



Research Paper

Urban tree isolation affects the abundance of its pests and their natural enemies

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HIGHLIGHTS

- Urban tree isolation affects the abundance of pests and their enemies.
- Urban tree isolation affects the top-down regulation of pests by their enemies.
- Monospecific *Eucalyptus* patches had more herbivore insects than isolated trees.
- Pest parasitism rate was 30-fold greater in urban forest patches than isolated trees.
- Pest-predator-parasitoid abundance interdependence differed by tree arrangement.

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ABSTRACT

The proximity to transportation hubs and the large movement of goods and people in cities make trees especially prone to invasive insect pests. Urban tree arrangements, in isolated tree sites or in forest patches, may alter their susceptibility to insect herbivory. Surprisingly little is known about how urban tree spatial arrangements influence pest abundance and top-down regulation by natural enemies. We sampled the abundance of an invasive pest of *Eucalyptus*, the psyllid *Glycaspis brimblecombei*, and of two of its natural enemies, the specialist exotic parasitoid *Psyllaephagus bliteus* and the generalist native predator *Anthocoris nemoralis* over two years. We measured insect abundances in isolated trees versus monospecific planted forest patches in 17 pairs of sites, each within a Portuguese city. The abundance of the exotic pest was three-fold higher in forest patches than in isolated trees. The parasitism rate was ~ 30 times higher in forest patches (11.5 %) than in isolated trees (0.4 %). The interdependence among insect species abundances also differed between spatial arrangements. In isolated trees, predator and parasitoid abundances depended markedly on prey abundance. In forest patches, we found a marked dependence of the predator on the composition of the surrounding landscape. Our study adds empirical data indicating that urban tree isolation matters for pest abundance and regulation by its enemies. In similar systems, avoiding dense monospecific patches of exotic trees and increasing the compositional heterogeneity of the landscape are promising paths to maintain the sustainability of urban trees and their environmental and societal benefits.

1. Introduction

Trees in urban landscapes provide ecosystem services and improve human well-being (FAO, 2016). They do this by reducing pollution and cooling the air, contributing to biodiversity conservation, sequestering

carbon and mitigating climate change, improving physical and mental health and increasing connectivity with rural areas (Fernández-Juricic & Jokimäki, 2001; Kang et al., 2015; Ossola et al., 2019; Gulsrud et al., 2018). Urban trees are usually grown isolated or in very small groups (isolated trees; e.g., along the streets), or as larger forest patches, such as

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in parks and gardens, according to aesthetic, ecological, and practical aspects (Endreny, 2018; FAO, 2016; Lawrence, 1988; Lawrence, 1993). While tree diversity can be high in urban parks or arboreta (sometimes even higher than in natural forests because of the accumulation of more exotic species), street trees are often of the same single species. Such is the case with some Mediterranean streets with *Eucalyptus* trees, which can have less biodiversity and serve as corridors for the spread of insect pests (Gilbert et al., 2003; Stemmelen et al., 2021). Because cities have high movement of people and goods and often serve as national or international entry points, urban trees are often exposed to the establishment of alien pests. Indeed, 89 % of alien forest pests in Europe were first detected in urban and peri-urban areas (Branco et al., 2019). Urban trees are also particularly exposed to stressors and pressures favoring pest outbreaks, such as pollution, soil compaction, heat island effects, and intensive management (Dale & Frank, 2017; Livesley et al., 2016; Long et al., 2019; Meineke et al., 2013).

However, little is known about the effect of the spatial arrangement of urban trees on the risk of establishment and outbreak of alien pests (Hanks & Denno, 1993; Parsons & Frank, 2019). According to the source-sink dynamics meta-population concept for habitat colonization, more isolated trees would be less likely to be colonized than well-connected trees in forest patches (Frouz & Kindlmann, 2015; Maguire et al., 2015). The presence of similar or alternative habitats in the surrounding landscape must also be taken into account to predict the probability of colonization of isolated patches (Ewers & Didham, 2006).

Herbivore insects are generally regulated by their natural enemies, such as predators and parasitoids. In urban forests, such enemies are also present and are expected to exert their top-down control. Notwithstanding, the abundance of natural enemies likely depends on the urban tree isolation as well (Parsons & Frank, 2019; Stemmelen et al., 2021). Land cover diversity in the surrounding landscape may further provide complementary habitats and alternative prey for natural enemies, especially the generalist ones, which in turn would promote pest top-down regulation. Still, how the spatial pattern of urban trees influences the relative importance of bottom-up and top-down forces controlling pest dynamics remains an understudied question (Long & Frank, 2020).

Exotic tree species are common in urban areas (Cowett & Bassuk, 2014). Interestingly, the “enemy escape hypothesis” (Keane & Crawley, 2002) suggests that non-native trees are more likely to avoid insect herbivory. There are, however, examples of non-native trees infested by insect herbivores, either native (e.g., Branco et al., 2015) or non-native (e.g. Hurley et al., 2016) from the original range of the introduced tree species. A good example is *Eucalyptus*, which is widely used as urban tree species, particularly in Mediterranean climates worldwide. The number of exotic pests attacking eucalypts outside their native region has increased exponentially since the 1980’s (Hurley et al., 2016; Mansfield, 2016). Most are sap suckers, such as the red gum lerp psyllid, *Glycaspis brimblecombei* (Moore). It is currently the most frequent and damaging *Eucalyptus* pest in urban areas (Laudonia et al., 2014; Paine et al., 2015) and has recently invaded Europe (Valente & Hodkinson, 2009). It can cause tree defoliation, produces abundant honeydew, and decreases tree aesthetical value (Brennan et al., 1999). The Australian parasitoid *Psyllaephagus bliteus* (Riek) is a specialist parasitoid of *G. brimblecombei* that has been introduced in California as biological control agent (Daane et al., 2012). Later, *P. bliteus* fortuitously established itself in Europe (Caleca et al., 2011). *Anthrenus nemoralis* (Fabricius) is a true bug native to Europe that has been found to prey on *G. brimblecombei*. This generalist predator seems to have adapted well to the new prey and its habitat by expanding its prey range. Females are able to lay eggs, reproduce and complete their development on *Eucalyptus* trees by feeding exclusively on *G. brimblecombei* (Garcia et al., 2019).

In this study, we evaluated the effect of two urban *Eucalyptus* spatial arrangements on the abundance of *G. brimblecombei* and of its natural enemies to guide efforts for better tree spatialization in healthier cities. We sampled over 2 years the abundance of *G. brimblecombei*, *P. bliteus*

and *A. nemoralis* in 17-paired urban sites with planted *Eucalyptus* arranged as isolated trees vs. monospecific forest patches in southern Portugal. First, we hypothesized that isolated trees would be less colonized by *G. brimblecombei* than forest patches. Second, because the parasitoid *P. bliteus* is a specialist whereas the predator *A. nemoralis* is a generalist, we would expect a marked response of the parasitism rate to the abundance of *G. brimblecombei* but not of the predator to prey ratio. Last, we hypothesized that the interdependence among abundances of the three insect species would differ between the two urban tree spatial arrangements, namely due to dissimilar effects of the surrounding land-use composition on the natural enemies. Because *A. nemoralis* feeds on a number of psyllid species of several host plants (e.g., Horton et al., 2004; Sigsgaard, 2010), the presence in the surrounding landscape of diverse land cover types would likely benefit this generalist species. On the contrary, because *P. bliteus* is an Australian parasitoid specialized on specific psyllids of the *Eucalyptus* genus, its abundance would be most affected by the type of arrangement.

2. Material and methods

2.1. Study sites and design

We conducted the study in southern Portugal from 2016 to 2017, between mid-May and mid-August, the period with the highest abundance of *G. brimblecombei* populations (Boavida et al., 2016). The mean daily temperature over the 3-months sampling periods ranged from 25 °C to 35 °C (IPMA, 2020).

To assess whether abundances of psyllids and their enemies would be similar between *Eucalyptus* spatial arrangements, we selected 17 pairs of sites, each pair including one isolated tree site and one forest patch site within the same city (Table S1, Supplementary Materials). We based the selection of sites with *Eucalyptus* trees on cross-checking various sources of information, including Google Earth® and Google Street View® images, our knowledge of the territory, and on-site reconnaissance and validation. The mean distance between pair member sites was 2.8 km (± 2.6 SE; range = 0.2–10.6 km). We only sampled *Eucalyptus* species susceptible to *G. brimblecombei*, mostly *Eucalyptus camaldulensis* (Dehnh.), the most common species planted in the region. Isolated tree sites had two to six trees (mean = 3.0 ± 1.8 SE) further than 0.2 km away from any other congeneric *Eucalyptus*. Isolated trees were located in parks, gardens, or hedgerows (Fig. S1A, S1B, Table S1, Supplementary Materials). Forest patches (>1000 m²) were dominated over 90 % by one *Eucalyptus* species — *E. camaldulensis* or closely related congeneric species, such as *E. rudis* and *E. tereticornis*. Forest patches were plantations of exotic species with no natural regeneration in the study area. Each pair was sampled on the same day, or up to 3 days in a few cases. In each pair, we sampled 2 trees from the isolated trees site and 2 trees from the forest patch site. At the isolated tree sites, the two trees were randomly selected 10–20 m apart. At forest patch sites, the two trees, 20 m apart, were randomly selected in a transect beginning 2–3 m from the patch boundary. Data were recorded per tree (68 trees = 2 trees \times 2 spatial arrangements \times 17 site pairs). Twelve of the 17 pairs were sampled in 2016 and the remaining 5 in 2017.

2.2. Data collection

Per sampled tree, we collected four 0.40 m-long branches at 1.70-m high in tree crown, one per orthogonal direction. Branches were carefully handled to avoid dislodging any psyllid, parasitoid, or predator and individually placed in a paper bag (0.40 m length \times 0.25 m width). To prevent insect dehydration and death until observation (24 h maximum), we carried the bags in a cooler box to the laboratory and stored them at 8–10 °C. Leaves of each branch were carefully observed under a stereomicroscope (Optika SZM-LED1 7 \times 45 \times). We recorded the total number of psyllids from each development stage and parasitoid mummies per sampled branch and then we summed up per tree

(Boavida et al., 2016). We also recorded the number of eggs, nymphs, and adults of *A. nemoralis* per branch. Parasitism rates were obtained by dividing the number of mummies (parasitized N5 nymphs) by the total number of N5 nymphs (including mummies) per branch. The ratio between the number of *A. nemoralis* (adults and nymphs) and the number of susceptible nymph stages of the psyllid (N1 to N3) was used as a proxy for predation rate. Because this predator can complete its development in the *Eucalyptus* trees where it feeds solely on *G. brimblecombei* (Garcia et al., 2019), the predator to prey ratio was a good predation rate proxy in our case study.

To assess the effect of the nearby land-use composition on insect abundances, we photo-interpreted the land cover within a 400-m circle of each plot. We delimited the land-use polygons based on high-spatial resolution of World Imagery (ESRI Online data 2020, through Esri, ArcGis® software), Google Street View® Imagery. We validated the land-use assignment by on-site reconnaissance. We photo-interpreted the classes *Eucalyptus* susceptible to *G. brimblecombei*, shrubs, urban areas (backyards, gardens, small parks, and a few pine areas), other non-eucalyptus areas, and crops (mostly orchards). After exploratory data analysis using mainly correlations, we opted to use in the statistical modeling only two landscape types: i) the combined land-use class including urban areas, shrubs, and permanent crops, which correlated best with the *A. nemoralis* abundance and provide habitat for the predator, and ii) forests with *Eucalyptus* species susceptible to *G. brimblecombei*, therefore correlating better with *G. brimblecombei* abundance.

2.3. Data analyses

2.3.1. Effect of *Eucalyptus* spatial arrangement on abundance of *Glycaspis brimblecombei* and its natural enemies

To evaluate the effect of the spatial arrangement of *Eucalyptus* trees on the abundance of *G. brimblecombei*, *P. bliteus*, and *A. nemoralis* we used three separate generalized mixed-effects models using a Bayesian framework. Because the response variable in all three models was expressed as a count and to handle over-dispersion, we used the log-normal Poisson family distribution (i.e., including individual tree-level random effects) with log link. Each variable was expressed per tree. Because tree sites were nested within the 17 site pairs across southern Portugal, we used both as random factors in the mixed-effects models following that hierarchical order (pair/site).

We created the Bayesian models in Stan computational framework (<http://mc-stan.org/>) accessed with *brms* package (Bürkner, 2017). To improve convergence while controlling against overfitting, we assigned weakly informative priors (see Gelman 2020) to the beta parameters of the effect sizes (normal (0, 10)) and to the intercepts (normal (0, 100)). For each model, we ran four parallel MCMC chains until convergence was reached (all \hat{R} at ≤ 1.1). Each chain had 4000 iterations (warmup = 1000, thin = 1), totaling 12,000 post-warmup samples. We assessed model adequacy using posterior predictive checks.

2.3.2. Parasitism and predation rates in isolated *Eucalyptus* trees vs forest patches

To evaluate the effect of the spatial arrangement of *Eucalyptus* trees on the parasitism rate of 5th instar nymphs (N5) by *P. bliteus*, we used a generalized mixed-effects model (GLMM). A binary logistic regression with log link function was used with the total number of N5 as denominator. The tree spatial arrangement was considered a fixed effect and the site a random effect. The effect of *Eucalyptus* tree spatial arrangement on the predator to prey ratio (*A. nemoralis* predation rate proxy) was tested using GLMM with a Gaussian distribution and log link function. Estimated means for the two types of spatial arrangement were compared with pairwise contrast. These two analyses were conducted using IBM® SPSS™ Statistics version 26.

2.3.3. Interdependence between *G. brimblecombei*, its enemies, and surrounding landscape features in isolated trees and forest patches

To investigate the interactions among the number of *G. brimblecombei*, *P. bliteus* and *A. nemoralis* in isolated trees and forest patches, we performed confirmatory path analyses (*sensu* Grace, 2006) using the D-separation procedure (e.g., Vaz et al., 2019). A path diagram denotes by arrows how variables influence (and are influenced by) other variables. This procedure tests whether any paths are missing in the model and whether it would be improved by the inclusion of a missing path (Shipley, 2009).

To assess how different were the pathways among variables between the two *Eucalyptus* spatial arrangements, we built one model for isolated trees and another one for *Eucalyptus* forest patches. In both models, we hypothesized that (1) *P. bliteus* abundance would be affected by *G. brimblecombei* abundance; and (2) *A. nemoralis* abundance would be affected by *G. brimblecombei* abundance and by the area of nearby land cover combining urban areas, shrubs, and crops.

Using the R package *piecewiseSEM* (Lefcheck, 2016), the path diagram was translated into a set of two mixed-effects models explaining *P. bliteus* and *A. nemoralis* abundances. We entered tree pair as random factor in both models. Both responses were fitted using a log-normal Poisson family distribution (including observation-level random effects) with log link. We tested for the validity of the hypothesized relationship pathways using the C-statistic (Shipley, 2009). Once the generalized path model was validated, we obtained the path coefficients by fitting the models. All variables were rescaled prior to analyses (i.e., value subtracted from the mean and then divided by the standard deviation). We performed all analyses in R v. 3.6.3 (R Core Team, 2020).

3. Results

Overall, the pest *G. brimblecombei* was more abundant in *Eucalyptus* forest patches than in *Eucalyptus* isolated trees in all its developmental stages (Table 1). Eggs and nymphs of first to third instar were the most common developmental stages. All sites had *G. brimblecombei* except one isolated tree site. The parasitoid *P. bliteus* abundance was also greater in forest patches than in isolated trees. *A. nemoralis* abundance was three times greater in forest patches relative to isolated trees (Table 2).

3.1. Effect of *Eucalyptus* tree spatial arrangement on *Glycaspis brimblecombei* and its natural enemies

The mean of the posterior distribution was 516 (credible interval = 203 – 1078) individuals of *G. brimblecombei* per tree (in the four sampled branches) in isolated trees and 1635 per tree (660 – 3408) in *Eucalyptus* forest patches (Fig. 1). Thus, in *Eucalyptus* forest patches, the number of *G. brimblecombei* was 3.2-fold greater than that in *Eucalyptus* isolated trees. After performing non-linear hypothesis testing (Bürkner, 2017; Clark, 2020) for contrast effects, we are 98 % confident that *Eucalyptus* forest patches had greater *G. brimblecombei* abundances (Table 3). Sampling the difference between *G. brimblecombei* in forest patches and isolated trees from the model's posterior distribution, the most credible difference was 1010 individuals (in 50 % of cases), 95 % CI [50, 2859].

Table 1

Mean number per four sample branches of individuals (\pm SE) of *Glycaspis brimblecombei* by developmental stage and *Psyllaephagus bliteus* in urban *Eucalyptus* isolated trees and forest patches.

Tree isolation	<i>Glycaspis brimblecombei</i>				<i>Psyllaephagus bliteus</i>
	Eggs	N1 to N3	N4	N5	Mummies
Forest patch	1135.6 \pm 912.5	530.3 \pm 597.5	74.4 \pm 91.8	74.2 \pm 86.6	18.1 \pm 33.3
Isolated trees	871.3 \pm 955.0	316.6 \pm 369.5	47.2 \pm 73.9	53.6 \pm 84.2	2.2 \pm 4.1

Table 2

Mean number (\pm SE) per four sampled branches of *Anthocoris nemoralis* individuals in *Eucalyptus* isolated trees and forest patches.

Tree isolation	Eggs	Nymphs	Adults
Forest patch	18.47 \pm 28.45	1.38 \pm 2.67	0.85 \pm 1.92
Isolated trees	6.47 \pm 12.90	0.32 \pm 1.25	0.03 \pm 0.17

As for the *P. bliteus* species, the posterior mean was 1 individual (0–2) in isolated trees and 5 (2–11) in *Eucalyptus* forest patches. We are 100 % confident that forest patches had greater *P. bliteus* abundances than in isolated trees. The most credible difference between *Eucalyptus* tree arrangements was 4 *P. bliteus* individuals (in 50 % of cases), 95 % CI [1, 10].

Last, *A. nemoralis* abundance was also greater in forest patches (mean = 5; 1–12) than that in isolated trees (2; 0–4). In this case, we have 97 % confidence that the largest number of individuals occurred in forest patches. The most credible difference between *Eucalyptus* tree arrangements was 3 *A. nemoralis* individuals (in 50 % of cases), 95 % CI [0, 10].

3.2. Parasitism and predation rates in isolated trees and forest patches

The parasitism rate by *P. bliteus* was 30-fold greater in forest patches than that in isolated trees ($t = 21.52$, $p < 0.001$) (Table 4). The estimated marginal mean for the parasitism rate was 11.5 % \pm 4.4 in forest patches and 0.4 % \pm 0.2 in isolated trees. The predator to prey ratio (predation rate proxy) did not differ between forest patches and isolated trees ($t = 0.137$, $p = 0.892$) (Table 5).

3.3. Interdependence between *Glycaspis brimblecombei*, its enemies, and nearby landscape composition in isolated trees and forest patches

Path analyses revealed different interdependence among abundances of the three insect species between *Eucalyptus* forest patches and isolated trees (Fig. 2). Both models had a good fit ($P > 0.7$ in both cases). The effects of *G. brimblecombei* on *A. nemoralis* and *P. bliteus* were not deemed significant in forest patches, while these were the effects of higher magnitude in isolated trees (0.65 and 0.72, respectively). Moreover, as

the path between *G. brimblecombei* and *P. bliteus* worsened the isolated trees model fit, it was dropped from that model. The forest patch model confirmed the significant effect of urban areas, shrubs, and permanent crops on the abundance of *A. nemoralis* and this was not deemed a significant effect in isolated trees.

4. Discussion

Our study provides empirical evidence that the level of urban tree isolation can affect tree pests and their regulation. We found that urban forest patches of *Eucalyptus* were clearly more infested than isolated trees by the red gum lerp psyllid, an insect pest originating from the

Table 3

Summaries of the fixed parts of the three log-normal Poisson mixed-effects Bayesian models predicting the effects of *Eucalyptus* tree spatial arrangement (forest patch, isolated trees) on the number of *Glycaspis brimblecombei*, *Psyllaephagus bliteus*, and *Anthocoris nemoralis*, respectively. CI = credible interval for the parameter; $\beta < 0$ = posterior probability under the hypothesis of whether effect is greater (less) than zero if positive (negative); Notable = asterisk on effects whose CI does not contain zero (or with margin very close to zero). Potential scale reduction factor on split chains (Rhat) was 1.00 in all parameters.

Parameter	Estimate	Error	2.5 % CI	97.5 % %CI	$\beta < 0$	Notable
<i>Glycaspis brimblecombei</i>						
Intercept	7.31	0.41	6.49	8.13	1.00	*
<i>Eucalyptus</i> tree type (reference = Isolated trees)	−1.16	0.54	−2.22	−0.07	0.98	*
<i>Psyllaephagus bliteus</i>						
Intercept	1.45	0.49	0.44	2.38	1.00	*
<i>Eucalyptus</i> tree type (reference = Isolated trees)	−2.06	0.46	−2.98	−1.18	1.00	*
<i>Anthocoris nemoralis</i>						
Intercept	1.46	0.52	0.40	2.45	1.00	*
<i>Eucalyptus</i> tree type (reference = Isolated trees)	−1.19	0.66	−2.52	0.09	0.97	*

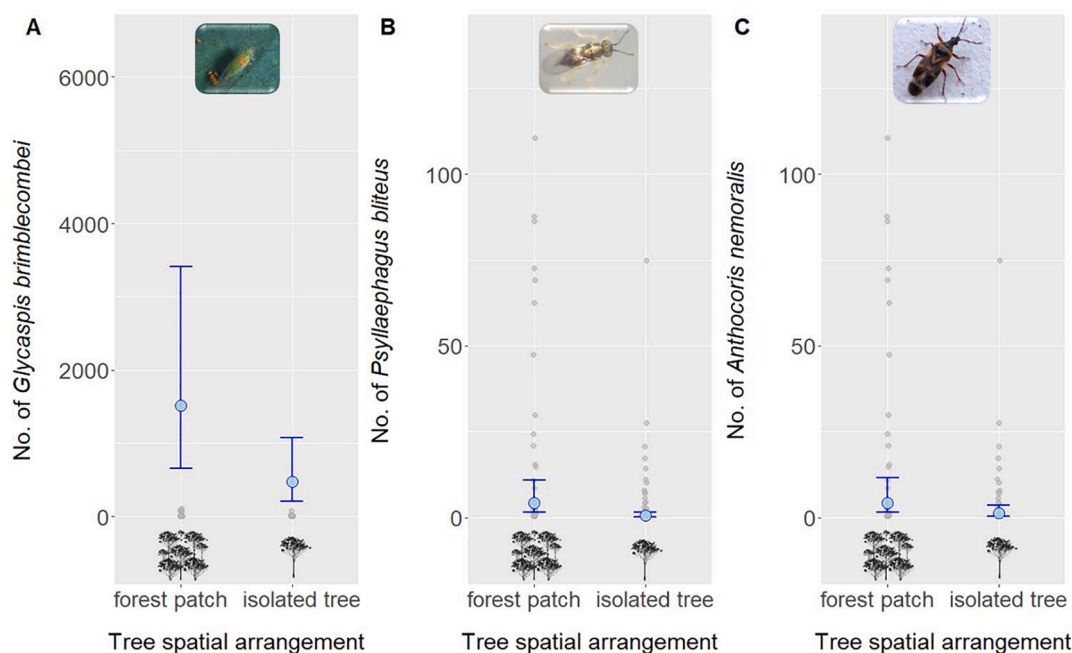


Fig. 1. Mean fitted values (\pm 95 % credible intervals) for the three log-normal Poisson mixed-effects Bayesian models predicting the effects of *Eucalyptus* tree spatial arrangements on the number of *G. brimblecombei* (A), *P. bliteus* (B) and *A. nemoralis* (C). Grey circles are predicted values.

Table 4Summary of the GLMM predicting the effect of *Eucalyptus* tree isolation (forest patch, isolated trees) on parasitism rate by the parasitoid *P. bliteus*.

Parameter	Coefficient	Standard Error	t	Sig	Exp (coeff)	95 % CI for Exp (coeff)	
						Lower	Upper
Intercept	−5.44	0.46	−11.81	<0.001	0.004	0.002	0.01
Tree isolation (reference = forest patch)	3.40	0.15	21.52	<0.001	29.98	21.84	41.13

Table 5Summary of the GLMM predicting the effect of *Eucalyptus* tree isolation (forest patch, isolated trees) on predator to prey ratio (*A. nemoralis* predation rate proxy).

Parameter	Coefficient	Standard Error	t	Sig	95 % CI for Exp (coeff)	
					Lower	Upper
Intercept	−2.65	0.40	−6.56	<0.001	−3.45	−1.84
Tree isolation (reference = forest patch)	0.08	0.55	0.14	0.89	−1.02	1.17

tree's native area. As hypothesized, the greater abundance of the psyllid in *Eucalyptus* forest patches was also associated with a much greater rate of parasitism, by the specialist parasitoid *P. bliteus*, but not with a higher potential predation by the generalist native predator *A. nemoralis*. Our results also showed that the surrounding landscape can affect the interactions among insect abundances. As *Eucalyptus* trees are now planted widely in Mediterranean climates, our results may apply to many comparable urban areas.

We shed light on the dynamics of the insect pests and their natural enemies of non-native urban trees which are commonly used in many cities (Helden et al., 2012; Jim & Chen, 2009; Sjöman et al., 2012). In systems without *Eucalyptus* trees worldwide, insect assemblages and urban tree isolation effects on pest-enemy interactions may differ. In addition to the great emphasis that has been placed on tree species

diversity when planning urban forests (Alvey, 2006; Laćan & McBride, 2008; Riley et al., 2018), we focused on the spatial organization of trees. We showed that large monospecific patches of exotic trees should be avoided. In contrast, large diverse patches combined with isolated individuals should be preferred. It is worth noting these tree species mainly form mixed stands with natural regeneration and multiple age strata in their native natural habitats. Due to multiple top-down and bottom-up forces, we hardly find most of the herbivores that become so noticeable in the invaded regions.

Lower abundances of *G. brimblecombei* in more isolated trees can be explained by the low functional connectivity among host trees (Maguire et al., 2015). To our knowledge, there are no specific studies on the dispersal ability of this psyllid. Yet, because of its small-size, we believe that wind-assisted dispersal can occur up to hundreds of meters as observed with other psyllids. Indeed, we found all but one isolated tree colonized by *G. brimblecombei*. Alternative explanations for the smaller population size of the psyllid on isolated trees compared to monospecific forest patches may be related with bottom-up and top-down forces.

The clear trend for greater pest abundance in monospecific *Eucalyptus* forest patches than in isolated trees is in line with the resource concentration hypothesis. An herbivore species specialist of a single tree species or genus (i.e., monophagous) is favored by the concentration of resources resulting from the presence of a high number of neighboring host trees in a given forest patch. On the other hand, the relative amount of host resources is by principle lower in more diverse plant communities (Jactel et al., 2021). Higher abundances of eucalypts in forest patches result in greater abundance of new growth flushes during spring and early summer, which are favorable for psyllid feeding activity and

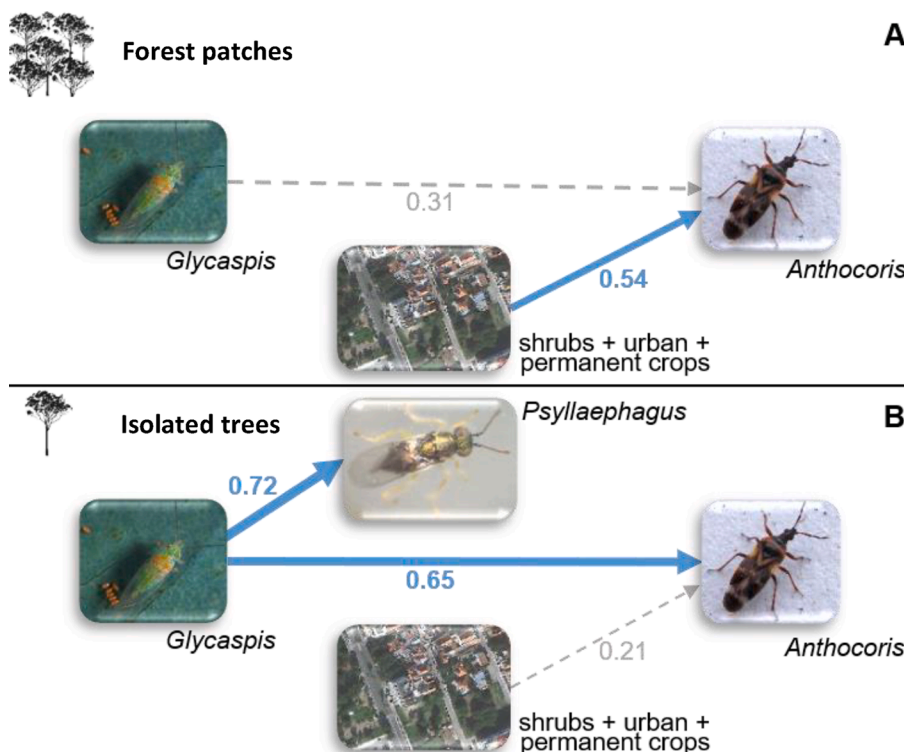


Fig. 2. Final path diagram for *Eucalyptus* forest patches ($P = 1$; $n = 34$; A), and *Eucalyptus* isolated trees ($P = 0.734$, $n = 34$; B). Arrows represent directed relationships between variables (paths) deemed significant (full lines) or not significant (dashed) at the 0.05 level, each having a standardized coefficient (sign indicates whether the relationship is positive or negative for that direct effect). The arrow thickness is proportional to the coefficients, which can be compared to assess the relative effects of the variables. *Glycaspis* = *G. brimblecombei*; *Psyllaephagus* = *P. bliteus*; *Anthocoris* = *A. nemoralis*; Shrubs + Urban areas + Permanent crops = land-use with urban areas, shrubs, and Perennial crops combined.

population growth. Conversely, habitat fragmentation resulting from the arrangement of *Eucalyptus* as isolated trees can lead to a lower probability of colonization and colony development.

Other factors may also be involved, such as microclimate differences depending on tree spatial arrangement. For example, Long et al. (2019) found that urban forest patches were 1.3 °C cooler than isolated trees and suggested that the higher densities of the gloomy scale, *Melanaspis tenebricosa*, in isolated trees compared to forest patches were related with an urban heat island effect.

Our observational study provides evidence that the level of isolation of urban trees matters for pest regulation by their enemies. We studied the specialist parasitoid *P. bliteus*, introduced from Australia for classical biological control of *G. brimblecombei* and the generalist predator *A. nemoralis*, native to Europe. Both *P. bliteus* and *A. nemoralis* showed higher abundances in forest patches than in isolated trees, following the higher abundance of their host or prey. Especially striking was the 30-fold higher parasitism rate by *P. bliteus* in forest patches versus isolated trees. Still, parasitism rates were low and did not guarantee the control of the psyllid at low abundance. Interestingly, no differences were detected in the predator to prey ratio (*A. nemoralis* predation rate proxy), between forest patches and isolated trees. In both cases, the number of predators and therefore the predator to prey ratio were small. In general, specialist natural enemies are expected to benefit from the abundance and concentration of their host (herbivore) resources, which were higher in forest patches. Considering that prey habitat fragmentation is greater in isolated trees than in forest patches, our results partially support the predictions of the theory that prey habitat fragmentation will have negative effects on specialist predators, but may increase predation by generalists (Ryall & Fahrig, 2006). Although the abundance of the generalist predator *A. nemoralis* was higher in forest patches, the increase in their population size was probably not sufficient to compensate for the increase in prey population size and thus improve the predator to prey ratio.

Despite the positive response of *P. bliteus* to prey abundance, parasitism rates were modest, i.e. 11.5 % in forest patches and 0.4 % in isolated trees. This result is in agreement with other works showing the low efficiency of this parasitoid to control *G. brimblecombei*, in different regions, including North America (Daane et al., 2012), South America (Cuello et al., 2021), and Europe (Boavida et al., 2016).

Path analysis indicated that the abundance of the two natural enemies, *A. nemoralis* and *P. bliteus* were not influenced by their prey and host abundances in forest patches, while the opposite was observed in isolated trees. This suggests that the psyllid is more likely to escape regulation by its natural enemies in forest patches, than in isolated trees. Therefore, *G. brimblecombei* outbreaks are expected to occur more often in forest patches.

We also analyzed how the composition of the landscape surrounding eucalypt isolated trees or patches influenced the abundance relationships of the pest and its natural enemies. The path analysis showed that *A. nemoralis* abundance was influenced by the composition of the landscape but only in forest patches. The land cover types included in the varying surrounding landscapes such as backyards, gardens, orchards and scrublands may provide different habitats for the predatory bug, thus serving as sources. The forest patches were large monospecific *Eucalyptus* forest areas. Understandably, the availability of predator sources in the surrounding landscape will likely influence predator abundance in these forest patches. On the other hand, isolated trees, often planted along roadsides or in public gardens, are more likely to be surrounded by a heterogeneous landscape and greater plant diversity on different strata, so it is expected that the surrounding landscape will not be an important, additional explanatory variable.

It is also interesting to note that in isolated trees *P. bliteus* responded positively to host abundance but was not influenced by the surrounding landscape comprising other land uses than *Eucalyptus* patches. This corroborates the hypothesis that specialist and generalist predators respond differently to land-use, as observed in other studies (Bouzar-

Essaïdi et al., 2021).

Our results provide evidence that the level of isolation of urban trees may influence the population abundance of insect pests, interactions with their natural enemies, and thus the risk of pest outbreaks. Therefore, our findings have implications for the management of urban forests. Similar works may further investigate pest-enemy interactions in other spatial arrangements such as stand-alone trees, trees aligned in urban streets, and in urban parks. For example, it remains possible for the latter to have similar effects to monospecific forest patches but this prediction must be tested in mono- and multi-specific stands. Furthermore, improving the spatial patterns of a given tree species in urban areas needs to be combined with adequate tree diversity. Diverse tree communities may reduce the abundance of specialist herbivores, decreasing the likelihood of outbreaks through bottom-up regulation (Castagneyrol & Jactel, 2012; Jactel et al., 2021). Higher tree diversities can be effective in reducing the infestation of monophagous or oligophagous pests of major concern (Klapwijk et al., 2016). Diverse plant communities can also host greater diversity and abundance of natural enemies by providing habitat and diverse food sources (Haddad et al., 2009).

Our study highlights the caution that should be taken when planting non-native tree species in urban areas, and suggests avoiding their concentration in forest patches. Because non-native trees like *Eucalyptus* spp. in Europe may be phylogenetically distant from native ones, they might also be less prone to attacks by native herbivores. Indeed, non-native trees often exhibit fewer pests than native congeners (Branco et al., 2015; Frank et al., 2019). However, non-native tree species are prone to receive herbivore insects from their original area over time and may overall facilitate the establishment of invasive herbivores, thus posing a biosecurity risk. Further, herbivores on non-native trees may escape their natural enemies after introduction in the non-native range, especially specialized ones. Therefore, their damage is likely to be higher than in their native range.

4.1. Conclusion

By analyzing abundances of a pest and its enemies in isolated trees and forest patches, this study indicates that the level of isolation matters for planning sustainable urban tree assemblages. Our results are relevant as urban trees are at the forefront of exposure to forest pests, being under challenging microclimates and nearby invasion pathways. Much emphasis had hitherto been directed to the diversity of urban trees, but less to their spatial arrangement. We show that not only urban tree diversity should be considered for urban spatial planning, but also how these trees are arranged in the urban space. Specifically, our study suggests isolated trees can be preferable to monospecific forest patches in the study area, as they had three times less pest abundance and there was a marked effect of the pest on predator and parasitoid abundances. Because previous work indicates greater tree diversities can reduce the infestation of monophagous pests, isolated trees combined with large diverse patches can also be an option. As *Eucalyptus* trees are now planted widely in Mediterranean climates, our results can apply to many comparable urban areas. Yet, because the system with *Eucalyptus* trees may not be representative of other systems, further work might delve into specific pest-enemy interactions in other arrangements and urban systems. In similar Mediterranean areas, it appears that avoiding excessive concentration of exotic trees in parks and gardens, increasing the species diversity of urban forests, and increasing the compositional heterogeneity of urban landscapes are promising avenues for limiting infestation risks.

CRedit authorship contribution statement

André Garcia: Data curation, Investigation, Writing – original draft. **Pedro Gonçalves Vaz:** Data curation, Formal analysis, Writing – original draft, Visualization, Writing – review & editing. **José Carlos**

Franco: Conceptualization, Writing – original draft. **Pedro Nunes:** Investigation. **Hervé Jactel:** Writing – original draft. **Manuela Branco:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2022.104515>.

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