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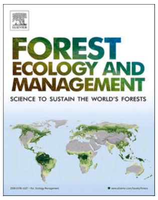

Simulated flood-stress and X-ray tomography unveil susceptibility of different tree taxa to ambrosia beetles

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ABSTRACT

Climate change will lead to higher frequencies of natural disasters, including flooding events. Consequently, more severe and widespread attacks by invasive ambrosia beetles associated with stressed trees are predicted to occur. In this scenario, understanding which tree species are expected to be more susceptible, as well as which ambrosia beetle species could be expected to have the biggest impacts, represent a research priority. To this aim, potted-trees of eight tree species (four in the order Fagales and four in the order Rosales) were first exposed to flood-stress in a common garden experiment; then emerging insects were counted and logs obtained from infested trees were analyzed through X-ray tomography to evaluate host selection patterns (entry holes), colonization success (percentage of branched galleries and offspring production), and potential damage to the tree (volume of the log occupied by galleries) by native and exotic ambrosia beetle species. Four ambrosia beetle species attacked flood-stressed trees: the native *Anisandrus dispar* and *Xyleborinus saxesenii*, and the exotic *Xylosandrus crassiusculus* and *Xylosandrus germanus*. Flood-stressed Rosales species were consistently more attacked than Fagales species, with different ambrosia beetle species showing distinct preferences for certain tree species. Rosales were also generally more suitable for ambrosia beetle reproduction than Fagales, even though differences were also evident among tree species within the two orders. The exotic *X. crassiusculus* was the most successful species, showing higher percentage of branched galleries and higher offspring production. Our study showed a differential susceptibility of common tree species to native and exotic ambrosia beetles in a flood-stress scenario. In addition, it highlighted that X-ray tomography provides a novel method for characterizing the host selection and colonization of trees by ambrosia beetles and can be considered a reliable methodology to improve our comprehension of these mechanisms.

1. Introduction

There is strong scientific evidence that the climate is changing due to anthropogenic activity (Karl and Trenberth, 2003; Berrang-Ford et al., 2011). Since the industrial revolution, the surface temperature of the planet has increased by 0.66–1.00°C (i.e., comparing the years 1850–1900 and 1995–2014) and is predicted to warm further to ten degrees by 2300 unless greenhouse gas emissions are significantly reduced (IPPC, 2021). Frequent increases in temperature extremes alter precipitation patterns, triggering a higher risk of natural disasters, such as floods, storms, and droughts (Strzepek et al., 2010; Hirabayashi et al., 2013). Such extreme weather events and the increased seasonal variability are critical for agriculture and forestry (Berrang-Ford et al., 2011). For example, water stress caused by floods is projected to cause crop value losses of more than 60 % over 100 years of production (Chau et al., 2015; Agovino et al., 2019) and it also strongly damages trees commonly planted in urban areas, forests and orchards (Chapman et al., 2008; Bremond et al., 2013; Basak et al., 2015). Outbreaks, range expansion, and human-assisted movement of insects among continents are also predicted to increase following global warming (Walther et al., 2009; Pureswaran et al., 2018), inevitably leading to higher pressure on natural and anthropized ecosystems.

Fungus-growing ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) are one of those insect groups that are predicted to be strongly affected by climate change and extreme climatic events (Urvois et al., 2021; Pureswaran et al., 2022). While they are

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mostly native in tropical and subtropical regions of the world (Kirkendall et al., 2015; Hulcr and Stelinski, 2017; Hulcr and Skelton, 2023), the interest towards them has exponentially increased over the last two decades following the rising number of new species introductions and interceptions outside their native ranges (Lantschner et al., 2020; Marchioro et al., 2022), and the economic and ecological damages that some of them cause in the invaded areas (Hughes et al., 2017; Gugliuzzo et al., 2021; Hulcr et al., 2021). Several ambrosia beetle species are associated with stressed trees producing and emitting ethanol (Ranger et al., 2015a, 2021; Cavaletto et al., 2023), which serves as an olfactory cue to locate stressed host trees (Ranger et al., 2015b; Reding et al., 2017; Rassati et al., 2020; Cavaletto et al., 2021). The presence of ethanol within host tree tissues also promotes the growth of ambrosia beetles' nutritional symbiotic fungi, and could inhibit fungal competitors (Ranger et al., 2018; Lehenberger et al., 2021). Given that the frequency and intensity of water-related stresses are expected to increase due to climate change, more severe and widespread attacks by ambrosia beetles are also predicted to occur in the near future.

Among water-related natural stressors, flooding is more important than drought for inducing attacks by ambrosia beetles (Frank and Ranger, 2016; Ranger et al., 2013, 2023; Parajuli et al., 2023). Gallery establishment and offspring production is higher in flood-stressed trees than drought-stressed trees (Ranger et al., 2023), perhaps because the low moisture level tends to inhibit fungal growth (Rousk and Bååth, 2011; Frank and Ranger, 2016; Frank et al., 2017). Several studies have elucidated patterns of host selection on flood-stressed trees, demonstrating that ambrosia beetles preferentially attack flood-intolerant tree species over flood-tolerant species and mostly during the early to intermediate stages of the stress (Ranger et al., 2016, 2021). Instead, patterns of gallery development within stressed trees infested by ambrosia beetles are largely understudied. Reconstructing what occurs within the wood of trees infested by ambrosia beetles is necessary to more deeply understand the impact of flood-stress on host tree colonization by ambrosia beetles. The manual dissection of infested woody material used so far (e.g., Cavaletto et al., 2021, 2023; Reding et al., 2021) provides limited quantitative data on gallery development and can cause the potential destruction of the sample, whereas novel imaging techniques such as X-ray tomography can help to overcome these limitations. Notably, X-ray tomography has been used on other insect taxa (e.g., Perna et al., 2008; Watanabe et al., 2015; Himmi et al., 2016; Yang et al., 2022; Seibold et al., 2022) or on ambrosia beetles but for different purposes (Li et al., 2018; Jiang et al., 2019).

In this study, we investigated how several tree species, varying in their tolerance to flooding, may influence attacks and colonization of ambrosia beetles under simulated flooding conditions. To this aim, we first exposed eight tree species (four in the order Fagales and four in the order Rosales) to flood-stress, and then we counted the emerging adult beetles and used X-ray tomography to evaluate host selection patterns (i.e., entry holes), colonization success (i.e., percentage of branched galleries and offspring production), and potential damage to the tree (i.e., volume of the log occupied by galleries) by native and exotic ambrosia beetle species. This study aids in our understanding of how extreme precipitation events associated with climate change could facilitate the success of invasive ambrosia beetles and improves our understanding of their attack patterns and colonization success in various tree species. We also provide insight into which species of ambrosia beetles can be expected to have major impacts on trees following flooding events.

2. Materials and methods

2.1. Study site, experimental design and treatments

The experiment was conducted in spring 2022 in a broadleaf-dominated forest located in north-eastern Italy (Riserva Naturale Integrale Bosco Nordio, Chioggia Veneto, 45°07'30" N, 12°15'47" E) (Fig. S1A,B). This forest represents the remains of old native forests that covered the upper part of the Adriatic coastal area and is dominated by holm oak (*Quercus ilex* L.) and manna ash (*Fraxinus ornus* L.). Pedunculate oak (*Quercus robur* L.), wild linden (*Tilia cordata* Miller), stone pine (*Pinus pinea* L.), and white poplar (*Populus alba* L.) were the most common secondary species.

Eighty potted trees (diameter at the base 3.0–4.5 cm, approximate height 3.5 m) were bought from a tree nursery located in Ferrara, Emilia Romagna, Italy (44°39'52" N; 12°07'38" E). The trees belonged to eight species, four in the order Fagales (i.e., *Carpinus betulus* L., *Corylus avellana* L., *Q. ilex*, and *Q. robur*) and four in the order Rosales (i.e., *Malus sylvestris* L., *Prunus armeniaca* L., *Prunus avium* L., and *Pyrus pyraster* L.), which were selected because they i) are widespread in forest, urban or orchard settings, ii) belong to genera that are known to be susceptible to ambrosia beetle colonization (Cavaletto et al., 2021; Viloria et al., 2021; Monterrosa et al., 2022), and iii) show different degrees of flood tolerance, even though this info was not available for all the selected species. In particular, some species are known to be susceptible to flooding, showing low (i.e., *C. betulus*, *C. avellana, M. sylvestris*) to very low (i.e., *Prunus avium*) ability to tolerate it, while others are more tolerant (i.e., *Q. robur*) (Glenz et al., 2006). Potted trees were brought to the experimental site in April and were located in five clearings corresponding to different blocks (Fig. S1B). At each clearing, 16 potted trees were positioned, two for each of the eight selected tree species. These two individuals were randomly assigned to one of the two treatments (i.e., control, flooding) and then arranged along the forest edge (Fig. S1C). All potted trees were secured with metal wires to the closest tree to avoid falling and they were irrigated with tap water once per week during the experiment.

Trees used as controls were not subjected to any experimentally imposed stress. This approach allowed us to verify that the potted trees used in the experiment were healthy enough to not trigger ambrosia beetle colonization unless artificially stressed. Flood-stress condition was established using a pot-in-pot system, whereby a pot was first lined with a plastic bag and then a second pot containing a single tree was placed within the plastic-lined pot (Ranger et al., 2023). Flood stress was initiated by irrigating the internal pot until standing water was present around the base of the trees. The flooding conditions were maintained throughout the whole duration of the experiment by refilling the water lost by evapotranspiration.

2.2. Analysis of entry holes, galleries and emerging adults

The experiment started on 26 April 2022, corresponding to the application of flood stress, and lasted for 28 days. Then, potted trees were cut and the portion 20 cm – 1 m from the tree base was divided into two logs of 40 cm (Fig. S2A) which were brought to the laboratory and enclosed in individual rearing chambers (Fig. S2B). Once a week and for five consecutive weeks emerging adults were collected, counted, and then morphologically identified (Gomez et al., 2018) to the species level.

Each log showing signs of attacks by ambrosia beetles (i.e., entry holes) was first heat treated at 105°C for 5 days to kill all eventual beetles still present inside the galleries and then analyzed through X-ray tomography. Tomography analyses were performed using a ZEISS METROTOM MT 1500 industrial computed tomography system located at the Carl Zeiss S.p.A. (Zeiss Quality Excellence Center, Reggio Emilia, Italy). For the scans, five or six logs were wrapped in polystyrene packaging material and placed vertically in the machine carrier so that they were separated one from the other. The logs were then exposed to 10 min of scanning within the Metrotom MT 1500 using an acceleration voltage of 160 kV at 1.5 K resolution (32.6 μm). Image reconstruction was performed using ZEISS METROTOM OS 3.10 software, and image analysis was performed using VG Studio MAX version 2022.1 (Volume Graphics GmbH, Heidelberg, Germany) (Fig. 1A).

Each individual ambrosia beetle tunnel/gallery system was characterized in terms of diameter, volume, and type. For the diameter, a mean value was calculated from 5–10 measures taken at an equal distance for

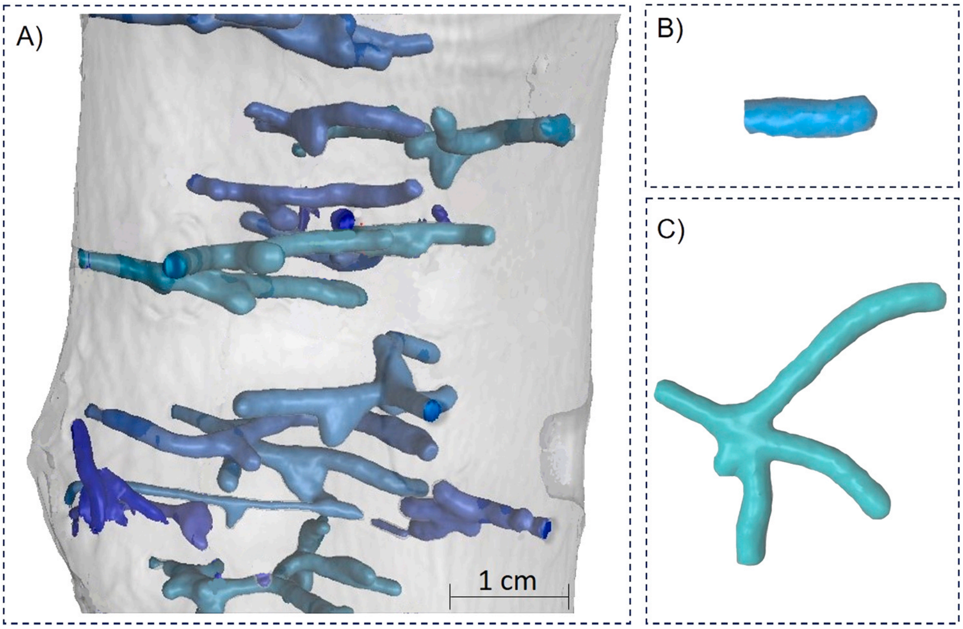

Fig. 1. Stem section from a flood-stressed tree analyzed using X-ray tomography in which ambrosia beetle galleries can be observed (A), and example of a straight (B) and branched (C) galleries.

each gallery (Fig. S3A). Measurements were obtained using the "wall thickness analysis (sphere method)" tool available in the program myVGL, a free viewer app for projects created with Volume Graphics software (VGSTUDIO and VGSTUDIO MAX format). Each gallery was then assigned to one of the ambrosia beetle species colonizing the trees. Diameter classes of entry holes and tunnels were determined after having measured the width of 40 beetles of each species among those emerged from the logs (Fig. S3B,C), an approach established in previous studies to assign ambrosia beetle species to individual tunnels (Rassati et al., 2020; Cavaletto et al., 2021). For the volume of the tunnel, we used the porosity/inclusion analysis tool also available in the program myVGL. The volume was used as a proxy for the damage created by a beetle to the plant. For the gallery type, we classified galleries as straight (Fig. 1B) or branched (Fig. 1C), which can be considered a proxy for unsuccessful vs. successful colonization, respectively (Rassati et al., 2020).

2.3. Statistical analysis

Generalized linear mixed models were used for all analyses. The response variables were: i) the number of entry holes per unit area of the host tree (cm^2) (negative binomial distribution with a ln link function, using as offset the ln-transformed log surface); ii) the percentage of number of branched galleries on total number of galleries (binomial distribution with a logit link function); iii) the number of emerged adults pooled over the five weeks (negative binomial distribution with a ln link function); and iv) the ln-transformed percentage of volume occupied by galleries (Gaussian distribution). The statistical unit was represented by the pooled values of the two logs for each tree. Ambrosia beetle species, tree species, and tree taxonomic order were included as categorical explanatory variables in separate models. The block (i.e., clearing) identity was included in all models as a random factor. Pairwise comparisons among tree species were not carried out as the number of multiple comparisons was judged too high to provide reliable results. All the analyses were performed in R software version 4.1.1 (R Core Team, 2021). Models were fitted using the 'glmmTMB' package (Brooks et al., 2017) and validated using the 'DHARMa' package (Hartig, 2021).

3. Results

3.1. General results

Four ambrosia beetle species colonized the potted trees, namely the native species *Anisandrus dispar* (Fabricius) and *Xyleborinus saxesenii* (Ratzeburg), and the exotic species *Xylosandrus crassiusculus* (Motschulsky) and *Xylosandrus germanus* (Blandford). Attacks were observed on flood-stressed trees but not on control trees. The mean number of entry holes, percentage of branched galleries, number of offspring, and volume occupied by galleries were all significantly affected by the ambrosia beetle species (Table 1). In particular, values of all these four variables were higher for *X. crassiusculus* than for the other three ambrosia beetle species (Fig. 2A,B,C,D). No branched galleries and no offspring were recorded for *A. dispar* (Fig. 2).

3.2. Effect of tree species and tree order on ambrosia beetle entry holes

Tree taxonomic order and tree species significantly affected host selection patterns of *X. saxesenii*, *X. crassiusculus*, and *X. germanus* (Table 2). For tree taxonomic order, significantly more entry holes per unit area were observed in Rosales than Fagales in all cases (Table S1 and Fig. 3A,B,C). For tree species, some general trends were observed in ambrosia beetle entry holes. *Malus sylvestris* was consistently one of the most attacked tree species, whereas *C. betulus*, *C. avellana* and *Q. robur* were among the less attacked ones (Table S2 and Fig. 3A,B,C). However, the preference for *M. sylvestris* was more evident in the exotic

Table 1
Omnibus chi-square tests of generalized linear mixed models testing the effect of ambrosia beetle species on the number of entry holes per cm^2, percentage of branched galleries, number of emerged adults, and percentage of volume occupied by galleries. *df* = degrees of freedom.

	Ambrosia beetle species		
	χ^2	*df*	*p-value*
No. entry holes/cm^2	134.340	3	< 0.001
% branched galleries	11.258	2	< 0.001
No. emerged adults	17.877	2	< 0.001
% volume	72.740	3	< 0.001

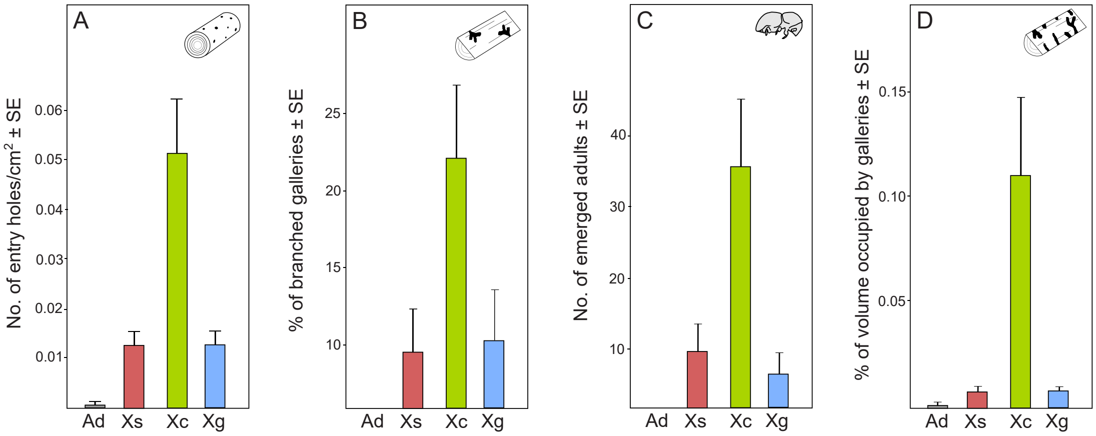

Fig. 2. Mean number of entry holes per cm^2 (A), percentage of branched galleries (B), number of emerged adult beetles (C) and percentage of volume occupied by galleries (D) for each of the species found to attack flooded trees. Species: Ad = *A. dispar*; Xs = *X. saxesenii*; Xc = *X. crassiusculus*; Xg = *X. germanus*.

Table 2
Omnibus chi-square tests of generalized linear mixed models testing the effect of the flooded stressed tree species and tree taxonomic order on the number of entry holes per cm^2, percentage of branched galleries, number of emerged adults, and percentage of volume occupied by galleries for *X. saxesenii*, *X. crassiusculus*, and *X. germanus*. *df* = degrees of freedom.

	Tree species			Tree order		
	χ^2	*df*	*p-value*	χ^2	*df*	*p-value*
X. saxesenii						
No. entry holes/cm^2	44.619	7	< 0.001	12.562	1	< 0.001
% branched galleries	8.008	4	0.091	8.480	1	0.004
No. emerged adults	35.967	6	< 0.001	23.219	1	< 0.001
% volume	36.478	7	< 0.001	20.021	1	< 0.001
X. crassiusculus						
No. entry holes/cm^2	105.540	7	< 0.001	21.237	1	< 0.001
% branched galleries	169.270	6	< 0.001	50.674	1	< 0.001
No. emerged adults	14.291	7	0.046	4.817	1	0.028
% volume	81.165	7	< 0.001	44.144	1	< 0.001
X. germanus						
No. entry holes/cm^2	41.103	7	< 0.001	9.075	1	0.002
% branched galleries	9.416	4	0.052	4.822	1	0.028
No. emerged adults	36.290	7	< 0.001	11.859	1	< 0.001
% volume	45.050	7	< 0.001	19.583	1	< 0.001

X. crassiusculus and *X. germanus* than in the native *X. saxesenii*, for which a high number of entry holes was observed also on *P. armeniaca*. In addition, among Fagales, both *X. germanus* and *X. saxesenii* attacked *Q. ilex* more often than the other three tree species, whereas this preference was less evident for *X. crassiusculus*.

3.3. *Effect of tree species and tree taxonomic order on percentage of branched galleries*

Tree taxonomic order significantly affected colonization patterns in all the three tested ambrosia beetle species (Table 2), whereas the effect of the tree species was significant only for the exotic *X. crassiusculus* (Table 2). For tree taxonomic order, the percentage of branched galleries on the total number of galleries was significantly higher in Rosales than Fagales in all cases (Table S1 and Fig. 3D,E,F). For tree species and *X. crassiusculus*, the latter value was higher in *P. armeniaca* and *P. avium* than in all the other tested tree species (Table S2 and Fig. 3E).

3.4. *Effect of tree species and tree taxonomic order on emerged adults*

Tree taxonomic order and tree species significantly affected offspring production in all the three tested ambrosia beetle species (Table 2), even though the effects were more evident for *X. saxesenii* and *X. germanus* than *X. crassiusculus*. For tree taxonomic order, a higher number of emerged adults was observed in Rosales than in Fagales (Table S1 and Fig. 3G,H,I). For tree species, different trends were observed in different ambrosia beetle species (Table S2 and Fig. 3G,H,I). For the native *X. saxesenii*, the highest number of adults emerged from *P. avium* (Fig. 3G). For the exotic *X. germanus*, the highest number of adults emerged from *P. avium* and *M. sylvestris* (Fig. 3I). The exotic *X. crassiusculus* produced a high number of offspring in *M. sylvestris, P. avium* and *P. armeniaca,* but it was also the only ambrosia beetle species for which the highest value was observed for a tree species belonging to Fagales order (i.e., *Q. ilex*) (Fig. 3H).

3.5. *Effect of tree species and tree taxonomic order on volume occupied by galleries*

Tree taxonomic order and tree species significantly affected digging activity in all the three tested ambrosia beetle species (Table 2). Higher gallery volume was again observed in Rosales than in Fagales in all cases (Table S1 and Fig. 4A,B,C). At the tree species level, different trends were observed for the different ambrosia beetle species. Digging activity was particularly high in *P. armeniaca* both for the native *X. saxesenii* and the exotic *X. crassiusculus*, but differences with other Rosales were more evident in the latter ambrosia beetle species (Table S2 and Fig. 4A,B). For the exotic *X. germanus*, the volume occupied by galleries was higher in *M. sylvestris* and *P. avium* than in the other tested species (Table S2 and Fig. 4C).

4. Discussion

Understanding which tree species are more susceptible to ambrosia beetle attacks in a scenario of increasing frequency of flooding events and which ambrosia beetle species can be expected to have major impacts represents a research priority. Using X-ray tomography, our study clearly highlighted a differential susceptibility of eight widespread tree species to ambrosia beetles, including native and exotic species, as well as a higher ability of one of these exotic ambrosia beetles to attack and successfully reproduce in flood-stressed trees. In particular, trees belonging to the order Rosales were consistently more attacked and colonized by ambrosia beetles relative to trees belonging to the order Fagales, and the exotic *X. crassiusculus* showed the highest attack rate and colonization success in flood-stressed trees.

Tree taxonomic order and tree species consistently affected host selection of the native species *X. saxesenii* and the two exotic species *X. crassiusculus* and *X. germanus*. Ambrosia beetle attacks have been reported both on Fagales and Rosales tree species, including those used in this study (Kovach and Gorsuch, 1985; Batt, 2000; Agnello et al., 2017;

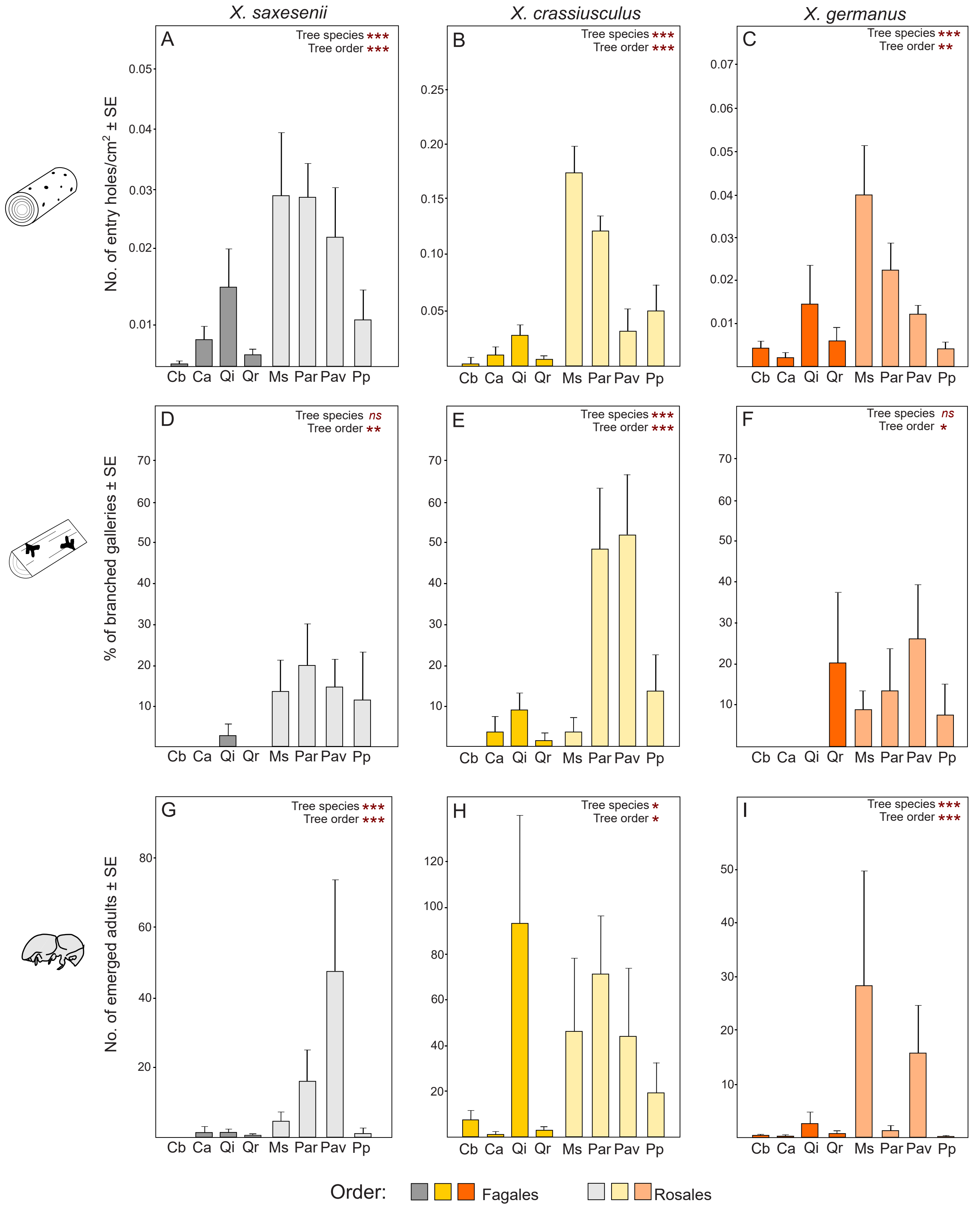

Fig. 3. Effect of tree species and tree taxonomic order on the number of entry holes per cm^2, the percentage of branched galleries, and the number of emerged adults for *X. saxesenii* (A,D,G), *X. crassiusculus* (B,E,H), and *X. germanus* (C,F,I). *P*-values: ns > 0.05; * = 0.05 – 0.01; ** = 0.01 – 0.001; *** = < 0.001. Tree species: Cb = *C. betulus*; Ca = *C. avellana*; Qi = *Q. ilex*; Qr = *Q. robur*; Ms = *M. sylvestris*; Par = *P. armeniaca*; Pav = *P. avium*; Pp = *P. pyraster*.

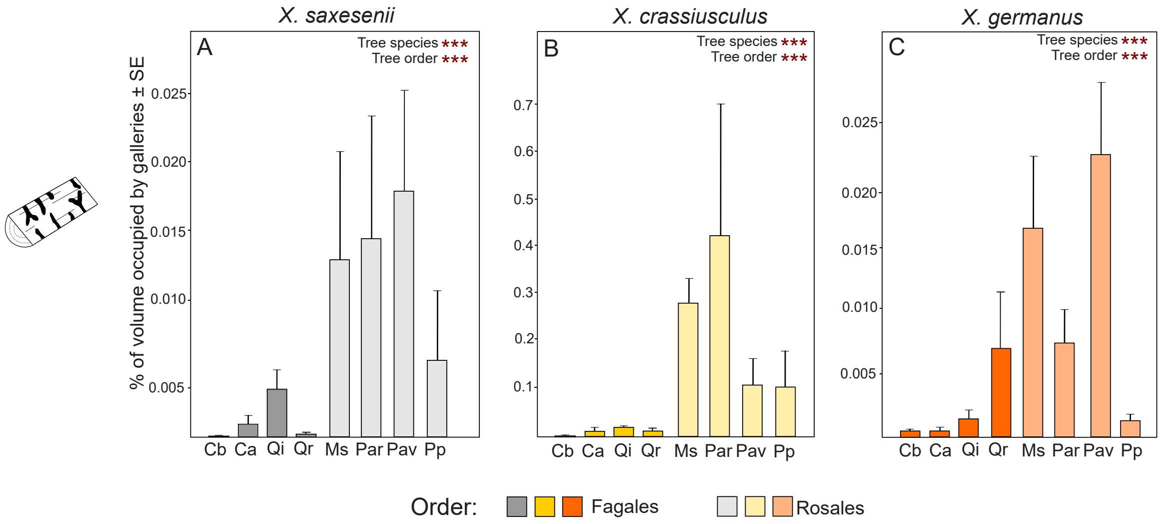

Fig. 4. Effect of tree species and tree taxonomic order on the percentage of log volume occupied by galleries for *X. saxesenii* (A), *X. crassiusculus* (B), and *X. germanus* (C). P-values: ns > 0.05; * = 0.05–0.01; ** = 0.01–0.001; *** = < 0.001. Tree species: Cb = *C. betulus*; Ca = *C. avellana*; Qi = *Q. ilex*; Qr = *Q. robur*; Ms = *M. sylvestris*; Par = *P. armeniaca*; Pav = *P. avium*; Pp = *P. pyraster*.

Monterrosa et al., 2022; Ruzzier et al., 2023), but the higher attractiveness under flood-stress condition of Rosales trees compared to Fagales trees, as well as the differential attractiveness of the single species within the two orders, was not demonstrated so far. Previous studies indicated that the selective host choice of ambrosia beetles can be attributed to a different tolerance of the tested tree species to flooding, which is correlated to varying amounts of ethanol being produced upon stress (Ranger et al., 2015a). The lack of data on the ability of all the tree species tested in this study to tolerate flooding and on their ethanol production under flooding conditions did not allow us to confirm whether the same mechanism can also explain the pattern observed in our study. Nonetheless, the comparison of the attacks counted on tree species for which flooding tolerance is known (i.e., more attacks on the more tolerant *M. sylvestris* than on less tolerant *P. avium*, Glenz et al., 2006) suggested that other non-mutually exclusive mechanisms acting pre- or post-landing on host trees might have contributed to determining the number of attacks. These might include bark thickness and bark roughness (Ferrenberg and Mitton, 2014; Boland and Woodward, 2021; Kuma et al., 2021), amount of attractive or repellent host-derived compounds other than ethanol (e.g., benzaldehyde) released by stressed trees (VanDerLaan and Ginzel, 2013; Byers et al., 2018; Yang et al., 2018; Chen et al., 2021; Romero et al., 2022), as well as self-induced defense responses of the tree (Mendel et al., 2021).

As for host selection, the colonization success of *X. saxesenii*, *X. crassiusculus*, and *X. germanus* was also affected by tree taxonomic order and tree species, even though the effect was generally more evident on offspring production than on percentage of branched galleries. Our results indicated that tree species in the order Rosales are generally more suitable for ambrosia beetle reproduction than those in the order Fagales. A differential reproductive success in potted trees or logs of different species or in rearing media prepared with sawdust of different tree species was already shown for the same and other ambrosia beetle species (Castrillo et al., 2012; Mayfield et al., 2012, 2013; Cavaletto et al., 2021), but in this study we also showed that the most suitable tree species changed depending on the ambrosia beetle species. The exotic *X. germanus*, for example, produced more offsprings in *M. sylvestris* and *P. avium*, the native *X. saxesenii* in *P. avium*, and the exotic *X. crassiusculus* in *Q. ilex* and *P. armeniaca*. The different suitability of the tested tree species to support ambrosia beetle colonization might be related to the potentially different amount of ethanol they produced upon flood-stress. Given that the optimal concentration maximizing growth of symbiotic fungi and thus offspring production can vary among ambrosia beetle species (Cavaletto et al., 2023), tree species producing a certain amount of ethanol might be more suitable than others to support colonization by a certain ambrosia beetle. Another possible explanation can be related to the presence of secondary metabolites in the host trees (Aljbory and Chen, 2018), which act as defensive compounds that might reduce the success of ambrosia beetles by inhibiting the growth of those fungal and bacterial mutualists having fundamental nutritional and defensive roles (Hofstetter et al., 2015; Cambronero-Heinrichs et al., 2023). The clear effect on ambrosia beetle microbiome of rearing media prepared with sawdust of different tree species seems to support this hypothesis (Ibarra-Juarez et al., 2018). However, so far only a few reports have compared the antioxidant and antimicrobial capacities of different tree species. It is known, for example, that *C. betulus* has higher antioxidant power than other species of Fagales (Tálos-Nebehaj et al., 2017), which might explain the very low attacks and colonization success we observed on this tree species. A different nutrient content in host tissues of different tree species (André and Ponette, 2003) may also affect fungal growth, and in turn, colonization success. Finally, plants are generally colonized by a diverse endophytic community that might be affecting ambrosia beetle colonization as certain endophytic microbes are known to protect plants against herbivore consumption (Breen, 1994; Omacini et al., 2001).

X-ray tomography analysis also confirmed that the mismatch between entry holes and branched galleries in ambrosia beetles can commonly occur in nature (Cavaletto et al., 2021; Mendel et al., 2021). The generic olfactory and visual stimuli indicating a potential host tree (Cavaletto et al., 2020; Ranger et al., 2021) might lead adult females to land on non-suitable hosts (Yamasaki et al., 2023); on these hosts the beetles can start digging galleries but then leave before laying eggs if wood tissues do not support growth of symbiotic fungi (Biedermann et al., 2009; Cruz et al., 2018; Biedermann, 2020). Thus, an attractive host can become a non-suitable host, or vice-versa, a less attractive host can become a highly suitable host (Mendel et al., 2021). Patterns that we observed for the exotic *X. crassiusculus* on *M. sylvestris* (high number of entry holes but low number of branched galleries) and *Q. ilex* (low number of entry holes and branched galleries but high offspring production), respectively, are examples of the first and the second mechanism, respectively. However, the lack of data on the ability of all the tree species tested to tolerate flooding does not allow us to confirm whether the observed mismatches can be linked to tree tolerance to flooding. A mismatch was also observed when comparing the number of entry holes and the number of branched galleries with the percentage of volume occupied by galleries. This indicated that potential damage on trees caused by beetle digging activity could also occur on hosts that are less suitable for ambrosia beetles. Whether the tree can tolerate this damage and survive after the attacks or not, as suggested for short-flooding events (Reding et al., 2021), requires further investigation.

In general, the exotic *X. crassiusculus* was by far the most aggressive and successful species, as evident by the higher number of attacks, percentage of branched galleries, offspring, and volume occupied by galleries compared to the other three ambrosia beetle species. We can hypothesize that the observed trend for the attacks is related to a possible higher population density of *X. crassiusculus* at the experimental site. All four ambrosia beetle species analyzed in this study are known to attack flood-stressed trees (Ranger et al., 2015a; Tanasković et al., 2016; Prathapan and Hiremath, 2018; Reding et al., 2021), but the attack density of different ambrosia beetle species was shown to vary depending on the study site and thus likely on their population density (Reding et al., 2021). For the other variables, the observed trend might be explained by a general higher ability of the exotic *X. crassiusculus* to colonize and reproduce in flood-stressed trees or might indicate that a different intensity or duration of the flood-stress is required by the other ambrosia beetle species to create the optimal conditions inside wood tissues that can increase their colonization success.

5. Conclusion

Climate change due to anthropogenic activities will inevitably augment the frequency and intensity of flooding events, which in turn will lead to increased attacks by those ambrosia beetles that are associated with stressed trees. Our study demonstrated that tree species belonging to the order Rosales that are commonly used for fruit production are more likely to be attacked and consequently potentially damaged by ambrosia beetles compared to tree species belonging to the order Fagales that are commonly present in forest areas. In addition, we highlighted that the exotic *X. crassiusculus* might benefit more than the other species of ambrosia beetles from the increasing frequency of flooding events, potentially becoming a pest species in those areas where this phenomenon will become more common. Future studies should evaluate whether the trend we observed in this study can also be considered valid for other climatic regions and different ecosystems. This study was carried out in a forest area where the microclimate and the tree species composition might have affected the presence and the reproductive success of the different ambrosia beetle species, and it would be important to investigate whether other ambrosia beetle species might become more aggressive and more successful in colonizing stressed-trees in other contexts. Additionally, the validity of our conclusions can be partially limited by the low number of replicates used for each tree species; a more extensive experiment including more replicates for each selected tree species could allow to strengthen the results obtained in our study. Further studies could also focus on other tree species in the same taxonomic orders, to determine whether they show the same trends or not. Finally, we showed that X-ray tomography can be considered a reliable method that can allows for the precise reconstruction, quantification, and measurement of gallery development, also aiding our comprehension of the mechanisms underpinning ambrosia beetle host selection and colonization processes.

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CRediT authorship contribution statement

J.C. Cambronero-Heinrichs:Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **C.M. Ranger**:Writing – review & editing, Supervision, Conceptualization. **E. Scabbio**:Visualization, Methodology, Investigation. **D. Rassati**:Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition, Conceptualization. **G. Santoiemma**:Investigation, Formal analysis, Data curation. **A. Battisti**:Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **G. Cavaletto**:Methodology, Investigation. **F. Meggio**:Writing – review & editing, Supervision, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122106.

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