Primary Research Paper (Original Article)

# Mast seeding mitigates the negative demographic effects of conspecific adults on rowan seedling survival

Seget Barbara[1]*, Bogdziewicz Michał[2], Piechnik Łukasz[1], Holeksa Jan[3], Ledwoń Mateusz[4], Żywiec Magdalena[1]

[1]W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland

[2]Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland

[3]Department of Plant Ecology and Environmental Protection, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland

[4]Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland

A running title: Masting increases seedling survival and reduces conspecific vicinity costs

* b.seget@botany.pl

ABSTRACT

**Background and Aims** Seedling mortality filters tree recruitment, yet we know little about whether the year in which a seedling is produced leaves a demographic signal after emergence. This gap is central for mast-seeding species, where seed crops vary widely among years and may generate cohorts that differ in offspring quality. We tested whether the size of the seed crop from which a seedling cohort comes predicted subsequent seedling survival, and whether this effect depended on seedling size, age, and conspecific neighbourhood context.

**Methods** We used 15-years of data monitoring the establishment, survival and growth of 4678 individually marked rowan (*Sorbus aucuparia*) seedlings in a natural subalpine spruce forest in West Carpathians. We modelled annual survival in relation to seedling age, leaf area, crop size, and establishment beneath conspecific rowans or heterospecific spruces.

**Key Results** Seedling survival increased with age, leaf area, and establishment beneath heterospecific spruces compared with conspecific rowans. The effect of crop size depended on neighbourhood context. Beneath the crowns of conspecific rowans seedlings from high-crop years survived better than seedlings from low-crop years, whereas survival beneath heterospecific spruces changed little with crop size. As a result, the seedling survival disadvantage associated with establishment beneath conspecifics was reduced for cohorts from high-crop years.

**Conclusions** Masting can shape recruitment beyond seed production and seedling emergence by influencing the survival of established cohorts. Our results suggest that variation in cohort quality among years may determine how many seedlings pass through the establishment bottleneck. By increasing survival in conspecific neighbourhoods, high-crop years may also alter the spatial pattern of recruitment, allowing more seedlings to persist near conspecifics.

KEY WORDS

Distant-dependent mortality, Janzen-Connell effect, masting, seed production, seedling age, seedling size, temporal variability of seedling mortality, spatial pattern of recruitment, subalpine spruce forest, *Sorbus aucuparia*

## INTRODUCTION

Tree population dynamics depend on both recruitment and survival, yet the processes shaping survival during early establishment remains understudied (McDowell *et al.*, 2020; Hanbury-Brown *et al.*, 2022). The seedling stage is a key demographic bottleneck in the life cycle of trees, because a large proportion of seedlings die within the first year, or even within weeks of emergence, and this stage is therefore exposed to strong selection pressure (Moles and Leishman, 2008). Seedlings are vulnerable to mortality from numerous biotic and abiotic factors that often act simultaneously, and death commonly results from the combined effects of insect and vertebrate herbivory, fungal pathogens, drought, low-light in understory, nutrient limitation, physical damage, burial under litter and competition with established vegetation or other seedlings (Moles and Westoby, 2004 *b*; Green *et al.*, 2014; Yao *et al.*, 2020; Jiang *et al.*, 2022). Despite the central demographic importance of this stage, the factors determining which seedlings persist and which are lost remain incompletely understood, partly because resolving this question requires long-term, labour-intensive monitoring of individually marked seedlings across multiple years.

The demographic fate of seedling cohorts may be linked with the pattern of seed production through variable resource allocation to seeds in high- and low-crop years. This issue is especially relevant in mast-seeding species, in which seed production varies widely among years (Bogdziewicz *et al.*, 2024 *c*). The variation in reproductive output can alter per-seed investment in contrasting ways. High crop years may reduce investment per seed through a seed size–number trade-off, with negative consequences for seedling germination and establishment. For example, in *Castanopsis fargesii* a 30% decline in seed mass during high-seeding years translated into a fivefold decline in germination rate (Huang *et al.*, 2021). Seed mass also declined with increasing seed production in *Pinus armandii* (Wang and Ives, 2017). However, high-seeding years may also increase seed quality if they coincide with greater reproductive allocation or improved pollination and cross-fertilization, leading to heavier or better-provisioned seeds (de Jong and Klinkhamer, 2005). In support, size of European beech seeds increase by 14% between low and high-seeding years (Kondrat *et al.*, 2026). Such interannual variation in seed provisioning can, in turn, influence subsequent seedling size and survival.

Seedling size is a key determinant of subsequent seedling survival. Increasing evidence shows that relationship between environmental conditions and demography are

mediated by plant functional traits (Umaña *et al.*, 2018; Jiang *et al.*, 2022), and seedling size appears to be most important, with strong positive impact on seedling survival (Comita *et al.*, 2009; Bianchi *et al.*, 2019; Yao *et al.*, 2020). For example, in Central European temperate forests, greater seedling height and a higher number of leaves were associated with higher survival (Bianchi *et al.*, 2019). The same pattern was found in tropical forest where probability of seedling survival increased with seedling height (Comita *et al.*, 2009). Seedling height may positively influence survival both directly and indirectly through correlated traits such as leaf area, which tends to increase with seedling height (Jiang *et al.*, 2022). Because mortality is size-dependent, the effects of biotic and abiotic drivers on seedling survival may also change with seedling age or developmental stage (Comita *et al.*, 2014; Liu *et al.*, 2021; Huang *et al.*, 2022).

Another major biotic driver of seedling survival is the conspecific neighbourhood. According to the Janzen-Connell hypothesis, seedlings establishing beneath or near conspecific adults often experience lower survival than those associated with heterospecific trees because they are exposed both to high local densities of conspecific seedlings and to host-specific natural enemies, such as pathogens and herbivores, whose effects increase with conspecific density or proximity to adult trees (Connell, 1971; Janzen, 1970). As a result, mortality of seedlings is often density- and/or distance-dependent (Packer and Clay, 2000; Yamazaki *et al.*, 2009; Metz *et al.*, 2010; Comita *et al.*, 2014; Yao *et al.*, 2020; Song *et al.*, 2021). While masting generates positive density-dependence that helps escaping natural enemies in time (Zwolak *et al.*, 2022), the Janzen-Connell processes are negative density and/or distance-dependent and facilitate escaping seed or seedling predators in space (Xiao *et al.*, 2017; Bogdziewicz *et al.*, 2018; Davies *et al.*, 2025). The Janzen-Connell processes likely interact with the variable allocation of resources to seeds in high- and low-crop years described above, because the advantage of larger seeds should be stronger under stressful habitat conditions. For example, in Scots pine (*Pinus sylvestris*), the positive effect of seed mass on seedling recruitment was more evident in the more stressful soil environment, suggesting that size-related advantages become stronger when establishment conditions are harsher (Castro, 1999).

Here, we used 15-years long monitoring on rowan (*Sorbus aucuparia*) seedling establishment and growth in a natural subalpine spruce forest in West Carpathians. We analysed seedling survival in relation to the size of the seed crop from which a cohort come, while also accounting for seedling size, seedling age, and whether seedlings grew under

conspecific or heterospecific trees. We hypothesize that survival of seedlings increase with seedling size and age and that survival is higher under heterospecific than conspecific trees. The relationship between the seed crop and subsequent seedling survival could operate in opposite directions. If high crop years reflect years of high resources and/or high level of cross fertilization, seedlings coming from such years could be larger and survive better. By contrast, if high crop arise through a size-number trade-off and large number of seeds is produced at the expense of their quality (for example, lower mass or nutrient content), seedlings from those years should be smaller and have lower survival. The effect of seed crop size on seedling survival should also be also habitat-dependent. Specifically, to the extent that habitat under crowns of conspecifics is stressful, the possible positive effect of crop size on seedling survival should be stronger for seedlings growing under rowan crowns.

## METHODS

### Study area

The study was conducted in the Western Carpathians in a subalpine old-growth spruce forest growing on the Babia Góra massif (Poland). The tree stand consists two species: Norway spruce (*Picea abies*) and rowan (*S. aucuparia*). The percentage of rowan is usually below 5%, and the distribution of rowan is distinctly clumped. Rowan trees usually form small groups in spruce stand gaps resulting from bark beetle outbreaks or windstorms. The mean density of rowan trees was 8.4-11.5 individuals/ha (Holeksa *et al.*, 2017; Żywiec and Ledwoń, 2008). The climate of the study site is cold, with mean annual temperature of 3.3°C, mean annual rainfall of 147 cm and a snow-free period of 7 months.

### Study species

Rowan *Sorbus aucuparia* L. (Rosaceae, Maloideae) is deciduous fleshy-fruited tree reaching 15–20 m in height and living 100–150 years. It is distributed through Europe, Asia Minor, the Caucasus, western Siberia and North Africa (Raspé *et al.*, 2000). Its flowers are pollinated by a wide range of insects, and pollination increases from 20% to 80% with increasing tree-level flower abundance, showing no pollinator satiation (Szymkowiak *et al.*, 2026). Fruit production is highly variable among years and synchronized among individuals (Żywiec *et al.*, 2012; Seget *et al.*, 2022 *a*, *b*; Bogdziewicz *et al.*, 2024 *a*, *b*). Fruits of rowan are predated

by larvae of the apple fruit moth *Argyresthia conjugella* Zell. (Lepidoptera, Yponomeutidae) which is a specialized rowan seed predator that cause considerable seed losses (Kobro *et al.*, 2003; Żywiec *et al.*, 2013; Seget *et al.*, 2022 *b*). The seed predation is lower for more synchronized individuals (Bogdziewicz *et al.*, 2021). The seedling recruitment is enhanced through predator satiation and increased seed dispersal by frugivores (Seget *et al.*, 2022 *a*, *b*). The years of high population-level fruit production are followed by increased seedling recruitment (number of new seedlings per produced fruit) proving that masting improves recruitment success in rowan (Seget *et al.*, 2022 *a*, *b*).

In the Polish Western Carpathians, the primary seed dispersers of rowan include local breeding species such as *Turdus merula*, *T. pilaris*, *T. viscivorus*, *T. philomelos*, and *Erithacus rubecula* as well as short-distance migratory birds, specifically *Bombycilla garrulus* and *Turdus iliacus*. Among these, the European robin (*E. rubecula*) is the dominant breeding disperser within subalpine spruce forests. Mammalian dispersers present in the subalpine spruce forests of the Babia Góra study area include *Martes martes* and *Vulpes vulpes* ( Seget *et al.*, 2022 *b*).

The rowan seeds show deep and absolute dormancy (an embryo dormancy and a dormancy imposed by the seed coat) which can be broken by cold stratification (Raspé *et al.*, 2000; Paulsen and Högstedt, 2002; Dinçer, 2023). The germination occurs in the first and second year after seed dispersal (Tiebel *et al.*, 2021). The germination is epigeal. The hypocotyl is 2-4 cm long and woody. The cotyledons are elliptically oblong, their length reaches 5.5-8.5 mm, a petiole has 1-2 mm. The first leaves are alternate, with a petiole 2-5 mm, pinnatipartite-pinnate, 1-1.5 cm long (Raspé *et al.*, 2000). Rowan seedlings can be attacked by numerous pathogens such as e.g. *Phytophthora sp.*, *Botrytis cinerea*, *Fusarium solani*, (Orlikowski *et al.*, 2004), *Ochropsora ariae* (van Dijk *et al.*, 2022), and *Cytospora rubescens* (MacBrayne, 1981).

Rowan seedlings and saplings are very tolerant to shade (Raspé *et al.*, 2000). It is important as due to avian post-foraging behavior, rowan seeds are predominantly deposited beneath spruce crowns (Żywiec and Ledwoń, 2008). They persist in a suppressed state for years establishing a seedling and sapling bank beneath the living canopy (Żywiec and Holeksa, 2012).

Data collection

Data were collected on the permanent plot (27-ha; 564 × 480 m; 1170 – 1310 m above sea level) located on the northern slope of Babia Góra massif (West Carpathians). We measured fruit production in September (2008 and 2024) counting the number of infructescences on all living rowan trees with the use of binoculars (N = 228‑310 depending on the year). The number of reproductive trees changed over the years due to mortality and maturation to the reproductive stage. In randomly sampled five infructescences from each tree all fruits were counted. The fruit production of an individual tree was estimated as the product of the number of infructescences and the average number of fruits in five infructescences (Pesendorfer *et al.*, 2019; Żywiec *et al.*, 2012; Żywiec *et al.*, 2018; Seget *et al.*, 2022 *a*, *b*) (Fig. S1).

On the same site, we placed 100 plots (each 1 $m^2$) for seedling monitoring, 50 plots were located under the crown of 50 rowan trees and 50 – under the crowns of 50 spruces nearest to each rowan tree (Fig. S2). Each July from 2010 to 2025, we counted and individually marked all new rowan seedlings recruiting in these plots and monitored their survival once per year (Żywiec, 2013; Seget *et al.*, 2022 *a*, *b*). During 16 years, some spruce and rowan trees died. Such mortality events drastically alter microsite conditions (e.g., light availability and litter dynamics) and seed shadows, thus we excluded seedlings growing on these plots from the primary dataset. Our final dataset included 4532 seedlings.

In 2020 we measured size of all seedlings growing on the seedling monitoring plots, which included height, number of leaves, length (l) and width (w) of longest leaf were included. Then, leaf area of the longest leaf (a) was calculated using formula for the area of an ellipse ($a= \Pi \times l/2 \times w/2$). Leaf area was chosen as representative seedling functional trait as it is a trait related with light capture, mechanical support and transport functions of leaves (Westoby *et al.*, 2002).

Data analysis

We started by testing whether older seedlings were larger, had larger and more numerous leaves. We analysed seedling size as measured in 2020. We fitted three separate models (for seedling height, leaf area, and leaf number) with age in 2020 as the predictor, and in each model we also included habitat, i.e. whether a seedling was growing under a conspecific tree (rowan) or a heterospecific tree (spruce). Seedling height and leaf area were analysed using linear models with a quadratic age term to allow for non-linear relationships. The number of

leaves was analysed using a generalized linear model with a Poisson error distribution and log link, also including a quadratic age term.

To test whether seedling size in 2020 predicted subsequent survival, we analysed annual survival from 2020 to 2025 using a generalized linear mixed-effects model (GLMM). Survival was modelled at the interval level (year t to t+1) as a binary response with a binomial error distribution and logit link. The model included seedling leaf area measured in 2020, seedling age in the given interval, and habitat (whether the seedling grew under a conspecific rowan or a heterospecific spruce tree) as fixed effects. We have also explored models where leaf area was replaced with seedling height, which provided qualitatively the same results (see Table S1 for correlations among seedling traits). We also included plot-level density of rowan seedlings in given year to account for density-dependence. Seedling identity and seedling plot were included as a random intercepts to account for repeated annual observations of the same individual and correlation among seedlings occurring at the same plots. This approach allowed us to test whether initial size predicted subsequent survival probability while accounting for age, habitat context, and within-individual temporal dependence.

To test whether long-term survival depended on fruit crop size at recruitment, we analysed annual survival of seedlings from cohorts established between 2010 and 2024. Survival was modelled at the interval level (year *t* to *t*+1) as a binary response with a binomial error distribution and logit link. For each recruitment year, fruit production was quantified as the sum of fruit production in the two years preceding recruitment, and log-transformed prior to analysis. The fruit production was summed over the last two consecutive years as rowan seeds germinate 1 or 2 years after seed dispersal (Tiebel *et al.*, 2021; Seget *et al.*, 2022 *a*, *b*). The model included fruit crop size, seedling age in the given year, and habitat (whether the seedling grew under a conspecific rowan or a heterospecific spruce tree) as fixed effects, as well as the interaction between fruit crop size and habitat to test whether fruit effects differed between conspecific and heterospecific neighbourhood. We also included plot-level density of rowan seedlings in given year to account for density-dependence. Seedling identity and seedling plot were included as a random intercepts to account for repeated annual observations of the same individual and correlation among seedlings occurring at the same plots. Note that in both models described above we could not include both habitat and distance to nearest rowan, as these were strongly correlated (Fig. S2). Nonetheless, replacing habitat with distance provided qualitatively similar results.

Model assumptions were assessed using quantile–quantile plots of residuals, plots of residuals against predicted values, and tests for dispersion and outliers; no substantial deviations were detected. We also checked for multicollinearity using variance inflation factors (VIFs) and found no problematic collinearity. We also tested residuals for spatial autocorrelation and found no evidence of remaining spatial dependence.

The analysis was conducted in R version 4.5.2, models were fitted via glmmTMB package version 1.1.14 (Brooks *et al.*, 2017), and validated using DHARMa version 0.5.0 (Harting 2026).

## RESULTS

In sum, the emergence and survival of 4532 rowan seedlings was determined, they represented 15 cohorts: 2010-2024 (Fig. S3). The size of 971 seedlings (alive in 2020 and representing cohorts 2010-2020) was measured (Table S2).

**Seedling size and age**. Seedling height, leaf area, and leaf number increased with seedling age (Fig. 1). For seedlings growing under rowan conspecific trees, predicted height increased by 0.93 cm per year, from 3.83 cm (95% CI 3.55–4.12) at age 2 to 9.43 cm (95% CI 8.99–9.86) at age 8. Habitat had a significant effect on height, with seedlings growing under spruce (heterospecific trees) being on average 0.80 cm shorter, corresponding to approximately a 9% reduction in height relative to rowan across ages ($\beta = -0.80 \pm 0.20$ SE, $p < 0.001$) (Fig. 1A). In contrast, habitat had no detectable effect on the number of leaves ($p = 0.94$) or leaf area ($p = 0.12$) of seedlings. The predicted number of leaves increased by 0.24 leaves per year, from 2.93 (95% CI 2.81–3.07) at age 2 to 4.35 (95% CI 4.12–4.60) at age 8, although the negative quadratic term indicated partial levelling-off at older ages (Fig. 1B). Leaf area showed the strongest relative change, increasing by 1.92 mm² per year, from 2.73 mm² (95% CI 2.17–3.29) at age 2 to 14.23 mm² (95% CI 13.41–15.04) at age 8 (Fig. 1C).

**Seedling survival.** Annual survival was primarily driven by seedling age, with positive contributions of leaf area and growing under spruce rather than rowan (Fig. 2, Table S3). Age had the positive effect on survival ($\beta = 0.15 \pm 0.02$ SE, $p < 0.001$). For example, predicted annual survival of seedlings growing under spruce increased by 0.02 per year, from 0.71 (95% CI 0.64–0.77) at age 2 to 0.85 (95% CI 0.80–0.89) at age 8 (Fig. 2A). Annual survival was higher under spruce ($\beta = 0.38 \pm 0.19$ SE, $p = 0.05$); for an average seedling, survival was 6.2

percentage point higher under spruce than those under rowan (0.829 vs 0.767, Fig. 2B). Leaf area also positively influenced survival ($\beta = 0.03 \pm 0.009$ SE, $p < 0.001$). For seedlings under spruce, predicted survival increased from 0.71 (95% CI 0.70–0.82) at low leaf area (1.0 mm²) to 0.76 (95% CI 0.70–0.82) at high leaf area (9.5 mm²), corresponding to a 7.6% increase (Fig. 2C).

In the model based on the larger dataset (2010-2025), annual survival depended on the interaction between fruit crop size at recruitment and habitat (interaction = $-0.49 \pm 0.11$ SE, $p < 0.001$; Fig. 3, Table S4). Under rowan, survival increased significantly with increasing fruit crop size ($\beta = 0.46 \pm 0.07$ SE, $p < 0.001$). For cohorts from relatively low fruit years (25% quantile, Fruits $T_{1+2} \approx 4{,}450$; 8.4 on the log-scale), predicted annual survival under rowan was 0.44 (95% CI 0.37–0.52), increasing to 0.55 (95% CI 0.48–0.62) for cohorts from high fruit years (75% quantile, Fruits $T_{1+2} \approx 11{,}400$, 9.3 on the log-scale). This corresponds to a 10.9 percentage-point increase and a 24.6% relative increase in annual survival across a ~2.6-fold increase in fruit production. In contrast, under spruce the effect of fruit crop size was not statistically supported ($\beta = -0.03 \pm 0.09$ SE, $p = 0.72$), and predicted survival changed little across the same fruit production range. Consequently, the extent to which seedling survival differed between habitats was determined by fruit crop size. After low fruit years, survival under spruce exceeded that under rowan by 17.6 percentage points (0.62 vs 0.44), corresponding to a 39.7% relative difference. After high fruit years, this difference was reduced to 6.0 percentage points (0.61 vs 0.55; 10.9% relative difference).

Note that because these estimates refer to annual survival, even modest percentage differences can accumulate over successive years, leading to substantial divergence in cumulative survival probabilities and, consequently, in long-term recruitment outcomes. For example, an annual survival of 0.85 sustained over five years results in a cumulative survival probability of 0.44 ($0.85^5$), whereas a survival of 0.80 over the same period yields 0.33 ($0.80^5$). Thus, a 5 percentage point difference in annual survival translates into a 33% higher probability of surviving five years, illustrating how relatively small annual effects can generate substantial long-term differences in recruitment.

## DISCCUSION

Seedling survival was higher for cohorts coming from years of high fruit production, it also increased with seedling age, seedling size, and establishment under heterospecific rather than

conspecific trees. The effect of crop size on seedling survival depended on habitat context. Seedlings from high crop years had higher annual survival under conspecific rowans compared to seedlings from low crop years, whereas survival under heterospecific spruces changed little with crop size. Consequently, the survival disadvantage associated with establishment beneath rowans was reduced for cohorts recruited after high crop years. Our results show that the demographic consequences of masting extend beyond seed production and seedling emergence to post-establishment survival, and that this advantage is expressed most strongly in the conspecific neighbourhood.

Seedling survival increased with the fruit crop size. This suggests that, in rowan, years of high reproductive output may increase both the number of offspring produced (Bogdziewicz *et al.*, 2024 *a*) and their probability of persistence after establishment. One possible explanation is that seeds produced in high crop years are of higher quality, for example because these years are associated with greater cross-fertilization (Szymkowiak *et al.*, 2026), higher seed mass, or better provisioning (Kondrat *et al.*, 2026). This interpretation is consistent with recent evidence from European beech, where high seed production was associated with higher seed mass and lipid content (Kondrat et al. 2026). Nonetheless, the relationship between crop size and seed quality remains unresolved, with studies reporting negative, neutral, and positive covariation between reproductive output and seed provisioning for species within the Fagaceae and Pinaceae families (*Quercus lobata*, *Pinus armandii*, *Castanopsis fargesii*; Koenig *et al.*, 2009; Wang and Ives, 2017; Huang *et al.*, 2021). This question is important because reduced seed quality during high crop years could strongly weaken the demographic benefits of masting, as shown in *Castanopsis fargesii*, where lower seed mass in high-seeding years reduced early survival and recruitment gains (Huang *et al.*, 2021). Our results highlight the need to quantify how seed quality covaries with crop size and to test the demographic consequences of this variation for seedling performance.

The positive effect of seed crop size on seedling survival was restricted to seedlings establishing beneath conspecific rowans. This pattern suggests that the advantage associated with high crop years was expressed primarily in the habitat where establishment conditions were most stressful (Song *et al.*, 2021; Liu *et al.*, 2021; Huang *et al.*, 2022). In our study, survival was consistently lower under rowan than under spruce crowns, which is consistent with Janzen–Connell effects arising under conspecific adults. Such effects have been documented in many systems and are often attributed to the accumulation of host-specific natural enemies, including soil-borne pathogens and herbivores, near adult trees (Packer and

Clay, 2000; Yamazaki *et al.*, 2009; Bagchi *et al.*, 2010; Metz *et al.*, 2010; Comita *et al.*, 2014; Song *et al.*, 2021). In rowan, the most probable mechanism involves host-specific soil pathogens, given that negative plant–soil feedback is common in tree seedlings and has been reported in Rosaceae (Packer and Clay 2000; Brinkman et al. 2010). While enhanced insect herbivory near conspecifics could also contribute to this pattern, vertebrate herbivory is far less likely to be a driver, as the short distance between plots beneath rowans and spruces would probably not generate a significant difference in browsing pressure. Therefore, the seed quality may play an important role under high densities of seedlings, being the key for the persistence of the early stage individual in harsh conditions, like those generated by conspecific density-dependent mortality (Castro, 1999; Landergott *et al.*, 2012). Masting may partly offset the survival costs associated with conspecific neighbourhoods, allowing a greater proportion of seedlings to pass through the bottleneck of early establishment.

Differences in seedling survival between conspecific and heterospecific neighbourhoods may reflect not only the action of host-specific natural enemies, but also other differences in microsite quality. Tree species can modify soil chemical and physical properties through litter production, effects on soil moisture and temperature, nutrient cycling, and mycorrhizal communities (Packer and Clay, 2003). In our system, rowan and spruce create contrasting litter environments. Rowan litter decomposes more rapidly and improves nutrient availability, soil respiration, and other soil properties relative to spruce litter (Emmer *et al.*, 1998), suggesting that conditions for seedling establishment and growth should in some respects be more favourable beneath rowan than beneath spruce. Despite these potential advantages, rowan seedlings had lower survival beneath rowan than beneath spruce, indicating that the negative effects associated with conspecific neighbourhoods outweigh these benefits. Conditions beneath spruce may also impose costs, including lower light availability, drought, nutrient limitation, or burial under litter.

For fleshy-fruited species such as rowan, establishment beneath conspecific trees may involve an additional disadvantage linked to dispersal mode. Beneath rowan crowns, seeds often arrive within intact fruits, whereas beneath heterospecific trees they are typically deposited by frugivorous birds after gut passage. This creates the difference in germination conditions, because fruit pulp may inhibit germination and early growth, whereas gut passage removes pulp and may additionally enhance recruitment through scarification or fertilization by fecal material (Cipollini and Levey, 1997; Fedriani and Delibes, 2009; Fedriani *et al.*, 2012). In rowan, seeds enclosed in intact fruits germinate poorly and germination increases if

pulp is removed mechanically, decomposes, or fruits pass through bird guts (Yagihashi *et al.*, 1998; Paulsen and Högstedt, 2002). These constraints on establishment beneath rowan may further increase the importance of cohort quality, helping explain why the positive effect of high crop years on seedling survival was expressed most strongly in conspecific neighbourhoods. This is in line with Howe (1989) who suggests that seedlings of species dispersed by small frugivories are vulnerable to pathogens and herbivores and their recruitment near parent trees is rare.

Seedling size was an important predictor of survival. Annual survival increased with leaf area, indicating that larger seedlings were more likely to persist through subsequent years. This agrees with the evidence that seedling performance is influenced by functional traits linked to carbon gain and resource capture (Umaña *et al.*, 2018; Jiang *et al.*, 2022). In our study, older seedlings were taller and had larger and more numerous leaves, indicating that ontogenetic development was accompanied by increasing structural capacity. Nonetheless, the effects of age and leaf area remained significant when included in the same survival model, indicating that the positive effect of age was not explained solely by the fact that older seedlings had larger leaves or were taller. Rather, age likely captured additional aspects of seedling development that were not measured directly, such as a more developed root system, greater carbon storage, or improved physiological tolerance to stress. This interpretation is consistent with the general pattern that mortality risk is highest during the earliest life stages (Beckage *et al.*, 2005; Moles and Leishman, 2008). Very young seedlings are especially vulnerable because they have limited reserves and poorly developed structural and defensive traits, which makes them more susceptible to abiotic stress and natural enemies (Wright, 2002; Moles and Leishman, 2008; Comita *et al.*, 2014). Seedling size contributes directly to persistence during establishment, whereas age reflects a broader suite of developmental changes that further enhance survival.

In closing, our results show that survival during early establishment is shaped jointly by cohort identity, habitat context, and ontogenetic status. In rowan, seedlings survived better if they were from years of high fruit production, were larger, were older, and established beneath heterospecific rather than conspecific trees. The survival advantage of cohorts from high crop years was expressed primarily beneath conspecific rowans, where neighbourhood-dependent mortality was strongest. These findings indicate that the consequences of masting extend beyond seed production and seedling emergence to later stages of recruitment, and that variation in offspring quality among years may influence how many seedlings pass through

the demographic bottleneck of establishment. By increasing survival in the otherwise unfavourable conspecific neighbourhood, high crop years may also modify the spatial pattern of recruitment, allowing a greater fraction of seedlings to persist near adult rowans.

## SUPPLEMENTARY DATA

Supplementary data are available at Annals of Botany online and consist of the following.

Table S1. Correlations between seedling traits. Table S2. Descriptive statistics for seedling traits in 2020 and seedling survival (2010-2024), separated by habitat. Table S3. Summary of the generalized linear mixed-effects model testing effects of seedling age, leaf area, habitat, and local seedling density on annual survival. Table S4. Summary of the generalized linear mixed-effects model testing effects of fruit crop size at recruitment, habitat, seedling age, and local seedling density on annual survival. Figure S1. Annual fruit production across the study period. Figure S2. Distance from seedling plots to the nearest rowan tree, shown separately for plots located under rowan and spruce crowns. Figure S3. Recruitment dynamics and cohort persistence across microhabitats. (A) Cumulative number of recruited seedlings from 2010 to 2024, shown separately for seedlings established under rowan and spruce crowns. (B) Decline in the number of surviving seedlings within each recruitment cohort over time since recruitment, shown separately for the two microhabitats.

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## AUTHOR CONTRIBUTIONS

B.S., M.Ż., M.B. and J.H. conceived the ideas and designed the study; B.S., J.H., M.L., Ł.P., and M.Ż. collected the data; B.S. led data curation; B.S. and M.B. analyzed the data; B.S. and

MŻ led the writing of the manuscript. M.B. and MŻ. revised the text. All authors contributed critically to the drafts and gave final approval for publication.

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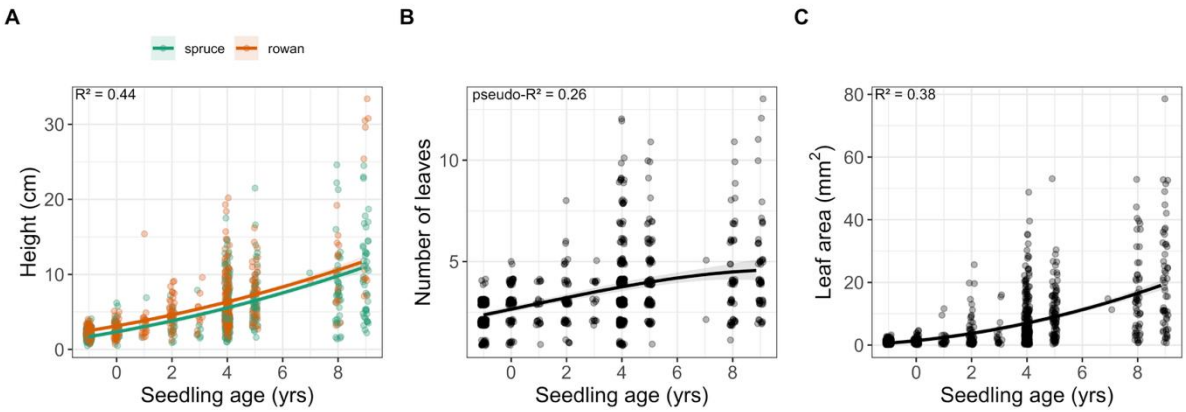
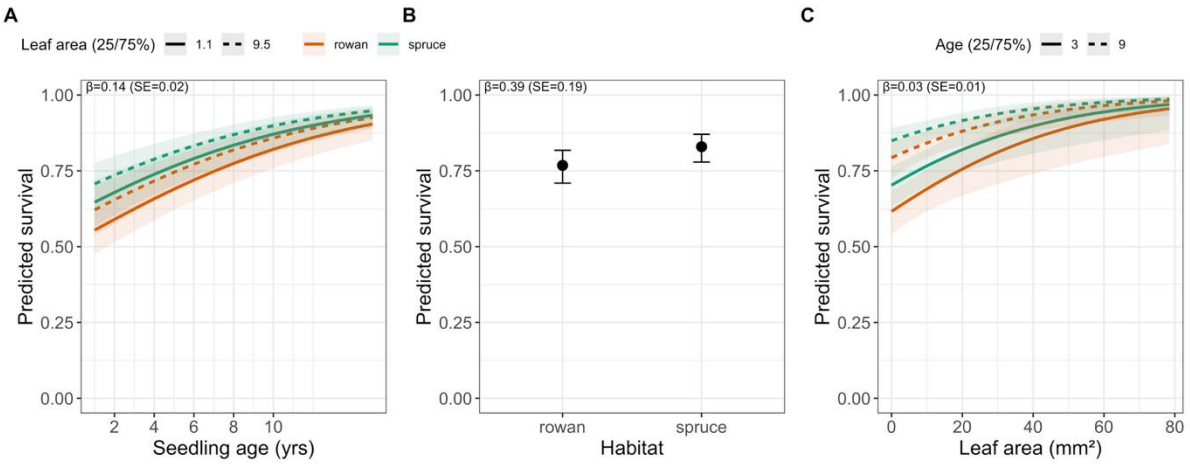



Fig. 1. Seedling size (height, leaf area, and leaf number, as measured in 2020) as a function of age and habitat. Points represent individual seedlings measured in 2020 (n = 971). Lines show model predictions from quadratic age models, and shaded areas indicate 95% confidence intervals. Panel A shows seedling height (cm), panel B the number of leaves, and panel C leaf area ($mm^2$). $R^2$ (linear models, A, C) and pseudo-$R^2$ (Poisson model, B) values are shown within panels. Note that regression lines for both habitats are presented exclusively for seedling height, as habitat type was statistically significant only in that model.




660

661 Fig. 2. Annual survival probability (2020–2024) as a function of seedling age, habitat, and
662 leaf area. Predictions are based on a generalized linear mixed-effects model (binomial error,
663 logit link) including seedling identity as a random intercept (3,109 annual intervals from 971
664 seedlings). Lines show population-level predicted survival probabilities and shaded areas
665 indicate 95% confidence intervals. (A) Effect of seedling age, shown separately for seedlings
666 growing under crowns of rowans (orange) and spruces (green); solid and dashed lines
667 represent low and high leaf area (25th and 75th percentiles), respectively. (B) Estimated
668 annual survival under rowan and spruce at mean age and leaf area. (C) Effect of leaf area,
669 shown separately for seedlings growing under crowns of rowans and spruces; solid and
670 dashed lines represent low and high age (25th and 75th percentiles), respectively.

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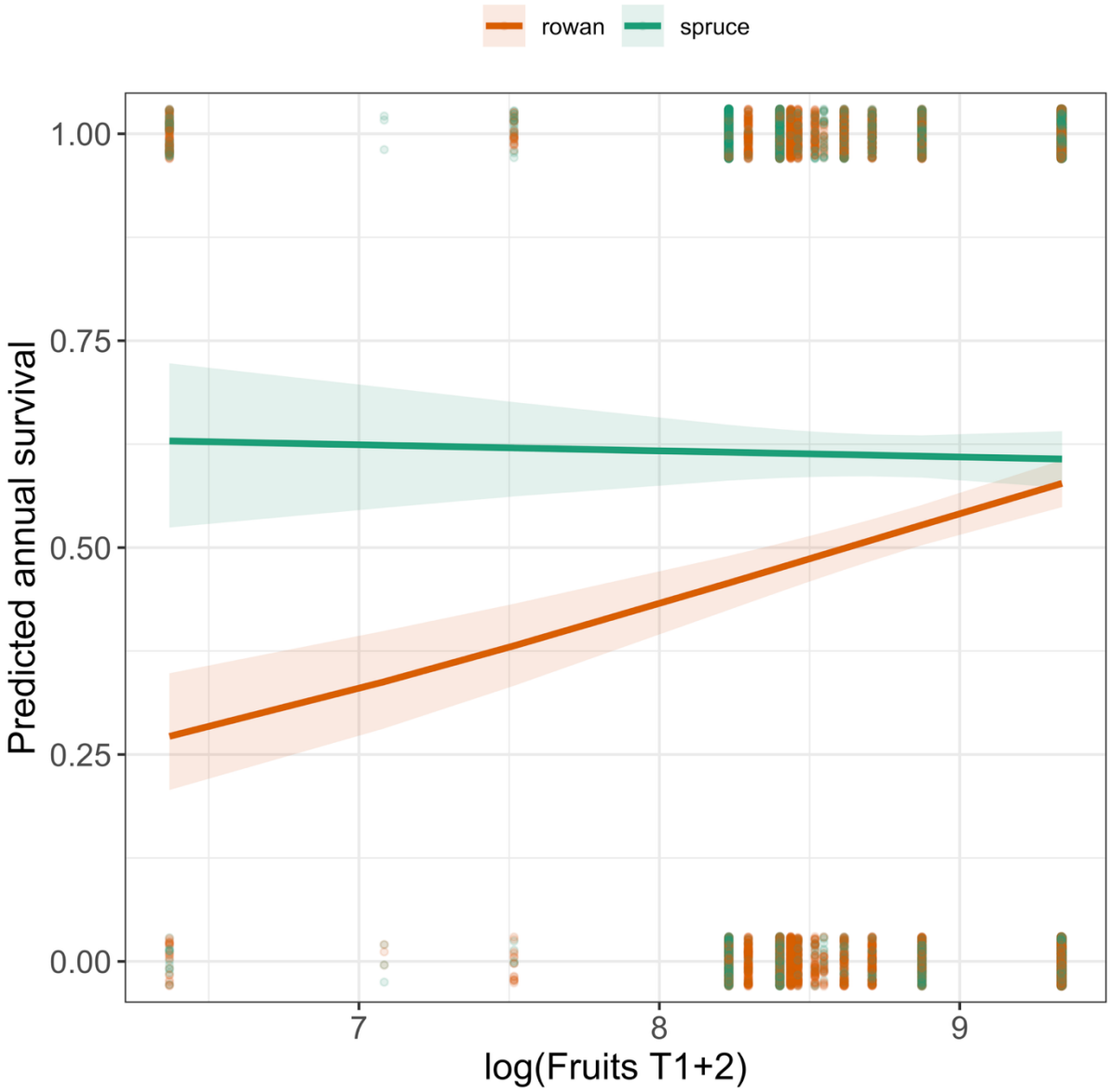


672

673 Fig. 3. Annual survival probability as a function of fruit crop size (Fruits $T_{1+2}$) and habitat.
674 Predictions are based on a generalized linear mixed-effects model (binomial error, logit link)
675 including seedling identity as a random intercept (12,401 annual intervals from 4,532
676 seedlings). Lines show population-level predicted survival probabilities and shaded areas
677 indicate 95% confidence intervals. Colors distinguish seedlings growing under rowan
678 (orange) and spruce (green). Points represent observed annual survival means for each
679 recruitment cohort × habitat combination. Fruit crop size is expressed as log-transformed
680 production summed over the two years preceding recruitment (Fruits $T_{1+2}$).