Action D1.
Analyses of data and samples, evaluation
and optimisation of techniques

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Deliverable: Main pathways driving insect and symbiotic fungi introduction

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Summary

We studied *Xylosandrus compactus* and *X. crassiusculus* genetic structure using a mitochondrial marker to understand their invasion history in Europe. After sequencing native and invasive specimens collected in different parts of the world, we only found one haplotype for *X. compactus* in Europe, also found from individuals sampled in Shanghai. This suggests a single introduction from the native area, maybe in Italy, followed by a spread to other European regions. This is supported by the study of the taxonomical structure of *X. compactus*' associated fungal community. Indeed, out of the 6 taxa identified in Italy whose records were limited to native areas or areas of introduction of *X. compactus*, 5 were recorded in *X. compactus*' native area in Eastern Asia. For *X. crassiusculus* the situation is more complex. We confirmed the existence of two differentiated clusters, with only one detected in Europe so far. We found four haplotypes in Europe, two of which were found exclusively in Europe. Two of the European haplotypes were found in the native area, one in Shanghai and the other in several localities in Japan. We thus hypothesise that there were several introductions from native areas, followed by invasion from European localities. The presence of shared haplotypes between Europe and Shanghai for both species suggests that the region of Shanghai could be a main source of invasions. We hypothesise that both species invasion is mainly human-mediated, probably through ornamental plant trade, known to be the biological invasions' main pathways worldwide.

We also performed species distribution modelling on both species. Our analyses showed that *X. compactus* has not been reported in all potentially suitable areas yet. Its current distribution in Europe is localised, whereas our results predicted that most of the periphery of the Mediterranean Sea and most of the Atlantic coast of France could be suitable. Outside Europe, our results also predicted Central America, all islands in Southeast Asia and some Oceanian coasts as suitable. For *X. crassiusculus*, the models could not be used for predictions. We hypothesise that this result could result from pooling together the two clusters in the analysis instead of performing a SDM on each cluster separately.

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1. Introduction

Biological invasions are one of the main threats to biodiversity worldwide, and their number has been increasing steadily in the last decades. Invasion scenarios can be diverse, whether human-mediated or unassisted, through unique or several introductions, with only a few or many founders. Understanding where an invasive species comes from and how it disperses after establishment is critical for management.

Xylosandrus crassiusculus and *X. compactus* are two ambrosia beetles native from Southeast Asia. They are known invaders worldwide and share apparently similar invasion histories. Both have been detected outside of their native range more than one century ago in Madagascar before spreading to continental Africa and later in the New World. Both species were recently reported from Europe, where they were first detected in Italy, *X. crassiusculus* in 2003 [1] and *X. compactus* in 2011 [2], before being detected in France in 2014 and 2015 [3], respectively. *X. crassiusculus* was then detected in 2016 in Spain [4] and 2017 in Slovenia [5], whilst *X. compactus* was detected in 2019 in Greece [6] and on the island of Majorca in Spain [7]. Like other ambrosia beetles, their ecological characteristics tend to favour invasion. They live in galleries dug in wood but feed exclusively on their fungal symbiont. Indeed, before leaving the maternal galleries, the females load spores from their fungal symbiont in a specialised structure called mycangium, which they will cultivate in their own galleries as a food source for their offspring. We thus expect the insect and the symbiotic fungi's invasion pathway to mirror each other. This feature allows them to attack a broader range of host tree [8], which is a major reason for their success as invaders [9]. They are also commonly associated with a non symbiotic fungal community, whose study could help give insight into the beetles' invasion pathways. Xylosandrus crassiusculus and X. compactus both originated from subtropical areas and succeeded in invading tropical and subtropical regions in a first step. However, both are now established under temperate and Mediterranean climates. *X. crassiusculus* is now established as far North as South Canada [10] and was intercepted several times in the Netherlands during the last decade [11].

Our first goal was to study both species' main introduction pathways using their genetic structure (for a full analysis, see the deliverable "*Xylosandrus* spp. distribution in Europe and population genetic structure"). To do so, we sequenced mitochondrial and nuclear DNA (using RAD sequencing) on specimens from a maximum of localities, including samples from non-European regions, to infer the origin of both species' invasion. We also studied the main pathways driving *X. compactus* introduction based on associated fungal community taxonomical structure using High Throughput Sequencing on insect captured from galleries on different hosts at the Circeo National Park. Our second goal was to identify the regions where these invaders still do not occur but could be at risk, to understand the invasion pathways, to anticipate their expansion and help develop preventive management strategies. To do so, we estimated both species potential geographical distribution according to present and future climate using species distribution modelling (SDM) [12].

2. Main pathways driving insect introduction

For a more in-depth analysis of *Xylosandrus compactus* and *X. crassiusculus*' genetic structure, see the deliverable "*Xylosandrus spp.* distribution in Europe and population genetic structure".

Xylosandrus crassiusculus

Worldwide

The sequences obtained from the 183 studied individuals raised 49 different haplotypes worldwide named, corresponding to 8 haplogroups (A – H). A phylogenetic analysis using MEGA software showed that the haplotypes could be grouped in 2 clusters (cluster 1 corresponding to haplogroups D to F and cluster 2 to Haplogroups A to C). Our results are in line with the literature.

The 12 haplotypes found in invaded areas belonged to either haplogroup A (all A2 except A3 and A11) or E (E1 – E3) (Figure 1 and 2). The other haplogroups were only found in native areas. As opposed to what we observed with *X. compactus*, some localities in the invaded area had more than one haplotype, such as Podsabotin (Slovenia). We even found haplotypes from both clusters in two Hawaiian localities, Poamoho Ridge and Manoa Valley, suggesting that they might have been invaded several times from different sources. We hypothesise that this invasion happened through plant importation, which is coherent because Hawaii relies on importing plants and parts of plants, in which insects can sometimes slip from border controls.
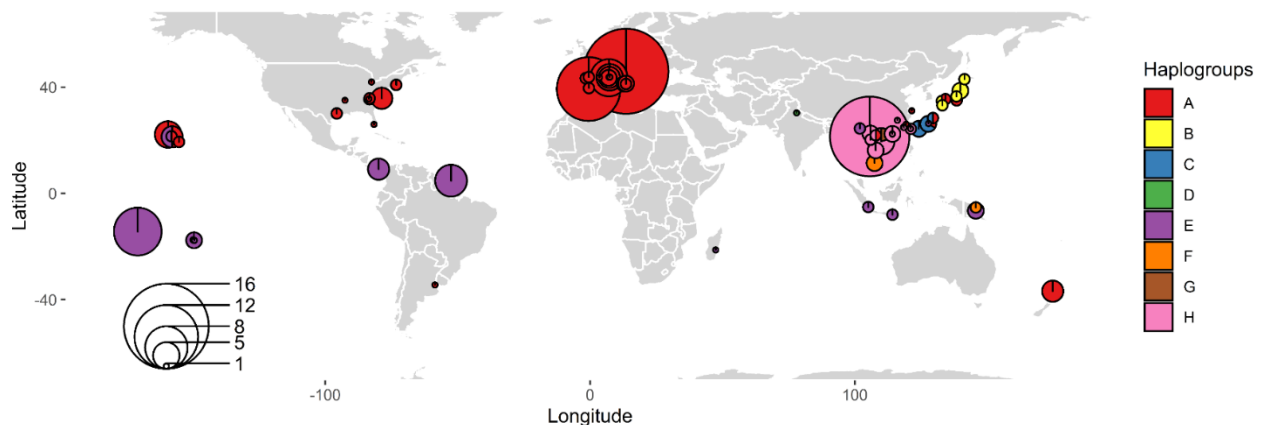
Figure 1: Map representing the different mitochondrial haplogroups sequenced for Xylosandrus crassiusculus.
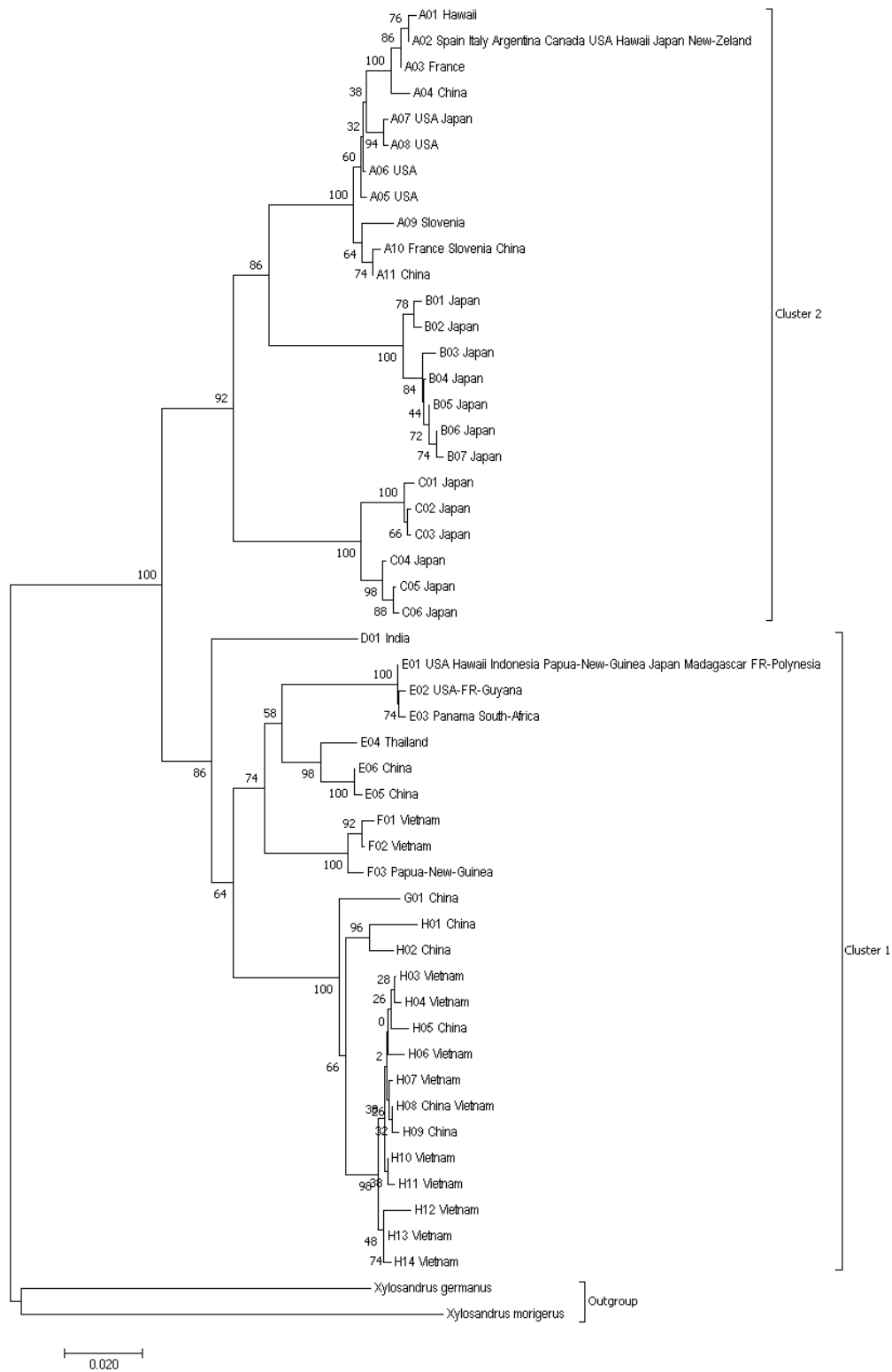
Figure 2: Xylosandrus crassiusculus' evolutionary tree using the Neighbor-Joining method.

Focus on Europe

We found four haplotypes in Europe, all belonging to cluster 2, haplogroup A (Figure 3).

The haplotype A2 is widespread worldwide and was the only one found in Spain and Italy. It is also present in several localities in *Xylosandrus crassiusculus*' native area in Japan, which could be the origin of this haplotype's invasion in Europe. *X. crassiusculus* was detected in Italy in 2003 and Spain in 2016, suggesting that Italian populations spread to Spain. Another possible explanation would be that Italy and Spain's invasions resulted from multiple introductions from one or several origins.

Figure 3: Map representing the distribution of Xylosandrus crassiusculus' *haplotypes found in Europe a) worldwide and in b) Europe.*

The haplotype A10 was found in Western France and Shanghai. We hypothesise that a part of *X. crassiusculus*' introduction in Europe might come from Shanghai, through ornamental plant trading.

The haplotype A9 was found exclusively in Slovenia. This could be the result of a separate introduction from an area that we did not sample or a haplotype that we failed to detect. However, as it coexists with A10, which is present in France, this does not seem like the most straightforward explanation. Another explanation would be that it has the same origin as A10 but somehow did not reach Western France, possibly due to random effects when shipping ornamental trees.

The presence of 4 haplotypes in Europe and only one in Italy contradicts our hypothesis that Italy was the first area invaded and acted as a source for further invasions in Europe.

Xylosandrus compactus

Worldwide

The mitochondrial DNA sequences obtained for the 102 studied individuals raised 9 different haplotypes worldwide named A1 – A5 and B1 – B3, three of which were found in invaded areas. A phylogenetic analysis using MEGA software showed that they could be grouped in 2 clusters (A and B). Haplotype A1 was found in Europe and Shanghai, A2 exclusively in the Americas and the Pacific Islands and B3 in Uganda, India and Vietnam (Figure 4). The haplotypes A1 and A2 were highly similar (99.8%), differing by only one substitution. The other haplotypes were exclusively found in native areas.

The haplotypes A1, A2 and B3 were each detected in several very distant places, indicating that the invasion was probably human-mediated and that the same origin might have invaded several regions. However, every locality studied in the invaded area showed only one haplotype, suggesting that each invasion probably occurred from a single introduction with low genetic diversity. This is in line with our expectations as *X. compactus* allows for invasion with a single-mated female.

No genetic variation was found in the Americas and the Pacific Islands, where only the haplotype A2 was found. This could result from multiple invasions from the same source, bridgehead effect and invasion from already invaded areas, or a combination of both. *X. compactus* can disperse more than 8km between two flying seasons [13], which would be enough to disperse actively between close sites (e.g. between our sampling sites in Hawaii for example). Between remote places, the spread of the A2 haplotype was mainly probably human-mediated through international trade. The similarity between the haplotype A1 and A2 is surprising, suggesting a recent divergence and maybe a common origin of these two invasions.

The haplotype B3 was found in Ouganda and two localities in *X. compactus*' native area, India and Vietnam, suggesting that it might originate from one of these localities.
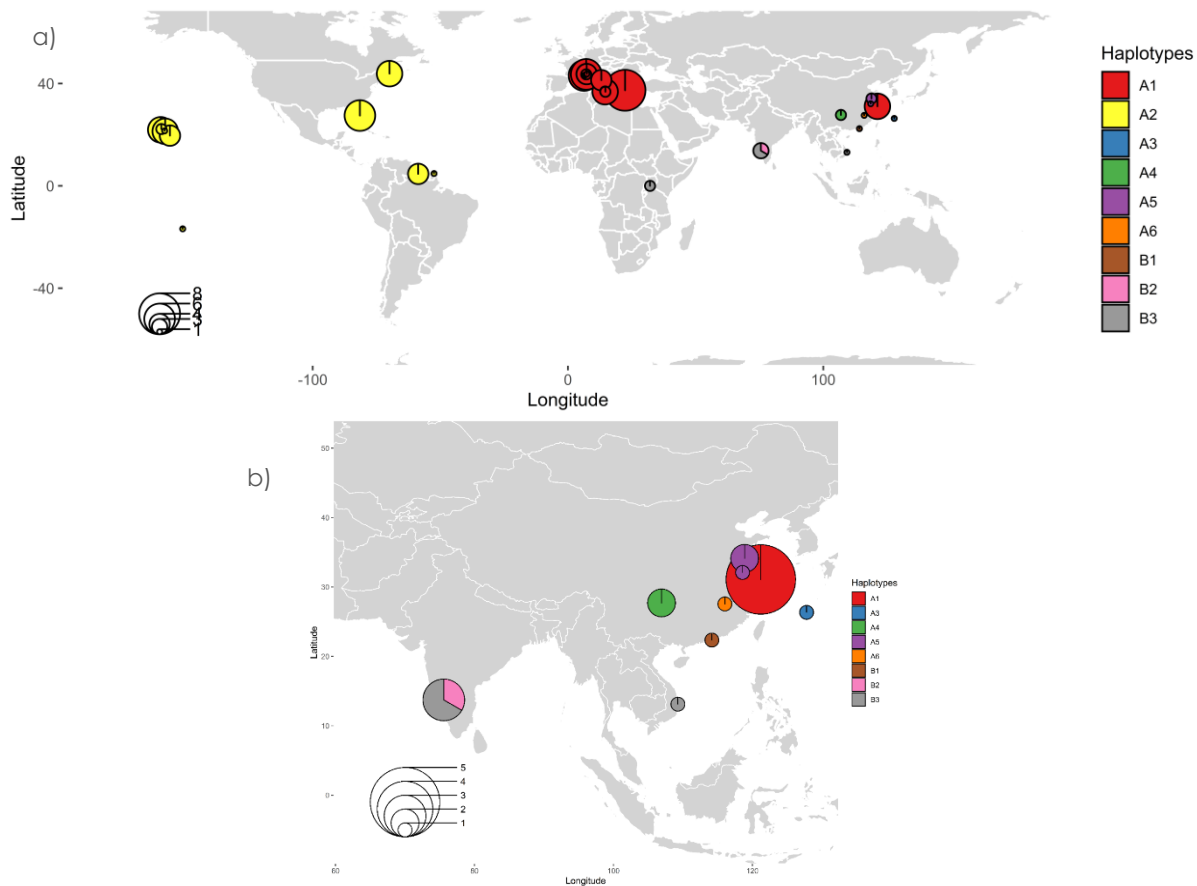
Figure 4: Map representing the different mitochondrial haplotypes sequenced for Xylosandrus compactus a) worldwide and b) with a focus on Asia.

Our first RAD sequencing results showed the same pattern, with two clusters, high similarity between specimens from the localities of the haplotypes A1 and A2, and specimens from Shanghai falling in the same group as the European ones (Figure 5).

To conclude, cluster A is present in China and invaded Europe, the Americas and the Pacific. Cluster B is present in India and Vietnam and invaded at least a part of Africa (Ghana, Uganda). We have no information on the other genetic structure of the other invasive populations in Africa, so we cannot tell whether cluster B is the only one present in Africa.
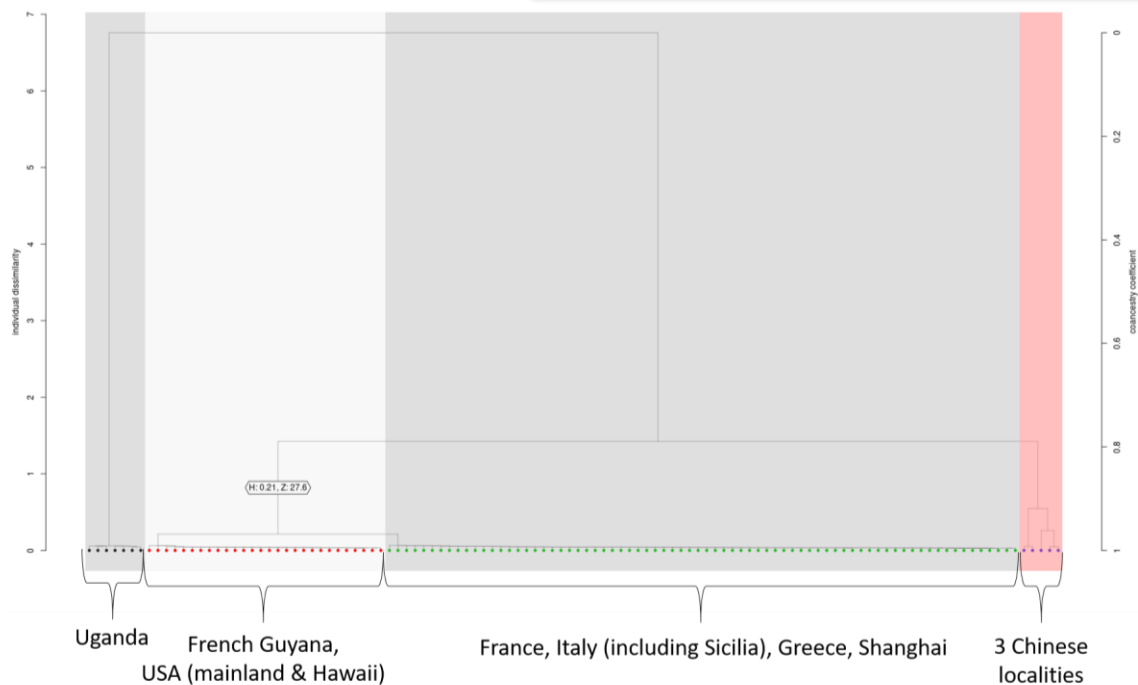
Figure 5: Xylosandrus compactus' *evolutionary tree according to RAD sequencing results.*

Focus on Europe

No genetic diversity was found in Europe, where only haplotype A1 was found despite a dense sampling in France, Italy and Greece. In the native area, this particular haplotype was only found in Shanghai, suggesting that *X. compactus*' introduction in Europe might come from Shanghai through ornamental plant trading.

X. compactus was found in Mallorca in 2019, but we did not manage to get specimens. It was also found in Corsica during summer 2020, and we are still waiting for the sequencing results. We expect to find haplotype A1 and confirm a plausible unique introduction event in Europe followed by a geographic expansion in several Mediterranean regions.

Based on associated fungal community taxonomical structure

The results reported in this deliverable are extracted from Morales et al., (2021)[14] in which the taxonomy and functionality was analysed of the fungal community associated with the ambrosia beetle *Xylosandrus compactus* invading the Mediterranean maquis in central Italy. The fungal community was analysed by mean of High Throughput Sequencing (HTS) of rDNA amplicon libraries from total DNA extracted from the bodies of adults captured from galleries on different hosts at the Circeo National Park.

Six taxa were identified whose literature records were limited to native areas or areas of introduction of *X. compactus* other than Europe. These species' distribution is showed in Table 1 and mapped in Figure 6.

Five over six taxa were recorded in eastern Asia [14,15], in the native area of *X. compactus*, where the same haplotype found in Europe, A1, was prevalent, supporting the hypothesis above formulated that EU population of the insect was introduced from eastern Asia.

Four of these five taxa were also recorded in the Americas, including Hawaii, considered an area of introduction of the insect, where the A2 haplotype was exclusive.
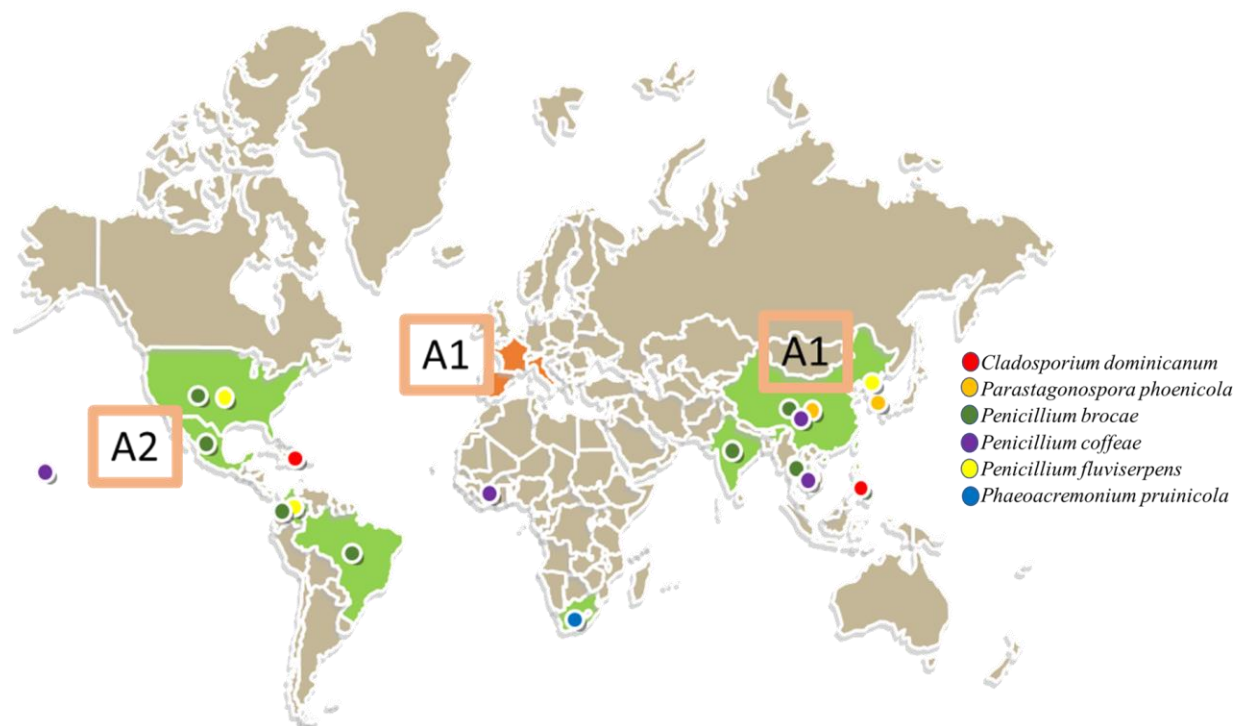
Figure 6: Distribution according to current literature of the records of 6 fungal taxa found associated with adults of X. compatus *in the Mediterranean maquis of the Circeo National Park (Italy), and whose detection represent the first record for Italy (and EU).*

Table 1. Taxonomic position, life strategy, occurrence and recorded hosts/substrate for each of the sixty-four fungal species identified by HTS analysis (from Nguyen et al., 2020; Morales-Rodriguez et al., 2021)

	Fungus	Functional guild	Occurrence	Reported host/substrate	Reported plant host (this study)
OTU	Species				
31, 56	*Cladosporium dominicanum*	saprotroph	Philippines (NA[#] of *Xc*) and Dominican Republic (AoI of *Xc*)	*Citrus* spp. and *Dracaena* spp.	Core-biome
143	*Parastagonospora phoenicicola*	endophyte	New Zealand; China, Taiwan (NA of *Xc*)	*Phoenix canariensis*; *Acanthus ilicifolius* (Mangrove plant)	*L. nobilis*
11	*Penicillium brocae*	endophyte	Mexico; Thailand (NA of *Xc*) China, India, Turkey, Brazil, USA, Colombia	*Hypothenemus hampei* coffee berry borer (ambrosia beetle) in Mexico; rice	*C. siliqua*
43, 45	*Penicillium coffeae*	endophyte	Hawaii (AoI of *Xc*); China (NA of *Xc*) Vietnam, Ivory Coast	*Coffea arabica* (main host of *Xc*); *Laguncularia racemosa* (Mangrove plant)	*L. nobilis*; *C. siliqua*
66	*Penicillium fluviserpens*	endophyte	Korea; Colombia; USA	Tomato fruits; *Coffea arabica* (main host of *Xc*)	*L. nobilis*
35	*Phaeoacremonium prunicola*	endophyte/ weak pathogen	South Africa (AoI of *Xc*)	hardwoods	*C. siliqua*

* A= Ascomycota; B= Basidiomycota   ** nd= not determined *** *Xc= Xylosandrus compactus*   ¥ AoI= Area of Introduction   # NA= Native Area according to CABI

3. Current and future distribution

Since the beginning of SAMFIX, *Xylosandrus compactus* was newly observed in Greece [6], Spain (Mainland [16] and Majorca [4]) and Corsica, and *X. crassiusculus* was detected in Western France. It means that the expansion is still in progress. A critical step in invasion management is to assess where they can establish or not, and by which pathways.

Several pest risk analyses have been performed on our two species of the *Xylosandrus* in Europe in the last decade (UK [17], France [18], Slovenia [19]), but they mostly focused on the presence of host species when assessing the species' establishment probability. For monophagous or oligophagous invasive species, the invasion pathways and currently suitable areas can be determined using host species transportation and distribution. However, both *X. compactus* and *X. crassiusculus* are known to have a broad range of hosts [7,20], and more are added to the list as they invade new regions [21]. Hence, managers should not rely on pre-existing host lists as a way to consider an area as unsuitable.

We performed species distribution modelling (SDM) using the MaxEnt algorithm, using worldwide occurrence records for *X. compactus* and *X. crassiusculus* and 126 combinations of 11 environmental descriptors assumed to be potential drivers of *X. crassiusculus* and *X compactus* distributions.

Xylosandrus crassiusculus

Out of the 126 environmental datasets tested in the first step of the analysis, none fulfilled the evaluation criteria for *Xylosandrus crassiusculus*. Consequently, we could not perform ecological niche modelling on this species.

Our first hypothesis to explain this result is that we may have overlooked crucial information when performing SDM on *X. crassiusculus*. According to the literature, *X. crassiusculus* is genetically structured and could be divided into two or more differentiated clades, corresponding to potential cryptic diversity [22,23]. It has been shown that integrating phylogeographical information into SDM can alter the results when performing SDM on different clades of a species [24,25]. Yet, as genetic studies concerning *X. crassiusculus* in different regions of the world did not rely on similar molecular markers, it is not possible at present to determine which clade occurs in a given region. We thus tested the SDM approach at the species level, possibly grouped clades with potentially different ecological features, hence building models with weak predictive power.

The results we showed in the previous section confirmed the existence of these two clusters. Moreover, our preliminary results showed that they look geographically structured, with Cluster 1 in the tropical and subtropical areas and Cluster 2 stretching polewards (Figure 7). We worked on a comprehensive genetic analysis of *X. crassiusculus* worldwide, allowing us to assign some localities to a cluster. Our next step will be to check whether the two clusters have different ecological preferences and then perform a SDM for each clade separately.
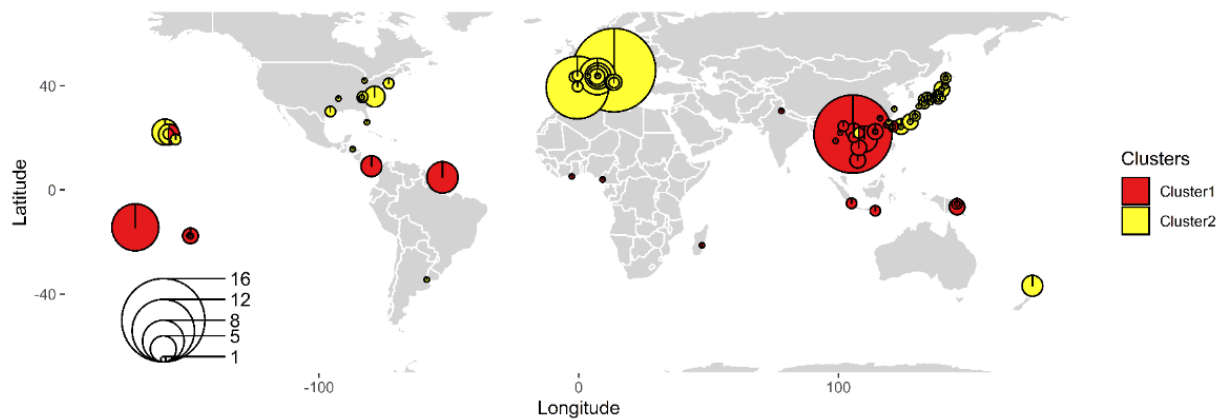
Figure 7: Geographical distribution of Xylosandrus crassiusculus' *two clusters.*

Xylosandrus compactus

Current climate

According to our model, *X. compactus*' distribution in America could expand to Chile and Argentina, all Central America and the Western coast of North America (Figure 8). In Europe, most of the Mediterranean coasts and the UK's westernmost parts are predicted as suitable (Figure 9). Besides Northwest Australia, almost all Oceania and South East Asia is expected to be suitable. This suggests that even in its native area in Asia, *X. compactus* might colonise new areas or islands where it is not present yet. Even though *X. compactus* has proven to be very adaptable, invading different climatic regions in the last century, our models unanimously predicted more than 50% of the world's area as not suitable. Most of these areas are considered arid or semi-arid [26] whether hot (e.g. Sahara or Arabian Peninsula) or cold (e.g. Canada or Andean Mountains).

Our models predicted the Greek province of Peloponnese, the Balearic Island Mallorca and the new occurrence in mainland Spain, where it was reported as established after our study, which suggests that the models have good predictive power.
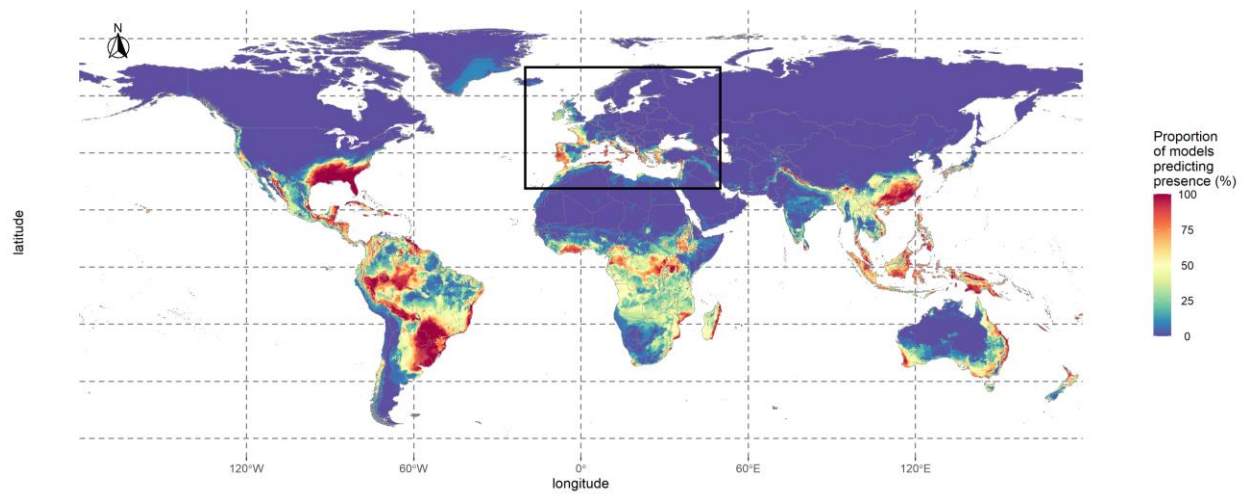
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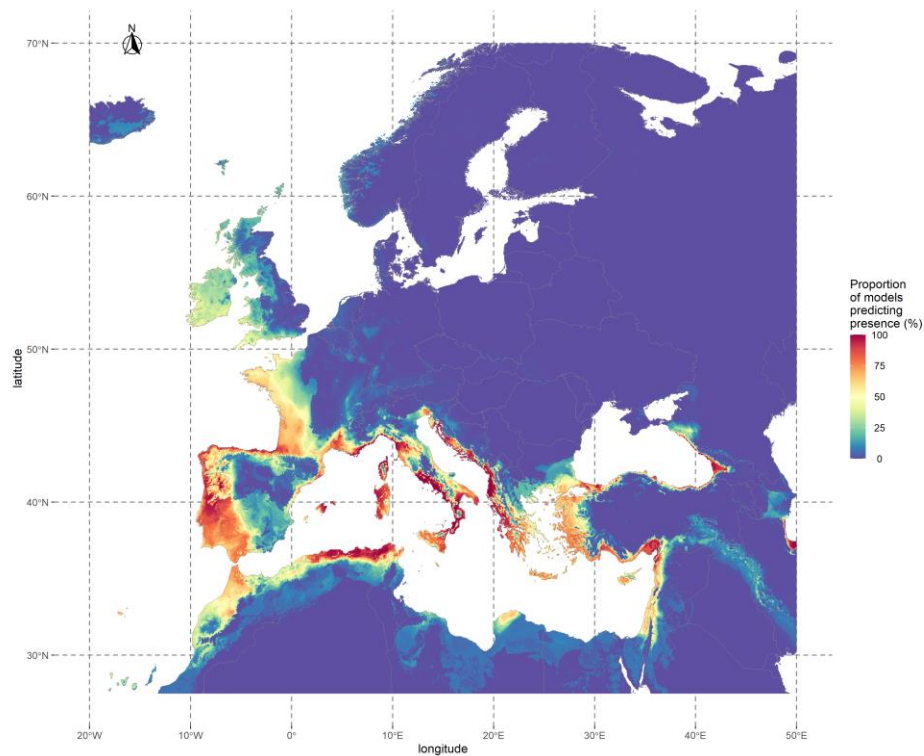*Figure 8: Map showing habitat suitability for* Xylosandrus compactus *under current climate*

Figure 9: Map showing habitat suitability for Xylosandrus compactus *under current climate conditions.*

Future climate

The direction and magnitude of a range shift depend on how climate change will affect the environmental parameters constraining the species' distribution [27]. Being generalist and carrying

its symbiotic fungi to feed on, *X. compactus*' distribution is expected to be mostly dependent on temperature and humidity. However, *X. compactus* lives most of its life in galleries, where wood acts as a buffer, protecting individuals from ambient air temperature and extreme events [28]. The uncertainties of predictions were higher when dealing with future conditions than the consensus obtained under the current climate.

In Europe, the habitat suitability is predicted to increase going North and Northeast, reaching Central Europe, the Balkans and the Black Sea. However, outside the focal area, no new country is projected to become suitable between now and 2050 or 2070 (Figure 10).

Our result relies on environmental parameters to show which areas are suitable for *X. compactus*. This could significantly improve the future pest risk analyses, in addition to being a helpful tool for decision-makers when making policies about trapping for early detection of *X. compactus*. Indeed, our results show that some areas are still free of *X. compactus* even though they are predicted as suitable, today or in the future. We suggest that such areas should be prioritised for early detection strategy, while efforts could be partially relaxed in regions unanimously predicted as unsuitable in the present study.

4. Conclusion

Both species are still spreading through Europe, where they manage to invade several countries in a matter of years. Our models show that – for *Xylosandrus compactus* at least – suitable areas in Europe are not only localised in the Mediterranean area and will probably increase in the future with climate change.

The invasion history of *X. compactus* seems relatively straightforward. We found a low genetic diversity for *Xylosandrus compactus*, with only 9 haplotypes worldwide. The only haplotype found in Europe was present in Shanghai too, suggesting a single invasion in Europe followed by dissemination via active and human-aided dissemination.

Xylosandrus crassiusculus' invasion seems more intricate. We found much more genetic diversity with 49 haplotypes worldwide, divided into two differentiated clusters. Only one cluster was found in Europe, probably originating partly from Japan and China. The presence of 4 haplotypes in Europe and only one haplotype in Italy contradicts our hypothesis that Italy was the first and only area invaded, and acted as a source for further invasions in Europe. The presence of shared haplotypes between Europe and Shanghai for both species suggests that the region of Shanghai could be a main source of invasions, possibly for other non *Xylosandrus* species too.

Although *Xylosandrus compactus* and *X. crassiusculus* have different invasion history, they share similarities. Both species can disperse a few kilometers, which is be enough to disperse actively between close sites but cannot explain their invasion worldwide. Between remote places, their spread was mainly human-mediated, probably through international plant trade.
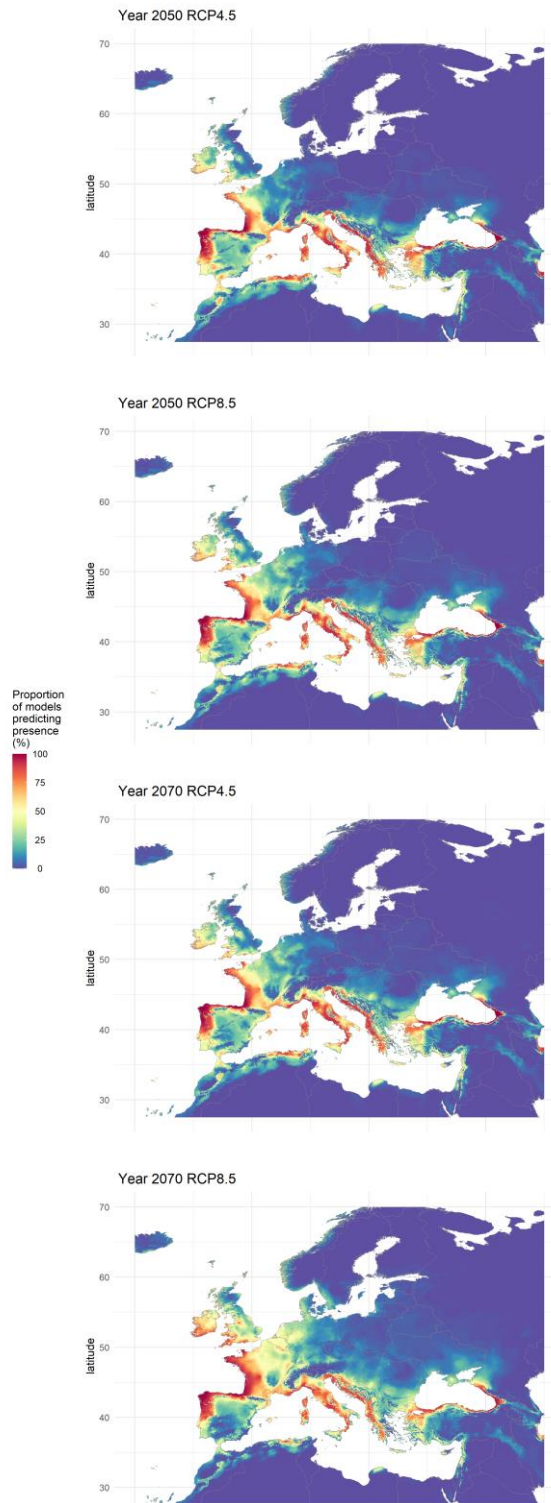
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Figure 10: Maps showing habitat suitability for Xylosandrus compactus under future climate for 2 greenhouse gases concentration scenarios (RCP4.5 and 8.5) and for 2 years (2050 and 2070).

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