

# Population dynamics of an invasive tree, *Sorbus aucuparia*, in the understory of a Patagonian forest

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**Abstract** Exotic fleshy fruited plants are often dispersed by generalist frugivores into undisturbed or weakly disturbed forests. The establishment and spread of these plants in the understory may pass unnoticed until their abundance and size turns them a nuisance. *Sorbus aucuparia* is a fleshy fruited tree recently established in temperate forests of northwestern Patagonia. Our aim was to determine the invasion

dynamics of *S. aucuparia* in a *Nothofagus pumilio* forest. We analyzed age structure, minimum age of reproduction, the time from colonization to effective recruitment (lag time), and demographic parameters to pinpoint critical stages for management. Currently, the population of *S. aucuparia* is increasing. Large numbers of suppressed, potentially reproductive individuals were found. Lag time was relatively short (25 years) in comparison to other invasive woody plants. The minimum reproductive age was 10 years, and all reproductive individuals were located in high light conditions. The number of trees at the reproductive stage made the most significant contribution to population growth; a 5 % reduction in this number would be enough for the population growth rate to be negatively affected. Thus, the reproductive stage is key to the control of *S. aucuparia*. Forest disturbance leading to increase light availability may result in higher rates of growth and reproduction among currently suppressed individuals, triggering further expansion events and increasing the number of invasion foci. Management strategies for tree species which present an inconspicuous bank of individuals in the understory, like *S. aucuparia*, should focus on early detection and eradication of reproductive individuals while avoiding the increase in light availability in the affected environment.

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Matrix demographic analysis

## Introduction

Invasive species are frequently related to environments with high light availability, but some of them grow and increase in abundance over time under tree canopy (Martin et al. 2008). Shade tolerance allows some species to endure closed-canopy conditions at the sapling stage with little growth until light conditions become more favorable. Examples of this are *Acer pseudoplatanus* and *Prunus serotina*, two invasive trees of North American and European forests, respectively, which maintain a bank of suppressed saplings in the understory until forest clearings allow them to grow faster and produce seeds (Martin and Marks 2006; Closset-Kopp et al. 2007). The low growth rate that exhibit shade-tolerant species in the understory may be misleading, as their potential impact on the forest ecosystem may be high in the long term (Martin et al. 2008).

Whenever an exotic species colonizes a novel environment, local dispersion does not occur for some time, due to low propagule availability and the failure of potential dispersers to adopt the newcomer's fruit as a resource (Theoharides and Dukes 2007; Lockwood et al. 2007; Aslan and Rejmánek 2012). This time period, referred to as "lag time," varies between species (Crooks and Soulé 1999). An exotic species may pass unnoticed without causing significant impacts during its lag time but may become a troublesome organism after a relatively short period of population increase (Lockwood et al. 2007; Simberloff 2011). Knowledge about the lag time of introduced and potentially invasive exotic species within a community is considered relevant both to prevent future invasions and to develop effective management plans to minimize the negative effects of an eventual invasion (Crooks 2005; Amodeo and Zalba 2013).

Matrix demographic analysis has become a powerful tool in population biology studies. It has been widely used in the study of threatened or invading species, and in the design of management plans (Golubov et al. 1999; Menges et al. 2006; Caswell 2001; Satterthwaite et al. 2002). Matrix models are relatively simple to construct and analyze (Online Resource 1) and have the advantage of representing a species' life cycle quite plainly. Moreover, several matrix properties have a clear biological interpretation (Jongejans et al. 2008). Population management requires the identification of life history stages and processes with the highest contribution to population

growth, so that management efforts can be properly focused (Benton and Grant 1999). Population matrix models and perturbation analysis are good tools in this regard. Once the projection model of a specific population is constructed, two analyses can be applied to assess the impact that small changes on the vital rates (i.e., survival, growth, or reproduction) may have on population growth rate: (1) elasticity analysis, which estimates the effect of a proportional change in the vital rates on population growth rate, and (2) the sensitivity analysis, which estimates the impact of absolute changes in vital rates on population growth rate (Benton and Grant 1999).

In the Andean region of Argentina and Chile, several exotic woody plants have dispersed from gardens and plantations and are invading areas currently dominated by native species (Fernández 2007; Damascos 2008; Quiroz et al. 2009; Pauchard et al. 2014). The population dynamics of these exotic species and their colonization histories could be inferred from the current age structures of their invading populations. Population age-structure provides relevant information about the invasiveness of a species, the length of its lag time, the critical stage for recruitment, and the tendency of the population to vary in size over time (Deckers et al. 2005; Rice et al. 2012; Amodeo and Zalba 2013). We investigated the population dynamics of the invasive tree species *Sorbus aucuparia* L. (Rosaceae) so as to identify the critical stages for its recruitment and recommend procedures to control its incipient invasion. In order to reach a better understanding of this species' invasion in native Patagonian forests, a retrospective analysis of stand dynamics was conducted for a population of *S. aucuparia* in a native *Nothofagus pumilio* forest. For this *S. aucuparia* population, we analyzed age structure, minimum reproductive age, and lag time, estimated demographic parameters to construct the matrix demographic analysis, calculated the long-term population growth rate and stable structure, and studied the population projection under small changes in demographic processes, through sensitivity and elasticity analyses.

## Materials and methods

### Study species

*Sorbus aucuparia* (rowan) is a deciduous tree up to 15–20 m in height native to Europe and Asia and

invasive in New Zealand (Webb et al. 1988). It produces white hermaphroditic flowers in terminal inflorescences and fleshy red fruits, each containing 1–6 seeds (Herrera 1987; Lediuk et al. 2014). *Sorbus aucuparia* has been recently identified as an invasive species in the Andean forest region of Argentina (Lediuk 2015), where it was introduced as ornamental (~1960) and is often planted as a street tree and for hedging (Rovere et al. 2013). At the invaded area of Argentina, flowers of *S. aucuparia* trees are in full bloom in late spring, fruits ripen in late summer–early autumn, and seeds are dispersed by birds during autumn–winter (Lediuk et al. 2014). For *S. aucuparia* growing in invaded communities of Argentina, mean productions of 37.6 (SE = 4.5) ripe fruits and 130.6 (SE = 12.5) seeds per infructescence (Lediuk et al. 2014), and about 600 infructescences per tree (Lediuk, unpublished data) have been estimated; fruits are consumed by native birds (Lediuk, personal communication), and seeds exhibit high levels of viability (80 %; Lediuk et al. 2014). Within its native distribution, *S. aucuparia* is very tolerant to shade at seedling and sapling stages but demands sunny conditions for flowering and fruiting (Raspé et al. 2000). This last also appears to be the case in the invaded areas of Argentina, where seedlings and saplings of *S. aucuparia* develop under lower light availability than reproductive individuals (Online Resource 2).

#### Study area

The study took place in a northwestern Andean-Patagonian forest of Argentina dominated by the deciduous tree species *N. pumilio*. The study site was delimited on a 20 ha area located on the hillside of Cerro Otto in a forest at the surroundings of San Carlos de Bariloche city (41°08.758'S, 71°21.977'W, 1285 m a.s.l.), where a *S. aucuparia* population has established. This forest is crossed by one road; minor paths and off-path trampling cause low levels of disturbance. No dead reproductive individuals of *S. aucuparia* were observed. The regional climate is temperate cold, with a mean temperature of 5–8 °C (Ezcurra and Brion 2005) and annual precipitations between 1100 and 1400 mm in S. C. de Bariloche (Pereyra 2007). The period of plant growth corresponds with the dry season (spring and summer).

#### Sampling

The study was conducted at the end of the 2010–2011 growth period, before the abscission of *S. aucuparia* leaves (autumn). Sampling was carried out in ten 5 m × 10 m randomly established plots located below the forest canopy and within an area where *S. aucuparia* was present. Main stem height and diameter at soil level were measured for all individuals within the plots. Individuals with trunk diameter <40 cm were cut at soil level, and a trunk disk was taken. Increment cores were taken from the trunk of larger trees at breast height. For the counting of growth rings, both disks and increment cores were mounted and sanded to make the rings clearly visible. The same measurements and increment cores were also taken from a random sample of reproductive plants growing in sunny conditions (the only light condition that appear reproductive individuals), around the study plots, as well as from the putative founder trees, i.e., trees located less than 100 m away from the sample plots which, according to interviews with local people, had been planted.

We analyzed the age structure of the *S. aucuparia* population and estimated its lag time: the period between the establishment time of the oldest spontaneously recruited (not planted) tree, and the time when population recruitment started to increase exponentially (Lockwood et al. 2007; Theoharides and Dukes 2007; Amodeo and Zalba 2013).

#### Data analyses

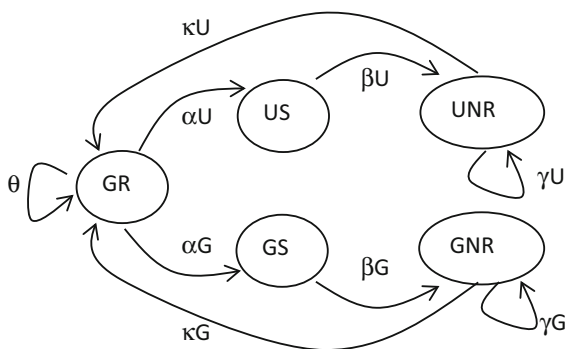
##### *Morphometric characteristics: height and basal diameter*

Pairwise relationships between the variables height (m) and basal diameter (mm) with plant age were evaluated with linear and non-linear regressions using functions that could describe patterns of plant growth; three types of non-linear functions were selected after exploratory visualization of the data: exponential, saturation (Michaelis–Menten), and sigmoid (Holling type III) (Bolker 2007). In all cases, both variables involved were normally distributed. Akaike's information criterion (AIC) was used to rank the models and select the model with the lowest AIC (with  $\Delta AIC < 2$  considered equivalents, Burnham and Anderson 2002).

The models were fitted using “bbmle” package in R 2.12.0 (R Development Core Team 2012).

### Demographic modeling

A basic stage-based life-cycle graph (Caswell 2001) was applied to two light conditions: under canopy and gaps. The percentage of gap surface in the study area was estimated to be around 15.1 %. This surface was determined in two 150 m<sup>2</sup> plots in the study area employing free map tools (<http://www.freemaptools.com/area-calculator.htm>). We divided the life cycle of *S. aucuparia* into three categories: seedlings (plants up to one year old), non-reproductive individuals (more than one year-old plants), and reproductive individuals (those that have developed flowers and/or fruits). By combining these categories with light conditions, each *S. aucuparia* plant in the sample area was assigned to one of six categories (Fig. 1): (1) Gap seedling “GS,” (2) Under-canopy seedling “US,” (3) Gap non-reproductive individuals “GNR,” (4) Under-canopy non-reproductive individuals “UNR,” (5) Gap reproductive individuals “GR,” and (6) Under-canopy



**Fig. 1** Conceptual model of *Sorbus aucuparia*'s life cycle in temperate forests of northwestern Patagonia. The circles represent stage categories: Gap reproductive plant (GR), Under-canopy seedlings (US), Gap seedlings (GS), Under-canopy non-reproductive plant (UNR), and Gap non-reproductive plant (GNR). Arrows represent the contribution of each category to another from one time step to the next.  $\alpha U$  and  $\alpha G$  represent the per capita number of seedlings that established from 1 year to the next;  $\beta U$  and  $\beta G$  represent the proportion of seedlings that survived and established as non-reproductive individuals and  $\gamma U$  and  $\gamma G$  represent the survival of non-reproductive plants (stasis of non-reproductive classes);  $\kappa U$  and  $\kappa G$  represent the probability of a non-reproductive plant becoming a reproductive plant, under-canopy and in-gap areas, respectively. The parameter  $\theta$  represents the probability of annual survival of reproductive individuals (stasis of Gap reproductive class)

reproductive individuals “UR.” The UR category was later disregarded in the analyses, as none of the under-canopy plants had reached the reproductive stage. “Seed class” was not included in the model because as seed availability was not considered a factor that may become limiting for recruitment under ordinary conditions (Lediuk 2015; see Study species). The contribution of each category to another from one time step to the next is included in this model. We supposed that seedlings will establish under the canopy or in gaps, with  $\alpha U$  and  $\alpha G$  probabilities, respectively, related to the available percentage of gap surface in the study area. Seedlings growing under the canopy and in gaps will grow with  $\beta U$  and  $\beta G$  probabilities, respectively. Non-reproductive individuals under canopy (URN) and in gaps (GRN) can stay in the class from 1 year to the next (stasis) with  $\gamma U$  and  $\gamma G$  probabilities, respectively, or become reproductive with  $\kappa U$  and  $\kappa G$  probabilities respectively. The stasis of reproductive is representing with  $\theta$  probability.

### Parameter estimation: survivorship, growth, and germination

Based on the age structure obtained from the sampling carried out at the end of the 2010–2011 growth period, we reconstructed the life history of the invading population of *S. aucuparia* from 2011 back to 1955, i.e., all parameter of the model is estimated from that age structure. Due the short spread distance that currently exhibited by *S. aucuparia* at the study site, we considered that the founder trees that had been planted in this area and the reproductive individuals that developed spontaneously were the only seed sources for the population under survey. In an experimental study on a nearby invasive population of *S. aucuparia*, it was determined that its seeds fail to remain viable in the soil after one year (Lediuk 2015). Therefore, when calculating fecundity rates, we assumed no seed bank for this species. Annual seedling emergence per capita was estimated by counting the number of new seedlings per year and dividing this number by the number of reproductive individuals in the previous year. Then we divided proportionally the emergence rate between under-canopy ( $\alpha U$ ) and gap ( $\alpha G$ ), according to the percentage of the total area in each of these two conditions. For these two parameters, we assumed that the transition from reproductive individual fecundity to

seed germination does not differ between light conditions. That transition includes several processes such as reproductive adult fecundity, seed dispersal, seed survival, and germination that could be different between both light conditions but could not be investigated here; we consider this topic in discussion section. Annual transition probabilities from seedling to non-reproductive classes ( $\beta_U$ ,  $\beta_G$ ) and the probabilities of survival of non-reproductive individuals (stasis,  $\gamma_U$ ,  $\gamma_G$ ) were estimated by assessing the numbers of dead plants from one year to the next (based on the age structure database) and dividing this number by the total number of plants, regarding the surface of the area under canopy or in gaps. The probability of transition from non-reproductive class to the reproductive class in gaps ( $\kappa_G$ ) was estimated by counting the new reproductive plants in a year, and referring it to the number of non-reproductive plants in gaps. In the study area, we did not observe under-canopy reproductive individuals. In nearby areas, we observed that a very low proportion of under-canopy individuals can reach reproductive status once they overpass the canopy. Then, based on this observation, we set the probability of non-reproductive under-canopy plants becoming reproductive ( $\kappa_U$ ) at a very low value. The probability of annual reproductive survival (stasis of Reproductive class,  $\theta$ ) was inferred by counting dead reproductive individuals per year.

Once the projection matrix was constructed, the dominant eigenvalue  $\lambda$  (the population growth rate), and the associated right column eigenvector  $\mu$  and left row eigenvector  $\nu$  were calculated. The associated right and left eigenvectors  $\mu$  and  $\nu$  provide the stable class distribution and the reproductive values of each class, respectively (Caswell 2001). The stage-specific reproductive values, given by the left eigenvector  $\nu$ , estimate the expected per capita contribution of individuals in each class to population growth. The elasticity and sensitivity matrices were also built (Eq. (2) and (3); Online Resource 1). Numerical analyses were performed with PopTools (Hood 2005).

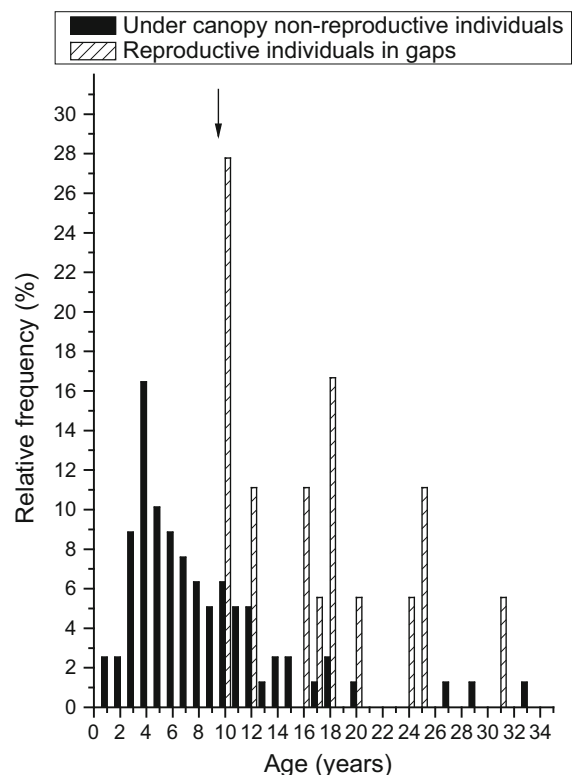
## Results

### Age structure

In the total sampled surface beneath canopy forest (500 m<sup>2</sup>), 79 individuals of *S. aucuparia* were found,

i.e., 0.15 individuals/m<sup>2</sup>. The population under forest canopy was relatively young: none of the plants were reproductive and young plants were abundant (Fig. 2). Understory non-reproductive individuals older than nine years accounted for 32 % of the total sample (25 individuals, Fig. 2); the oldest one was 33 years old (Fig. 2). All reproductive individuals (21 reproductive individuals sampled) were out of the study plots. The founder trees were close to a house, whereas spontaneously recruited reproductive trees were in gaps, along paths and roadsides through the forest. The youngest, and also most frequent, reproductive individuals were 10 years old (Fig. 2).

Founder trees (three planted trees) were between 56 and 45 years old, i.e., they were planted around 1955–1966, 150 m from the study plots (Fig. 3). Considering ten years as the earliest age to reach the reproductive phase in *S. aucuparia* (present study;

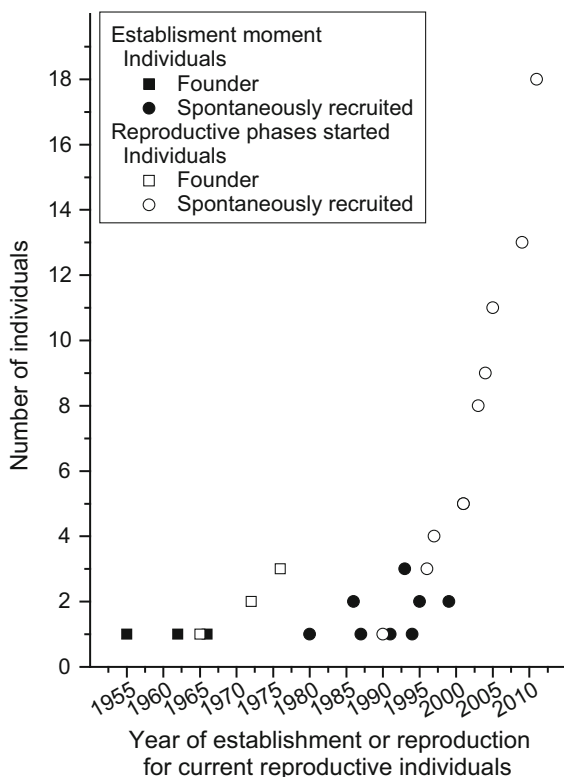


**Fig. 2** Age structure of a *Sorbus aucuparia* population in a temperate *Nothofagus pumilio* forest of northwestern Patagonia. UNR under-canopy non-reproductive plants, GR gap reproductive plants growing in gaps. The arrow indicates the age at which non-reproductive plants can pass to the reproductive stage if the environmental conditions improve



Myking et al. 2013), we estimated that founder trees started to produce seeds between 35 and 46 years ago (between 1965 and 1976; Fig. 3). The first spontaneously recruited individual (currently suppressed under the canopy) established 13 years after the founder trees started to produce fruits (in 1978); spontaneously recruited individuals entered the reproductive stage 15–35 years later (between 1980 and 2000; Fig. 3).

According to age structure, spontaneously recruited *S. aucuparia* individuals entered the reproductive stage no less than 12 years after the first spontaneous emergences of this species at the study site. Thirty-five years after the beginning of fruit production by founder trees and 25 years after the establishment of the first spontaneously recruited individuals, the *S. aucuparia* population below the canopy of *N. pumilio* started a phase of exponential increase (Fig. 4).



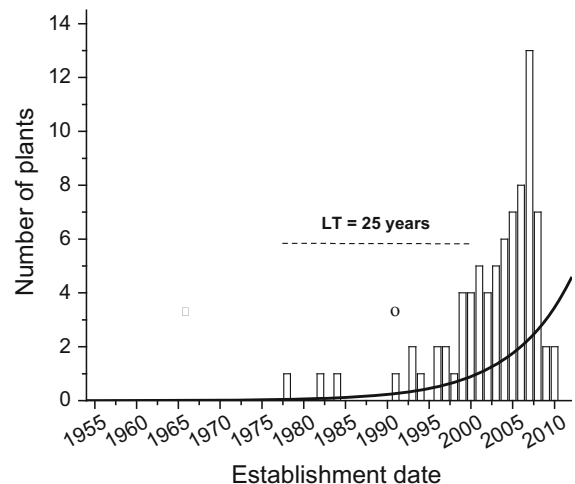
**Fig. 3** Dates of establishment (*fill symbols*) and of the beginning of the reproductive phase (*empty symbols*) for founder (*squares*) or spontaneously recruited (*circles*) reproductive *Sorbus aucuparia* trees growing in open areas or *Nothofagus pumilio* forest gaps. The cumulative number of reproductive individuals is indicated for each date

## Height and basal diameter as related to tree age

According to AIC, variations in stem height and basal diameter with tree age were best described by sigmoid functions (Table 1; Fig. 5). However, individuals between 10 and 35 years old exhibited high variability regarding stem height and basal diameter, which depended, to some extent, on whether the individuals were reproductive or not (Fig. 5).

## Analytic results of the demographic model

The population projection matrix for *S. aucuparia* and its right ( $\mu$ ) and left ( $\nu$ ) eigenvectors are presented in Table 2. The projected growth rate (the matrix dominant eigenvalue) was  $\lambda = 1.0367$ , representing a 3.67 % annual growth. The stable stage distribution ( $\mu$ ) was dominated by under-canopy non-reproductive and reproductive individuals (56 and 26 %, respectively), whereas seedlings and gap non-reproductive individuals summed up less than 20 % of the population. The reproductive values ( $\nu$ ) were higher for individuals in gaps at all stages (45, 31, and 21 % for



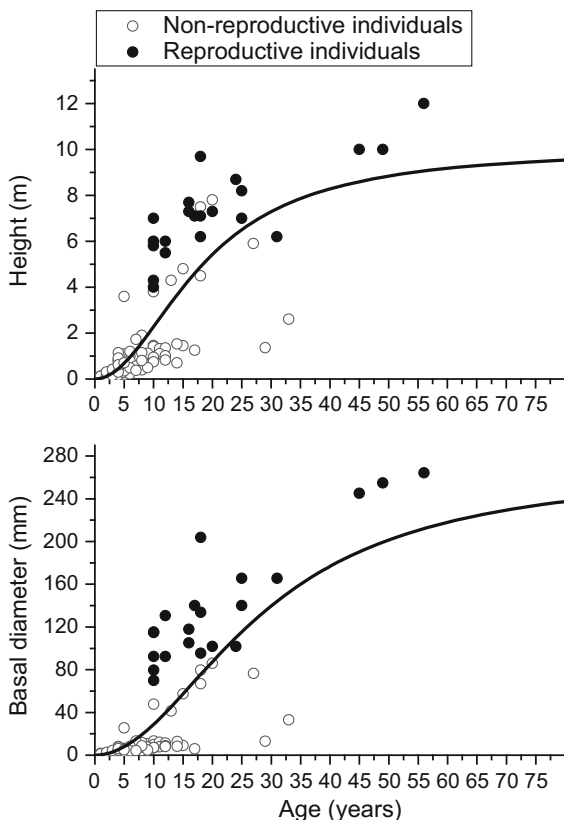
**Fig. 4** Number of non-reproductive individuals of *Sorbus aucuparia* spontaneously recruited beneath the canopy of *Nothofagus pumilio* trees. The years when founder trees (*square*) and spontaneously recruited trees (*circle*) started to develop flowers are indicated. The *black dashed line* indicates the lag time (LT), i.e., the time from the first spontaneous recruitment to the time when population increase was first noticed. The *solid curve* represents the function fitted to the data:  $\text{Log}(\text{number of plants}) = -271.65 + 0.135 \text{ year of establishment}$  ( $F = 92.05$ ;  $P < 0.001$ ;  $R^2 = 0.63$ )

**Table 1** Differences in Akaike’s information criterion ( $\Delta$  AIC) between models fitted to the variation in stem height (m) and basal diameter (mm;  $y$ : dependent variables) with

respect to plant age ( $x$ : independent variable) for *Sorbus aucuparia* in temperate forest of northwestern Patagonia

Variables	Models	$\Delta$ AIC	Best fit model
Height (m)	Sigmoid	0.0	$y = (10.05 \times x^2)/(18.45^2 + x^2)$
	Lineal	22.2	
	Saturation	26.2	
	Exponential	34.9	
Basal diameter (mm)	Sigmoid	0.0	$y = (268.11 \times x^2)/(28.76^2 + x^2)$
	Exponential	16.1	
	Lineal	107.5	
	Saturation	145.3	

The best fit was that of the sigmoid curve (Holling type III:  $y = (a \times x^2)/(b^2 + x^2)$ ), where  $a$  is the maximum height or basal diameter, and  $b$  is the age of maximum increase rate of the dependent variable (inflection point)



**Fig. 5** Relationships between stem height (m) and plant age (year; A), and between stem basal diameter (mm) and plant age (B) for *Sorbus aucuparia* plants. Non-reproductive individuals (empty symbol) and reproductive individuals (fill symbol) are discriminated. The Holling type III sigmoid curve fitted to each relationship is indicated (solid line)

reproductive plants, non-reproductive plants, and seedlings, respectively).

Sensitivity and elasticity matrices are shown in Table 3. The highest sensitivity values corresponded to the probabilities of understory non-reproductive individuals reaching the reproductive stage ( $\kappa U$ ) and of the survival of reproductive individuals ( $\theta$ ) (1.75 and 0.80, respectively). A reduction of  $\kappa U$  (even setting it in 0) still produces  $\lambda$  values higher than 1, which means that the population keeps growing (Fig. 6a). For example, a reduction of 10 times in  $\kappa U$  (from 5 every 1000 to 5 every 10,000 individuals becoming reproductive each year) reduces the annual population growth rate only by 0.9 %. However, if  $\kappa U$  is duplicated (from 5 every 1000 to 1 every 100 individuals becoming reproductive each year), the annual population growth rate changes from 3.7 to 4.5 %, and if  $\kappa U$  is duplicated, again the annual population growth rate increases to 5.9 % (Fig. 6a). A reduction of 4.0 % in the current reproductive stage stasis  $\theta$  (from 0.99 to 0.94) would stabilize population growth ( $\lambda = 1$ ), and simultaneous 4.75 % reductions in both  $\kappa U$  and  $\theta$  would be necessary to cause  $\lambda$  to fall below 1 (Fig. 6b).

The elasticity analysis showed that the contribution of reproductive stage stasis ( $\theta$ ) to  $\lambda$  was more than three times higher than that of all other demographic processes together (76 vs. 24 %). Reproduction was the demographic process with the lowest contribution to  $\lambda$  (3 %), followed by the transitions from seedling to the non-reproductive stage and from this to the

**Table 2** Population projection matrix for *Sorbus aucuparia* in temperate forests of northwestern Patagonia

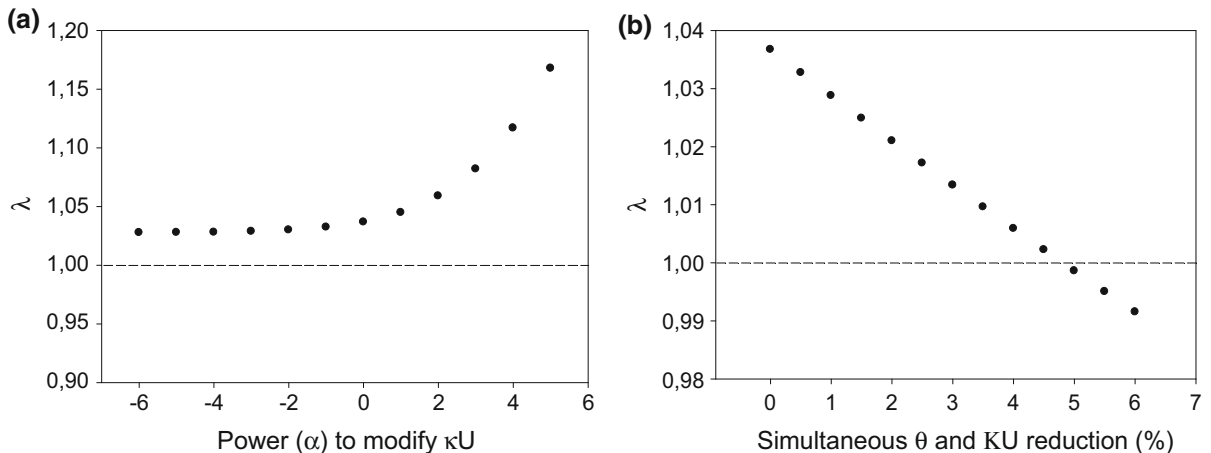
	Projection matrix					Stable structure	Reproductive values
	GS	US	GNR	UNR	GR		
GS	0	0	0	0	0.07	0.02	0.21
US	0	0	0	0	0.42	0.11	0.01
GNR	0.72	0	0.76	0	0	0.05	0.31
UNR	0	0.72	0	0.90	0	0.56	0.02
GR	0	0	0.19	0.005	0.99	0.26	0.45

Stage categories: Gap seedling (GS), Under-canopy seedling (US), Gap non-reproductive plant (GNR), Under-canopy non-reproductive plant (UNR), and Gap reproductive plant (GR). Stable structure (right eigenvector) and reproductive values (left eigenvector) corresponding to the dominant eigenvalue,  $\lambda = 1.0367$ , are expressed as proportions

**Table 3** Population sensitivity and Elasticity Matrices for *Sorbus aucuparia* in temperate forests of northwestern Patagonia

	Sensitivity matrix					Elasticity matrix				
	GS	US	GNR	UNR	GR	GS	US	GNR	UNR	GR
GS	0	0	0	0	<b>0.40</b>	0	0	0	0	0.02
US	0	0	0	0	0	0	0	0	0	0.01
GNR	0.04	0	0.09	0	0	0.03	0	0.07	0	0
UNR	0	0.01	0	0.06	0	0	0.01	0	0.06	0
GR	0	0	0.14	<b>1.75</b>	<b>0.80</b>	0	0	0.03	0.01	<b>0.76</b>

Stage categories: gap seedling (GS), Under-canopy seedling (US), gap non-reproductive plant (GNR), Under-canopy non-reproductive plant (UNR), Gap reproductive plant (GR). High values are shown in bold



**Fig. 6** Variation in the population growth rate ( $\lambda$ ) of *Sorbus aucuparia* **a** when the probability of under-canopy non-reproductive individuals reaching the reproductive stage ( $\kappa U$ ) is modified, and **b** when reproductive individual stasis is reduced

simultaneously with the decrease in  $\kappa U$ . The horizontal axis of **(a)** represents the power  $\alpha$  in the equation  $\kappa U = \kappa U_0 \times 2^\alpha$ , where  $\kappa U_0$  is the value estimated from field data. The dotted line represents the threshold under which population size decreases



reproductive stage (8 %), and the stasis at both non-reproductive categories (13 %).

## Discussion

### Early invasion phases of *S. aucuparia* in Patagonia

The structure of the *S. aucuparia* population under survey showed a reversed J-shaped frequency curve (Kimmins 1997), which suggests that this population is expanding and complies with the 3.67 % annual population growth obtained through modeling. The majority of this population consisted of non-reproductive individuals up to 1.5 m in height growing in understory conditions. In many shade-intolerant species, seedlings are unable to establish in understory conditions, even though seed germination may take place in such conditions, as found for the invasive species *Ailanthus altissima* in North America (Knapp and Canham 2000), and for *Pinus radiata* in Chile (Bustamante and Simonetti 2005). In the *S. aucuparia* population studied here, saplings varied notably in age, which indicates that this species is able to establish and survive for decades beneath a deciduous forest canopy. By this means, this species may be able to colonize relatively undisturbed forests.

Estimating the age of trees growing in the understory by measuring their height or diameter at breast height or at the base of the trunk (as in Suzán-Azpiri et al. 2002; Bustamante and Simonetti 2005; Hernández-Apolinar et al. 2006) can hide important information about the behavior of the species concerned. In the case of *S. aucuparia*, the relationship between either height or trunk diameter and plant age was sigmoidal rather than linear, with high levels of variation in the size of intermediate-age plants (those between 10 and 35 years old). Such variations could be due to differences in light conditions among plants within the population (Closset-Kopp et al. 2007; Żywiec and Ledwoń 2008). In the model proposed here, reproductive values were indicated by the left eigenvector  $v$ , which estimates the expected per capita contribution to population growth of individuals in each category (Table 2). Reproductive values were notably higher for individuals in gaps than for those under-canopy cover, thus supporting the idea that light availability plays a major role in the reproduction of *S.*

*aucuparia* in the invaded environment, as described for this species in its native range (Raspé et al. 2000). Usually, a plant species that grows under different light conditions may not show optimal performance throughout the entire light gradient; for instance, many species that grow in environments with high and low light availability are unable to reproduce in the latter condition (Valladares and Niinemets 2008; Silvertown and Charlesworth 2009). *Sorbus aucuparia* is capable of recruiting under closed canopy and develop a bank of slow-growing, stunted juveniles which reach the reproductive stage only after the formation of canopy gaps. This behavior has been described for other invasive tree species, such as *Prunus serotina* and *Acer platanoides* (Martin and Marks 2006; Wangen and Webster 2006; Closset-Kopp et al. 2007; Phartyal et al. 2009). Other factors such as soil type and water availability could affect the habit and vegetative growth of woody plants (Girona et al. 2005; Zalba and Amodeo 2015). For example, trees of the invasive species *Prunus mahaleb* increase in size at a different rate depending on soil type: trees growing in deep soils grow larger than plants growing for the same period in rock crevices (Zalba and Amodeo 2015). These variables, together with light condition, could be responsible of the high level of variability in stem height and basal diameter exhibited by >10-year-old reproductive and non-reproductive individuals of *S. aucuparia*. Future studies should consider soil type and water availability when assessing the likelihood of *S. aucuparia* becoming reproductive under forest canopy gaps. The capacity to maintain a bank of relatively small, shade-tolerant seedlings and saplings for a long time may result in the invasion process passing unnoticed for a long period, until the formation of gaps in the canopy boosts the growth of seedlings and non-reproductive individuals, and makes possible the transition of non-reproductive individuals to the reproductive stage.

The present study, like a previous one (Lediuk et al. 2014), indicates that *S. aucuparia* is exhibiting an apparently slow invasion rate in Patagonia but is likely to have significant environmental impact on at least some types of Patagonian forests in the long term (Martin et al. 2008). Those factors that increase light availability in the understory of native forests, such as disturbance related to trampling and path opening, and the natural decay of the native forest trees

(Bongers and Popma 1988), would cause many small *S. aucuparia* plants to reach the reproductive stage and increase seed production exponentially.

#### Lag times in woody plants

A better knowledge about the factors that affect the length of the lag time of a particular invasive species is necessary in order to gain insight into its population growth and prevent its becoming a troublesome invader in a new area (Larkin 2012). Lag times of about 170 years and 131 years have been found, respectively, for trees and shrubs that were introduced in Europe (Kowarik 1995), 149 years for species introduced in South Australia (Caley et al. 2008), and less than 22 years for woody species introduced in tropical environments (Daehler 2009). A lag time between 8 and 18 years was found in central Argentina for *Prunus mahaleb* (Amodeo and Zalba 2013). At the *N. pumilio* forest studied here, *S. aucuparia* colonization started without severe human-related disturbance about 13 years after the time when those trees that had been planted in the native forest reached the reproductive phase. Twenty-five years after the founder *S. aucuparia* trees reached sexual maturity, many spontaneously recruited individuals started to produce seeds, so that population growth rate increased. This lag time is relatively short for a woody species in a temperate climate. Larkin (2012) reported that lag times of invasive and potentially invasive species in North America is shorter for woody than herbaceous species. This author considered that the reason for this difference could be that the former species are widely planted as ornamentals and have fleshy fruits that are often consumed by birds and other animals, facilitating seed dispersal. Both plantation as ornamental and fruit consumption by birds could explain the short lag time of *S. aucuparia*. In its native range, seed dispersal by birds has been found to influence the spatial distribution pattern of *S. aucuparia* (Żywiec and Ledwoń 2008). Birds assist the reproduction of *S. aucuparia* not only by means of seed dispersion but also by increasing the seed germination rate and seedling growth (Paulsen and Högstedt 2002). In Patagonia, the bird species most likely involved in the seed dispersal of *S. aucuparia* is the native *Turdus falcklandii*, which is a key disperser of native species with fleshy fruits during the autumn

period (Amico and Aizen 2005), when ripe fruits of *S. aucuparia* are still attached to the fruiting trees (Lediuk et al. 2014). Therefore, the feeding ranges of *T. falcklandii* would be indicative of the distance of seed dispersal of *S. aucuparia*. *Turdus falcklandii* tends to collect large sets of fruits from the same plant (Amico and Aizen 2005; Lediuk, field observation). The fate of seeds produced by a given plant species could be affected by the composition of the frugivores assemblage, plant location, and fruit availability from other plants (Morales et al. 2013). Seed dispersal patterns by birds of the same genus (*Turdus* spp.) in the native range of *S. aucuparia* are highly directional, i.e., seed deposits are denser in habitats with fleshy fruited trees than in habitats with other tree types or in open habitats (Carlo et al. 2013). Seed sources may be in gaps where *S. aucuparia* can reach the reproductive stage, but the dispersers' behavior could lead to a higher extent of seed deposition in the understory than in gaps. Thereby, the habitat preference and behavior of the birds (movement, perching, and gut passage time) and landscape structure (distribution, cover, and fruit availability of plants) could be key factors determining the distribution of seeds in the different light conditions (gaps and understory). Future studies should focus on comparing seed dispersal and seedling establishment between sites with contrasting light conditions. A better ethological knowledge about frugivorous seed dispersers would be helpful in determining the distances and directions of seed spread and would allow an appropriate and effective management of *S. aucuparia* (Buckley et al. 2006). It would be recommendable, a priori, not to plant this species close to nature reserves, and to eradicate *S. aucuparia* trees from urban and suburban areas located at short distances from reserves or National Parks.

#### Modeling the population dynamics of an invasive species

The persistence of adult *S. aucuparia* trees was found to be a demographic process with high elasticity, i.e., the number of reproductive individuals is the feature contributing most significantly to population growth (76 %). Therefore, management strategies aimed at preserving *N. pumilio* forests should focus on eradicating *S. aucuparia* trees that have reached the reproductive stage. Under the current environmental conditions, the presence of a relatively low proportion

of adult plants (26 % of the population) would be enough to keep the population growing ( $\lambda > 1$ ), even without assuming any increases in light availability, which would promote the passage of non-reproductive individuals to the reproductive stage (i.e., if  $\kappa U = 0$ ). Although the contribution of seedlings to population growth rate is comparatively low (3 %), and their mortality rate is high (28 %), the low mortality rates of reproductive and non-reproductive individuals imply that the invading population of *S. aucuparia* keeps growing in size. A decrease of only 5 % in the number of reproductive individuals would be enough for the population growth rate to be negatively affected ( $\lambda < 1$ ), i.e., to begin the control of this *S. aucuparia* population. The matrix demographic projection of population trends thus provides key information for the control of exotic species at early stages of the invasion process. The development of management plans for *S. aucuparia* in the Patagonian forests should be focused on the removal of reproductive individuals and controlling those factors that may help increasing light availability and, indirectly, seed production in *S. aucuparia*. Management plans that include the removal of adult *S. aucuparia* plants should go together with post-removal revegetation plans, and the monitoring of eventual transitions of plants from the non-reproductive stage to the reproductive stage.

## Conclusion

*Sorbus aucuparia* plants can establish and remain beneath the canopy of *N. pumilio* forests in Patagonia for several decades. In these forests, low light availability seems to be the factor that restricts the passage of *S. aucuparia* plants from the sapling to the reproductive stage. The formation of canopy gaps, e.g., during path and road openings, or due to partial or total crown deaths, would increase the growth rate of *S. aucuparia* trees already present in the understory and trigger flower production in some of them. The consequent increments in fruit production and, probably, attraction of frugivorous birds, would favor the spread of *S. aucuparia* and cause a sharp increase in its impact on Patagonian forest ecosystems. Reducing the number of reproductive trees would be key to the control of *S. aucuparia*: a 5 % reduction may cause a decrease in population size. Management strategies for invasive tree species that form inconspicuous

understory seedling/sapling banks, such as *S. aucuparia*, must focus on the early detection, control, and eradication of reproductive individuals while preventing light availability to increase in the understory.

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