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Plant phylogenetic relatedness and herbivore specialization interact to determine pest biocontrol efficiency in mixed plantations

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Pest herbivory regulation is one of the key functions provided by diverse ecosystems, especially when compared to species depauperate agro-ecosystems and in the context of increased pest outbreaks due to global change. The dilution effect of host diversity on insect herbivory suggests that mixed plantations are feasible for regulating pest herbivory in agroecosystems. Dilution effect of increased plant diversity on insect herbivory has been widely observed, yet little is known about how it may change with plant phylogenetic relatedness and herbivore specialization, especially at the community level. Here, we compared herbivore richness, abundance, and degree of herbivory (i.e., the ratio of trees damaged by pest and total trees in a given area) among the two monocultures and the four mixed plantations in Wenchang city, Hainan Province, China. We also respectively assessed the effects of phylogenetically close or distant species on generalist and specialist herbivores in monocultures and mixture. We found that increasing the number of phylogenetically closely-related tree species could dilute generalist herbivore richness, abundance, and degree of herbivory but amplify specialist herbivore richness, abundance, and degree of herbivory. In contrast, increasing the number of phylogenetically distant tree species increased generalist herbivore richness, abundance, and degree of herbivory, while reducing specialist herbivore richness, abundance, and degree of herbivory. Our results suggest that plant phylogenetic relatedness and herbivore specialization can indeed interact to influence pest control efficiency when using mixed plantations to manage pest herbivory in agroecosystems. Thus, both herbivore specialization and plant phylogenetic relatedness should be taken into account in the management of agro-ecosystems and biodiversity conservation with respect to herbivory.

KEYWORDS

phylogenetic relatedness, herbivore specialization, plant-insect herbivore interaction amplification effect, dilution effect, generalist, herbivory, specialist

1. Introduction

The anthropogenic acceleration of biodiversity loss (Pimm et al., 2014) and its detrimental effects on ecosystem functions remain one of the major concerns in ecology (Tilman et al., 2014). Pest herbivory regulation is one of the key functions provided by diverse ecosystems, which is especially important for agro-ecosystems in the context of increased pest outbreaks due to global change (Jactel et al., 2012; Klapwijk et al., 2012; Castagneyrol et al., 2014; Andrew and Hill, 2017). Given the widely acknowledged phenomenon that increasing plant diversity can have a dilution effect (i.e., increasing plant diversity results in decreased pest herbivory)

on insect herbivory, mixed plantations can potentially provide a key ecosystem service for the regulation of pest herbivory in mono-plantation in agroecosystems (Castagneyrol et al., 2014). However, the magnitude of the dilution effect of plant diversity on pest herbivory is known to vary according to the composition of plant and herbivore communities (Jactel and Brockerhoff, 2007; Vehvilainen et al., 2007; Barbosa et al., 2009). Moreover, evidence refuting this effect (i.e., that increasing plant diversity leads to increased pest herbivory) has also been found in other studies (Schuldt et al., 2015; Zhang et al., 2017; Grossman et al., 2018). As a result, it remains unclear whether increasing plant diversity through mixed plantations can be used to help manage pest herbivory in agroecosystems.

Recent synthesis studies highlight two primary factors that may be responsible for the lack of consensus regarding plant diversity-herbivory relationships (Jactel and Brockerhoff, 2007; Castagneyrol et al., 2014). First, host specificity of herbivores, particularly herbivory by specialist species (feeding on a specific plant genus), is usually reduced in diverse communities compared to monocultures (but see Plath et al., 2012). In contrast, the response of generalist species (feeding on different plant genus) is asynchronous in terms of its direction and magnitude (Schuldt et al., 2015). The second possibility regards the plant diversity being examined. Previous studies have shown that plant functional and phylogenetic diversity of the host community, and the relative abundance of the focal plant species, is more important than plant species richness in regulating the magnitude of herbivory (Mouquet et al., 2012). Moreover, herbivore specificity and plant phylogenetic relatedness interact to regulate the intensity of herbivory (Castagneyrol et al., 2014).

Till now, the associational resistance hypothesis has been recognized as the primary mechanism driving the dilution effect of increased plant diversity on specialist herbivory (Root, 1973; Agrawal et al., 2006; Lewinsohn and Roslin, 2008). This hypothesis claims that specialist herbivores prefer homogeneous neighbors to the same host plants for increase their herbivore loads (Lewinsohn and Roslin, 2008). As such, mixing closely related plant species with a mono-plantation may amplify herbivory caused by specialist herbivores. In contrast, mixing phylogenetically distant plant species with mono-plantations may dilute the effects from specialist herbivores (Figure 1). Likewise, the associational susceptibility hypothesis has been considered key to explaining the dilution effect of increased plant diversity on generalist herbivory (Unsicker et al., 2008; Plath et al., 2012). The hypothesis assumes that generalist herbivores require heterospecific neighbors to a focal plant to increase their herbivore load (Plath et al., 2012). As a result, mixing phylogenetically distant plant species with mono-plantation consumed by generalist herbivores may amplify herbivory due to generalist herbivores. In contrast, mixing closely related plant species with mono-plantations can dilute generalist herbivory (Figure 1). To the best of our knowledge, however, little is known about whether and how herbivore specificity and plant phylogenetic relatedness interact to alter the efficiency of mixed plantation on controlling herbivore in monoculture agroecosystem.

Current knowledge regarding the effect of plant phylogenetic diversity on generalist vs. specialist herbivores is largely based on comparisons of generalist and specialist herbivore intensity

between monoculture and mixed plantations (Castagneyrol et al., 2014). By doing so, however, herbivore-herbivore interactions are largely overlooked. In fact, more complexity and even inverse patterns may emerge when multiple hosts and herbivores are taken into account as in the reality. For instance, phylogenetic relatedness of a host community may have different effect on the mean intensity of herbivory for multiple generalist herbivores and a specific herbivore respectively. An assemblage of phylogenetically distant plants may harbor more generalist herbivore species, and may also suffer from a higher level of herbivory through the sampling effect (i.e., higher possibility of attracting herbivores with high herbivory) (Schuldt et al., 2014). Similarly, phylogenetically similar species can also trigger many new specialist species, which may also lead to higher specialist herbivory via the sampling effect. As a result, pest species diversity (species richness and abundance) and the herbivore intensity by the targeted generalist or specialist herbivores should be compared simultaneously among monocultures and mixed plantations. However, experimental studies addressing the specificity of multiple herbivores and their community composition at the community level remain scarce.

Here, we sampled two monocultures in Wenchang City, Hainan Province, China. One was one subspecies of *Cocos nucifera* (we called “green *Cocos nucifera*”) stand and the other is a pure stand of *Pinus elliottii*. Based on 20 years’ pest herbivore survey in this area, “green *Cocos nucifera*” is attacked by generalist herbivores (e.g., *Brontispa longissima*, *Rhynchophorus ferrugineus*, *Oryctes rhinoceros*, *Diocalandra frument*, *Aspidiotus destucto*, and *Aleurocanthus spiniferus*) (Lin et al., 2010). In contrast, *Pinus elliottii* is attacked merely by a specialist herbivore (*Dendrolimus punitatus*) (Xu et al., 2014). We mixed ten tree species which are phylogenetically distant with the two monocultures (Supplementary Figure S1) to simulate the influence of mixture of phylogenetically distant species on generalist and specialist pest herbivory respectively. These ten tree species are *Litsea glutinosa*, *Calophyllum inophyllum*, *Casuarina equisetifolia*, *Rapsnea linearis*, *Rhodomyrtus tomentosa*, *Psychotria rubra*, *Clerodendrum cyrtophyllum*, *Zanthoxylum piperitum*, *Wikstroemia indica*, and *Atalantia buxifoli* (Supplementary Figure S1). We also mixed another subspecies of *Cocos nucifera* (we called “red *Cocos nucifera*”) with the pure “green *Cocos nucifera*” stand “red *Cocos nucifera*” is phylogenetically close to “green *Cocos nucifera*” stand (Supplementary Figure S1), so we use this design to assess the effect of mixing phylogenetically close species on generalist pest herbivory. Similarly, since *Pinus caribaea* is phylogenetically close to *Pinus elliottii* (Supplementary Figure S1), we mixed *Pinus caribaea* with the pure *Pinus elliottii* stand to assess the impacts of mixing phylogenetically similar species on specialist pest herbivory too. Specifically, we compared herbivore richness, abundance, and degree of herbivory (i.e., the ratio of trees damaged by pest and total trees in a given area) among the two monocultures and the four mixed plantations. This experimental design aims to test: (1) if the addition of distantly related plant species can amplify herbivory by generalist herbivores, but dilute herbivory caused by specialist herbivores in a diverse host community; and (2) if adding closely related species to a host community can dilute herbivory caused by generalist herbivores, but amplify herbivory caused by specialist herbivores.

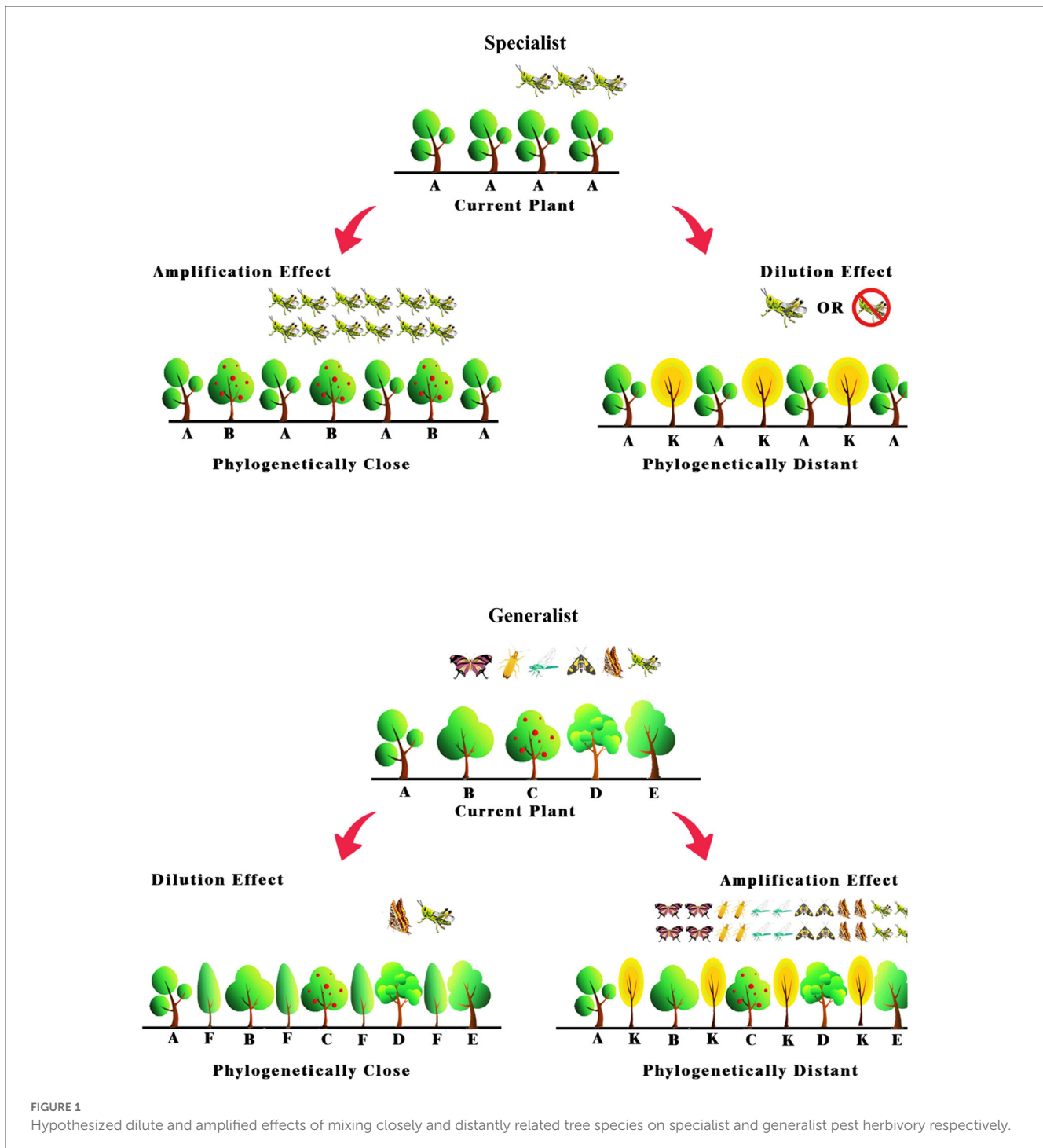


FIGURE 1 Hypothesized dilute and amplified effects of mixing closely and distantly related tree species on specialist and generalist pest herbivory respectively.

2. Materials and methods

2.1. Study sites

Our study site included four mixed stands (mixed stand 1, 110°57'34"E, 19°43'58"N; mixed stand 2, 110°56'39"E, 19°44'4"N; mixed stand 3, 110°58'34"E, 19°44'23"N and mixed stand 4: 110°49'24"E, 19°32'29"N), one monoculture pure "green *Cocos nucifera*" stand (110°51'15"E, 19°34'58"N), and one monoculture pure *Pinus elliottii* stand (110°43'19"E, 19°34'01"N) in Wenchang

City, Hainan Province, China (Supplementary Figure S2). These sites have a mean annual temperature (1978–2010) of 23.9 °C, with a low monthly mean temperature of 16.2 °C in January and high of 33 °C in August. Average annual precipitation is 1,729 mm, most of which occurs from April to October.

One hundred stems from each of ten species (i.e., *Litsea glutinosa*, *Calophyllum inophyllum*, *Casuarina equisetifolia*, *Rapsnea linearis*, *Rhodomyrtus tomentosa*, *Psychotria rubra*, *Clerodendrum cyrtophyllum*, *Zanthoxylum piperitum*, *Wikstroemia indica*, and *Atalantia buxifoli*) were randomly mixed with 1,000

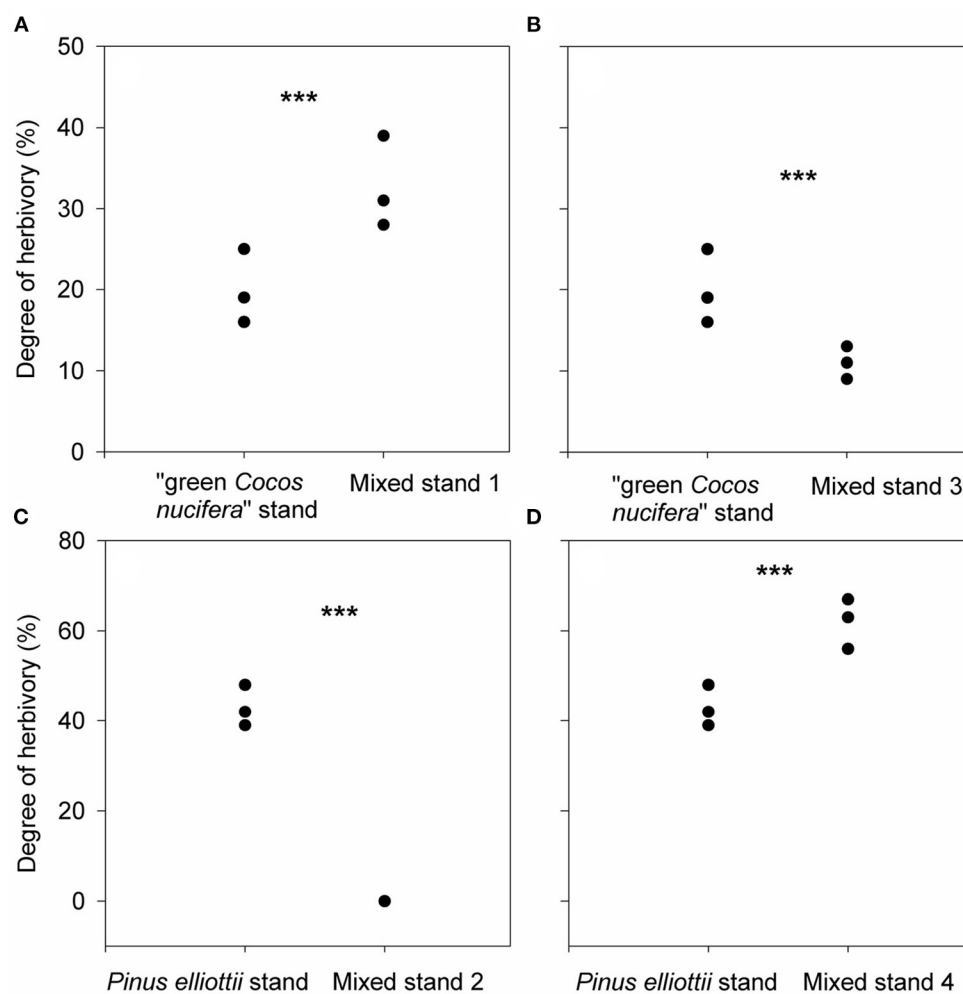


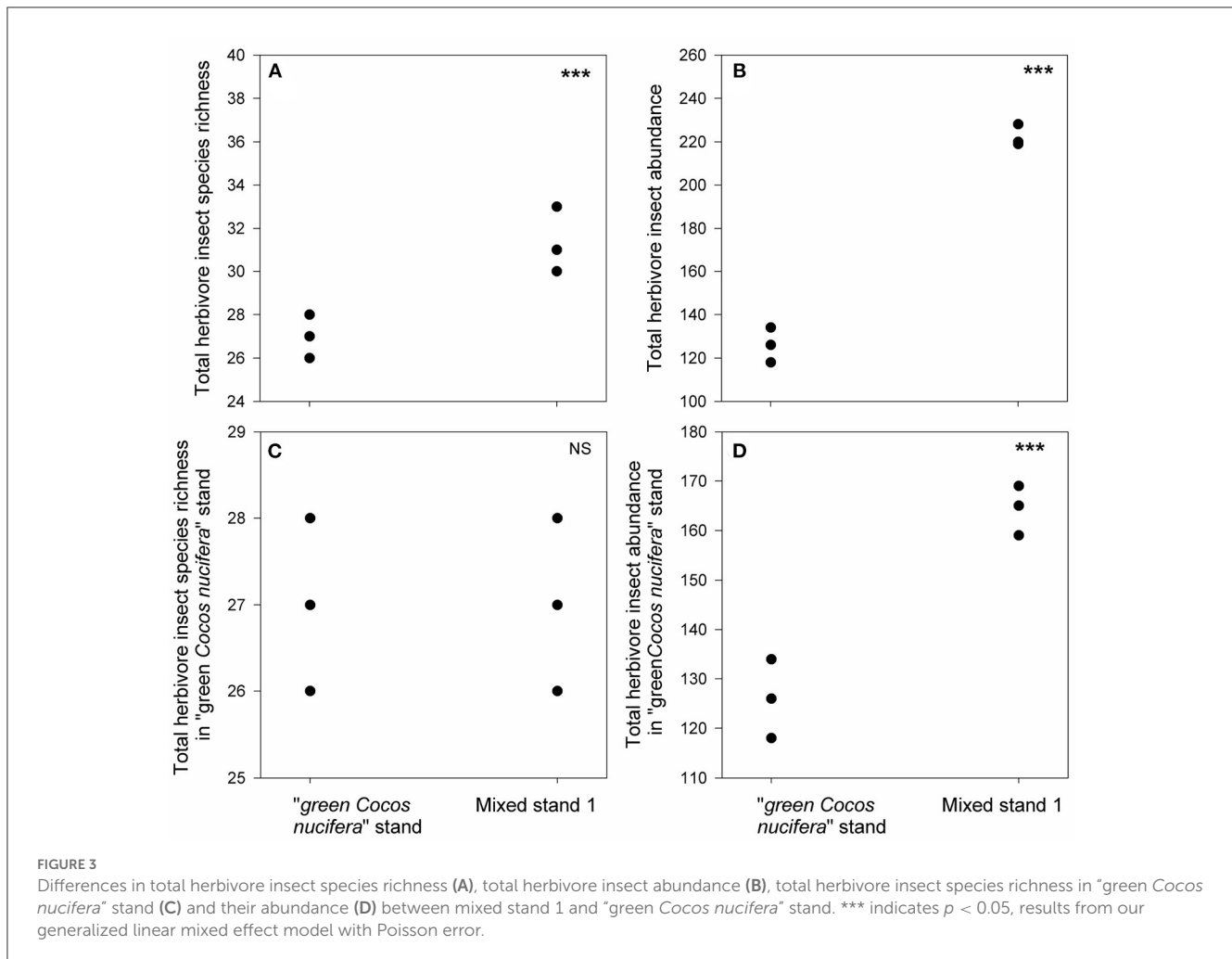
FIGURE 2 Differences in degree of herbivory [the percentage of trees damaged by a pest (%)] of "green *Cocos nucifera*" and *Pinus eliottii* between mixed stand 1 and the pure "green *Cocos nucifera*" stand (A), mixed stand 2 and the pure *Pinus eliottii* stand (C), mixed stand 3 and the pure "green *Cocos nucifera*" stand (B), and mixed stand 4 and the pure *Pinus eliottii* stand (D), respectively. ***indicates $p < 0.05$, results from our generalized linear mixed effect model with Poisson error.

individuals of "green *Cocos nucifera*" in mixed stand 1 and 1,000 individuals of *Pinus eliottii* in mixed stand 2. Thus, this planting was used to test the influence of mixing phylogenetically distant plant species on generalist and specialist pest herbivory individually. In mixed stand 3, 1,000 individuals of "green *Cocos nucifera*" and 1,000 individuals of "red *Cocos nucifera*" were planted to determine the influence of mixing phylogenetically similar plant species on generalist pest herbivory. In mixed stand 4, 1,000 individuals of *Pinus eliottii* and 1000 individuals of *Pinus caribaea* were therefore randomly mixed to assess the impact of mixing phylogenetically similar plant species on specialist pest herbivory. Pure "green *Cocos nucifera*" and *Pinus eliottii* stands of at least 1000 ha were established in Wenchang for nearly 30 years. Pure "green *Cocos nucifera*" and *Pinus eliottii* stands, mixed stand 1, 2, 3, and 4 have been planted for at least 20 years, and their planting densities were all kept at 500 stems per hectare. Since all six stands were very near the ocean, the local government forbids any human management (e.g.,

pesticide spraying and fertilization), thereby to avoid any potential ocean pollution.

2.1.1. Measurements of degree of herbivory for "green *Cocos nucifera*" and *Pinus eliottii*

We randomly selected three 20×20 m² subplots from each of the six stands described above. The subplots within each stand were at least 500 m apart from one another and from the edges of the stands. We then checked all "green *Cocos nucifera*" and *Pinus eliottii* trees in the three 20×20 m² subplots from each of the six stands to see how many "green *Cocos nucifera*" and *Pinus eliottii* trees were damaged by pests. Examples of different types of pest herbivory in "green *Cocos nucifera*" and *Pinus eliottii* stands are shown in [Supplementary Figure S3](#). Then we calculated the degree of herbivory as the ratio of trees damaged by a pest by the total number of trees found in each of the three 20×20 m² subplots within each of the six plantation stands.



2.1.2. Insect species richness and abundance trapping

Following Xue et al. (2021), we used 18 insect nets trap that were 50 cm in diameter and 160 cm in length to collect all flying insects during the day from July 26–28, 2019 in the three 20×20 m² subplots from each of the six stands. We also used 18 mercury lamps (450W) and 18 white cloths (2×3 m) (Supplementary Figure S4) to trap nocturnal insects from 8:00 pm to 10:00 pm during the same period. All non-larval herbivore insects were sorted and identified to species, and the abundance of each species was also recorded within each subplot.

2.1.3. Constructing phylogenetic tree of the 12 tree species and two subspecies of *Cocos nucifera*

The chloroplast genome of the 12 tree species and two subspecies of *Cocos nucifera* ("green *Cocos nucifera*" and "red *Cocos nucifera*") were measured to quantify the phylogenetic relationships of the 12 tree species and two subspecies of *Cocos nucifera*. The chloroplast genome for *Pinus elliottii*, *Casuarina equisetifolia*, *Clerodendrum cyrtophyllum*, *Litsea glutinosa*, *Rhodomyrtus tomentosa*, *Zanthoxylum piperitum*, and

Wikstroemia indica can be directly found in NCBI. Thus, we only sequenced chloroplast genome for "green *Cocos nucifera*" and "red *Cocos nucifera*", *Pinus caribaea*, *Calophyllum inophyllum*, *Rapsnea linearis*, *Psychotria rubra*, and *Atalantia buxifolia*. Detail descriptions of the chloroplast genome for these seven tree species or subspecies were described in detail in Supplementary Table S1. A maximum likelihood tree (Supplementary Figure S1) was then constructed using RAxML (Stamatakis, 2014).

2.2. Statistical methods

Since species richness and abundance are discrete random variables (count data here), we used the generalized linear mixed effect model (GLMM) with Poisson error to test whether phylogenetic relatedness, herbivore specialization and their interactive effects can significantly influence degree of herbivory, total insect species richness and abundance, and total herbivore insect species richness and abundance. Specifically, we used a GLMM model [Degree of herbivory or Richness or Abundance \sim herbivore specialization \times phylogenetic relatedness + (1|plantation type)]. Here *richness* and *abundance* indicate total insect or herbivore species richness and insect or herbivore

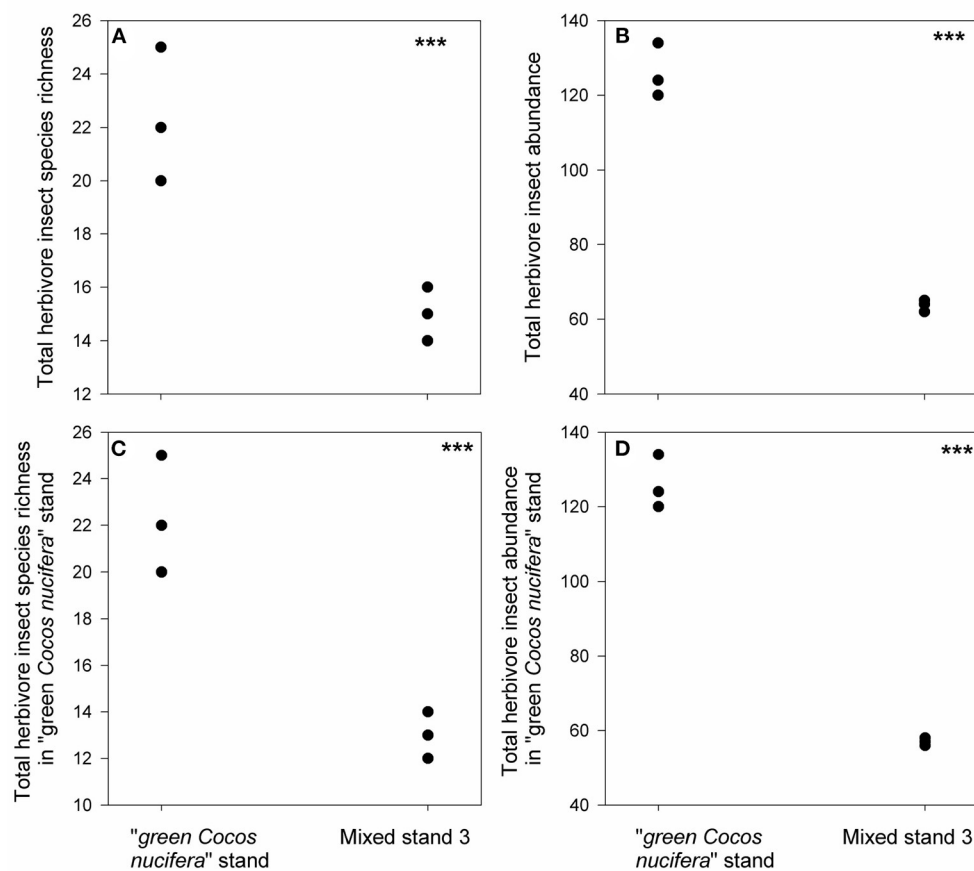


FIGURE 4

Differences in total herbivore insect species richness (A), total herbivore insect abundance (B), total herbivore insect species richness in "green *Cocos nucifera*" stand (C) and their abundance (D) between mixed stand 3 and "green *Cocos nucifera*" stand. *** indicates $p < 0.05$, results from our generalized linear mixed effect model with Poisson error.

insect abundance respectively. Herbivore specialization was either generalist or specialist. Phylogenetic relatedness coded phylogenetically close and distant individually. Plantation type indicated the six stands (green *Cocos nucifera* stand, mixed stand 1, mixed stand 3, *Pinus elliottii* stand, mixed stand 2, and mixed stand 4).

3. Results

The GLMM model results demonstrated that herbivore specialization, phylogenetic relatedness and their interactive effects all significantly influenced degree of herbivory, total insect species richness and abundance and total herbivore insect species richness and abundance (p of GLMM < 0.05 , Supplementary Table S2). Our GLMM model results showed that degree of herbivory of "green *Cocos nucifera*" in mixed stand 1 was 1.63 times higher than that in the pure "green *Cocos nucifera*" stand (Figure 2A). The degree of herbivory of *Pinus elliottii* decreased from 43% in the pure *Pinus elliottii* stand to 0% in mixed stand 2 (Figure 2C). Degree of herbivory of "green *Cocos nucifera*" in mixed stand 3 was 1.82 times lower than that in the pure "green *Cocos nucifera*" stand, while the

degree of herbivory of *Pinus elliottii* in mixed stand 4 was 1.44 times higher than that in the pure *Pinus elliottii* stand (Figures 2B, D).

We found 25 herbivore species in the pure "green *Cocos nucifera*" stand, all of which were generalist feeders (Figure 3A, Supplementary Figure S2, Supplementary Table S3). They also emerged in mixed stand 1 (Figure 3C, Supplementary Table S3), but their total abundance in mixed stand 1 increased to 1.4 times higher than that in the pure "green *Cocos nucifera*" stand (Figures 3B, D). Moreover, 10 generalist herbivore species that were absent from the pure *Cocos nucifera* stand appeared in mixed stand 1 (Figure 3A, Supplementary Table S3). In contrast, although one new generalist species emerged (Figure 4A, Supplementary Table S3), only 14 out of the 25 generalist herbivore species observed in the pure "green *Cocos nucifera*" stand were found in mixed stand 3 (Figure 4C, Supplementary Table S3). Moreover, herbivore abundances in mixed stand 3 decreased 2-fold compared with the pure "green *Cocos nucifera*" stand (Figures 4B, D, Supplementary Table S3).

In the *Pinus elliottii* stand we only found one specialist herbivore species (*Dendrolimus puntatus*), which was absent from mixed stand 2 (Figure 5C, Supplementary Figure S2, Supplementary Table S3). However, another 24 generalist herbivore species were found in mixed stand 2, leading to both

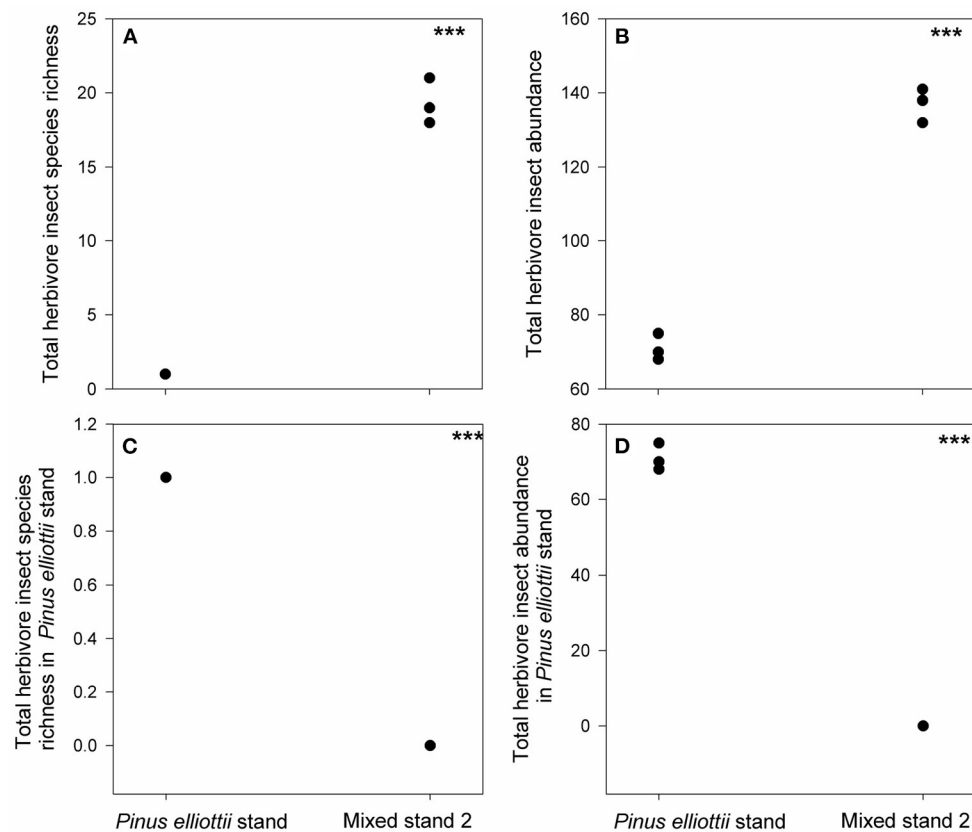


FIGURE 5

Differences in total herbivore insect species richness (A), total herbivore insect abundance (B), total species richness of herbivore insects found in *Pinus elliotii* stand (C) and their abundance (D) between mixed stand 2 and *Pinus elliotii* stand. ***indicates $p < 0.05$, results from our generalized linear mixed effect model with Poisson error.

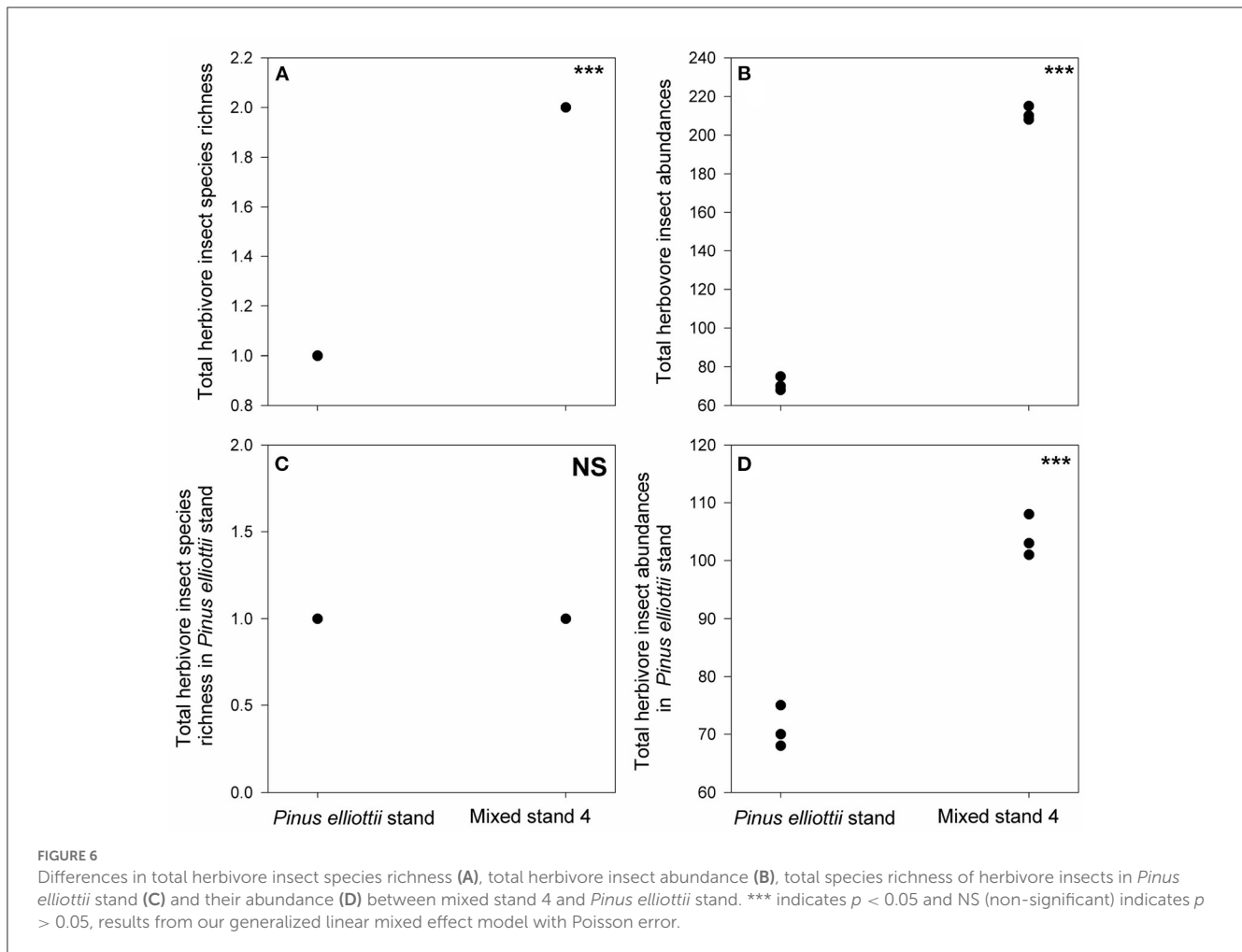
higher total herbivore species richness and total abundance than those found in the *Pinus elliotii* stand (Figures 5A, B, D, Supplementary Table S3). In contrast, in mixed stand 4, one more new specialist herbivore (*Dioryctria splendidella*) emerged, except for *Dendrolimus punctatus* (Figures 6A, C, Supplementary Table S3). Moreover, the abundance of *Dendrolimus punctatus* increased 2-fold compared to that in the mono-*Pinus elliotii* stand (Figures 6B, D, Supplementary Table S3).

4. Discussion

Herbivores play key functions in ecosystems across the world, and multiple herbivore species can interact to regulate ecosystem processes and functions (Schemske et al., 2009). Hence, studies focusing on herbivory of a single focal plant species and by a single herbivore species may provide misleading information regarding biodiversity conservation and agroecosystem management. By investigating herbivory from multiple herbivores and across six different plant communities, we found that the addition of phylogenetically distant plants and the mixture of phylogenetically close plants can have opposite effects on herbivory. Specifically, mixing closely related tree species diluted herbivory of generalist pest herbivores, but amplified the impact of specialist pest. In contrast, mixing phylogenetically distant tree species enhanced the

herbivory of generalist pest while diluting the herbivory effects from specialist pest. As mixed plantations are widely acknowledged as a useful management strategy, our results highlight the need to carefully consider the combined effects of multiple herbivore types on overall herbivore load and damage. Our results also emphasized the importance of which plants being added into monoculture forests.

By comparing mixed stands 1 and 3 with the pure “green *Cocos nucifera*” stand, we found that increasing the number of distantly related tree species can increase herbivory from generalist pest (i.e., increasing “green *Cocos nucifera*” generalist pest degree of herbivory). This is consistent with some previous studies (Schuldt et al., 2010, 2012, 2014) which find that increasing plant diversity can dilute pest herbivore. This finding can be explained, in part, by the widely acknowledged “associational susceptibility hypothesis,” which claims that generalist herbivores need many distantly related plants to increase their herbivore load, thereby increasing herbivore intensity (i.e., increased damage percentage) (Brown and Ewel, 1987; Jactel and Brockerhoff, 2007; Unsicker et al., 2008; Plath et al., 2012). For instance, more distantly related plants in a community may benefit the growth of generalist herbivores via dietary mixing (Bernays et al., 1994). Likewise, high diversity stands may increase damage from non-preferred host species due to spillover effects from preferred hosts (Power and Mitchell, 2004). However, we propose an alternative explanation, which is that phylogenetically



distant plant species may support many new generalist herbivore species and increase total abundance of generalists found in monocultures, which may in turn lead to a higher possibility of obtaining high generalist herbivory intensity (i.e., sampling effect). Indeed, in mixed stand 1, the number of generalist herbivores was 1.4 times greater than the pure “green *Cocos nucifera*” stand. Moreover, 10 new generalist herbivore species were found in mixed stand 1.

We found that increasing the number of closely related tree species can reduce the generalist degree of herbivory in stand of pure “green *Cocos nucifera*”. This can also be explained by the associational susceptibility hypothesis. Nevertheless, another potential reason is that phylogenetically similar plant species may result in new generalist species for “green *Cocos nucifera*”, which may in turn compete with or directly prey upon the generalist pest of “green *Cocos nucifera*”. Indeed, although one new generalist species emerged, 11 generalist pest herbivore species in the pure “green *Cocos nucifera*” stand disappeared in mixed stand 3. Moreover, herbivore abundance in mixed stand 3 decreased 2-folds compared with the pure “green *Cocos nucifera*” stand.

By comparing mixed stands 2 and 4 with the pure *Pinus elliottii* stand, we found the effects of phylogenetic relatedness on herbivory differed for specialist pest herbivores compared

with generalist pest herbivores. For *Pinus elliottii*, the degree of herbivory of the specialist pest, *Dendrolimus punctatus*, was reduced to zero when it was mixed with ten phylogenetically distant tree species (i.e., mixed stand 2). This result suggests that mixed plantation of phylogenetically distant plant species can have a clear dilution effect on herbivory intensity from specialist pest. This pattern can be explained by the associational resistance hypothesis, which claims that specialist herbivores prefer more homogeneous neighbors to their preferred host plants to increase their loads (Root, 1973; Agrawal et al., 2006; Lewinsohn and Roslin, 2008). Thus, increasing the numbers of phylogenetically distant tree species will dilute specialist herbivores, thereby decreasing the abundance of specialist herbivores (Tahvanainen and Root, 1972; Barbosa et al., 2009). However, another possibility is that phylogenetically distant tree species are favored by generalist herbivores that may compete with or directly prey upon the specialist herbivores (Brown and Ewel, 1987). Indeed, we observed 24 generalist herbivore species in mixed stand 2, but we cannot observe original specialist pest (*Dendrolimus punctatus*) anymore.

The degree of herbivory of *Pinus elliottii* by the specialist pest herbivore was 1.44 times greater when it was mixed with phylogenetically close tree species (mixed

stand 4), thus providing support for the associational resistance hypothesis. However, it is also highly possible that phylogenetically close tree species (*Pinus caribaea*) can trigger new specialists, which in turn results in higher specialist degree of herbivory via sampling effects. Indeed, we ended up sampling a new specialist (*Dioryctria splendidella*) in mixed stand 4.

5. Conclusions

Our study provides clear evidence that herbivore specialization and plant phylogenetic relatedness interact to influence the efficiency of mixed plantations on the regulation of pest herbivory in agroecosystems. Mixing phylogenetically distant tree species with monocultures enhanced herbivory by generalist herbivores, while simultaneously diluting herbivory by specialist herbivores. In contrast, mixing phylogenetically close tree species with monocultures can give rise to totally opposite influences on generalist and specialist herbivory. Our results may differ with those observed on a single focal plant species attacked by a single herbivore species. Although investigations in other agroecosystems are needed to test the generality of the conclusion, our results suggest that both herbivore specialization and plant phylogenetic relatedness should be taken into account when using mixed plantations to manage pest herbivory in agroecosystems.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

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QY and XC: conceptualization, methodology, writing—original draft preparation, and writing—reviewing and editing. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1187996/full#supplementary-material>

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