

Arthropod diversity sheltered in *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) larval nests

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Abstract. 1. In pine ecosystems, the role of the larval nests of the Mediterranean defoliator *Thaumetopoea pityocampa* as shelter of other arthropods, was studied for the first time. In Portugal, *Pinus* stands which differed in understorey plant diversity and level of attack by *T. pityocampa* were compared.

2. The arthropod fauna found sheltering inside the nests consisted of 60 species, representing 12 foraging types. Both arthropod richness and abundance were positively correlated with nest size, expressed as larval biomass. Arthropod richness was further positively correlated with understorey plant diversity, while no correlation was detected between arthropod richness and nest density.

3. Spiders accounted for up to 50% of the species richness, while 80% of the individuals collected were either juveniles, or females with brood, implying that *T. pityocampa* nests are used for overwintering and brood care. Seventy-six per cent of the Araneae were nocturnal ground foragers and specialised cryptic hunters, demonstrating the occurrence of indirect interactions among species belonging to different communities, namely ground vegetation layers and forest pine coppice.

4. It was concluded that, in Mediterranean pine ecosystems, *T. pityocampa* nests (i) create habitat diversification and contribute to improve overwintering survival of a wide range of arthropod species; (ii) play a functional role in the food web of pine ecosystems, by promoting indirectly mediated interactions among species from different communities; and (iii) do not contribute to create habitat for sympatric phytophagous arthropods, since contrary to literature references for different types of shelters, 98% of the associated species belonged to foraging types other than *T. pityocampa*.

Key words. Araneae, arthropod diversity, larval nests, pines, *Thaumetopoea pityocampa*, understorey diversity.

Introduction

The pine processionary moth, *Thaumetopoea pityocampa* Denis & Schiffer is a defoliator attaining ecological and economic importance across the Mediterranean region. The larvae are social and feed communally upon the needles located in the vicinity of the maternal egg-batch, around which they spin silk nests. Development takes place throughout the winter

and larvae from different batches sometimes merge, nest size being positively correlated with larval growth and survival (Pérez-Contreras *et al.*, 2003). Nests are believed to afford protection against predation, parasitism and adverse weather conditions, while improving larval thermoregulation and nest temperatures (e.g. Breuer & Devkota, 1990). Additionally, they may enclose food sources to the advantage of the primary shelter maker, co-existing organisms and secondary users (e.g. Fukui, 2001). In pine stands, nest densities of over 200 nests ha⁻¹ may be attained, thus pointing to the role of *T. pityocampa* as ecosystem engineer, that is in creating habitat (Jones *et al.*, 1994, 1997).

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Social larval behaviour is a rare ecological strategy among lepidopterous species (Costa & Pierce, 1997), apparently associated with outbreak traits (Hunter, 1991). Although the role of leaf shelters in fostering interactions within, and among trophic levels has been documented (e.g. Cappuccino, 1993; Cappuccino & Martin, 1994; Kudo, 1994; Larsson *et al.*, 1997; Martinsen *et al.*, 2000; Lill & Marquis, 2004), similar studies of communal tents, built by gregarious, or social lifestyle Lepidoptera larvae, were seldom conducted and mainly focused on natural enemies (e.g. Arevalo, 1992), while disregarding other arthropod nest inquilines.

Indirect interactions among species (Schmitz & Suttle (2001) are important drivers shaping community assemblage and functioning (e.g. Werner & Peacor, 2003). Most studies focus on interactions mediated by plant trait responses and habitat alterations which affect community dynamics (e.g. Cappuccino & Martin, 1994; Jones *et al.*, 1997; Martinsen *et al.*, 2000; Werner and Peacor, 2003). However, within communities the role of inter-specific interactions, indirectly mediated by other species (e.g. Bolker *et al.*, 2003; Ohgushi, 2005) is still poorly documented.

The present work aimed at establishing if *T. pityocampa* communal tents might also benefit the associated syntopic arthropod fauna, as observed for leaf shelter builders (e.g. Fukui, 2001). Furthermore, if the abundance and diversity of arthropods, establishing interactions with *T. pityocampa* nests, would be a function of (i) understorey plant diversity, assuming that arthropod diversity increases with plant diversity (e.g. Altieri, 1999); (ii) nest density, that is, number of nests per area; and/ or (iii) nest size, expressed as larval biomass. The topics studied have not been addressed before.

Material and methods

Stand location, larval nest sampling and nest density

Ten to 15 winter nests of *T. pityocampa* were randomly collected from each one of four pine stands (Table 1), at monthly intervals between October and March 1999–2000, in order to cover the period of *T. pityocampa* larval development from L2 to L5. Ten additional nests were further collected in late March, after nest abandonment by the larvae. Nest density per hectare was determined by counting the number of nests per tree, and either the number of trees in plots of 50 × 50 m, or if not possible, those falling inside three transects of 50 × 3 m each.

Understorey diversity

Plant diversity and species composition were studied by setting up two to four line transects, 20 m long each, separated from the nearest one by 20 m, by placing a measuring tape straight over the vegetation. All plants were identified to species, and the length of the canopy intersected by the tape was measured. The length of the bare ground intersected by the tape was also recorded. Plant diversity was estimated by applying the Shannon Index, using both the number of individuals and the percentage cover of the different species, recorded along the line.

Larval density, biomass and nest size

Nest volume was determined by measuring the three main axes of 15 to 18 nests in total, sampled at the peak of the L2, L3 and L4/L5 larval stages. Larval biomass was determined by sampling 10 to 15 larvae of each instar, randomly collected from different nests, in each stand. Dry larval weight was determined after 48 h drying. Nest biomass was determined by multiplying the number of larvae at each instar by the respective mean larval dry weight.

Arthropod identifications

The nests collected were opened in the laboratory, thus implying destruction, where all arthropods were counted and identified to either family, genus or species, or to operational taxonomic units, OTUs (Sneath & Sokal, 1973). Immature stages were separated and placed in rearing chambers to complete development. The following foraging types were individually assigned to nest dwelling arthropods: parasitoids, predators, omnivorous, fungi feeders, necrophagous and phytophagous. Aranea were further subdivided into seven types: jumping hunters, nocturnal foragers, cryptic hunters, scattered line weavers, orb builders, sheet weavers, diurnal hunters (e.g. Marc *et al.*, 1999; Uetz *et al.*, 1999). Their stage of development was also recorded, to allow for the establishment of trophic relationships.

Diversity indices and statistical treatments

Species richness (*s*) was defined as the total number of arthropod species per nest and stand. The mean number of arthropods

Table 1. Characterisation of the *Pinus pinaster* Ait. stands studied, Portugal.

Stand	Coordinates (N; W) elevation a.s.l. (m)	Number nests ha ⁻¹	Sampled nests	Understorey plant species diversity	
				Mean Shannon Index	Mean richness <i>S</i>
Leiria	39°50'N, 8°57'W; 50 m	55†	203	0.97	6.5
Apostiça	39°30'N, 9°11'W; 35 m	110‡	157	1.23	5.5
Pucariça	39°26'N, 8°04'W; 160 m	38†	131	0.33	1.5
Barrada	39°32'N, 8°15'W; 230 m	397†	160	0.43	2.0

†Monoculture, even aged, approximately 10–15 years old. ‡natural regeneration, mixed with low numbers of *Pinus pinea* L. and *Quercus suber* L.

Table 2. Number and percentage of arthropods from different taxa, found sheltering inside *Thaumetopoea pityocampa* nests and respective feeding groups. Portugal, 1999–2000.

Class/Order	Family/Species	Total and (percentage)	Foraging types	
Araneae		263 (9.74)	Predators	
	Salticidae	57	Jumping hunter	
	Clubionidae	112	Nocturnal forager	
	Gnaphosidae	18	Nocturnal forager	
	Thomisidae	20	Cryptic hunters	
	Philodromidae	27	Cryptic hunters	
	Theridiidae	1	Scattered line weavers	
	Araneidae	1	Orb builders	
	Linyphiidae	1	Sheet weavers	
	Liocraniidae	13	Diurnal hunter	
	Unidentifiable	13		
Chilopoda		3 (0.11)	Predators	
Diplopoda	Julidae	67 (2.48)	Omnivorous	
Blattoidea	Polyphagidae	1 (0.04)	Omnivorous	
Collembola	Entomobryidae	18 (0.67)	Omnivorous	
Coleoptera	Coccinellidae	5 (0.19)	Predators	
	Cryptophagidae <i>Micrambe perrisi</i> Brisout	723 (26.77)	Fungi feeders	
	Curculionidae	5 (0.19)	Phytophagous	
	Dermestidae <i>Dermestes aurichalceus</i> Küster	12 (0.44)	Necrophagous	
	Scolytidae <i>Tomicus</i> sp.	1 (0.04)	Phytophagous	
	Staphilinidae	4 (0.15)	Omnivorous	
	Other	14 (0.52)	?	
	Dermaptera	Forficulidae <i>Forficula</i> sp.	55 (2.04)	Omnivorous
	Diptera	Mycetophilidae	2 (0.07)	Fungi feeder
		Phoridae	19† (0.70)	Necrophagous
Tachinidae <i>Phryxe caudata</i> Rond.		1147 (42.47)	Parasitoid of <i>Thaumetopoea pityocampa</i>	
Hemiptera	Syrphidae <i>Xanthandrus comtus</i> Harr.	9 (0.33)	Predators	
	Aphididae (Lachninae) <i>Cinara</i> sp.	21 (0.78)	Phytophagous	
	Anthocoridae	1 (0.04)	Predators	
	Cercopidae	5 (0.19)	Phytophagous	
	Cixiidae	3 (0.11)	Phytophagous	
	Lygaeidae	1 (0.04)	Phytophagous	
Hymenoptera	Formicidae	13 (0.48)		
	<i>Crematogaster scutellaris</i> Olivier	1	Predators	
	<i>Formica fusca</i> Vikberg	1	Predators	
	<i>Lasius</i> sp.	5	Predators	
	<i>Lasius emarginatus</i> Laus.	6	Predators	
	Braconidae <i>Meteorus versicolor</i> Wesma	27 (1.00)	Parasitoid of <i>T. pityocampa</i>	
	Braconidae <i>Orthostigma</i> sp.	7‡ (0.26)	Parasitoids of Phoridae	
	Ichneumonidae <i>Erigorgus femorator</i> Aubert	6 (0.22)	Parasitoid of <i>T. pityocampa</i>	
	Ichneumonidae (Diplazontinae)	3‡ (0.11)	Parasitoids of Syrphidae	
	Pteromalidae <i>Dybrachis cavus</i> Walk.	212§ (7.85)	Parasitoid of <i>P. caudata</i>	
	Pteromalidae <i>Habrocytes</i> sp.	50§ (1.85)	Parasitoid of <i>P. caudata</i>	
	Lepidoptera	Unidentified larvae	4 (0.15)	Phytophagous

†Collected in March from nests with many dead larvae; ‡emerged from pupae of *Xanthandrus comtus* (Syrphidae); §emerged from pupae of *Phryxe caudata*.

sheltered per nest was also calculated. Species richness and the mean number of arthropods per nest among stands were compared using a Kruskal–Wallis H test, followed by a Mann–Whitney U test, to detect differences between pairs of stands. Spearman's correlation coefficient (r_s) was used to detect variable association.

Results

Patterns of diversity and abundance

A highly diverse arthropod fauna, approximately 60 species of 36 families, representing 12 foraging types, was found in *T.*

pityocampa nests (Table 2). The taxa of the arthropods sheltered in the nests varied seasonally. Omnivorous, predators and fungi feeders were present in higher numbers between October and December, whereas from January to March parasitoids made up the largest percentage (Fig. 1). Arthropods remaining in abandoned nests (Fig. 2) consisted mainly of the parasitoid *Phryxe caudata* Rond. (20–60%), omnivorous millipedes and Dermaptera (10–30%), and arachnids (10–50%).

Spiders accounted for 10% of all arthropods collected, representing 9 families and 11 genera (Table 2). The families Clubionidae (genera *Clubiona* and *Cheiracanthium*), Salticidae, Thomisidae (*Synaema* sp.), and Gnaphosidae, (genus *Aphantaulax*) were the most abundant, accounting respectively for 44%, 22%, 8% and 7% of all specimens. Spiders were found as early as October inside L2 nests and their abundance increased with nest size, until March. Empty nests collected in March were still inhabited by individuals of the genera *Clubiona*, *Synaema* and *Aphantaulax*. Broods of arachnids including adults with egg sac, or juveniles, were found in higher numbers than adults, consequently dominating the arachnid collection (71%). Hunting

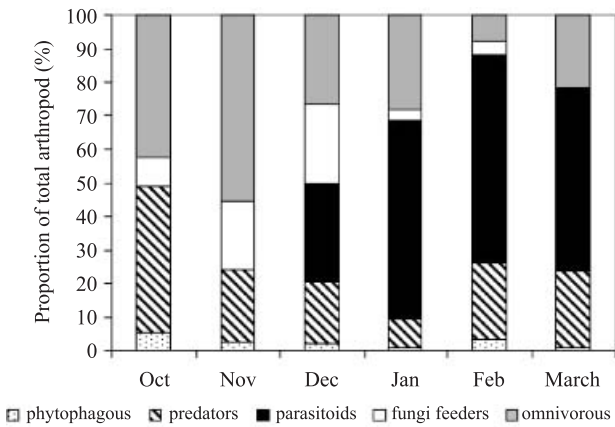


Fig. 1. Variation throughout the winter of the proportions of arthropods belonging to different foraging types, in relation to the total observed in four stands. Portugal, 1999–2000.

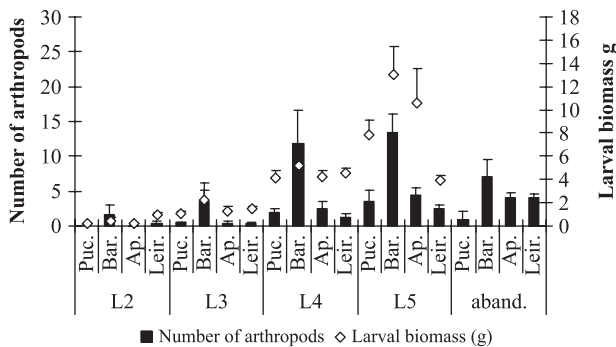


Fig. 2. *Thaumetopoea pityocampa* larval biomass (g of dry weight) per nest ($\bar{X} \pm SE$) (open diamonds) and number of arthropods per nest, for each stand ($\bar{X} \pm SE$) (dark bars). Portugal, 1999–2000.

spiders, including jumping spiders (23%), nocturnal foragers (56%) and specialised cryptic hunters (19%) were the most common foraging types, by contrast with web-building spiders, which reached less than 3% of the total.

Parasitoids represented 44% of the arthropods and were only present from the fourth *T. pityocampa* larval instar onwards. According to location and year, between 75–98% of the specimens were collected either as late larvae, or pupae, which later developed into adults in the laboratory. Apart from *P. caudata*, two other *T. pityocampa* parasitoids, *Meteorus versicolor* Wesma and *Erigorgus femorator* Aubert, were found in lower numbers, while a few species and individuals of Phoridae and Syrphidae, were mostly collected as pupae. The hyperparasitoids *Dybrachis cavus* Walk. and *Habrocytus* sp. emerged in high numbers, parasitising 3% to 16% of the *P. caudata* pupae.

Insect predators were seldom found, consisting of nine syrphids, *Xanthandrus comtus* Harr., mostly in the pupal stage, 13 ants, five coccinelids and one anthocorid. Fungi feeders, *Micrambe perrisi* Brisout (Coleoptera, Cryptophagidae), were common in November and December and constituted 27% of the arthropods.

Omnivorous and necrophagous arthropods represented 7% of the total and were often found in recently abandoned nests. This foraging type was dominated by two species, one forficulid (Dermaptera) and a millipede of the family Julidae (Diplopoda). The dermestid *Dermestes aurichalceus* Küester is a probable scavenger of *T. pityocampa* dead larvae (Herrmann & Bahillo de la Puebla, 2003). In total herbivores, mainly phloem feeders such as *Cinara* sp. and Cercopidae, accounted for only 1.4% of the arthropods collected.

From the end of the first until the fifth instar, individual larval dry weight increased by a factor of about 1000. Consequently, mean density of larvae per nest decreased and nest larval biomass followed an increasing trend, from L2 to L5 (Figs 2 and 3). Concomitantly, nest volume ($\bar{x} \pm SE$) increased from 9.3 cm³ \pm 1.16, ($n = 15$) in mid-October (L2), to 104.4 cm³ \pm 11.03 ($n = 18$) at the end November (L3), and finally to 404.4 cm³ \pm 11.03 ($n = 18$) in February, when all larvae had completed development. The number of larvae per nest decreased between October and November, due to the mortality occurring in the L1 and L2 instars

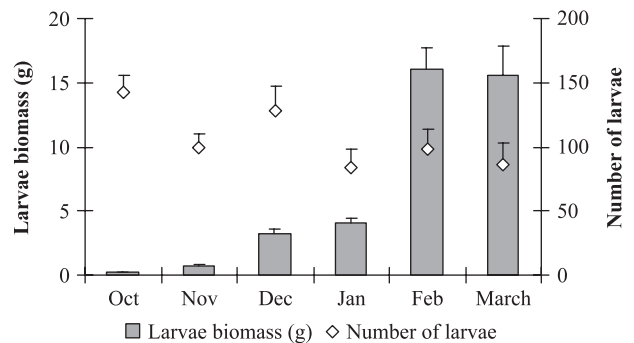


Fig. 3. *Thaumetopoea pityocampa* larval density and biomass per nest ($\bar{X} \pm SE$) throughout the period of larval development, from October (L2) to March (L5), data pooled for all stands, considering the nests occupied with live larvae. Portugal, 1999–2000.

(Pérez-Contreras *et al.*, 2003), followed by an increase in December, resulting from group merging, a trend which was particularly noticeable in Apostiça and Barrada (Fig. 3). In stands having a high density of nests per tree, several colonies can merge so that one nest may contain up to 1334 larvae, as observed in Barrada. As from January onwards, high numbers of dead larvae were found in L4/L5 nests. In March, larvae descended to the ground for pupation and most nests contained only dead larvae, if any.

Association patterns at nest and stand level

At nest level, both the abundance and richness of arthropods per occupied nest, were positively related to mean larval biomass ($r_s = 0.97$; $n = 562$, $P < 0.001$ and $r_s = 0.97$; $n = 562$, $P < 0.001$, respectively). The number of nest-associated arthropods increased throughout the winter, following nest size and total larval biomass (Fig. 2), attaining a factor as high as 22, between instars L2 and L5. Larval biomass also varied significantly among stands $\chi^2 = 13.3$ (d.f. = 3, $P = 0.004$). In addition, the mean number of arthropods per nest was seven times higher in the stand with the largest larval biomass per nest, Barrada, than in the stand with the smallest one, Leiria.

A significant positive correlation was further encountered between the number of arthropods per nest, and spider richness ($r_s = 0.75$, $n = 351$, $P < 0.001$).

At stand level, arthropod species richness per nest, differed significantly according to stand, $\chi^2 = 24.25$ (d.f. = 3, $P < 0.001$). Furthermore, a significant positive correlation was detected between the mean richness of arthropods per nest, and understorey plant diversity ($r_s = 1.00$, $n = 4$, $P < 0.001$). In Apostiça a significantly higher mean number of species per nest was found, than in Barrada, Leiria and Pucariça, $Z = -2.06$, $P = 0.039$, $Z = -2.33$, $P = 0.020$ and $Z = -5.05$, $P < 0.001$, respectively (Fig. 4), with Leiria and Barrada having similar values ($Z = -0.23$, $P = 0.817$). In contrast, no significant correlation was found between the number of nests per hectare, and arthropod richness ($r_s = 0.40$, $n = 4$, $P = 0.60$). However, nest density was positively correlated with the mean number of arthropods per nest ($r_s = 1.00$,

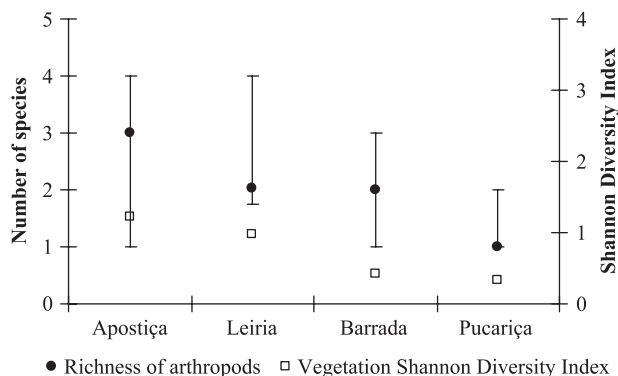


Fig. 4. Richness of arthropods per nest, median (black circles) and inter-quartile range (line), and Shannon Diversity Index for the vegetation (open squares). Portugal 1999–2000.

$n = 4$, $P < 0.001$), a result mainly due to the high numbers of the parasitoid *P. caudata*.

Spider abundance also differed significantly according to stand, $\chi^2 = 16.3$ (d.f. = 3, $P = 0.001$). The average number of spiders per nest (\pm SE) was higher in Leiria (1.14 ± 0.01), followed by Apostiça (0.76 ± 0.09), Barrada (0.50 ± 0.03) and Pucariça (0.21 ± 0.09). Araneae represented approximately 49% of the total species richness in the two stands having the highest understorey diversity, Leiria and Apostiça, 33% in Pucariça, and 28% in Barrada.

Discussion

The rich and abundant arthropod fauna sheltered inside *T. pityocampa* nests was studied in detail, for the first time. Most of the ca. 60 species identified, representing 12 foraging types, belonged to trophic levels other than *T. pityocampa*, while phytophagous arthropods accounted for 1.4% of the total only. It can thus be inferred that *T. pityocampa* nests promote interactions among trophic levels, a finding which is innovative. On the other hand, contrary to observations for leaf rollers (Cappucino, 1993; Cappucino & Martin, 1994), nests did not contribute to foster interactions among phytophagous species.

Although the number of stands sampled was small, arthropod species richness was significantly higher in pine stands having higher vegetation diversity, regarding both stand composition and understorey vegetation, than in young monocultural plantations with scarce understorey. These findings are in accordance with predictions which couple variations of the diversity of plant and arthropod communities, regarding both herbivores and higher trophic levels (e.g. Siemann, 1998). They further agree with Santos *et al.* (2002), who detected significant positive correlations between understorey species richness of pine stands in Portugal and Hymenoptera diversity.

Araneae heavily influenced the overall abundance and diversity of *T. pityocampa* nest-associated arthropods, leading us to conclude that (i) spiders use nests for brood care, since 80% of the individuals collected were juveniles, or females with egg sacs; (ii) 99% of the spiders were non-web builders, including jumping hunters (Salticidae), cryptic hunters, (Thomisidae, and Philodromidae), and nocturnal ground foragers (Clubionidae and Gnaphosidae); (iii) the two later groups accounted for 75% of the spiders collected, providing evidence of the occurrence of an interaction between communities of the pine coppice, and of the ground vegetation layers, similarly to suggested for other agroecosystems (e.g. Bogya & Markó, 1999); and (iv) nests are extensively used by Araneae, even after larval abandonment. In general, communal tents protect from climatic elements and facilitate the accumulation of thermal energy during the winter (e.g. Bryant *et al.*, 2000; Ruf & Fiedler, 2000; Ruf & Fiedler, 2002).

Our results show that *T. pityocampa* nests provide shelter and habitat for non-web-builder spiders, by supplying a microclimate suitable for arachnid juvenile development, a novel finding. Previous authors have shown that adult Clubionids occur both on the ground and canopy throughout the summer (e.g. Bogya *et al.*, 2000). It can thus be inferred that nests contribute to improve the survival of large numbers of spiders.

Throughout the season, larval biomass was positively correlated with arthropod abundance and diversity, demonstrating the importance of nest size regarding the number of interactions established.

By the end of the winter, peak larval biomass was attained and a large amount of faeces, exuviae, fungi and dead arthropods were accumulated inside the nests. This substantial food resource attracted decomposers, scavengers and fungi feeders, such as *Micrambe perrisii* (Coleoptera, Cryptophagidae), which also inhabits nests of *Thaumetopoea pinivora* L., while a sympatric species, *Micrambe unbripennis* Reitter, associates with different caterpillar species (Reska, 1994; Otero, 2001). Observations thus appear to indicate a co-evolutionary nature for the relationship established between social caterpillars and nest cleaning arthropods.

Although this study did not aim at studying host–parasitoid density relationships, a positive correlation was found between *T. pityocampa* nest density and its main larval parasitoid, *P. caudata* (e.g. Triggiani *et al.* 1993). The apparent direct density-dependent relationship detected is probably justified by the fact that *P. caudata* is a specialist parasitoid of *T. pityocampa*, as confirmed by, for example, Biliotti (1958).

By contrast, few generalist predators and parasitoids, such as *M. versicolor* were present, which agrees with the theory relating the effectiveness of shelter protection with the level of natural enemy specialisation (e.g. Jones *et al.*, 2002; Weiss *et al.*, 2004). Since hyperparasitoids and parasitoids of Phoridae and Syrphidae were also collected, we postulate that *T. pityocampa* nests are involved in multiple links of the pine ecosystem food web.

Since over two-thirds of the parasitoid specimens were sampled in late larval, or pupal stages, and considering that adult parasitoids and predators remain inside the nests for shorter periods than immature stages, their numbers could have been overlooked. This could also apply to predators such as *Xanthandrus comtus* (Syrphidae), the larvae of which prey on gregarious caterpillars (Rotheray & Gilbert, 1999), including *T. pityocampa* (e.g. Biliotti, 1958). Two ant species, *Formica fusca* and *Lasius* sp. were observed in nests containing aphids, probably collecting honeydew, similarly to observed by Nakamura and Ohgushi (2003) for other types of shelters.

Novel data were obtained clarifying the role of *T. pityocampa* nests in Mediterranean pine ecosystems, a topic not addressed before. The indirect interactions documented, mainly with generalist predators, parasitoids, scavengers and fungi feeders, evidence the important functional role of *T. pityocampa* nests in pine ecosystem food webs. By contrast, only a negligible percentage of the arthropods using the caterpillars shelters were phytophagous, thus showing that nests do not promote direct interactions with other potential pests. Finally, a relevant link between habitat and insect conservation was identified, considering that arthropod diversity, sheltered in the nests, was positively correlated with understorey vegetation diversity.

Considering that defoliations of up to 25%, caused by *T. pityocampa*, do not significantly affect the growth rate of *Pinus pinaster* (Barrento *et al.*, 2008) and nests may contribute to biodiversity conservation, the present findings have practical implications regarding forest management strategies.

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