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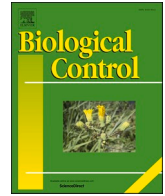
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Conservation biological control in forest: A case study with the pine processionary moth

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HIGHLIGHTS

- More predation by birds on dummy caterpillars in pine plantations when adjacent to hedgerows.
- Positive correlation between dummy caterpillar predation and great tit activity.
- Lower infestation of pine processionary caterpillars in pine plantations adjacent to hedgerows.

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ABSTRACT

In forest ecosystems, the damage caused to trees by insect pests is increasing as a result of global change. Classical biological control has proven effective in managing exotic pests by introducing natural enemies from the pest's native range. For native pests, however, conservation biological control, which aims to improve the habitats and resources for native natural enemies, is more appropriate. While widely studied in agricultural systems, this method has been rarely, if ever, tested in forest. In this study, we aimed to test whether broadleaved hedgerows could improve the control of the pine processionary moth (*Thaumetopoea pityocampa*) in adjacent pine stands by providing a favorable habitat for an insectivorous bird, the great tit (*Parus major*). To this end, we assessed PPM infestations on the edges of pine plantations adjacent to broadleaved hedgerows or mature pine plantation, recorded the vocal activity of great tit using sound recorders, and experimentally measured bird predation using dummy caterpillars. The density of processionary caterpillar nests was lower at the edge of pine stands adjacent to hedgerows than at the edge adjacent to mature pine stands. We showed that bird predation was more frequent on pine edges adjacent to hedgerows. Predation by birds was also positively correlated with the vocal activity of the great tit, the main predator of pine processionary caterpillars in winter. In conifer monocultures, broadleaved hedgerows not only help to control the pest but could also promote biodiversity and protect pine plantations from abiotic hazards, thereby enhancing the multifunctionality of plantation landscapes.

1. Introduction

Forests are facing the increasing impact from insect pests due to climate change (Jactel et al. 2019). This has been well documented for bark beetles (Forzieri et al., 2024; Patacca et al., 2023), but damage caused by tree defoliators are also on the rise (Château, 2024; Ministère des forêts, de la faune et des parcs., 2020; Toigo et al., 2020; FOREST EUROPE., 2020). Higher temperatures can lead to a higher survival rate, particularly in winter, a more rapid rate of development and a wider distribution area, with more frequent or larger outbreaks of forest

defoliators (Jactel et al., 2019; Pureswaran et al., 2018; Robinet & Roques, 2010).

To control these forest pests, several methods have been tested. Insecticides, which were commonly applied at the end of the 20th century, are no longer used, mainly because of their high cost-effectiveness ratio and growing concern about their negative impact on the environment, which has led to a ban on their use in many European countries (Jactel et al., 2021; Liebhold, 2012). Genetic selection of trees for resistance to forest insects has never really been implemented because of the length of the process, the often-negative correlations with growth and the lack of

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durability (Henery, 2011; Woodcock et al., 2018). Forest management strategies can improve pest control while preserving the environment. Mixing tree species is known to improve forest stand resistance to many insect pests, including defoliators (Jactel et al. 2021). However, forest managers are still reluctant to apply it because of the difficulty of managing mixed forests and questions about the value of timber (Klapwijk et al., 2016). Another environmentally friendly solution is biological control. Classical biological control is meant to control non-native pests by introducing natural enemies from the native range of the introduced pest into the invaded area (Cock et al., 2016). As far as native pests are concerned, it is more appropriate to apply conservation biological control. It consists of enhancing the control of native pests by their local (native) natural enemies by offering the latter a greater abundance and diversity of resources and habitats for reproduction or protection against adverse environmental conditions (Holland, 2016). Semi-natural habitats adjacent to crops, as for example hedgerows, can provide natural enemies with resources, shelters and corridors for dispersal (Hatt et al., 2020; Holland, 2016; Montgomery et al., 2020). Hedgerows (or linear woody habitats) can benefit arthropod predators such as ground beetles, rove beetles, insect parasitoids and spiders (Brooks et al., 2012; Morandin et al., 2014), particularly older, well-structured hedgerows (Pywell et al., 2005). Bats can use hedgerows as navigation routes to hunt moth prey in nearby areas, and insectivorous birds can find complementary feeding resources in hedgerows, thus increasing their abundance (Coulthard et al., 2016; Montgomery et al., 2020; de Zwaan et al., 2024). Although few studies have assessed the direct impact of hedgerows on pest control, recent research has shown that their presence enhances the activity of avian and arthropod predators in adjacent fields (Ferrante et al., 2024). Although practical applications of conservation biological control have been widely used in agricultural landscapes, to the best of our knowledge, no published article mentions its use in forest ecosystems. However, this concept could be applied in monospecific plantation landscapes, that are particularly prone to pest damage (Jactel et al. 2021) and where semi-natural habitats such as remnants of mixed forest or hedgerows could be useful for natural enemies by providing complementary resources as well as corridors for dispersal (Marini et al., 2022). To represent a case of conservation biological control in intensively managed forests such as plantations landscapes, hedgerows should therefore 1) provide a favorable habitat for native natural enemies and 2) thus enhance the control of insect pests in adjacent forest stands.

We tested this hypothesis using *Thaumetopoea pityocampa* (Notodontidae, Denis & Schiffermüller, 1775), the pine processionary moth (hereafter referred to as 'PPM') as an example of a forest pest, and the Landes de Gascogne forest as model plantation landscape. Established in the 19th century in south-west France, the Landes de Gascogne forest covers nearly one million hectares and consists almost entirely of monospecific maritime pine stands (*Pinus pinaster* Ait.) (Barbaro & van Halder, 2009). PPM is the main native insect defoliator of pine forest in southern Europe (Roques, 2015). Like other defoliating insects, PPM experiences cyclic outbreaks, approximately every 7–9 years (Li et al., 2015), leading to severe defoliation that can result in important growth losses for trees (Jacquet et al., 2013). It has been shown that PPM makes more damage in pure than in mixed forests, both at stand (Castagneyrol et al., 2020; Damien et al., 2016; Poeydebat et al., 2021) and landscape scale (Samalens & Rossi, 2011), where the moths can easily locate host trees and spread through a continuous, homogeneous, and favorable matrix. The life cycle of PPM has been well documented, as have the various vertebrate predators associated with each phase of this cycle. PPM caterpillars develop and feed on pine needles from late summer to end-winter, while protecting themselves from colder temperatures within their winter nests (Roques 2015). Attacked trees are mainly located at stand edges (Régolini et al., 2014). During this period, specialist predators (the common cuckoo, *Cuculus canorus*; the great spotted cuckoo, *C. glandarius*) and a generalist predator (the great tit, *Parus major*) prey on PPM caterpillars, using adapted physiological

structures or behavior to avoid the caterpillars' urticating setae (Barbaro & Battisti, 2011). At the end of winter, the caterpillars procession along the trunk of infested trees down to the soil where they burry themselves before to enter the pupal stage. The pupae enter into diapause in the ground, for a few months until early summer, or up to several years in the case of prolonged diapause (Salman et al., 2016). The Eurasian hoopoe (*Upupa epops*) is the only bird species capable of feeding on PPM pupae in the soil (Barbaro et al., 2008). Adult moths emerge and fly during the summer, where they are predated by bats, mainly of the genus *Pipistrellus* in the study area, and the Eurasian nightjar (*Caprimulgus europaeus*) (Charbonnier et al., 2014). After mating, females lay their eggs on needles in the crown of pine trees (Uemura et al., 2020). Egg masses and first larval instars (non-urticating) are then preyed upon by tits, including the great tit, the crested tit (*Lophophanes cristatus*), and the coal tit (*Periparus ater*). While PPM provides an abundant food resource in pine plantation landscapes, habitat availability, particularly nest cavities, is a limiting resource for certain predators such as the Eurasian hoopoe, great tits, and bats (Barbaro et al., 2008; Charbonnier et al., 2014; Mänd et al., 2009). Since broadleaved trees offer more natural nest cavities than conifers (Acloque et al., 2023; Larrieu et al., 2012), broadleaved hedgerows could provide nesting habitats for vertebrate natural enemies of PPM. However, the ability of these predators to regulate PPM populations remains to be demonstrated. Dulaurent et al. (2012) showed that PPM infestation at the edges of pine stands was significantly reduced by the presence of broadleaved hedgerows in front of the pine edge. But it was unclear whether this was due to the visual or chemical barrier effects exerted by non-host trees (i. e., the 'Host Apparency Hypothesis'; (Castagneyrol et al., 2014b; Jactel et al., 2011) or the result of a regulation by natural enemies living in the hedgerows (Castagneyrol et al., 2014a; Charbonnier et al., 2014). To better address this question, we chose to focus on a single PPM predator: the great tit.

Great tits can prey on various life stages of PPM, including egg masses (in summer), first larval instars (in autumn), and late urticating larval instars (in winter) (Barbaro et al., 2008). When feeding on caterpillars during the winter, great tits consume only the inside of the body, thus avoiding the urticating setae located on the caterpillar integument (Halperin, 1990). They can prey on caterpillars while they are feeding on pine needles or in their winter nests (Barbaro & Battisti, 2011). Previous studies have demonstrated how great tit populations can rapidly respond numerically to the abundance of a food resource (Carrascal et al., 2012). Pimentel & Nilsson (2007) showed that great tits were more abundant in winter in forest stands with classic life-cycle PPM populations, and more abundant in summer in the Portuguese stands where PPM population exhibits a shifted phenology, with caterpillars present during the summer. At local scale, Barbaro et al. (2013) found that great tit abundance was positively correlated with the number of PPM nests along pine edges during winter, highlighting their ability to adapt to food availability, particularly when other resources are scarce. Great tits are more abundant in broadleaved than in coniferous forests due to the greater availability of nest cavities and food resources during the breeding season (Gosler et al., 2020; Mänd et al., 2009). In pine plantation landscapes, broadleaved hedgerows could therefore supply the great tit with these microhabitats for nesting in spring, while also providing corridors for their dispersal. In winter, the increase in great tit abundance in broadleaved hedgerows could then contribute to the control of PPM in adjacent pine stands, as PPM becomes the main food source during this season. Supporting this hypothesis, a previous study found that great tits were more abundant along pine edges adjacent to broadleaved hedgerows (Castagneyrol et al., 2014a). However, when PPM egg masses were experimentally placed along pine edges, great tits abundance did not affect egg predation during the summer. This lack of effect may be attributed to the availability of numerous alternative prey in broadleaved trees as well as the great tits' preference for larger caterpillar prey during this period (Royama, 1970; Ulfstrand et al., 1981).

In this study, we aimed to evaluate the suitability of broadleaved hedgerows as complementary habitat for great tits in order to improve their predation activity on PPM during the winter in adjacent pine stands. To investigate this case of conservation biological control in forests, we combined field observations of PPM infestations in pine plantations edges located adjacent to or distant from broadleaved hedgerows, recorded great tit activity using sound recorders, and experimentally assessed bird predation using dummy caterpillars. Specifically, we tested the following predictions:

H1: The number of PPM winter nests is lower on the edge of the focal pine stands adjacent to broadleaved hedgerows than on the edge adjacent to mature pine stands.

H2: Great tits are more abundant on the edge of the focal pine stands adjacent to broadleaved hedgerows than on the edge adjacent to mature pine stands.

H3: Bird predation on dummy caterpillars is higher on the edge of the focal pine stands adjacent to broadleaved hedgerows than on the edge adjacent to mature pine stands.

H4: Bird predation on dummy caterpillars is positively correlated with great tit activity in the corresponding pine stand edge.

2. Methods

2.1. Study area

The study was carried out in the “Landes de Gascogne” forest, in south-west France. This vast plantation forest of around 1 million ha, created in the 19th century, is mainly composed of pure, even-aged stands of the native maritime pine (*P. pinaster*), under intensive management. The forest landscape also includes a small number of isolated broadleaved remnants, mainly composed of native oaks (*Quercus robur* L. and *Q. pyrenaica* Willd.) in dry stations, and *Alnus glutinosa* L. along the rivers (Barbaro & van Halder, 2009). Linear broadleaved structures are also present at the edge of maritime pine stands, along roads, forest tracks, or ditches. They have been preserved mainly as property boundary markers and for their amenity value (aesthetics, hunting, mushroom picking, firewood). We defined them as “broadleaved forest hedgerows” (hereafter called “hedgerows”, by analogy with the hedgerows found in agricultural bocage landscapes, Montgomery et al. 2020). In the study, we focused on hedgerows that were mainly composed of *Q. robur* and *Q. pyrenaica*, measuring at least 100 m long, 10 m wide, and 8 m high, with continuous tree crowns.

2.2. Experimental design

To evaluate the effect of hedgerows on PPM infestation and bird predation, we selected 14 focal pine plantations adjacent to a hedgerow on one side and a mature maritime pine stand on the other side. We then compared PPM abundance, bird activity and predation on the two opposite edges (adjacent or not to the hedgerow) of the same focal pine stand. By nesting the studied edges within the site, we sought to improve the robustness of our results, since PPM abundance has been shown vary widely, even at a small spatial scale (i.e., 2 km; Samalens & Rossi, 2011). These 14 focal pine stands were located in a 70,000 ha study area of the “Landes de Gascogne” forest (center coordinates: X: -0.776865; Y: 44.560623). The average distance between study sites was 3.8 km (ranging from 1.7 to 9.2 km). On average the selected hedgerows were 244 ± 34 m long (mean \pm standard error), 14.4 ± 1.4 m wide and 11.2 ± 0.4 m high. The opposite mature pine stands were at least 10 m in height, and the borders between the focal and adjacent pine stands were 245 ± 30 m long (similar to the hedgerow length). The width of the focal pine stands, i.e. the distance between the adjacent hedgerow and mature pine was longer than 200 m, in order to avoid overlapping bird detection by acoustic recorders. Mean pine tree height in focal pine plantations was 7.6 ± 0.6 m, to detect the pine processionary nests clearly and easily reach the crown to expose the plasticine caterpillars. As PPM winter

nests are more often located on South and West facing pine edges to benefit from warmer micro-climate (Régolini et al., 2014), we selected focal pine plantations oriented in these directions. Although it would have been interesting to verify the presence of tits prior to the experiment, we prioritized factors such as hedgerow quality (length, width, height, and tree species), stand orientation, and pine age for the selection of study sites. Consequently, to reinforce the robustness of the experimental design, we chose to increase the number of study sites rather than distribute them along a gradient of great tit activity. As great tits may prefer to feed on seeds in winter (Gosler et al., 2020), we controlled for the landscape composition surrounding the focal pine plantations, ensuring that there was little land cover by crops and urban settings.

2.3. Pine processionary nest monitoring

PPM silky nests were monitored in February 2024, as a proxy for PPM infestation level. Since the number of PPM nests is always higher at the edge of pine stands (Régolini et al., 2014), they were recorded on 30 pines from the first pine tree row. Nests were counted on sunny days by two trained observers using binoculars and observing from two opposite directions (Dulaurent et al., 2012). Nests were counted on both edges of the focal pine plantation, adjacent to the hedgerow or to mature pine stand.

2.4. Evaluation of bird predation

Bird predation rate was evaluated using plasticine caterpillars (Lövei & Ferrante, 2017). We used brown plasticine (Staedtler brand, model 8421-7) shaped to 3 cm in length and 0.7 cm in width. We chose longer and wider caterpillar than those commonly used in other studies in order to better mimic pine processionary caterpillars in their late instar and minimize the likelihood of attacks by other bird species than great tits (Chahbar et al., 2021; Pérez-Miles & Perafán, 2015). Plasticine caterpillar shape and size were standardized using a sugar paste extruder. For the field experiment, it was impossible to directly attach the dummy caterpillars to the crown of a living tree for obvious reasons of accessibility. We therefore developed a specific device. First, 8 caterpillars were glued to a freshly cut maritime pine branch, 1 cm from each other, to mimic a procession of PPM larvae. The cut branch was then fixed perpendicularly to a 4 m long wooden stick (Fig. 2). Finally, the stick was attached vertically along the trunk of a pine tree at the edge of the focal pine stand. The height of the stick was adjusted so that the cut branch with the eight exposed caterpillars was in the middle of the crown of the pine tree. In each of the 14 focal stands, six pine trees (distant at least 15 m apart) on the edge adjacent to the hedgerow were equipped with the experimental device. Similarly, six pine trees were equipped on the opposite side (adjacent to the mature pine stand). In total, 1,344 dummy caterpillars were deployed on 168 trees in early February 2024. We chose this period because PPM caterpillars had reached their final larval stage, during which great tits are the only bird species known to prey on them, while the common cuckoo does not begin its return migration until late February in the study area (Theillout, 2015). Dummy caterpillars were exposed for 14 days, exceeding the period recommended by Lövei & Ferrante (2017), but consistent with studies conducted in the same area (Castagneyrol et al., 2017; Valdés-Correcher et al., 2019). We opted for a longer exposure period with a larger number of caterpillars rather than replicating the experiment over time. This decision was influenced by the logistical difficulties involved in placing caterpillars in the tree crown and by the tendency of bird predation rates to decrease over time, as birds learn to recognize and avoid plasticine caterpillars (Mrazova & Sam, 2018). At the end of the experiment, dummy caterpillars were collected, stored individually in plastic tubes and transferred to the lab. Caterpillars were examined under a magnifying glass. Predation marks were assessed by two trained observers (NP and CT) using a predation mark guide (Low et al., 2014), a reference set of

dummy caterpillars attacked in a previous experiment (Valdés-Corcher et al., 2019), while following recommendations by Lövei & Ferrante (2017). Plasticine caterpillars were classified as having been attacked by birds if at least one beak or claw mark was present. Three types of predation marks were identified (birds, arthropods and mammals), but only bird marks were included in the analysis. We chose to evaluate predation at the procession level (8 close caterpillars) rather than at the individual caterpillar level (as commonly evaluated in the literature; Lövei & Ferrante, 2017) because the latter were grouped on the same branch to mimic a PPM procession and thus could not be considered independent of each other (i.e. pseudoreplicates). We considered that a procession was attacked if at least one of the eight caterpillars showed bird marks during the fortnight of exposure. As six processions were exposed on each pine edge, we used the proportion of attacked to non-attacked processions as the response variable for the statistical models.

2.5. Evaluation of great tits activity

We used passive acoustic monitoring coupled with the BirdNET automated detection algorithm (Kahl et al., 2021) to assess great tits activity. We proceeded as follows. We recorded audible sounds for 30 min each hour during 14 days using AudioMoth recorder devices (Hill et al., 2018). Recorders were deployed during the same period in which plasticine caterpillars were exposed. On each focal stand, one recorder was installed at a height of 2 m at the edge adjacent to the hedgerow, and at the opposite pine edge (Fig. 1). Recorders were set up to start recording 30 min before sunrise and end 30 min after sunset (so between 8 AM and 7 PM in winter in the study area). We selected eight consecutive days, common to all the sampled pine edges, with low levels of precipitation and wind speeds of less than 30km/h. Of the 28 recorders installed, six were unable to collect acoustic data due to technical problems. To maintain the consistency of our sampling design we decided to remove the acoustic data from the opposite pine edge. This resulted into a sub-sample of eight focal pine stands, corresponding to a

total recording period of 704 h (44 h spread over 96 recordings per pine edge).

We used the BirdNET algorithm to identify every great tit vocalizations (songs or calls) in the selected recordings. The default input parameters for BirdNET were used, with a sensitivity of 1.0 and a confidence threshold of 0.1. An overlap of 1 s was chosen to minimize the loss of bird activity detection. In cases of overlapping detections (e.g. one great tit detected between 1 and 3 s and one other between 2 and 4 s), only the first one was retained for analysis. Although bird vocal activity is often considered a territorial behavior for defending territory or mating purpose (Catchpole & Slater, 2003), we hypothesize that this metric is correlated with the time spent on the study site and therefore with the time spent hunting potential prey. Additionally, in winter, great tits can vocalize while foraging in heterospecific flocks (Gosler et al., 2020).

As it is recommended to verify BirdNET identification (Pérez-Granados, 2023), an expert ornithologist (LM) listened a 20-minute subsample of recordings from each pine edge (5 min during the morning chorus x 4 days x 8 focal pine stands x 2 pine edges, resulting in 5 h and 20 min of listening) and identified every great tit vocalization. To avoid misidentification, the ornithologist used a sound bank containing the calls of the great tit and the blue tit (the two most difficult tit species to distinguish in the study area). No activity were counted when the sound of the calls was too low (due to the distance of the audiomoth). By comparing the expert and BirdNET identifications, we were able to determine that BirdNET identifications were over 95% accurate when we selected only the vocalizations for which BirdNET assigned a confidence threshold above 0.31. We therefore applied this confidence threshold to all BirdNET data over the 704 h of recording to obtain a conservative estimate of total great tit activity per pine edge. We then defined two metrics of great tit activity. The “BirdNET great tit activity” was calculated as the number great tit calls or songs lasting 3 s (with no overlap between two detections) identified by BirdNET over the 8 days of recording. The “Expert great tit activity” was calculated as the mean number of seconds per day (during the 5 min listened to) that the great

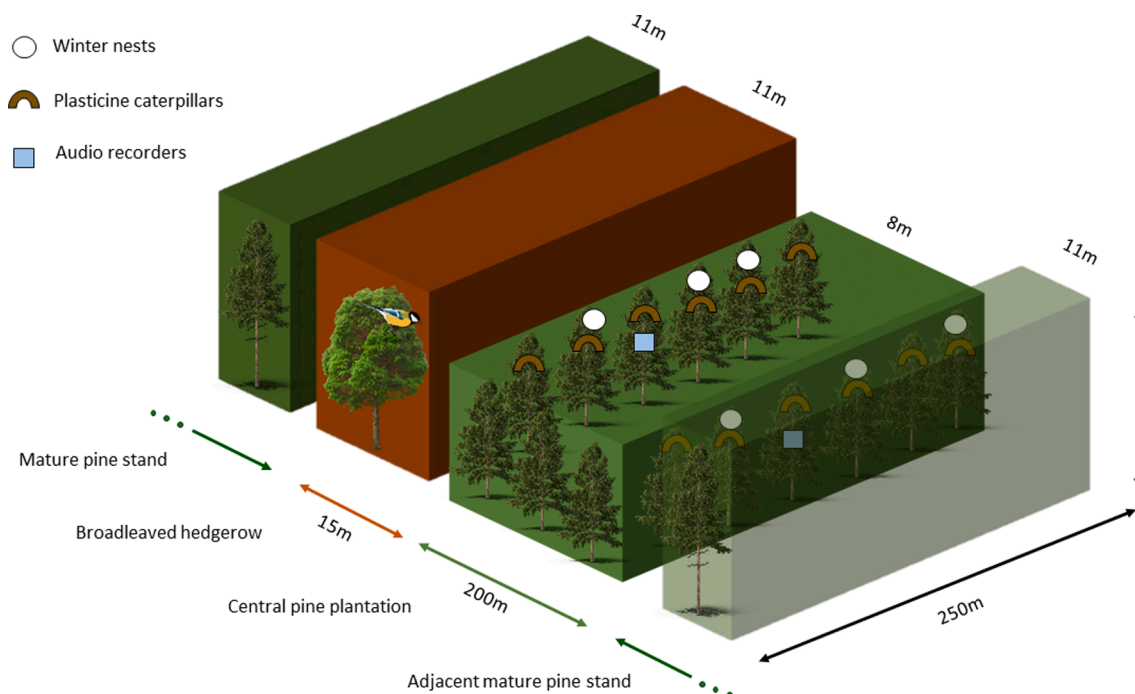


Fig. 1. Experimental design of the study. Data were collected on the number of pine processionary moth winter nests (white dots), predation on plasticine caterpillars by birds (brown caterpillars) and great tit activity (blue square). These three metrics were collected on both sides of the central pine plantation (i: adjacent to broadleaved hedgerow and ii: adjacent to maritime pine stand). Values correspond to mean height, width or length of pine stands and adjacent hedgerows in the 14 study sites. Figure not at scale.



Fig. 2. Pictures of the experimental device: (A) Arrangement of plasticine caterpillars on a freshly cut maritime pine branch (B) Beak mark from a bird on a caterpillar (C) A branch with caterpillars attached to a 4 m wooden stick (D) A stick attached to a 10 m high pine (red circle indicates the position of the artificial branch in the tree).

tits were heard singing or calling. Both metrics were significantly correlated (Fig. S1). This result was expected because BirdNET is particularly effective at recognizing very common species, such as the great tit, as its training dataset includes a greater representation of these species (Funosas et al., 2024). For the rest of the analyses we thus used the “BirdNET great tit activity” because it could be assessed for a longer period of time at each location (44 h instead of 20 min by the expert).

2.6. Data analysis

To address our four different hypotheses, we used Generalized Linear Mixed effect Models (GLMM) and Linear Mixed effect Models (LMM) based on three different response variables (Table 1). Since the focal pine edges were analysed in pairs (adjacent and opposite to hedgerow), we accounted for this pairing by including focal pine stand *Id* as a random effect in all models.

H1 – Effect of hedgerows on PPM infestation level. We evaluated the effect of hedgerows (vs. adjacent mature pine) on the number of PPM nests recorded on edges of the focal pine stands using a GLMM with a Poisson distribution, which is appropriate for count data.

H2 – Effect of hedgerow on great tit activity. We first evaluated the effect of hedgerows (vs. adjacent mature pine) on the great tit activity on edges of the focal pine stands using a GLMM with a Poisson distribution. As the residuals of the model deviate from the assumptions of normality and homoscedasticity we log transformed the variable to fit a Gaussian distribution and tested it with an LMM. This effect was evaluated only on the sub-sample of 8 focal stands on which great tits activity had been evaluated.

H3 and H4 – Effect of hedgerows and great tit activity on predation by birds. The proportion of dummy caterpillars processions predated by birds per pine edge was used as a response variable in a GLMM with a binomial distribution and a logit link function. The effect of hedgerows

(vs. adjacent mature pine) was tested in a first model that included all sampled focal pine stands (H3, n=14). As great tit activity was recorded only in 8 focal pine stands, this explanatory variable was added in a second model (H4, n=8). Due to low statistical power, we decided not to include interactions between explanatory variables. Explanatory variables were scaled and centered prior to modeling to ensure comparability of coefficients (Schielzeth, 2010).

Given that the number of PPM winter nests on focal pine edges could influence bird activity and behavior by serving as a potential food resource (e.g. optimal foraging theory), we included this variable as a predictor in models H2, H3 and H4 (Table 1). All statistical analyses were conducted in R (R Core Team, 2016, version 4.4.0) using the *lmerTest* library.

3. Results

3.1. H1 and H2. Effect of hedgerows on pine processionary moth infestation and on great tit activity

Based on observations of 30 pines in the first tree row, the mean number of PPM nests detected per edge was 14.1, ranging from 1 to 45 nests. The hedgerows contributed significantly to the reduction in the number of PPM nests in the pine edge, with an average of 12.00 ± 3.12 (mean \pm standard error) nests adjacent to the hedgerows compared to 16.29 ± 3.43 nests adjacent to mature pine stand ($P = 0.002$; Table 1, H1; Fig. 3A).

Great tit activity was detected by the expert in 11 pine edges (among 16) including 6 edges adjacent to the hedgerows and 5 edges adjacent mature pine stand. BirdNet identified great tit activity on all the 16 pine edges, ranging from 144 to 1886 activities (i.e: 3 s calls or song). Great tit activity was not significantly higher in focal pine edges adjacent to hedgerows, with 800 ± 194 activities, than adjacent to mature pine

Table 1

Summary of GLMM and LMM testing the effect of the type of pine edge (adjacent to a mature pine stand vs a broadleaved hedgerow) on the number of PPM nests (H1), great tit activity (H2) and predation by birds (H3). For H4 the GLMM tested the effect of both pine edge type and great tit activity on predation by birds. Significant variables are indicated in bold. R2m and R2c correspond to the variance explained by fixed and fixed plus random factors, respectively. Values of n indicate sample size.

H	Response	Predictors	x ²	Df	Coeff. \pm SE	P	R2m (R2c)	n
H1	Number of PPM nests per pine edge	Type of pine edge	9.01	1	-0.31 ± 0.10	0.002	0.02 (0.94)	28
H2	Great tit activity	Type of pine edge	0.29	1	0.29 ± 0.24	0.271	0.05 (0.70)	16
H3	Bird predation	Number of PPM nests per pine edge	0.06	1	0.01 ± 0.01	0.596		
		Type of pine edge	4.22	1	1.92 ± 0.82	0.019	0.24 (0.43)	28
H4	Bird predation	Number of PPM nests per pine edge	1.47	1	0.04 ± 0.03	0.218		
		Type of pine edge	0.29	1	-0.75 ± 0.98	0.440	0.36 (0.36)	16
		Number of PPM nests per pine edge	0.30	1	-0.25 ± 0.53	0.640		
		Great tit activity	5.70	1	1.18 ± 0.50	0.017		

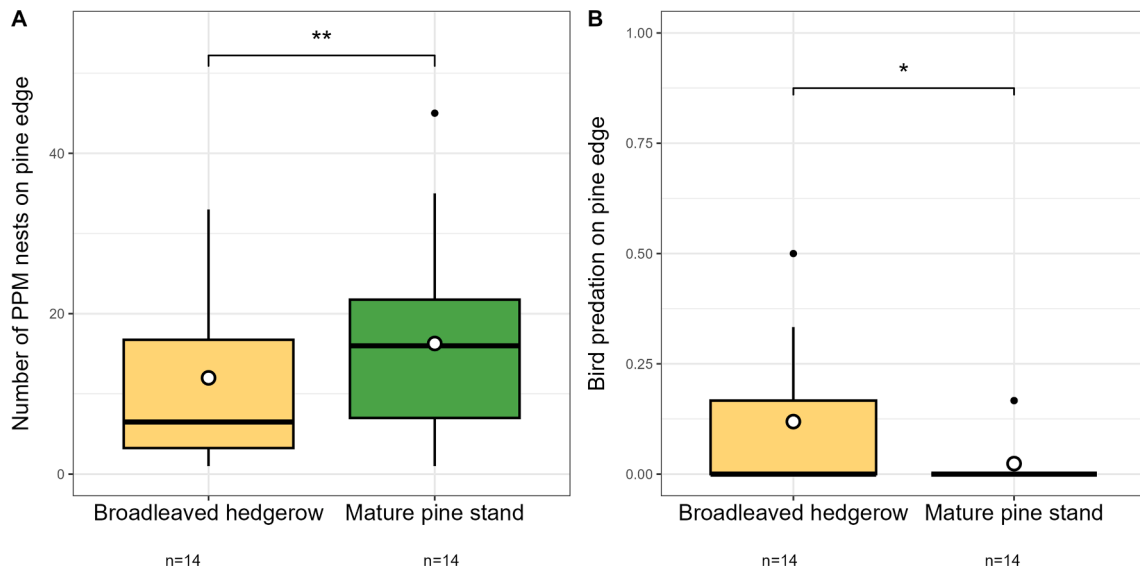


Fig. 3. Box plots showing (A) the number of PPM nests in focal pine plantation edges adjacent to a broadleaved hedgerow vs adjacent to a mature pine stand; (B) proportion of caterpillar procession attacked by birds in focal pine plantation edge adjacent to a broadleaved hedgerow vs adjacent to a mature pine stand. Boxes indicate the lower and upper quartiles. Thick horizontal lines represent the median, white dots indicate the mean value. Values of n below boxes indicate the sample size. Black dots show extreme values. Stars represent significant differences between treatments according to GLMM (Table 1, H1 and H3).

stands, with 717 ± 202 activities ($P > 0.05$; Table 1, H2). The number of PPM nests on edges of focal pine stand did not affect great tits activity nor predation by bird ($P > 0.05$; Table 1, H2, H3, H4). For both models (H1 and H2), the random effect of the focal stand explained an important proportion of the variance observed (Table 1), indicating a substantial effect of spatial variation in the dynamics of PPM and great tit.

3.2. H3 and H4. Effect of hedgerows and great tit activity on predation by birds

Overall, among 168 plasticine caterpillar processions exposed for two weeks, 12 showed at least one bird mark (7.14%). Only 2 processions showed bird attacks on two different caterpillars. Based on the complete dataset (n=28 pine edges), the proportion of processions predated by birds was significantly higher on pine edge adjacent to the hedgerows with 0.12 ± 0.04 than adjacent to mature pine stands 0.02 ± 0.02 ($P = 0.019$, H3, Table 1, Fig. 3B).

When using the subsample of focal pine stands (n=16 pine edges)

where great tit activity had been recorded, the proportion of caterpillar processions predated by birds was still higher on pine adjacent to hedgerow than to mature pine stand but this effect was no longer significant ($P = 0.440$, Table 1, H4) probably due to the low predation rate by birds in our experiment. However, bird predation was significantly and positively correlated with great tit activity, with greater bird predation in pine edges where great tit activity was higher ($P = 0.017$, Table 1, H4, Fig. 4).

4. Discussion

Based on an experimental approach using dummy caterpillars mimicking pine processionary processions on trees at the edge of pine plantations, our study showed that bird predation activity was more intense next to broadleaved hedgerows and that it was positively correlated with great tit activity. We also found that natural PPM infestations were significantly lower on the edges of pine stands adjacent to broadleaved hedgerows. These results suggest that broadleaved

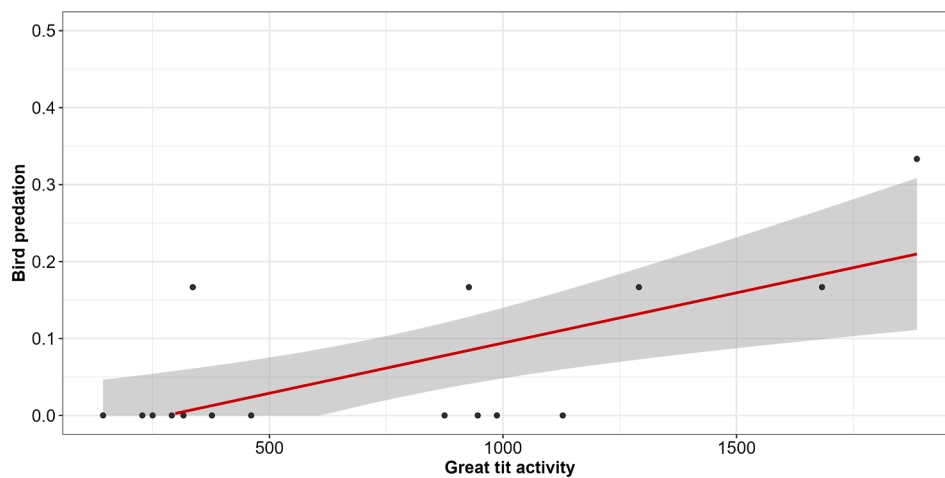


Fig. 4. Effect of great tit activity (as evaluated with BirdNET) on predation by birds (i.e: proportion of plasticine caterpillar processions attacked per pine edge) ($P = 0.017$; Table 1, H4) on a focal pine edge adjacent to a broadleaved hedgerow (n = 8) or a mature pine stand (n = 8). Dots showed the raw data distribution. Shaded areas indicate standard deviation.

hedgerows are likely to provide a suitable habitat for insectivorous birds, and in particular great tit, allowing better control of the pine processionary, which represents a case of conservation biological control.

The role of hedgerows as favorable habitat for insectivorous bird species has already been reported in agricultural landscapes. Heath et al. (2017) found a positive impact of hedgerows on bird species richness and evenness, comparable to the effects of riparian forests. A large-scale study conducted in Ontario (de Zwaan et al., 2024) showed that 44% of bird species (20 out of 45) increased in abundance in landscapes with a higher proportion of hedgerows, while only 11% (five species) were negatively impacted by the presence of hedgerows.

Although bird abundance and species richness increase with the presence of hedgerows in agricultural systems, their impact on pest control for adjacent crops is still debated (Albrecht et al., 2020). In our study, we found an increase of bird predation in maritime pine stands adjacent to a hedgerow. This result is consistent with a recent study using plasticine caterpillars in wheat field, which showed a higher predation rate by both arthropods and vertebrates (birds and rodents) next to hedgerows (33.7%) vs next to grassy margin (17.7%) (Ferrante et al., 2024). In a forest context, Vázquez-González et al. (2024) found an increase in predation by birds on plasticine caterpillars with increasing tree diversity at stand level. The total bird predation rate of 7.14% found in our study is consistent with another study, which found a bird predation rate of 2.5% on dummy caterpillars placed in oaks plots adjacent to pine stands in the same study area (Valdés-Correcher et al., 2019). As previous methodological studies have shown (Lövei and Ferrante, 2017; Nimalrathna et al., 2023), plasticine caterpillars are relevant for comparing predation rate between habitats but underestimate real predation pressure.

We found a significantly lower number of PPM winter nests on pine stand edges adjacent to a hedgerow than on pine edges adjacent to another pine stand. This reduction confirms the results of Dulaurent et al. (2012) in the same forest landscape. However, their study could not disentangle the respective contribution of host tree apparency and natural enemies in explaining lower PPM infestation behind hedgerows. Subsequent research has primarily focused on host tree apparency effects, attributing the reduction in PPM nests to the visual or chemical barrier effects of non-host (broadleaved) species (Castagneyrol et al., 2014b; Jactel et al., 2011). These studies did not report any significant role of natural enemies on PPM predation. Therefore, our study is the first to demonstrate that hedgerows not only can act as a physical or chemical barrier but also provide suitable habitat for natural enemies, such as birds, which can prey on PPM caterpillars in adjacent maritime pine stands. The high variance explained by the random effect in our model suggests a considerable influence of site-specific factors on PPM infestation within the landscape. PPM populations can exhibit substantial variability in winter nest density, even across small spatial scales (e.g., 2 km). This variability may be influenced by factors such as the length and configuration of sand tracks, which provide caterpillars with opportunities to burrow into the soil, or the density and connectivity of pine stands in the landscape (Samalens & Rossi, 2011).

Given the methodological difficulties involved in assessing predation by birds on PPM adults (flying) or pupae (buried in the soil), our study focused mainly on the control of PPM caterpillars by great tits. However, other natural predators of the PPM, such as the Eurasian hoopoe, also benefit from hedgerows and broadleaved woodlands that provide suitable nesting cavities (Barbaro et al., 2008). As a specialist predator, the hoopoe primarily feeds on PPM pupae near the pine stand edges (Barbaro et al., 2008). Bats are also known to prey on PPM flying moths (Charbonnier et al., 2014; Garin et al., 2019). Bats can use broadleaved trees as roosting sites and benefit from the diversity of food resources offered by these habitats (Charbonnier et al., 2016).

According to our results, great tits were not more active on the edge of the focal pine stands adjacent to hedgerows than on the edge adjacent to mature pine stands. This finding contrasts with two previous studies.

Using radiotracking in orchard system, Bouvier et al. (2022) demonstrated that hedgerows were more frequently visited by great tits for foraging than other land type. In the same pine plantation landscape as our study, Castagneyrol et al. (2014a) reported that great tits and blue tits were three times more abundant along pine edges adjacent to hedgerows during the summer than on pine edges adjacent to other pine stands. This discrepancy in locating great tit activity may be attributed to methodological differences, as we used vocal activity to estimate their presence, whereas the previous studies employed radiotracking or point counts (which estimate abundance). The distance between our two recording devices ranged from 200 to 500 m. Great tits have a home range of 1–2 ha in spring (Bouvier et al., 2022), which means that they can fly hundreds of meters from their nest. They can roost and nest on the hedgerow but forage and vocalize within pine plantations, resulting in similar levels of vocal activity on both edges of the pine stand in our case (adjacent or opposite to the hedgerow). This is particularly plausible in winter, when great tits may form mixed-species flocks and expand their foraging range up to 3.9 ha (Gosler et al., 2020; Saitou, 1979). The large variability in great tit activity observed across the study sites (as shown by the part of variance explained by the random effect in our model H2, Table 1) may be partly attributed to differences in hedgerow structure. Although we attempted to standardize hedgerow height as much as possible in our sample sites, larger hedgerows—characterized by greater width and volume—are known to positively influence bird species richness and abundance by providing a wider range of habitats and more abundant food resources (Hinsley & Bellamy, 2000; Kratschmer et al., 2024).

We found a positive correlation between the predation marks on the caterpillars and the great tit activity. However, it is worth questioning whether the increased bird attacks on pine edges adjacent to hedgerows were truly due to great tits. Due to the urticating hairs of PPM caterpillars, great tit is the only known bird species able to predate upon PPM at this time of the year. However, the use of plasticine caterpillars in our study did not allow for the identification of the bird species responsible for the attacks. Other methods under development should help fill this gap. Environmental DNA analysis could facilitate the detection of bird species through saliva traces left during attacks on caterpillars, but this method had only been tested for mammals (Röbler et al., 2020). Camera traps could also be used to record predation events on dummy caterpillars or directly on PPM nests. However, the current technology is not optimized for capturing images of birds, particularly passerine species, as these birds are often too small and fast to activate motion detection systems designed primarily for larger mammals (Schillé et al., 2025). We cannot exclude the possibility that our plasticine caterpillars were not sufficiently similar to those of PPM, potentially attracting other insectivorous birds. Barbaro et al. (2013) found that, in addition to great tits, three other bird species—blue tits (*Cyanistes caeruleus*), short-toed treecreepers (*Certhia brachydactyla*), and chaffinches (*Fringilla coelebs*)—showed abundances correlated with PPM nest densities in winter in south-east France. Although these species do not prey directly on PPM caterpillars, they may have opportunistically tried to prey on the plasticine caterpillars. Contrary to the results obtained by Barbaro et al. (2013) in mountain pine forests, we did not observe any relationship between the total number of PPM nests at stand edges and bird predation or great tit activity. This difference may be explained by the generally higher abundance of PPM nests in our study area, which made this food resource readily available to birds across the landscape. As a result, birds may not concentrate their foraging efforts on the more heavily infested pine edges.

Our findings suggest that great tits can contribute to pest control service by preying on PPM caterpillars. Although the territorial behavior of great tits can limit the number of breeding pairs per hedgerow (depending on hedgerow length), tits may expand their foraging range during winter by forming flocks, thus extending their regulatory effect over a larger area (Bouvier et al., 2022; Gosler et al., 2020). The role of great tits in pest control has been studied in orchard systems. Génard

et al., (2017) estimated that great tits could potentially consume up to 25,000 codling moth larvae per hectare during winter. In similar systems, Mols & Visser (2002) demonstrated that great tits reduced damage to apple crops and increased fruit yield per tree. In the case of PPM, the number of caterpillars consumed by great tits may be lower due to the urticating setae, which can reduce feeding efficiency (Barbaro et al. 2013). However, great tits can also open a hole into PPM nests to gain access to the caterpillars inside, which can lead to an increase in caterpillar mortality by lowering the temperature of the nest.

5. Conclusion

Our study has shown that broadleaved hedgerows help to reduce pine processionary moth infestations in adjacent pine stands. As well as acting as physical or chemical barriers against PPM colonization of pine stands, hedgerows also provide habitat for insectivorous birds, increasing predation pressure in adjacent pine stands. Our results suggest that this predation is primarily exerted by great tits, the most abundant predator of PPM larvae during winter. Broadleaved hedgerows thus represent a case of conservation biological control in forest ecosystems. Long-term studies are nevertheless needed to evaluate the impact of natural enemies associated with broadleaved hedgerows on the successive life stages of PPM, and hence their collective ability to control PPM population and mitigate its outbreaks intensity. In homogeneous coniferous forests, some studies (Pimentel & Nilsson, 2007, 2009) recommend the installation of nest boxes to compensate for the lack of suitable nesting habitats. We believe that broadleaved hedgerows offer a more sustainable solution, simultaneously providing habitat and resources for avian predators and acting as dispersal corridors. Additionally, hedgerows can shelter biodiversity distinct from that found in pine plantations, as well as providing protection against abiotic hazards (Cui et al., 2019; Montgomery et al., 2020). Planting hedgerows of broadleaved species in conifer monocultures could therefore improve the multifunctionality of plantation landscapes.

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CRedit authorship contribution statement

Nattan Plat: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Lucas Moreews:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Laura Schillé:** Writing – review & editing, Software, Methodology, Formal analysis, Conceptualization. **Jean-Baptiste Rivoal:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Hervé Jactel:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2025.105702>.

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