

Article

Fruit Color Preference of Frugivorous Birds in an Agroecosystem in Southcentral Mindanao, Philippines

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Simple Summary: Plant–animal interactions play a crucial role in the functioning of ecosystems by promoting biodiversity, maintaining ecological balance, and facilitating the provision of resources for both fauna and humans. Failure to maintain these interactions could lead to numerous plant and animal species' inability to survive, potentially resulting in ecological imbalances. We examined the effects of fruit color and the local landscape on plant–bird interactions in an agroecosystem in Southcentral Mindanao, Philippines. Using artificial fruit models, we found that the proportion of predation and risk was significantly higher in the red fruit model (ripe fruits) compared to the green model (unripe fruits). Furthermore, birds were the dominant predators and were more likely to consume ripe fruits compared to unripe ones, compared to other predators such as mammals and arthropods. Our study showed that fruit color significantly promotes mutualistic interactions, especially for birds, within an agroecosystem.



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Abstract: The removal of fruit is a consequence of plant–animal interactions, and is a vital step in the natural regeneration cycle of plant populations. This research aimed to determine the effect of fruit color and local landscape on plant–bird interactions in an agroecosystem in Southcentral Mindanao, Philippines. We set out 1500 artificial fruit models in ten sampling locations within an agroecosystem. We measured the difference in the proportion of predated/removed (%) fruit models and the risk between sites, fruit color, and predators. Approximately a quarter (24.53%) of the artificial fruit models deployed were predated, and the proportion of predation was significantly higher in the red fruit models (mean = 18.74 ± 9.84) compared to the green fruit models (mean = 11.67 ± 6.17). Birds were the most dominant predators compared to mammals and arthropods, and contributed to at least 60% of the predation of red fruits. Our findings are consistent with previous evidence showing birds' preferences for darker fruit colors. Although landscape variables did not significantly affect fruit predation, tree cover may help increase these interactions. Overall, our study showed that agroecosystems can still support species of frugivorous birds, as indicated by high fruit predation rates, particularly by birds that can permeate different layers of the agroecosystem. Our findings demonstrate an important implication for habitat quality management within agroecosystems. Enriching agroecosystems with pioneer trees with dark-colored fleshy fruits is a sustainable greening strategy that would benefit frugivores and producers in this system.

Keywords: agriculture; avifauna; plant–bird interaction; tree cover; visual cues

1. Introduction

Many vital ecological processes in different habitats, such as seed dispersal and pollination, depend on interactions between plants and animals [1–3]. Vertebrate frugivores are important indicators of the environmental health and changes in terrestrial ecosystems [4–6]. For example, the composition and abundance of fruit bats are significantly higher in a more pristine ecosystem, and even vary in two monocultural systems [7]. Similarly, frugivorous birds are more diverse in pristine habitats compared to disturbed habitats with less vegetation [8,9]. Furthermore, a diverse community of frugivores plays a critical role in providing key ecosystem services, such as the dispersal of seeds in forested and successional zones, which aids in the restoration of many degraded habitats [2,9–12]. Fruit removal is a primary consequence of many plant–frugivore interactions and is a vital part of the natural regeneration cycle of plant populations and diversification, in which fruit dispersers play a critical role [13–15]. Yet, agricultural expansion threatens biodiversity in many countries and is primarily responsible for the widespread destruction and fragmentation of natural vegetation worldwide [16–18]. The rise and expansion of urbanization and conversion to monoculture agriculture have exacerbated negative impacts on biodiversity, particularly in developing countries [19,20]. While some frugivores, such as birds, benefit from agricultural landscapes, particularly in rural areas, by providing alternative food sources when food resources are scarce in urbanized area. Yet, some studies have also shown that frugivorous birds would primarily prefer to search and forage for fruits in less disturbed sites (e.g., more rural areas) compared to more urbanized areas. Even within urbanized areas, frugivores would consume berries from trees that are located in less urbanized gradient [21,22].

Fruits commonly undergo color changes, from a cryptic green that blends in with vegetation to brighter and more conspicuous colors such as red, blue, yellow, or black which are visible to frugivores with color vision [13,23]. The color of the fruit substantially affects the probability of fruit consumption by frugivores [24,25]. Understanding the connection between fruit and frugivores requires linking the fruit morphology and accessibility to removal rates by birds and other frugivorous species [25–27]. Furthermore, it is important to understand the predation rates by frugivores with various habitat modifications to predict the consequences and maintain biodiversity and ecosystem services provided by seed dispersers [28–31]. However, studies to understand the effects of local landscape structure and fruit color on plant–animal interactions within tropical agroecosystems are limited, especially in light of growing global agricultural development [32–34]. An investigation is necessary to fill the gaps and provide valuable evidence to support the sustainable management of agricultural lands.

The use of artificial fruit models is one of the standard techniques to test the effects of fruit colors on bird detection in different habitat types [27,35,36]. This study aimed to test the effects of fruit color and the local landscape on plant–bird interactions in an agroecosystem in Southcentral Mindanao, Philippines. Specifically, our goals were (1) to assess and compare the proportion of predation (%) by birds versus other predators between fruit colors and (2) to determine the effects of local landscape-level and plot-level variables in explaining the predation risks of fruit models. We hypothesize that the proportion and likelihood of fruit predation within an agroecosystem vary depending on the type of fruit predator and fruit colors. Specifically, we predict that birds, which locate fruits by visual cues, will exhibit higher levels of fruit predation compared to mammals and arthropod predators, which rely on smell for locating fruits. Furthermore, we hypothesize that landscape variables may also influence plant–frugivore interactions within an agroecosystem. Specifically, we predict that higher vegetation characteristics will positively influence plant–frugivore interactions.

2. Materials and Methods

2.1. Study Areas and Sampling Design

A common garden experiment was carried out in the agricultural areas of the University of Southern Mindanao in the Southcentral Mindanao region of the Philippines (Figure 1) from July to December 2022. The study site has a warm and humid tropical climate, with temperatures ranging from 23 °C to 35 °C. The dry season begins in November and ends in May, while the wet season peaks in June, with an average annual rainfall of 172 mm. The study area is predominantly classified as an agroecosystem, consisting of remnants of forest cover surrounded by urban built-up structures, fruit orchards, and monoculture Oil palm (*Elaeis guineensis*) and Rubber (*Hevea brasiliensis*) plantations. During the sampling period, we observed several patches of fruit-bearing plant species, including common figs (*Ficus* spp.), Nasturtium tree (*Macaranga* spp.), Soursoap (*Annona muricata*), Aratiles (*Muntingia calabura*), Papaya (*Carica papaya*), Rambutan (*Nephelium lappaceum*), Chico (*Manilkara zapota*), Mabolo (*Diospyros blancoi*), Bell fruit (*Syzygium aqueum*), Guava (*Psidium guajava*), Star fruit (*Averrhoa carambola*), and Lanzones (*Lansium* sp.), which are potential plant foods of frugivores in the area.

We selected ten sampling locations with a radius of 75 m and at a minimum distance of 100 m apart (Figure 1) (see Pena et al. [37]). We selected sites with trees to set up our clay model experiments. Four (4) 4 × 5 m plots with 7 m distance intervals from the centroid of each sampling site were established. We used an oil-based and non-toxic clay to create artificial fruit models. In each plot, we placed 30 clay balls (20 mm in diameter) (15 red and 15 green) on a sturdy tree branch using a steel wire, and placed them at a minimum of 1 m apart (Figure 1). Trees with fruit models were marked with transparent ribbons at least 25 m away to reduce the effect of visual bias on predator behavior. We then exposed the artificial fruit models for seven (7) days to measure the predation rates, the probability of predation and the removal of fruits.

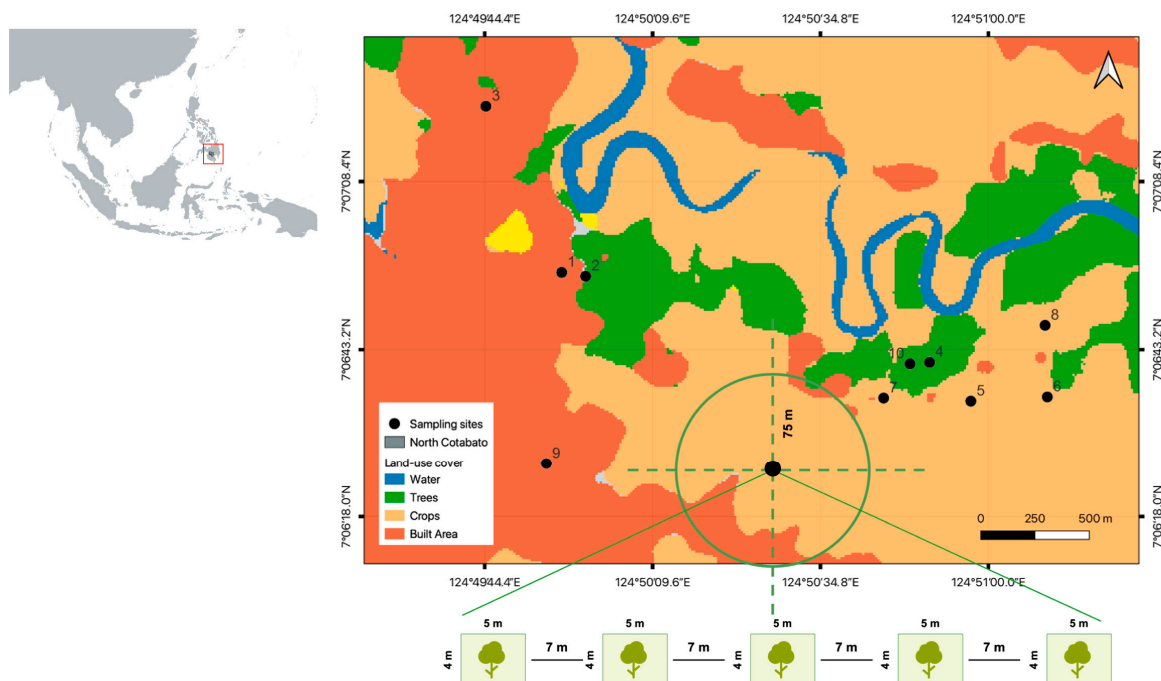


Figure 1. A map of the sampling sites showing the land-use cover of the agroecosystem. The land-use cover is based on Sentinel-2 10 m land-use/land cover data [38]. The sampling plots are also shown.

We considered artificial models to be predated by the presence of a distinct bite mark on the model [39,40]. Predator bite marks were visually distinctive and identified based on the shape of the following bite marks [40]. Birds are indicated with V-shaped marks, predatory

arthropods leave cut-shaped marks (mandibles), and mammals leave incisor-shaped or square-shaped teeth marks (Figure 2). Unidentifiable bite marks and missing models were excluded from the analysis. Models attacked by multiple predators (e.g., mammals and arthropods) were counted separately (i.e., two types of predator damage recorded in one model). The proportion (%) of predated fruit models per site was calculated as the number of predations per area divided by the number of predations in all areas multiplied by 100 [39]. On the other hand, the risk of predation was based on the likelihood (1—attacked, 0—not attacked) of the fruit model being attacked by any of the predator types based on the fruit color (i.e., the frequency of fruits being attacked).

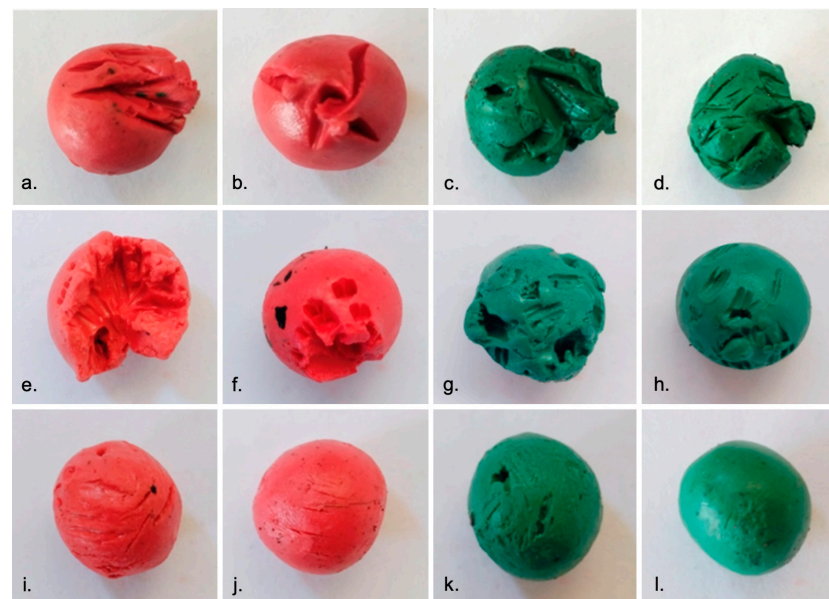


Figure 2. Examples of typical attack marks of birds (a–d), mammals (e–h), and arthropods (i–l).

2.2. Land Use Cover and Environmental Variables

We aimed to determine the effects of environmental variables at the plot level and in the local landscape. At the plot level, all trees within the 4 × 5 m grid were measured for their diameter at breast height (DBH). The diameter of the tree from the base to the height of the breast was used to calculate the DBH (1.2 m from the tree base). We used the mean DBH of all trees in the analysis. Using the Canopeo mobile application (<https://canopeoapp.com/>) (accessed on 2 October 2022), canopy openness (%) was measured from the center of the grid. At the local landscape level, we calculated the proportion of land use cover within a 75 m radius of the sampling site using spatial statistics and the buffer zone function in QGIS [41]. We used spatial data from the Sentinel-2 10 m land use/land cover to quantify the percentage of local landscape structure and agricultural area [38].

2.3. Statistical Analyses

We performed all our statistical analyses based on the fruits recovered from the study sites. A Kruskal–Wallis H test was used to compare the proportion of predated fruit models (%) between sites and predator types, and a Mann–Whitney U test was used for comparison of artificial fruit colors. A Chi-square test of association (χ^2) was used to determine the relationship between the frequency of attacks and site, fruit colors, and predator types. We used a generalized linear mixed model (GLMM) with a binomial error distribution (log-link) to investigate the effects of fruit color, predator types, plot level, and local landscape-level variables. Fruit color (red and green), predator types (birds, mammals, arthropods), DBH, canopy cover, and tree cover were included as explanatory variables. We had study sites and plots as random effects. We selected the best model based on the lowest values of the corrected Akaike information criterion (AICc) and Akaike weight (wAICc) [42]. Using the

significant predictors from the best model, we built another separate binomial generalized linear mixed model (GLMM) to determine the risk of predation between fruit colors. We used predator type and tree cover as explanatory variables, and sites as random effects. We tested all continuous data for collinearity prior to the final modeling.

All statistical tests and data visualization were performed using the open software JAMOVI 2.3.22 [43] and GraphPad Prism 9 [44]. All spatial analyses were performed in QGIS 3.26 [41]. The significance level was set at $p < 0.05$.

3. Results

3.1. Fruit Predation Proportion (%) in an Agroecosystem

Of the 1500 artificial fruit models set up within the agroecosystem sites, 368 (24.53%) were predated, with a higher proportion of predation in red fruit models ($n = 255$, 69.3%) compared to the green fruit models ($n = 113$, 30.7%) (example of predation of fruits shown in Figure 2). Forty-two ($n = 42$, 2.8%) fruit models were reported missing (red, $n = 28$; green, $n = 14$). We found that the proportion of predation based on the color of the fruit model did not differ between the study sites within the sampled agroecosystem (KW test, Red: $H = 10.70$, $df = 9$, $p = 0.297$; Green: $H = 5.96$, $df = 9$, $p = 0.744$).

3.2. Risk of Predator Attack

Predation proportion by predators only significantly differed in birds (MWU test = 276, $p < 0.001$) and mammals (MWU test = 161, $p = 0.031$) but not in arthropods (MWU test = 91.50, $p = 0.277$) (Figure 3). Among fruit predators, bird predation represented the majority of identifiable marks (red = 20.9%, $n = 223$; green = 8.8%, $n = 66$) ($\chi^2 = 43.619$, $df = 1$, $p < 0.001$), followed by mammals (red = 8.5%, $n = 64$; green = 3.7%, $n = 28$) ($\chi^2 = 15.059$, $df = 1$, $p < 0.001$), and arthropods (red = 4.5%, $n = 34$; green = 2.5%, $n = 19$) ($\chi^2 = 4.422$, $df = 1$, $p = 0.035$).

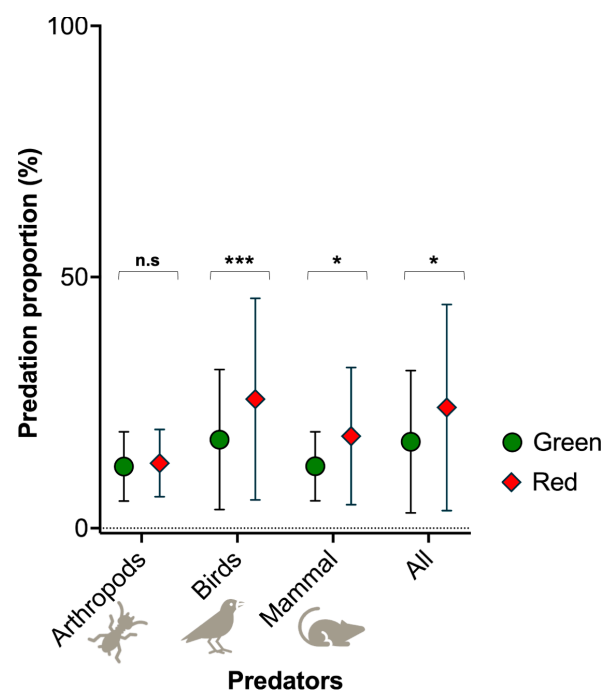


Figure 3. Comparison of the predation proportion (%) of different predator types in red and green artificial fruit models. Whiskers represent the SD, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = not significantly different.

3.3. Risk of Predation by Fruit Color

Our field experiment showed that red-colored models (i.e., ripe fruits) have a higher probability of being attacked (i.e., predation risk) than green-colored (i.e., unripe fruits) ($\chi^2 = 59.813$, $df = 1$, $p < 0.001$). The mean proportion of predation (%) of red-colored models (18.74 ± 9.84) was significantly higher than that of the green-colored models (11.667 ± 6.172) (MWU test = 1609, $p < 0.001$). Furthermore, the predation risk did not differ between study sites ($\chi^2 = 11.409$, $df = 9$, $p < 0.249$).

Among the six (6) GLMM models built (Table 1), the combination of color, predators, their interactions, and tree cover was the best model to predict predation risk (Model #6, AICc = 741.285) (Table 1, Figure 4). The red-colored models were more likely to be predated than the green-colored models ($\beta = 0.869$, $p < 0.001$). Compared to arthropods, birds are the more dominant predictor ($\beta = 1.421$, $p < 0.001$) of predation probability. On the other hand, mammals ($\beta = 0.288$, $p = 0.377$) did not significantly affect the likelihood of fruit model predation. Meanwhile, tree cover only showed a marginally significant effect on predation. The separate models consistently demonstrated that birds were a significant predator in determining the probability of fruit removal, with a stronger effect observed in the red-colored models ($\beta = 1.724$, $p < 0.001$) compared to the green-colored model ($\beta = 1.126$, $p = 0.013$). (Figure 5). Contrary to our expectations, increased tree cover significantly influences the likelihood of predation in green-colored fruit models ($\beta = 0.968$, $p = 0.008$).

Table 1. List of candidate models for the best binomial generalized linear mixed model (GLMM) predicting the risk of fruit removal. The best model is shown in bold.

Models	Terms	AICc	Δ AICc	RL	wAICDc
1	Color + Predator + Color \times Predator + DBH + Canopy + Tree cover	747.160	0.510	0.775	0.510
2	Color + Predator + Color \times Predator + DBH + Canopy	747.760	1.110	0.574	0.378
3	Predator + DBH + Canopy	765.100	18.450	0.000	0.000
4	Predator + Color + Predator \times Color	747.060	0.410	0.815	0.536
5	DBH + Canopy + Tree Cover	808.780	62.130	0.000	0.000
6	Color + Predator + Color \times Predator + Tree Cover	746.650	0.000	1.000	0.658

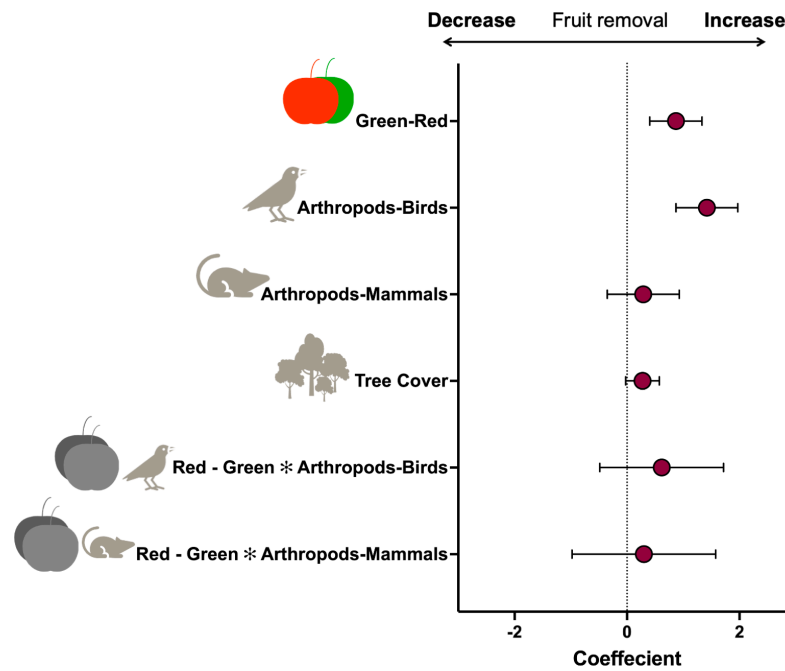


Figure 4. Visualized results of the best binomial generalized linear model (GLM). The dots represent the coefficients, and the whiskers represent the lower and upper bounds of the 95% CI. Silhouettes in dark colors represent significant relationships at $p < 0.05$.

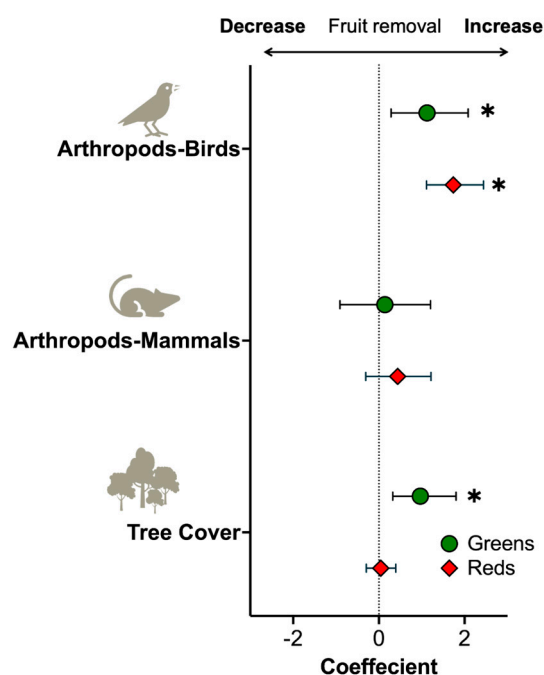


Figure 5. Comparison of the binomial generalized linear mixed models (GLMM) results between the predation risk of two artificial fruit models. The diamonds and dots represent the coefficients, and the whiskers represent the lower and upper bounds of the 95% CI. The * denotes significant relationships at $p < 0.05$.

4. Discussion

Our field experiment found the usefulness of clay models in understanding plant–animal interactions in an agroecosystem. Various ecological studies have used modeling clays to study plant–animal interactions under different habitat conditions and successfully regulated the variables [45], since artificial fruits can change fruit characteristics independently [36]. Our present study utilized clay models to demonstrate the proportion of fruit removal and the variations in risk from various frugivores in an agroecosystem in Southcentral Mindanao, Philippines. We found that birds were the dominant fruit predators within the agroecosystem, contributing to at least 61% of predation success. More importantly, we found that fruit color is a significant factor in increasing the probability of predation of fruits, particularly by birds.

The dominance of bird predation on our model fruits can be attributed to their highly developed color vision and excellent visual acuity; therefore, they often use visual cues such as the color of the object during their foraging to locate and identify foodstuffs [26]. Preferences for fruits based on colors have been widely studied in several species of birds, and it has been shown that they prefer red and darker fruits [25,27,46], which can signal the ripeness of the fruit. Galleti et al. [26] demonstrated that darker fruits, such as red and black fruits, were more predated than less conspicuous colors, such as white models. They also showed that artificial fruit experiments could quantify the influence of habitat structure on fruit removal. In a separate field experiment using three colors of artificial fruits (red, brown, and white), around 62.2% of artificial red fruits were pecked the most, followed by brown (57.2%) and white (26.7%) [47]. Their findings suggest that darker fruit colors significantly predict fruit removal. The color of the fruits functions mainly to attract the attention of potential dispersers who use vision as the key sense to find food and to influence the selective pressure of birds in foraging [24,25,45,47]. Cazetta et al. [25] stressed that fruit color is an important factor in plant–bird interactions because it aids in attracting potential dispersers and increases plant diversity. Although some species prefer less appealing colors such as green, the predation of green fruits is lower compared to more apparent colors [48]. This provides insight into the co-evolution of plants and seed

dispersers, as immature green fruits of plants that disperse their seeds primarily through ornithocoric means are not yet ready to germinate [24,49].

An alternative explanation for the observed patterns is that bird predators may have a preference for red-colored fruit models over green-colored ones, not necessarily due to an innate color preference, but because they are more easily noticeable in the area due to their greater conspicuousness [27]; this shows that predators perceive artificial fruits as a type of natural fruit. Among predators, birds are dominant compared to mammals and arthropods. This is possibly because birds rely on visual signals, as artificial fruits do not have scent or taste. Most mammals and arthropods would not be attracted to visual cues, but instead to the olfactory [50,51]. Furthermore, fruit dichotomy is a strong determinant of the removal of fruits by predators; for example, mammals consume more orange, yellow, or brown fruits, and birds consume more red or black fruits [13,52]. Although mammals are less attracted to red-colored fruits and contribute lower fruit model predation, they can still be a potential predator and aid in seed dispersal.

Although we did not find any of the local landscape variable to be a significant factor in predation risk, our analysis showed that increasing tree cover and habitat structure would enhance bird–fruit interactions. Forest fragmentation and conversion to agricultural land impact frugivory and seed dispersal through several mechanisms, such as habitat loss [53], fragment isolation and edge effects, and modifications in habitat quality [54]. Without an appropriate approach, quantifying the impact of the land modification on plant–animal interactions is challenging [55]. Previous field investigations showed that seed dispersal interactions are negatively affected by forest loss and fragmentation [15,56]. Frugivores in tropical regions are key conservation priorities due to their higher risk of extinction than other trophic levels, and their sensitivity to habitat modifications, such as agricultural land conversion [57]. However, some species occupy agricultural space and benefit from fruit production and suitable habitats available for foraging [7,28]. In our study, although the investigated agroecosystem is degraded, the plant–bird interaction remained comparable to previous studies in other ecosystems, such as Arruda et al. [47] and Gagetti et al. [58]. The high abundance and proportion of common frugivorous birds, such as Yellow-vented Bulbul (*Pycnonotus goiavier*), Black-naped Oriole (*Oriolus chinensis*), Asian Glossy Starling (*Aplonis panayensis*), and several species of fruit doves that mainly forage at the edge of the forest compared to the inner part of the forest, may also explain the dominance of birds as fruit predators at the study sites [8,59–62]. This suggests that frugivorous birds can still function, as bird-dispersed fleshy fruits within agroforests are often consumed and dispersed primarily by generalist species that are least sensitive to habitat changes [8,63].

Our results also show that the risk of predation of green-colored fruit models increases with tree cover. This means that increasing tree cover, for example, with more extensive fruit orchards, agroforests, or more forests adjacent to the fruit orchard (i.e., within a 75 m radius in this study), increases the probability of premature fruit removal from fruit trees. This could be due to the increased number of predators, as predicted by the species–area relationship [64], competing for food resources. The availability of forests around the study site also served as a source of frugivore species that can immigrate or colonize the area [65]. Maintaining the remaining native and intact vegetation within the agroecosystem would enhance the diversity of frugivore species, especially birds, within fragmented habitats. Therefore, to effectively ensure the population of frugivorous birds and maximize their ecosystem services as seed dispersers (consequently maximizing habitat quality improvement), an enrichment strategy for agroecosystems and adjacent forests with pioneer trees with dark fleshy fruits such as Aratiles (*Muntingia calabura*), Mulberry (*Morus* spp.), Currant tree (*Antidesma bunius*), Java plum (*Syzygium cumini*), and figs (*Ficus* spp.) is highly recommended. This approach would be a sustainable alternative and may benefit frugivores and farmers by increasing the availability of stable food sources for frugivores, rather than relying entirely on the food provided by fruit crops in a monoculture production system, and reducing the disservices of frugivorous birds to crop yields.

Our observed high predation proportion of fruit models showed that agroecosystems can still support frugivorous species, particularly birds. Although most frugivores in agroforests may be generalist species [8,60], frugivorous birds are more mobile, can permeate various habitat types, and disperse seeds more efficiently than other predators [10,12]. Overall, our study provides important management implications, especially in improving habitat quality within an agroecosystem.

Although we conducted our study in a small area and on a localized scale, we have demonstrated the effectiveness (i.e., high predation turnover of clay models) of using clay models to study plant–animal interactions in an agroecosystem. Studying the ecology of plant–animal interactions in different habitat settings is also possible using this technique. Lastly, we acknowledge several caveats in our study. For instance, we did not consider the potential impact of visually attractive fruit colors or olfactory cues that might be more effective for other frugivores, such as mammals. Further research with different fruit colors is needed to explore this aspect. Additionally, the scent of the clay may have influenced the predation rate, which should also be investigated in future studies. We also did not consider the species diversity of frugivores that predated the fruit models in the area. We recommend future studies to integrate methods to study this, for example, using camera traps to identify fruit predators [66,67]. Frugivore communities can vary depending on the types of agroecosystems [8,68], as some systems have higher and better vegetation cover than others [69]. Future studies in the Philippines should also investigate fruit removal and preference in different habitat types and other ecological conditions, including seasonal variation.

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