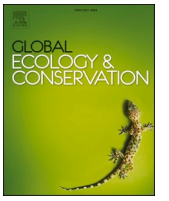
Global Ecology and Conservation 56 (2024) e03303



Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Original research article

Non-native palm affects arthropod communities and litter decomposition in an ongoing biome shift

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ARTICLE INFO

Keywords:
Arthropod herbivores
Arecaceae
Functional traits
Novel ecosystems
Ecosystem functioning
Invasive species

ABSTRACT

The emergence of novel ecosystems, characterized by shifts in species composition and interactions, abiotic conditions and altered ecosystem functioning, is a major and inevitable challenge to contemporary ecosystem management. This study examines the ecological implications of *Trachycarpus fortunei*, a non-native evergreen palm, currently involved in a biome shift from deciduous temperate forest to evergreen laurophyllous forest in the Southern European Alps. Specifically, we investigated the effects of *T. fortunei* encroachment in peri-urban forests on flying and ground-dwelling arthropod communities as well as on leaf-litter decomposition. We found that the presence of *T. fortunei* altered arthropod community composition, mostly by reducing the number of herbivore species. This effect was likely driven by the lower quality of palm leaves as a food source compared to deciduous, dicotyledonous tree leaves and by a lower plant richness in the herb and shrub layer. Furthermore, we observed higher rates of leaf-litter decomposition associated with increasing abundance of young palm trees, which was not explained by predictors commonly associated with litter decomposition (i.e., detritivore abundance, litter depth and air temperature). Hence, the slow decay of palm leaves appears to be counterbalanced by the favourable conditions for litter decomposition within dense palm stands. Overall, our findings indicate that high densities of the non-native palm species (*T. fortunei*) impacts herbivore

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https://doi.org/10.1016/j.gecco.2024.e03303
Received 24 April 2024; Received in revised form 6 November 2024; Accepted 10 November 2024
Available online 12 November 2024
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arthropod communities in the Southern European Alps, providing first evidence of possible effects on ecosystem functioning of this ongoing biome shift. These outcomes are integral components of the broader process of laurophyllisation in the study region, a phenomenon linked to climate warming and land use change, encompassing both native and non-native species.

1. Introduction

In the current era, the Anthropocene, ecosystems with altered species compositions and abiotic conditions are becoming more prevalent (Hobbs et al., 2006). These novel ecosystems often arise through the introductions of non-native species by human intervention, often in combination with changes in land use (Hobbs et al., 2009). Concurrently, human activities are increasingly causing climate to shift (IPCC, 2023), thereby also driving the emergence of novel ecosystems (Ordonez et al., 2016). While these novel ecosystems are generally categorized as of poorer biodiversity value, due to negative effects of the invaders on the local biota (Vilà et al., 2011), an increasing body of evidence is suggesting that non-native species can enhance biodiversity and ecosystem services (Fehr et al., 2020; Schlaepfer, 2018; Stohlgren et al., 2008). For example, in light of rapid climate change, ecosystems comprising non-native species might exhibit greater resilience compared to those composed solely of native species (Thomas, 2020). Yet, despite the growing prevalence of novel ecosystems, our understanding of the changes in the trophic structures and underlying processes within these ecosystems remains limited. Given the inevitability of novel ecosystems, addressing these knowledge gaps is crucial for the preservation of robust and diverse ecosystems (Hobbs et al., 2009).

The emergence of novel ecosystems can be intertwined with biome shifts, where changes in climate, land use or other human activities, such as the introduction of non-native species, contribute to rapid changes in biome distribution and composition (Boonman et al., 2022; Elsen et al., 2022). On the southern slope of the European Alps, the biome shift from temperate, deciduous forests to warm-temperate, evergreen, laurophyllous forests is termed "laurophyllisation" (Gianoni et al., 1988; Klötzli and Walther, 1999). These novel ecosystems, combining evergreen laurophyllous species with deciduous broadleaved species, have experienced substantial alterations in plant species, structure, and function, potentially influencing litter quality, decomposition processes, nutrient cycling, and carbon storage. However, the dynamics and processes of these emerging laurophyllous ecosystems remain poorly understood.

A plant family with high potential to create novel ecosystems, e.g., via laurophyllisation, is the Arecaceae palm family (Fehr et al., 2020) due to several reasons: (1) palms have been widely introduced beyond their native ranges, with some becoming naturalized or invasive, primarily due to extensive cultivation in agriculture and horticulture, particularly as ornamentals (Balslev et al., 2016; Broschat et al., 2014; Fehr et al., 2020). (2) The generally warm/tropical-adapted nature of palms makes them responsive to global warming, expanding their climatic range to higher latitudes and altitudes as observed in the Southern United States (Butler et al., 2011; Butler and Larson, 2020; Butler and Tran, 2017). (3) Within their native habitats, palms serve as ecosystem engineers, reshaping ecosystems through their unique physiognomy. Their large leaves alter the physical structure, affecting native plant communities and functioning. Dense palm stands can reduce light availability, supressing shade-intolerant plant species (Farris-Lopez et al., 2004; Wang and Augspurger, 2006). Accumulating palm litter impedes dicotyledonous tree seedling recruitment (Farris-Lopez et al., 2004; Peters et al., 2004; Young et al., 2014), and slow decomposition of palm leaves influences forest floor biomass (Arnason et al., 1982). (4) Palms often act as keystone species in their natural ecosystems, participating in mutualistic relationships with pollinators and influencing animal distribution and behaviour (Eiserhardt et al., 2011; Galetti et al., 2001; Henderson, 2002). However, several non-native palm species have been demonstrated to have detrimental impacts on local arthropod communities (Holmquist et al., 2011; Talley et al., 2012). Hence, given their multiple ecological roles, non-native palms could impact local ecosystem composition, interactions, and functioning, leading to the emergence of novel ecosystems (Fehr et al., 2020).

This study focuses on a specific case of a novel ecosystem in the Southern European Alps (Switzerland and Italy), generated by the process of laurophyllisation and undergoing a biome shift (Fehr et al., 2024; Klötzli and Walther, 1999). The non-native Chinese windmill palm (*Trachycarpus fortunei*) is driving this process, having escaped from cultivation as an ornamental species during the 20th century (Fehr et al., 2024). It is now widely naturalized in peri-urban forests, forming dense stands in the forest understory, particularly close to urban areas at low altitudes (Fehr et al., 2024; Fehr and Burga, 2016; Walther et al., 2007). Within the temperate deciduous forests of the Southern European Alps, *T. fortunei* represents a novel functional type of vegetation cover (Fehr et al., 2024). Compared to the leaves of the local tree community, *T. fortunei* leaves are bigger, evergreen and differ in physical and chemical characteristics (Kissling et al., 2019; Tomlinson et al., 2011). In alluvial forests and on northern slopes, dense *T. fortunei* stands have been demonstrated to reduce native plant species richness in the herb and shrub layers, as well as the richness (though not the abundance) of woody recruiting species (Fehr et al., 2024). However, no significant effects on native vegetation were observed on southern, western, and eastern slopes (Fehr et al., 2024). The Swiss national authorities for the environment classify *T. fortunei* as an invasive species (Info Flora, 2023; Tonellotto et al., 2022). Currently, empirical evidence regarding the effects of these novel palm-generated ecosystems on mesofauna communities and key ecosystem processes, such as litter decomposition, is still lacking.

To fill this knowledge gap, we compared arthropod community composition, richness and abundance and leaf litter decomposition in *T. fortunei*-invaded forests versus non-invaded forests. Arthropods, classified into different feeding guilds, served as biodiversity indicators due to their crucial roles in supporting higher trophic levels and ecosystem functions like decomposition and pollination (Handa et al., 2014; Obrist and Duelli, 2010). Our hypothesis posits that naturalizing *T. fortunei* in native forests induces changes in leaf functional type, physical habitat structure, microclimate and light regime, consequently affecting the distribution of multiple arthropod groups (Litt et al., 2014).

We also explored leaf litter decomposition as a representative of key ecosystem functions, such as organic matter decomposition, nutrient cycling, and soil structuring and fertilization (Cornwell et al., 2008; Lavorel et al., 2002). Key factors influencing this process include leaf litter traits, climate, and decomposer communities (Cornwell et al., 2008; García-Palacios, Mckie, et al., 2016; Handa et al., 2014), all likely affected by the presence of the non-native palm. The distinct physical and chemical characteristics of the palm's leaves differ from those of native deciduous trees (Kissling et al., 2019; Tomlinson et al., 2011). Furthermore, we anticipate that the large, evergreen leaves influence the microclimate by providing shading, potentially leading to increased moisture levels the creation of darker habitats favorable for decomposers (Hassall and Tuck, 2007).

2. Methods

2.1. Study region

The study took place in the Southern European Alps in Southern Switzerland and Northern Italy, in areas surrounding the cities of Locarno, Lugano, Varese and Verbania (Table A.1). The climate there is characterized as warm-temperate. According to the climate normals 1981–2010 (MeteoSwiss, 2023), mean annual precipitation of Lugano (273 m asl) is 1567 mm with monthly minima in winter and monthly maxima in early summer. Mean annual temperature of Lugano is 13 °C. Mean temperature of the coldest month (January) is 3.8 °C whilst the mean temperature of the warmest month (July) is 22.6 °C. Most bedrock in the study region is crystalline rock but a few areas with limestone exist (Labhart, 2005).

The vegetation on crystalline rocks consists of chestnuts (*Castanea sativa*), oaks (*Quercus robur*, *Q. petraea* and *Q. pubescens*) or linden (*Tilia cordata* and *T. platyphyllos*) (Conedera et al., 2018). On limestone, the dominant tree species include the European hop-hornbeam (*Ostrya carpinifolia*) and the manna-ash (*Fraxinus ornus*) (Ceschi, 2006). Since the 1980s, non-native evergreen species mainly originating from Asia (*T. fortunei*, *Cinnamomum* spp., *Prunus laurocerasus*, and *Elaeagnus* spp.) are escaping from cultivation as ornamentals and are spreading in the peri-urban forests (Gianoni et al., 1988; Walther et al., 2001) with the Chinese windmill palm (*T. fortunei*) being one of the most widespread ones (Walther et al., 2007).

2.2. Sampling design

We randomly selected ten sites with high density populations of *T. fortunei*. At each site, we installed paired plots: one invaded plot (20 m × 20 m) with a high density of *T. fortunei* and one control plot (20 m × 20 m) where *T. fortunei* was (nearly) absent. Paired plots were at least 25 m apart to minimize effects of neighbouring palms (mean distance = 111.13 m; maximum distance = 469.98 m). To ensure consistency in geomorphological and environmental conditions, paired plots were deliberately chosen with similar forest community, slope, elevation, and aspect (Figure A1).

2.3. Arthropod sampling and identification

In each plot, we installed two window traps (i.e., polytraps from Brustel, 2012) and two pitfall trap triplets to capture flying and ground-dwelling arthropods respectively (details in Appendix B). Sampling occurred in two four-week periods (May 24 - June 19, 2019, and July 24 - August 24, 2019), with traps emptied weekly to minimise bad weather impacts. All arthropods were preserved in 70 % ethanol. Due to heavy rain in two weeks (August 2 - August 16, 2019), samples from those weeks were discarded. To mitigate short-term fluctuations or outliers, samples from all periods were pooled for both trap types in each plot.

Table 1
Litterbag treatments.

Treatment ID	Treatment	Exposure time	Species composition	Mass [g]
F	Fast-decomposing litter of common deciduous broadleaved species	72 days	*Fraxinus excelsior*	0.67
			Robinia pseudoacacia	0.67
			Tilia cordata	0.67
FP	Fast-decomposing litter of common deciduous broadleaved species + non-native palm litter	72 days	*Fraxinus excelsior*	0.5
			Robinia pseudoacacia	0.5
			Tilia cordata	0.5
			Trachycarpus fortunei	0.5
P	Non-native palm litter	72 days	*Trachycarpus fortunei*	2.0
S	Slow-decomposing litter of common deciduous broadleaved species	254 days	*Castanea sativa*	1.33
			Quercus sp.	0.67
SP	Slow-decomposing litter of common deciduous broadleaved species + non-native palm litter	254 days	*Castanea sativa*	0.67
			Quercus sp.	0.67
			Trachycarpus fortunei	0.67
PP	Non-native palm litter	254 days	*Trachycarpus fortunei*	2.0

To compare arboreal arthropod communities between *T. fortunei* and native broadleaved woody species, we collected arthropods by beating the leaves of 10 randomly selected palm trees in invaded plots and branches of 10 randomly selected native woody species individuals in control plots 20 times using a wooden stick and capturing the falling arthropods with a beating sheet. Beating was done on two sunny days (May 21, 2019 and August 19, 2019).

All individuals were identified at the species level by experts (see Acknowledgements) and assigned to three main feeding guilds (herbivores, carnivores and detritivores) based on own data, literature (Gossner et al., 2015; Sattler et al., 2010), different taxa-specific databases such as Fauna Indicativa (Klaiber et al., 2017), BETSI for different soil and ground-dwelling groups (Pey et al., 2014), and Syph the Net for overflies (Speight, 2017), as well as expert knowledge (see Acknowledgment). If a species occupied a single trophic level, it was assigned a value of 1 (100 %). When its trophic level was split between two or three levels, each was assigned a value of 0.5 (50 %) or 0.33 (33 %), respectively. We determined arthropod biomass by drying and weighing most specimens to obtain direct measurements. For individuals retained by experts for collection purposes post-identification, biomass values were estimated using two approaches. For taxa within Coleoptera and one Araneae species, biomass was extrapolated based on the mean weight of other individuals of the same species or genus. For all bees and wasps, biomass was estimated using an allometric regression model based on length, taxon and region (Model 5: log 10 (mass) ~ TaxReg × log 10 (length)) derived from Sohlström et al. (2018).

2.4. Litter decomposition experiment

To examine the effect of *T. fortunei* on litter decomposition, we monitored mass loss of leaf-litter (Graça et al., 2005) in invaded and control plots using six litterbag treatments containing palm leaves and leaves of deciduous broadleaved tree species (Table 1). The deciduous tree species represented the five most common species along the slow-fast decomposition rate continuum (Finerty et al., 2016) across all 20 plots, and with at least one present in each plot. Grouped into fast- and slow-decomposing species (Finerty et al., 2016; Handa et al., 2014), the different treatments enabled us to test the decomposition rate of leaves of fast-decomposing species (F), slow-decomposing species (S) and the non-native palm *T. fortunei* (P for short exposure - 72 days - and PP for long exposure - 254 days), in response to the presence of *T. fortunei*. Treatments with a mix of deciduous and palm leaves (FP and SP) allowed testing for possible interactive effects of *T. fortunei* leaves on decomposition rates of common broadleaved species, e.g., by changing the chemical or biotic environment. Each litterbag contained 2 g of fully developed, undamaged, senescent leaves (Handa et al., 2014), with the amount weighted based on species abundance in the plots (details in Appendix C). Litterbags had a 5 mm mesh size on top for macrofauna access and 1 mm mesh size on the bottom to prevent leaf fragment loss while allowing access for decomposing mesofauna and microorganisms.

On March 7, 2019, three replicates of the litterbag set, each containing six litter treatments, were randomly positioned in each of the 20 plots (totalling 360 litterbags). Our aim was to retrieve the bags after approximately 50 % of the initial weight had been lost. We estimated the experiment duration by regularly weighing additional litterbags under similar conditions. After 72 days, we collected litterbags with fast-decomposing leaves (F), fast-decomposing and palm leaves (FP) and palm leaves alone (P). Litterbags with slow-decomposing litter (S, SP and PP) were collected after 254 days. Of the initially positioned 360 litterbags, we successfully retrieved 349, with the remaining 11 lost or destroyed. After collection, the remaining leaf litter was gently cleaned, dried for 48 hours at 70°C and weighed.

To compare leaf litter traits of the common deciduous species (data from Finerty et al. 2016; Table C.1) with those of *T. fortunei*, we quantified total carbon and nitrogen concentration (%), along with leaf tensile strength (N mm^{-1}) of *T. fortunei* leaves. These traits are recognized for their substantial influence on leaf litter decomposition (Finerty et al., 2016; Garcia-Palacios et al., 2016).

2.5. Environmental variables

For each plot, all plant species were identified to the species level. The coverage of each species was estimated for each forest layer (i.e., herb layer: < 1 m; shrub layer: 1–3 m; lower tree layer: > 3–5 m; upper tree layer: > 5 m) using the Braun-Blanquet scale (Braun-Blanquet, 1964). Shrub cover (excl. palms) and shrub cover (incl. palms) represented the sum of species cover without and with palms, respectively. In a 5 m × 20 m rectangle (centered in the plot and parallel to the contour lines on slopes), *T. fortunei* individuals were counted and classified into the following height classes: < 50 cm; 50–130 cm; > 130 cm and maximum stem diameter not reached. In the entire plot (400 m^2, 20 m × 20 m), *T. fortunei* individuals that have reached the maximum stem diameter were counted and their stem height was measured (Rivera et al., 2023). Individuals with a stem height below 1.5 m were classified as juvenile, while those above 1.5 m were considered mature trees. Each plot was subdivided into eight small subplots (2 m × 2 m) (Figure S1). In each subplot, litter depth was measured at two random locations (separated by a minimum distance of 50 cm). Litter depth per plot represented the average of the 16 measurements. Data collection occurred between March 2019 and September 2020.

In each plot, we installed one temperature logging iButton (DS1922L, temp. resolution 0.5°C, logging interval 1.5 hours) to measure air temperature. In invaded plots, the loggers were attached to a mature *T. fortunei* individual, while in control plots, they were attached to a broadleaved tree, 20 cm above the ground on the north-facing side. Temperature was recorded from the beginning of the litter decomposition experiment (March 7, 2019) to October 17, 2019 (one month before the litter experiment ended on November 15, 2019)). Using daily mean temperatures, we calculated growing degree days (GDD >10 °C) for each plot, serving as an index for available heat affecting plant and arthropod growth and maturation.

2.6. Data analysis

All statistical analyses were performed in R (R Core Team, 2022). For the binary comparisons of arthropod species richness, abundance and biomass between control and invaded plots, we performed non-parametric, paired Wilcoxon tests. Compositional patterns of arthropod communities between control and invaded plots were visualized through non-metric multidimensional scaling (NMDS) based on Hellinger-transformed Bray-Curtis dissimilarity using the 'metaMDS' function with three dimensions in the R package 'vegan' (Oksanen et al., 2020). Compositional differences between arthropod communities in invaded and control plots were assessed via pairwise permutational multivariate analysis of variance (PERMANOVA) on Hellinger-transformed Bray-Curtis dissimilarity using the 'adonis2' function in the R package vegan (Oksanen et al., 2020). To examine the relationship between arthropod species richness, abundance, and biomass (response variables) and juvenile and mature palm abundance (predictor variables), generalized linear mixed models (GLMMs) were employed. Models for species richness and abundance used a Poisson distribution, while models for biomass used a Gaussian distribution. Plot pair was included as a random effect in all models. To identify further environmental variables affecting arthropod species richness and abundance, we fitted Poisson-distributed GLMMs with total plant species richness, shrub cover (excl. palms), total shrub cover (incl. palms) for window traps. For pitfall traps, the same predictor variables plus litter depth were fitted and site was treated as a random effect.

To investigate differences in litter mass loss between litter bag types, GLMMs were employed with litter mass loss as the response variable, treatment as the predictor variables and plot ID as a random effect. Litter mass loss differences between control and invaded plots were tested using GLMMs with litter mass loss as the response variable, plot type as the predictor variable and site as a random effect. To identify potential environmental variables affecting litter mass loss after 72 and 254 days, two GLMMs with a Gaussian distribution were fitted. The predictor variables included detritivore abundance in pitfall traps, juvenile palm abundance, mature palm abundance, litter depth and growing degree days ($> 10^{\circ}$ C) with plot ID as a random effect. All GLMMs were performed with the 'glmer' and 'lmer' functions in the R package lme4 (Bates et al., 2015). The marginal and conditional R^2 for all the GLMMs were calculated with the 'r2_nakagawa' function in the R package performance (Lüdecke et al., 2021). The marginal R^2 represents the proportion of variance explained solely by the fixed effects, while the conditional R^2 describes the variance explained by both the fixed and random effects (Schielzeth and Nakagawa, 2013)

To test for potential non-additive effects of palm leaves on the leaf litter decomposition rate of common broadleaved species, we compared the average measured mass loss of treatment FP and SP within each plot with the expected mass loss of the treatment FP and SP. The expected mass loss for treatments FP and SP is the sum of mass loss of the treatments F and P divided by 2, and S and PP divided by 2, respectively, assuming a homogenous decomposition rate for treatments F, S, P and PP in each plot. We then tested, if the difference between the measured and the expected mass loss was significantly different from zero using a t-test. Prior to the t-test, we checked the normality of the variables using a Shapiro–Wilk test.

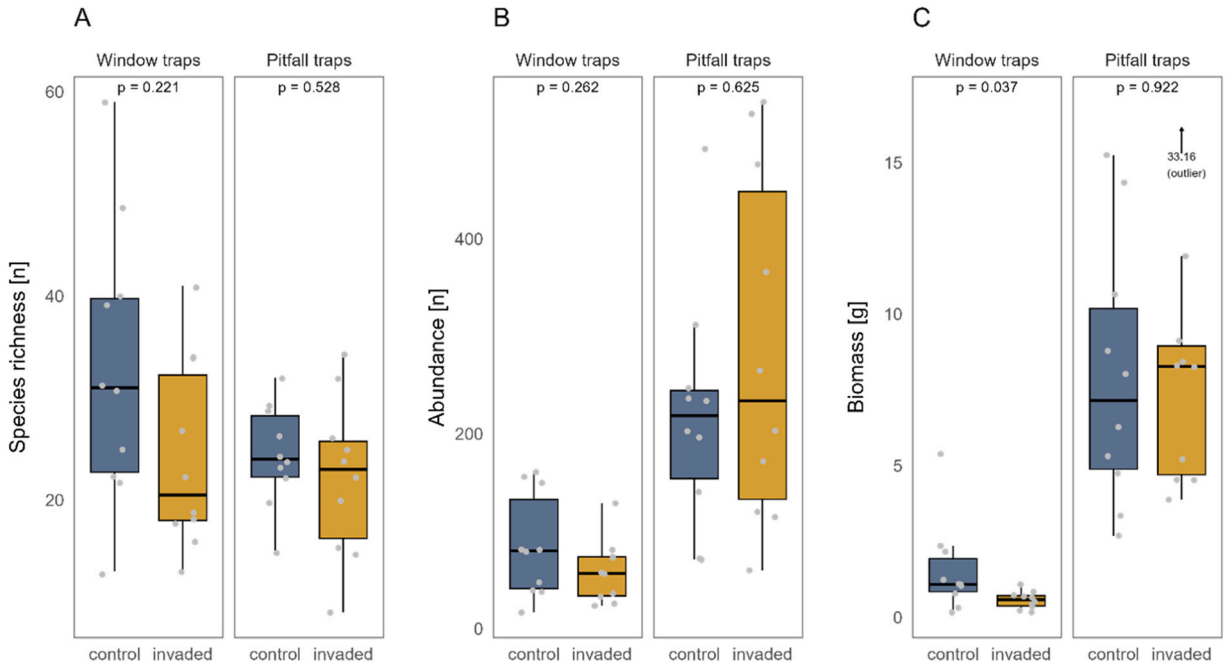


Fig. 1. Species richness (A) abundance (B) and biomass (C) for all arthropods per trap type (window traps and pitfall traps combined). Blue boxes represent control plots and yellow boxes represent invaded plots. P-values refer to the paired Wilcoxon-tests, testing the difference of the arthropod species richness, abundance and biomass, respectively, between control and palm-invaded plots.

3. Results

3.1. Arthropod communities from window and pitfall traps

In total, we captured 6488 arthropods (mean per plot = 324, min = 118, max = 601) belonging to 357 species (mean per plot = 49.8, min = 28, max = 85) using pitfall (5048 individuals, 151 species) and window traps (1440 ind., 257 spp.). Mean arthropod species richness showed no significant difference between control and invaded plots for both window ($p = 0.221$) and pitfall traps ($p = 0.528$). Similarly, there was no significant difference in mean arthropod abundance between control and invaded plots in both window traps ($p = 0.262$) and pitfall traps ($p = 0.625$) (Fig. 1A & 1B). In contrast, arthropod biomass in window traps was reduced by 36.5 % in invaded compared to non-invaded plots ($p = 0.037$), whilst for pitfall traps, no significant difference of the biomass between control and invaded plots was detected ($p = 0.922$) (Fig. 1C).

Comparing arthropod species richness and abundance of the three main feeding guilds between control and invaded plots, we found a significantly reduced species richness ($p = 0.041$) of herbivores in pitfall traps in invaded plots (Fig. 2A). We also identified weak trends of a reduced herbivore species richness in invaded plots in window traps ($p = 0.202$) (Fig. 2A) and for a reduced herbivore abundance in window ($p = 0.275$) and pitfall traps ($p = 0.114$) (Fig. 2B). For carnivores and detritivores, no significant differences in species richness and abundance between invaded and control plots were detected for both window and pitfall traps (Fig. 2A & 2B). However, the variation of the detritivore abundance in pitfall traps in invaded and control plots was large (Fig. 2B).

Arthropod composition differed significantly between invaded and control plots for both window ($R^2 = 0.08$, $p = 0.008$) and pitfall traps ($R^2 = 0.08$, $p = 0.014$) (Fig. 3, Table D.1). The composition of the different feeding guilds differed significantly between invaded and control plots for detritivores ($R^2 = 0.10$, $p = 0.018$, Figure D.1), but not for herbivores ($R^2 = 0.05$, $p = 0.176$, Figure D.2) or carnivores ($R^2 = 0.05$, $p = 0.101$, Figure D.3).

The patterns when investigating the relationship of arthropod species richness, abundance and biomass with varying palm abundance are consistent with our previous findings (Fig. 1 & 2; Table D.2 and Table D.3): We found that for window traps, total arthropod species richness (R^2 cond. = 0.628, R^2 marg. = 0.201, $p = 0.034$) and herbivore species richness (R^2 cond. = 0.619, R^2 marg. = 0.181, $p = 0.006$) were negatively related to mature palm abundance (Fig. 4A; Table D.2). Neither arthropod biomass, total arthropod abundance, herbivore abundance nor species richness and abundance of carnivores and detritivores were significantly related to mature palm abundance in window traps. For pitfall traps, we found that mature palm abundance was negatively related to

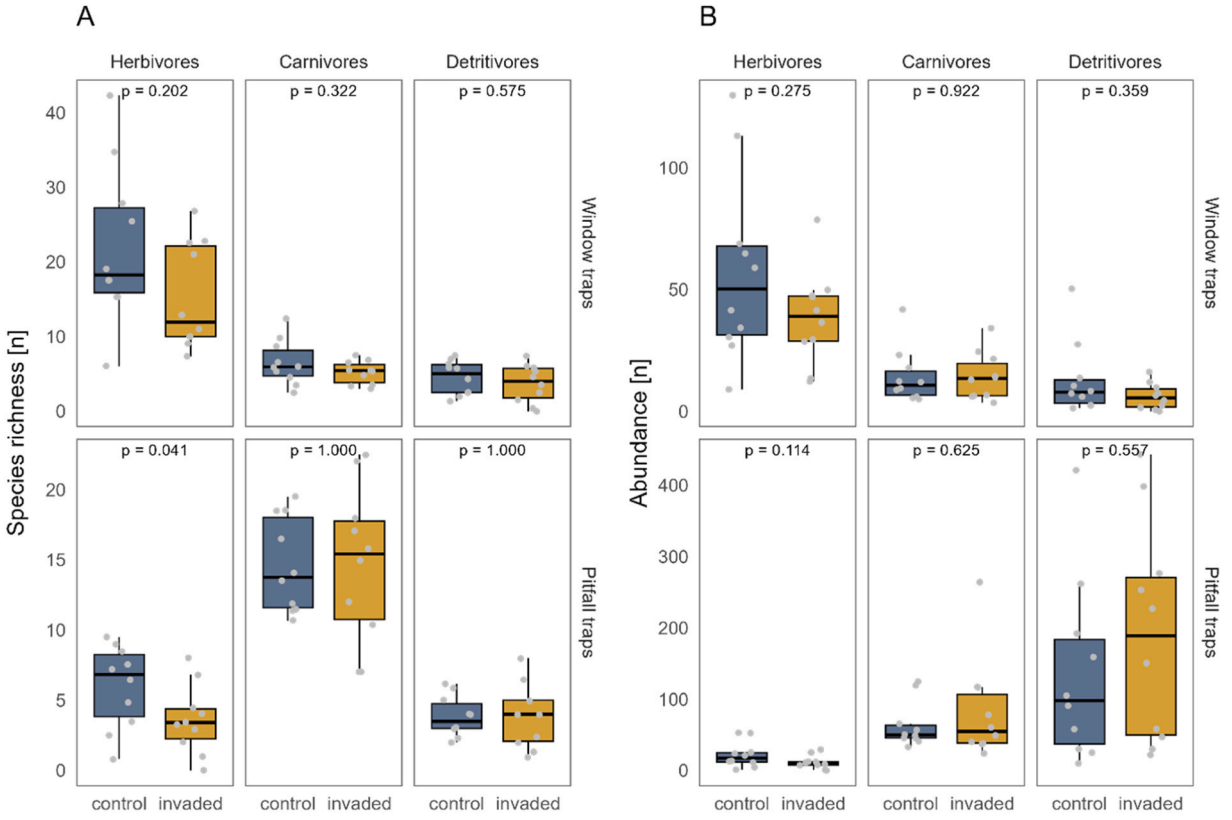


Fig. 2. Arthropod richness (A) and abundance (B) for the three main feeding guilds for each sampling method (window and pitfall traps). Blue boxes represent control plots and yellow boxes represent invaded plots. P-values refer to the paired Wilcoxon-tests, testing the difference of the arthropod richness and abundance, respectively, between control and palm-invaded plots.

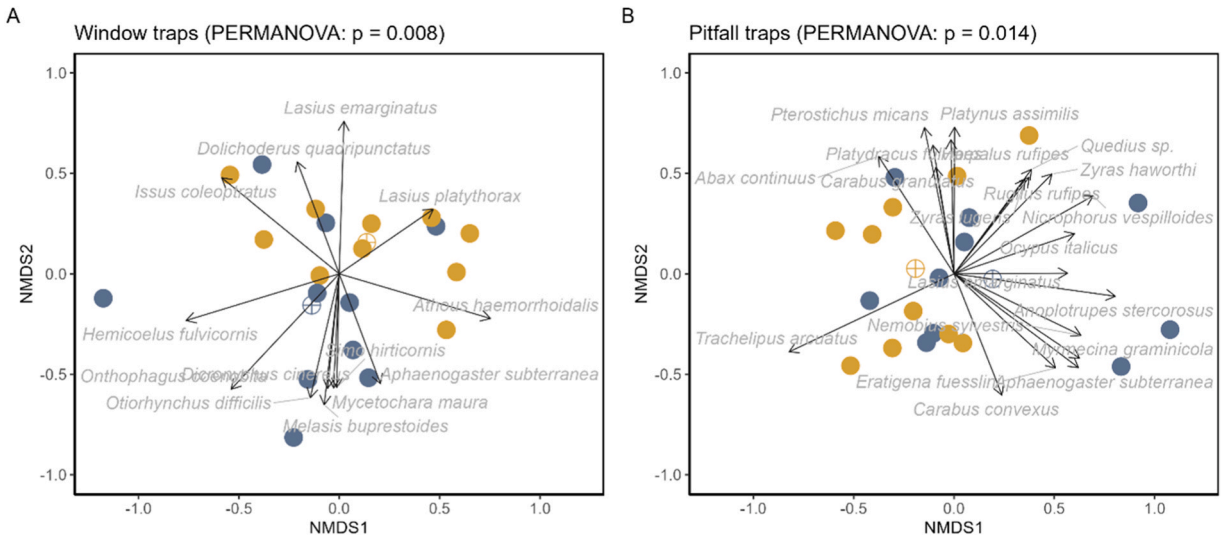


Fig. 3. Non-metric multidimensional scaling (NMDS) ordination plot for arthropods sampled with pitfall (A) and window traps (B) in the 20 plots. Blue dots represent control plots with no or very few individuals of *T. fortunei* and yellow dots represent invaded plots dominated by *T. fortunei*. The blue and yellow circle plus symbols show the centroids of the control and invaded plots, respectively. The pairwise PERMANOVA (strata = site) was conducted using the adonis2 package.

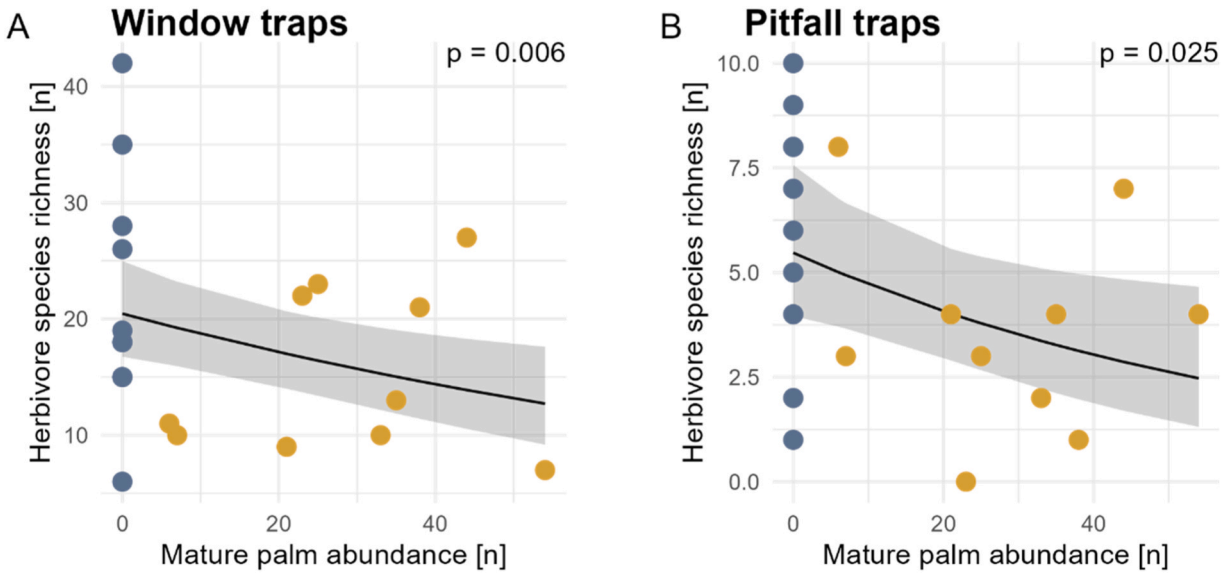


Fig. 4. Herbivore species richness in window (A) and pitfall traps (B) in relation to mature palm abundance. Blue dots represent control plots, yellow dots represent palm-invaded plots. The black line represents the best fit of the generalized linear mixed model and the grey shading represents the ±95 % confidence interval.

herbivore species richness (R^2 cond. = 0.475, R^2 marg. = 0.188, p = 0.025) (Fig. 4B), but as for window traps, the other predictors were not significant.

Juvenile palm abundance was negatively correlated to total arthropod species richness (R^2 cond. = 0.663, R^2 marg. = 0.335, p < 0.001) and herbivore species richness (R^2 cond. = 0.682, R^2 marg. = 0.305, p < 0.001), captured by window traps, but not with other tested response variables (Table D.3).

3.2. *Arthropod communities from branch beating*

From branch beating we captured 259 arthropods (mean = 14, min = 1, max = 56) belonging to 60 species (mean = 7, min = 1, max = 13) which is much less than what we captured using window and pitfall traps. We found that arthropod richness on native

woody species was significantly higher than that on individuals of *T. fortunei* ($p = 0.038$; Figure D.4). There was also a trend for a higher arthropod abundance on native woody species than on *T. fortunei* individuals ($p = 0.052$; Figure D.4). These differences can be mainly attributed to the higher richness ($p = 0.009$) and abundance ($p = 0.014$) of herbivores on native woody species Figure D.5). Richness and abundance of carnivores and detritivores did not differ significantly between native woody species and individuals of *T. fortunei*.

3.3. Environmental variables affecting arthropod communities

In window traps (Table D.4, Figure D.6), total arthropod species richness (R^2 cond. $= 0.689$, R^2 marg. $= 0.421$, $p < 0.001$) and herbivore species richness (R^2 cond. $= 0.666$, R^2 marg. $= 0.453$, $p < 0.001$) were positively related to shrub cover (excluding palm cover). Additionally, herbivore species richness (R^2 cond. $= 0.666$, R^2 marg. $= 0.453$, $p = 0.023$) was negatively related to shrub cover (including palm cover).

For the arthropods sampled with pitfall traps (Table D.5, Figure D.7), litter depth was positively related to total arthropod species richness (R^2 cond. $= 0.492$, R^2 marg. $= 0.464$, $p = 0.004$) and herbivore richness (R^2 cond. $= 0.477$, R^2 marg. $= 0.410$, $p = 0.009$) and negatively related to detritivore abundance (R^2 cond. $= 0.748$, R^2 marg. $= 0.302$, $p = 0.035$). Shrub cover (including palm cover) was positively correlated with total arthropod richness (R^2 cond. $= 0.492$, R^2 marg. $= 0.464$, $p = 0.012$) and abundance (R^2 cond. $= 0.434$, R^2 marg. $= 0.237$, $p = 0.023$), as well as carnivore (R^2 cond. $=$ NA, R^2 marg. $= 0.172$, $p = 0.048$) and detritivore abundance (R^2 cond. $= 0.748$, R^2 marg. $= 0.302$, $p = 0.004$).

3.4. Leaf-litter decomposition

The litter of common broadleaved deciduous species decomposed significantly faster than palm litter, with mixed litterbags (broadleaved plus palm litter) showing intermediate decomposition rates (Fig. 5). On average, litter of fast-decomposing deciduous species decomposed 4 times faster than palm litter after 72 days, while litter of slow-decomposing deciduous species decomposed 1.5 times faster than palm litter after 254 days. Comparing decomposition rates between invaded and control plots for various litterbag types (F, FP, P, S, SP, PP) revealed no significant differences (Figure E.1). However, a positive relationship between litter



Fig. 5. Percentage litter mass loss per day for litterbags consisting of fast-decomposing litter of common broadleaved species (F), a mixture of litter of fast-decomposing common broadleaved species and palm litter (FP) and for palm leaf litter (P) after 72 days and for slow-decomposing litter of common broadleaved species (S), a mixture of litter of slow-decomposing common broadleaved species and palm litter (SP) and palm leaf litter (PP) after 254 days. Mass loss differences between litter bag types were tested using GLMMs with site as random effects.

decomposition rate (after 254 days) and juvenile palm abundance was found (R^2 cond. = 0.263, R^2 marg. = 0.177, p = 0.023; Fig. 6A). Additionally, decomposition rate correlated positively with herb layer cover (including palms) (R^2 cond. = 0.263, R^2 marg. = 0.177, p = 0.003; Fig. 6B), while mature palm abundance, detritivore abundance, litter depth and growing degree days (> 10 °C) showed no significant relation to litter decomposition rate. No significant relationships were found in the short-term (after 72 days) between the decomposition rate and the above-mentioned predictor variables (see Table E.1 for details).

An interactive antagonistic effect of palm litter was observed for fast-decomposing litter after 72 days, but not for slow-decomposing litter after 254 days (Figure E.2): Fast-decomposing litter exhibited reduced decomposition when mixed with palm leaves in both invaded (p = 0.002) and control plots (p = 0.027) after 72 days. In contrast, adding palm litter to slow-decomposing broadleaved litter did not affect decomposition rate in either control or invaded plots after 254 days.

Senescent *T. fortunei* leaves exhibited higher tensile strength (M = 40.15 N) and a higher C:N ratio (M = 62.42) compared to senescent leaves of broadleaved species (Table C.1).

4. Discussion

In the Southern European Alps, where peri-urban forests are experiencing an influx of the non-native palm *Trachycarpus fortunei*, we investigated its impact on local arthropod communities and litter decomposition. This invasion is part of a larger climate change-driven biome shift, from deciduous temperate to evergreen subtropical vegetation in areas near evergreen plant source populations, in line with emerging warming-linked biome shifts around the world (Boonman et al., 2022; Penuelas and Boada, 2003). This shift signifies the emergence of a novel ecosystem (Hobbs et al., 2006), notably as palms of the genus *Trachycarpus* have been absent from Europe since their cooling-linked extinction millions of years ago (e.g., Gregor, 1980; Postigo Mijarra et al., 2009). While we did not observe significant differences in total arthropod species richness and abundance between plots with a high density of palms and without the palm, we did detect a change in community composition. Dense palm stands negatively impacted herbivore richness, although no significant differences were observed in the richness of carnivores and detritivores, or the abundance of feeding guilds (herbivores, carnivores, and detritivores) between invaded and uninvaded plots. Long-term litter decomposition rates were positively correlated with juvenile palm abundance but were decoupled from mature palm abundance, detritivore abundance, litter depth, or temperature. Overall, the majority of the results of this study, despite being significant, show weak to moderate effects. Our findings suggest that *T. fortunei* affects herbivore communities in the Southern European Alps, with potential implications for future ecosystem functioning, that remain to be fully understood and quantified. These effects also shed light on the broader consequences of the ongoing laurophyllisation process in the study region, involving both native and non-native species (Alessi et al., 2019; Fehr et al., 2024).

4.1. Arthropod species richness, abundance and composition

Our findings suggest a more pronounced impact of *T. fortunei* palms on flying arthropods than on ground-dwelling arthropod

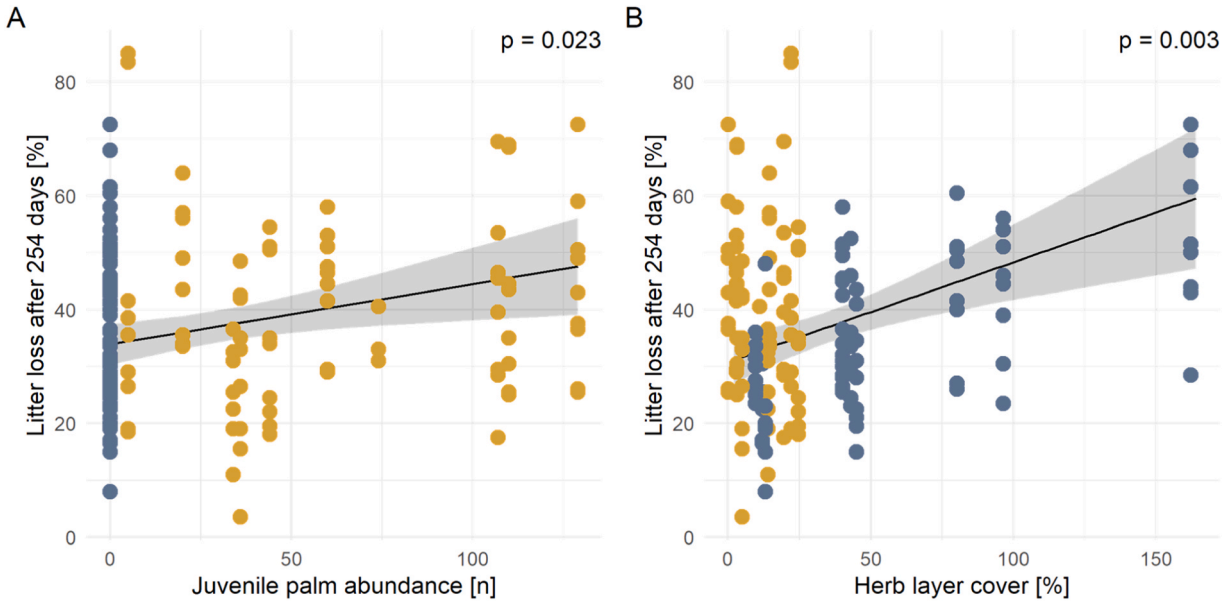


Fig. 6. Percentage leaf-litter loss of litter bags after 254 days in relation to juvenile palm abundance (A) and herb layer cover (B). Blue dots represent control plots, yellow dots represent palm-invaded plots. The black lines represent the best fit of the generalized linear mixed model and the grey shadings represent the ±95 % confidence interval.

communities, indicating a greater susceptibility of above-ground habitats and resources to *T. fortunei* influence compared to ground habitats. This could be attributed to alterations in the physical structure of the forest understory, particularly the increased closure in high-density stands of *T. fortunei* (Fehr et al., 2024) as non-native palms have been frequently reported to influence the physical structure, further impacting the ecological dynamics within these ecosystems (Fehr et al., 2020). However, uncertainties persist regarding whether the observed weak effect on total arthropod species richness and abundance results from a time delay in response (Crooks et al., 1999) or remains weak due to the still small size of monodominant palm stands relative to the matrix vegetation.

We also found that *T. fortune*i negatively affects herbivorous arthropods likely due to lower native plant richness in the herb and shrub layer (Fehr et al., 2024) that are essential food sources for many native herbivores (Schirmel et al., 2016). More generally, this impact can be attributed to the recalcitrant, lignified leaves of *T. fortunei* compared to common deciduous species (Table C.1). These leaves, typical of palm family members (Dominy et al., 2008; Tomlinson et al., 2011), likely make *T. fortunei* leaves an unsuitable food source for most herbivorous arthropods (Grubb et al., 2008; Peeters et al., 2007), as demonstrated for other palm species outside their native range (Holmquist et al., 2011; Talley et al., 2012). This finding aligns with research in subtropical deciduous and evergreen forests, indicating that even within their native range, evergreen trees attract fewer herbivores than deciduous species (Liu et al., 2022).

Arthropods dwelling on *T. fortunei* leaves showed significantly lower richness and abundance compared to arthropods on native woody species, further supporting the palm's limited suitability as a food source and habitat. Flying herbivore richness was positively linked to native plant cover, emphasizing the reliance of resident herbivores on native plants. In contrast, total shrub cover (including *T. fortunei*), correlated positively with ground-dwelling carnivore and detritivore abundance, suggesting that the dense shrub layer supports suitable habitats and resources for these arthropods. Increased shrub cover may facilitate carnivores in hunting prey (Pearson, 2009), while detritivores, mainly isopods, benefit from the more humid and shaded microhabitats created by the increased shrub cover (Warburg et al., 1984). In line herewith, a recent study in a wet deciduous Canadien woodland invaded by the alien shrub species *Frangula alnus* showed inly weak decreases in detritivore diversity indices (Roberge et al., 2024).

The overall arthropod richness and abundance appeared only little impacted by this palm invasion, but there was a significant change in arthropod community composition, indicating a species turnover driven by dense *T. fortunei* stands. The palm likely alters environmental conditions, favouring certain species while displacing others or altering their functional contribution in the ecosystem. We hypothesize that despite these changes, the trophic functioning of palm-invaded ecosystems is likely still be upheld, albeit by different organisms. Our results underscore the need to consider changes in community composition alongside traditional abundance and diversity metrics when evaluating the impact of invasive species.

In summary, our findings show a substantial impact of dense *T. fortunei* stands on herbivorous arthropod communities and arthropod community composition, suggesting a complex relationship between arthropods, native and non-native evergreen and deciduous plants, and climate change within the ecosystem. Furthermore, our results indicate that the emerging novel ecosystems in the region may be able to maintain ecosystem functioning through a reorganisation of trophic interactions.

The expansion of *T. fortunei*, driven by climate change, is part of a broader biome shift from deciduous temperate to evergreen subtropical vegetation, involving various other evergreen plant species (Fehr et al., 2024). In addition to impacts from invasive palms, arthropod communities are therefore likely influenced by other evergreen species. Furthermore, arthropod communities likely also experience direct climate change-induced shifts, which may alter trophic dynamics, affecting ecosystem functionality (Di Marco et al., 2023). These large-scale and irreversible dynamics highlight the need for further studies on the functioning of novel ecosystems, including the resilience and rewiring capacity of trophic processes in arthropod communities.

4.2. Litter decomposition

Comparing *T. fortunei* litter decomposition rates with common deciduous broadleaved tree species (i.e., *Fraxinus excelsior*, *Robinia pseudoacacia*, *Tilia cordata*, *Castanea sativa*, *Quercus* sp.) across all plots, we found slower decomposition in *T. fortunei* leaves. This aligns with our expectations based on inherent monocot leaf traits (Dominy et al., 2008) and palms in general (Ewel, 1976) and more specifically, in the case of *T. fortunei*: Our measurements on *T. fortunei* leaves revealed very high tensile strength and a high C:N ratio (Table C.1). Such toughness and rigidity make these leaves less prone to detritivore consumption (Brousseau et al., 2019; Pérez-Harguindeguy et al., 2000) resulting in a slower decomposition compared to the leaves of the broadleaved species. Despite anticipating higher litter accumulation in dense palm stands, *T. fortunei* exhibits a pattern quite common for palms (Hodel, 2009): a significant portion of leaves remains attached to the stem after desiccation (authors observation), leading to decomposition when still attached. Consequently, the expected conspicuous accumulation of palm leaf litter in densely populated *T. fortunei* stands does not occur as anticipated.

When comparing the decomposition rates of different litter treatments (leaves of common deciduous broadleaved tree species versus palm leaves) between palm-invaded plots and non-invaded control plots, no significant differences were found. However, the mass loss of more recalcitrant, slow-decomposing litter of broadleaved species (*Castanea sativa* and *Quercus* sp.) and the non-native palm after 254 days, was positively correlated with juvenile palm density and herb layer cover (including palms). Given the established role of moisture in governing decomposition processes (García-Palacios, Shaw, et al., 2016), the increased humidity resulting from the shaded conditions created by the large palm leaves may have accelerated decomposition. Direct shading could also play a role, as decomposers often avoid light to reduce predation risk (Hassall and Tuck, 2007). Other factors known to influence litter decomposition rates, such as detritivore abundance, litter depth, and growing degree days ($>10\,^{\circ}C$) showed no significant relationship, possibly due to their negligible effects or being overshadowed by other drivers of litter decomposition.

The investigation into interactive effects of palm leaves on the decomposition of common broadleaved tree species revealed that,

after 72 days, fast-decomposing litter decomposed more slowly when mixed with palm litter. However, the addition of palm leaves to slow-decomposing leaves of broadleaved species did not significantly affect the decomposition rate after 254 days. This suggests that palm leaves can reduce the decomposition rate of fast-decomposing litter in the short term but do not substantially impact the decomposition rate of slow-decomposing leaves of broadleaved species over the long term. This antagonistic effect of combined non-native palm litter with fast-decomposing litter may be attributed to inhibitory plant secondary compounds with anti-microbial properties observed in fruits of *T. fortunei* (Ahmed et al., 2017).

Overall, our findings reveal that palm leaves decompose slower than common broadleaved trees in dense *T. fortunei* stand, but favourable environmental conditions within dense palm stands counterbalance this, accelerating decomposition.

4.3. Future dynamics and ecosystem-level implications

While observing moderate effects of dense stands of *T. fortunei* on arthropod communities at the plot level, the broader ecological consequences depend on the future extent of dense palm populations. If dense non-native palm populations remain confined to limited areas (mainly in peri-urban forests) as is currently the case, they might generate landscape-level heterogeneity. Environmental heterogeneity, an important determinant of biodiversity (Stein et al., 2014), are generally associated with higher species richness (Katayama et al., 2014). Thus, the non-native palm could enhance the landscape-scale beta-diversity (i.e. diversity among patches), whilst at the same time causing a decline in species richness at the local, alpha-diversity, level. On the contrary, if habitats colonized by the non-native palm become dominant in the landscape, heterogeneity might decline, resulting in biotic homogenization with possible further implications on ecosystem processes and functioning and overall resilience (Bartley et al., 2019). However, abiotic heterogeneity might result in mosaics of evergreen and deciduous trees and impede the formation of extensive, continuous stands of non-native palms (Fang et al., 2017). The future spreading dynamics of *T. fortunei* beyond peri-urban forests depend on factors such as dispersal behaviour and disequilibrium dynamics (Svenning and Sandel, 2013) triggered by climate change, the immigration of pests and competing evergreen native and non-native species.

High-density populations of *T. fortunei* are likely to primarily establish in peri-urban forests, facilitated by seed input from birds associated with cultivated individuals (Fehr et al., 2024). The long maturation period of over 15–20 years for naturalized fertile *T. fortunei* individuals, along with the short dispersal distance of less than 200 m by birds (Conedera et al., 2018), suggests a slow spread away from initial escaped individuals. Also, limited light availability in the understory often leads to irregular flowering, reduced fruit production, and premature shedding of immature fruits (Koike, 2006). Consequently, *T. fortunei* stands, except those near settlements, are expected to be confined to sites with ample light availability such as disturbed forests, riversides, cliffs, and forest edges (Koike, 2006). Recent observations note recurring abiotic stress factors and biotic disturbances in dominant chestnut forests, including summer drought, chestnut blight, ink disease, and chestnut gall wasp (Conedera et al., 2021). These disturbances may result in increased forest clearings, creating suitable conditions for new colonization by *T. fortunei* and other plant species (Dalle Fratte et al., 2019).

Accumulating evidence suggests that non-native species, initially experiencing milder pressures from predators and competitors than native species (enemy-release hypothesis) (Keane and Crawley, 2002), may subsequently decline due to the arrival of natural enemies like pathogens and pests (Blossey et al., 2021; Crous et al., 2017), as has been observed in a tree invasion system (Medzihorský et al., 2023) and in non-native palm stands (Milosavljević et al., 2019). Notably, the palm moth (*Paysandisia archon*), which already infests palms in the Insubrian region (Lake Garda, Mori et al., 2022), and the red palm weevil (*Rhynchophorus ferrugineus*), already attacking palms in the Mediterranean region (Buchsbaum and Fuchs, 2016; Muñoz-Adalia and Colinas, 2020), are expected to reach the Southern European Alps soon, potentially impacting both cultivated and naturalized palms and reducing their abundance.

Moreover, the formation of monodominant palm stands may be hindered by other evergreen woody species, both non-native (e.g., *Prunus laurocerasus*, *Cinnamomum* spp., *Elaeagnus* spp., *Ligustrum lucidum*) and native (*Ilex aquifolium*, *Laurus nobilis*, and *Taxus baccata*) species. These evergreen species could possess a competitive advantage, similar to *T. fortunei*, compared to native and non-native deciduous species (Conedera et al., 2018), as they have been documented as successful invaders in various regions (Campagnaro et al., 2022; Fernandez et al., 2021). Additionally, they might share some effects with palms (e.g., due to similar leaf characteristics such as leaf toughness), but likely less intensely (Dominy et al., 2008). Together with *T. fortunei*, these species are suggested to induce a biome shift, transforming the deciduous temperate forest into an evergreen (laurophyllous) forest (Fehr et al., 2024; Klötzli and Walther, 1999). Besides land use changes (e.g., increased propagule pressure due to increased urbanization (Fehr et al., 2024) and abandonment of intensively managed chestnut forests (Conedera et al., 2018)), this biome shift is further driven by the changing climate regime, which increasingly provides more favourable conditions for laurophyllous species (Boonman et al., 2022; Elsen et al., 2022). Similar climatic conditions prevailed during the late Cenozoic period when evergreen laurophyllous species, including several palm species, dominated in southern Europe (Alessi et al., 2019; Gregor, 1980; Kissling et al., 2012). Due to extinctions during the ice ages and post-glacial dispersal limitations, unoccupied niche space for palms and other laurophyllous species exists (Klötzli and Walther, 1999), with anthropogenic warming expanding the occurrence of these conditions (Walther et al., 2007). The ecosystems resulting from this biome shift can be considered as a novel ecosystem, characterized by persistent presence of many non-native species and modified dynamics (Hobbs et al., 2006; Kerr et al., 2023).

5. Conclusion

Our study reveals nuanced shifts in arthropod communities within dense *Trachycarpus fortunei* stands compared to native stands. While overall arthropod species richness and abundance exhibit only subtle changes, herbivores were negatively affected, possibly due

to reduced native vegetation and the unsuitability of the tough, fibrous palm leaves as a food source for many herbivorous arthropods (Grubb et al., 2008). Additionally, our examination of litter decomposition unveils a balance between the palm's slow leaf decay and favourable conditions for litter decomposition in dense palm stands. Future expansion dynamics of *T. fortunei* driven by climate and land use change, will dictate broader ecological consequences in the Southern European Alps. Confined expansion may generate landscape heterogeneity and promote biodiversity, while landscape-level dominance could lead to regional biotic homogenisation. The potential arrival of pests and competitive interactions with other (evergreen) plant species may limit the formation of monodominant palm stands. The expansion of *T. fortunei* is part of a broader climate change-driven biome shift from deciduous temperate to evergreen laurophyllous forests and can be considered as the emergence of a novel ecosystem generated by combined effects of alien species introduction and climate and land use change. These dynamics, intensified by trophic interactions triggered by *T. fortunei*, echo typical roles observed in other palms (Fehr et al., 2020) and monocots in forest understories, offering a degree of predictability in these dynamics.

How these novel ecosystems, characterized by a substantial presence of non-native species, in addition to *T. fortunei,* will impact the functioning of forest ecosystems in the Southern European Alps poses important areas for future investigation.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jens-Christian Svenning reports financial support was provided by Villum Foundation. Jens-Christian Svenning reports financial support was provided by Danish National Research Foundation. Sergio Rasmann reports financial support was provided by Swiss National Science Foundation. Gianni Boris Pezzatti reports financial support was provided by Federal Office for the Environment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank VILLUM FONDEN for economic support via JCS' VILLUM Investigator project "Biodiversity Dynamics in a Changing World" (grant 16549). We also consider this work a contribution to Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by Danish National Research Foundation (grant DNRF173 to JCS). Fieldwork was partially funded by a Swiss National Science Foundation grant (310030_204811) to SR and by the Swiss Federal Office of the Environment FOEN (grant 18.0111.PJ/S025–0632) to GBP. We thank Matty Berg and Jurgen van Hal for their measurements of the tensile strength of palm leaves. We thank the experts that identified the arthropods at the species level:

Martin Riha, Aculeata, Apoidea, wasps
Isabella Forini, Aculeata, Formicidae
Xavier Heer, Araneae
Valeria Trivellone, Auchenorrhyncha
Yannick Chittaro, Coleoptera
Alexander Szallies, Coleoptera, Staphylinidae
Christoph Germann, Coloeptera, Curculionidae
Andrea Sanchez, Coleoptera, Scolitinae
Christoph Germann, Coleoptera, Curculionidae
Vivien Cosandey, Coleoptera, Scarabaeidae
François Claude, Gastropoda
Ralf Heckmann, Heteroptera
Pascal Stucki, Isopoda
Christian Monnerat, Orthoptera

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03303.

Data availability

Data will be made available on request.

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