# Exploring Competitive Interactions: A Comparative Species Association and Ecological Niche Study of *Bactrocera cucurbitae* and *Bactrocera tau* (Diptera: Tephritidae)[1]

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**Abstract** *Bactrocera cucurbitae* (Coquillett) and *Bactrocera tau* (Walker) (Diptera: Tephritidae) are two invasive pests that pose a great threat to melon and fruit crops in tropical and subtropical regions. Previous studies have indicated that there may be a competitive relationship between these two pests because they have similar morphologies and a tendency to damage the same range of hosts. However, no studies have yet confirmed this competitive relationship, which is crucial for predicting the tephritid community structure and population dynamics, as well as for designing management strategies for these pests. In this study, we combined field investigations, literature reviews, and host preference tests to analyze the species association, niche width, and overlap of the two fruit flies to confirm their competitive relationship. We found that *B. cucurbitae* was more abundant in the wild than *B. tau*, and there was a negative correlation between them regardless of habitat types. The niche widths of *B. cucurbitae* and *B. tau* were 7.50 and 7.42, respectively, and the niche overlap was 0.87 when we analyzed the data from the selected literature. Similarly, the niche widths were 4.95 and 4.44, with a niche overlap of 0.95 when we analyzed data from host preference tests. These results indicate that the two fruit flies co-occur and have a competitive relationship due to their similar niche widths and high niche overlap. The findings offer insights into predicting the field population dynamics and structures of these pests, important for pest monitoring and management.

**Key Words** biological invasion, interspecific relationship, host diversity, *Bactrocera* pests, integrated pest management

*Bactrocera cucurbitae* (Coquillett) and *Bactrocera tau* (Walker) (Diptera: Tephritidae) are invasive pests widely distributed in tropical and subtropical regions (Dhillon et al. 2005, Dorla and Laurent 2017, Jaleel et al. 2018). These two invasive pests have similar ecological and physiological characteristics (Huang et al. 2020, Jacquard et al. 2013, Singh et al. 2010) in that they exhibit similar host range, feeding habits, and morphology. The adults lay eggs inside the fruit, and the larvae bore into and feed on the fruit, causing decay and fruit drop. This can lead to a reduction in fruit production with significant economic impacts (Nath and Bhushan 2006, Wu et al. 2011).

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Due to their similar ecological characteristics, combined with a large number of field observations and laboratory research, studies have suggested that these two invasive pests have a competitive relationship (He et al. 2019, Li et al. 2023, Shen et al. 2014, Zhang et al. 2017). However, few studies provide data to determine their relationship, such as specific associations observed in the field and the niche widths and overlap of the two species, which are important for determining their competitive interactions.

Interspecific competition involves interactions between different species that share the same environment and compete for the limited food or habitats (Bursali et al. 2024, Fortuna et al. 2022, Sokame et al. 2021). The association between species, as well as the width and overlap of their ecological niches, can be used to estimate their competitive strength and predict the outcome of competition (Bolnick et al. 2010). A positive species association between species may benefit their co-existence; however, a negative association may cause competitive exclusion (Gao et al. 2021, Yang 2023, Zhao et al. 2021). For example, in the desert grassland, there was a significant positive correlation among the *Microdera kraatzi* (Reitter), *Anatolica pandaroides* (Reitter) and *Anatolica planata* (Reitter), resulting in a mutually beneficial coexistence among the populations, with the community remaining relatively stable (Yang et al. 2021). In the subtropical degraded forests, species with negative interspecific correlation, for example, *Quercus serrata* (Thunberg), *Castanopsis tibetana* (Hance), and *Cyclobalanopsis gracilis* (Rehder and E. H. Wilson) have different habitat requirements, and interspecific competition will occur in the case of scarce resources (Liu et al. 2019). In addition, higher overlap may lead to fierce interspecific competition, and lower niche overlap may lead to stable coexistence (Smith 1978). For example, in both rearing and wild environments, the high ecological niche overlap between the seven-spotted ladybug and the nine-spotted ladybug leads to strong competition between them, that is, the competitive advantages of *Coccinella septempunctata* (L.) in food consumption and developmental speed can lead to delayed development and reduced body weight in *Coccinella novemnotata* (Johann) (Petersen and Losey 2024).

Previous studies on the ecological niche width and overlap have often used literature review methods (Adler et al. 2018). For example, by using keywords to retrieve eligible literature and collecting literature data, the niche relationships in plant communities were calculated, and the competitive coexistence relationships within plant communities were explored (Adler et al. 2018). However, the variability in collection and analytical methods may not accurately reflect the actual niche breadth and overlap status of species (Li et al. 2012). An integrated approach that combines literature search, laboratory studies, and field investigation should offer a comprehensive interpretation of the interspecific relationships of these two invasive pests.

This study aimed to determine the competition relationship among the two invasive pests, *B. cucurbitae* and *B. tau*, by studying their species association in different habitats and exploring the ecological niche width and overlap through literature review, and host preference experiments in the laboratory. Firstly, field surveys were conducted to assess the occurrence and their interspecific association in various habitats. Secondly, the niche width and overlap of these two pests were calculated by reviewing existing literature and by conducting host preference tests in the laboratory. The findings of this study will offer valuable insights into the competitive relationships of these two invasive pests and contribute to predict community structure change, and field population dynamics.

## Materials and Methods

**Species association.** In order to study the species association of the two fruit flies, two types of habitats (e.g., fruit orchards and melon farmland) where these flies frequently occur, were selected for investigation from July to October 2022. Five survey sites were established in each type of habitat, with each site covering an area of more than 10 mu and ensuring a distance of $>$ 5 km between sites. The 5 melon farmlands were located in Fengmu and Xinxing Town, Tunchang, Wancheng and Liji Town, Wanning, and Longtang Town, Haikou. The first 3 sites were planted with *Momordica charantia* (L.), while the last 2 were planted with *Cucumis sativus* (L.). The 5 fruit orchards were located in Baocheng Town, Baoting (planted with *Nephelium lappaceum* (L.)), Dazhipo and Sanmenpo Town, Haikou (planted with *Psidium guajava* (L.)), and 2 orchards in Poxin Town, Tunchang (one was planted with *Artocarpus heterophyllus* (Jean-Baptiste) and the other was planted with *Citrus maxima* (Bum.)).

The 5-point sampling method was used to determine the occurrence of *B. cucurbitae* and *B. tau* in each site for both habitats, thus, there were 25 survey points for each habitat. The attractant, 1 mL of ethyl acetopyruvate (Kunke Trading Co., Ltd, Heze, China), was added dropwise into the cotton inside a white trap bottle (h $=$ 15 cm, d $=$ 6 cm, Duoyuduo Biotechnology Co., Ltd, Guangzhou, China). The trap bottle was hung at each survey point. In the melon farmlands, the trap bottle was suspended on the central support pole of covered structure at a height of 1 to 1.5 m from the ground, while in the fruit orchards, the trap bottle was hung on the main trunk of the fruit tree at the same height. After 24 h, the trap bottle was removed, and the number of captured fruit flies of both species was recorded.

**Ecological niche width and overlap.** Two methods, literature review and oviposition preference tests, were used to evaluate the ecological niche width and overlap of *B. cucurbitae* and *B. tau*. For the literature review method, we used academic databases such as China National Knowledge Infrastructure (CNKI), Google Scholar, Web of Science (WOS), and PubMed as data sources. This approach ensures the comprehensiveness and thematic relevance of the literature review and analysis. The search formula was: "*Bactrocera cucurbitae*", "*Bactrocera tau*" combined with "oviposition frequency", "ecological and physiological character", "specific interactions", "management", "population", "behavior". The study screened literature based on titles, abstracts, and full texts, and extracting data on the oviposition of the two fruit fly species on different hosts from the selected literature.

For host preference tests, these two species of fruit flies were collected and reared for use. *Bactrocera cucurbitae*, originating from the Chinese Academy of Tropical Agricultural Sciences, was reared in the laboratory for 10 generations to establish a stable laboratory population. *Bactrocera tau*, collected from the fruits of *M. charantia* in the Haidian campus of Hainan University, Haikou, were also reared in the laboratory for 10 generations to establish a laboratory population.

In the laboratory, larvae of both *B. cucurbitae* and *B. tau* were fed with *Cucurbita pepo* (L.). *C. pepo* containing larvae were placed in plastic trays, with sand as the substrate for pupation. Every 3 d, the sand was sifted to collect the pupae, which were then placed into plastic boxes and reared under controlled conditions of 26 ± 1°C; relative humidity (RH) of 65 ± 3%; photoperiod of 16 L:8 D. After emergence, adults were immediately transferred to 60 × 60 × 60 cm insect-rearing cages and provided with food and water. The adult diet consisted of a mixture of yeast extract and glucose (1:3).

According to the results of the literature review (see above), 10 common host fruits were selected. These included *Cucurbita pepo* (L.), *Cucumis sativus* (L.), *Momordica charantia* (L.), *Luffa cylindrica* (L.), *Cucurbita* spp (Joseph), *Citrullus lanatus* (Mansfeld), *Solanum lycopersicum* (L.), *Musa* spp (L.), *Lagenaria siceraria* (L.), *Citrus sinensis* (Osbeck). All host fruits were from local supermarkets and washed several times to reduce any pesticide residue.

**Host preference tests.** Ten host fruits (see above) were cut into small cuboids each with a volume of $2 \times 2 \times 3$ cm$^3$, and specimens of each species were placed in a Petri dish (d = 7 cm). Thus, 10 Petri dishes were used and randomly arranged in a circular pattern within the cage (30 × 30 × 30 cm) to avoid errors caused by different placement positions. Then, ten 15-d-old female adults of *B. cucurbitae* or *B. tau* were introduced into the cage. The test hosts were removed after 24 h of oviposition and examined under an anatomical microscope to observe and record the number of eggs on the fruits. Twenty replicates were conducted for each of host.

**Data analysis.** To determine the difference in the number of fruit flies (*B. cucurbitae* and *B. tau*) captured between the two habitats, the Kruskal-Wallis test was used, followed by Šídák multiple comparison tests. Then, the variance ratio (*VR*) test, which is based on species presence or absence, was used to examine the overall association (Chow et al. 1993, Schluter and Dolph 1984). The *VR* was calculated using the following formula:

$$\delta_T^2 = \sum_{i=1}^{S} P_{i(1-P_i),\ \ P_i = \frac{n_i}{N}}$$

$$S_T^2 = \frac{1}{N}\sum_{j=1}^{N} \left(T_j - t\right)^2$$

$$VR = S_T^2/\delta_T^2$$

where $S$ = total number of species, $N$ = total number of quadrats, $n_i$ = number of quadrats where species $i$ appears, $T_j$ = total number of species in quadrat $j$, and $t$ = average number of species in the quadrat, that is, $t$ is the average number of species in the quadrats (Pandey et al. 2023). When $VR = 1$, there is independence of the species, $VR > 1$ indicates a positive association of the species, and $VR < 1$ indicates a negative association of the species in the community. The statistic $W$ was used to test for the significance of the deviation of $VR$ value from 1 using the formula:

$$W = VR \times N$$

where $W$ follows the chi-squared distribution, with $0.00393 < X^2 < 3.841$. If $W < X^2_{0.095N}$ or $W > X^2_{0.05N}$, the interspecific association is significant ($P < 0.05$).

Conversely, if $X^2_{0.95N} < W < X^2_{0.05N}$, the interspecific association is not significant ($P > 0.05$) (Gu et al. 2017, Ludwig et al. 1988, Zhou et al. 2015, Zou et al. 2024).

The searched literature was categorized into four main topics: management strategy, ecological and physiological characteristics, host preference and literature reviews. We further analyzed and compared the number of papers that studied the type of host of two fruit flies. The fecundity data across various hosts of two fruit flies were extracted from chosen papers and standardized by converting the data into the number of eggs laid per female in 24 h. Finally, the niche breadth and niche overlap of *B. cucurbitae* and *B. tau* were calculated using Levins niche breadth index, Simpson diversity index, and Pianka niche overlap index.

The niche breadth calculations for *B. cucurbitae* and *B. tau* utilized the niche breadth by Levins (Levins 1968, Regmi et al. 2022):

$$\mathrm{B_i} = \frac{1}{\mathrm{r}\sum_{\mathrm{j}=1}^{\mathrm{r}} \mathrm{P_{ij}^2}}$$

where $B_i$ = the niche breadth of species $i$, $j$ = the quadrat, $P_i$ indicates the proportion of individuals consuming the $i$ type of resource within the total population. A higher value of the Levins' ecological niche breadth index signifies greater variation in resource utilization by the species within the niche, while a lower value suggests less variation (Song et al. 2024).

Host diversity was described by Simpson diversity (Simpson 1949):

$$D = 1 - \sum \mathrm{P}_i^2$$

where, $D$ = the Simpson diversity index, and the value of the Simpson index ranges from 0 to 1. Over all $i$, where $P_i$ represents the proportion of each category $i$. The closer the value is to 0, the higher the diversity of the community, because the distribution of individuals among different species is more uniform. On the contrary, the closer the value is to 1, the lower the diversity of the community, which indicates that most individuals belong to a few species (i.e., there are dominant species) (Measey et al. 2017).

Niche overlap was described by Pianka niche overlap (Pianka 1973):

$$\mathrm{Q_{ik}} = \frac{\sum_{\mathrm{j}=1}^{\mathrm{r}} \mathrm{P_{ij}P_{kj}}}{\sqrt{\left(\sum_{\mathrm{j}=1}^{\mathrm{r}} \mathrm{P_{ij}}\right)^2 \left(\sum_{\mathrm{j}=1}^{\mathrm{r}} \mathrm{P_{ij}}\right)^2}}$$

where, $Q_{ik}$ represents the ecological overlap value between species $i$ and species $k$. $P_{ij}$ and $P_{kj}$, respectively, denote the proportion of individuals of species $i$ and species $k$ in resource state $j$ relative to the total number of individuals of species $i$ and species $k$. $r$ is the total number of units in the resource set. The value of $Q_{ik}$ ranges from 0 to 1, with a higher $Q_{ik}$ indicating a greater ecological niche overlap between the two species (Bewick et al. 2015).

In the host preference tests, the number of eggs laid by *B. cucurbitae* and *B. tau* on different hosts did not follow a normal distribution. A general linear model

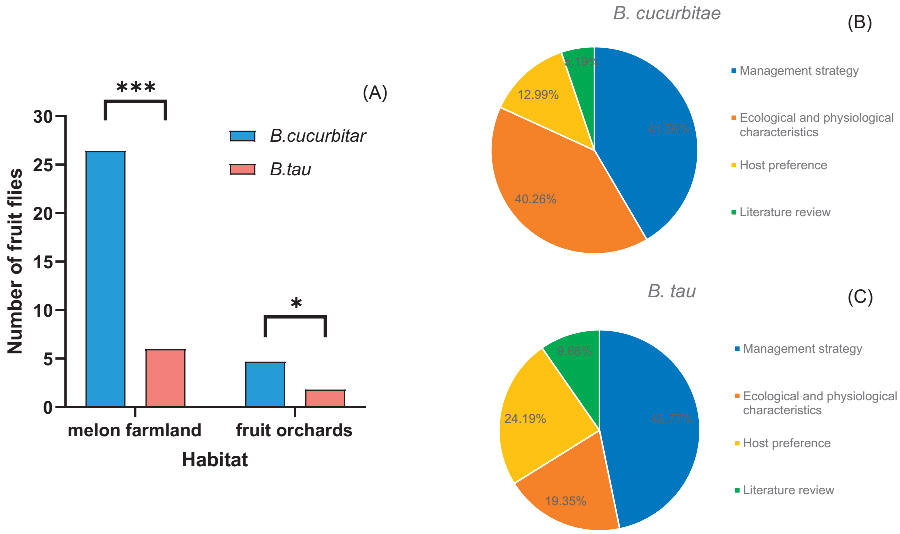


**Fig. 1. Number of *B. cucurbitae* and *B. tau* adults in fruit orchards and melon farmland, in this context, "***" indicates $P < 0.01$; "**" indicates $P < 0.05$ (A). The proportion of literature on management strategy, ecological and physiological characteristics, host preference, and literature review for *B. cucurbitae* (B) and *B. tau* (C).**

(GLM) was used for the analysis, and the fly species and host types were considered as the predicted variables, and assumed a Poisson distribution. The Tukey's tests were used for multiple comparisons. The calculation method of niche breadth and overlap was the same as that proposed above.

All data analyses were completed in R 4.3.3 (R Core Team 2014).

## Results

**Species association.** The number of fruit flies captured was affected by the types of fruit flies ($\chi^2 = 13.48$, $df = 1$, $P < 0.0001$, Fig. 1A) and the habitat type ($\chi^2 = 8.36$, $df = 1$, $P < 0.05$). The number of *B. cucurbitae* captured was higher than that of *B. tau* in both habitats, and the number of both fruit flies captured in the melon farmlands was higher than those captured in the fruit orchards (Fig. 1A).

In both melon farmlands and fruit orchards, there was a negative association between *B. cucurbitae* and *B. tau*, indicated by a Variance Ratio (*VR*) of 0.30 ($< 1.00$). The *W* statistic for melon farmlands was 7.84, and for fruit orchards it was 10.78. Both values exceeded the critical values for the 95% confidence interval ($X^2_{0.95N} < W < X^2_{0.05N}$).

**Ecological niche breadth and overlap.** A total of 205 articles were collected, including 154 studies on *B. cucurbitae* and 51 studies on *B. tau*. For *B. cucurbitae*, the proportion of research on management strategy was the highest, reaching 41.56% (Fig. 1B). The proportions for ecological and physiological characteristics, host preference, and literature review were 40.26%, 12.99%, and 5.19%, respectively.

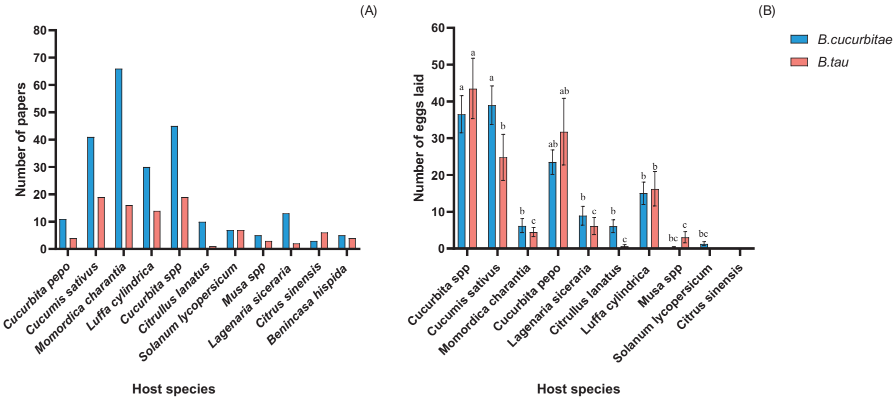


**Fig. 2. Number of papers that cite each type of host for *B. cucurbitae* and *B. tau* (A). Number of eggs laid by *B. cucurbitae* and *B. tau* on 10 different hosts. Statistical differences between different hosts is expressed in lowercase letters ($P < 0.05$) (B).**

For *B. tau*, the highest proportion of research was focused on management strategy, at 46.77%, while the proportions for host preference, ecological and physiological characteristics, and literature review were 24.19%, 19.35%, and 9.68%, respectively (Fig. 1C).

Regarding host preference, *M. charantia* was the most frequently mentioned host for *B. cucurbitae*, followed by *Cucurbita* spp., *C. sativus*, and *L. cylindrica* (Fig. 2A). The most frequently reported ovipositional host was *L. siceraria*, followed by *C. melo*, *L. cylindrica*, and *C. sativus* (Table 1). For *B. tau*, *C. sativus*

**Table 1. Mean (±SD) number of eggs laid by *B. cucurbitae* and *B. tau* on different hosts. These data were extracted from selected papers and converted to the number of eggs laid per 24 h.**

| Hosts | *B. cucurbitae* | *B. tau* |
|---|---|---|
| *Citrullus lanatus* | 3.86 ± 2.41 | 0.00 ± 0.00 |
| *Cucumis melo* | 10.56 ± 5.28 | 13.65 ± 5.60 |
| *Lagenaria siceraria* | 11.51 ± 1.00 | 0.00 ± 0.00 |
| *Cucumis sativus* | 7.91 ± 1.77 | 6.02 ± 1.99 |
| *Cucurbita pepo* | 3.80 ± 2.67 | 4.19 ± 3.35 |
| *Cucurbita* spp. | 6.05 ± 1.65 | 3.76 ± 3.09 |
| *Luffa aegyptiacas* | 9.16 ± 3.41 | 11.56 ± 5.48 |
| *Momordica charantia* | 7.00 ± 1.61 | 12.26 ± 4.30 |
| *Solanum lycopersicum* | 2.14 ± 2.14 | 9.36 ± 7.86 |

and *Cucurbita* spp. were the most frequently mentioned hosts, followed by *M. charantia* and *L. cylindrica* (Fig. 2A). The most frequently reported ovipositional host was *C. melo,* followed by *M. charantia*, *L. cylindrica*, and *S. lycopersicum* for *B. tau* (Table 1).

Based on data extracted from the literature, we calculated the niche breadth for *B. cucurbitae* and *B. tau*, and their niche overlap. The niche breadths for *B. cucurbitae* and *B. tau* were 7.50 and 7.42, respectively. The host diversity index for *B. cucurbitae* and *B. tau* was 0.87 for both. Additionally, the niche overlap between the two fruit flies was 0.89.

**Host preference tests.** The number of eggs laid by *B. cucurbitae* and *B. tau* was affected by host types ($\chi^2 = 5961.20$, $df = 9$, $P < 0.001$), but not by the types of fruit flies ($\chi^2 = 2.80$, $df = 1$, $P = 0.093$, Fig. 2B). For *B. cucurbitae*, a significantly higher number of eggs was laid on *C. sativus*, *Cucurbita* spp, and *C. pepo* than on other hosts. The number of eggs laid on *M. charantia*, *C. pepo*, *L. siceraria*, and *L. cylindrica* was also significantly higher than that on *M.* spp. No eggs were laid on *C. sinensis*. For *B. tau*, a significantly higher number of eggs was laid on *Cucurbita* spp. and *C. pepo* than on other hosts, followed by *C. sativus* and *L. cylindrica*, which have a significantly higher number of eggs than *M. charantia*, *L. siceraria*, and *Momordica* spp. No eggs were laid on *C. sinensis* (Fig. 2B).

The niche breadths for *B. cucurbitae* and *B. tau* were 4.95 and 4.44, respectively. The host diversity index for *B. cucurbitae* and *B. tau* were 0.80 and 0.77, respectively. Additionally, the niche overlap between the two fruit flies was 0.95.

## Discussion

In this study, we aimed to create an improved understanding of the competition relationship between two invasive fruit flies, *B. cucurbitae* and *B. tau*, by testing their species association in the field and by using a literature review method and host preference tests for evaluating their niche width and overlap. The results show that the number of *B. cucurbitae* was more than that of *B. tau* in the field, and there was a negative correlation between the two fruit flies regarding the habitat types. The niche breadth and host diversity index of *B. cucurbitae* and *B. tau* were similar, and the niche overlap between these two flies was high, indicating the potential for high competition between them. These results are important for predicting their population structure and dynamics, which are crucial for pest monitoring.

In field observation, we found that *B. cucurbitae* were the most abundant species compared to *B. tau*, and there was a negative correlation (both *VR* values were 0.30, which is less than 1.00) between them in the field regardless of habitat type. These results indicate that *B. cucurbitae* may be the dominant species and has a competitive advantage over *B. tau*. Similar patterns have been reported in other species. For example, both *Helicoverpa zea* (Boddie) and *Spodoptera frugiperda* (J.E. Smith) can infest and damage either the whorl or the ear of *Zea maize* (L.), and there was a negative correlation between the two pests, which led to competition as they competed for space and food (Rodríguez-del-Bosque et al. 2012). *Platyneura testacea* (Comstock) and *Ceratosolen fusciceps* (Mayr), which were on *Ficus racemosa* (L.), exhibited a negative interspecific association and competed for flower resources in order to reproduce (Zhang et al. 2003). The competitive advantage of *B. cucurbitae* is probably due to its higher fecundity than *B. tau* on most of the host plants, as shown in our results (Fig. 2B). Furthermore, the higher fecundity may contribute to its higher number of larvae than *B. tau* on a single host, which further enhances its competitive ability. To confirm this, the competitive ability of larvae on a single host should be considered to test if the competitive ability of *B. cucurbitae* is stronger than that of *B. tau*, which would further confirm our field results and their competitive relationship. A comprehensive experimental design that considers multiple growing seasons would better reveal their species associations, because reports have found that *B. cucurbitae* and *B. tau* reach their peak occurrence and damage in the autumn. However, in other seasons, the field occurrence and damage caused by these two fruit fly species differ significantly (Mao et al. 2019, Wei 2011, Wu 2021).

As for the niche width and overlap, the information from the collected papers showed that these two pests had a similar niche width and exhibited a high niche overlap. These results were further confirmed by the laboratory host preference tests. Therefore, these results indicated that there is a competitive relationship between these two pests. It is well studied that species with similar niche widths or high niche overlap may have a high competitive relationship (Abrams 2022, Regmi et al. 2022, Voeten and Prins 1999). For example, Huang et al. (2005) found that *Myzus persicae* (Sulzer), *Asiarposina sasakii* (Matsumura), and *Didesmococcus koreanus* (Borchsenius), which damage the fruit of *Armeniaca mume* (Martius), had similar niche breadth and higher niche overlap, and would compete with each other for spatial resources. However, studies also indicated that the competitive relationship could be further influenced by the resources available (Hurtado et al. 2018, Schoener 1983). For example, when there is a large amount of oilseed rape resources, there was no competition between *Apis mellifera* (L.) and *Bombus terrestris* (L.) despite high niche overlap (Bernhardsson et al. 2024). Thus, when confirming the competitive relationship in the field, additional factors should be considered.

The present results were from few studies as we found that most of the papers were focused on studying the ecological characteristics and finding a proper method to control these pests. However, revealing a competitive relationship between them should provide more detail on their ecological characteristics and contribute to the design of a proper management strategy. It is necessary to have a full understanding of the pest community, population structure, and dynamics of the target pests, as well as non-target pests before initiating management tactics. The competitive relationship may help to predict the potential community structure of the fruit fly on cropland based on the host and their competitive ability. Since these two fruit flies have the same niche, but *B. cucurbitae* has a high competitive ability, the population size of *B. cucurbitae* should be larger than that of *B. tau* regardless of the host, as we have shown in the field observation. However, these two pests should be given equal attention when designing management strategies, because if we only control *B. cucurbitae*, *B. tau* may develop as the dominant pest.

Combined field and laboratory studies, as well as utilizing species association, niche breadth, and niche overlap studies, we revealed that there was a high negative association, similar niche width, and high niche overlap between *B. cucurbitae* and *B. tau*, which confirms the competitive relationship between these two pests. These results provide a comprehensive method for confirming species competition relationships and help to predict the occurrence and population dynamic of these pests in the field, which is significant for their managements.

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