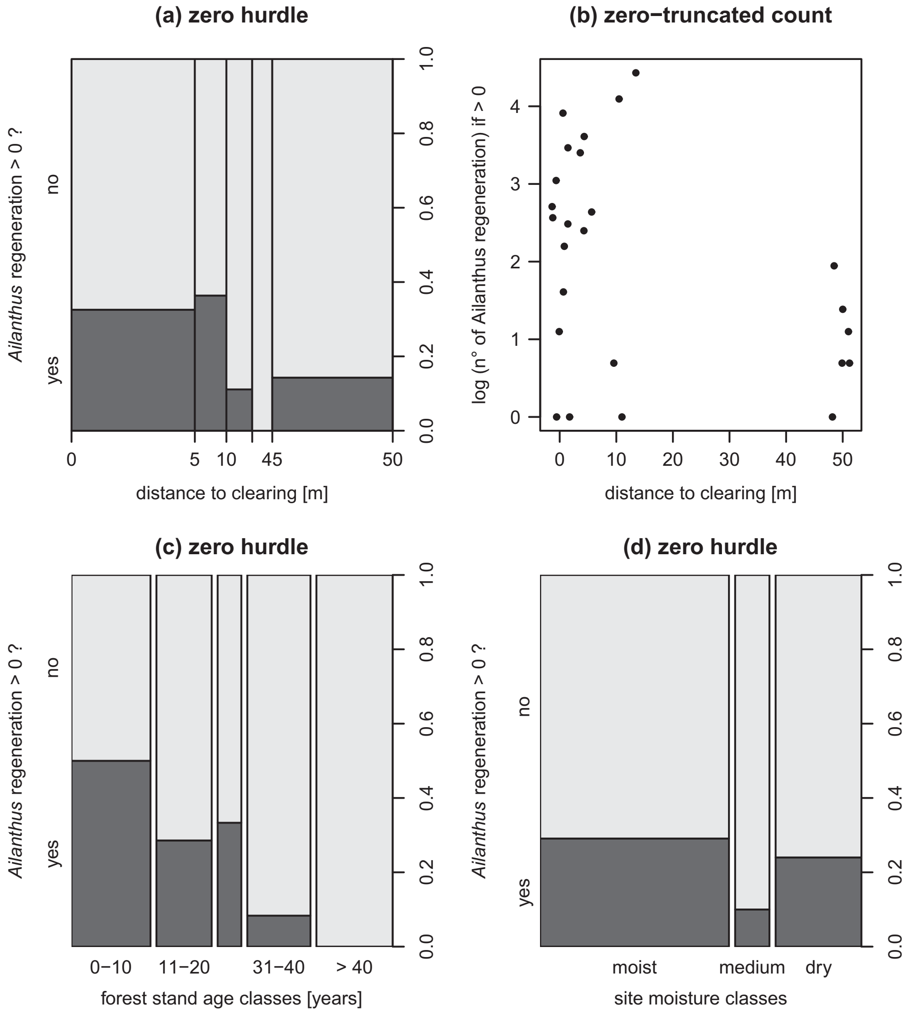

Fig. 2. Visualized results of the significant predictor variables in the hurdle model of *Ailanthus*. Presence of *Ailanthus* regeneration in relation to (a) 'distance to clearing', (c) forest stand age class and (d) soil moisture class. For the interpretation of spinograms see methods section. (b) Abundance of *Ailanthus* regeneration in relation to 'distance to clearing'.

only 'distance to clearing' showed a significant relation to the number of saplings (Table 3). The probability of *Ailanthus*' occurrence as well as the number of saplings decreased with increasing 'distance to clearing' (Fig. 2a and b). *Ailanthus* saplings mainly occurred in

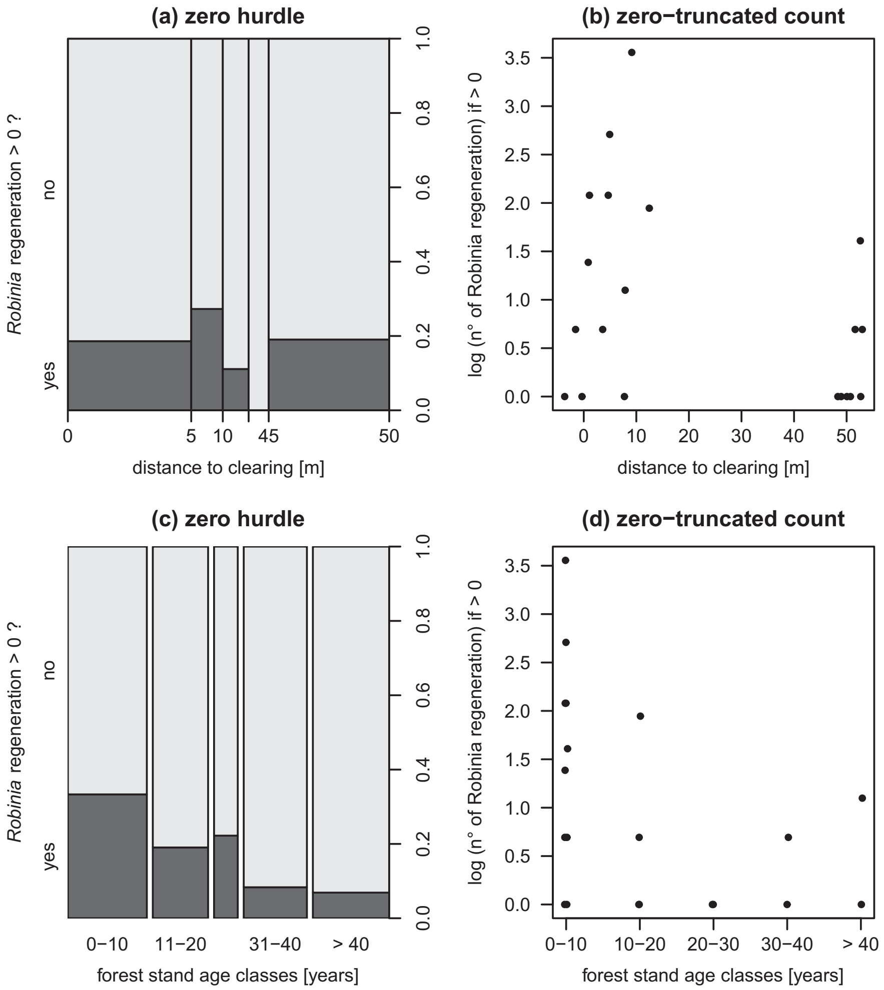

Fig. 3. Visualized results of the significant predictor variables in the hurdle model of *Robinia*. Presence of *Robinia* regeneration in relation to (a) 'distance to clearing', (c) forest stand age class, and abundance of *Robinia* regeneration in relation to (b) 'distance to clearing', (d) forest stand age class. For the interpretation of spinograms see methods section.

stands younger than 30 years (Fig. 2c), and slightly more often on moist sites than on dry sites (Fig. 2d). *Ailanthus*' occurrence was more probable with the co-occurrence of mature *Ailanthus* trees.

The presence and the abundance of *Robinia* regeneration were negatively correlated to forest stand age (Table 3, Fig. 3c and d), and positively to the presence of mature trees. Although the occurrence of *Robinia* regeneration was not correlated with 'distance to clearing', the number of saplings decreased with increasing 'distance to clearing' (Table 3, Fig. 3a and b).

To sum up, both presence and abundance of the two species were positively correlated to the presence of mature trees of the respective species and decreasing forest stand age. Decreasing 'distance to clearings' had a positive influence on *Ailanthus*' presence and the abundance of both species.

3.3. Proportion of non-native to native saplings and height class distribution

The proportion of non-native saplings to native ones differed significantly between forest stand age classes (non-parametric Kruskal–Wallis-Test: $\text{Chi}^2 = 25.14$, $\text{df} = 4$, $p < 0.001^{***}$), being highest in the youngest patches (Fig. 4a). A closer look onto those patches ($n = 30$) revealed that the proportion of non-native saplings increased from the smallest to the largest height class (Fig. 4b).

4. Discussion

The invasion of *A. altissima* and *R. pseudoacacia* into the studied coppice forest may well be explained against the background of their ecological characteristics (Table 4). Both species are good colonizers, e.g. their propagules can be dispersed over long distances and their seedlings grow fast. As the studied coppice forest is located close to a rural area where mature *Robinia* and *Ailanthus* trees grow, seed sources have been and continue to be present. Thus, as soon as a forest patch is cut, *Ailanthus* and *Robinia* seeds find suitable germination sites where light is abundant and competition is low. Both species grow fast and quickly and make up a considerable part of the canopy soon. Due to the relatively short cycle of coppice forests, the time of forest development is too short for native species to out-shade the light-demanding non-natives, like it was observed for longer periods of forest development (Huntley, 1990; Call and Nilsen, 2003; Motta et al., 2009).

In the studied forest, both invasive species were more abundant in younger forest patches than in the oldest ones (research question 1). This pattern was consistent for the canopy cover as well as for the regeneration. However, the invasion of *Robinia* is much further progressed than that of *Ailanthus* in this forest. First, *Robinia* is more abundant in the canopy and second, while the majority of mature *Ailanthus* trees occurred in patches younger than 20 years, *Robinia* trees occurred numerously in 30-to-40-year old patches as

Table 3
Results of the hurdle models for a) *Ailanthus* and b) *Robinia*. The categorical variable ‘moisture class’ is split into its three levels.

	Estimate Std.	Error	*z* Value	*p* Value
(a) Ailanthus				
Zero hurdle model coefficients (binomial with logit link)				
(Intercept)	3.04083	1.47722	2.058	0.03954*
Distance to clearing	−0.09452	0.03237	−2.920	0.00351**
Forest stand age	−1.45878	0.45746	−3.189	0.00143**
Mature *Ailanthus*	3.01670	1.05168	2.868	0.00412**
Moisture class 2	−2.02774	1.78209	−1.138	0.25519
Moisture class 3	−3.28775	1.51274	−2.173	0.02975*
Count model coefficients (truncated negbin with log link)				
(Intercept)	3.04525	0.46211	6.590	$4.4e^{-11}$***
Distance to clearing	−0.05345	0.02033	−2.629	0.00855**
Log(theta)	−0.86981	0.67607	−1.287	0.19825
(b) Robinia				
Zero hurdle model coefficients (binomial with logit link)				
(Intercept)	−0.669012	1.104344	−0.606	0.54465
Distance to clearing	−0.024223	0.016845	−1.438	0.15042
Forest stand age	−0.518765	0.225482	−2.301	0.02141*
Mature *Robinia*	2.541274	0.797094	3.188	0.00143**
Slope	0.013101	0.008671	1.511	0.13079
Soil skeleton	−0.048337	0.035944	−1.345	0.17869
Count model coefficients (truncated negbin with log link)				
(Intercept)	0.96273	0.40145	2.398	0.016480*
Distance to clearing	−0.04808	0.01455	−3.304	0.000952***
Forest stand age	−0.59169	0.22856	−2.589	0.009631**
Mature *Robinia*	2.25286	0.56584	3.981	$6.85e^{-05}$***
Log(theta)	0.88518	0.79557	1.113	0.265869

p-Values are encoded:
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

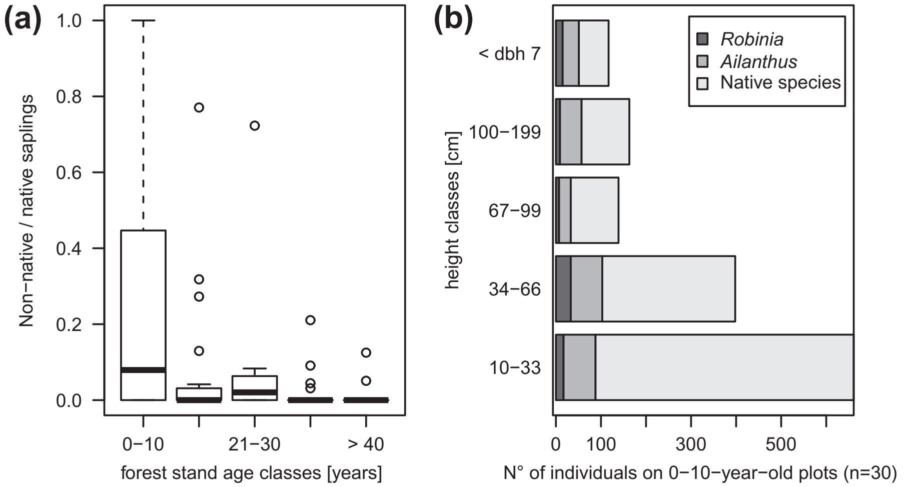

Fig. 4. (a) Boxplot of the non-native to native saplings proportion per forest stand age class. (b) Cumulative sapling numbers per species and height class from all young forest patches (0–10 years old).

well. The recurrent clear-cuts of the coppice management have probably hindered the out-shading of *Robinia* by native species during late succession (Motta et al., 2009). The same might happen now, 20 years later, with *Ailanthus*. After colonizing competition-free and light-abundant clearings, it grows into the overstory. Before *Ailanthus* can be out-shaded by native species, the coppice cycle starts again.

Future studies might shed light onto the influence of positive feed-back loops, which might additionally reinforce the invasion of the two species, such as positive interactions with mycorrhiza or seed dispersers (Alpert et al., 2000), an increasing number of mature trees producing more seeds, *Ailanthus*’ excretion of allelopathic substances (Heisey, 1990; Tsao et al., 2002) and *Robinia’s* natural soil fertilization (Hoffmann, 1961).

Ailanthus and *Robinia* saplings were more often found in younger than in older forest patches. This decrease of saplings with increasing forest age was steeper for *Ailanthus* than for *Robinia.* In other words, the number of colonized plots from one forest stand age class to the next was higher. This indicated higher invasion speed for *Ailanthus* compared to *Robinia*. Overall, the results show that disturbance events like clear-cuts facilitate the invasion of both non-native species by creating competition-free sites and

Table 4
Ecological characterization of non-native *Ailanthus altissima* and *Robinia pseudoacacia* in Europe according to a literature review. References: 'A' refers to *A. altissima* while 'R' refers to *R. pseudoacacia.*

	Ailanthus altissima (Simaroubaceae)	*Robinia pseudoacacia* (Fabaceae)	References
Native range	Deciduous forests in large parts of China and North Vietnam	Humid broad-leaved forests in the eastern parts of the USA	A: Kowarik and Säumel (2007) R: Huntley (1990)
Introduction to Europe	Middle of 18th century	Begin of the 17th century	A: Kowarik (2010) R: Böhmer et al. (2001)
Current distribution in Europe	– in Central Europe mostly urban biotopes – in Southern Europe also natural biotopes	– core area: Hungary – additionally many parts of Central and Southern Europe	A: Kowarik and Säumel (2007) and Kowarik (2010) R: Basnou (2009) and Rédei et al. (2010)
Zones of spontaneous dispersal	Mediterranean and sub-Mediterranean Zone	(sub)continental and sub-Mediterranean zone	A: Kowarik and Säumel (2007) R: Kohler (1963), Kowarik (2010)
Through invasion endangered ecosystems	– abandoned grassland, vegetated bedrock, alluvial forests, meso- und xerothermic forests – in South Tyrol: Subpannonic steppes and dry grasslands	– abandoned grassland, xero-thermic forests – in South Tyrol: Subpannonic steppes and dry grasslands, ravine forests	A: Lasen and Wilhalm (2004), Punz et al. (2004), Essl and Walter (2005), Kowarik and Säumel (2007) R: Paar et al. (1994), Lasen and Wilhalm (2004), Essl and Walter (2005), Kowarik (2010)
Urban habitats	Wasteland, along roadways and embankments, walls	Wasteland, along roadways and embankments	A: Celesti-Grapow and Blasi (2004), Kowarik and Säumel (2007) R: Celesti-Grapow and Blasi (2004) and Kowarik (2010)
Soils	Wide range (except permanently wet soils)	Wide range (except water-logged and compacted soils)	A: Kowarik and Böcker (1984) R: Huntley (1990)
Warmth and Drought tolerance	High – very high	High	A: Trifilò et al. (2004) and Kowarik (2010) R: Kohler (1963) and DeGomez and Wagner (2001)
Frost tolerance	Moderate (young plants low)	Moderate (sensitive to early frosts)	A: Scheerer (1956) and Kowarik and Säumel (2007) R: Kohler (1963)
Light requirements	High	High	A: Kowarik (1995) and Knapp and Canham (2000) R: Call and Nilsen (2003) and Kowarik (2010)
Age of fruiting	3–5 Years	ca. 6 Years (seldom 3 years)	A: Kowarik (2010) R: Barrett et al. (1990) and Huntley (1990)
Seed dispersal	Anemochorous, hydrochorous	Mainly barochorous, also anemochorous	A: Kowarik and Säumel (2008), Säumel and Kowarik (2010) R: Huntley (1990) and Kowarik (2010)
Distances of fruit distribution	>200 m	Mostly just a few meters, within seed pods – 100 m	A: Kota et al. (2007) R: Huntley, 1990; Kowarik, 2010
Germination capacity	ca. 1 Year	Several years	A: Kota et al. (2007) R: Kowarik (2010)
Height increment of seedlings per year	>1 m	>1 m	A: Kowarik (2010) R: Gould et al. (2004)
Height increment of clonal shoots per year	−3 m	−5 m	A: Kowarik and Säumel (2007) R: Ertle et al. (2008)
Ability of vegetative reproduction	Strong	Strong	A: Kowarik and Säumel (2007) R: Wolf (1985) and Kowarik (2010)
Maximum Height	27–30 m	25 m (in USA up to 30 m)	A: Kowarik (2010) R: Boring and Swank (1984) and Grosser (1998)
Economic value and use	Low (mainly ornamental tree)	High (agri- and silvicultural crop plant)	A: Kowarik and Säumel (2007) R: Kowarik (2010) and Rédei et al. (2010)
Impacts on ecosystem	Allelopathy	Nitrogen fixation, Eutrophication of soils	A: Heisey (1990) and Tsao et al. (2002) R: Hoffmann, 1961, Danso et al. (1995)
Control measures	– mechanical: costly, limited success – chemical: use of herbicides, moderate to good success – biological: debated, but not applied so far	– mechanical: costly, moderate to good success – chemical: use of herbicides possible – biological: rarely debated, not applied	A: Burch and Zedaker (2003), Essl and Walter (2005), Ding et al. (2006), Meloche and Murphy (2006), Constán-Nava et al. (2010) R: Böcker and Dirk (2008) and Basnou (2009)

increasing resource availability. In the same way, *A. altissima* and *R. pseudoacacia* numerously appeared after a forest fire in Southern Switzerland (Maringer et al., 2012). It is believed that habitats with a long history of recurrent disturbances, like e.g. forest ecosystems where natural fires occur in regular intervals, are less invasible than habitats which are naturally not used to disturbances (Catford et al., 2012). However, our study area seems highly invasible, even though coppice management has been practiced there for a long time.

The factors favoring the regeneration of the two invasive species were low forest stand age, short distance to clearing, and presence of mother trees (research question 2).

Since clearings are light-abundant and represent disturbed sites, we expected the presence and abundance of *Ailanthus* and *Robinia* regeneration to be positively correlated to decreasing distance to clearing. Indeed, we found this relation for *Ailanthus* (presence and abundance) and *Robinia* (abundance only), which confirms the high light requirements of *Ailanthus* seedlings and saplings (Kowarik, 1995, 1996; Kota et al., 2007). The fact that we did not find the same relation for the presence of *Robinia* regeneration might be the result of the high percentage of vegetative offspring which require less light than generative regeneration (Kowarik, 1996). Predominantly vegetative reproduction is typical for *Robinia* in forest habitats (Böhmer et al., 2001) and is likely to prevail in our forest as well because *Robinia* rejuvenation was found on only 7 plots without mature trees. A similar strategy was described for *Ailanthus* whose vegetative offspring are much more shade-tolerant than the seedlings, thus allowing a certain persistence during succession through a ramet bank (Kowarik, 1995; Knapp and Canham, 2000).

In general, *Ailanthus* and *Robinia* are regarded as drought resistant species and occur in various types of dry habitats, such as *Quercus pubescens* forests (Kohler, 1963; Lohmeyer, 1976; Celesti-Grapow and Blasi, 2004; Walter et al., 2005; Ließ and Drescher, 2008; Constán-Nava et al., 2010; Liesebach and Schneck, 2011). Even young *Ailanthus* individuals can survive in dry conditions (Trifilò et al., 2004) by increasing root growth (Kowarik and Säumel, 2007). At the study site, *Ailanthus* colonized even screes, i.e. primary sites where rocks from above have been newly deposited. The complete absence of competitive vegetation there favors the germination of *Ailanthus* (Kowarik, 2010). Later, it grows, thanks to its intensive root system, vigorously pervading even hardly penetrable soils (Call and Nilsen, 2005). In the studied forest, *Ailanthus* and *Robinia* regeneration did not differ among soil moisture classes. This suggests that the whole area can potentially be invaded if sufficient light is available.

In this study, the proportion of non-native to native saplings decreased with increasing forest age (research question 3). Additionally, non-native saplings were proportionally more frequent in higher height classes than in lower ones. That indicates better performance of non-native saplings compared to native saplings with two possible explanations: (a) non-native saplings have a higher survival rate and/or a higher probability to grow from one height class into the next, (b) non-native saplings grow faster compared to native ones, so that saplings of the same age (plot) can be found in different height classes. The latter suggestion is supported by the growth potential of the two species (Table 4). Moreover, *Robinia* may benefit also from its thorns preventing it from being browsed.

5. Conclusions

- Our study about the invasion of *Robinia pseudoacacia* and *Ailanthus altissima* into a deciduous forest exemplified how coppice forest management can govern invasion dynamics. It showed that forest stand age (i.e. time since last cutting), distance to the next clearing, and the presence of mother trees have a larger influence on the regeneration of the two invasives than microsite conditions like soil moisture, stone cover, slope, or vegetation cover.
- The current coppice management with its regular clear-cuts creates light-abundant sites (‘safe sites’ *sensu* Harper et al., 1961) which are suitable for the generative and vegetative regeneration of the invasive tree species. Over time, the invasion will thus most likely continue to the over-30-year-old forest stands, as soon as they are cut. Unless expensive effort is undertaken to suppress non-native tree species by mechanical means, their presence has to be accepted and actively integrated into the forest development planning, acknowledging also the services they provide (e.g. timber production, rockfall protection).
- Without mechanical or chemical control measures, the invasion of the two light-demanding species could be hindered by reducing the light availability by a conversion into high forest management with an alternative cutting system instead of clear-cuts. This measure has turned out to be an effective way of controlling the impact of unwanted species (Ammer et al., 2011; Wagner et al., 2011) but it would likely reduce the rockfall protection (Jancke et al., 2009) and might affect tree species diversity. The second possibility could be to prolong the rotation length as much as possible and to release a high number of standards on the clear-cuts.
- Forest management should be continuously monitored in order to assess its success and to test a critical number of standard trees, i.e. trees which are kept longer than one rotation cycle. A direct comparison of the native and non-native tree species regarding growth rates of saplings and vegetative sprouts after coppicing would be necessary to make more detailed predictions about the future stand development.

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