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► **To cite this version:**

Thomas Boivin. The Interplay Between Climate Change and Insect Threats in Narrow Mediterranean Forest Habitats. Narrow Mediterranean Forest Habitats. Handbook for the sustainable management and long-term conservation of a narrow endemic habitat type in a limited area of occupancy-The case of the habitat type 9590\* Cedrus brevifolia forests (Cedrosetum brevifoliae)., 2021. hal-04235249

**HAL Id: hal-04235249**

**<https://hal.inrae.fr/hal-04235249v1>**

Submitted on 10 Oct 2023

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# The Interplay Between Climate Change and Insect Threats in Narrow Mediterranean Forest Habitats

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## 6.1. Introduction

Insects represent three-quarters of the described animal species on the planet with about six million known species. There are currently nearly 300,000 known species of plants and they represent the highest biomass on Earth. Plants and insects have coexisted for some 400 million years and their interactions play a key role in the functioning of ecosystems, and more generally of the biosphere (Stam et al. 2014). These interactions can be of a mutualist type, as in the case of entomophilic pollination or protective associations between trees and ants (Bronstein et al. 2006). They can also be antagonistic since about half of the known insect species are phytophagous, i.e. they consume different parts of the plants (leaves, stems, roots, conductive vessels, flowers, fruits or seeds). They can do so in a more or less selective way and with very different intensities depending on the species. In forest ecosystems, insect phytophagy has consequences for trees from the individual to the community levels. Indeed, insect outbreaks can slow down the growth or kill trees (Kanat et al. 2005), and the consumption of reproductive structures (pollen, flowers, seeds) can interfere with reproductive success and consequently with the regeneration processes of a tree population (Boivin et al. 2019). Interspecific differences in plant exposure to phytophagy can also influence the rate of ecological succession in plant communities (Strauss and Zangerl 2002).

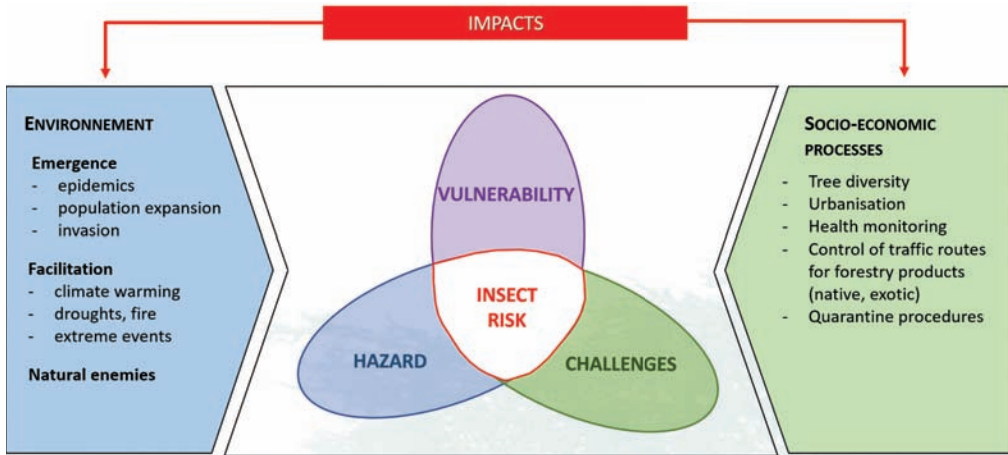
## 6.2. The concept of entomological risk in forest ecosystems

### 6.2.1. *Interactions between trees and phytophagous insects and forest ecosystem services*

Forests produce timber, firewood and a wide variety of non-timber forest products. They also play a protective role against soil erosion, landslides, they help maintaining the water balance at the landscape level, and they have an important recreational role. Forests are increasingly expected to play a mitigating role in the context of global warming through carbon sequestration (in the ecosystem and in wood products) and through substitution for fossil resources. Consequently, phytophagy of forest insects and its consequences for forest health generate strong interferences with human activities and forests ecosystem services. Insect damages can lead to quantifiable economic losses and/or losses in amenity and amenity value associated with decreases in ecological and social services provided by forests (Nagelheisen et al. 2010). In Europe, over the period 1950-2000, damage caused by phytophagous insects accounted for 8% of the total damage caused by forest disturbances (about 2.88 million m<sup>3</sup> per year between 1958 and 2001), and in North America, large bark beetle outbreaks over the past 20 years have been the leading cause of major forest disturbances, ahead of hurricanes, tornadoes and fires, with average costs exceeding USD \$2 billion (Grégoire et al. 2015). Insects specialized on tree reproductive structures can reduce the supply of high quality seeds for ornamental plants, reforestation, afforestation and conservation in established orchards and selected tree populations (Boivin and Auger-Rozenberg 2016). There are also health risks to humans and domestic animals associated with the expansion and spread of urticating insects (e.g. processionary caterpillars) in visited and exploited forests (Moneo et al. 2015).

### 6.2.2. *Definition of the risk associated with phytophagous insects in forests*

The risk of phytophagous insects for forests is defined as the combination of a hazard, the vulnerability of tree populations and the ecological and socio-economic challenges associated with insect impacts in forest ecosystems (Fig. 6.1).



**Figure 6.1:** Definition of interacting risk and impacts of forest insect damages

The *hazard* is determined by the existence of populations of insects at low abundance (endemic phase) likely to show progressive or eruptive population growth (epidemic phase) in response to favourable environmental factors (e.g. resource abundance, climatic conditions, droughts, disturbances). Hazard can also be determined by the probability of invasion of one or more exotic insect species. Insect hazard analysis can be done by mapping: (i) areas of potential presence by modelling ecological and climatic niches, (ii) areas of presence carried out by observations and monitoring of established populations, or (iii) changing areas of occurrence by observations and modelling of natural or assisted expansion. These approaches are based on knowledge of the distribution and abundance of insect species and their impact on trees (e.g. mortality, dieback, growth loss). Adaptive processes in insect populations, their ecological impacts in new colonized areas, and the role of biotic interactions (e. g. with natural enemies) in modulating insect dynamics can also be investigated (Liebhold and Tobin 2008). The establishment and updating of lists of alien species (Roques et al. 2009), the development of tools for early detection and prediction of invasiveness potential in native areas (Mansfield et al. 2019), and tools for detection and tracing of invasion routes of invasive alien insect species are essential approaches to biological invasion-related hazards (Hulme et al. 2008).

The *vulnerability* is a change in the level of attractiveness of trees for insects and in the ability of insects to exploit these trees. It is primarily related to levels of fruiting, defoliation, dieback, and tree mortality. Vulnerability of forest stands to phytophagous insects is often related to tree size, stand structure and species composition, and stand proximity to human activities. Such characteristics directly influence insect demography and damage intensities to trees. Increased tree diversity can for instance increase the resistance of planted forests to insect pest attacks at different spatial scales through association effects between tree target and non-target species for insects (Jactel and Brockerhoff 2007). Moreover, vulnerability depend on the occurrence of predisposing factors to insect attacks that are generally considered as stress factors for tree. These can be biotic (parasites, pathogens, inter- and intraspecific competition) and abiotic (droughts, heat waves, fires), or a combination of the two (Manion 1981; Jactel et al. 2012).

The *challenge* is linked to the consequences of insect pest damage at the levels of economy (tree species with market value), ecology (diversity and functioning of the ecosystem) and health (transmission of pathogens to trees and species dangerous to human health). The challenges associated with phytophagous insects in forests are the economic or ecological importance of the species of trees attacked, the extent of damage caused by insects or the possibility of entomophilic transmission of highly problematic pathogens (e.g. the pine wood nematode). Such challenges respond to the alteration of ecosystem services related to the supply of forest reproductive material or timber, to the structuring of habitats of patrimonial or ecological importance, and human health issues in exploited, recreational, urban and peri-urban tree areas. Challenge issues can be addressed through links with forest managers, observation and monitoring networks, municipalities and health services. The ability to develop tools for insect population control (biological or environment-friendly) and decision support in control also define these issues.

### 6.3. Phytophagous insect-tree interactions and climate change

Changes in the abiotic environment are likely to directly affect various characteristics of tree populations (e.g. phenology, seed production, growth, mortality). Direct effects of climate are also expected on phytophagous insects whose survival, reproduction, dispersal and distribution are closely related to temperature and precipitation conditions (Bale et al. 2002). In addition, there are indirect effects of the environment on insect populations through alterations of tree health and through responses of insect competitors, facilitators or natural enemies to environmental change. Finally, abiotic changes can indirectly affect tree populations through their direct effects on the abundance and distribution of phytophagous insects. Successive episodes of drought can directly limit tree survival through irreversible physiological alterations (Allen et al. 2010), or indirectly when these conditions weaken trees sufficiently to reduce their ability to resist bark beetles (killing-tree insects that feeds on their host's phloem). This generally limits the resilience of trees, which may prevent them to avoid death before more favourable conditions return (Manion 1981). However, drought may also induce significant changes in the nutritional quality of trees (e.g. water content, carbohydrates, nitrogen) and can trigger the synthesis of antagonistic compounds to phytophagia, particularly in leaves (Jactel et al. 2012). In Spain, a remarkable disruption in the population dynamics of phytophagous insects may have been associated with the impacts of droughts on holm oak (Carnicer et al. 2011).

Climate change also alters the spatial and temporal patterns of interspecific interactions, and in this respect phenological divergences between insects and their host plants can be observed with potentially strong population consequences (Singer and Parmesan 2010). Many forest phytophagous insects affect their host plants only during specific vulnerable periods that often result from drastic changes in the abiotic environment (Rouault et al. 2006). Successive drought episodes can affect directly tree physiology and survival (Allen et al. 2010), or indirectly when higher temperatures and lower tree resistance trigger severe forest insect outbreaks (Durand-Gillmann et al. 2014). However, the interdependence between climate, biotic factors and tree dynamics remains complex to predict. Drought-induced changes in tree nutritional quality (water, carbohydrates and nitrogen contents) or in tree defence mechanisms can limit the development and the damages of parasites (Jactel et al. 2012). Extreme droughts may even be directly involved in the collapse of herbivorous populations at wide scales, but drought can also affect negatively tree physiology and decrease the effectiveness of tree resistance mechanisms to pathogens and parasites (McIntyre et al. 1996).

Fire ecology provides interesting additional examples of the complexity of integrating interdependencies between trees, biotic and abiotic factors. Bark beetle outbreaks and forest fires have jointly increased in extent and severity during the last decades in the USA, raising concerns about their possible interactions (Simard et al. 2011). Bark beetle outbreaks may increase the risk of active crown fire due to the great quantities of dead and ladder fuels that they generate. However, Simard et al. (2011) suggested that risk of active crown fires may not change in the short term but it may rather increase in the decades following an outbreak. Importantly, bark beetles are thus likely to

indirectly affect non-attacked trees through subsequent enhanced fire risks. This clearly illustrates the critical need to integrate the interplay between the abiotic environment, biotic interactions and trees health. This is a major issue with regard to narrow endemic habitats where climate warming is supposed to be a major threat to range-restricted species by shrinking the area of their suitable habitats.

#### **6.4. Interactions between trees, insects and climate in Mediterranean areas**

The Mediterranean basin is a major former glacial refuge that is now considered a hot spot for plant and animal diversity at the inter- and intra-specific levels (Lefèvre and Fady 2016). There are nearly 201 species of woody plants, 100 species of trees (compared to 30 species in the rest of Europe for a surface area 4 times larger) and a high level of endemism (60%, Quézel and Médail 2003). Phytophagous forest insects also show particularly high levels of diversity and endemism in many groups. These are most likely the result of tree biodiversity and endemism, the diversity of habitats available for insects on a single tree and the diversification of insect guilds, particularly for specialists (Boivin and Auger-Rozenberg 2016). Mediterranean forests are at the forefront of the global change effects on terrestrial ecosystems due to the increased frequency and intensity of disturbances (fires, droughts, urbanisation and fragmentation, pest epidemics), compared to other European forest ecosystems (Lefèvre and Fady 2016).

Mediterranean phytophagous insect communities show that they are already affected by global change, however, global change effects and their consequences on tree-insect interactions remain much less documented in Mediterranean areas than in temperate or boreal ones. It is also difficult, if not risky, to extrapolate observations made in northern areas to southern areas. For example, temperature increases in temperate and boreal zones are expected to be more favourable to insects in terms of development and winter survival, while the threshold of lethal maximum temperatures can be reached more quickly in Mediterranean areas (Lieutier and Paine 2016). The effects of increased CO<sub>2</sub> on tree growth are most often always positive in temperate and boreal regions, but they are already largely negative for some tree species in the Mediterranean due to water limitations (Nageleisen et al. 2010). This is therefore likely to affect different groups of phytophagous insects differently. For instance, defoliators may be negatively affected by climate change effects on their host plants as they generally seek for good quality leaves, while bark beetles may be favoured by weakened tree defenses resulting for successive droughts (Jactel et al. 2012). Increased temperatures and drought frequency are expected to make southern and continental parts of Europe less suitable for heat-sensitive species, which is likely to result not only in range shifts to the north, but also in contractions of distribution areas (Netherer and Schopf, 2010). Many projections therefore remain to be made, and such direct and indirect climate effects on both insects and trees make long-term predictions for sensitive Mediterranean forest ecosystems more complex.

#### **6.5. Seed predators and bark beetles, two potentially important insect threats for narrow forest habitats**

Seed predators and bark beetles directly affect tree survival at the embryo and adult stages, respectively. The demographic and evolutionary consequences of their feeding activities in narrow habitats are thus likely to differ from most forms of herbivory which often result in only the partial removal of tissue from individual plants.

##### *6.5.1. Predispersal seed predators*

*General features:* A distinction is usually made between pre-dispersal seed predators that feed on tree reproductive structures (buds, flowers, pollen, fruits, cones and seeds) as long as they remain on their parent plants, and post-dispersal predators that forage for reproductive structures after they have been dispersed. The clumped and conspicuous nature of seeds before dispersal tends to favour specialization in pre-dispersal predators, while post-dispersal seed predators often share generalist habits to forage for an inconspicuous and scattered resource that is often at

low density. Insects are considered the most important animal predators of reproductive structures during the pre-dispersal phase of seed development (Crawley 2014). Seed loss to insects, such as ants, weevils or bruchids, can also reach important levels during the post-dispersal phase (van Klinken and White 2014).

*Damages and impacts:* Conifer predispersal seed predators affects trees' reproductive output in two, possibly cumulative, ways. First, insects' feeding activity on the seed storage organs reduces the amount of reserves available for germination and early development of seedlings (Lesieur et al. 2014). Second, consumption of the seed embryo makes further seed germination impossible. Aside from direct seed consumption, insect attacks can also result in the abortion of the seed-bearing structures or selective abortion of co-occurring seeds (Meyer et al. 2014), a constraint to seed release due to resin spill or seed fusion to cone scale following insect attack (Lesieur et al. 2014), or the introduction of tree pathogens (Luchi et al. 2012). Important concerns arose on the potential impacts of seed predators on endangered tree species with poor natural regeneration success (Guido and Roques, 1996). Similar concerns relate to the potential impact of these insects on the adaptation of natural forest ecosystems to climate change as well as adaptation strategies such as assisted migration and the implications of altered seed productivity. Finally, reforestation and afforestation programs require high quality seeds from selected genotypes that represent high value material, for which the establishment and maintenance of high seed outputs relies on low tolerance for cone and seed damage.

*Management options in narrow habitats:* Protection of cones and seeds from insects is generally a complex task, especially in narrow endemic habitats. This is partly due to the cryptic internal feeding habits of many seed predators that makes them difficult to detect and control, and to the spatial heterogeneity of cones at both tree and stand levels. Predispersal seed predators are essentially controlled within seed orchards and tree stands providing seeds or fruits as food, which share some of the features of an agro-ecosystem but also those of a forest ecosystem. This adds significant complexity in establishing effective pest management programs. Seed orchard managers conduct integrated pest management (IPM) programs aiming at combining all suitable direct (e.g. insecticide treatments) and indirect (e.g. use of natural enemies) techniques to maintain populations below a desired economic threshold, but such procedure are nearly impossible to conduct in protected areas such as narrow endemic habitats. In seed orchards, prophylaxy remain the most easily applicable management practice of seed insects and it may also affect insect densities and hinder population growth in seed orchards. The removal of all cones or fruits at harvest is an effective strategy to reduce local seed predator populations (Turgeon et al. 1994). Alternatively, destruction of unharvested cones or fruits left on the soil surface by tilling and discing the seed orchard floor may contribute to reduce overwintering populations of many pest species. Such prophylactic tactics are likely to prevent the formation of local pest inoculums. This can be particularly useful against species in developmental arrest over several years (i.e. prolonged diapause), and this make new stand infestations only rely on immigration from surrounding areas. When possible, combining the limitation of a local inoculum with the removal of host trees from within a substantial radius of a seed orchard may be thus a major obstacle to seed losses to seed insects. Finally, careful inspection of collected seed lots can prevent or limit long-range dispersal of seed insects at the regional scale, to other countries of the Mediterranean Basin, and beyond.

### 6.5.2. *Bark beetles*

*General features:* Declines in tree populations are usually triggered by repeated droughts and heat waves, but tree individuals can display resilience abilities, which in some cases allow them to avoid mortality and benefit from the return of favorable conditions. One factor driving resilience opportunities is the presence or the absence of biotic aggravating factors such as bark beetles (Durand-Gillmann et al. 2014). Bark beetles commonly feed on cambial tissues of dead, recently wounded and even heavily defended healthy trees. Dispersing adult bark beetles colonize their host tree by boring an entrance hole through the bark. Females dig a tunnel near the cambium where they

lay their eggs, from where developing broods dig their own tunnel by feeding on the phloem. In conifers, tree defense mechanisms against bark beetle attacks involve a system of toxic resin ducts of variable size and number and the synthesis of defensive chemicals to the entrance site. The likelihood of tree survival to bark beetle attacks is closely linked to the interplay between tree's ability to mobilize defense mechanisms and the abundance of attacking bark beetles. Stress factors that weaken tree defenses have been usually associated with the start of bark beetle epidemics (Marini et al. 2012). Drought is particularly prone to increase tree susceptibility to insect attacks and to induce changes in tree's physiology (Netherer et al. 2015). Bark beetles are inherently labile forest insect populations displaying transitions between endemic states, during which they reside in stands at very low densities and kill only a few weakened trees, playing an important role by preparing the substrate for a high diversity of saproxylic organisms. In epidemic states they reach very high densities over large areas and cause high tree mortality at both stand and landscape scales (Kausrud et al. 2011). Knowledge on the impacts of insect epidemics on tree individuals and populations benefited from extensive research, but less attention has been paid to those associated with endemic states. Global warming increases the risk of damage in the Mediterranean basin and of northward extension of some species in current temperate regions. Life cycles of Mediterranean bark beetles display diverse types of voltinism, sister broods and various type of feeding habits (Lieutier et al. 2016)

*Damages and impacts:* During epidemics, bark beetles generally infest trees by a sudden and massive attack, with adverse effects on tree vitality. Attacked trees may initially show no specific symptoms, but the canopy of the trees infested in spring and early summer turn yellow within a few weeks, then reddish and finally dries up completely. In conifers, massive fall of green needles can be observed (Lieutier et al. 2016). Following late summer or autumn attacks, the infested trees can keep green foliage throughout the autumn and winter as canopy symptoms may appear only in the following spring. In these cases, the attack is often discovered months later because absence of symptoms on the canopy does not allow a prompt identification of the infested trees. However, infested plants die within a few months. Insect galleries alter the functionality of the bark tissues (cambium and phloem), which dry out and die in a few months. Tree mortality generally follows exhaustion of tree defenses by associated fungal species and beetle boring activity, and probably involves several factors including various fungal species (Lieutier et al. 2009). Bark beetle epidemics often result from extensive damage both directly, through death of plants, and indirectly through the economic reduction of timber quality due to possible wood discoloration by symbiotic blue-staining fungi. Some species can carry pathogenic fungi to living trees. Severe mountain pine beetles (*Dendroctonus ponderosae*) outbreaks can lead to up to 90% mortality of tree basal area as observed in North America (Harvey et al. 2014) and European forests and plantations are regularly managed to reduce bark beetle impacts (Kausrud et al. 2011). Bark beetles are thus considered as important disturbance agents in forested areas worldwide, affecting critical processes in forest dynamics and forest services with important subsequent societal issues (Weed et al. 2013; Morris et al. 2018).

*Management options in narrow habitats:* The management of bark beetle populations includes two main approaches that are based on the monitoring of forest stands for early detection of attacks and on the control of new tree infestations. The effectiveness of bark beetle management practices in natural and protected areas varies considerably depending on whether they are implemented in a timely and sustained manner, one objective being the anticipation of epidemic phases. The rapid identification of currently infested trees is essential to maximize efficient management response before bark beetle outbreaks. Phytosanitary survey carried out once or twice a year to assess general forest health conditions and damage caused by main bark beetle species is a first step to decide about management strategies and action priorities. Such survey should be conducted by trained field operators in collaboration with entomologists and scientific institutes, with the objective of controlling the initial infestations to prevent more serious damage. More specific survey

may be carried out in case of rapid increase in population density of target bark beetle species, or after climatic events known to trigger outbreaks. Additional field monitoring activities rely on the assessment of bark beetle occurrence and population density using traps baited with attractive lures. Inferences on the flight activity, phenology and voltinism can be made from trapping. Such information may be used as a decision-making tool for control in sensitive areas if mean catches per trap can be correlated with damage, i.e. infested cubic meters or killed trees (Wermelinger et al. 2004). Efficient trapping techniques may provide estimates of spatio-temporal variation in bark beetle population density. Traps may be baited with commercial specific aggregation pheromones of the most common bark beetle species (see [www.pherobase.com](http://www.pherobase.com)), or with host volatiles (mainly  $\alpha$ -pinene and ethanol) if pheromones are not available.

Control strategies of bark beetle populations in natural forests can be both indirect and direct. Indirect control options primarily rely on silvicultural management including clearing, thinning and pruning. This may help sustainability of forest health and increase forest resiliency of forests to bark beetle infestations and other disturbances. Moreover, all silvicultural practices that reduce excessive tree density likely reduce the vulnerability of individual trees, stands, and forests by strengthening insect resistance mechanisms (Fettig and Hilszczanski 2015). Tree felling and harvesting should be carried out in winter or early spring to reduce the risk of attacks during the spring-summer flight of bark beetles. When felled logs cannot be removed from the forest for several months, log debarking may be efficient in preventing further bark beetle colonization and insect population building. Direct control options mainly rely on sanitation felling, i.e. the felling and removal or treatment of infested trees in order to kill bark beetle brood before adult emergence. If economically feasible, transportation of felled trees to mills allows to kill brood during timber processing. Otherwise, felled trees have to be burned or debarked *in situ* (Fettig and Hilszczanski 2015). The efficiency of sanitation felling depend on its timing relative to the phenology and biology of the target bark beetle species. Tree debarking after adult emergence may be useless and unfavorable to bark beetle predators which usually emerge later than their prey. The target period should be during full larval development, when females have already laid all their eggs. One should however note that, in natural forests, remaining dead or dying trees likely constitute breeding substrate for bark beetle natural enemies. Semiochemicals (aggregation pheromones or host-volatiles) can also be used to employed to attract and concentrate the bark beetle population in a baited trapping device. But such mass-trapping control technique may affect insect population density only with an available efficient aggregation pheromone, which is more likely to ensure high levels of insect captures (several thousands of insects per trap and season). Attractants may also be used on individual trees or small groups of trees or logs (namely trap-trees or trap-logs) to favour and concentrate insect attacks prior sanitation. Trap-trees should be baited and set up vertically to maximize their attractiveness to insects, and then removed or debarked.

## 6.6. Conclusion

One important outcome of this chapter is that the interdependence between the components of global change, tree populations and forest insect populations results in a number of constraints to prediction. These result from the different directions (favourable/ unfavourable effects) and the expected levels (direct/ indirect effects) of interactions, a multi-trophic dimension in which other actors (predators, competitors, facilitators) can modulate tree-insect interactions, and significant variability in the response of hosts, phytophagous insects and associated communities to environmental change. In addition, from the point of view of entomological risk to forests, global change and forest management practices can both play a major role. Global change will mainly act through its effect on the occurrence of hazards (e.g. pest outbreaks, spread of invasive species, higher frequency of storms) and on forest vulnerability (e.g. water stress reducing insect resistance). Forest management will mostly influence forest vulnerability (e.g. thinning to improve the vigour and therefore the resistance of trees to pests) and the impacts of insect damage (e.g. reducing the standing volume of forests by short rotation).



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