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RESEARCH ARTICLE

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# Apparent effect of range size and fruit colour on palm diversification may be spurious

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## Abstract

**Aim:** Fruit selection by animal dispersers with different mobility directly impacts plant geographical range size, which, in turn, may impact plant diversification. Here, we examine the interaction between fruit colour, range size and diversification rate in palms by testing two hypotheses: (1) species with fruit colours attractive to birds have larger range sizes due to high dispersal ability and (2) disperser mobility affects whether small or large range size has higher diversification, and intermediate range size is expected to lead to the highest diversification rate regardless of disperser.

**Location:** Global.

**Taxon:** Arecaceae (palms).

**Methods:** Palm species were grouped based on likely animal disperser group for given fruit colours. Range sizes were estimated by constructing alpha convex hull polygons from distribution data. We examined disperser group, range size or an interaction of both as possible drivers of change in diversification rate over time in a likelihood dynamic model (Several Examined State-dependent Speciation and Extinction [SecSSE]). Models were fitted, rate estimates were retrieved and likelihoods were compared to those of appropriate null models.

**Results:** Species with fruit colours associated with mammal dispersal had larger ranges than those with colours associated with bird dispersal. The best fitting SecSSE models indicated that the examined traits were not the primary driver of the heterogeneity in diversification rates in the model. Extinction rate complexity had a marked impact on model performance and on diversification rates.

**Main Conclusions:** Two traits related to dispersal mobility, range size and fruit colour, were not identified as the main drivers of diversification in palms. Increased model extinction rate complexity led to better performing models, which indicates that net diversification should be estimated rather than speciation alone. However, increased complexity may lead to incorrect SecSSE model conclusions without careful consideration. Finally, we find palms with more mobile dispersers do not have larger range sizes, meaning other factors are more important determinants of range size.

KEYWORDS
Arecaceae, dispersal, diversification rate, evolutionary dynamics, frugivory, fruit colour, geographical range size, macroecology, palm distribution, plant traits

## 1 | INTRODUCTION

In order to disperse, plants produce fruits for seed ingestion by frugivorous animals. To increase the chance of consumption, and thereby dispersal, fruits exhibit colours that increase the probability of detection by desirable dispersers and reduce detection by less desirable ones (Melo et al., 2011). Animals better detect fruits that contrast against background colours. Bird and mammal frugivores are the most significant seed dispersers in terrestrial habitats (Fleming & Kress, 2011), but due to variation in colour vision these groups perceive fruit colour contrasts differently.

Birds have the ability to discriminate between red and green (Vorobyev et al., 1998), whereas mammals generally cannot distinguish red from green (Jacobs, 1993). The mammalian exception that do distinguish red from green is certain primate groups: apes, old world monkeys and a few new world monkeys (Onstein et al., 2020; Regan et al., 2001). Birds are therefore more likely to consume fruits that are red, black and intermediate shades of purple (Duan et al., 2014; Schaefer et al., 2014). These fruits are often collectively termed 'bright' in the literature, and may include orange and yellow (Knight & Siegfried, 1983; Onstein et al., 2019). Fruit colours equally detectable and often preferred by mammals are often termed 'dull' and include green, brown, orange and yellow fruits (Janson, 1983; Sinnott-Armstrong et al., 2018). Whether it is birds or mammals that more likely consume any specific orange or yellow-coloured fruit may be determined by the brightness of the colour or whether it is perceptually closer to bird- or mammal-dispersed fruit colours. For example, orange colours with wavelengths closer to reds would be more likely consumed by dispersers that distinguish red hues better (birds). Orange colours with wavelengths close to yellow or browns would be more likely consumed by frugivores that better distinguish yellow and brown hues (mammals).

Frugivory-related traits such as fruit size and colour are important drivers of angiosperm diversification (Lu et al., 2019; Onstein et al., 2018, 2020). However, the mechanisms by which particular fruit colours influence diversification remain unclear. One potential mechanism is that certain fruit colours promote diversification due to their synergistic effects with geographical range (Lu et al., 2019; Onstein et al., 2019). The specific dispersers associated with a certain plant will determine its dispersal ability; thus, the fruit colour used to attract one disperser or another can be an important predictor of plant geographical range. Overall, birds travel and disperse seeds further (Santos et al., 1999; Stevenson et al., 2021), and cross geographical barriers with greater ease than (non-flying) mammals do (Lu et al., 2019). Therefore, plants that produce red, black and purple fruits often disperse further due to their association with bird dispersal, resulting in a wider geographical range for that plant species (Lu et al., 2019).

Different mechanisms that facilitate or hinder speciation and extinction are associated with different range sizes (Gaston, 1998). Furthermore, range size is correlated with dispersal ability (Estrada et al., 2015; Faurby & Antonelli, 2018; Penner & Rödel, 2019; Sinnott-Armstrong et al., 2018). Therefore, plants dispersed by animals with high dispersal ability may have larger range sizes, and be influenced by mechanisms impacting speciation and extinction at large range size (Bacon et al., 2013). Species with high dispersal ability are more likely to colonise new areas, meaning that geographically isolated populations arise. These geographically isolated populations are, in turn, more likely to speciate (Lester et al., 2007). For example, a large range size may facilitate parapatric speciation through isolation by distance (Baptestini et al., 2013), ecological speciation due to variation in environmental conditions (Bacon et al., 2021; Chen & Schemske, 2015; Keller & Seehausen, 2012) or differences in pollinator communities (Neves et al., 2020). However, high dispersal ability may also hinder diversification through the maintenance of gene flow between distant populations (Claramunt et al., 2012).

Diversification rate may, alternatively, be higher in small- or intermediate-ranged species (Gaston, 1998). For large range sizes that have geographical barriers embedded within the range, connectivity around the barrier for species unable to cross it would hinder allopatric speciation. However, small-ranged species are more prone to extinction, which lowers net diversification (O'Grady et al., 2004). Small-ranged species may not benefit as often from the speciation-facilitating factors suggested for large-ranged species such as ecological speciation. Owing to the hindrances of diversification associated with either range size extremity, intermediate ranges are expected to balance gene flow and isolation, and thus lead to the highest diversification rate (Gaston, 1998; López-Villalta, 2014).

With a wide variety of fruit colours, sizes, shapes and amount of fruits, palms are a keystone resource for dispersing animals (Zona & Henderson, 1989), with 14 unique fruit colours described (Kissling et al., 2019). Palms rely on a wide array of animals (e.g. birds, bats, non-flying mammals, reptiles, insects and fishes) to disperse their seeds (Zona & Henderson, 1989). This mutualistic interaction has been important in shaping palm distribution patterns over space and time (Lim et al., 2020; Onstein et al., 2018; Sales et al., 2021). Here, we test the impact of the interplay between fruit colour on range size and diversification rate in palms (Arecaceae). Palms are a taxonomically (c. 2600 species; Baker & Dransfield, 2016) and functionally diverse clade (Kissling et al., 2019) characteristic of tropical regions (Couvreur et al., 2011), and have rich phylogenetic (Faurby et al., 2016), trait (Kissling et al., 2019) and distribution data (Global Biodiversity Information Facility, GBIF; https://www.gbif.org/) available. Range size in palm species is highly variable, where certain species are known from single localities while others have intercontinental distributions (Dransfield et al., 2008). Taken together, palms are an excellent case to study the potential interaction between fruit colour and range size on diversification rate.

Plants have dynamic dispersal systems in that a single individual may rely on a multitude of different animal species to disperse its seeds (Stevenson et al., 2015). These interactions have shaped global plant diversity and biogeography. It is therefore important to examine how the colour of a fruit ultimately leads to more diverse lineages through time and has large-scale impacts on biogeography and evolution. With this, we hypothesise that (1) large range size is associated with fruit colours that are dispersed by frugivorous birds, owing to their mobility and high dispersal ability. We also hypothesise (2) that net diversification varies between fruit colour groups associated with different dispersers, revealing how dispersal ability impacts diversification at different range sizes. Due to the potential effects that hinder speciation at either range size extreme (small and large), we expect that diversification rate is higher for palms with intermediate range size. Testing these two hypotheses will aid the understanding of how ecological relationships and geography interact to influence diversification.

## 2 | MATERIALS AND METHODS

### 2.1 | Data

We obtained fruit colour data for 1485 palm species (ca. 57% of all recognised species; Baker & Dransfield, 2016) from the PalmTraits 1.0 database (Kissling et al., 2019). For phylogenetic analyses, we used a set of 30 trees sampled from an updated version of the posterior distribution of the all-evidence species-level phylogeny from Faurby et al. (2016). The phylogeny by Faurby et al. (2016) was constructed by combining novel data with a backbone constructed from nine plastid and four nuclear markers combined with a morphological dataset and a restriction fragment length polymorphism dataset (Baker et al., 2009). The phylogeny was time-calibrated using five calibration points. Species without data were placed in the phylogeny using Bayesian modelling, leading to a probability distribution of phylogenies. The following changes have been made to the updated version 1.1 from 2018 that was used in our study: Iriarteeae was reanalysed, all at one time, based on data from Bacon et al. (2016). It was rooted internally with *Iriartea*, and *Dictyocaryum* was set as sister to remaining genera based on the same source. The clade comprising *Balaka*, *Veitchia*, *Adonidia*, *Jailoloa*, *Manjekia* and *Wallaceodoxa* was reanalysed based on Heatubun et al. (2014) and on Alapetite et al. (2014). It was rooted with *Adonidia* as sister to the rest. *Sabinaria* was added as sister to *Itaya* based on Bogotá-Angel et al. (2015). The taxonomy was then updated.

Species occurrence records for 1785 species were obtained from GBIF (last consulted on 31 January 2019; GBIF Occurrence Download https://doi.org/10.15468/dl.rjmqfy). We performed analyses using R version 3.6.3 (R Core Team, 2019) except for Several Examined and Concealed States-dependent Speciation and Extinction (SecSSE) analyses, where R version 4.1.2 was used on a high-performance computing system.

### 2.2 | Combining fruit colour categories

To determine whether our examined traits (disperser type and range size) drive diversification, and to estimate net diversification associated with the character states, we used SecSSE models (Herrera-Alsina et al., 2019). The reasoning behind using SecSSE models is discussed in Appendix S1-S2., Supporting Information. Due to the complexity of SecSSE models, it is desirable to minimise the number of character states and therefore keep the modelled likelihood space low. To decrease the number of parameters, distinct fruit colours in the dataset were combined. Combining similar colours also reduced any effect from when colour, which is a complex trait where colours are not always unambiguously delineated, was assigned into discrete categories for the dataset.

All polymorphic species, 403 in total, were removed from the data (i.e. species with more than one fruit colour assigned). Ambiguous colour definitions that are not typically mentioned in the frugivory-related literature, but are present in PalmTraits: 'ivory', 'straw-coloured', 'cream', 'pink' and 'grey' (70 species total) were excluded. To reduce the number of character states, we first classified the palm species into five fruit colour categories based on likely disperser group (bird or mammal): (1) black, purple; (2) red, orange; (3) yellow; (4) brown, green, blue; (5) white. The categories containing (1) black and purple and (2) red and orange were assumed to be bird-dispersed because they are preferred by birds and/or contrast against green background vegetation and/or are bright (Duan et al., 2014; Knight & Siegfried, 1983; Onstein et al., 2019; Schaefer et al., 2014). The other groups contain colours preferred by mammal dispersers and/or do not contrast against green background vegetation and/or are dull, groups: (3) yellow, (4) brown, green, blue and (5) white (Janson, 1983; Sinnott-Armstrong et al., 2018).

To further decrease the number of character states used in the SecSSE models, we tested which of the five fruit colour categories could be further merged without significant loss of model fit. For this, we used a simpler SSE model (MuSSE, 'diversitree' version 0.9–13; FitzJohn, 2012), where the model simplicity allows for more parameter-rich models. While MuSSE models can lead to incorrectly attributing diversification parameters to a trait, the likelihoods of MuSSE models are comparable to equivalent zero state SecSSE models (Herrera-Alsina et al., 2019) and MuSSE can therefore be leveraged for model selection.

Starting with the most complex model (five colour categories), we tested all 10 possible combinations of merged categories from the five initial categories. In each case, two of the five groups were combined, while the other three were kept separate. Each model was fit on 30 phylogenetic trees randomly sampled from the posterior distribution of trees. To compare Akaike information criterion (AIC) scores between models with fruit colour states merged differently, we calculated the median ΔAIC scores. This was done by subtracting the AIC scores for each model (values from each of the 30 models on 30 trees) by the AIC scores of the 30 trees from the full five-category model. We then calculated the median of these ΔAIC values. The best model (highest ΔAIC) from the first round (which had four categories per model) was selected and used as a starting point for the second round of merging. The best model from this round (which had three categories) was tested in a third round to check if additional simplification was possible, but these produced ΔAIC scores that dramatically reduced model fit. All model setup and their AIC scores are described in Table S2 in Appendix S2, Supporting Information.

The best model had the following fruit colour categories: (1) black, purple, red, orange, white; (2) yellow; and (3) brown, blue, green. Based on the likely most frequent frugivorous dispersers for the selected model fruit colour groups we hereafter refer to the groups as (1) bird, (2) mammal-1 and (3) mammal-2.

With the selected model, there were some species from the original dataset which, based on the colour combinations in the selected model were no longer polymorphic as their colours were now grouped into a single category. We added these species back into the fruit colour dataset for the remaining analyses. This resulted in 1063 palm species with fruit colour data, representing ca. 41% of all recognised palms species (Baker & Dransfield, 2016).

## 2.3 | Range size calculations

We estimated the range size of all species with available, filtered data. Fossil data, records without coordinates, duplicates and occurrence records nearby science institutions, within bodies of water, or country centroids with a buffer of 5000 m were filtered out using 'CoordinateCleaner' version 2.0–3 (Zizka et al., 2019). We also removed records outside the species native 'botanical country', which is the level three geographical division defined by the International Working Group on Taxonomic Databases for Plant Sciences (TDWG) (Brummitt et al., 2001), using a custom Python script.

(https://github.com/mftorres/palm_leaf/blob/master/notebooks/01_GBIF_variables_data_prep.ipynb).

We built alpha hull polygons to estimate the range (extent of occurrence) for species with three or more records using 'rangeBuilder' version 1.5 (Rabosky et al., 2016), keeping only terrestrial range (clipping to land). The package optimises the alpha value to create the smallest possible polygon(s) for each species. Because alpha hull polygons allow for concavities in the outer perimeter of the species range, they are a more conservative range estimate compared to convex hulls (Meyer et al., 2017). Alpha hull area was calculated in 'raster' version 3.0–12 (Hijmans, 2020). For our analyses, we did not need precise areas for all species but only the relative sizes (grouped into small, medium and large range). We were therefore able to include relative range size for some species with fewer than three records if available data suggested that they have small ranges. More specifically, we included species that occur exclusively within a single TDWG unit and with fewer than three occurrence records in that unit. These species were added into the range size dataset with an arbitrary range size that was lower than any of the alpha hull areas (0.1 $\text{km}^2$), meaning they were categorised as small ranged.

Species were then ordered based on ascending range size and then split into three range size categories: small, intermediate and large. Each range size category contained a third of the species each. We used three range size categories because this is the minimum number of categories to be able to assess if the relationship between range size and diversification was non-linear. We chose to have all three groups be equally large since this maximises the power of the analyses by minimising tip ratio bias (Davis et al., 2013). Species in these range size categories were further split by their associated fruit colour group into nine total groups based on both fruit colour and range size. The number of species in each disperser group's range size categories (small, medium and large range, respectively) were as follows: Bird: 250, 243 and 208 (black, purple, red, orange and white; 701 species total); Mammal-1: 22, 16, 28 (yellow; 66 species total); Mammal-2: 85, 93, 118 (brown, green and blue; 296 species total).

## 2.4 | Testing the relationship between fruit colour, range size and diversification rate

We tested whether there was a relationship between disperser group and range size with a Fisher's exact test (Mehta & Patel, 1983). To examine diversification dynamics related to disperser group and range size, we built SecSSE models (in the R package 'SecSSE' version 2.3.1) based on the nine combined categories of range size and fruit colour from the model selection (fruit colour and range size categories are mapped on a palm phylogeny in Figure 1). SecSSE models can be examined trait dependent (ETD) or concealed trait dependent (CTD). ETD models test for heterogeneity in diversification parameters related to the coded traits, in our case fruit colour and range size. CTD models test for heterogeneity in diversification parameters related to a concealed trait. The relative model fit of an ETD and CTD model reveal whether the examined or concealed trait respectively is the driver of the diversification parameters estimated by the model. Model fit between the ETD and CTD models for a given setup was compared using AIC. This comparison is made to avoid falsely attributing diversification parameters for the examined trait when they are more likely related to a trait not examined as indicated by a CTD model fitting better than an ETD model.

Phylogenetic tree tips lacking trait data were removed from the tree. This left 1063 species with fruit colour and range size data to be used in the analysis (about 41% of palms in the phylogeny; analysis of

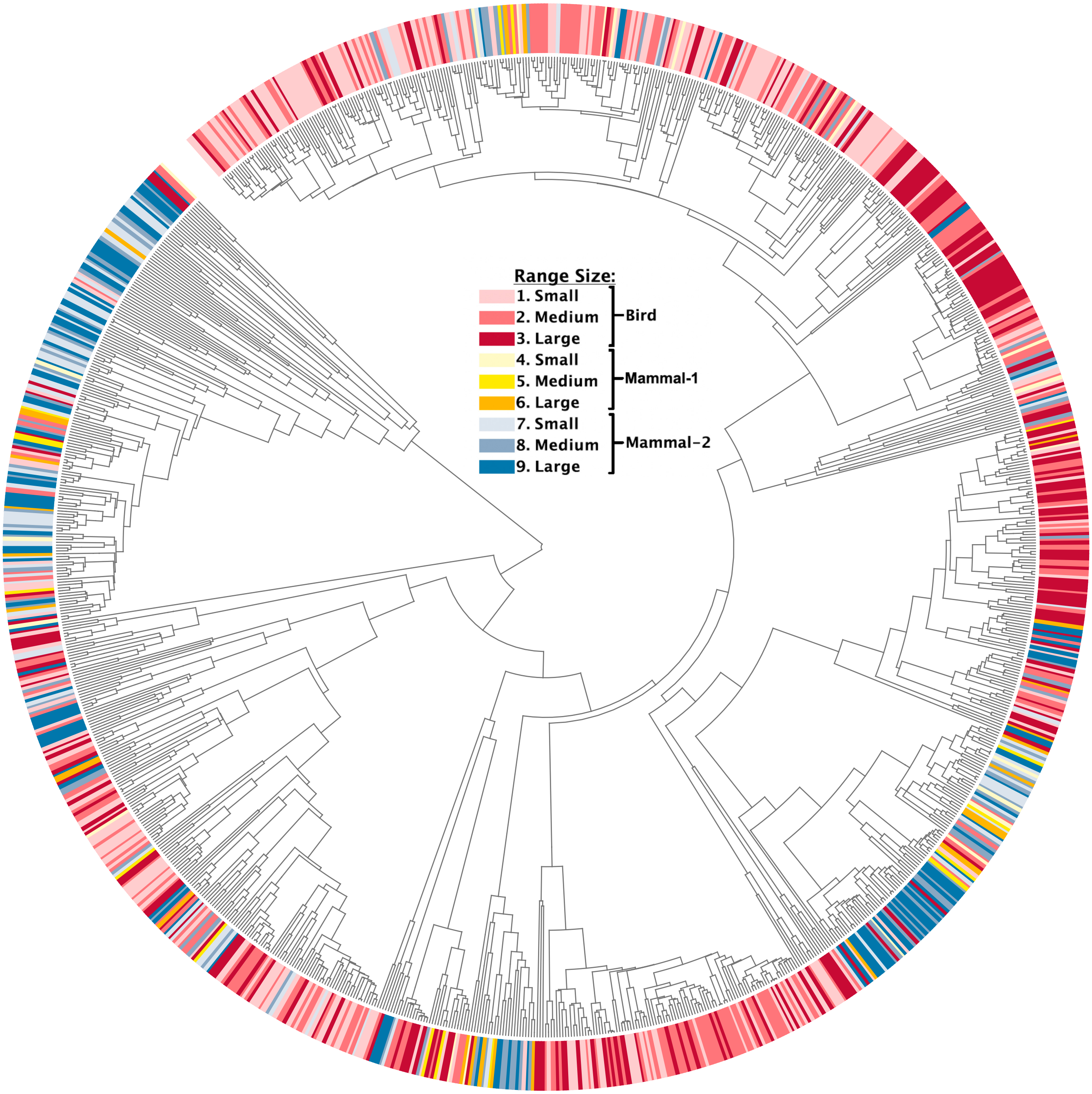

FIGURE 1 Fruit colour categories mapped onto the palm phylogenetic tree. Categories are described based on their range size and disperser group.

the effect of this sampling is described in section 2.5). The sampling was relatively even across the tree (Figure 1). To simplify the model and reduce overfitting, we disallowed changes between categories that would effectively mean two character transitions at once. This means a state could only change range size while keeping the same disperser, or only change disperser while keeping the same range size. Transitions between range sizes could only occur between adjacent ranges at one time, small-medium (and vice versa) and medium-large (and vice versa). Our SecSSE models had nine hidden states to match the model complexity of the nine examined trait states (Herrera-Alsina et al., 2019). Concealed state transitions followed the same constraints to disallow double transitions as the examined state transitions did. Transitions between examined and concealed states could only occur between the equivalent examined and concealed states. In SecSSE, examined states are numbered, in our case 1–9, and hidden states are denoted alphabetically, in our case A-I, so our constraint means that transitions were allowed only between states 1 and A, 2 and B, 3 and C and so on. The examined and concealed state transitions are visualised in Figure S2.1, Appendix S2.

We tested nine different model designs that had different parameters jointly estimated. Model naming convention is thus: 'interaction' models study the interaction of fruit colour and range size and therefore include both, while 'independent' models examine either trait independently. Models with 'all' in the name have all possible transition rates and extinction rates (mu), while others specify whether they have fewer transition ('trans') rates and/or extinction rates (mu). For each setup, we constructed an ETD and a CTD model and ran these on a maximum clade credibility (MCC) tree. The mean AIC of the ETD and CTD model for each setup was calculated (ETD AIC + CTD AIC / 2), and the different models were ranked based on mean AIC. The three best-fitting model setups were selected and the ETD and CTD version of each setup was run on a posterior distribution of six trees. These six trees were the first six of the random 30 trees used for model selection. The median AIC of the ETD and CTD models run on six trees was used to compare ETD and CTD model fit for each setup. All results for the models run on six trees are shown in Table S2.2, Appendix S2. Net diversification was calculated (speciation rate-extinction rate) from the optimised speciation and extinction parameters of the best three models.

## 2.5 | Statistical validation of sampling size

The nine state SecSSE models were fit to a phylogeny containing the 41% (1063) of palm species that have both fruit colour and range size data. To assess whether our level of sampling had significant effects on our results, we performed statistical validation based on simulations. A total of 100 randomly simulated phylogenetic trees containing 2550 species each, with unique three-state traits that influence diversification were simulated. The parameter values for speciation and extinction from our results were used to simulate the trees. These simulation models had three states rather than nine to keep the number of free parameters low. Therefore, each simulated state was given the mean parameter values from each range size category. The parameters used for the simulations were as follows: (1) mean of bird, mammal-1 and mammal-2's small range parameter values; (2) mean intermediate range parameters and (3) mean large range parameters.

We leveraged the simplicity of MuSSE models to run the simulations. The problem of MuSSE models falsely attributing diversification parameters to specific traits (Herrera-Alsina et al., 2019) was not an issue here, as we were interested only in testing whether combining character states significantly lessened model fit, not drawing conclusions of whether higher diversification is associated with specific traits. We fit MuSSE models to the simulated trees, with a single model constraint preventing state changes to occur directly between states one and three. After fitting a model to each of the full trees, 41% of the species were sampled at random and the tree was pruned to only contain the sampled species. MuSSE models were fit to the pruned trees, also with adjacent state changes disallowed. Net diversification values were then calculated from the resulting parameter values, for the full tree parameters and for the pruned tree parameters. A two-tailed binomial test was used to assess whether the pruned trees were biased compared to the full trees.

## 3 | RESULTS

We found that disperser group and range size were not independent based on a Fisher's exact test ($p = 0.0089$; Mehta & Patel, 1983). The three SecSSE models with the lowest average AIC were selected to run on a distribution of six trees. An ETD and a CTD version of these three best models were run. These three best-fitting SecSSE models differed only in the number of parameters jointly estimated for extinction rate (μ). In order of best fit to worst, the models had nine-, three- and one-parameter value for extinction rate estimated. This means either every trait had an independent extinction rate, only fruit colour groups had a separate extinction rate (μ1: states 1,2,3—bird; μ2: 4,5,6—mammal-1; μ3: 7,8,9 mammal-2) or a single extinction rate was estimated for all states, respectively. These results indicate that estimating extinction rate separately is important for good model fit when using SecSSE. CTD AIC was lower than ETD AIC for each respective model (Table 1), indicating that for our three best fitting models, the examined trait is not the primary driver of the parameter values observed. Furthermore, the three best models have different net diversification rates associated with different character states compared to one another (Figure 2). These different diversification rates are driven by the concealed trait, so cannot be interpreted as driven by our examined trait. However, the large variance in diversification rates that arises from changing the number of extinction rate parameters to be estimated indicates sensitivity of parameter estimates to differing extinction rates.

For both the mammal-1 and mammal-2 groups, we found that large-ranged species made up the largest proportion of species (representing 28 species, 42.4% of total and 118 species, 39.9% of total for the respective groups; Figure 3). The mammal-1 group had more small- than intermediate-ranged species (22 species, 33.3% of total small versus 16 species, 24.2% of total intermediate), whereas the mammal-2 group had more intermediate- than small-ranged species (85 species, 28.7% of total small versus 93 species, 31.4% of total intermediate). For bird-dispersed palms, we found a roughly equal proportion of small and intermediate-ranged species (250 species, 35.4% of total small versus 243 species, 34.9% of total intermediate), whereas 208 species, 29.7% of total species were large ranged.

Our analyses assumed complete sampling even though our trees only included 41% of the existing species. Based on simulations, we show that this did not bias our conclusions. In all, 100 phylogenetic trees with traits driving diversification were simulated. Each trait had three character states, and therefore three speciation, extinction and net diversification rates. Each of these 100 trees were sampled, keeping 41% of the tips. A binomial test was then used to test for significant bias in the results of the full compared to the sampled trees. Results are biased if the p-value for the binomial test are significant ($p < 0.05$) and non-biased if non-significant ($p > 0.1$). For the first and second simulated traits, the speciation rate parameters showed bias in the pruned compared to the full tree ($p = 4.3 \times 10^{-9}$ and $p = 1.8 \times 10^{-4}$, respectively), while the third trait showed no bias ($p = 0.62$). The second extinction rate parameter showed bias in the pruned compared to the full tree ($p = 3.5 \times 10^{-3}$), while the first and third were not found to be biased ($p = 0.37$ and $p = 0.62$, respectively). Even though both speciation and

TABLE 1 Model design of all nine SecSSE models ordered from low to high AIC (better to worse model fit).

| Model name | ETD/CTD | Lambda | Trans rates | Mu | Parameters | lnLik | AIC | avg_AIC | Set rank |
|---|---|---|---|---|---|---|---|---|---|
| Interaction all | ETD | 9 | 4 | 9 | 22 | −5335.325 | 10714.65 | 10655.695 | 1 |
| **Interaction all** | **CTD** | **9** | **4** | **9** | **22** | **−5276.369** | **10596.74** | | **1** |
| Interaction 3 mu | ETD | 9 | 4 | 3 | 16 | −5324.269 | 10680.54 | 10666.12 | 2 |
| **Interaction 3 mu** | **CTD** | **9** | **4** | **3** | **16** | **−5309.851** | **10651.7** | | 2 |
| Interaction 1 mu | ETD | 9 | 4 | 1 | 14 | −5345.7 | 10719.4 | 10718.5 | 3 |
| **Interaction 1 mu** | **CTD** | **9** | **4** | **1** | **14** | **−5344.8** | **10717.6** | | **3** |
| Fruit colour independent | ETD | 3 | 4 | 1 | 8 | −5362.616 | 10741.23 | 10,731,965 | 4 |
| **Fruit colour independent** | **CTD** | **3** | **4** | **1** | **8** | **−5353.349** | **10722.7** | | **4** |
| Range size independent 1 mu | ETD | 3 | 4 | 1 | 8 | −5390.692 | 10797.38 | 10772.345 | 5 |
| **Range size independent 1 mu** | **CTD** | **3** | **4** | **1** | **8** | **−5365.655** | **10747.31** | | **5** |
| Range size independent all | ETD | 3 | 4 | 3 | 10 | −5522.744 | 11065.488 | 11025.07 | 6 |
| **Range size independent all** | **CTD** | **3** | **4** | **3** | **10** | **−5482.326** | **10984.652** | | **6** |
| **Fruit colour independent all** | **ETD** | **3** | **6** | **3** | **12** | **−5516.61** | **11057.22** | 11085.318 | **7** |
| Fruit colour independent all | CTD | 3 | 6 | 3 | 12 | −5544.708 | 11113.416 | | 7 |
| **Interaction 1 trans** | **ETD** | **9** | **1** | **9** | **19** | **−5519.494** | **11076.99** | 11140.2 | **8** |
| Interaction 1 trans | CTD | 9 | 1 | 9 | 19 | −5582.703 | 11203.41 | | 8 |
| Interaction 1 trans 1 mu | ETD | 9 | 1 | 1 | 11 | −5580.946 | 11183.89 | 11170.645 | 9 |
| **Interaction 1 trans 1 mu** | **CTD** | **9** | **1** | **1** | **11** | **−5567.698** | **11157.4** | | **9** |

*Note*: The columns, in order of left to right, have the model name, whether it was the ETD model or CTD edition of each model, lambda value (speciation rate), number of transition rates, mu value (extinction rate), total number of model parameters estimated, model likelihood, AIC value, average AIC for the ETD and CTD model, and the average AIC rank. The values are based on running on the maximum clade credibility tree. Only the top three best fit models were run on a posterior distribution of six trees. Rows in bold indicate whether the ETD or CTD model had better fit given each model design.

Abbreviations: AIC, Akaike information criterion; CTD, concealed trait dependent; ETD, examined trait dependent; SecSSE, Several Examined and Concealed States-dependent Speciation and Extinction.

extinction rates may have been biased by our approach these biases cancelled each other out and net diversification was not biased. For all three categories, net diversification rate was equally likely to be higher in the full or in the pruned simulated tree ($p=0.37$, $p=0.13$ and $p=0.62$ for character states one, two and three, respectively).

## 4 | DISCUSSION

Fruit colour is tightly linked to dispersal and therefore to geographical range in plants (Lu et al., 2019). Here we combined macroecological and macroevolutionary approaches to determine the impact of fruit colour (and hence seed dispersal interactions) on palm range size and diversification rate. We tested two hypotheses: That (1) fruit colours attracting frugivorous bird dispersers have larger range size due to high dispersal ability. That (2) the distribution of diversification rate at different range sizes differ between fruit colour groups associated with different disperser groups, and that diversification rate is higher for palms with intermediate range size. Our findings show that both the mammal-dispersed fruit colour groups have greater proportions of large-ranged species than the bird-dispersed ones. Therefore, we reject our first hypothesis. Our evolutionary dynamic SecSSE models suggest that the differences in diversification rates across lineages are not associated with either trait or an interaction of the traits. Because heterogeneity in diversification rates is better explained by a concealed trait than the traits examined in our study, the result for the second hypothesis is inconclusive, as the potential differences in diversification rates are not statistically significant.

### 4.1 | Frugivore disperser ability and species range size

While a positive correlation between dispersal ability and range size is not ubiquitous (Gaston, 1998), several studies have demonstrated

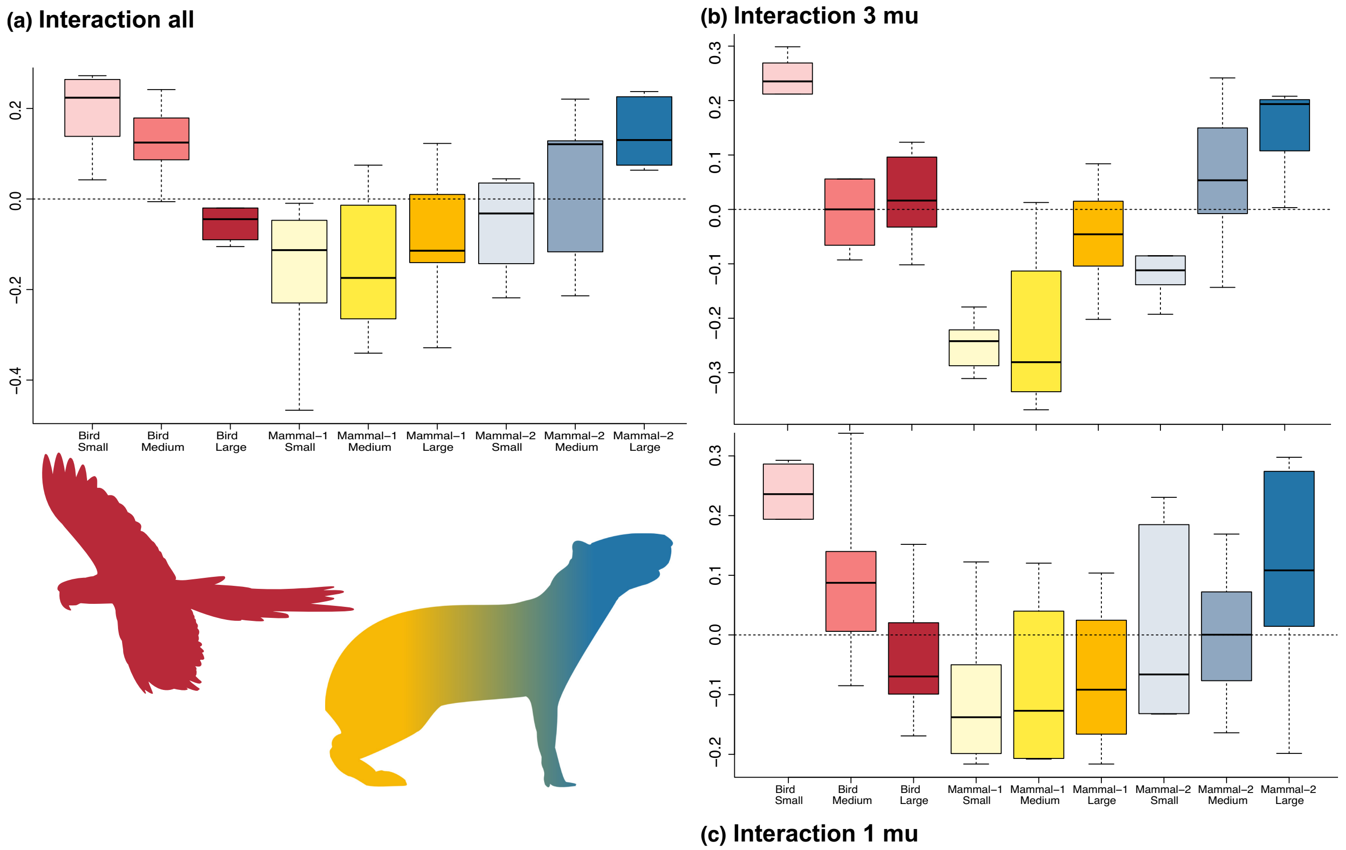

**FIGURE 2** Boxplots showing net diversification rates from the three best fitting SecSSE models. Boxes show the distribution of values from SecSSE models fit to a posterior distribution of six phylogenetic trees. All models had nine speciation rates and four transition rates but vary in number of extinction rates jointly estimated. The x-axis shows the character states and the y-axis shows diversification rate. Ordered from better to worse fit, the models were: (a) Interaction all: nine extinction rate SecSSE, (b) Interaction 3 mu: three extinction rate SecSSE and (c) Interaction 1 mu: one extinction rate SecSSE. A concealed trait is the primary driver of the observed diversification rates, but it is notable that they vary significantly depending on the number of extinction rate parameters estimated. SecSSE, Several Examined and Concealed States-dependent Speciation and Extinction

such an effect (e.g. Estrada et al., 2015; Faurby & Antonelli, 2018; Penner & Rödel, 2019; Sinnott-Armstrong et al., 2018). Our study did not identify such an effect in palms (Figure 3). This is assuming, as we have done, that the substantiated claim that birds generally have higher dispersal ability than mammals is true (Lu et al., 2019; Santos et al., 1999). Our finding is that in both mammal-dispersed fruit colour groups (mammal-1 and mammal-2), large-ranged species make up the plurality of species (42.4% and 39.9%, respectively; Figure 3). For bird-dispersed fruit colours, species with large range size is the smallest group (29.7%; Figure 3). It is however notable that our range size groups were defined to have an equal number of species in each, potentially constraining results.

Dispersal ability is just one of many factors that influence range size. After speciation, there are multiple ways that the parent species range is divided among the two daughter species (Gaston, 1998). For one, it may be asymmetrically divided to various extents. The division is determined by the process by which speciation occurred: allopatric, peripatric, parapatric or sympatric. The speciation of a small-ranged species will invariably result in small-ranged daughter species. Given our categorisation of range size, a large-ranged species could speciate into daughter species with any initial combination of range sizes, given that a parent species could have a range large enough to fit two large ranges. Even within modes of speciation there may be different outcomes of range division depending on specific mechanisms, for example whether allopatric speciation occurs through vicariance or peripheral isolation (Gaston, 1998).

In our study, bird-dispersed palms more frequently have small and medium range size than large range size. A possible reason the bird-dispersed group has a lower proportion of large-ranged species is the reduction in range size post-speciation for daughter lineages (Pigot, Phillimore, et al., 2010), followed by limits to range expansion post-speciation (Pigot, Owens, & Orme, 2010). A daughter species that has speciated through adaptation to a novel habitat may be limited to this specific habitat. If this novel habitat is geographically small, dispersal ability does not matter—the daughter lineage range size would remain small. With speciation through isolation by distance over a large range, a daughter lineage may not be limited by habitat in such a way, but could potentially expand its range to match the range of the ancestral species. High dispersal ability could hinder isolation by distance by maintaining gene flow. This means that speciation modes that occur most frequently for species with better dispersal ability, for example by ecological speciation after range expansion into novel habitat, can hinder subsequent range expansion.

If better dispersal ability does tend to correlate positively with range size, our results indicate that daughter lineages dispersed by long-distance dispersers (some birds) are limited from achieving a large range by, for example, ecological factors. It is possible that there are other dispersal-range size dynamics that impact diversification, for example, high dispersal could result in very fragmented small populations that simply go extinct. Other dispersal mechanisms exist for certain plants that produce fruit, such as non-sexual reproduction (Sheth et al., 2020). Furthermore, frugivores may be selecting fruit based on other factors than colour, such as scent and taste. Taken together, our results demonstrate the importance of other determinants of range size than dispersal ability tied to fruit colour in palms.

## 4.2 | Drivers of diversification in palms

We ran ETD and CTD versions of the three best fit SecSSE models. Each model was run on a distribution of six phylogenetic trees. For all three SecSSE models, the CTD version has better fit than the ETD version based on AIC. This means that a concealed trait is the main driver of the differences in diversification rates estimated in our SecSSE model, rather than our examined traits, disperser type and range size. Two models show support for examined trait diversification, but these were not among the three best fit. This means that an interaction of range size and fruit colour or either trait independently is not the primary determinant of the diversification dynamics observed. Although we find that fruit colour and range size are not the sole drivers of diversification, it is likely that they contribute to the evolutionary process. There is a need for evolutionary models that measure the contribution of each trait in macroevolutionary patterns.

Other studies have found similar results regarding range size. Simpson et al. (2022) found that a different trait than range size or different combinations of traits including range size are more important than range size alone in explaining diversification. Hernandez-Hernandez and Wiens (2020) found that geographical range size is a dominant driver of diversification at the clade level only.

In contrast to our study, others have found relationships between diversification and fruit colour (Lu et al., 2019) or other fruit traits (Onstein et al., 2017). However, none of these studies tested whether the diversification heterogeneity inferred for examined traits were better explained by another related trait, as is done with HiSSE or SecSSE models. Our study highlights, as other studies have (Herrera-Alsina et al., 2019), the importance of factoring in the effect of hidden traits when inferring trait–diversification relationships. Range size and/or fruit colour may influence net diversification, but our results indicate that other unconsidered traits explain diversification better. Therefore, our study is inconclusive about our second hypothesis, whether disperser mobility influences diversification differently or if intermediate range size leads to higher net diversification.

## 4.3 | Complex evolutionary scenarios are supported

In general, model complexity led to better fit based on AIC, indicating that rates of speciation, extinction and transitions between character states are highly variable between species with different fruit colours and range sizes in palms. In other words, joint estimation of these diversification parameters does not adequately reflect the actual trait evolution, and therefore lead to worse model fit. However, SecSSE requires joint estimation of several parameters in order to keep the likelihood space low enough that finding the diversification parameters that maximise the model likelihood is possible. A SecSSE model with too many parameters will finish optimising, but likely not in the global likelihood optimum. Herein lies a cautionary tale: increasing the number of parameters to be estimated leads to better fitting models, but after a certain number of parameters to be estimated, convergence will be impossible without any indication that the search algorithm has become stuck in a local optimum. It is desirable to increase model complexity when it leads to better fit and to more accurately mimic complex biological systems. However, with the added complexity the chance of non-convergence increases. To ensure the global optimum has been found, running several iterations of parameter optimisation with different starting values are recommended.

Our nine hidden state SecSSE models were all initially run on MCC trees for model selection and ranked based on AIC (Table 1). Both models that were ranked last had a common denominator: a single transition rate (Table 1). Regardless of overall model complexity, a low transition rate led to poor fit. This indicates that character state shifts in palms are variable—some character state shifts happen more frequently than others, although in this case, these shifts are driven by a concealed trait. The three best fitting models had the highest as well as the third and fourth highest number of overall parameters. They varied in the number of extinction rates, where the best had nine, the second had three and the third had one extinction rate to be estimated (Table 1). It is notable that having more extinction rates increased model fit. Whether extinction rates can be accurately inferred from phylogenies has long been controversial. However, more recent studies show that extinction rate cannot be reliably estimated from phylogenetic data (Rabosky, 2016).

## 4.4 | Best practices when using SecSSE

Given that altering model design regarding number of parameters to be optimised in any model can change the distribution of optimised parameter values (Figure 3), careful planning and consideration must be done to draw valid conclusions about trait evolution. There are potentially a large number of possible model designs for a multi-state

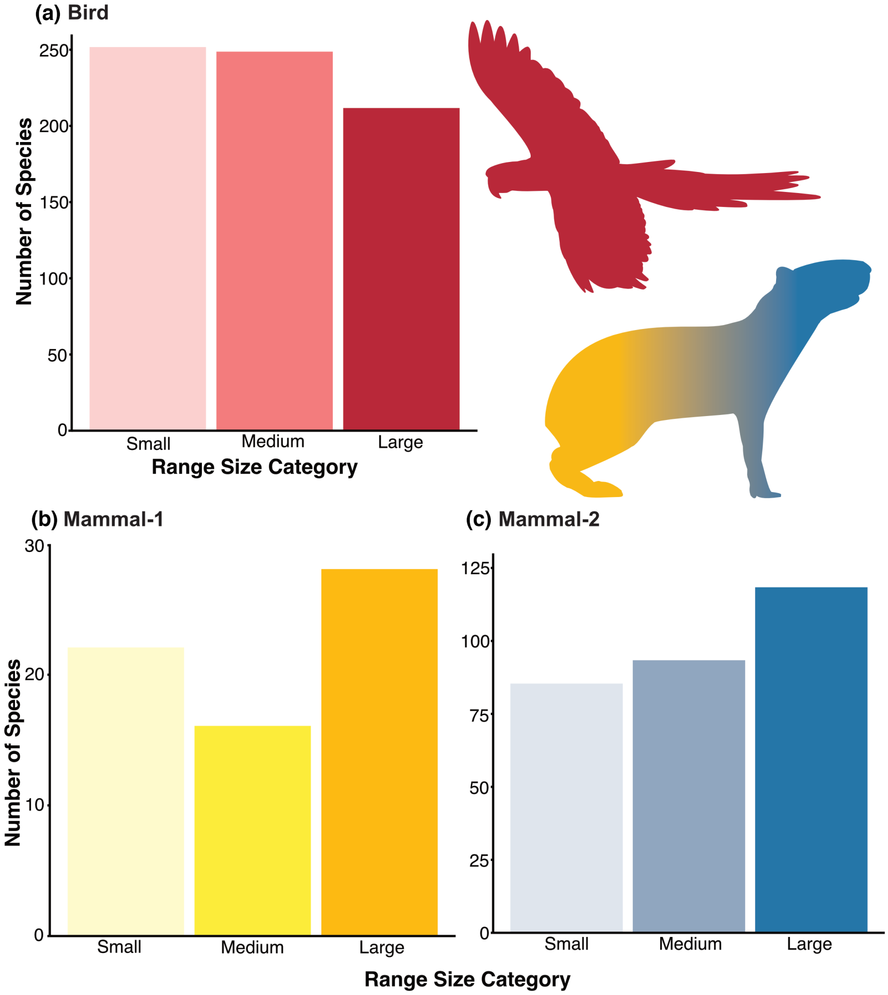

FIGURE 3 Number of species classified as small, medium, or large range within the fruit colour categories: (a) Bird, (b) Mammal-1 and (c) Mammal-2.

system. It is likely that a study implementing SecSSE will use only a fraction of the possible evolutionary scenarios. Without testing every single model, there will be uncertainty regarding whether the set of tested models contain the best fitting global model. If for example, four basic models are tested with a single transition rate for the sake of computational efficiency, with the best fit model favouring the ETD over the CTD model, the conclusion would be trait-dependent diversification has occurred. However, if another version of these models with two different transition rates was tested, at least one of these fitting the data better, supporting CTD over ETD, it would mean there is no trait-driven diversification for the trait of interest. Quantifying uncertainty around whether the best global model may be found in the set of models tested relative to the number of models possible is a good practice to ensure validity regarding results from SecSSE models.

Similar to the uncertainty that the true global optimum-fit model has been found, bias can easily occur. There may be a propensity to stop testing additional models when one that has been shown to favour examined trait dependence has been found. To avoid this form of data dredging, we suggest some form of pre-registration (Ioannidis, 2022). Pre-registration defines what models to test prior to running the models, either more or less formally (e.g. providing a time-stamped document or simply keeping a note between project authors, respectively). If, after running these models, something is learned from the outcome warranting additional models to be run, an additional pre-registration could be done.

As we have shown, minor changes in model design can change model outcome and therefore biological conclusions (Figure 2). The suggestions above not only prevent falsely concluding state-driven diversification when there is none, but would prevent concluding that the parameters of a suboptimal ETD model are correct when minor changes may produce an ETD model that is better fit and leads to different conclusions regarding optimal parameter values.

## 5 | CONCLUSION

Our study demonstrates that dispersal ability does not correlate positively with range size in palms. Furthermore, we find a trait (or traits) not considered in our study is a more significant driver of the diversification parameters that we estimated for our trait. Because we cannot decouple these effects, our study is inconclusive regarding what disperser and what range size positively influences diversification rates. We find striking differences in optimal parameter values for models assuming or not differences in extinction rates across states. Model sensitivity results call for well-defined best practices to avoid drawing incorrect conclusions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The palm fruit colour and geographical occurrence data used for the analyses are publicly available in Kissling et al. (2019) (https://doi.org/10.6084/m9.figshare.9766919) and Global Biodiversity Information Facility (GBIF; ttps://doi.org/10.15468/dl.rjmqfy), respectively. The code for cleaning the data is available on GitHub.

(https://github.com/mftorres/palm_leaf/blob/master/notebooks/01_GBIF_variables_data_prep.ipynb)

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## BIOSKETCH

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All authors excluding L. H-A. are members of the Gothenburg Global Biodiversity Centre, which is hosted at the University of Gothenburg and provides a platform to better understand and communicate biodiversity sciences among its 17 partner organisations around Western Sweden. The centre's goal is to better understand biodiversity and address issues related to the ongoing biodiversity crisis to build a biodiversity-positive future.

**Author contributions**: C.D.B. conceived the ideas and all authors together designed the methodology; A.H., M.F.T.J. and S.F. collected the data, A.H. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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